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BISHOP MUSEUM OCCASIONAL PAPERS

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FEATURE ARTICLES

Introduction to the Hawaiian Terrestrial Invertebrate Survey

Scott Miller[1] and Allen Allison[2]

IN NOVEMBER 1988, the Bishop Museum, with sponsorship of the John D. and Catherine T. MacArthur Foundation, hosted a workshop on the conservation of Hawaiian terrestrial invertebrates. The goal of the workshop was to develop strategic plans for understanding the terrestrial invertebrate biodiversity of Hawai'i in order to provide for their protection through conservation means. Heretofore, it has been difficult or impossible to answer conservation questions for the over 8,000 species of insects and related arthropods and 1,000 species of land snails because of poor knowledge of their taxonomy, biology, and, especially, their current distribution and population status.

Specialists in invertebrate biology, Hawaiian natural history, and conservation, from major institutions in Hawai'i and throughout the United States and Canada, examined means for filling the major gaps in knowledge of this fauna that hinder conservation efforts. Separate survey plans for land snails and terrestrial arthropods have evolved from the foundation established at this workshop. The Museum is currently soliciting funds for the implementation of the first phase of survey activities.

The first 2 papers in this volume of *Occasional Papers* summarize knowledge of the conservation status of 2 groups that include much of the biological diversity of the Hawaiian Islands—terrestrial arthropods and land snails. These papers provide overviews of past and current research, as well as a perspective on needs for future research. The Bishop Museum hopes that these papers will encourage interest in these important subjects. Similar papers within the Museum's interests will be published from time to time.

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Hawaiian Terrestrial Arthropods: An Overview

Francis G. Howarth[1]

ABSTRACT

The Hawaiian Islands are the most isolated group of islands in the world. The 8 main southeastern islands, with their sequentially younger ages, great physiographic and climatic variation, and the repetition of climatic regimes and ecosystems on each island, are ideal natural laboratories for evolutionary and ecological research. Few organisms crossed the vast oceanic distances and successfully colonized the islands. About 400 colonizers gave rise to over 5,000 endemic species of arthropods, with probably at least as many more undescribed species awaiting study. This dearth of knowledge of the total fauna makes it difficult to assess their conservation status and formulate conservation programs for native arthropods. Over 3,200 alien species of arthropods have been purposefully or inadvertently introduced by human activities. Possibly 2,500 of these are established residents. Declining populations of native species indicate the impacts of these aliens may be severe. Systematic studies, field surveys, and long-term ecological research programs are needed to determine the status of native and alien species and formulate conservation programs for the remaining native species. Recent biological discoveries demonstrate that no habitat should be excluded from survey.

INTRODUCTION

The Hawaiian Islands, which extend 2,400 km from the northern subtropical to tropical Pacific, are the most isolated high islands on earth (ca. 3,850 km from any continent and about the same distance from the nearest high islands, the Marquesas in French Polynesia). The Hawaiian Islands are the summits of giant submarine volcanoes emanating from a hot spot in the mantle below the Pacific Tectonic Plate. The Hawaiian Hot Spot has been relatively stationary over time, producing volcanoes in assembly-line fashion as the Pacific Plate moved northwest. Each island or island group is progressively older in a northwest direction and each has always been isolated from the others by deep straits 40 km or more wide (Dalrymple, Silver & Jackson 1973).

The island chain originated over 70 million years (ma) ago and is comprised of 3 parts (Fig. 1): the youngest 8 main islands (originated <5.6 ma ago) with their satellite islets at the southeast end, the relict volcanic islands and coral atolls (ca. 6–30 ma) in the middle, and a long chain of progressively more sunken seamounts (35–>70 ma) stretching to the Aleutian Trench. Undoubtedly, additional islands once existed but are now subducted into the trench (Clague & Dalrymple 1987).

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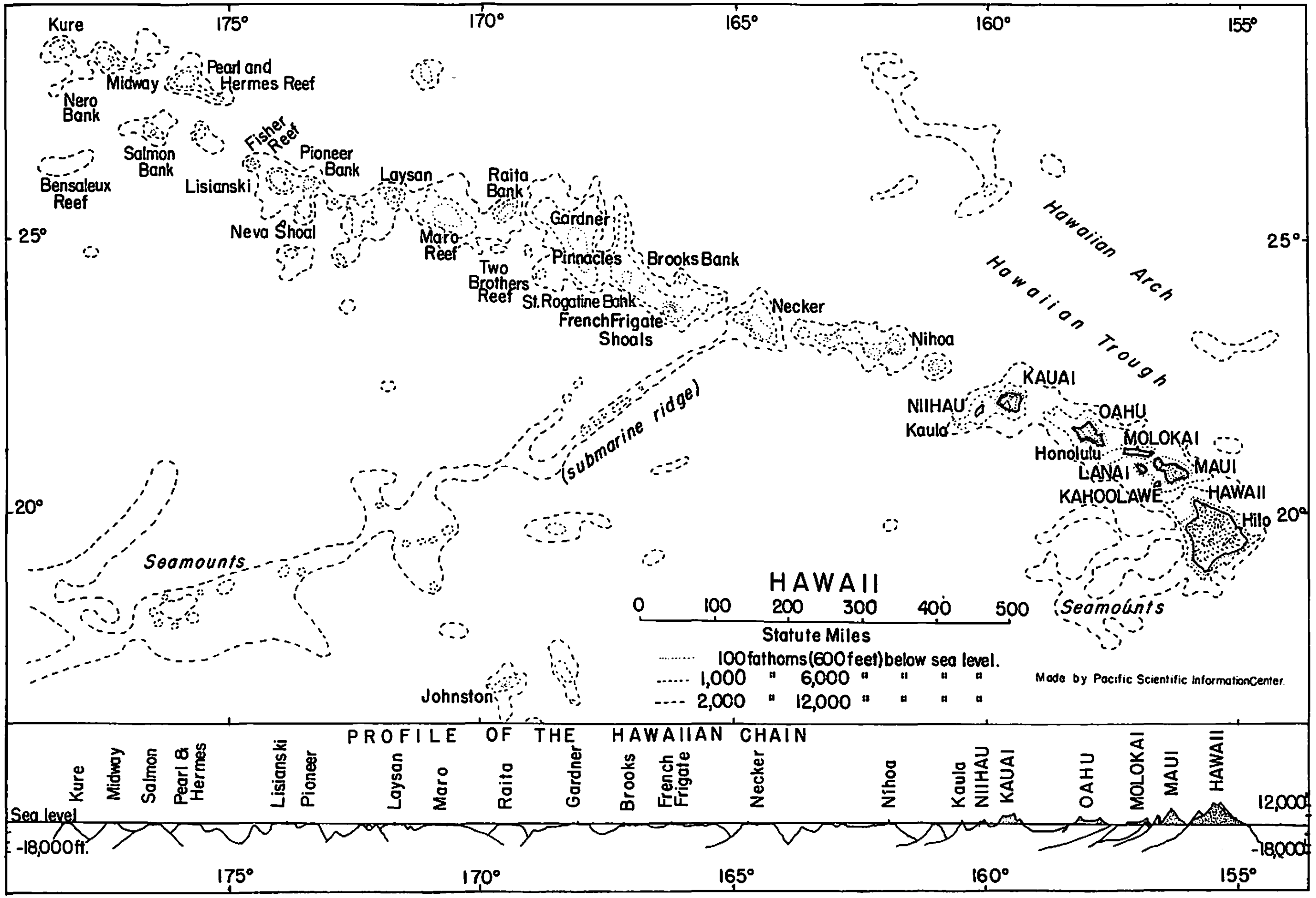

Fig. 1. Map of the Hawaiian Islands, showing both plan and profile view of the island chain. (Copyright Bishop Museum. Geography and Map Collection, Bishop Museum.)

The major ecosystems in the Hawaiian islands are: littoral (on both rocky and sandy shores), strand plant community, lowland dry scrub, desert, grassland, partly deciduous dry forest, mesic forest, and (on the windward sides of some islands) lowland rain forest grading into a montane rain forest near 900 m. On the higher mountains a cool dry forest or savannah (mountain parkland) occurs above 1,500 m, which grades into alpine scrub (above 2,000 m) and a stone desert supporting an aeolian community (above 3,000 m) (Fig. 2). The boundaries of these ecosystems are dictated by climate, local topography, lava morphology, age, soil development, altitude, and degree of human disturbance. These ecosystems have been further subdivided into about 120 different communities on the basis of dominant plants (Gagné & Cuddihy 1990), and all of the world's major plant formations occur within the islands (Mueller-Dombois, Bridges & Carson 1981). Young unvegetated lava flows in each climatic regime also support aeolian communities, and lava tubes and other voids in young lava support diverse communities of cave animals (Howarth 1987). More than 180 distinct natural communities (i.e., discrete groups of interacting species in a common area) are found in the Hawaiian Islands, comparable to the number of communities found in continental areas (Mueller-Dombois, Bridges & Carson 1981; Gagné & Cuddihy 1990; Daws 1988). Part of the reason for this great diversity of habitats and natural communities results from the great rainfall gradients created orographically by the northeast tradewinds. Rainfall varies from between 25 cm on leeward coasts to over 1,000 cm at mid-elevation windward sites.

The Southeastern Hawaiian Islands

Hawai'i Island, locally known and referred to hereinafter as the "Big Island," is the youngest, largest, and highest island in the chain (500,000–700,000 years old, 10,000 km^2 in area, and 4,205 m above sea level). It was formed by the coalescing of 5 volcanoes: Kohala, Mauna Kea, Hualalai, Mauna Loa, and Kīlauea. Mauna Kea (4,205 m) bears the scars of past glaciers and broke the ocean surface at least 380,000 years ago. Mauna Loa (4,170 m) and Kīlauea (1,220 m) are still very active.

Lava flows create continuous strips of new substrates with similar chemical structure for animal and plant succession along altitudinal and climatic gradients. These flows are more or less regular in time and space and cover parts of older flows, allowing comparisons of recolonization and succession on different age lava flows, in different climates. Islands of older vegetation surrounded by younger lava flows, called "kipukas" are abundant on the younger volcanoes. These are often rich in native species and provide benchmarks for later successional stages. In spite of the locally high rainfall, Kīlauea and Mauna Loa lack surface streams because of the high porosity of the young lava. The aquatic fauna of Mauna Loa and Kīlauea is meager and restricted to leaf axils and other small pools in the rain forest and in coastal pools in lava. The oldest volcanoes on the Big Island have young but well-developed streams and a better developed aquatic biota.

Northwest of the Big Island is an island complex, sometimes called Maui Nui, consisting of 6 volcanoes on 4 islands (Maui, Kaho'olawe, Lana'i, and Moloka'i), which have been separated by subsidence and erosion (Clague & Dalrymple 1987). Biologically, they comprise 5 distinct areas: East Maui or Haleakalā (0.8 ma), West Maui (1.3 ma), Kaho'olawe (>1.3 ma), Lana'i (1.3 ma), and Moloka'i (1.3–1.8 ma). Lana'i, West Maui, and Moloka'i are similar biogeographically, sharing many taxa, often with closely related species on neighboring mountains. East Maui (Haleakalā) is younger and higher (3,050 m) than these 3 islands and shares taxa with them but shares more with the Big Island than do the others. Kaho'olawe is the lowest island and has been badly degraded through human disturbance.

The geologically defined cave and aeolian habitats, found on the Big Island, disappear on the older islands, except locally on post-erosional flows and on the younger Haleakalā volcano.

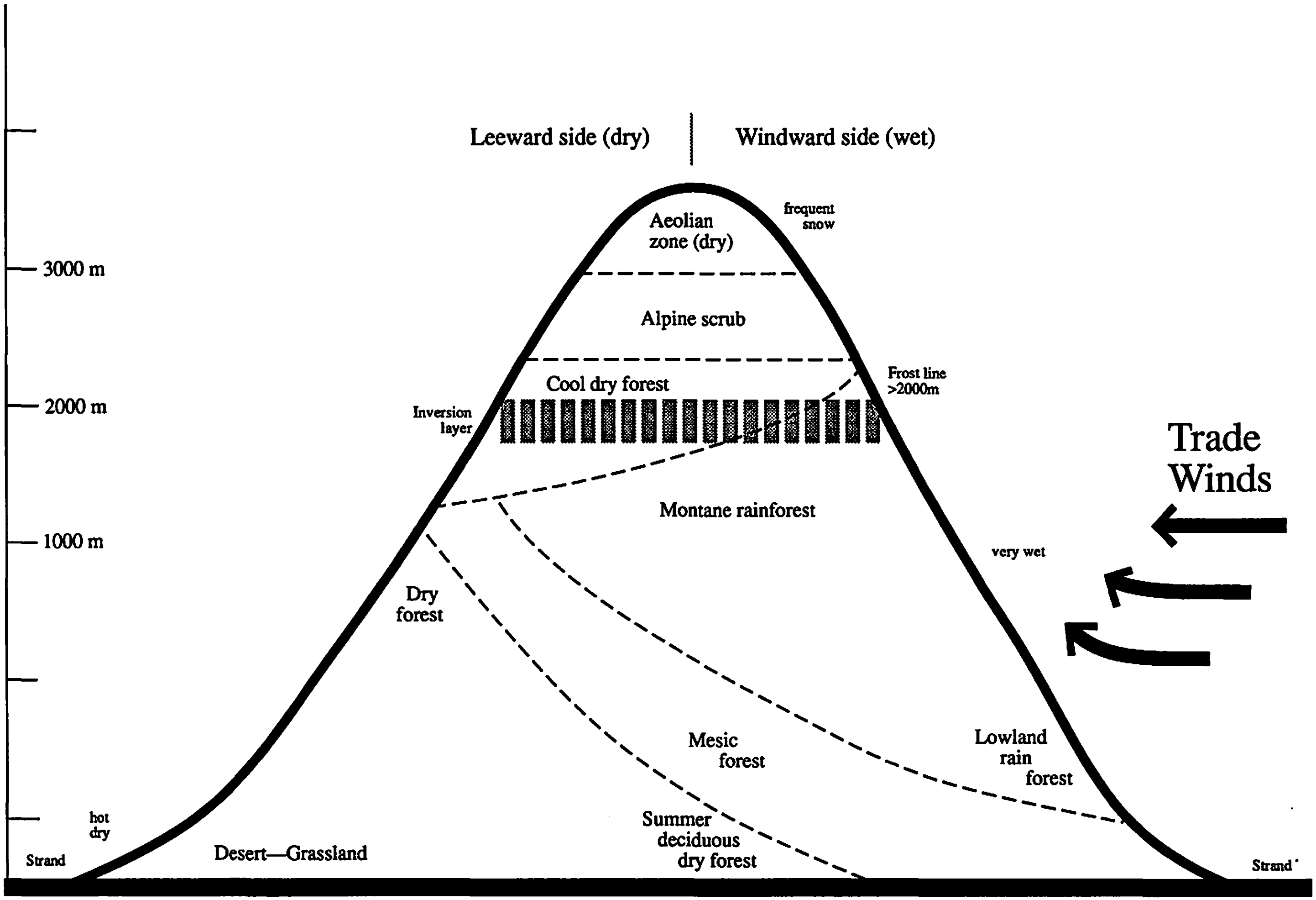

Fig. 2. The major vegetation zones show on a generalized cross-section through a higher Hawaiian mountain. Altitude not to scale.

Table 1. Number of species of selected native insect groups endemic* or (indigenous**) to each island.

	NW	Kaua'i	Oah'u	Maui Nui***	Hawai'i
Diptera:					
Drosophila (all infuscate winged sp.)	0	23(4)	50(7)	70(7)	52(10)
Discritomyia	0	2(3)	4(3)	6(3)	9(3)
Lispocephala	0	12(0)	18(1)	45(3)	28(3)
Campsicnemus	0	6(2)	30(6)	54(12)	31(12)
Eurynogaster	0	14(2)	17(4)	14(4)	5(4)
Scaptomyza (Elmomyza)	0	19(6)	5(6)	25(14)	19(13)
Limonia (Dicranomyia)	0	1(7)	1(8)	3(8)	1(7)
Coleoptera:					
Oodemus	4	20(0)	12(2)	14(6)	6(4)
Plagithmysus	1	19(0)	20(0)	52(0)	44(0)
Mecyclothorax	0	0(0)	6(0)	63(0)	16(0)
Bembidion	0	7(4)	2(3)	3(3)	2(0)
Odonata:					
Megalagrion	0	9(1)	5(4)	5(6)	3(6)
Orthoptera:					
Banza	1	2(0)	2(0)	4(0)	1(0)

* Endemic refers to species naturally occurring only on the listed island.

** Indigenous refers to species naturally occurring on the listed island as well as on other islands.

*** Maui Nui includes the islands of Maui, Lana'i, Moloka'i, and Kaho'olawe.

However, streams are more numerous and the aquatic fauna better developed. Many more groups have colonized Maui Nui than the Big Island, and speciation within this four-island complex gives it the most diverse arthropod fauna in the archipelago (cf. Table 1).

O'ahu was formed by 2 volcanoes 2.6 and 3.7 ma ago, respectively. The highest ridges, though highly eroded, rise up to 1,230 m. Despite the pressures from a metropolitan population, a significant portion of the native biota survives. For example, some of the best remaining lowland dry forests occur on O'ahu because of the greater hunting pressures on alien ungulates than on other islands. Additionally, the stream fauna and bog communities are well developed. However, aeolian and alpine communities have completely disappeared, and the cave fauna is reduced to relictual pockets. The island, along with many habitats, has been reduced in size by subsidence and erosion, but the spectacularly dissected topography and greater age have led to speciation through *in situ* isolation which has resulted in extreme local endemism in some groups.

Kaua'i is the oldest of the main islands but is still a mere 5.1–5.6 ma old. It rises nearly 1,600 m and has one of the wettest spots on earth, with rainfall up to 1,500 cm/yr. Kaua'i is more isolated, being 116 km from Oahu, and supports many relicts and more primitive members within many native groups. Habitats are older and seem to be more mature with more species sharing resources. In relation to land area, the insect fauna of Kaua'i is probably the most diverse but least known of any in the Hawaiian islands. The large central plateau, the Alakai Swamp, has a diverse rain forest biota, but it is threatened by introduced ungulates and invasive weeds. An episode of voluminous post-erosional lava flows rejuvenated the island 0.6–1.4 ma ago, and a small but interesting relictual cave fauna survives.

The Northwest Hawaiian Islands

Most of the northwestern Hawaiian Islands are administered by the U. S. Fish and Wildlife Service as a wildlife sanctuary. However, the main emphasis of management and protection has been devoted to birds and near-shore marine vertebrates (mammals and turtles). The insect faunas of these low islands are still poorly known, yet they offer an exciting opportunity for future research on what was once the lowland insect fauna of the main islands. Insects associated with sea birds and marine littoral habitats on these islands are often widespread. In addition, endemic members of many typical Hawaiian insect groups are, or were at one time, found on these islands, indicating a stepping-stone progression of the fauna along the chain.

Nihoa and Necker islands, 250 km and 540 km northwest of Kaua'i, respectively, are volcanic remnants with relict lowland biotas. Many plant and animal groups still survive on these islands and provide a partial view of what the lowland biota of the main islands was before the arrival of humans (Conant et al. 1983). Necker Island is unique in resting on the shoulders of a much older sea mount (Rotondo et al. 1981), but there is no biological or geological evidence that any part of this sea mount was above sea level or had a terrestrial biota when it joined the Hawaiian chain (Simon et al. 1984). Of special concern to the native and endangered biota on both islands is the recent invasion by several alien insect pests. Some of these immigrants may have arrived by natural dispersal from the main islands, though dispersal as stowaways on landing craft is more likely.

The islands northwest of Necker become successively more eroded and sunken (reduced to lava pinnacles, shoals, and atolls). Early incidental collections indicate they once had a unique Hawaiian biota, but all of them have been more or less disturbed by human intervention (Bryan 1926; Butler & Usinger 1963; Beardsley 1966). The cascading demise of a major portion of the native biota of Laysan after the introduction of rabbits remains one of the best examples of detrimental effects of alien species on an island ecosystem. Many native insect species still survive, however.

Northwest of Kure Atoll, the oldest of the emergent Hawaiian islands, the chain angles northward as the Emperor Sea Mounts. At least some of these are guyots indicating that they were once above sea level. These guyots very likely acted as stepping stones for some of the current Hawaiian biota.

ORIGIN OF THE BIOTA

The biota of the Hawaiian Islands has been constrained by the extreme isolation, youth, and climate of the islands. Only those groups that could disperse across vast oceanic distances and were able to establish viable populations became successful colonizers. Many propagules arrived only to find their beachhead unsuitable or were unable to reproduce, and so they perished. The terrestrial fauna is composed primarily of 3 characteristically vagile groups: arthropods (especially insects), land snails, and birds. Native terrestrial mammals are represented by only 2 bats, 1 of which is extinct (Tomich 1986, Ziegler & Howarth, unpubl. data).

The youth of the islands is reflected in the fauna. Most groups present are young, widespread, successful groups on the continents (e.g., among the insects *Agrotis*, *Nysius*, *Odynerus*, *Crabro*, *Hyleaus*, *Drosophila*, Curculionidae, and Carabidae). Many primitive continental groups are absent, although *Proterhinus* (a primitive weevil that is most speciose in Hawai'i) and others are exceptions.

Those that successfully established evolved to exploit jointly the full range of available habitats. Insects, disproportionately well-represented on oceanic islands, are theoretically among the most important groups in nutrient cycling in most island ecosystems (Howarth 1985; Wilson 1987). Those arriving by air were phoretic on birds, flew themselves, or drifted with wind as aerial plankton. Those arriving by sea swam, drifted with waves, or rode on

Table 2. Tentative summary of Hawaiian terrestrial arthropods.

Order	Endemic* species	Indigenous** species	Alien*** species
Palpigrada			1
Pseudoscorpionida	4		5
Scorpionida			1
Schizomida			1
Acari†	92	6	396
Araneae†	101		73
Amphipoda†	4	1	2
Isopoda†	3	?	17
Diplopoda†	15		10
Chilopoda†	4?		22
Pauropoda			2
Symphyla			4
Protura			1
Diplura			4
Collembola†	9		57
Thysanura	2		5
Ephemeroptera			3
Odonata	31	2	6
Orthoptera†	52		27
Blattaria			21
Mantodea			6
Dermaptera	7	1	11
Isoptera			6
Embioptera			2
Zoraptera			1
Psocoptera†	75	5	41
Mallophaga†	4	15	47
Anoplura			14
Thysanoptera	26		122
Heteroptera†	216	1	100
Homoptera†	385		294
Neuroptera†	51		8
Lepidoptera†	952		194
Trichoptera			3
Coleoptera†	1373	15	610
Strepsiptera			4
Diptera†	1115	10	431
Siphonaptera	1		9
Hymenoptera†	641	16	624
Totals	5163	72	3185

Source: Nishida & Miller 1989.

* Endemic refers to species naturally occurring only in Hawai'i.

** Indigenous refers to species naturally occurring in Hawai'i as well as elsewhere.

*** Alien includes both inadvertent and purposefully introduced species.

† Indicates groups in which significant number of additional species are known, but not yet described.

Table 3. Relative representation of major insect groups in different regions.

	Number of species in major insect groups as a percentage of the total regional fauna			
		North	Hawai'i	
	World	America	*1948*	*1989*
Order	(762,659)*	(93,728)*	(3,722)*	(5005)*
Coleoptera	39	32	37	28
Diptera	16	19	7	22
Lepidoptera	15	12	23	19
Hymenoptera	14	19	17	13
Other Orders	16	18	16	18

Sources: World and North American data from Danks (1988), Hawaiian data from Zimmerman (1948) and Nishida & Miller (1989).

*Number of currently recognized native species.

flotsam (Carlquist 1981). The oceanic distances to Hawai'i have always been so vast that, except for halophilic species, the sea was a poor avenue for the dispersal of arthropods. Wind, especially storms and jet streams, carried most of the successful propagules of arthropods to the isles (cf. Holzapfel, Clagg & Goff 1978).

Biologists visiting the islands are at first struck by what is not present because relatively few colonizers succeeded in becoming established. Only about 50% of the known orders and just 15% of the known families of insects are represented in the native fauna (Table 2). Only 350–400 separate colonizations can account for the total estimated insect fauna (ca. 10,000 endemic species), an average of 25 species per colonization (Zimmerman 1948; Gagné 1988; Nishida & Miller 1989). Over the 70 ma age of the islands only 1 long-distance dispersal event every 175,000 years could account for the current fauna. Even if they all arrived during the age of the present high islands, only 1 arrival every 12,750 years would account for just the insect fauna. The specific numbers are less extreme for other groups, but the pattern of only a few colonizers giving rise to many closely related species is a characteristic of the Hawaiian biota (Zimmerman 1948; Howarth, Sohmer & Duckworth 1988; Wagner, Herbst & Sohmer 1990).

Most native insects are representatives of modern, small, vagile groups that are often found dispersing as aerial plankton on the continents and over the oceans (Gressitt & Yoshimoto 1963; Hespenheide 1977; Holzapfel, Clagg & Goff 1978). These include small flies, beetles, wasps, moths, bugs, leafhoppers, and planthoppers. Large showy insects and the primitive, flightless, moisture-loving soil forms are poorly represented. Many groups important in continental areas are missing. There are no native chrysomelid, scarabaeid, or buprestid beetles, swallowtail butterflies, termites, short-horned grasshoppers, cockroaches, mayflies, stoneflies, horse and deer flies, bumblebees, sawflies, ants, and only one flea. Beetles, flies, moths, and bugs are perhaps proportionately better represented in Hawai'i than elsewhere (Table 3).

Each island received propagules from neighboring older islands with the infusion of rarer colonizers from greater distances. Hawai'i, being in the northern mid-Pacific, has received these long-distance propagules from all points of the compass, but unfavorable equatorial ocean and air currents greatly restricted groups from crossing the equator (Armstrong 1983; Hourigan & Reese 1987). The majority arrived from the Oriental region and could have island-hopped across part of the western Pacific. A large percentage belong to Holarctic groups and could have come from the north, east, or west. The *Drosophila* most likely came from north Asia

(Carson 1987a), the butterflies *Udara* and *Vanessa* from the west, the *Manduca* hawkmoth from the east, and *Hyles* hawkmoths from the east, west, or north. Some representatives, such as *Plagithmysus* beetles, are from the Nearctic region (Gressitt 1978) and a few, such as the prognathogrylline crickets and the *Oodemus*, *Rhynchogonus* and *Proterhinus* weevils, are characteristic Hawaiian or Pacific groups without clear continental affinities.

HISTORY

Polynesians knew the native insects and developed cultural and verbal traditions concerning the native insect fauna of the Hawaiian Islands. Unfortunately, little of this oral tradition was recorded by westerners before this aspect of Hawaiian culture was lost. Some of the Hawaiian insect names are listed in Kent (1986).

Scientific knowledge of Hawaiian biology developed during 3 periods: the exploration period (1778–1850), the resident naturalist period (1820–1900), and the modern period (1900 to the present) (Kay 1976). Unfortunately, arthropods were neglected by most of the early explorers, and even specimens brought back were ignored by the scientists in Europe and North America. Insects were collected by the naturalists on Cook's initial voyage to Hawai'i in 1778 and 1779, but only 2 wasps were described from the material. Plants, snails, and birds captured the curiosity of the early naturalists, and a myth developed (which at first proved hard to break) that insects were uncommon or rare on oceanic islands.

Entomological studies began in earnest late in the resident naturalist period with the arrival of the 1st resident naturalist to concentrate on insects, the Reverend Thomas Blackburn who lived in Hawai'i for 6 years (1877–1883). He supplied scientists at the British Museum (Natural History) and elsewhere with a steady stream of specimens, finally dispelling the myth that insects were poorly represented in Hawai'i. Unfortunately, many of Blackburn's species have not been recollected. Human activities and invasions of alien biota, especially cattle and other ungulates, destroyed much of the native biota before insects were seriously collected. We owe much of our understanding of the native lowland insect fauna to Blackburn's work.

The modern period of Hawaiian entomology began just before the turn of the century with the arrival of professionally trained scientists. At about this time plantation agriculture was growing as the principal economic base. Newly arriving alien insect pests were a continual concern, especially to sugar cane crops. In 1893 the Hawai'i National government hired Albert Koebele, who had just established a successful pest control program in California using alien insect predators. Koebele traveled throughout the world sending alien species to Hawai'i and is credited with introducing hundreds of beneficial species for biological control (Swezey 1931; Funasaki et al. 1988). It was a grandiose experiment in ecology, but, unfortunately, accurate records of specific introductions, their fate, and resultant impacts on the native biota were not kept. Additionally, important questions on the impact on nontarget organisms were never researched or answered.

Growing awareness of the diverse and unique fauna of Hawai'i, as well as the specter of extinctions, led to the commissioning of a faunal survey sponsored jointly by the Royal Society of London and the British Association for the Advancement of Science in collaboration with the Bishop Museum, Honolulu. They hired the British entomologist R.C.L. Perkins for the formidable task of conducting the survey's fieldwork that eventually resulted in the *Fauna Hawaiiensis* (Sharp 1899–1913; Perkins 1913). From 1892 to the early 1900s, he made truly remarkable collections of many groups, concentrating especially on Coleoptera, Lepidoptera, Hymenoptera, Odonata, and some minor orders. Only a few groups, including the Diptera and Heteroptera, were less well covered. His ability to procure good material and identify species in the field is now legendary, and his accounts include a wealth of biological information

(Manning 1986). The 3 volumes of *Fauna Hawaiiensis* (Sharp 1899–1913) remain as the baseline of our knowledge of many arthropod groups.

Early successes with biological control encouraged further development of the program. In 1904 the Hawaiian Sugar Planters' Association (HSPA) commenced with its program of biological control. For more than half a century, HSPA was the largest employer of entomologists in Hawai'i. A number of prominent entomologists passed through their ranks, including R.C.L. Perkins, O. H. Swezey, F. X. Williams, and E. C. Zimmerman. Swezey (1931), listed 300 species purposefully introduced up until 1929, of which 92 definitely established. He lamented the fact that perhaps another 3,000 species were experimented with but were not recorded! Most of these 3,000 species did not become established, but many of our currently established immigrant insect predators and parasitoids may have arrived in this way. The biocontrol program in Hawai'i continues today under the aegis of the State Department of Agriculture (Funasaki et al. 1988). Between 1890 and 1985, the documented intentional introductions and releases into the state totalled 639 species of arthropods, of which 230 became established (Funasaki et al. 1988).

In addition to his duties at the HSPA, O. H. Swezey conducted studies on the biologies of native Hawaiian insects, especially moths. Most of what is known on this subject is the result of his work, which spanned 50 years. His notes were collated in *Forest Entomology in Hawaii* (Swezey 1954), which continues as the primary source of host data for many Hawaiian groups.

The Bernice P. Bishop Museum (BPBM), founded in 1889, was instrumental in providing local support for Perkins and the *Fauna Hawaiiensis* and in encouraging other biological surveys of the islands. It remains the premier natural history institution in the islands. The Hawaiian Entomological Society was founded in 1906 and is one of the oldest entomological societies in the country. The *Proceedings of the Hawaiian Entomological Society* and publications by Bishop Museum Press and the University of Hawaii Press, have been the principal outlets for Hawaiian entomological research since *Fauna Hawaiiensis*.

E. C. Zimmerman at BPBM and HSPA began cataloging the Hawaiian fauna and describing new species in 1934. He also began a long-term project documenting the insect fauna in the monumental series, *Insects of Hawaii*. The 1st of 14 currently-produced volumes was published in 1948. Only the large orders Hymenoptera and Coleoptera have not been treated. D. Elmo Hardy at the University of Hawaii joined the project in 1949 and published accounts of the Diptera as volumes 10–14 (1960–1981). Tenorio (1969) added a supplement on the Dolichopodae. The 300% increase in relative representation of Diptera in the fauna between 1948 and 1989 (Table 3) resulted from Hardy's encouragement of systematic studies. Volume 1 (Zimmerman 1948) remains the best overall treatment of the natural history of Hawai'i to date. The earlier systematic volumes are 40 years out of date but remain useful compilations. Except for those in Hardy's Diptera volumes, few new species were described, hence there is a large accumulation of undescribed taxa in collections.

Systematics Resources

Steffan (1976) reviewed the systematics resources in Hawai'i. The premier collection of arthropods from Hawai'i and the Pacific is housed at the Bishop Museum. The Hawaiian insect collection consists of nearly 1 million specimens, representing more than ¾ of the described species. The collection houses early historical material, especially from *Fauna Hawaiiensis*, which mirrors the fauna as it was at the time of collection in the early 1900s, and a wealth of newer material, some unworked from biosurveys and environmental impact statement assessments. Amy Suehiro maintained a card catalog of Hawaiian entomological literature and taxa from 1928 to 1968. This card file has served as the foundation for the database of Nishida & Miller (1989). Additional significant collections are housed at the State Department of Agriculture (DOA) and the University of Hawaii at Manoa. The DOA collection includes valuable historical material from the former HSPA collection and vouchers of biological control programs. Primary type specimens formerly in HSPA are now in the Bishop Museum. Significant historical collections are also housed at the British Museum (Natural History), which was the primary depository for voucher material from the *Fauna Hawaiiensis* survey.

HAWAIIAN INSECT EVOLUTION

The isolation of the Hawaiian Islands from each other, their sequential ages, and the repetitive occurrence of similar climatic zones, habitats, and ecosystems on each island, along with the formation of isolating barriers within each island by erosion, have favored speciation.

Most speciation events are hypothesized to follow founding of new isolated populations (Carson 1987b). The founding cohort was often small, sometimes only a single gravid female, which could carry only a subset of the genetic repertoire of its parental population, changing gene frequencies and fixing some alleles (Carson 1987b). As the founder population expanded and adapted to its new surroundings, it could diverge from its parental population. This process was repeated on each island with less frequent return of a derived species to its ancestral home (Carson 1987a). On top of this pattern has been an incredible array of adaptive shifts, wherein a subpopulation of a successful population exploits a totally new resource or habitat. Again it may have been a small closely related cohort, possibly a single female, within the population that made the switch. Not all of these would give rise to new species, and it is not known at what stage the speciation event occurs.

These adaptive shifts placed the new population under the influence of new selective pressures, leading to surprisingly rapid morphological changes. In many cases the degree of change has been so great that the original describers placed many species in endemic genera, either to highlight the spectacular changes or to indicate that the affinities to other species were so obscure. For example, the 5 beetlelike flightless lacewings were placed in 2 endemic genera (*Pseudopsectra* and *Nesothauma*), yet Zimmerman (1957) concluded that each flightless species evolved independently from a separate flighted ancestral species in the genus *Nesomicromus*. Therefore *Pseudopsectra*, with 4 described species, is polyphyletic and not a good genus. Also, native *Drosophila* were placed by Hardy (1965) in 3 endemic genera and a number of subgenera before modern work showed them to all belong to the subgenus *Drosophila*; yet according to Kaneshiro (1976), the degree of morphological change within this group far exceeds the range for the whole family Drosophilidae outside of Hawai'i! Furthermore, the native *Plagithmysus* beetles were placed in 6 genera until Gressitt (1978) showed them to represent a single closely related group.

An epitome of rapid morphological change associated with adaptive shifts is exhibited by some of the cave species. The cave fauna contains examples of macro-evolution on micro-continents in mini-time. For example, there are 80 described endemic species in the worldwide cixiid planthopper genus, *Oliarus*. Most *Oliarus* are big-eyed, flighted, somber colored denizens of forests, but no less than 5 evolutionary lines have independently invaded caves and are now obligate subterranean species with reduced or absent eyes, wings, and body pigment. One line occurs on Moloka'i, 2 on East Maui, and 2 occur on the Big Island. The 4 lines (with 5 species) on Maui and the Big Island all evolved within the last million years. The degree of convergence shown by the different cave species on different islands is striking. Despite the complete change in life style and morphology, characters of the male genitalia place them within the native complex of surface species. At least 1 line containing 2 cave species on the Big Island can be placed in a known group of big-eyed surface species (Howarth 1988).

A new population created by an adaptive shift may disperse up or down the chain, becoming the ancestor to additional species (Carson 1987a; Gagné 1983). These 2 phenomena, founder events and adaptive shifts, have been reoccurring down and up the chain in parallel, creating swarms of closely related species within many native groups. Hawai'i is the premier locality for study of the results of this process, called adaptive radiation. Hawaiian *Drosophila* (more than 450 species) and *Hyposmocoma* (350–500 species) head a list of 9 genera that each contain more than 100 described native species (i.e., the beetles *Proterinus* and *Plagithmysus*, the flies *Campsicnemus*, *Scaptomyza*, and *Lispocephala*, and the wasps *Sierola* and *Odynerus*). This list will expand greatly as additional systematic studies are completed. The vast majority of Hawaiian invertebrate species are endemic to a single island (e.g., Table 1).

Adaptive radiation may fill available niches in a brief time. In fact, evidence from the Big Island suggests that ecological niches (defined as functional roles in ecosystems) become occupied in ecological time, like succession, rather than evolutionary time as is commonly assumed (Mueller-Dombois & Howarth 1981, Howarth 1987).

The evolutionary processes in Hawai'i have great predictive value. One can find new species on an unusual host or in an unusual habitat and successfully predict that a close relative exploits a similar niche on the neighboring islands. This has been done on several occasions with the cave fauna and aeolian communities (Howarth 1987) and in studies on specific groups (e.g., in cerambycids *Plagithmysus* [Gressitt 1978], in mirids *Nesiomiris* [Gagné, unpublished data], in geometrids *Eupithecia* [Montgomery 1983], and with flies *Drosophila* [Montgomery 1975]). In each of these groups it was correctly predicted that one would find a new species in a given habitat, based on the ecology of the group on another island.

On the oldest islands of Kaua'i and O'ahu are representatives of taxa that have not yet dispersed down the chain to the younger islands and species believed to be close to the ancestors of taxa found on the younger islands. On Kaua'i one finds the hawkmoth *Tinostoma*, and the lucanid beetle *Apterocyclus*, and the most primitive species of many speciose Hawaiian lineages (e.g., *Drosophila* [Carson 1987a], the mirids *Nesiomiris* [Gagné 1983], and the damselflies *Megalagrion*). In *Megalagrion* the species on the younger islands from O'ahu to the Big Island, inclusive, can be placed easily into 4–5 distinct species-groups, with usually a single species of each group on each island. However, on Kaua'i these species groups blend into a confusing array of mixed morphological traits among the 9 endemic species. Many of the individual species endemic to O'ahu and Maui can be traced back to presumed ancestral species on Kaua'i, but these ancestors on Kaua'i cannot be so easily placed in species groups (Zimmerman 1948, Maciolek & Howarth 1978). In 1–2 million years, O'ahu will be faunistically like Kaua'i once additional Kaua'i species jump to O'ahu and more autochthonous O'ahu species evolve. In a few groups (e.g., *Banza* [katydids] and *Plagithmysus* [beetles]), the hypothesized primitive species occur on the even older island of Nihoa.

Flightlessness

A conspicuous theme among island insects is the evolution of flightlessness. The Hawaiian fauna contains some of the finest examples: flightless beetlelike lacewings, moths, beetles, flies, bugs, planthoppers, leafhoppers, crickets, katydids, and wasps. In fact of the 11 orders of alate insects that dispersed to the islands, only 1, the odonates (dragonflies and damselflies), has not evolved flightless species.

Flightlessness is not unique to islands or to wind-swept, harsh environments, but is common in every ecosystem, including competitive continental ones. In fact, at nearly every trophic level, most resource exploitation is carried out by flightless organisms. Furthermore, nearly all insects spend the majority of their active lives in flightless stages. Consider the ants, termites, cockroaches, scales, springtails, silverfish, etc., of the home and garden. Since most of the dominant flightless continental groups did not disperse to Hawai'i, many of the alate Hawaiian natives have evolved to fill these roles. What makes this process exciting in Hawai'i is that alate and flightless sibling species often live side-by-side and that sometimes intermediate forms are also extant. With the generally young and less complex geological history of Hawai'i, the pieces to such interesting evolutionary puzzles as flightlessness still exist and can be evaluated. Independent adaptive radiation has occurred on each island. Often flightlessness has evolved within each group independently from separate ancestral species on each island (e.g., hemerobiids [Zimmerman 1957], dolichopodids [Hardy & Delfinado 1974], cixiids [Howarth 1988], and tipulids [Byers 1985]).

Evolutionary Ecology Laboratory

The evolution of the Hawaiian fauna has paralleled the geological evolution of the islands. The 6 largest inhabited islands, with their great diversity of habitats and species, present almost ideal evolutionary laboratories. Each island acts as a mini-continent, having obtained its biota from trans-oceanic dispersal. Each is a microcosm of evolutionary and ecological processes on the continents. The isolation and youth make these processes especially clear. A series of similar habitats has developed sequentially on each island down the chain. The repetition of habitats with regularly varying ages allows one to study the role of time in both evolution and ecology.

The Hawaiian biota has been locked in a series of differently aged and isolated "laboratories" for hundreds of thousands to millions of years, where intricate substantive evolutionary ecology "experiments" have been carried out. Each experiment was established at regular intervals on the newer islands and then allowed to run under similar constraints of climatic, geologic, and biological parameters.

The Hawaiian *Drosophila* has been studied more than any other taxon, but other opportunities exist, especially among other speciose groups. In addition, species of the native cutworms, *Agrotis* and *Peridroma*, and the corn earworm complex, *Helicoverpa*, represent unique and valuable resources in applied evolutionary biology. Since each of these groups is closely related to important continental pest species, there is an opportunity to conduct genetic research and find genetic controls for pest species. Such a project is now under way with the corn earworm complex. The Hawaiian species of *Agrotis* and *Peridroma* range from widespread successful species to rare precinctive species and would be good candidate groups for determining the comparative ecological genetics of rarity and extinction. They are also conspicuous and would be good indicator species of the status of many native species in reserves. Similarly, the 22 closely related species in the pyralid genus *Omiodes* range from endemic agricultural pests to endangered or extinct species.

CONSERVATION STATUS OF HAWAIIAN ARTHROPODS

The conservation status of a few groups will be described to illustrate major problems and indicate possible solutions. Some of the major problems affecting conservation biology of Hawaiian arthropods include (1) taxonomic ignorance, (2) small geographic ranges, (3) impacts of invasive alien species, (4) loss of habitat from agricultural conversion, (5) fire, (6) land clearing, (7) military maneuvers, (8) pollution, (9) water diversion, and (10) mining.

Taxonomic Ignorance

The most serious problem is the taxonomic impediment (Ramsay 1986), which results from the lack of both information on invertebrates and trained personnel to obtain that knowledge. Some Hawaiian groups are so poorly known taxonomically that they currently cannot be identified; thus their management is largely ignored. For example, the 3 major terrestrial crustacean groups, the crabs, amphipods, and isopods, were recognized as components of the native fauna only within the past 2 decades. They remain largely unstudied. Native terrestrial crabs are now all extinct and known only from fossil remains. The native terrestrial amphipods are represented in collections by over 30 species, but only 4 have been described. These amphipods represent a number of different founders and separate adaptive radiations (Bousfield 1984). The situation is even worse with isopods, in which only 3 native species have been described, but the total fauna is known to consist of over 60 species, most of them recently established aliens (Taiti & Ferrara, in press). The populations of some of these alien species occasionally reach phenomenal levels, but their ecological effects are unknown.

The situation among the insects is similar. Zimmerman (1978) lamented that the paratype series of the endemic moth genus *Hyposmocoma* with ca. 350 described species sometimes contained a mix of up to 10 closely related species. Many of these are synonyms, but clearly this exciting native group is badly in need of revision. More telling is the fact that Perkins, who collected for the *Fauna Hawaiiensis* survey, never had a chance to collect Lepidoptera and some other invertebrate groups on West Maui or portions of the other islands. Not a single microlepidopteran has been described from West Maui! Based on what is known of the island distribution of species of *Hyposmocoma*, at least 80 new species in this genus alone are presumed to live on West Maui. Described species of native leaf bugs (Miridae) now total almost 50 species, but a manuscript by Gagné (1983) will double that number with a revision of only 1 genus (*Nesiomiris*). An additional 100 to 200 new species wait in collections for a trained taxonomist's eye. The group is undoubtedly the largest native heteropteran family in the islands.

In nearly every native group that has been studied using modern methods new species are recognized. The best example is clearly the *Drosophila*, the number of known endemic species of which has risen from 48 in 1948 to over 400 under the University of Hawaii *Drosophila* Project, and the asymptote of new species has not yet been reached (Kaneshiro & Boake 1987). The percentage representation given in Table 3 reflects more the level of systematic effort devoted to each group.

The lesson for conservation biology is that it is the population that must be saved. There is a human bias toward saving rare things, and conservationists often exploit this trait to save unique rare species. However, for both scientific reasons and conservation goals, it is also important to save the numerous closely related populations of a widespread variable species. The more populations of endemic species we can preserve for future studies, the greater their combined value is to science and the better our understanding will be of evolutionary ecology, behavior, and biology in general.

Cultural Problems

There are cultural problems that hinder conservation programs. The primary problem concerns the advertising industry's view that the only good bug is a dead one. The public is continually being bombarded with the idea that all insects are harmful and should be killed. This is so persuasive that even many applied insect textbooks imply that all predators of insects are beneficial regardless of their prey. The second problem results from the great cultural diversity of Hawai'i. Each immigrant ethnic group has brought to Hawai'i a portion of its natural world, especially organisms considered "useful" or aesthetic. Often invertebrates ride as hitchhikers on these introductions or find suitable hosts when they finally get here by other means. With the introduction of each new alien, the chance of its associated biota becoming established increases (Howarth 1985). Humans are homogenizing the world's biota.

There is also a cultural bias that species are discrete units in nature. However, the more critical our studies become, the less support such a thesis engenders. If conservation biologists are successful in saving only "good species," then the resultant research is a priori biased and the resources to disprove the myth are lost. Current reserve management, with its emphasis on rare unique distinct species may mean our understanding of evolution will be an artificial result of biased management rather than good science.

Small Geographic Range

Many Hawaiian species have extremely restricted geographic ranges. For example, the cave wolf spider (*Adelocosa anops*) is restricted to caves within a single small lava flow on Kaua'i. Its entire known range is threatened by urbanization and recreational developments (Wells, Pyle & Collins 1983). The Big Island species of *Rynchogonus* weevils (*giffardi*) is known from a dry gulch barely 100 m X 10 m—an oasis within a sea of barren pastureland. The once widespread coastal species on O'ahu, *R. simplex*, is now restricted to a few hectares on the southeast tip of that island and possibly some offshore islets (R.C.A. Rice, pers. comm.).

Impacts of Invading Species

Humans have ruined the splendid isolation that allowed the evolution of these spectacular island species. Biological pollution (the impact of invading alien species) is the most insidious, pervasive, and perhaps the most serious conservation threat. Biological pollution is virtually irreversible and has the potential to undo all other conservation programs. Alien species do not respect human boundaries, but can invade all suitable habitats within their dispersal range. The destruction caused by ungulates, rabbits, and certain other vertebrates is well known (Tomich 1986; Vitousek, Loope & Stone 1987), but invertebrates can also be terribly destructive.

About 3,200 species of alien arthropods have been either intentionally or unintentionally introduced to Hawai'i (Table 2). However, the present status of most of these in the islands is unknown. Many populations did not survive to become permanent residents. Some populations subsequently died out for the same reasons that some native populations are declining. Currently there may be 2,500 species of alien arthropods successfully established in Hawai'i (Funasaki et al. 1988). Some alien invertebrates (including both intentionally and unintentionally introduced species) can now be found in virtually all habitats from sea level to the summits of the highest mountains. They have become pests and threaten native species (Howarth 1983, 1985; Gagné & Howarth 1985).

Social and colonial alien insects historically have had far greater adverse effects than most other invertebrates (Howarth 1985). Ants have been strongly implicated in the extinction or extirpation of many native species. Ants with large aggressive colonies, such as the big-headed ant, Argentine ant, long-legged ant, and 2 fire ants, have been the most damaging (Zimmerman 1948; Medeiros, Loope & Cole 1986). In 1977 an aggressive race of the yellowjacket (*Paravespula pennsylvanica*) became established in Hawai'i and quickly spread throughout suitable habitats on all the main islands. Its phenomenal population explosion and spread corresponded with an alarming decline in many native arthropods and may have affected native bird numbers (Gambino, Medeiros & Loope 1987).

The effects of alien species is often unpredictable. Alien invertebrates prey on or parasitize native plants and animals, spread diseases or toxins among native species, supply food or shelter for and help disperse other invading organisms, and alter soils. The reduction of insect prey by alien predators during the critical nesting period of the native forest birds is considered a major factor in the decline of these endangered avian species. Alien parasites, especially mosquitoes, are also considered a major problem in the conservation of native birds (van Riper et al. 1986). Earthworms and termites drastically alter soil structure and nutrient cycling and probably adversely affect regeneration of native plants. Alien seed predators and alien pollinators (especially the honey bee) also restrict regeneration of native plants and favor establishment and spread of alien plant species. Some invertebrate species are food for detrimental vertebrates (e.g., dung beetles for mongooses; slugs and earthworms for pigs) and thereby support greater numbers of these animals than otherwise would be the case (Howarth 1985; Vitousek, Loope & Stone 1987).

Many parasites and predators purposefully introduced for biological control of pest species have expanded their diets to include native species and even alien plant-feeding species introduced to control weeds (Howarth 1983, 1985; Funasaki et al. 1988). The endemic pentatomid stink bugs (*Oecalia* with 14 described endemic species and *Coleotichus* with 1 specie) are disappearing with alarming rapidity. Their demise appears to be the result of parasitism by the biological control agents introduced against the southern green stink bug. Two well-established agents, a scelionid wasp and a tachinid fly, are known to attack *Coleotichus* and other pentatomids (Funasaki et al. 1988). Some native moths, scale insects, and psyllids may also be at special risk from biological control introductions (Howarth 1985) because alien species in these groups have been common targets for biological control (Funasaki et al. 1988).

Land Conversion

Land conversion was begun by the early Hawaiians (Kirch 1982) and is a continuing process, often with devastating effects on the native biota (Gagné 1988). The current land tax structure favors clearing native forests for pasture, plantations, and other ventures. Some prime native habitats have recently been cleared for dubious economic reasons. Fire, wood chipping for biomass energy and for pressed board manufacture, silviculture, mining, pollution, military bombing and resultant fires, geothermal development, and powerline construction also take their toll (Gagné 1988).

Many Hawaiian insects are extremely host specific. In some groups related sympatric species (e.g., *Drosophila* [Montgomery 1975], Cerambycidae [Gressitt 1978], and many Lepidoptera and Homoptera [Swezey 1954]) even divide up the resources of a single host species. As their host plants become rarer and more scattered, these host specific species become vulnerable to extinction. Most of the native leafhoppers (Cicadellidae) and planthoppers (Delphacidae) remain undescribed and many may be going extinct without any documentation. Say "aloha" to the planthoppers in the genus *Aloha*. Most of the species in the endemic moth genus *Mapsidius* are of special concern because their known tree host (*Charpentiera*) is now rare.

The freshwater aquatic fauna is being impacted by stream channelization, impoundments, diversion, pollution, and alien introductions. The last includes introductions for control of mosquitoes and snails as well as escapees from the aquarium trade.

Some moth groups demonstrate the full range of conservation problems. Gagné and Howarth (1985) assessed the native macrolepidoptera and listed 6 major perturbations, not mutually exclusive, that were important in the extinction of 27 species. They are, in order of importance, introductions for biological control, habitat loss, alien mammals, host loss, alien arthropods, and hybridization with an invading alien relative. The native *Hypena* appear to be entirely extinct. Except for the Laysan species, the reasons for their demise are obscure. Their undocumented extinction underscores the vulnerability of some Hawaiian groups and the urgency of beginning a conservation biology program for invertebrates. A large segment of our native fauna may be lost. This loss could have repercussions in other groups.

SOLUTIONS

Recent interdisciplinary evolutionary biology programs have generated considerable publicity and interest in the native Hawaiian biota, and numerous smaller studies were created as spin-offs of these larger ones. The 2 larger studies are the University of Hawaii's *Drosophila* Project, which since the 1950s has been studying the genetics and evolution of the remarkable Hawaiian Drosophilidae (Carson 1987a; Kaneshiro & Boake 1987), and the International Biological Program (IBP) sponsored by NSF and jointly administered by the University of

Hawaii and the Bishop Museum in the 1970s (Mueller-Dombois, Bridges & Carson 1981). This growth in interest, along with the realization that the native biota is at extreme risk, has led to conservation biology initiatives, which have been encouraged by exposure in special issues of scientific and popular conservation and natural history magazines devoted to the Hawaiian biota (Barrett 1975; Dodge 1982; Ternes & Simon 1982; Simon & Sugden 1987; Miller 1988). Leading agencies involved in this shift of emphasis and in the development of a conservation biology program are the U.S. National Park Service, the U.S. Fish and Wildlife Service, The Nature Conservancy of Hawai'i, the Natural Area Reserves System, the Bishop Museum, and the University of Hawaii.

Recent biological discoveries, including new species (even a new genus of living bird), new caterpillars with a unique feeding strategy, and surprising new ecosystems in caves and lava flows, show that there is a great deal remaining in Hawai'i, which is worth saving, and that island biology is not yet fully known. Discoveries in ecology and evolutionary biology demonstrate that the Hawaiian islands are ideal laboratories and can elucidate how fundamental life processes work. Potential for further programs is great, especially in conservation biology. For here we can, unfortunately, examine all stages in the extinction process, assess the role of invading species, and study in isolation the effects of various novel perturbations (Vitousek, Loope & Stone 1987).

Species diversity in Hawai'i is so high that conservation efforts in selected areas will save many endangered species. The Hawaiian fauna is not inherently fragile. Recent conservation efforts have clearly demonstrated that native species respond remarkably to appropriate management actions (Mueller-Dombois, Bridges & Carson 1981; Stone & Scott 1985). Species do recover. However, small population size, the severity of the novel perturbations, and the close interrelationships within native groups act in concert to increase their vulnerability to extinction.

Establish Reserves

To prevent this extinction, each of the distinct habitats needs to be identified and as many examples as possible protected. However, setting aside reserves does not guarantee the long-term survival of the ecosystems unless biological surveys and long-term ecological studies of selected invertebrate and vertebrate groups are initiated. As the knowledge base on biodiversity and the ecology and systematics of arthropod groups grows, management requirements will become more clear.

Determine Indicator Species

To solve the taxonomic impediment, Ramsay (1986; 1989) suggested the identification of a few invertebrate indicator species for each reserve. These indicator species should be chosen on the basis of ease of sampling and recognition as well as their vulnerability to disturbance. Land managers could then be trained to recognize and monitor the indicator species on their reserves to assess the health of invertebrate populations in general. Coupled with knowledge of ecosystem processes, such a system should work.

In other habitats, knowledge of key host plants and appropriate associated invertebrate herbivores could be used as indicator species. The moth genus *Tamsica* occurs mostly in lowland dry habitats and many species may already be extinct. Good populations still exist on some of the small offshore islets around the main islands and on Nihoa. Arthropods should be a recognized resource of these small offshore islands, and the appropriate invertebrate biosurveys and management recommendations for the native invertebrates should be initiated. *Tamsica* would make good indicator species for other possible surviving arthropods on the islets. Many of these offshore islets are sea bird refuges, where management is currently strongly biased and strictly for the birds. Arthropods are given scarce mention or consideration.

Other potential indicator species can be found in the native Amphipoda, Aranae, Odonata, Orthoptera, Neuroptera, Heteroptera, Homoptera, Lepidoptera, Diptera, Coleoptera, and Hymenoptera. In fact, nearly every speciose native group contains appropriate indicator species, if there are trained systematists and ecologists available to identify them.

Biological Survey of Hawaiian Invertebrates

The biological survey of Hawaiian invertebrates is woefully incomplete. Less than ½ to perhaps ⅓ of the native species are described, making it virtually impossible to recognize problems or to formulate effective conservation management plans. Avise (1989) reviewed several examples where inadequate knowledge of systematics led to inappropriate endeavors to save endangered vertebrates. Such problems are more acute among the less well known invertebrates. It cannot be overemphasized that studies in conservation biology, like all other biological disciplines, can only be as good as the systematics research upon which they are based (Wilson 1985; Avise 1989). Whether a population under study represents an alien species or an endemic species, and whether the population represents one or 20 or 200 closely related species, all have direct bearing on valid management recommendations.

Ecological Research

The role of invertebrates, including alien species, in ecosystems is less understood than is the role of vertebrates. In part, this results from our human bias toward being able to recognize the activities of larger organisms, while not noticing the smaller creatures until the damage is done and the causes obscure. Long-term ecological studies are needed to find better management strategies for mitigating the harmful impacts of aliens and to better assess and predict the impacts of intentional introductions. This research is imperative because increasing world commerce continually worsens the problem. We must revise several myths in ecology, especially concerning unfilled niches, immigration potential, ecosystem fragility, etc. This research should be done in both natural and seminatural areas and on key invertebrate species.

Currently, our knowledge of the status of native groups is anecdotal at best. Several native groups of Hawai'i disappeared alarmingly fast: *Megalagrion* damselflies, *Dyscritomyia* flies, and *Achatinella* snails on O'ahu, Collembola, Vespidae, Sphecidae, and Colletidae on most islands. Some of these groups still have good populations on 1 or more islands. These present a once-in-a-species lifetime opportunity for conservation biology. By monitoring these surviving populations in a long-term effort, there is an excellent chance to recognize the beginning stages of decline and their causes and to develop ameliorating strategies.

Reducing Foreign Species Introductions

Strictly enforced quarantines, regulating potentially harmful introductions, are highly cost-effective in preventing undesirable invasions. Quarantine programs are not only effective against the intended organisms but also have 2 very important side benefits: interception of a great number of other intentional and unintentional introductions and, most importantly, impressing on the public that introductions are potentially harmful.

Persons or agencies desiring to introduce an alien species, including those for biological control, must convincingly demonstrate in a critical open public review process that the alien species poses little potential risk to native species, human health, and the local economy. This review should be modeled after environmental impact studies. Organisms introduced for biological control should be monitored with long-term ecological studies to determine the true fate of these species and make applied ecology a predictive science.

Develop Environmentally Sound Pest Controls

In the political and economic arenas, both real and perceived pests are often controlled by whatever arsenal seems expedient, with often detrimental effects on the native biota. It should be clear that there are no panaceas in pest control. Any action to kill or limit one species must also impact other species.

High priority should be given to separating the serious pests requiring control from innocuous species causing no damage or minor damage. Review of pest status would facilitate development of environmentally sound control methods for bona fide pests, while innocuous species and less serious pests could be dealt with more pragmatically. Biological control, being largely irreversible, unpredictable, and self-dispersible, should be used only in exceptional circumstances.

Conflicts of interests arise in identifying pests. One state agency has imported predators to reduce insect damage to the legume, haole koa *(Leucaena leucocephala)*, while many land managers expend considerable resources to control this major alien weed. Even now, public agencies are planting lantana, several melastomas, and other weeds in public places, while other government agencies introduce alien herbivores to control them.

Environmental Education

Successful educational programs that overcome the public's fear of the perplexing array of strange invertebrates and instill an appreciation of the aesthetics and importance of invertebrates for human welfare should be encouraged and developed. These programs would make many environmentally risky control procedures unnecessary. The western cultural bias and fear of invertebrates needs to be changed. The media's message that "the only good bug is a dead bug" does a great disservice to the natural world.

CONCLUSIONS

The Hawaiian fauna is in transition, as profound changes are now occurring in its composition. Many native groups are declining, with concurrent population explosions of alien species. Is it cause and effect and replacement of one group by another? Or is it coincidence, and the native species declining from some unrecognized cause or change in the environment? Most extinction studies are done in hindsight, after the game is lost. Conservation biologists must act now and get into the field to study population dynamics of native species in natural settings in order to understand extinctions and to develop valid conservation strategies. We presently have that opportunity in Hawai'i and urgently need to field a team of biologists to monitor populations of selected native groups.

Long-term ecological studies are needed to separate population fluctuations from irreversible changes, to assess the impacts of aliens, and to develop mitigative measures. Unfortunately, research on the role of invertebrates lags far behind that for the vertebrates, despite the theoretical importance of invertebrates in maintaining the health of ecosystems. In addition, old assumptions concerning island biology must be thrown out.

Some 2,500 different kinds of alien arthropods are believed to be established in Hawai'i, and probably no native species of plant or animal escapes the effects of this biological pollution. Furthermore, control programs, including biological control, aimed at aliens may adversely affect nontarget native species. More effective quarantine measures and more effective review and regulation of importations of living organisms are desperately needed. Society must discourage alien introductions.

The biological survey of Hawai'i should be completed. Perhaps ⅔ of Hawaiian invertebrates remain unknown, making it difficult to develop appropriate conservation programs. As demonstrated in young Hawaiian caves and on the cold stone desert on Mauna Kea (Howarth 1987), one has to actually search all potential habitats for native species before writing them off as devoid of life.

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How Many Hawaiian Land Snail Species Are Left? and What We Can Do for Them

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ABSTRACT

Probably only 25–35% of the 1,461 species level taxa of endemic Hawaiian land snails that have been described are still extant. Unless immediate actions are taken, most of the 25% to 35% still left will vanish in a very few years. The extensive collections and research publications that resulted from the efforts of the late C. Montague Cooke, Jr. give us a good data base from which to start assessing what part of the fauna remains and where it lives. Extensive field surveys covering both previously collected and very remote areas will identify places that still shelter significant numbers of native land snails. Continued survival of the vegetation communities that contain land snails and other groups of native organisms will require careful management. We must encourage regeneration and expansion of the native plant communities, not just static preservation.

INTRODUCTION

The Hawaiian Islands had the world's most extensive and spectacular radiation of land snails. The use of the past tense is deliberate, reflecting the extinction of probably more than half of this fauna since 1900. Much of this loss has occurred since the mid–1930s. Field surveys by d'Alte Welch and W. Meinecke in the early 1930s demonstrated the presence of many taxa that have not been found during field work from 1960 to 1988. These taxa are thus presumed to be "gone forever." Extinction is not spread equally, but appears to be concentrated within the most diverse taxa, which are endemic at the family or subfamily level. Use of the terms "probably" and "appears" is necessary when discussing the status of these snails, since we lack the data needed to establish what species still exist—and where they can be found today.

Evidence exists for a *minimum* of 1,461 recognizable endemic taxonomic units of Hawaiian land snails, comprising 931 species, 332 subspecies, and 198 unjudged "varieties" (Table 1). For comparison, the land snail fauna of North America north of Mexico (as of 1947) included 719 species and 416 subspecies (Pilsbry 1948: ix). The Hawaiian taxonomic statistics are based upon a combination of published monographs and preliminary reviews of unstudied materials in museum collections. There is no reason to assume that these figures represent anywhere near the actual land snail diversity that existed when the Polynesians first arrived in Hawai'i. Much lowland vegetation had been destroyed prior to initial sampling of the land snail fauna in the mid–1800s. Some record of the vanished lowland fauna can be retrieved from archaeological excavations (see references in Gagné & Christensen 1985; Christensen & Kirch 1986), but most

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disappeared without a trace. An important remnant of this fauna recently has been found to exist on the isolated island of Nihoa (Conant et al. 1984). Many mountain tops and remote valleys still have not been sampled and can be expected to yield a number of additional endemic species.

Undoubtedly the pace of land snail extinction is continuing, although subtractions are now coming from a rapidly shrinking faunal base. The time left in which to seek out and protect remnant patches of Hawaiian land snail diversity is, at best, a *very* few years. It can certainly not be measured in decades.

The reasons for this loss are many and complex, involving human cupidity, stupidity, ignorance, incompetence and, finally, a long period of silence and inactivity by those of us who knew better (including myself). Good summaries of specific catastrophic changes wrought by man have been given by Gagné and Christensen (1985), Hadfield (1986), and Hadfield, Miller and Carwile (1988). Aspects of the factors that led to this drastic loss are mentioned below as a warning. My focus here is on why I consider that parts of this fauna still survive.

If we are to save what is left of the Hawaiian land snails, we must (1) find out what still exists, (2) identify areas retaining significant diversity, and (3) protect both the species themselves and the habitats in which they survive. The damage to native vegetation by feral pigs and other hoofed mammals must be stopped, halting the spread of alien plants into native forest, and protecting the remnant forests from both logging and wood-chipping are minimum initial steps that must be taken *now.*

Land snails do not live in an ecological vacuum. The places where they survive contain members of many other phyla that often are much more difficult to sample and whose taxonomy is poorly known. Snails can serve very effectively as indicator organisms. The extremely small geographic ranges of many land snail taxa (see below) also mean that areas of less than an acre, if protected against major disturbance, may be adequate to provide "thousand year" survival for some Hawaiian species.

SUMMARY OF HAWAIIAN LAND SNAILS

The native land snail fauna of Hawai'i is typically disharmonic and characteristic of "oceanic" islands, including only 10 of the more than 65 land snail families. Extensive diversity is restricted to only 7 family units (Table 1). Members of several other land snail families have been introduced accidentally (at least the Veronicellidae, some "pupilloids," Valloniidae, Ferussaciidae, Philomycidae, Arionidae, Limacidae, Zonitidae, Subulinidae, Bradybaenidae, Helicidae) or deliberately (Streptaxidae, Achatinidae, Oleacinidae). They are flourishing, often in both synanthropic habitats and native forests. Quite probably additional alien taxa are established, but not yet represented in collections or noticed by malacologists.

One aspect of the Hawaiian land snail fauna cannot be overemphasized. There is endemism at both the subfamily and family level, in contrast with other groups of native animals. There are no endemic subfamilies or families of terrestrial arthropods in Hawai'i. Even the justly famed radiation of Hawaiian honeycreepers is now judged to consist of somewhat aberrant finches, rather than a separate family of birds, the Drepanididae.

Although many Hawaiian publications have linked the amastrid land snails with the Holarctic family Cochlicopidae based on a parenthetical paragraph by Watson (1920:24), monographers have followed the judgement of Pilsbry and kept the Amastridae as a separate family (Zilch 1959; Solem 1978; Tillier 1989). The Cochlicopidae and Amastridae may be sister taxa, but their differentiation is at the family level. Both subfamilies of the Amastridae, the Amastrinae and Leptachatininae, are found only in Hawai'i. The family Achatinellidae consists of several Pacific Basin subfamilies: the Achatinellinae are restricted to Hawai'i and most other subfamilies to other parts of eastern Polynesia. These 3 Hawaiian family-level groups account for 753

Table 1. Known Hawaiian endemic land snail diversity.

Family unit	Species	Number of subspecies	Varieties*
Prosobranchia			
Hydrocenidae	1		
Helicinidae	16		43
Pulmonata			
Orthurethra			
Achatinellidae			
"Tornatellininae"	106	11	
Achatinellinae	103	106	6
Amastridae			
Leptachatininae	129		113
Amastrinae	202	94	
"Pupillacea"**	58	26	1
Sigmurethra			
Endodontidae	195	85	35
Punctidae	7		
Helicarionidae			
Euconulinae	6	2	
Microcystinae	54	8	
Zonitidae	10		
Succineidae	44		
Total	931	332	198
Grand total = 1,461			

* Some "varieties" may be polymorphisms within populations, but the status of most remains undetermined, reflecting the pre-1920 systematic literature.

** Family limits within the "Pupillacea" are uncertain, and no attempt has been made to determine the affinities of the Hawaiian taxa.

(51.5%) of the 1,461 recognized Hawaiian land snails. The family Endodontidae (Solem 1976), restricted to Polynesia, Lau Archipelago, and Palau, had about 315 (21.6%) Hawaiian representatives. The achatinellid subfamily Tornatellininae is a Pacific Basin taxon with 117 (8.0%) Hawaiian taxa, and the helicarionid subfamily Microcystinae is another Pacific Basin group with 62 (4.2%) Hawaiian taxa described. These are the most speciose groups of the Hawaiian land snails (Table 1), accounting for 1,229 (84.1%) of the total fauna.

These families are not recently evolved or weakly differentiated. The Achatinellidae includes several of the earliest known land snails (Anthracopupinae) from the late Paleozoic of western Europe and eastern North America (Solem & Yochelson 1979), and the Endodontidae have a Miocene record in other parts of the Pacific (Solem 1976, 1983). They are best viewed as "island hopping relicts" that have been replaced on continental areas by more recently evolved taxa.

The family restricted endemicity for much of the Hawaiian land snail fauna has major practical consequences in terms of systematic and biological study. Specialists in other phyla may obtain their systematic training through overseas work on a particular group and then be attracted by the special problems presented by Hawaiian members of "their" family; in contrast, students of the Hawaiian-Polynesian land snail fauna must be developed locally, or "transfer their interest" from, at best, distantly related taxa residing in other parts of the world.

Soundness of Species Concepts

Especially where organisms are colorful, variable, and popular with collectors, there is a universal pattern of describing all variations as "species." The resulting inflated species numbers are dramatically (and often uncritically) reduced in a succeeding generation of workers. This is followed by later discovery of cryptic or sibling species, and the number of recognized species increases.

Where in this cycle does knowledge of the Hawaiian land snail fauna stand? There is a natural tendency, especially among vertebrate biologists, to view the number of described Hawaiian land snail species very sceptically (Diamond 1977). Particularly when they see the dates of the major monographic studies. I contend that the initial drastic reduction in "species numbers" has *already* taken place, and present 2 examples to support this argument.

Pilsbry and Cooke (1912–1914:xxxiii), in introducing their revision of the highly colorful and very popular tree snail genus *Achatinella*, stated that "While many conchologists may consider the treatment of *Achatinella* in this work an extreme example of 'lumping' (since we recognize but 43 species in place of 171 described), it really belongs to the splitting school. Both authors hold that a considerable further reduction would have to be made to make the species of equal value with most Hawaiian species of *Leptachatina* or *Amastra*." Christensen (1985) estimated that there might be as few as 12–16 "biological species" of *Achatinella*. Hadfield (1986) and Hadfield, Miller and Carwile (1989) implied recognition of 41 *Achatinella* species, although believing (pers. comm.) that adequate study might reduce this number significantly. No such study has been published. It is significant that the very people who published most of the systematic monographs on Hawaiian land snails held the above view of species in the most variable genus.

Only 1 genus has been revised subsequent to the early 1900's burst of study. Hyatt and Pilsbry (1911:100–18) monographed the amastrid genus *Carelia*. With very limited material available, they recognized 11 species and several varieties. By 1930, some 5,500 specimens had accumulated at the Bernice P. Bishop Museum. Cooke (1931), in an exhaustive study, recognized 20 species and 9 subspecies. Five of the latter (Cooke 1931:13) probably represent species. Cooke and Kondo (1952), in the only subsequent study, described another species, 2 new subspecies, and a "geographic race" of uncertain status. Species numbers thus have increased, not decreased.

I have pointed out elsewhere (Solem 1978:52–55) that Pilsbry had an extraordinary ability to recognize actual species from very limited material. It is very probably, on balance, that modern reviews of the Hawaiian land snails will result in increased, not decreased, species numbers.

Background

The obvious attractiveness and bewildering shell variation of the Oahu endemic genus *Achatinella* seized the interest of several generations. Collections by voyagers starting just after Captain James Cook's visit in 1778 resulted in descriptions of numerous species and varieties. In the 1820s, local collecting interest developed. The huge pre–1900 collections by J. T. Gulick and D. D. Baldwin, followed by later efforts of, among many, the Emersons, Irwin Spalding, W. D. Wilder, W. Meinecke, D. Thaanum, G. Arnemann, and d'Alte Welch, provided a massive data base for studies of not only this genus but also many others. J. T. Gulick (1905) produced a classic evolutionary study based upon his years of collecting and study in Hawai'i.

As is typical in early stages of biological inventorying, with the notable exception of Gulick's monograph, most synoptic and first analytical study was by overseas scientists. The early summary reports by a Frenchman (Ancey 1889, 1899, 1904) and an Englishman (Sykes 1900) set the stage for the classic revisionary studies, but a modest, locally produced checklist

(Baldwin 1893) probably had the most effect. Both local and overseas collectors could use this to document personal progress in "completing their collection" and as a challenge to collect or exchange for rare or newly named forms. How many collections this booklet inspired is unknown, but its effect was substantial.

In this century the influence of a most remarkable individual, Charles Montague Cooke, Jr., and his cooperation with the dean of terrestrial malacologists, Henry A. Pilsbry, from the Academy of Natural Sciences of Philadelphia, dominated. "Monte" Cooke died in 1948, leaving a still unfilled gap of interest and concern about Pacific land snails. The flavor of this very remarkable person is found in the highly readable bio-bibliography by Kondo and Clench (1952).

Pilsbry's publication career spanned 75 years. He started this century by publishing 2 of his most important contributions, which were based in large part on Hawaiian data. He established the basic ordinal units of land snails (Pilsbry 1900a) and made a major contribution to biogeographic theory and speculation concerning the Pacific Basin (Pilsbry 1900b). Following publication of 2 descriptive papers (Pilsbry and Vanatta 1905, 1906) based on very limited material, Pilsbry launched a period of intensive cooperation with Cooke. Major monographs of the endemic family Amastridae (Hyatt & Pilsbry 1911; Pilsbry & Cooke 1914–1916); native Helicinidae (Pilsbry & Cooke 1908); Achatinellidae and Tornatellinidae (Pilsbry & Cooke 1912–1914); and "pupilloid" taxa by Pilsbry and Cooke or Cooke and Pilsbry (Pilsbry 1918–1920, 1920–1921) covered several of the main groups. Pilsbry (1916, 1921) continued some Pacific biogeographic work, but then moved on to other projects.

Cooke, realizing that the Hawaiian fauna could not be fully understood without knowledge of taxa from the other Pacific islands, turned his attention to other parts of Polynesia and the Micronesian fauna. He promoted or participated in 3 major expeditions through Polynesia and Micronesia: the Mangarevan Expedition through eastern and southern Polynesia (15 April–28 October 1934); the Micronesian Expedition (8 December 1935–10 June 1936); and the Henry G. Lapham Expedition to Fiji (27 June–28 September 1936). Yoshio Kondo, who served first as an assistant, then collaborator, and finally as successor to Cooke as malacologist at the Bishop Museum, obtained his initial field training and malacological interests on these trips. Additionally, 2 generations of Bishop Museum staff and "mainland" scientists passing through on their way to the South Pacific, were cajoled, inspired, and persuaded by Cooke to collect land snails wherever they visited. Although Cooke continued to encourage active collecting throughout Hawai'i, little of the incoming Hawaiian material, except for specimens of *Achatinella*, were identified to species. They were cataloged and filed under a generic name.

The unparalleled collections at the Bishop Museum are a monument to Cooke's efforts and his inspiration of others. Like many "collection builders," Cooke published comparatively little, choosing instead to promote collaborative efforts or work by others. An important paper on the Succineidae (Cooke 1921); an excellent review of the largest Hawaiian land snails, members of the amastrid genus *Carelia* (Cooke 1931); a significant popular article on the land snails (Cooke 1941); and a posthumous collaborative monograph revising the genera and focussing on the anatomy of mostly non-Hawaiian Achatinellidae (Cooke & Kondo 1960), were his major publications, along with the monumental monographs published in cooperation with Pilsbry. Among the most significant publications that he promoted were an updated checklist of Hawaiian land snails (Caum 1928); a conchological revision of the Hawaiian Helicinidae (Neal 1934); and the landmark monographs of the Pacific Island Zonitidae and Helicarionidae (H. B. Baker 1938, 1940, 1941), which combined anatomical and shell data in an elegant fashion.

Under Cooke's guidance, a detailed program of collecting and analyzing variation in *Achatinella* on a colony by colony basis was started by d'Alte Welch. Welch's massive collection

Table 2. Changing species numbers, 1928–1988.

Family	Number of Recognized Taxa Caum (1928)	Current
Helicinidae	22	59
"Zonitoids"	35	80
Endodontidae	27	ca. 300
Succineidae	44	?

effort began in 1931. This effort was made possible by the publication of detailed maps (Welch 1938:4), which allowed the plotting of each colony with great accuracy. These maps and collections still exist and form the basis for future surveys of Oahu land snails. Welch left Hawai'i to spend the rest of his career as a college professor in Ohio. While he managed to produce studies on geographic and altitudinal variation in *Achatinella mustelina* (Welch 1938), *A. apexfulva* (Welch 1942), and *A. bulimoides* (Welch 1954, 1958), study of the remaining probable species of *Achatinella* was not completed. Parallel collecting and mapping efforts by William Meinecke from 1930 to 1941 and George Arnemann's collections of *Carelia* provide additional highly significant records.

Thus, Cooke was responsible for monographic work on 5 of the 7 diverse taxa—Helicinidae, Achatinellidae, Amastridae, "Pupillacea," and the Helicarionidae plus Zonitidae. Only the Succineidae and Endodontidae remained basically untouched at his passing.

Caum (1928:59–61) listed 44 taxa of Succineidae and 26 in the Endodontidae. While I used Cooke's collection legacy to monograph the 265 species level taxa of Polynesian and Micronesian endodontoid land snails (Solem 1976, 1983), time was not available to study the more than 300 Hawaiian taxa represented in the Bishop Museum collection by about 50,000 specimens in 5,197 lots (Solem 1976:3, Table II). Table 2 contrasts the number of taxa listed by Caum (1928) and those recorded in the few subsequent monographs. Known diversity in these taxa has significantly increased.

Despite all the monographic work accomplished, no overall summary of the Hawaiian land snail fauna was produced. It was left to an entomologist, Elwood C. Zimmerman, drawing upon the knowledge of Cooke and Kondo, to prepare what is still the best outline of the Hawaiian snail fauna that exists (Zimmerman 1948:97–104).

The periods of study can be roughly grouped into 3 eras: (1) the pre–1900 period of survey efforts by residents and description of the taxa, usually by overseas workers; (2) the 1905–1921 period of intensive cooperative work by Cooke and Pilsbry; and (3) the 1928–1948 period in which Cooke primarily promoted studies by others. The later publications by Welch (1954, 1958) belong intellectually to the latter period, and the monograph by Cooke and Kondo (1960) was essentially finished in 1948, although its publication was long delayed.

Except for the evolutionary study of Gulick (1905), published work through 1960 was almost exclusively systematic in content. Then began a period of malacological silence. Neither systematic nor biological work was accomplished for 2 decades. The popular article by Hart (1978) stimulated conservation of Hawaiian land snails and led to the listing by the Office of Endangered Species of all *Achatinella* species as endangered. Subsequently, the seminal report of Hadfield and Mountain (1981) on the life history of *Achatinella mustelina*, reviews on extinction in *Achatinella* by Christensen (1985) and Hadfield (1986) provided much useful data.

It is not that the Hawaiian land snails lack unusual biological features that make them "good organisms" for research studies. The fact that they have basically been ignored stems from other reasons. Perhaps it is simply that they did not have a spokesperson. Nobody proselytized non-systematic biologists touting the opportunities that they present. There was no malacological equivalent to Elwood C. Zimmerman's challenge to *Drosophila* specialists (Zimmerman 1958) concerning the 300 Hawaiian species. The latter paper led directly to the current huge literature and the many evolutionary insights provided by study of the Hawaiian picture wing flies.

Time is very late, and much remains to be done.

Probable Status of Hawaiian Land Snail Families

The low-diversity families (Table 1) comprise the Hydrocenidae (an Indo-Polynesian group known from one collection on Kaua'i), the Punctidae (worldwide with perhaps 5 to 9 Hawaiian species in collections), and the Zonitidae (10 species of recent Holarctic origin). Probably both of the latter families are extant at higher elevations. Hydrocenids are easily overlooked because of their minute size. No comments can be offered on the basis of only 1 collection made many years ago.

Many of the Helicinidae were low elevation taxa and probably are extinct. Recent collections of living helicinids in Mākua Valley (1983) and several places in the Wai'anae Mts indicate that at least some helicinids persist (C. C. Christensen, pers. comm.). In other parts of the Pacific, helicinid taxa are still commonly found, often in mixed vegetation situations or even banana patches. As the only non-hermaphroditic land snails that diversified in Hawai'i, helicinids present many opportunities for biological studies. They are common in fossil deposits and adult shells are highly variable in size, which correlates with moisture differences. Thus, they can be good indicators of minor changes in climate.

The Succineidae are reported by Hadfield (1986:79–80) as "still abundant in many Hawaiian mountain locales." The little anatomical work on Hawaiian species (Odhner 1950; Patterson 1971; Solem unpubl.) shows that Hawaiian radiation is based on the subfamily Catinellinae. Species of Catinellinae have the lowest chromosome numbers (5–6) yet found in any land snail. Twenty years ago, I suggested that this low chromosome count was the result of a chromosome number reduction series, limiting variation in these inhabitants of often temporary habitats (Solem 1969). Unfortunately, no one has attempted to either test this hypothesis or to study the Hawaiian taxa, which represent the largest number of succineid species reported anywhere in the world. The several hundred lots in the Bishop Museum indicate 5 named species from Kaua'i, 7 named and 7 new from Oahu, 2 named and 17 unnamed from Hawai'i. Ranges of species on Kaua'i and Oahu appear extensive, with Hawaiian species very limited. The fact that *S. caduca* is listed from Kaua'i, Oahu, Moloka'i, and Hawai'i may indicate either an actual range (since it is a lowland "species") or that this is a generalized shell form, found in several anatomically distinct species.

The Helicarionidae often are arboreal. In many parts of the Pacific they remain abundant. Because of their uniform shell color and simple shell, they never have been popular with collectors. The latest systematic review of this complex (H. B. Baker 1938, 1940, 1941) was based on very limited material. Accurate species ranges cannot be delimited at present, and the actual diversity level remains to be determined.

The minute "pupilloids" are mostly extinct with only *Pronesopupa* common and persisting even in low elevation, non-native forest. Lowland *Lyropupa* (especially the subgenus *Lyropupilla*), *Pupoidopsis*, and *Nesopupa* have vanished, despite the recent record of *Lyropupa* from Barbers Point (Christensen & Kirch 1986). Some *Nesopupa* and sinistral *Lyropupa* still remain in upland native forests.

Catastrophic extinction has occurred in the remaining three families: Endodontidae, Amastridae, and Achatinellidae. Unfortunately, they were the most diverse families.

The Endodontidae were mostly ground dwellers. Many species laid their eggs in the umbilicus of the shell. Throughout Polynesia, wherever the ant *Pheidole* has become established, endodontids no longer exist. To my knowledge, no live material of *Endodonta* has been collected on the main islands since 1940 (both it and *Cookeconcha* survive on Nihoa). In 1962 I did find a few *Cookeconcha* alive on Wai'anae Mts high ridges on 2 occasions, and M. Hadfield (pers. comm.) once saw two "*Cookeconcha* chasing each other on a leaf" in the 1980s. Low and mid-elevation species, accounting for nearly all of the described taxa, were extinct by 1960. I would guess that less than 5% of the endodontid species may still exist, and these only at high elevations.

Within the Amastridae, the genus *Carelia*, which included the largest native Hawaiian land snail species, is restricted to Kaua'i and 1 species on Ni'ihau. A few living colonies of *Carelia* may exist on the isolated small valleys of the Na Pali coast, but no live specimens have been seen since George Arnemann's collections in 1950. Cooke, in a note on his copy of the *Carelia* monograph, stated in April 1946 that only 10 forms had been taken alive "in the last thirty years." We do not know the current status of most other genera, but since many were ground dwellers, we can predict that considerable extinction has occurred.

Hadfield (1986:80) reported that minute tornatellinids and "a few hardy *Auriculella* species persist in areas from which the achatinellines have disappeared." The status of the species belonging to *Achatinella* was summarized as "22 species of *Achatinella* as extinct, with the remaining 19 species endangered" (Hadfield 1986:67). Subsequently, Hadfield, Miller and Carwile (1988) revised this to "16 species extinct (no living specimens have been observed over 25 years); another 5 species have not been seen for over 15 years." Most of the rest are restricted to a tiny fragment of their historic ranges. The status of most tornatellinids remains unknown, but the degree of extinction must be large. The long life span and low fecundity of *Achatinella* (Hadfield & Mountain 1981; Hadfield 1986) present many interesting opportunities for developmental and ecological studies. Some taxa still exist, but the spread of the introduced carnivorous land snail *Euglandina rosea* quite possibly will do to both the larger Amastridae and Achatinellidae of Hawai'i what it has already done to the *Partula* of Moorea, Society Islands (Clarke, Murray & Johnson 1984; Murray et al. 1988)—eat them unto extinction, except for a few experimental laboratory and zoo colonies. Another temporary option is to establish captive breeding colonies in Hawai'i (see Hadfield, Miller & Carwile 1988), with future hopes of reintroduction into natural areas that are (by then) *Euglandina*-free.

Given the above notes, my earlier statement that 50% of the Hawaiian land snail fauna is extinct probably is wildly optimistic. It may be much higher, since no comprehensive surveys have been made since the late 1930s. But the critical point is that many species still exist, although precariously. Even if only 25% of the documented forms are still extant, these 365 land snail taxa from such a small area represent extraordinary high diversity compared with any other area of the world. They merit study and strenuous efforts toward their preservation.

The fact that many represent families or subfamilies that are *restricted* to Hawai'i, without living representatives elsewhere in the world, increases the urgency. Their loss will be the equivalent of the dodo and elephant bird extinctions, the only island restricted families of vertebrates to become extinct in historic times. This must not be permitted to happen to the Hawaiian land snails.

CAUSES OF LAND SNAIL EXTINCTIONS

"Human interference," be it habitat alteration to complete destruction; chance and deliberate introduction of predators or competitors; or exploitation by collecting activities, is the summary reason for the crisis of 20th century extinctions in all groups of organisms. What had been the gradual pattern of change through geological time (= evolution), of which extinction was a natural part, has become a "momentary" and immediate crisis, which will strip from

Earth many of its species. The fragile and wonderfully diverse biota of oceanic islands lead the list of the vanished.

Much of the damage no longer can be remedied. The process of rapid extinction began when people first arrived on islands. In Hawai'i, the cutting of lowland forests and introduction of foreign land snails started when the initial Polynesian settlers landed (Christensen & Kirch 1986). Habitat destruction and the number of exotic introductions accelerated after 1778. While the Polynesians had carried with them Polynesian and probably a few Indonesian species, Caucasian commerce added taxa from Africa, the West Indies, and India. Such introductions have reached jet speeds today (see Gagné & Christensen 1985; Christensen 1985; Hadfield, Miller & Carwile 1988).

Hadfield (1986) presented a superb summary of the probable causes for the apparent 50% extinction of *Achatinella* species and endangerment of the remainder. His paper should be required reading for Hawaiian biologists.

Unless an island area is clear-cut and burned, total and immediate land snail extinction does not occur. A clear distinction must be made between ground dwelling and arboreal species. Species that forage or shelter in the litter die out first. A change in the ground plant cover, scratching by chickens, trampling by cattle, pigs or goats, the presence of alien ground snails, predation by introduced ants, other arthropods, or predatory flatworms—any or all of these catastrophies can lead to almost immediate extinction of the ground taxa. The arboreal species will have a short reprieve. If the native bushes and trees form a near natural canopy, the tree snails seem to survive. But this may be very short term. Invasive alien plants can choke out the seedlings of the native plants, preventing replacement as the older plants succumb, and trampling by ungulates also can kill off the seedlings. Either of these factors limits the patch as suitable snail habitat to the remaining lifetime of the mature trees.

Until very recently, vegetational changes probably have been the primary causes of tree snail extinction (Gagné & Christensen 1985). Introduced rats also are implicated in the decline of the arboreal snails. Hadfield (1986) has demonstrated how overcollecting could and almost certainly did result in local extinction. Hopefully this no longer will be a factor. But the most immediate and serious threat resulted from State of Hawai'i agricultural officials who introduced a Floridian carnivorous snail, *Euglandina rosea* (Férussac) in an attempt to control the results from the equally stupid introduction of the Giant African Snail, *Achatina fulica*. The introduction of *Euglandina* was against the unanimous protests of malacologists, whose advice obviously was ignored.

Clarke, Murray and Johnson (1984) documented the spread of *Euglandina* on the island of Moorea in the Society Islands. They could thus predict the rate of extinction for the endemic tree snails of the genus *Partula*. Their prediction unfortunately was fulfilled (Murray et al. 1988). *Partula* is the ecological equivalent of *Achatinella*, although independently derived and belonging to a different family. Hadfield (1986:74) noted the extinction of specific *Achatinella* colonies through predation by *Euglandina*.

The above picture is gloomy. If *Euglandina rosea* can be exterminated in Hawai'i, then the salvage of many larger land snails would be relatively simple. A very high conservation priority should be given to the study of ways to exterminate *Euglandina*, 1st in Hawai'i, then from the other islands of Polynesia, and Micronesia, where it is exterminating many other native land snails. If this project fails, we may have to resign ourselves to the inevitable loss of at least the larger native land snails. There are suggestive observations that *Euglandina* may have some altitudinal limitations that could spare the comparatively few higher elevation endemic taxa.

HOPE STILL EXISTS

Despite the above, I think it is possible to save and protect a significant portion of the native Hawaiian land snail fauna. A small portion, perhaps less than 5% of the species, will be found to have adjusted to introduced plant cover or mixed vegetation. So long as any combined forest remains, they will survive. But we do not know currently which species they are or what their minimum requirements may be.

Neither vertebrate biologists nor botanists, who have been much more active in conservation matters than malacologists, appreciate how small an area is adequate to maintain a viable colony of many land snail species.

They must be educated. The view of Diamond (1977) that only Madagascar, New Guinea, and possibly New Zealand, of all Pacific islands, were large enough for *in situ* speciation of land birds, stands in sharp contrast to the situation found in land snails.

Unfortunately, the Hawaiian examples of exceedingly small ranges are based upon the memory of formerly active collectors and involve areas now stripped of trees. But several situations were known in which "father and son," over much more than half a century, repeatedly visited a grove of trees to collect a special form of *Achatinella.* They found that the colony continued to be restricted to 1 or 2 trees only, even though their branches interdigitated extensively with many neighboring trees of the same species, and the whole grove contained 50–100 trees. While this is an extreme situation, the diversity of Hawaiian land snails was not based upon many species living in the same place. It was based upon many species having small, mainly allopatric ranges. Altitudinal zonation, rain shadow changes in moisture and vegetation, plus single ridge effects, combined to provide the opportunity for many local speciation events.

This contrasts, for example, with the situation in wetter parts of the mid North Island of New Zealand, where up to 72 relatively small land snail species can be microsympatric (Solem, Climo & Roscoe 1981). The Hawaiian pattern parallels the situation found in the monsoon fringe habitat of the Ningbing Ranges in the northeast corner of Western Australia (Solem 1988). An endemic radiation of camaenid land snails has resulted in over 28 relatively large species (shell diameter 15–25 mm), which are mainly allopatric, and have area ranges of only 0.01–7.45 km^2 (median 0.825 km^2). In fact, most areas of the world have only 5 to 10 sympatric land snail species (Solem 1984).

The contemporary Hawaiian pattern of low sympatric land snail diversity, perhaps 5 to 10 species present in 1 patch of bush only 10 meters^2 in size, may complicate initial conservation efforts. Hopefully there still will be large numbers of such bush or tree clusters found to contain snail colonies. The plant or vertebrate-oriented conservationist, raised in the "species/area" dogma, will view such patches as inconsequential and incapable of sustaining populations. This is not true for land snails!

In the emergency situation that exists, we must think initially of "hundred year survival." If two trees can hold a colony for over a half century, then 10–20 trees should be good for at least 1 century, buying time for longer range solutions to be implemented. And this is where our view must start.

ACTIONS TO TAKE

The following statement, taken from Pilsbry and Cooke (1915–1916:68) is nearly 75 years old, but remains as true today as when first penned to paper. "The higher mountain slopes of the Hawaiian Islands offer an almost unlimited field of study to the painstaking collector of small or minute species of land Mollusca. This region, especially on Oahu, Molokai and Lanai, has been pretty well covered for the larger arboreal species (*Achatinellidae*), but in what is known to the average collector as "small trash" (such as *Tornatellina* [used as a general descriptive term for small, brownish, conical or globular land snails]), it is practically an unexplored country."

The collections of land snails in the Bishop Museum and private collectors provide a wonderful data base. They demonstrate where species were from the 1900s through 1930s and what the species look like. They can be used immediately to demonstrate where collections have not yet been made—usually because of remoteness and difficulty of access. It is in these remote and upland areas of Hawai'i that we are most apt to discover healthy colonies of land snails and then focus our efforts on salvage and preservation.

Collecting and study of the Hawaiian land snails followed the typical pattern of coast 1st, low level forest next, midlevel forest later, and high forest only after the rest became extinct. For altitudinally zoned taxa, such as the endodontid genus *Libera* in the Society Islands (Solem 1976:385–86), species collected by early explorers were not found after 1840, and similar situations will be documented for Hawai'i.

Our 1st priority must be extensive survey work, not only reinvestigating areas sampled in the early 1930s (the last period of rigorous sampling), but also working the "areas out of reach." Because of the existing collection and monographic data base, it will be relatively simple to identify places that contain land snail colonies and differentiate those places containing only widespread taxa from those with mainly local endemics. Considerable mapping of ranges will be required and the data for major systematic revisions will accumulate. It is hoped that this initial phase will gain the enthusiastic cooperation of local biologists, and that work on many aspects of snail biology and evolution can be started. At the very least, establishing "Baseline 1990s," where native land snails still persist, will permit intelligent attempts at preservation and recovery for those taxa remaining.

Perhaps 3–5 years of primary field survey and identification work can accumulate the data needed to carry out the 2nd phase of work. If such survey work is done on an island by island basis, it will be possible very early in the survey to begin targeting areas of snail and biotic diversity worth saving, identify immediate threats to these areas, and start the difficult process of managing them back to a healthy state.

Identification and legal protection of colonies is only the 1st step. Perhaps 15–20 small clusters of trees in an upper valley may have snail colonies, but they will be surrounded and isolated by dense stands of alien vegetation. The snails may enable targeting such areas, but the patches will contain many other organisms. Regeneration and expansion of the native plant stands must be encouraged over a period of decades, allowing the now isolated patches to coalesce and thus turn these remnants into an approximation of the native stands of yesteryear. This is the only way that longer term survival of the biota can be achieved.

Innumerable systematic and biogeographic problems will be encountered, especially as the field surveys of remote areas are completed. If we are fortunate, the successors and intellectual equals to Pilsbry and Cooke will rise to these new challenges and opportunities for study. The lengthy process of major monographic work must be emphasized. The monograph on the anatomy and classification of the Achatinellidae by Cooke and Kondo (1960:3) was in progress nearly full-time from late 1941 through most of 1948, required additional time for polishing, and did not appear in print until 19 years after its inception. My own studies on the Pacific Island Endodontidae and Charopidae (Solem 1976, 1983) were initiated in 1961. The time needed for completion of writing was extended by three and four-year "in press" periods, respectively.

SUMMARY AND CONCLUSIONS

Protection for and possible recuperation of the Hawaiian land snail fauna thus requires: (1) surveys to identify where native land snails persist; (2) identification of immediate threats to these colonies; (3) legal and managerial protection for selected areas; (4) work to permit regeneration of the native vegetation to provide expanded habitat; and (5) systematic and biogeographic studies of the material collected and the colonies protected.

These objectives cannot be carried out during occasional visits of overseas specialists. It must be the responsibility of the people of Hawai'i to provide the energy, efforts, dedication, and funding needed to save important natural elements of their wonderful land that they are in immediate danger of losing.

Only because of the lifetime dedication by a single person, C. Montague Cooke, Jr., do we have the knowledge and collections that will permit salvaging an important portion of the natural heritage of Hawai'i. Committees may come and recommend, but they will go. So often in human affairs, it is the action of a single person, or at most a few people, who provide real progress.

Who will be the next "Monte Cooke?"

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The Cult of Pele in Traditional Hawai‘i

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ABSTRACT

This paper is an attempt to reconstruct the cult of Pele, volcano goddess of Hawai‘i, as it existed in pre-European Hawai‘i. It is based on English language sources, including translations from Hawaiian and various European languages, and is intended to be a compilation of the earliest descriptions of the Pele cult. Primarily descriptive with minimal interpretation and analysis, the discussion includes (1) Pele within the context of Hawaiian religion; (2) the mythology of Pele; (3) traditional beliefs about Pele; (4) the ritual leaders or priesthood of Pele; (5) ceremonies for Pele; (6) offerings to Pele; and (7) the role of Pele in sorcery. The conclusion presents a summary of the major features of the traditional cult and a brief discussion of the continuing belief in Pele in contemporary Hawai‘i.

INTRODUCTION

The volcano goddess Pele was the central deity of an important religious cult in pre-European Hawai‘i.[2] The cult attracted worshippers from the districts of Hawai‘i Island, most frequently inundated by volcanic eruptions, and had its own temples, priests, rituals, and mythology. Although Pele was the most important of the volcano deities, other members of her family, such as her sister Hi‘iaka-i-ka-poli-o-Pele and her brother Ka-moho-ali‘i, also received ritual attention in the traditional cult.[3]

Present knowledge of the Pele cult, and of traditional Hawaiian religion in general, is based on a few written records of what was once a complex, elaborate religious system. This sparse and scattered literature includes the writings of the earliest explorers, the first missionaries, the first literate Hawaiians, and various other observers who passed through the islands before traditional Hawaiian culture was dramatically altered by Western contact. These sources must be used with caution, however. By the time most of the early descriptions were written, the culture had already been significantly altered by Western contact (Kelly 1967:401). The writings of early Hawaiians (e.g., Samuel Manaiakalani Kamakau and David Malo) are invaluable sources for the study of traditional Hawaiian religion but they, too, must be used cautiously since these men were Christianized and frequently critical of the traditional religion. Also, for the most part, they were writing from memory of a religion once practiced, rather than from intimate knowledge of one still functioning. Equally important, they were not themselves religious specialists, and their writings represent a very limited view of the complex, diverse

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2. Unless otherwise stated, orthography of Hawaiian words and deities follows *Hawaiian Dictionary* (Pukui & Elbert 1971). Orthography of place names is from *Place Names of Hawaii* (Pukui, Elbert, & Mookini 1974). Spellings of words not found in either of these books are based on the accounts in which they appear.

3. *Pele* is used in Hawaiian not only as the name of the volcano goddess, but also to mean "lava flow, volcano, eruption" (Pukui & Elbert 1971:298). According to Kamakau, *pele* is also the name for a volcanic manifestation or spirit (1964:64, 89).

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religion of traditional Hawai'i. Many of the other early observers remained in the islands only briefly, and their observations are often based on hearsay and are extremely superficial.

Thus, the details of Hawaiian religion and, more specifically, of the cult of Pele within that religion will probably never be known. This paper presents a compilation of the earliest descriptions of the Pele cult in an attempt to describe the general outlines of the Pele religion. It is based on English language sources, which include translations from Hawaiian as well as various European languages. The most important sources for data on the traditional cult of Pele are the writings of William Ellis (1979 [1827]), Samuel Manaiakalani Kamakau (1964), and Mary Kawena Pukui (Handy & Pukui 1972 [1958]; Pukui, Haertig & Lee 1972). William Ellis, an English missionary, visited the island of Hawai'i in 1823, and his journal has the earliest published references to Pele. Although his observations are biased by his Christian religious fervor and he was observing Hawaiian culture some 40 years after Western contact, he nonetheless left some of the earliest and most important documentations of the Pele cult. Samuel Manaiakalani Kamakau wrote a series of articles in Hawaiian newspapers on various aspects of Hawaiian culture during the mid-19th century. The most important of his works were translated by Mary Kawena Pukui and published by Bishop Museum (Valeri 1985:xxv). Kamakau's accounts of Pele worship are perhaps the most important sources on the traditional worship of Pele. The writings of Mary Kawena Pukui herself are much later than the other sources used in this paper, but are relevant because they are based on data from Ka'ū district of Hawai'i, where the Pele cult was very important and where Pukui conducted considerable field research. Pukui's family believed itself descended from Pele and continued to worship the goddess long after the Christianization of the islands. Thus her writings, although late, provide important insights into the traditional cult. In addition to these major sources, dozens of other early observers have contributed bits and pieces of information about the Pele cult. The resulting mosaic provides a general picture of the cult, albeit one filled with tantalizing lacunae.

This paper, then, is an attempt to reconstruct the cult of Pele as it existed in traditional Hawai'i. It is primarily descriptive and offers minimal interpretation and analysis. The following text includes discussions of (1) Pele within the context of Hawaiian religion; (2) the mythology of Pele; (3) traditional attitudes toward Pele; (4) ritual leaders or the priesthood of Pele; (5) ceremonies for Pele; (6) offerings to Pele; and (7) the role of Pele in sorcery. The conclusion presents a summary of the major features of the traditional cult and a brief discussion of the continuing belief in Pele in contemporary Hawai'i.

THE PELE CULT WITHIN HAWAIIAN RELIGION

Hawaiian religion, like most Polynesian religions, was an Olympian-type religious system with shamanistic elements. Hierarchical gods dominated the various realms of human concern and were the objects of religious ritual. Kū and the goddess Hina were the male-female godhead who presided over all the male and female gods (Beckwith 1970 [1940]:13). Kū, Lono, Kāne, and Kanaloa are usually regarded as the 4 major gods (Beckwith 1970 [1940]:3–4), although local and ancestral gods (*'aumakua*) were probably more important to the majority of the people. Kū is perhaps best known as the god of war. Associated with agriculture, rain, and peace, Lono was the central god in the *Makahiki* harvest festival. Kāne "represented the god of procreation and was worshipped as ancestor of chiefs and commoners" (Beckwith 1970 [1940]:42). Kanaloa, an important deity in other parts of Polynesia but less important in Hawai'i, was almost always found in association with Kāne. The rank and importance of these gods doubtless varied by region within an island as well as from island to island throughout the archipelago. These individual gods had various manifestations (e.g., Kamakau lists 36 for Kāne [1964:57–58]) that reflected their control over different domains of Hawaiian concern, and each was associated with different colors, directions, days of the month, periods of the day, natural phenomena, plants, animals, and seasons (Valeri 1985:15). Some were also ancestral gods (*'aumakua*) to those Hawaiians who could trace their ancestry directly to them. All had priests learned in the proper ritual for their appeasement, which was performed in special *heiau* (temples).

Beneath these major gods were literally hundreds of other gods who included the children of the major gods, such as Pele and other members of her family. Pele had a special relationship with the god Lono, who is associated both with rain in the Ka'ū district of active vulcanism on the island of Hawai'i, and with agriculture, especially in the celebration of the *Makahiki* harvest festival. Handy and Handy suggest this association may be due to the tradition of Pele and Lono coming from the south and the fact that rain clouds and rain often accompany volcanic eruptions (1972:333). Ka'ū traditions claim Lono is the uncle of Pele (Handy & Pukui 1972 [1958]:31). All the traditional myths relate Pele in one way or another to the highest gods. Thus, the chiefly families who traced their genealogy to Pele could trace their relationship to the highest gods and ultimately to the very beginning of the cosmos.

The genealogical relationships of these different gods are confusing and conflicting in the mythology that has survived. Probably this was also the case in traditional Hawai'i because of regional variations, marriages that brought different families (and thereby different gods) together, the political ups and downs of chiefs and their gods, and the genealogical juggling occasionally done to enhance family pedigrees. Consequently, the genealogies of related families may conflict with each other; nonetheless, the individual genealogies provided a coherent statement of the family's position within the cosmogony as well as within Hawaiian society.

Pele and members of her family are frequently described as *'aumakua*, or ancestral deities (Kamakau 1964:28; Kihe n.d.:566; Poepoe Collection n.d.:37). These *'aumakua* tended to be regional and were the most important objects of ritual concern for the majority of the population. Some *'aumakua* became *akua*, or major gods, in some areas. Such seems to be the case with Pele. Pukui claims Pele was worshipped both as an *akua* by some people who were not directly descended from her, and as an *'aumakua* by her descendants (Pukui, Haertig & Lee 1972:1:24,36). Ellis (1979 [1827]:216) and Bingham (1981 [1847]:255) also refer to Pele as an *akua*. Kamakau reports that "she [Pele] was consecrated and made a god . . . by persons not related by blood descent; and that is how Pele became an *akua* for this race" (1964:69). Emerson claims that the 4 great gods, Kū, Kāne, Kanaloa, and Lono, were occasionally dependent on or intimidated by Pele (1915:40,201).

Most Hawaiians living in the volcano areas of Hawai'i, the districts of Ka'ū, Puna, and Kona, at the time of European contact traced their ancestry to Pele. Kamakau elaborates:

> The persons who have a *kuleana* [a right or privilege because of a blood relationship] in *Ka lua o Pele* are the direct descendants . . . of Haumea, Kanehekili, Kaho'ali'i, Kanewawahilani, Kauilanuimakehaikalani, Nakoloilani, Kamohoali'i, Pele, Hi'iaka, and Namakaokaha'i. If one of these *'aumakua* is in the family of a person, they are all in his family. . . . Only through the blood lineage . . . of the ancestors does the *kuleana* come. The god recognizes that blood kinship and clings forever to his descendants in the living world. Persons who can claim such birth, even those who live on Oahu or Kauai, or those who have sailed away to foreign lands, have a *kuleana* in *Ka lua o Pele*. (1964:66)

Kamakau further claims that upon the death of a person believed to be descended from Pele, a volcanic spirit came to lead the deceased's spirit to the volcano (1964:50). He adds: "Only her [Pele's] actual relatives . . . commemorated her and observed the kapus of their ancestress" (1964:69). In discussing the *kapu* associated with the *'aumakua*, Kamakau states:

> The kapus of the third division, those with volcanic *'aumakua* . . . and those who had been changed into *pele* [a volcanic spirit], had to be combined with the kapu of another *'aumakua.* A volcanic spirit, a *pele,* as I have said, had no kapu thing of its own; only a gift of a bit of salt was required. But if the *pele* was combined with Puna'aikoa'e, then the *koa'e* bird became kapu; if combined with the kapu of the *mo'o* Kalamainu'u, then the kapu was a very strict one, and several articles of food were forbidden. (1964:89)

There is no evidence that Pele was worshipped extensively beyond the volcano area of Hawai'i, although her mythology was apparently widespread throughout the Hawaiian Islands and members of her family were important in ritual throughout the archipelago. For example, Laka, described as both her daughter and her sister in the myths, and Hi'iaka-i-ka-poli-o-Pele, her youngest sister, were objects of ritual concern during aspects of hula training (Emerson 1965 [1909]:23–25). Another sister, Kapo, as well as other family members, assisted the malevolent ends of sorcery (Emerson 1892:7). Her brother, Kanehekili, a thunder god, was the center of a cult on Maui (Thrum 1908:48–49).

Pakele writes of specific chiefs and the gods they worshipped (1864:3196–98). Not surprisingly, he mentions "Pele-wahine" and "Hiiaka-akua" as gods of a chief from Hawai'i. Other members of Pele's family are mentioned as gods of chiefs from other islands, specifically "Kapo-wahine" (Pele's sister) for a Moloka'i chief, "Haumea-akua" (Pele's mother) for an O'ahu chief, and "Lono-pele" (Pele's uncle) for a Ni'ihau chief. Chiefs who traced their ancestry directly to Pele were most likely from Hawai'i Island, more specifically the volcano districts. However, because of the web of kinship that related all the gods, most chiefs could probably trace a kinship tie to the Pele family. Kamakau notes that "from Kauai to Hawaii come visitors with their bones and their gifts and their offerings vowed to Pele" (1964:67), suggesting that people from throughout the Hawaiian archipelago felt closely enough related to Pele to want their bones deposited in the volcano with the goddess. This is 1 of 2 references in the early literature I encountered of people coming from other islands to worship Pele.

A variety of epithets were used to refer to Pele indirectly since the direct use of her name was not always considered proper. Among those found in the literature are: "Pele-ke-ahi-'a-loa" (Pele-of-the-lasting-fire) (Manu 1899:38); "the Woman" (Emerson 1915:10), "the Woman who dwells in the Pit" (25), "God of the Pit" (77), "Woman of Kilauea" (95), and "the Goddess" (167); "Pele-honua-mea (Pele-the-sacred-earth-person)" (Handy & Pukui 1972 [1958]:28); "Honuamea" (Kamakau 1964:14); "mountain dweller," "earth devourer," and *wahine kapu* (sacred woman) (Pukui, Haertig & Lee 1972:1:200); "Akua lehe 'oi. *Sharp-lipped goddess*" (Pukui 1983:13), "Ka wahine 'ai honua. *The earth-eating woman*" (177), "Ka wahine 'ai pōhaku. *The stone-eating woman*" (177), "Ka wahine 'ai la'au o Puna. *The tree-eating woman of Puna*" (177), "Ke kua a kānāwai. *The back guarded by law*" (188), and "Luahine moe nonō. *Old woman who sleeps and snores*" (218).

THE MYTHOLOGY OF PELE

Although the actual worship of Pele was most important in the districts of Hawai'i that experienced active vulcanism, the mythology of the goddess was widespread throughout the Hawaiian Islands. The body of Pele myths is a major myth cycle of Hawai'i and is, in fact, one of the most elaborate found throughout Polynesia. The collection of myths constitutes a biography of the goddess with the individual myths relating: (1) her birth and genealogy in a mythical homeland; (2) her migration to Hawai'i with family members; (3) her search for a suitable home in the Hawaiian Islands; (4) her love affair with Lohi'au, as related in the well-known Pele and Hi'iaka cycle (Emerson 1915); (5) her tempestuous encounter with

Kamapua'a, the hog-man demigod from O'ahu; and (6) numerous minor accounts of her role in shaping geological formations and her encounters with various real and mythical characters. Discussions and/or summaries of the major myths occur in Kalakaua (1972 [1888]:137–54), Emerson (1915), Beckwith (1970 [1940]:167–200), Anderson (1967 [1928]:267–87), Westervelt (1963 [1916]), Charlot (1987:41–47), and Nimmo (1987).

As with many Hawaiian gods, the myths are contradictory regarding Pele's genealogy. Most agree that her parents were among the major gods, with Kū as her father and Haumea, or Hina, as her mother. As noted, Kū and Hina were believed to preside over all gods, while Haumea was considered one of the original gods and "ancestress of the Hawaiian people" (Beckwith 1970 [1940]:276). Although the myths provide a variety of other names for Pele's parentage, they generally agree that she was the child of the highest gods. She was not an only child; in fact, an examination of the mythology reveals she had dozens of sisters and brothers (Nimmo 1987:12–16). Some of the siblings, like Pele, had both human and spirit forms, but most had only spirit forms (Kamakau 1964:67). The siblings who play significant roles in the mythology include: Ka-moho-ali'i, a brother who steered the canoe that brought Pele to Hawai'i and later became important as a shark-god; Nā-maka-o-kaha'i, an older sister whose jealousy of Pele resulted in Pele's expulsion from her homeland; Hi'iaka-i-ka-poli-o-Pele, Pele's youngest sister, best known in Hawaiian mythology for her adventures in seeking Pele's lover, Lohi'au, as recounted in the Pele–Hi'iaka cycle (Emerson 1915);[4] Laka, sometimes a sister and sometimes a daughter of Pele, associated with the hula; and Pele's sister, Kapo, also associated with the hula, but equally important in traditional Hawai'i as a sorcery goddess.

Pele was born in a mythical land, usually Kahiki, a place of origin that occurs frequently in Hawaiian religious literature. Because of a conflict, usually with her older sister, Nā-maka-o-kaha'i, she is forced to emigrate to Hawai'i with some of her relatives. The entourage visits various mythical places en route, but eventually lands in the Hawaiian Islands, usually at Ni'ihau, or one of the nearby islets. Upon arriving at Ni'ihau, Pele digs into the earth to build a home, but she soon encounters water, or her sister Nā-maka-o-kaha'i, sometimes described as a sea goddess, and she must look elsewhere. She moves from island to island in a northwest to southeast direction, seeking a home, always encountering water or Nā-maka-o-kaha'i, and having various adventures along the way, until she arrives at Kī-lau-ea Volcano on Hawai'i Island where she finally finds a home suitable for her extensive family. Kī-lau-ea becomes her permanent home, and from there she has the various adventures recounted in Hawaiian mythology.

Many traditional stories and chants of Pele reflect a duality in the nature of the goddess. For example, sometimes she is presented as a beautiful young woman and at other times as an ugly old hag. She may be benevolent or malevolent. She is a creator of new lands as well as a destroyer of old lands. This duality may be partly explained, perhaps, by the unpredictable and multifaceted nature of the volcanoes she personifies, but it is also a characteristic of Hawaiian, as well as Polynesian, world view.

Pele is regarded as a newcomer in some Hawaiian traditions—that is, she arrived in the islands after they had become inhabited by gods and humans. In fact, she is frequently referred to as "*akua malihini* (foreign deity)" in traditional stories and chants (Handy & Pukui 1972 [1958]:123). Some have interpreted this to mean she was introduced to Hawai'i by later Polynesian immigrants who arrived after the initial colonization of the islands. Fornander believed she was a historical person who arrived in Hawai'i after the islands were settled and was apotheosized at the volcanoes (1969 [1878]:44). The cycle of Pele myths, an indigenous

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[4] Brigham claims that *Hi'iaka* was a general name used for all the gods of the volcano (n.d.:31). Kepelino uses the name similarly (Kirtley and Mookini 1977:46).

Hawaiian development, probably began after the early period of colonization as Hawaiians moved into the volcano regions. This may partly explain the tradition of recency. It is certainly apparent both that the body of myth evolved in the volcano area of Hawai'i and that it shares many themes and motifs from Hawaiian and Polynesian myth in general. The name "Pele" appears in the mythologies of other Polynesian peoples, but always as a very minor deity (Nimmo 1987:34–35). It is unclear whether she was introduced to these areas after European contact (Beckwith 1970 [1940]:178), or whether she represents an ancient, albeit minor, deity in the Polynesian pantheon.

TRADITIONAL BELIEFS ABOUT PELE

In addition to the myths, various other beliefs were associated with Pele. The earliest accounts consistently report that Pele was a deity to be feared. Some of the accounts may be biased by the Christian ethnocentrism of the observers, and what was interpreted as fear in some cases may have been awe and respect. Nonetheless, the consistency of the descriptions of Pele as inspiring fear, by a wide variety of writers, suggests that such was the view of many early Hawaiians. Such descriptions appear throughout Ellis's book:

> Excepting the deities supposed to preside over volcanoes, no god was so much dreaded by the people. (Ellis 1979 [1827]:54)
>
> Whenever the natives speak of them [i.e., the volcano gods], it is as dreadful beings. (172)
>
> They [the volcano gods] never journeyed on errands of mercy; to receive offerings, or execute vengeance, were the only objects for which they left their place. . . . Great indeed is the number of men slain by them; . . . (173)
>
> [If proper respect were not paid the volcanic deities] they filled Kirauea [Kī-lau-ea] with lava, and spouted it out, or, taking a subterranean passage, marched to some one of their houses (craters) in the neighbourhood where the offending parties dwelt, and from thence came down upon the delinquents with all their dreadful scourges. . . . They would go down, with fire kill the fish, fill up with pahoehoe (lava) the shallow places, and destroy all the fishing grounds. (173)
>
> . . . for Pele was a dreadful being. (185)
>
> They . . . answered, that . . . [Pele] was very powerful, and capable of devouring their land, and destroying the people. (251)

Menzies similarly "found that the natives regarded volcanoes as the habitations of evil spirits who, when anywise engaged [*sic*], vomit up fire and hot stones" (1920:160).

The missionary Richards writes: "The volcanoes had, moreover, a superintending power, the goddess Pele, who was much dreaded" (1825:48).

Kamakau notes that "in the old days men feared the volcano; they did not descend into Kilauea as they pleased" (1964:67).

Stewart writes that "under the name of Pele, this volcano was one of the most distinguished and most feared of the former gods of Hawaii" (1970 [1830]:388). Charles de Varigny claims that "a god was born of each of their terrors. Pele, the volcano goddess, swallowed up villages, devoured crops, sowed across her path seeds of sterility and of death" (1981:13). Joseph Emerson provides one of the most fearful portraits of Pele:

> She could at times . . . assume the appearance of a handsome young woman. . . . At other times the innate character of the fury showed itself, and she

> appeared in her usual form as an ugly and hateful old hag, with tattered and fire burnt garment, scarcely concealing the filth of her person.
>
> Her blood-shot eyes and fiendish countenance paralyzed the beholder, and her touch turned him to stone. She was a jealous and vindictive monster, delighting in cruelty and at the slightest provocation overwhelming the unoffending victims of her rage in wide spread ruin. (1892:7)

Emerson further claims that the "deformity of the eyelids, especially of the lower eyelid, called *makahelei*, is charged to the malice of this goddess, who is herself represented as suffering with the most aggravated ophthalmia" (1892:7).

Elsewhere, Emerson says Pele was "represented as a hideous, ill-dressed hag, continually shifting her dwelling-place, tearing down and building up as suited her ever changeful mood" (n.d.a:606).

David Malo writes: "From the fact that people had with their own eyes seen . . . solid rocks, houses and human beings melted and consumed in the fires of Pele, the terror inspired by this class of deities [i.e., the volcano gods] was much greater than that caused by other deities" (1951 [1903]:116).

Judd translates and interprets 2 Hawaiian proverbs that associate Pele with fear: "Weliweli ino Puna i ke akua wahine: Puna is fearful of the goddess. Puna is afraid of Pele" (1930: 61); "Makau i ka hana, i ka uka o Puna: Afraid to do evil in the uplands of Puna. Afraid of disobeying the laws of Pele" (62).

Although elsewhere Kamakau describes Pele as fearful (1964:67), he also reveals a benevolent side of the goddess: "She, Pele, had built this place [Halema'uma'u] to warm strangers who came to the mountain through icy mists" (1964:65).

Handy and Pukui also depart from the general view of Pele as a dreadful goddess who is to be feared. In writing of the district of Ka'ū, they report:

> It is profoundly significant that the Hawaiians of Ka-'u did not fear or cringe before, or hate, the power and destructive violence of Mauna Loa. They took unto them this huge Mother mountain, measured their personal dignity and powers in terms of its majesty and drama. They named their land "The Breast" (*Ka-'u*). They loved Pele, whose home was their land: they endured her furies, and celebrated the drama of creation with which they lived so intimately in the songs and dances of the sacred *hula*. (1972 [1958]:22)

Two possibilities account for this departure from other observers. First, they were writing of Hawaiian beliefs a century after Ka'ū was Christianized. As noted elsewhere, in more recent years, Pele has come to be regarded as a protectress of all Hawaiian people (Nimmo 1986:164), and perhaps this view reflects this trend in contemporary Hawai'i. Second, Handy and Pukui were describing attitudes of the people who lived in Ka'ū, the district most frequently visited by volcanic activity and where Pele, consequently, was central to the lives of the inhabitants. In writing of the people of Ka'ū, Handy and Handy state: "They believed themselves to be of 'The clan of Pele'; many bore the names of the volcano goddess herself or of her sisters, the Hi'iakas. . . . [They] . . . both loved and feared Pele and her family" (1972:615). Since the Ka'ū people felt a greater kinship to Pele, worshipped her as their central *'aumakua*, and believed many of their deceased kinsmen lived in the volcano with her, it is likely they regarded her more warmly than did more distantly related Hawaiians. It is noteworthy that elsewhere, Pukui refers to Pele as "the dreaded fire goddess" (Handy & Pukui 1972 [1958]:153), reflecting perhaps an ambivalence of the Ka'ū people toward Pele.

Although eruptions were generally considered the result of Pele's anger, Kamakau claims

Hawaiians had no fear of the lava if they believed the spirits of their deceased were in the flames:

> Should Hawaii be overrun by lava, if they saw the *ho'ailona* [sign] of their own volcanic spirit (*pele*) in the fountains of fire the people had no fear of death—it was their own *kama'aina* who surrounded them with fire. If they were within the blazing fires, they would come to no harm; they had their guide, and they could go forward victoriously . . . and without harm. Such was the belief of some people about volcanic spirits in the old days. (1964:65)

The Hawaiians regarded Hale-ma'uma'u as the home of the volcano family who, except during the periodic eruptions, lived lives there similar to those of the Hawaiians. Ellis writes:

> They [i.e., Hawaiians] considered it [Hale-ma'uma'u] the primeval abode of their volcanic deities. The conical craters, they said, were their houses, where they frequently amused themselves by playing at Konane (the game resembling drafts . . .; the roaring of the furnaces and the crackling of the flames were the kani of their hura (music of their dance,) and the red flaming surge was the surf wherein they played, sportively swimming on the rolling wave. (Ellis 1979 [1827]:171)

Joseph Emerson writes that Hale-ma'uma'u, the fire pit at Kī-lau-ea where Pele was believed to reside, was the name used by Hawaiians for a temporary "small, rude house, or rather hut, thatched with the leaves of the ama'u fern. . . . The imaginative Hawaiians saw a fancied resemblance to these huts in the lava cones with their jutting peaks and rude unfinished apertures for the escape of smoke. On this view, Hale-ma'uma'u became a fitting name for the place where Pele was wont to build these temporary structures" (1913:729).

Hawaiians, however, approached the volcano area with great trepidation, fearful they might offend the volcano gods by intruding into their domains. Ellis's description of his visit to the volcanoes is filled with illustrations of such fears. When Ellis's guide learned of his intention to visit the volcano area, he refused to accompany him:

> He objected strongly to our going thither, as we should most likely be mischievous, and offend Pele or Nahoarii [Ka-moho-ali'i?], gods of the volcano, by plucking the ohelo, (sacred berries,) digging up the sand, or throwing stones into the crater, and then they would either rise out of the crater in volumes of smoke, send up large stones to fall upon us and kill us, or cause darkness and rain to overtake us, so that we should never find our way back. (Ellis 1979 [1827]:141)
>
> As we drew near one of the apertures that emitted smoke and vapour, our guide stopped and tried to dissuade us from proceeding any further, assuring us he durst not venture nearer for fear of Pele, the deity of the volcanoes. (150)
>
> As soon as the natives perceived us eating them ['*ōhelo* berries], they called out aloud, and begged us to desist, saying we were now within the precincts of Pele's dominions, to whom they belonged, and by whom they were rahuiia (prohibited), until some had been offered to her, and permission to eat them asked. (162)

Ellis's Hawaiian guides warned him not to "strike, scratch, or dig the sand, assuring us it would displease Pele, and be followed by an irruption of lava, or other expression of vengeance from this goddess of the volcano, of whose power and displeasure they had manifested the greatest apprehensions ever since our approach to Kirauea [Kī-lau-ea]" (1979 [1827]:166).

Dibble reports that the devastating eruption that destroyed part of Keoua's army was believed to be caused by Pele because stones were rolled into her crater (1909 [1843]:51). Ellis's party was unhappy with the spot "at the north-east end of the crater, on a pile of rocks over-hanging the abyss below, and actually within four feet of the precipice" (1979 [1827]:168) chosen by the Hawaiian guides as a sleeping place at Kī-lau-ea. "When we expressed our disapprobation, they said it was the only place where we might expect to pass the night undisturbed by Pele, and secure from earthquake and other calamity, being the place in which alone Pele allowed travellers to build a hut" (168).

> When they [the Hawaiians] learned that we had been to Kirauea, they were unwilling to believe we had broken the sulphur banks, eaten the ohelo berries, descended to the craters, or broken any fragments of lava from them, as they said Pele ma, Pele and her associates, would certainly have avenged the insult. However, when our boys shewed them the ohelo berries, with the specimens of sulphur and lava that we had brought away, they were convinced that we had been there, but said we had escaped only because we were haore [*haole*], foreigners. No Hawaiian, they added, would have done so with impunity, for Pele was a dreadful being. (Ellis 1979 [1827]:185)
>
> The violations of her sacred abode, and the insults to her power, of which we had been guilty, appeared to them, and to the natives in general, acts of temerity and sacrilege; and notwithstanding the fact of our being foreigners, we were subsequently threatened with the vengeance of the volcanic deity. (186)
>
> They [i.e., the Hawaiians] could not believe that we had descended into the crater, or broken off pieces of Pele's houses, as they called the small craters, until the specimens of lava, &c. were produced, when some of them looked very significantly, and none of them cared much to handle them. (194)

The missionary Elisha Loomis visited Kī-lau-ea in 1824 and wrote: "I ate plentifully of these [*'ōhelo* berries], notwithstanding the scruples of the [Hawaiian] boys who cautioned me against touching them, as they were sacred to Pele, the volcano" (Westervelt 1937:20).

Lady Franklin visited the volcanoes with David Kalakaua in 1861. He told her that Pele "did not like anyone to pluck flowers by the way: something was sure to happen if this was done" (Korn 1958:53).

Pukui reports that "the 'lava stones of *Pele*' were so filled with the power of the volcano goddess that they could be dangerous" (Pukui, Haertig & Lee 1972:2:179). Anyone who had to walk on volcanic land should say, "Forgive me, *Pele*, for walking on your domain" (246). A Hawaiian proverb in Pukui's compilation translates as, "*Wrongdoing is feared in the upland of Puna*," which she interprets as, "Wrongdoing in the upland of Puna brings the wrath of Pele" (1983:228).

The Hawaiian guides who accompanied Ellis told him that sometimes Pele and other volcanic deities were visible at the volcano. They said that when part of Chief Keoua's army died from poisonous volcanic gases, Pele appeared "in a column of smoke as it rose from the crater" (Ellis 1979 [1827]:175). When Ellis was camping at the volcano:

> Frequently during the night the natives thought they saw someone or other of the deities, but immediately afterwards they doubted. At these times, if we asked them where they saw Pele, they would sometimes point to the red lava, at others to the variegated flame; and on our saying we could not

> perceive any distinct form, they generally answered by assuring us, that during the night some one or other of them would certainly be seen. (175)

According to Pukui, when Pele appears, the colors of her clothes are significant: "Pele in white has traditionally been interpreted as a warning of sickness; Pele in red as a coming volcanic eruption" (Pukui, Haertig & Lee 1972:1:13).

Pele was believed to be very temperamental and easily offended, and to eject lava when she was affronted. Kamakau writes of an eruption:

> The people believed that this earth-consuming flame came because of Pele's desire for *awa* fish from the fish ponds of Kiholo and Ka'upulehu and *aku* fish from Ka'elehuluhulu; or because of her jealousy of Kamehameha's assuming wealth and honor for himself and giving her only those things which were worthless; or because of his refusing her the tabu breadfruit of Kameha'ikana which grew in the uplands of Hu'ehu'e where the flow started. (1961:184–85)

Ewaliko claimed that a Hawaiian man received a burn on his leg because "he had failed to keep a promise to Pele" (1863:2716).

Joseph Emerson reports that one of the most fearful oaths a Hawaiian can take involved Pele: "David's wife is greatly stirred up with jealousy of her husband and continually is making him take the oath Pau Pele Pau Mano that he has not been false to her. This oath, the most fearful a native can take, invokes the death by the dread fire goddess Pele and the mighty shark. 'If I run toward the land may Pele destroy me; If I run to the sea may the shark devour me' is another form of the same oath" (n.d.a:605).

Pukui presents a variant interpretation of the oath:

> Pau Pele, pau manō.
> *[May I be] devoured by Pele,*
> *[May I be] devoured by a shark.*
> An oath, meaning "If I fail . . . ." It was believed that if such an oath were not kept, the one who uttered it would indeed die by fire or be eaten by a shark. (1983:287)

Earthquakes were believed to be caused by Pele: "The superstitions of the natives lead them to believe they [earthquakes] are produced by the power of Pele, or some of the volcanic deities, and consider them as requisitions for offerings, or threatenings of still greater calamities" (Ellis 1979 [1827]:196). De Varigny observed Hawaiians "singing hymns to Pele to appease her anger" (1981:230) during a series of destructive earthquakes on Hawai'i. Westervelt writes that "earthquakes came when Pele stamped the floor of the fire-pit in anger" (1963 [1916]:13).

Collegiates, a Christianized Hawaiian of the mid-19th century, reports on the association of thunder and lightning with the volcano family:

> I have often heard them [i.e., the old Hawaiians] say that people were killed to cursing thunder and lightning. The thunder becomes angry when it is exclaimed at or when anything bad was done to it. They said that the thunder was the voice of the worthless gods of Hawaii nei, that is, Pele, Hiiaka, Kapo and so on. When the thunder pealed our grandfolks would say to us, "That is Hiiaka, for there are eight peals," or "that is Kapo for there are so many peals, those are her thunder peals". . . . They were used to the kinds of sounds of the thunder. When the thunder pealed, they made a guess that it was

> so-and-so and then began to chant some of the chants composed in honor of Hiiaka and Kapo.
>
> If anyone whispered during a thunder storm he was warned by an old person lest the thunder grew louder. If he exclaimed at the flash of lightning, he was warned again lest he be burnt. Pele was likely to turn him to stone. The old folks claim that Pele was in the lightning and so it was kapu to do any mischief. It was kapu to smack the lips in eating during a thunder storm; it was also wrong to whistle during a thunder storm; it was wrong to sleep face up lest the breath be stopped. If there were many people sleeping together in the house, they laid together on one side and in turning, all turn together to the other side. It would be well with them then and thunder would not be angry. Many people had been killed by thunder or lightning because of their mischief. If one drew down his eye lid, he would be burned. (1866:1–2)

Green and Beckwith, in a discussion of Hawaiian household beliefs, note that rainbows are considered signs of the approach of chiefs: "The predominating color in the rainbow is also important in determining the family of the chief to whom the sign belongs. If the dominant color is red, he claims the favor of Pe-le. The pure white rainbow belongs to Ka-moho-alii, king of the sharks and brother of Pe-le" (1928:14).

According to Pukui, menstruating women were offensive to Pele, and if they had to approach her domain, *ti* leaves were used to protect them: "*Ti* was [also] important in fire walking. No one was able to walk on lava beds cooled just enough to bear one's weight without carrying *ti* leaves. My great-great grandmother used to walk across hot lava this way and never got burned. Our family line is from the Pele priesthood and Pele is the volcano goddess. So the *ti* leaves invoked Pele's protection" (Pukui, Haertig & Lee 1972:1:191).

Pukui reports that people related to Pele were believed to be physically distinguishable: "Some Hawaiians believed that members of the Pele family were *'ehu* people, with lighter skin, brown eyes and curly brown hair, unlike the darker-skinned Hawaiians" (Pukui & Korn 1973:56).

The fine filaments of volcanic glass, formed from wind-blown lava, were called the "hair of Pele" by the Hawaiians (Ellis 1979 [1827]:178), while the occasional deposits of sulfur around the volcano area were known as "Pele's excrement" (Summers 1988:46).

Nathaniel Emerson reports that *opihi* is one of Pele's favorite foods: "There is an old saying. *He akua ai opihi o Pele*—'Pele is a goddess who eats the opihi.' In proof of this statement they [i.e., Hawaiians] point to the huge pile of opihi shells that may be found along the coast of Puna, the middens, no doubt, of the old-time people" (1965 [1909]:213).

RITUAL LEADERS

Kahuna is used in Hawaiian to signify one who is an expert in ritual knowledge. This knowledge may range from approaching the highest gods on the most important ceremonial occasions to knowing the proper chant to ensure the success of fishing. The religious specialists who contacted the gods reflected the hierarchy of the gods as well as that of Hawaiian society. The highest of the *kahuna* were the priests who officiated at the important ceremonies honoring the highest gods for the highest chiefs. At the lower end of the religious-social scale were *haka*, or mediums, who communicated with family spirits through trance and possession. Between these extremes were all the other religious intermediaries who dealt with the many religious needs of traditional Hawaiian society. Thus, the term *kahuna* is used for many kinds of ritual specialists. In reviewing the literature on *kahuna*, Valeri has suggested that the many different kinds of *kahuna* in traditional Hawai'i may be placed in 3 categories, namely: (1) *kahuna pule*, the *kahuna* who officiated in the temples of the *ali'i*; (2) "professional" *kahuna*, a large category that includes "specialists in different ritualized activities . . . and medical priests"; and (3) the *kāula*, or prophets (1985:135–40). The *kahuna* for Pele worship appear to fall into all 3 categories, although references in the literature are not always clear.

Most observers of traditional Hawai'i referred to the ritual leaders of the Pele cult simply as "priestesses" or "priests," terms that are used indiscriminately for several types of ritual leaders. The literature on Pele suggests that 4 types of ritual leaders were important in her worship. (1) The terms *priestess* and *priest* frequently refer to individuals, probably *kahuna pule*, who perform formal ceremonies, either in a *heiau* or at Hale-ma'uma'u. Their distinction from other ritual leaders is probably the greater formality of their ceremonies and their greater use of chants. (2) *Kāula*, translated as "prophet, seer" (Pukui & Elbert 1971:126), conducted ceremonies at Hale-ma'uma'u, and probably elsewhere. Their relationship to the goddess was apparently more direct with less of the formal ritual that characterized the *kahuna pule*. (3) *Kahu* assisted the ritual leaders by providing and offering the appropriate sacrifices for the ceremonies. Sometimes they also performed ceremonies. They apparently lived near Hale-ma'uma'u and seemingly served as caretakers of the premises. (4) *Haka* ("recipient; medium, one possessed" [Pukui & Elbert 1971:46]) refers to persons who were possessed by Pele, or who served as mediums of communication between the goddess and the people.

Kamakau mentions "gifts for the *priests* and *prophets* and *guardians* of the volcano" (1964:64; emphasis added) in a discussion of a ceremony held to deposit body remains at Hale-ma'uma'u. The original Hawaiian text uses *kahuna*, *kāula*, and *kahu* for the 3 positions (Kamakau 1870:12), terms almost identical to the categories I arrived at from an examination of the literature. It must be cautioned, however, that these categories are not as clear in the literature as the preceding discussion suggests. The terms were apparently used indiscriminately by the Hawaiians and may have had regional variations in meaning. In addition to these formal leaders, virtually every Hawaiian who lived in the volcano area knew the appropriate chants and offerings for Pele when passing near her domain. Furthermore, the heads of families who traced their ancestry to Pele performed ritual on a regular basis, often daily, to appease the goddess.

Kawaikaumaiikamakaopua claims that Ailaau was the first priest of Pele and that women were excluded from becoming "priestesses":

> Ailaau was the first priest of Pele and the Ai-laau (tree-eater) was given [*sic*] by Pele. There were many in the family, one boy and the rest girls. Pele did not want the girls to become priestesses of the volcano or to become Kaula-Pele, because women were said to be Opu-ukuuku [ōpū-'uku'uku] or Small clumps, lower (than the men).
>
> Therefore the brother went up in rank and called [*sic*] according to the male side, "Ahi-lapalapa" or "Blazing fire." (1923:1)

The literature provides no evidence, however, to support Kawaikaumaiikamakaopua's claim that women were excluded from performing rituals to Pele. Quite possibly he was referring only to the *kāula* who were apparently always males, according to Pukui (Pukui, Haertig & Lee 1972:2:269).

Numerous writers of the period under investigation simply refer to "priestesses" or "priests," with no elaboration of the nature of the positions. Ellis writes that when a luminous flame was seen in the sky above a village, "a priest of Pele and his family . . . immediately offered his prayer to the goddess, and told the inhabitants that no harm would befall them" (1979 [1827]:218). Ellis further notes that when the traditional religion was renounced by Hawaiian royalty in 1819 "several priests of Pele denounced the most awful threatenings, of earthquakes, eruptions, &c. from the gods of the volcanoes, in revenge for the insult and neglect then shewn by the king and chiefs" (218) and that "there are . . . many who . . . pay the most submissive and unhesitating obedience to the requisitions of her [Pele's] priests" (218). Manu notes: "and the people knew that Pele was the goddess of fire, therefore, they worshipped her, and some people were set apart to serve as priests of Pele. The practice became widespread among the people throughout the entire archipelago of Hawaii" (1899:990–91). This is the only mention of priests beyond Hawai'i Island in the early literature except the priestesses encountered by Stewart (1831:106–7), Ellis (1979 [1827]:186), and Bingham (1981 [1847]:226–27) on Maui. Lady Franklin visited the volcanoes in 1861 and noted in her journal that one of her party "was an old man with grey hair and a peculiar countenance who is one of the very few professed heathens left, and a priest of the Goddess Pele" (Korn 1958:55). She further notes the man's name was "Pauahilani" (Korn 1958:316). While Lady Franklin was at Kī-lau-ea, she "observed a remarkable-looking man seated on the very edge of the cliff, who began a sort of monotonous recitation, and we were told that he was another of Pele's priests" (Korn 1958:56). Writing of Puna and Hilo, a missionary wife recorded that "we knew the names of very many of the people of both districts, and among them were the old priest and priestess of Pele, who never failed to visit us when here" (Martin 1970:196).

The "priestesses" or "priests" who officiated at the formal ceremonies for Pele at the temples and at Kī-lau-ea were probably *kahuna pule*; at any rate they appear to have been supported by some organized body, and the position was apparently inherited. Descriptions of such persons from the literature include the following:

> On our return from the cascade of the Rainbow, Mr. Stribling and myself called at the mission house, and were, unexpectedly, gratified by an interview with the hereditary and last PRIESTESS OF PELE.
>
> In speaking of the volcano, Mr. Goodrich incidentally remarked, that this individual was now residing in the immediate neighborhood; and, at our suggestion, sent a messenger to invite her over. She almost immediately came, attended by her household, consisting of eight or ten individuals, male and female. I should judge her to be forty or forty-five years of age; a tall, finely formed, majestic woman, wrapped in a large, black mantle of native cloth, falling in thick folds like the Roman toga, from the bust to the ground. We were much impressed with her appearance, as she entered at the head of her train, and, after receiving our salutations, became seated on a mat in the centre of the apartment, in the attitude of a Turkish female on a divan. The style of her face is remarkably noble and commanding—indicative of strong traits of character—with a full, piercing black eye, which I can readily imagine, might be fearfully intimidating to the superstitious, when flashing in the wildness of an imaginary inspiration. There was not only a deep seriousness, but a decided cast of melancholy in her whole aspect, which reminded me in connection with the strongly marked and superior contour of her features, of a fine print of the tragic muse, which I recollect to have seen. . . .
>
> The priestess is now a firm believer in Christianity, and is one of the most attentive pupils of the station. . . .
>
> At the time of sacrifice, the priestess herself descended into the depths of the volcano, and, approaching the place most accessible and most active with fire, cast upon it the gifts, with the exclamation *"Here Pele is food for you"*—specifying the article or articles—*"and here is cloth,"* mentioning its name and varieties. In answer to the question, whether she was not afraid of the fire which she approached, she said no, for she then believed, that the goddess

> would defend her from harm—but, that now, when she knew, that there was no such being as Pele, she should be afraid to go to places where she once did without apprehension, lest she might perish in her temerity. (Stewart 1831:105–10)

Titus Coan describes some of the Hawaiian converts to Christianity he encountered in Puna: "Among these converts was the High Priest of the volcano. He was more than six feet high and of lofty bearing. . . . His sister was more haughty and stubborn. She was High Priestess of the volcano. She, too, was tall and majestic in her bearing" (1882:44–45).

It is perhaps significant that in both accounts the *kahuna* are described as "majestic," "noble," or somehow set apart from other people, suggesting they were from the *kahuna pule* class, who were *ali'i*.

The *kāula* were apparently always men (Kawaikaumaiikamakaopua 1923:1; Pukui, Haertig & Lee 1972:2:269) and wore their hair in deviant fashion. Pukui describes them:

> "*Kaula* of *Pele* were always men. *Pele* selected them when they were very young. These boys were *kapu* [sacred]. They had to let their hair grow—their beards, too—as they grew older. The only way they could cut their hair was to go to the volcano. Go right to the brink, then cut the hair and throw it in. Give it to Pele."
>
> These young men were excused from ordinary work. Instead, they studied, prayed, and meditated. Some concentrated on the rituals and prayers of *Pele* and eventually became *kahuna*. (Pukui, Haertig & Lee 1972:2:269)

Elsewhere, Pukui claims that ceremonies at the volcano were conducted by a "Prophet of Pele (*Kaula Pele*)" who lived at Kī-lau-ea (Handy & Pukui 1972 [1958]:153). In discussing the same ceremonies elsewhere, she notes that "the priests of Pele presented an odd appearance as their hair and beard were never trimmed. Some, to keep their hair and beard out of the way, braided them into braids and knotted up the ends" (1945:3).

I-lālā-ole, born in Puna in 1873, describes his grandfather who was a *kāula* (prophet) of Pele: "My grandfather was a kaula Pele. He was tabu, never cut long hair or beard, but he braided the hair and beard. He wore a white robe, cover whole body, no head piece. Like a cloak. Wore a malo—a red malo. I saw him. He was very old" (n.d.:3).

Kamakau writes that Kamehameha sought "Pele's seer (*kaula*), named Ka-maka-o-ke-akua," to determine the proper sacrifices to offer Pele in order to stop a devastating lava flow (1961:185). The sex of the seer is not indicated. Elsewhere, Kamakau claims the *kāula* conducted the ceremonies at the volcano for disposing of the remains of the dead (1964:64–65).

Malo's unflattering description of the *kahu* seems more in keeping with other descriptions of the *kāula*:

> The *kahu* of the Pele deities also were in the habit of dressing their hair in such a way as to make it stand out in great length, then, having inflamed and reddened their eyes, they went about begging for any articles they took a fancy to, making the threat, "If you don't grant this request Pele will devour you." Many people were imposed upon in this manner, fearing that Pele might actually consume them. (1951 [1903]:116)

Less is known about the *kahu* of Pele than about the *kāula*. Valeri defines *kahu akua* as "keeper of a god," or one who cares for a god (1985:135). The few mentions of such persons in the literature on Pele suggest the *kahu* were attendants who supplied offerings for ceremonies to Pele and maintained the grounds at Kī-lau-ea. Kamakau writes: "In the old days men feared the volcano; they did not descend into Kilauea as they pleased. Neither did most of the *kahu Pele*, the attendants of the volcano. Not more than ten of them made the dedications and took care of *Ka lua o Pele*" (1964:67). Elsewhere, Kamakau writes that "persons who were inspired by her to prophesy, and others who wanted her as a god, became the *kahu*, the 'administrators,' of Pele" (1964:69).

In describing a "priestess" of Pele, Stewart writes of the *kahu*:

> Her father was the hereditary kahu, or steward, as she was the priestess of Pele. The duty of the kahu was to provide the materials for the general sacrifices—the food and raiment of the supposititious deity: to grow the taro, potatoes, and sugar cane, and the cloth-plant, from which the garments for her were made; to provide the hogs and fowls, &c., and to have all things in readiness for the offerings, at the appointed seasons.
>
> Of the plantations sacred to this use, one was on the seashore, and another within the precincts of the crater—in the broken ground, described as that upon which we first came, in descending from our hut, on our late visit. The kahu and his family resided part of the time, on the coast; and part, in the neighborhood of the crater. (1831:109)

This is the only reference to special lands being set aside for growing offerings for Pele.

Pogue claims that "if any live person wished to call upon any of these spirits in their new residence [i.e., "the Crater of Pele"], he communicated with an attendant [*kahu*] of Pele, who accompanied him to the Crater, and called forth an invocation" (1978 [1858]:56).

More information is available regarding the *haka*, persons who claimed to be possessed by the goddess and/or were able to directly communicate with her. Again we are indebted to Ellis for the earliest accounts of such persons. During his journey around the island of Hawai'i, near Hilo, he encountered a woman who claimed to be possessed by Pele:

> As we arose to depart, an old woman, who during the discourse sat near the speaker, and had listened very attentively, all at once exclaimed, "Powerful are the gods of Hawaii, and great is Pele, the goddess of Hawaii, she shall save Maaro," (the sick chief who was present).
>
> Another began to chant a song in praise of Pele, to which the people generally listened, though some began to laugh.
>
> We supposed they were intoxicated, and therefore took no notice of them; but on our leaving the house, some of our people told us they were not ona i ka ruma (intoxicated or poisoned with the rum), but inspired by the akua (goddess) of the volcano; or that one of them was Pele herself, in the form of one of her priestesses. . . .
>
> I then asked if she thought Jehovah was good, and those happy who made him their God?
>
> She answered, "He is your good God, (or best God), and it is right that you should worship him; but Pele is my deity, and the great goddess of Hawaii. Kirauea [Kī-lau-ea] is the place of her abode. Ohiaotelani (the northern peak of the volcano) is one corner of her house. From the land beyond the sky, in former times, she came."
>
> She then went on with the song which she had thus begun, giving a long account of the deeds and honours of Pele. This she pronounced in such a rapid and vociferous manner, accompanied by such violent gestures, that only here and there a word could be understood. Indeed, towards the close,

> she appeared to lose all command of herself. When she had done, I told her she was mistaken in supposing any supernatural being resided in the volcano; that Pele was a creature of their own invention . . . and . . . Jehovah . . . was the Creator and Supporter of heaven and earth, and every thing she beheld.
>
> She replied, that it was not so. She did not dispute that Jehovah was a God, but that he was not the only God.
>
> Pele was a goddess, and dwelt in her, and through her would heal the sick chief then present. She wished him restored, and therefore came to visit him. . . .
>
> Assuming a haughty air, she said, "I am Pele; I shall never die; and those who follow me, when they die, if part of their bones be taken to Kirauea, (the name of the volcano), will live with me in the bright fires there."
>
> I said, Are you Pele?
>
> She replied, Yes: and was proceeding to state her powers, &c. when Makoa, who had till now stood silent, interrupted her, and said, "It is true you are Pele, or some of Pele's party; and it is you that have destroyed the king's land, devoured his people, and spoiled all the fishing grounds." . . .
>
> However, the pretended Pele said, "Formerly we did overflow some of the land, but it was only the land of those that were rebels, or were very wicked people. (Broke the restrictions of the tabu, or brought no offerings). Now we abide quietly in Kirauea." . . .
>
> She then added, "It cannot be said that in these days, we destroy the king's people." She mentioned the names of several chiefs, and then asked who destroyed these?
>
> Not Pele, but the rum of the foreigners, whose God you are so fond of. Their diseases and their rum have destroyed more of the king's men, than all the volcanoes on the island. . . .
>
> "I shall not die," she exclaimed, "but ora no," (live spontaneously). . . .
>
> The name of the priestess we afterwards learned was Oani. (1979 [1827]:215–18)

Later, while visiting Lahaina, Ellis encountered another "priestess of Pele":

> Some months after our visit to Kirauea, a priestess of Pele came to Lahaina, in Maui, where the principal chiefs of the islands then resided. The object of her visit was noised abroad among the people, and much public interest excited. One or two mornings after her arrival in the district, arrayed in her prophetic robes, having the edges of her garments burnt with fire, and holding a short staff or spear in her hand, preceded by her daughter, who was also a candidate for the office of priestess, and followed by thousands of the people, she came into the presence of the chiefs; and having told who she was, they asked what communication she had to make.
>
> She replied, that, in a trance or vision, she had been with Pele, by whom she was charged to complain to them that a number of foreigners had visited Kirauea; eaten the sacred berries; broken her houses, the craters; thrown down large stones, &c. to request that the offenders might be sent away; and to assure them, that if these foreigners were not banished from the islands, Pele would certainly, in a given number of days, take vengeance by inundating the country with lava, and destroying the people. She also pretended to have received, in a supernatural manner, Rihoriho's approbation of the request of the goddess. (1979 [1827]:186)

Bingham also provides an account of the event:

> A pseudo prophetess belonging to Hawaii visited Maui, and claiming authority from the god of the volcano, and even calling herself *Pele,* drew the attention of many to her vagaries. Her arrival in Lahaina caused an excitement among all classes; and some affirmed that she had been offended by the missionaries, who had rolled stones into her crater, and had plucked and eaten her prohibited *ohelos* without making offerings to her, and had dared to take away portions of her hair, and that she had come to induce the chiefs to dismiss the missionaries and suppress the *palapala.* Some seemed to think she would make some terrific display of her powers, unless the chiefs should yield to her demands. The day after she reached the village, she came to the chiefs with her insignia of office. Marching with haughty step, with long black, dishevelled hair, and countenance wild, with spear and *kahilis* in her hands, attended by her two daughters, bearing each a small flag, she attempted to make a display corresponding with her pretensions. As she approached, she was accompanied by an immense crowd, attracted some by curiosity, some by superstition, some with a desire to see her maintain her cause, and some to see her foiled by Kaahumanu and her coadjutors. Paying little attention to the throng, she drew near the chiefs and exclaimed, "I have come!" Kalakua . . . replied: "We are all here." "Good will to you all," said the prophetess. "Yes," said the chief, "good will perhaps." "I have come to speak to you," said the impostor. "Whence are you?" said Madam Hoapili. She replied: "From foreign lands, from England and America, whither I went to attend your king." Indignant at this falsehood, the chief rebuked her, saying, "Come not here to tell us your lies—what are these things in your hands?" "The spear and kahilis of Pele," she promptly replied. *"Lay them down,"* said the chief. Unwilling to lose her honor in the eyes of the world, she demurred, and put on the air of sullenness, as if insulted. "LAY THEM DOWN," was sternly repeated, and she complied. The chief continued with well sustained dignity, "Tell us not that you are *Pele.* There are other volcanoes than those on Hawaii. They are all under the control of the great God of Heaven. But you are a *woman,* like one of us. There is one God, who made you and us. We have one common Parent. Formerly we thought *Pele* a god, and gave our hogs, dogs, and cocoanuts. . . . Go back to Hawaii, plant potatoes, beat kapa, catch fish, feed swine, and eat of your own earnings; but demand not of the people this and that for Pele. . . . The impostor confessed, "I have been lying, but will lie no more." . . . She yielded, burned her mysterious flags, and was about to burn the spear which she had called Pele's; but one of the chiefs interposed, and claimed it to be used for tilling the ground. (1981 [1847]:226–27)

Stewart likewise reports an encounter with a "priestess" in Lahaina:

> I unexpectedly met her in an evening walk, followed by a considerable company; some, evidently under the influence of a superstitious feeling in reference to her; and others, as evidently disposed to deride her pretensions. She was dressed in a fantastic manner, with dishevelled hair—her eyes flashing in a half-frenzy, from the degree of excitement to which she had wrought herself—and appeared altogether like a maniac: such as I supposed her in reality to be, till undeceived by the exclamations of the crowd, *"it is a goddess—it is a goddess!"*

> As if to intimidate, she approached me with a fierce and daring look: and waving before her a small flag of tapa, appended to a light staff, supported the claim by the declaration, *"I am a goddess—a goddess indeed!—the palapala and the pule* (letters and religion) *are not good: they will destroy the people!"* (1831:106–7)

When the chiefess Ka-pi'o-lani visited Kī-lau-ea in 1824 to defy the power of Pele and exalt the Christian god, she was met by a "prophetess" of Pele:

> In approaching the region of the volcano, she [Ka-pi'o-lani] was met by a prophetess claiming authority from the veritable deity. This haughty female warned her not to approach the sacred dominions of Pele, and predicted her death through the fury of the god, should she make an invasion with the feelings of hostility and contempt which she professed. "Who are you?" demanded Kapiolani. "One in whom *ke akua* [the god] dwells," she replied. . . . Refreshments were kindly offered her; but in the haughtiness of her assumed dignity as a supernatural being, she said, "I am a god: I will not eat." She held in her hand a piece of bark cloth. "This," said she, "is a *palapala* from the god Pele." "Read it to us," said Kapiolani. . . . The prophetess cunningly carrying out her device, and with unexpected presence of mind holding her cloth before her eyes, poured forth a torrent of unintelligible words or sounds which she would have them believe was in the dialect of the ancient Pele.
>
> Kapiolani producing her Christian books . . . read several passages. . . . The haughty prophetess quailed; her head dropped, and her garrulity ceased. She confessed that *ke akua* [the god] had left her, and she could not therefore reply. (Bingham 1981 [1847]:254–55)

This account suggests that Pele spoke through mediums in a special language.

De Varigny encountered a male medium while visiting a village destroyed by earthquakes during an eruption:

> Their [the villagers'] terror had risen to such a pitch that they were ready to believe anything, blindly obeying the notions of a native fanatic; in fact, one whose unbalanced mind already dated back several years, and who insisted that Pele, the goddess of the volcano, had appeared before him and had informed him that she wished to avenge her repudiated cult by displaying the very power that the missionaries had denied. (1981:216)

This is the only mention of a male *haka* in the literature.

Malo notes that "Pele and Hiiaka also were *akua noho* . . . deities that took possession of people and through them made utterances" (1951 [1898]:116).

Handy and Pukui's discussion of *haka* in Ka'ū claims that the *haka* was chosen by the god, ate a restricted diet, and dressed in colors suitable to the god. "White is Pele's colour, pink is Hi'iaka's, red is Kapo's. . . . A woman could become a *haka* only after menopause" (1972 [1958]:132–33). When a spirit was coming to dwell in a *haka* a sign was given to members of the household. Pukui elaborates:

> When lightning flashes and the light darts into the house, the family observes whether it is red; if so, it is a Ka-uila-nui-makeha-i-ka-lani (. . . a brother of Pele); but if it is yellowish light, it was Hi'iaka. . . . There are many signs. If

> Lono, the sign he sends is a sudden heavy downpour, which quickly clears. If it is Hiʻiaka . . . who comes, no one must pass back and forth behind the back, because her back is *kapu*. Because the *kapu* belongs to her back, the back of her *haka* is also *kapu*, so no one must ever step across, or step on it. . . . Nor must anything unclean come in contact with it. The white dress and the pink were those that I have seen worn by her *haka* (Hiʻiaka's). Little lumps of salt were another requirement, for her *haka* or in her *hula*. . . .
>
> If it is Pele coming, she also has a *kapu* back, and it is so hot that it is impossible to go back and forth behind the *haka*—thus making it perfectly clear that the *akua noho* ["possessing god"] is the *Aliʻi Wahine* of Kilauea. If any *akua noho* claims to be Pele and the back of the *haka* is not hot, then those in the house may question indeed. From times way back this hotness of the back has been the sign. Pele likes *luʻau* (young taro leaves) when she comes but not *luʻau* already cooked. Wrap the green *luʻau* in *laʻi* (ti leaf). When the *akua wahine* sits on the *haka*, the body of the *haka* lies face down, and the package of *luʻau* is placed upon the back of the *haka* until the heat of her back has cooked it. When it is cooked, she (the *haka*) eats it all [See also Pukui 1983:188–89; Pukui, Haertig & Lee 1972:2:28]. . . .
>
> If it is Kapo-ʻula-o-Kinaʻu (Kapo-of-the-red-streak) the *papa hana* [ceremony, offering] would be covered with red, and so it was with respect to the colour of the dress of her *haka*. . . . Similarly for Ka-moho-aliʻi (Lord-of-Sharks) red also is called for, but not the same shade, one is a black red . . . the other is a clear red. . . . Ka-moho-aliʻi is a pleasant *akua*, although he was very *kapu*, having a playful manner of speaking and of joking with the helper and with others in the house, thus setting aside their fear of him. (Handy & Pukui 1972 [1958]:138–39)

Elsewhere, Pukui relates that "'When *Hiʻiaka-i-ka-pua-ʻenaʻena* possessed one, the skin reddened.' The red skin denoted the special and sacred attention of the sister *Pele*, goddess of the fiery volcano" (Pukui, Haertig & Lee 1972:2:291).

Handy writes of "seances" during which Pele visited mediums in Kaʻū in relatively recent times. His data is probably from Pukui.

> Until quite recently the cult of the volcano goddess and her sisters survived in mediumistic seances in which Pele and two of her sisters, Kapo and Hiʻiaka, have "sat upon" or "dwelt in" (*noho*) a medium, who was referred to as the "perch" (*haka*). This aspect or phase of the cult is not reported at all in early literature, but this is in no way strange since it would have been concealed from missionaries and other whites.
>
> The seances were by no means casual or informal; and they were strictly private, within a family who traced their ancestry to "the Pele clan." In every detail the seances were formally ritualistic, and the ritual was entirely in accord with Hawaiian religious practices. There is no reason to believe that this mediumistic phase of the cult was a result of any extraneous influence. The medium was dressed in a robe whose color denoted which sister was invoked (Pele, white; Kapo, red; Hiʻiaka, pink). There was a special mat on which the medium sat, and there were offerings of food and drink. The medium had a helper who was responsible for all the arrangements, and this helper was also the chanter whose invocation invited the spirit to enter or "sit upon" the medium. (1964:227–28)

CEREMONIES

The literature on Pele reveals that ceremonies to the goddess and her family were held at numerous locations, including the household; the hula *hālau*; tree-felling sites for canoe building; paths, steam vents, and craters throughout Pele's domain; active lava flows; temples; and Hale-ma'uma'u. Additional ceremonies were doubtless held at other sites not mentioned in the literature.

Household Ceremonies

Although no actual descriptions are available of household ceremonies to Pele, indications of the importance and frequency of such ceremonies to *'aumakua* are found throughout the literature. Most important in this context are the discussions by Pukui, since much of her data comes from the Ka'ū district and her own family members, who traced their ancestry to Pele. Handy and Pukui describe the traditional prayers and rituals held in the men's house at Ka'ū. Many of them probably involved Pele since she was one of the principal *'aumakua* in that district:

> The *Mua* was the men's eating and lounging house, and their sanctuary. At one end was an altar (*kuahu*) dedicated to the family *'aumakua* whose effigies stood there. Here the head of the household prayed and performed necessary rites and sometimes without, sometimes with the aid of a *kahuna pule*, when came the time for the rites of the life cycle such as birth, cutting the foreskin, sickness and death. Here the family rites during the monthly days of *kapu* were performed. . . . The common daily worship would seem to have consisted in offering a bit of food . . . at the time of eating. (1972 [1958]:95–96)

Pukui reports that in the Ka'ū district of Hawai'i the following chant to Pele "was sometimes offered as a morning prayer, performed on the beach after midnight and before dawn, at about two o'clock, to celebrate the beginning of the Hawaiian day."

From Kahiki came the woman Pele,
from the land of Polapola,
from the rising reddish mist of Kane,
from clouds blazing in the sky, horizon clouds.
Restless desire for Hawai'i seized the woman Pele.
Ready-carved was the canoe, Honua-i-Akea,
your own canoe, O Ka-moho-ali'i,
for sailing to distant lands.
Well-lashed and equipped, the canoe of high gods,
your canoe, Sacred-hewer-of-the-land,
stood ready to sail with the ocean current.
Pele-honua-mea embarked, the heavenly one
stepped aboard to sail round Kahiki island.
Multitudes of gods came aboard.
O royal companions, who handled the steering paddle
  at the stern?
Pele-the-redhead herself was helmswoman, ruler of
  the Menehune.
Ku and Lono bailed out the bilge water,
carried paddles, placed them in station.

> Hi'iaka, the wise sister, next embarked,
> boarded the craft to dwell with Pele in her sailing
> quarters,
> close to Pele on the long voyage.
> Jets of lava gushed from Kahiki.
> Pele hurled her lightning,
> vomit of flame, outpouring of lava was the woman's
> farewell. (Pukui & Korn 1973:52–55)

Elsewhere, Pukui recalled fragments of chants which her grandmother had addressed to Pele at dawn and dusk:

> From *Kahiki* came *Pele*,
> From the land of Borabora,
> From the smoky columns of *Kane*.
>
> . . . .
>
> *Pele* is my goddess,
> A chiefess of sacred darkness.
> And of sacred light.
>
> . . . .
>
> *Pele* is my goddess,
> Quiet reigns in the heavens,
> And reigns over the earth. (Pukui, Haertig & Lee 1972:2:126)

Handy and Pukui report that "on occasions of crisis or festivity" when the gods' presence and assistance was needed, "calling prayers" were used to call them to the ceremony. The following is such a calling prayer to Pele:

> Here is food, oh gods,
> Only a morsel of heavenly food,
> A gift from me, thy little child,
> Of the yellow-skinned *'awa* of Ke-ahi-a-laka.
> (My prayer) has gone to meet Pele,
> Who is gathering *lehua* blossoms,
> Who is stringing them into wreaths by the sea of Hopoe,
> Here is *'awa* for the men of heaven,
> Here is *'awa* for the women of heaven,
> Here is *'awa* for the men of the Pit,
> Here is *'awa* for the women of the Pit,
> Hither and yon,
> Come, rinse out your mouths and wash your hands,
> This (rite) is sacred and profound, let the *kapu* be released,
> Freed that we may stand, that we may walk about,
> Freed by the decree of the gods. (1972 [1958]:140)

The ceremonies already described were held in the household; during these, Pele and members of her family would possess mediums (Handy & Pukui 1972 [1958]:138–39).

Although included in a discussion of sorcery, the following prayer is said to be used to call upon the gods to grant health. The location of the ceremony is not mentioned, but it was probably held in the patient's home at the time of illness. It is called a "Prayer to the female aumakuas" and Pele, her sister Hi'iaka, and her mother Haumea are among the gods called upon:

> To you, O goddesses,
> From sunrise to sunset,
> From sunset to sunrise,
> From the firmament above to the earth below,
> From the zenith to the horizon (I pray),
> Come ye together.
> To thee, O Kahai, Haumea, Hiiaka,
> Pele, the goddess who devours the forests of Puna,
> And to thee, Kauhola, Kalahiki, Kauwila,
> Kaoaka, Kunaaioha, Moehaune,
> The women whose faces are hidden in the sea,
> O Laea, goddess of canoe builders,
> O Kamalei, goddess of the west,
> Goddesses who are deaf, who listened not to my words,
> Listen to my plea.
> Here is the patient (so and so) sick with the papaku,
> A sickness said to be incurable,
> May your gift be health for him,
> Take away the soreness, the pains,
> The chills, the drowsiness, the heaviness of the head,
> May health and strength be given him by you,
> Amen, it is freed. (Poepoe Collection n.d.:37)

The notes of Theodore Kelsey describe a household altar used by an old Hawaiian man who died in 1922 at the age of 104: "Kia'aina had an *akua* [god] named Mauna-loa, 'which he had on a shelf covered with a towel. It was a quadrilateral pyramid a foot or two high, with dark markings on the sides, where Fire Goddess Pele sat in spirit form'" (Gutmanis 1983:119). Although this altar is unique in the literature, it may represent a domestic altar once common in Pele worship.

Hula Ceremonies

During stages of hula training, ceremonies were conducted for Hi'iaka, Laka, and Kapo, sisters of Pele, at the altar in the *hālau*, the dwelling constructed for hula training (Emerson 1965 [1909]:23–25). Hawaiian myth relates that Hi'iaka, the youngest and favorite sister of Pele, danced the first hula at the request of Pele (Emerson 1965 [1909]:8). Some myths claim Laka and Kapo were contrasting aspects of the same goddess, others claim they were distinct and different goddesses, and others say Laka was a daughter of Pele. Regardless of the relationship to Pele, they all figure in the hula and its accompanying ceremonies. The most complete discussions of the traditional hula are found in Nathaniel Emerson (1965 [1909]) and Barrère, Pukui & Kelly (1980). Barrère summarizes Emerson:

> The *halau hula*, according to Emerson, was built on purified ground, and each stage of its building was accompanied by prayers. Within the *halau* was built a *kuahu* altar to Laka, the principal goddess of the *hula*. (The *kuahu* was usually a shelf or rack attached to the siding between wall posts.) Greenery from the forests was ritually gathered and the altar decorated, all with appro-

> priate *pule* (literally, prayer chants), which Emerson happily defines as "song offerings." (57)

Although the ritual prayers of the hula appear to have been directed to Laka or Hiʻiaka, some of the chants used in hula performances dealt with Pele. Emerson discusses "the hula Pele" and the ceremony that prefaced it:

> The ancient Hawaiians naturally regarded the Pele hula with special reverence by reason of its mythological importance, and they selected it for performance on occasions of gravity as a means of honoring the kings and alii of the land. They would have considered its presentation on common occasions, or in a spirit of levity, as a great impropriety.
>
> In ancient times the performance of the hula Pele, like that of all other plays, was prefaced with prayer and sacrifice. The offering customarily used in the service of this hula consisted of salt crystals and of luau made from the delicate unrolled ti leaf. This was the gift demanded of every pupil seeking admission to the school of the hula, being looked upon as an offering specially acceptable to Pele, the patron of this hula. In the performance of the sacrifice teacher and pupil approached and stood reverently before the kuahu [altar] while the former recited a mele, which was a prayer to the goddess. The pupil ate the luau, the teacher placed the package of salt on the altar, and the service was complete. (1965 [1909]:187)

Emerson later presents the following prayer to Pele, "said to have been used at the time of awa-drinking. When given in the hula . . . its recitation was accompanied by the sound of the drum." Other translations of this prayer are found in Titcomb (1948:129) and Gutmanis (1983:11–12).

> Lo, Pele's the god of my choice:
> Let heaven and earth in silence wait.
> Here is awa, potent, sacred,
> Bitter sea, great Hiiaka's root;
> 'Twas cut at Mauli-ola —
> Awa to the women forbidden,
> Let it tabu be!
>
> Exact be the rite of your awa,
> O Pele of the sacred land.
> Proclaim it, mother, Haumea,
> Of the goddess of Kilauea;
> She who dug the pit world-deep,
> And the Mau-wahine and Kupu-ena,
> Who prepare the awa for drink.
> A health to the stranger gods!
>
> . . . .
>
> Bedeck now the board for the feast;
> Fill up the last bowl to the brim;
> Then pour a draught in the sun-cave
> Shall flow to the mellow haze,
> That tints the land of the gods.
>
> All hail to the stranger gods!

> This my offering, simply a voice,
> Only a welcoming voice,
> Turn in!
> Lo, the feast! (Emerson 1965 [1909]:198)

Pukui summarizes a series of dances performed on Kaua'i that reenact the arrival of Pele in the islands. She claims that on Kaua'i, red was associated with Pele and green with Hi'iaka during the hula (Barrère, Pukui & Kelly 1980:79). In Ka'ū on Hawai'i, white is associated with Pele and pink with Hi'iaka (Handy & Pukui 1972 [1958]:138–39).

> Hula Pele followed by the hula hoe or canoe paddling hula. That signifies "The goddess Pele comes on a canoe." The hula kii or dance of the wooden images that follows conveys the idea that the spirits represented by the images shall man Pele's canoe. The dog deity Ku-ilio-loa, welcomes Pele ashore and so the dog dance or hula ilio follows. Then comes a feast in which a hog is served, hence the hog dance or hula puaa. But the hog must be cooked and the house built to receive the royal guest and here we have the hula ka-laau or stick dance, laau meaning stick or wood. After the feast, the entertainment, a royal one befitting her rank, and the pahu or drum is brought forth to entertain her with the hula pahu. The guest is a beloved one, and the dance of all favorite sitting and gesturing hula. This is the pattern or inner meaning of the program itself. (Barrère, Pukui & Kelly 1980:79)

Pukui elaborates on the "hula Pele":

> When Pele the volcano goddess came to these islands, her first home was on Kauai. Then going from island to island she found a permanent home on Hawaii. Pele herself did not dance, but her sister Hiiaka was numbered among the gods of the dance. Like all great rulers here in Hawaii, Pele had her particular dance. It was one in which no musical instruments were employed. The musicians sat in rows and kept the time by clapping their hands while one or two dancers stood up to dance. Kauai, her first home, had its version of the Pele dance and Hawaii, her present home, had another. Perhaps the other islands also had dances in honor of Pele. I have not heard of any. . . .
>
> For the hula Pele, a big fire was always built because she is the goddess of fire, and its hula was danced around it. . . .
>
> Mele for Hula Pele
>
> The woman Pele burst forth at Puukapele,
> She flashed to the heavens, on and on.
> The woman Pele burst forth at Nomilu,
> She flashed to the heavens, on and on.
> The woman Pele burst forth at Kakakalua,
> She flashed to the heavens, on and on.
> It was awe-inspiring, it was awe-inspiring.
> She flashed to the heavens, on and on.
> Amama, the kapu is freed, the kapu is freed.
> She flashed to the heavens, on and on. (Barrère, Pukui & Kelly 1980:80)

Canoe-Building Ceremonies

When Archibald Menzies climbed the slopes of Mauna Loa in 1794, he encountered a small group of canoe-makers and noted that "here and there on the sides of the path they have little maraes or spots consecrated to their deity, which none of them ever pass without leaving something, let it be ever so trifling, to obtain his good will" (1920:85). During a later climb up Mt Hualalai in 1794, he passed through an area where trees were cut

> for canoes, planks and other purposes. . . . We observed here and there on the path little maraes [i.e., altars], pointed out by taboo sticks stuck in the ground round a bush or under a tree. In passing these places the natives always muttered a prayer or hymn, and made some offering, as they said, to their akua [god], by leaving a little piece of fruit, vegetable or something or other at these consecrated spots. Even in this solitary hut [built by the Hawaiian wood-workers], we found a corner of it consecrated by one of these taboo sticks which the natives earnestly requested us not to remove when we took possession of it, and we very strictly obeyed their injunction. (1920:156–57)

Pele is not mentioned by name, but since Mauna Loa and Hualalai are both associated with her in Hawaiian mythology, it is quite likely that at least some of the small altars were intended for her. When Menzies and his party descended Hualalai, they spent the night in a "cavern." "None of the women durst follow us into the cavern because of a small marae which happened to be in the centre of it, where a variety of fruits and vegetables that had been offered to the Akua were in a decayed and rotten state. The natives, however, repaired it and made fresh offerings" (1920:164). Again, no mention is made of Pele, but because of the location, it may have been an altar for her.

Based on data from the unpublished notebooks of N. B. Emerson, Gutmanis reports that canoe-builders included Pele in their prayers during the ritual preceding the trimming of a tree for canoe building. Most likely such prayers were included when the trees were taken from the domains of Pele.

> Pele shakes the base of the mountains
> Mountains of the *koa* trees that stand here.
> Crookedly turn flat the tree tops.
> May the lesser deity, the major deity, cause growth,
> The long god, the short god
> Cut off the branches, the tops that reach to the heavens.
> Yours, to be sure, o heaven high one, is that canoe.
> Protected is the tree, tabu its shadow
> A little shadow, a long shadow.
> Trim the canoe that has fallen.
> It is free of tabu. (Gutmanis 1983:77–78)

Adze-making sites were sometimes located near craters (Kamakau 1961:240; Kirch 1985:179), and remains of shrines can still be found at them (Kirch 1985:180). Doubtless, some of the ceremonies at these sites were directed to Pele and her family. Byron observed that when sandalwood was cut and fern roots dug up, "locks of hair, and often more precious things" were offered to Pele (Byron 1826:186).

Apparently offerings were also made to Pele simply because it was believed she was in need of them. When Jules Remy drew a sketch of a very thin Pele which he told a group of Hawaiians he had seen, one of them said: "Pele is wasting away! Pele is suffering hunger! Beware lest she become angry and avenge herself! Let us make haste to offer her food and prayer" (Summers 1988:55).

Ceremonies in Pele's Domain

Descriptions abound of the small ceremonies and offerings made to Pele by Hawaiians when they approached her domain and craters. When Ellis visited the volcanoes, his Hawaiian guides refused to eat any *'ohelo* berries until they offered some to Pele.

> As we passed along, we observed the natives, who had hitherto refused to touch any of the ohelo berries, now gather several bunches, and, after offering a part to Pele, eat them very freely. They did not use much ceremony in their acknowledgement; but when they had plucked a branch, containing several clusters of berries, they turned their faces towards the place whence the greatest quantity of smoke and vapour issued, and, breaking the branch they held in their hand in two, they threw one part down the precipice, saying at the same time,
>
> "E Pele, eia ka ohelo 'au; e taumaha aku wau ia oe, e ai hoi au tetahi." "Pele, here are your ohelos; I offer some to you, some I also eat."
>
> Several of them told us, as they turned round from the crater, that after such acknowledgments they might eat the fruit with security. (1979 [1827]:163)

Elsewhere Ellis writes that "locks of human hair were among the offerings made to Pele. They were frequently presented to this goddess by those who passed by the crater of Kirauea, on which occasions they were thrown into the crater, a short address being made at the same time to the deity supposed to reside there" (250). Other early observers noted similar ceremonies:

> In this visit to the crater we observed that none of the natives went empty-handed, but carried pieces of taro, yams, plantains, etc., to make offerings, which they threw down at the mouth of the crater among other rotten remains of such offerings where they earnestly requested us to leave something too, which we did, such as beads, nails, and pieces of tape, which highly pleased them, and they seemed to think that such offerings would be highly acceptable. (Menzies 1920:161)
>
> In about three hours we reached the Okea tree, known as the boundary of the territory of Pele, or the goddess of the volcano. In bygone days no native dared venture beyond it without an offering to Pele, under penalty of her vengeance. (Wilkes 1852:145)

"Okea" is probably a misspelling of the *'ōhi'a* tree (*Metrosideros polymorpha*), one of the few trees that grows in lava areas and one traditionally associated with Pele. Probably this is the same tree described by Westervelt:

> About half way between the city of Hilo and the volcano Kilauea, there stood for many, many years an old ohia tree. It was so old that it had become legendary and was known as "Ka laau o Pele" (The tree of Pele). Whenever a native came near this tree, he began to search for certain leaves or fruit which he could lay beneath the tree as an offering before he dared to try to pass beyond. These sacrifices were supposed to appease the wrath of the goddess and assure the traveller safe passage through Pele's dominions. (1963 [1916]:36)

De Varigny describes a ceremony at Hale-ma'uma'u: "At the moment we drew near the edge, our Kanakas removed their shoes and bared their heads. After muttering several words in a low voice (the sense of which escaped us) they tied stones to a few small objects evidently carried for that purpose from Hilo—necklaces, glass beads, and so on—and threw these into the echoing abyss, as they called out three times this cry: 'Aloha, Pele! I salute you, Pele!' " (1981:78). Byron observed:

> Hence no ohelo berry was eaten on Peli [Kī-lau-ea] till some had been offered to the goddess of the same name: the sandal wood was not cut, nor the fern roots dug, without propitiating her by locks of hair, and often more precious things. Frequently, the hog and dog were sacrificed to procure her favour; and never was the ground disturbed or anything carried away from Kairauea [Kī-lau-ea]. (Byron 1826:186)

Kalakaua reports that "an offering was first made of everything eaten there [Kī-lau-ea]" (1974 [1888]:139).

A proverb in Pukui's compilation is based on the belief that *'ōhelo* berries must be offered to Pele:

> Mai hahaki 'oi i ka 'ōhelo o punia i ka ua noe.
> *Do not pluck the 'ōhelo berries lest we be surrounded by rain and fog.*
> A warning not to do anything that would result in trouble. It is *kapu* to pluck *'ōhelo* berries on the way to the crater of Kilauea. To do so would cause the rain and fog to come and one would lose his way. It is permissible to pick them at the crater if the first *'ōhelo* is tossed into the fire of Pele. Then, on the homeward way, one may pick as he pleases. (1983:222)

Ceremonies at Lava Flows

The literature provides ample documentation of ceremonies held at lava flows, especially when the flows threatened human habitations. Perhaps the best known of such ceremonies is the one attended by Ka-mehameha I when a lava flow threatened valuable lands in Kona. Kamakau provides a description:

> Kamehameha was in distress over the destruction of his land and the threatened wiping-out of his fish ponds. None of the kahunas, orators, or diviners were able to check the fire with all their skill. Everything they did was in vain. Kamehameha finally sent for Pele's seer (*kaula*), named Ka-maka-o-ke-akua, and asked what he must do to appease her anger. "You must offer the proper sacrifices," said the seer. "Take and offer them," replied the chief. "Not so! Troubles and afflictions which befall the nation require that the ruling chief himself offer the propitiatory sacrifice, not a seer or a kahuna." "But I am afraid lest Pele kill me." "You will not be killed," the seer promised. Kamehameha made ready the sacrifice and set sail for Kekaha in Mahai'ula.
>
> When Ka-'ahu-manu and Ka-heihei-malie heard that the chief was going to appease Pele they resolved to accompany him and if necessary die with him. Ulu-lani also went with them. . . . Other chiefs also took the trip to see the flow extinguished. . . .
>
> The flow had been destroying houses, toppling over coconut trees, filling fish ponds, and causing devastation everywhere. Upon the arrival of Kamehameha and the seer and their offering of sacrifices and gifts, the flow ceased; the goddess had accepted the offering. (1961:185–86)

During the course of the flow, a stream of lava "shot up the highest and . . . was the most brilliant in the bubbling mass" (Kamakau 1961:185). A chiefess attending the ceremony was told by a "seer" that the flame was her son, a common belief that deceased worshippers of Pele become flames (185). She responded by reciting the following chant composed in his honor:

> The eyes of my son are like a burning torch,
> Glowing like the red-hot *kukui* nut,
> It is the first flame to be seen in the burning fire,
> It is there in the bubbling fire,
> The body of Kanaloa-mahe-walu stands forth,
> I suppress my cry of affection,
> It overpowers me, my love, like that of a lover. (Kamakau
> 1961:185–86)

Kamakau continues: "It was said that Pele herself was seen in the body of a woman leading a procession composed of a multitude of goddesses in human form dancing the hula and chanting:

> 'Our husband has gone to carry the bigger load
> (Ka-heihei-malie)
> 'While the lighter load (Ka'ahu-manu) is neglected.' (1961:186)

It was believed that part of the reason Pele was erupting was because she disapproved of Ka-mehameha ("our husband") giving so much attention to Ka-heihei-malie and neglecting Ka'ahu-manu. Kamakau offers another account of the event elsewhere:

> The fishpond of Kiholo in North Kona, Hawaii, was constantly being threatened by lava flows while Kamehameha was ruler of the kingdom of Hawaii. A flow came down close to the pond of Kiholo; Kamehameha brought a pig and cast it in; the fires stopped. The flow had gone down as far as Ka'upulehu and Mahai'ula and had almost plunged into the sea. Kamehameha's bringing of a pig and offering it made the flow stop. There were eyes in the lava to see Kamehameha, and ears to hear his appeals and his words of prayer, and the great blazing lava flow died down. (1964:67)

Steen Bille provides another account of the same ceremony:

> In vain the unfortunate inhabitants made innumerable sacrifices to Pele, live pigs by the hundred were thrown into the boiling lava, the pigs burned and the lava continued its course. It lasted for many days; prayers, sacrifices, the songs of the priests, and the wailing of the people—nothing availed, nothing could appease the wrath of Pele. Then Kamehameha the Great stood forth at the head of his warriors. He went straight towards the stream, took a lock of his hair which was tabu and threw it into the fire, and then the torrent of lava ceased. Pele was satisfied, the sacrifice of Kamehameha had gratified her. (1851:225)

In 1881, another member of the Hawaiian royal family, Princess Ruth Ke'elikolani, conducted ceremonies to halt a flow approaching Hilo. The following is an eyewitness account:

> When we got to the flow it was advancing slowly but unmistakeably. The Princess walked to the flow, and I heard her give a long prayer. I was about 20 feet away from her. Then she took off her own red silk handkerchief and threw it into the red hot lava. Pele likes red silk.

> Then Ruth took other handkerchiefs and did the same thing.
>
> After the handkerchiefs were all gone, she took the brandy bottle and broke it by smashing it on the hot lava. It blazed into fire right away. Then she prayed again to Pele.
>
> We left the fire then and went to the tents where we spent the night.
>
> Early the next morning all of us went to the lava flow and we couldn't believe our eyes. The flow had stopped right there. (Zambucka 1977:70)

By this date, 1881, it appears that red silk was sometimes substituted for *kapa* and brandy for *'awa*.

Entries from a missionary diary also describe Princess Ruth's attempts to stop the flow: "There is a constant stream of visitors to the flow, and last night, Luka [Ruth] the old governess of Hawaii camped with a large number of people on the 3d hill, and rumor was rife yesterday in regard to the incantations which were to be made in order to stop the flow. If she does not succeed, it will be 'because the lands of Waiakea have been sold to haoles (white settlers)'" (Martin 1970:167). The flow stopped before reaching Hilo and the missionary notes in her journal: "I think that very many have been singing the doxology in their hearts ever since, whilst some few of the superstitious ones attribute the cessation of the flow to the influence of the chiefs" (168).

Coan also describes activities at the 1881 flow that approached Hilo:

> When the great eruption of 1881 was within a mile of the seashore, and threatened to destroy the town of Hilo, and seasons of fasting and prayer had proved of no avail, a deputation of pagan worshippers went quietly by night to the foot of the stream, made their sacrifices to the goddess Pele, the divinity of the volcano, and departed. The eruption, which had been flowing for nine months, stopped on the afternoon of the next day. (1889:156)

Coan describes the actions of a man who "belonged to the ancient class of native physicians or medicine-men" when a lava flow threatened his home: "When the burning flood struck the forest behind his house, he is said to have hoisted his flag in front of the slowly advancing lava, and to have forbidden it, in the name of the ancient gods of his race, to pass the flag" (1882:334).

Gutmanis provides 2 prayers from the Kelsey Collection that were recited to request Pele to desist from her destructive lava flows. She does not indicate where the prayers were recited, but seemingly the ceremony would have been held near the flows. The 1st is said "before eating," perhaps before giving offerings to Pele:

> Pele, Pele, eater of trees
> Yours is the small fire, 'Ula'ula-ke-ahi
> Pu'u-lena is the wind, the *'awa* is of Puna,
> That is joined by the *hala*, the *hala* of where?
> The *hala* the god continued
> For you deities, for us worshipers,
> Lest small be the land of the Pele worshipers
> Pele devoured the peace, the Pele worshipers
> Let the lightning flash, warm the earth.
> That we may live, your prophets
> Profoundly into tabu runs the prayer,
> Profound the lifting of the tabu.
> The tabu is lifted.

The 2nd prayer is recited "after eating," perhaps after offerings were made to Pele:

The land is free by the small attack, by the great attack,
For the release from the eating (of tabu) of the *haku.*
O depriver of bundles, o hinder who dwells in the pit
 turning a deaf ear,
Till the worshipers of Pele run away,
O Ku-wawa, o Ku ha'ili'ili-moe,
O Ha'iha'i-lau-ahea,
The women in the day, in the rain forest,
The *kahuna* in the hot raging of the fire,
O 'Imi'imi, o Nalo'wale, o Loa'a.
When you get the wrong, pay the native son
By love was the invitation given.
She comes . . . comes . . .
Profound the tabu; profound the freedom from tabu. (Gutmanis 1983:108)

Temple Ceremonies

Ceremonies to Pele and the other volcano gods were also conducted at formal *heiau*, or temples. Although Kamakau claims that "there were no formal prayer rituals for her [i.e., Pele], nor were heiaus erected for her where people bowed down; nor were people taught to worship her" (1964:69), other evidence in the literature refutes this.

Most references to *heiau* for Pele and her family are of a general nature. For example, Ellis says, "The whole island was considered as bound to pay them [i.e., the volcano gods] tribute, or support their heiaus" (1979 [1827]:173). When Ellis asked why Pele destroyed part of Keoua's army, he was told that "he had not sent sufficient offerings to the heiaus" (174). Kalakaua reports that "the temples of Pele were numerous, particularly in the neighborhood of old lava flows and their priests were always well sustained" (1974 [1888]:139).

Reference to a specifically named stone structure used in the worship of Pele is found in Ellis. While visiting Kī-lau-ea Iki, his Hawaiian companions "pointed out . . . the ruins of Oararauo, an old heiau, which crowned the summit of a lofty precipice on our left. It was formerly a temple of Pele" (1979 [1827]:179). Thrum describes the same temple: "Oalalauo—Kilauea Iki: on summit of precipice; temple of Pele, Kamakaakeakua its priest. In ruins in 1825" (1907:40). Reference to this *heiau* by Fornander (n.d.:265) appears to be from Ellis. Ellis provides a description of a *heiau* to Pele still used for ceremonies: "On descending to the bottom of the valley, we reached a heiau dedicated to Pele, with several rude stone idols, wrapped up in white and yellow cloth, standing in the midst of it. A number of wreaths of flowers, pieces of sugar-cane, and other presents, some of which were not yet faded, lay strewed around, and we were told that every passing traveler left a trifling offering before them" (1979 [1827]:250). Handy and Handy suggest this *heiau* that was in a "valley which marks the line between Hilo and Hamakua Districts . . . must have marked the point at which the domain of Pele ended and that of Kamapua'a commenced" (1972:335).

Ellis mentions "stone idols," but the only image from traditional Hawai'i identified as "Pele" is one currently in the Musée de l'Homme in Paris (Cox & Davenport 1974:132; Buck 1957:485). The authenticity of this identification is very doubtful (Rose 1978:270). Fornander claims that "tradition has it that image worship in the islands originated with her [Pele's] advent, though Pele was never represented by one" (1920:494).

Baker reports the remains of a *heiau* on Mauna Loa at 8,000 ft elevation that was associated with Pele-worship. He describes it as: "one large stone platform with long stones erected at the back, and further along a smaller stone platform. It has been learned from the Hawaiians that these platforms were for the priests, and the upright stones were offerings erected whenever there was a flow in this especially Pele-ridden section of Mauna Loa, to avert disaster" (1920:85).

Archaeologist Kirch writes that "Oalalauo and Uwekahuna were two important temples (*heiau*) situated at Kilauea, where rituals were performed for the propitiation of Pele" (1985:33).

Heiau to other members of Pele's family existed. Two stone structures to Hi'iaka are mentioned in the literature. Brigham provides the following brief description: "Heiau of Hiiaka, land of Lanihau, North Kona; situated on the rising ground at the head of Kailua Bay, 100 feet north of Pa-o Umi. Its site is now occupied by a hotel. . . . The name of Hiiaka was supplied by the late J. K. Nahale, Sheriff of Kona, and the late Malanui, the latter adding that it had been built by Umi" (n.d.:513).

Few accounts of temple ceremonies are found in the literature. One is from Ellis, who visited "a heiau dedicated to Pele" in 1823 during his journey around Hawai'i. His description of it continues:

> We were told that every passing traveller left a trifling offering before them [i.e., images].
>
> Once in a year, we were also informed, the inhabitants of Hamakua brought large gifts of hogs, dogs, and fruit, when the priests and kahu of Pele assembled to perform certain rites, and partake of the feast.
>
> The annual festival, we were told, was designed to propitiate the volcanic goddess, and secure the country from earthquakes, or inundations of lava. (1979 [1827]:250)

Although Ellis mentions an "annual festival" for Pele, he does not indicate the time of year it was held.

K. Kamakau writes of concluding ceremonies that were part of the elaborate "inauguration ritual of the *luakini* temple" (Valeri 1985:234) that involved Pele and her family:

> Then came certain prophets [*kāula*] to worship their goddess. Some for Pele, others for Hiiaka, Kapo, Pua and Kamohoalii. There were many prophets who came this day before the king's goddess, where they, every one of them, offered sacrifices of goods, pigs, chickens, sashes, and all other things, saying: "Here are the pigs, the chickens, and the sashes, gifts from us to thee. Save thou thy offspring; let us be strong before thee, and let the chiefs sustain us before them; and wilt thou see that we are forgiven on the day that we seek pardon." They then ceased their petitions and went away. The priest of the House of Papa then arose, waved the fire stick, sat down and prayed to the goddesses. The fires were then started for broiling dogs and chickens; these were brought together in the presence of the goddesses. Then the king offered the broiled dogs and chickens. (Fornander 1919b:28)

Kepelino writes of a child's naming ceremony that was held in a *heiau*. The reference to Pele is probably because she was an *'aumakua* of the participants.

> The prophet [*kāula*] held a position that was promised to a human being who was the devil's [god's[5]] assistant. When a new infant was born, the child's father took him to the *heiau*, later he sent for the prophet, who came to him. Then he offered a prayer calling the devil to come and see his helper, and afterwards a high priest gave a name, a nickname to this child. When this was

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[5] The Christianized Kepelino refers to all Hawaiian gods as devils.

> over, the baby was returned home. After two *anahulu* periods, (that is eight days), he took (the child) again to the *heiau*. There the child was circumcised, and a white tapa flag, a misty-white chicken, coconuts, bananas, red fish and other things were given as offerings. Afterwards, the real name of this child was announced, a name by which he was to be called and which was derived through prayer. That was how it was done. This ritual was associated always with the image-priests and the guardians of Pele. This child just mentioned then became a sacred child. All the knowledge and power of the devil were assumed entirely by this child. His name-chants were prayers addressed to the devil, and sacred, not to be chanted outside the *heiau*, only inside. When it was that period designed for prayers to the god-images, all the chants of this child were then performed. The priests chanted them in the *heiau*. When the fathered [sic] returned home, he chanted out the name-chants of his son, while the people in the house consequently were required to remain perfectly still and not walk about anywhere until the time of the prayer's final end. (Kirtley & Mookini 1977:60)

A ceremony described by an anonymous writer was held in the houses of the "keepers of the gods" (Anonymous 1860), seemingly a reference to the house within the *heiau* enclosure where images of the gods were kept, or to the *mua* (men's houses) where gods were sometimes kept (Kamakau 1976:132). References to the volcano suggest the ceremony was held in connection with Pele worship.

> In the houses of all the keepers of the gods, it is kapu to step over anything, or to walk to and fro when the awa is being chewed. When the awa is strained, it is kapu to utter a sound except by the one voice that responds to the one uttering the prayer. If one wishes to go outside or to come in, then a ti leaf shield is put where the awa container (kanoa) stands. Then the kapu is freed so that one can go out or come in. When the awa is strained, and poured into a cup then the gods are called by name. . . .
>
> "The rising smoke of the Pit breaks apart,
> Rising like terraces to the beloved clouds.
> Leaping upward, the cloud-like smoke arises from the Pit,
> Rising as Puuonioni does on the heights of Uekahuna,
> As Akanikolea does above Halemaumau,
> It is a customary sight.
> Here is your favorite food, O Kama,
> Come, come back.
> The back is protected, the face is shielded,
> Greetings to you" (Anonymous 1860)

Ceremonies at Volcanic Craters

Various writers mention ceremonies held at the volcano craters, but only brief descriptions of such ceremonies are found in the literature. Jules Remy observed 2 groups of Hawaiians who came to Hale-ma'uma'u for a ceremony in 1853.

> Two caravans, one of 26 people coming from Hilo, the other less numerous coming from Kau, arrived at almost the same time, and made a halt near our shelter. Three old men from the Hilo caravan descended into the crater with packets in their hands. "Are they, then, going fishing in the lake of fire?" I

> laughingly said to a young man who was acting eager around me. "It's just the contrary," he responded, giving himself the airs of being strong-minded, "they're going to scatter fish, they are idolaters!" (Summers 1988:62)

Westervelt found a brief entry in the Volcano House Records for 1865 made by a visitor, which notes a ceremony held at the crater by 37 Hawaiians. "They have been down to the lake of fire and have thrown in shoes, knives, handkerchiefs, coins, etc." (1904:12). Elsewhere, Westervelt describes a trip made by Hawaiians after they recovered from illness, which included ceremonies at Hale-maʻumaʻu:

> When Hawaiians, who had been ill, recovered, they frequently vowed to make a "journey of health." This meant that they came to the place now known as Hilo Bay. There they bathed by the beautiful little Coconut Island, fished up by the demi-god Maui. There they swam around a stone known as Moku-ola (The-island-of-life). Then they walked along the seashore day after day until they were below the volcano of Kilauea. They went up to the pit of Pele, offered sacrifices, and then followed an overland path back to Hilo. It was an ill omen if for any reason they went back by the same path. They must make the "journey of health" with the face forward. (1963 [1916]:28)

Bosserant d'Anglade describes what he calls "pilgrimages" to Kī-lau-ea in the early 1890s:

> As in earlier periods, the volcano is still the preferred place of pilgrimage for the Kanakas. Tradition holds that the goddess Pele had selected the volcano as her dwelling place, and so the Hawaiians journey there from all the other islands, displaying much the same robust faith as do the Mohammedans in their pilgrimages to Mecca. They bring with them offerings: the poorest of pilgrims come with a lei of rare flowers, the rich with a piglet or an exquisite kerchief destined to be thrown into the fire as a sacrifice. Throughout the visit they are sworn to keep in mind the fact that they are performing a religious act. They must not eat, nor can they even pluck a flower. Young men and girls do not even have the privilege of dreaming of their lovers. Instead, they chant their slow-measured sacred songs pausing from time to time only to celebrate their journey's progress, carefully placing some decorative leaves upon a wayside rock so as to compensate for a plant broken by the wind. (1987:138–39)

Handy and Pukui report that a betrothal on the island of Hawaiʻi "was sealed with a prayer and offering at Ka-lua-o-Pele (The pit of Pele, Halemaʻumaʻu). Later the betrothal was broken and subsequent troubles are believed to have been due to disregard of the *kapu* laid before Pele" (1972 [1958]:105). It is not mentioned how frequently such ceremonies were held at the volcano. Pukui writes that Ka wai hūnā a ka pāoʻo is "a pool not far from the crater of Kīlauea. The priests of Pele who knew of its location obtained water from it to mix the *ʻawa* drinks they offered to her. Like the pool on Lehua, a supernatural *pāoʻo* fish guarded it. This pool was destroyed during the making of a road" (1983:178).

Funeral Ceremonies

The most commonly described ceremony held at the crater is the one that accompanied the disposal of human bones. Various writers report the widespread Hawaiian belief that souls of persons who were related to Pele dwelt with her in the volcano (e.g., Holokahiki 1865:2). Such an eternal cohabitation seemed to be ensured if the bones of the deceased were deposited in the volcano crater. It was also believed that the presence of the spirits in the volcano would protect the living relatives from eruptions. Kamakau writes:

> When persons become volcanic spirits . . . , their *ho'ailona* [sign] are flames, earthquakes, or tidal waves within these volcanic manifestations. . . . They become the "worker slaves" . . . of the earth-devouring spirits . . . of the volcano who direct these "fires" to wherever they want them to go. The "fires" heed their desires, and from that place to this they are directed by these spirits. When the spirits are angry, these appease their anger and chagrin . . . by ruining the land and causing death to man. The only way to make them stop is for the ruler himself to take a pig and offer it as a "burnt sacrifice" to the gods with his own hand. (Kamakau 1964:66)

When John Papa I'i visited Kī-lau-ea in 1852, he sensed the spirits of the dead in the crater: "When they went down into the hollows of the pit and came to the crater proper, which was active, it seemed to Ii that the child's mother and aunts and her cousin Nahienaena [all deceased] were also there, sitting together on the other side where the lava gathered. The lava seemed to be dancing, and from where they stood, the flames appeared to go up and down" (1983:169). I'i does not say so, but presumably the deceased were kinsmen to Pele. K. Kamakau writes:

> Should a chief die, or any of his own men, or the servants of Pele, then their souls will go to the volcano, and the servants of Pele and other men will serve as they served in this world. And the servant of Pele will be his caretaker, who will lord it over his stewards or even over his own body servants. When the soul is living there, should some one wish to see it, then this is the process: go with a servant of Pele, and he will call by chanting one of the chants of that chief. (Fornander 1919a:572,574)

A "priestess" of Pele told Ellis: "I am Pele; I shall never die; and those who follow me, when they die, if part of their bones be taken to Kirauea, (the name of the volcano), will live with me in the bright fires there" (1979 [1827]:217). Kamakau writes that "if Pele and Hi'iaka were his *'aumakua*, then the pit of Pele would be the soul's resting place" (1961:200). Elsewhere, Ellis writes: "The worshippers of Pele threw a part of the bones of their dead into the volcano, under the impression that the spirits of the deceased would then be admitted to the society of the volcanic deities, and that their influence would preserve the survivors from the ravages of volcanic fire" (1979 [1827]:259). Pogue writes that "if the physical body of the Chief died, or those of his relatives, and the attendants (*kahu*) of Pele, their souls returned to the crater of Pele, where they were waited upon as in their earthly life" (1978 [1858]:56). Kirtley and Mookini translate an 1865 newspaper article, which reports: "Likewise, when corpses and bones are thrown into the crater at Ki-lau-ea, they become fire and lava, it is believed, and are worshipped" (1979:81).

Pukui describes a ceremony held at the crater to ensure that the spirit of the deceased would become an *'unihipili*, a spirit that could be called upon to assist a medium:

> The *kaku'ai* method [of creating an *'unihipili*] was more elaborate. After the death of a person, his body was prepared with the proper sacrifices and taken to the dwelling place of his *akua* or *'aumakua*. Those who claimed Pele as their *akua* and wished to take their dead to her, took the bones of the deceased, wrapped in red and black tapa, to the priests of Pele. At the pit the *kahuna* chanted a long prayer, threw in prepared *'awa* and a cooked pig, and then last

> of all the bundle of *kapa* containing the bones. If the deceased was accepted by Pele, the bundle made a circuit of the pit without being burned and then burst into flames and vanished. A flame appeared on the surface which was taken to be a spirit of the person just accepted by Pele. (Handy & Pukui 1972 [1958]:150)

Elsewhere, Pukui concludes the above description with: "If Pele would not accept the remains of the deceased, it was tossed back to the family or thrown up and its parts scattered on a ledge where the family gathered them up and took them home" (1945:3).

Von Kotzebue mentions that "dying persons sometimes desired that their bones should be thrown into the crater of the volcano at O Wahi [Hawai'i], which was inhabited by the revered god Pelai [Pele]" (1967:178).

H. B. Nalimu writes: "Pauahilani was a man who carried the bones of chiefs to Kilauea and threw them into the mouth of the crater in old times. This waha o Kilauea was a big open hole with a fire in it where smoke arose between ka pali kapu o Ka-moho-alii and Hale-ma'u-ma'u. Awa, pigs, etc were also sacrificed" (n.d.:802).

Various descriptions of the actual ceremonies are found in the literature. Kamakau writes most extensively of the ceremonies for disposing of the dead in the volcano:

> For a dead beloved one whom they wished to become a volcanic manifestation . . . of the crater . . . of Kilauea on Hawaii, the Hawaiians would act in this way: They would take to the volcano the bones, hair, fingernails, or some other part of the dead body, sacrifices and offerings for the gods . . . , gifts for the priests and prophets and guardians of the volcano, a pig, *'awa*, and a tapa garment of whatever color the relatives to whom the body belonged chose to be a visible sign to them . . . and they would ascend to the pit of Pele. . . . There they ritually killed the dedicatory pig . . . for the dead newcomer the *malihini*, to become a native, a *kama'aina*, of Kilauea. If the ritual went well . . . a pouring rain would pelt the uplands and the sounds of thunder would reverberate to the sea, as a sign of consent to the admission . . . of the *malihini*. In the morning, the pig was roasted, the *'awa* chewed, and all would feast. Then the prophet of Pele, the *kaula Pele*, and the relatives of the dead, from 10 to 40 as eyewitnesses, would take the corpse and the offerings—a live pig . . . and some *'awa* — to the very center . . . of the fire, where the fires were quiet and where fiery lava . . . welled up . . . instead of tossing about or rolling in great waves.
>
> The prophet stood and pleaded . . . for the acceptance of the *malihini* and for his being united with the *kama'aina* of the pit, and he recited the ancestry of the dead one so that his ancestors in the crater of Kilauea would know him as one of them. It was useless to make offerings to them, for they were just the *kama'aina* of the place, not the gods. When the *'awa* and the pig were thrown in, they were immediately consumed. When the body of the *malihini* was thrown in, it was as though it were being fondly lifted by a procession of people and borne tenderly upon fingertips into Halema'uma'u, the home of the *kama'aina* chiefess of this place. She, Pele, had built this place to warm strangers who came to the mountain through icy mists. The body was borne along for the distance of a chain or two without the tapa that covered it being scorched; then, like a swelling wave, a flame swept over it and the *malihini* vanished. Some minutes later a flame appeared and billowed, and a column

> of fire appeared, streaked with whatever color the relatives had chosen to wrap the body in. They would hear the sound of many voices making a din, chanting *hula* and *oli* and *mele*, and the colored column which was the *malihini* they had brought would move about joyfully. Then the people to whom the *malihini* belonged would wail and call out the name by which he had been known in life and say, "You live! You live!" The "sign" . . . which the relatives saw was their beloved one; this was the body of their beloved. . . .
>
> If the corpse was that of a chief, some people divided the body into 40 or more pieces and distributed the little pieces among the districts . . . of Hawaii. Those of each district could take their pieces to be made into a *pele* [volcano spirit]. There might be 40 or 100 pieces, and so each person might become a "multitude" . . . of volcanic spirits. The danger in making the body of a high chief, or perhaps a ruler, into so many spirits was that they might burst forth and devastate the land. The *kaula Pele*, therefore, did not like to do this. Those who did yield to the pleading of certain people and consent to do so were called "destroyers of the land" . . . and "troublemakers to the kingdom". . . . That is the reason why chiefs killed prophets of Pele in the old days, and why the prophets acted in great secrecy. If there was a great eruption that devastated the land, the people became greatly excited and believed that a high chief had been taken into the pit of Pele. The mistaken idea . . . that many spirits are banded together in the pit of Pele has persisted from ancient times to this. It is a place free from all defilement, according to the belief of these people.
>
> Many people wished to become volcanic spirits, and their relatives would make the appeal for them—perhaps because they believed that they would continue to live in the volcanic fires. There were many signs to be seen if one could not become a spirit of the volcano. A person did not become such merely by the making of a great many gifts and offerings; many are the eyewitnesses and prophets who can testify to this. When the prophet and the relatives of the dead one took his bones, hair, fingernails, or his spittle, perhaps, and the prophet made the appeal and threw the bundle into the glowing fire, if the bundle fell into the fire and was thrown back again to the place from which it was thrown without the tapa wrappings being burned, then the prophet would retrieve the bundle and ask what the obstructions . . . were that had caused it to be thrown back. If, when it was thrown a second time into the fire, it vanished into flame, then it had first been returned because of the obstruction that had now been cleared up. But if the bundle broke open and the bones or fingernails or whatever it was scattered, why was this? It was because the person had been spurned. He had no right . . . there, and had no relatives in that place. He became a wandering spirit at Kama'oma'o, a catcher of dragonflies, a shredder of spiders in the *wiliwili* grove of Kaupe'a. (1964:64–66)

Pukui quotes portions of the above from Kamakau and adds: "My great grandmother was taken to the volcano. This was after Christianity had come. But because we're related to the fire—the line of Pele—great grandmother's people took her secretly, after the flesh was removed from the bones. They wrapped the bones and took her [the bones] to the Halemaumau fire pit of Kilauea Crater and chanted and prayed and let her go happily to her people who were fire" (Pukui, Haertig & Lee 1972:1:116).

Reverend Nalimu describes the disposal of chiefs' bodies: "Chiefs were laid in caves until after decomposition then they were taken and thrown into the Pit of Pele. The bodies of chiefs were not stript of the flesh when they had just died but were left in an advanced stage of decomposition, one, two or three months" (n.d.:778).

Kalaaukumuole provides fragments of a ceremony held at the death of a child: "Unihilele: This god is there in Kilauea, the place of the women of the pit, in this way: the duty of this god, if a child dearly beloved died, Unihilele was appealed to: 'here is the taro top, restore my child,' and so forth" (1866). It is not clear whether bones were thrown into the pit at this time.

Green and Beckwith provide another account of a burial ceremony:

> The highest honor of all was conferred upon those dead whose bones were cast into the crater of Kilauea to be with Pele. Even to have their bones placed in fissures near the volcano was considered fortunate. The souls of those whose bones are cast into the crater are said to live with Pele in happiness.
>
> The description of such a burial was given to Miss Green two years ago by an intelligent Hawaiian woman over sixty years of age, who recalled an incident of her childhood life in Hilo where she was born and brought up. When she was ten or eleven years old her adopted father . . . then an elderly man, said to her, "We are going up to the crater to deposit bones of your ancestors." The two were accompanied by an old *kahuna*, or priest. When they reached the pit, a red handkerchief was spread near the edge and upon it was placed an *umeke*, or calabash, containing the bones. No mention was made of offerings, but probably these also were placed upon it. The three worshippers sat a little way back of the improvised table facing the pit, the girl sitting between the two men. Then the two men commenced to chant, calling upon Pele to receive the sacred bones. Gradually the lava rose in the pit until at length it reached the top, and then subsiding, took with it the calabash, cloth, and all. Instead of sinking immediately the calabash circled the pit, while at various points detonations were to be heard as if the gods or the spirits of the dead who inhabited Halemaumau were saluting the arriving company. After encircling the crater, the calabash sunk. Then the two men caught hold of the girl by the arms, telling her that soon would appear the visible forms of the dead and she must not leap into the pit after them in her excitement. They continued chanting, and sure enough, there in lava appeared the shapes of human figures, some of which she recognized as those not long dead, but whether the same as those just deposited she did not say. "You may believe this," said the old lady; "I wouldn't believe it if I hadn't seen it myself." (1926:185–86)

Pukui describes funeral ceremonies held by her family in Ka'ū:

> As my family belonged to the lineage of Pele, the bodies of our dead were laid away in a cave until after decomposition was all over. Then the bones were carried with the appropriate gifts to Kilauea fire pit where lived the Prophet of Pele (*Kaula Pele*). The *Kaula* went with the relatives to the rim of the Pit (*Ka Lua*) and with prayers the gifts (*mohai*) of pork and *'awa* were tossed to the Woman of the Pit (*Ka-Wahine-a-ka-Lua*). The bundle of bones were then thrown in with the words, "Here is your offering, O Pele, please accept him." The *'uhane* was then believed "to live with Pele for all time." If the dead was not acceptable to Pele, that is if she would not recognize the kinship, the bundle was thrown back to the feet of the priest. It was then

> carried back to the cave. There had never been a time when the bones of our own relatives were ever thrown back. This justified our belief that a kinship existed between our *'ohana* and the dreaded fire goddess. (Handy & Pukui 1972 [1958]:152–53)

Kaaie describes a similar type of burial on Maui at Hale-a-ka-lā where the entire body was thrown in the pit (1862:3148). A different translation of the same account is found in Fornander (1919a:570,572). Although Kaaie does not mention Pele, Handy and Handy assume such burials were conducted on Maui by people who believed themselves related to Pele (1972:336–37). If, indeed, Pele was appealed to in this ceremony, it is the only description of a ceremony held for Pele beyond the island of Hawai'i, except ceremonies associated with the hula. It is perhaps noteworthy that Maui is the only island except Hawai'i that has experienced volcanic eruptions since human habitation of the Hawaiian Islands.

> There are sacred burial places on the cliffs or on level places. There is a pit on Hale-a-ka-la called the Pit-of-Kaawa (Lua-o-Ka'awa), directly above Nu'u, on Maui. The bodies are prepared thus, just as it has been described. The bearer of the dead also takes with him the food of which he was fond, such as pork, banana, sugar cane or other things. These are taken according to one's fondness for them. Upon reaching the pit, the relative of the dead calls to a departed ancestor within, "So-and-so, here is your child." If the body (tossed in) falls into the water, he has no relative in this pit, but he who has a relative is caught as his corpse is thrown in. It lands on a ledge and does not drop into the water. After the corpse vanishes, the bearer returns home after which their [*sic*] is much crying and mourning. (Kaaie 1862:3148)

In addition to pit burials, deep chasms in the lava were also apparently used for disposing of the remains of those believed to be related to Pele. Green and Beckwith report that "even to have their bones placed in fissures near the volcano was considered fortunate" (1926:185). Byron writes: "Besides the roughness of our yesterday's march, to-day we had great chasms in the lava, which often demand our utmost care in walking. Near one of the largest of these, four poles had been erected to mark it as a burial-place, where the bones of many of the people, particularly the worshippers of the fire gods, used to be deposited" (1826:180).

OFFERINGS

'Awa and pigs were necessary offerings to Pele at the most important formal ceremonies—as they were for the other major gods of Hawai'i, also. Other offerings, however, of various types were made to Pele at domestic altars, when walking over her domain, at lava flows, at Halema'uma'u, and when conducting rituals in her *heiau*.

Numerous writers mention that *'ōhelo* berries could not be eaten until some were offered to Pele (e.g., Ellis 1979 [1827]:174; Byron 1826:186). Brigham reports "a broken fern leaf covered by a stone" (n.d.:5) was an offering still left to Pele at the turn of the century when passing through her territory.

Offerings were given to Pele at the lava flows. Brigham mentions a "bundle of awa done up in a red handkerchief found on the still hot flow of 1887" (n.d.:20). According to Ellis "many [hogs] were thrown into the rolling torrent of lava to appease the gods, and stay its progress" (1979 [1827]:173). At a lava flow in 1868, Lyman met "a native kahuna" who told him that if he were given "a black pig and a white hen, he would endeavor to appease the wrath of the Fire Goddess Pele" (1929:6).

At the crater of Kī-lau-ea offerings of "fruits, pigs, fowls, fish, and sometimes human beings" were given to Pele, according to Kalakaua (1974 [1888]:139). Ellis writes that fish were required offerings from people who lived near the seashore, and "vast numbers of hogs, some alive, others cooked, were thrown into the craters during the time they were in action, or when they threatened an eruption" (1979 [1827]:173). Kamakau reports that "a live pig . . . and some *'awa*" were offered during the ceremonies when the dead were deposited in the crater (1964:65). A Hawaiian account of Captain James Cook's death, published by de Varigny, claims that "sacred fish intended for Pele's altar" were forcefully taken by Cook's men (1981:17). Several writers (e.g., Byron 1826:186) mention locks of hair as suitable offerings at the crater. Stewart reports "taro, potatoes, and sugar-cane, and the cloth-plant . . . hogs and fowls" as items that were sacrificed at the crater (1970 [1830]:301). Pukui says that "*'awa* and a cooked pig" were thrown into the crater at the time bones were disposed there (1945:3; Handy & Pukui 1972 [1958]:150). Westervelt reports that because of Pele's enmity toward the hog-god Kamapua'a:

> The most acceptable sacrifice to Pele was supposed to be a puaa (a hog). If a hog could not be secured when an offering was necessary, the priest would take the fish humu-humu-nuku-nuku-a-puaa and throw it into the pit of fire. If the hog and the fish both failed, the priest would offer any of the things into which, it was said in their traditions, Kamapuaa could turn himself. (1963 [1916]:277)

Ellis observed "wreaths of flowers, pieces of sugar-cane, and other presents" at a temple, and was told that during an annual festival, "large gifts of hogs, dogs, and fruit" were brought to the temple (1979 [1827]:250). He was also told that at the ruined temple near Kī-lau-ea:

> Large offerings were frequently made of hogs, dogs, fish, and fruits, but we could not learn that human victims were ever immolated on its altars. These offerings were always cooked in the steaming chasms, or the adjoining ground. Had they been dressed any where else, or prepared with any other fire, they would have been considered polluted, and have been expected to draw down curses on those who presented them. (1979 [1827]:179–80)

In Titcomb's discussion of the use of *'awa* in Hawai'i, she quotes a letter which claims that "the priests used this kind [of *'awa*, i.e., *'awa mo-i*] in sacrificial ceremonies to Pele . . . obtainable today; *awa hiwa*: skin dark, also leaves; used in Pele worship, also at *heiaus* and *koas*" (1948:110). In a chant from Kepelino, *'awa* is offered to Pele and Hi'iaka (Titcomb 1948:156). An *'awa* offering prayer to Pele is also found in Emerson (1965 [1909]:199–200).

Ekaula claims that "*'awa* with greens" are suitable offerings to appease *'aumakua* of the Pele family (1865). Handy and Pukui write that Pele and Hi'iaka could be appeased during times of illness with offerings of "taro greens and salt" (1972 [1958]:143). Kamakau claims only "a gift of a bit of salt was required" for the volcano spirits (1964:89).

Kalakaua claims human sacrifices were made to Pele (1974 [1888]:139). Menzies, who visited Hawai'i in 1794, reports that Hawaiians "sacrifice their criminals by disposing of them in the same manner [i.e., throwing them into the volcano]" (1920:161). Whitman writes that "at the time of the eruption the poor natives were struck with consternation and apprehended the destruction of their little world. Thousands of victims are said to have been sacrificed to appease the angry gods" (1979:64). However, the more extensive discussions of the Pele religion (e.g., those of Kamakau, Ellis, and Pukui) do not mention human sacrifice. Ellis apparently inquired about human sacrifice, but received no confirmation of the practice (1979 [1827]:179–80).

SORCERY

Various members of the Pele family were involved in sorcery, but the only sorcerer's prayer directed to Pele discovered in the literature appears in Joseph Emerson's article (1918:28–30). This prayer, a type called "A Kuni Prayer (A Prayer with Fire)" is used to revenge the death of a person who "dies under suspicious circumstances" (23), and may be addressed to Uli, Kāne, Kanaloa, Pele, or Ka-moho-ali'i. The prayer invokes "the death of the victim . . . in a horrible, sometimes in a blood-curdling fashion" (24) after a fire is lighted.

> In all prayers to Pele the closing formulae, "Amama, ua noa," etc., or "Elieli kapu," etc., are omitted for the reason that she can be addressed in prayer only by those related to her, for whom she thus becomes an "aumakua." The "kuni" prayer is only used after the "kuni" fire is lighted which must be made of uhaloa wood. Upon it is thrown some "pupu-awa" and "opihi-awa," and, inclosed [*sic*] in a wrapping of ki leaves, are put some "pupu makaloa," "kua-paa," "limu-kala" and "kalo-lau-loa," which are roasted in the fire as a preliminary to the prayer. This ceremony is limited to no particular night. It may even be performed in the daytime. The word "Ku," to stand, is applied to any dry land where one may stand, and thus becomes an appellation of Pele, who made the dry land. This name for Pele should not be confused with that of Ku, one of the four principal gods. (Emerson 1918:25)
>
> O Ku,
> Unproven is the guilt of him who died,
> Slain by a god;
> Yea verily, slain by a god.
> He has built his house;
> The thunder has rolled;
> The earth has quaked;
> Their testimony to his innocence has reached to heaven.
> O thou rain, gift of Ku;
> And thou, Holani, god of agriculture;
> O ye heavens,
> And thou, Hamoea, goddess of the massage,
> Ye all are his witnesses.
> The heavens have declared for him.
> If during thy night, O Lono,
> Thou didst fail to see;
> Surely then it was on some common night, not thine, that this
>   deed was done.
> O Ku, Holani, ye heavens; and thou, Hamoea;
> The evidence is now clear as the dawning light.
> As I present the case
> The evidence will flash before your eyes.
> When Ku gives testimony
> The garment of the guilty kahuna will become his coffin.
> With the testimony of eye-witnesses,
> The death sentence will not be delayed.
> Ye winds in your wide circuit;
> And you, ye rains, present your testimony.

> Ye magical sands of Mahinahina,
> In close sympathy with those of Heihei;
> O Pele, maker of the earth;
> And this thy earth, O Pele,
> Nursed by the heavens,
> Snap then your jaws until the sound reaches the heavens.
> Ye rains, ye fruits, the gift of Holani,
> Stand as Holani.
> O ye heavens, Hamoea now gives her testimony.
> The heavens are ablaze with their verdict;
> The thunder shall be his coffin.
> The earth gives its verdict;
> An earthquake shall be his coffin.
> The mountains give their verdict;
> The mountain ridges shall be his coffin.
> The ocean gives its verdict;
> The raging surf shall be his coffin.
> Stand as Holani.
> O ye heavens,
> Hamoea approves the death sentence. (Emerson 1918:29–30)

The preceding prayer was addressed to Pele, the *'aumakua* of the person who composed it. "Its object is to destroy the evil-doer, the rival kahuna, who by his black art has caused the death of a well-known person by whom, it is claimed, no offence justifying such a fate has been committed" (Emerson 1918:24).

The literature frequently mentions Pele's sister Kapo as one of the deities used in sorcery (Poepoe Collection n.d.:31; Kirtley & Mookini 1979:76, 77, 79; Emerson 1888:1; Anonymous 1886:558; Anonymous 1888:555). In 1863, a letter to a Hawaiian-language newspaper reported that a woman of Kaua'i was using Kapo to practice sorcery (Anonymous 1863). Malo claims that possession by Kapo could result in "a swelling of the abdomen . . . which was a fatal disease. Many deaths were caused by obstruction of the bowels" (1951 [1903]:116). Joseph Emerson writes, "An inferior demon of the *Pele* family is the obscene *Kapo*, a conception of impurity too revolting to admit of description. She is continually employed by the *kahunas* as a messenger in their black arts, and is claimed by many as their *aumakua*" (1892:8). An anonymous writer reports:

> The goddesses that were usually sent in this kind of sorcery ["to destroy the intended victim"] were Kapo and Kuamu, two that were included in the one name of Kapo. . . . The trouble (death) caused by the two were hemorrhages above (nose and mouth) and below (womb and rectal). When sickness of this kind was seen, it was said "This is Kuamu's death" or perhaps "This is Kapo's". (Poepoe Collection n.d.:31)

Waiamau claims a sorcerer could send Kapo (as well as certain other gods) to harm a victim by reciting the following:

> Go to that person there . . . (to, for instance, Naimu, the person desired dead). . . . All of you go to Naimu, he will be your house to live in, your place to sleep. There will be your clothing, your poi, your fish, your water. All things for you will be there. Don't return here later. If you come back here excrement

> will be your food, urine your water. All of you go there and eat him to death. (Kirtley & Mookini 1979:79)

Pukui describes the dual nature of Kapo:

> Kapo established a school for the hula, ritual dance-drama. Her nature was dual. As Kapo-ʻula-Kinaʻu (Kapo-red-spotted) she was the Kapo invoked by *kahuna* when sending evil back upon a witch. This Kapo was a goddess whose temper was violent and vengeful. But when worshipped by dancers and chanters, this same person was the gentle Laka, the spirit of the wild wood. Yet when the *kapu* of seclusion was disregarded by a student or teacher during the period of devotion to *hula* training in the *halau*, the loving Laka quickly changed into vengeful Kapo and smote the culprit. So was the *hula* respected in the olden times; it was beneficent when rules were kept, yet deadly when they were not. The *hala-pepe* (*Draceaena aurea*), a plant used on the *hula* altar, was one of Kapo's *kino-lau*, as Laka; and the tree *ʻohe* (*Tetra plasandra Hawaiiensis*) was another. The tree was associated with sorcery, of which art Kapo also became the patroness, due to her ferocious side. (Handy & Pukui 1972 [1958]:124–25)

In some Hawaiian myths, Kapo is depicted as a beneficent deity. According to Manu, she and her sisters introduced trance and the healing arts to Hawaii before Pele arrived (1899). In another myth, she saves Pele from Kamapuaʻa by distracting him with her flying vagina (Beckwith 1970 [1940]:187).

Hiʻiaka-i-ka-poli-o-Pele, usually depicted in myth as Pele's favorite and youngest sister, was also called upon by sorcerers to assist in their malevolent rituals (Emerson 1888:476). Malo reports, "Hiiaka caused hemorrhage from the head of the *kahu* of whom she took possession" (1951 [1903]:116). Emerson elaborates on the role of Hiʻiaka in sorcery: "Her younger sister, *Hiiaka i ka poli o Pele*, after slaughtering many of the inferior gods that formerly dwelt near Waimea, on Hawaii, on the famous Mahiki road, became an active agent in the destruction of the Hawaiian race. She is the especial *aumakua* of those sorcerers who practice the murderous arts of *poʻi-uhane*, *apo leo*, and *hoonoho uhane*" (1892:7). Alexander writes that "the goddess Hiiaka-i-ka-poli-o-Pele was also much employed by this class of *kahunas* [i.e., sorcerers]." He elaborates on the kinds of sorcery Hiʻiaka assisted:

> *Kahuna Hoonoho*. The practices of the *kahuna hoonoho* strongly resembled those of modern spiritism. The medium was called the *kahu* or *ipu* of the spirit, which was often called a *makani* or wind. Sometimes the spirit descended upon the *kahu*, and sometimes it spoke from the roof of the hut. . . . The necromancer always demanded *awa* before commencing operations. . . . After drinking the *awa* the wind descended upon the *kahuna*, and showed him the cause of the sickness, whether the patient had been bewitched by a sorcerer, and by whom. The same practitioners were employed in cases of theft to recover stolen goods, and to detect the thief. (Alexander 1891:68)
>
> *Apo leo* was the art of depriving a person of the power of articulate speech. In order to do this, the *kahuna* prayed at night to Uli and Hiiaka, presenting them with the usual offerings of *awa*, etc. The next day he sought out his intended victim and entered into conversation with him, during which (as was believed) he caught and took away his voice, or paralyzed his vocal organs, so that he could never speak again. He might linger a long time in this wretched condition, or die in a few days if the sorcerer so willed. (1891:71)

> The *po'i-uhane*, who worshipped *Hiiaka*, had the faculty of not only seeing the souls of living persons, *kakaola*, but of catching them with the hand, *po'i*, and of either squeezing them to death or imprisoning them in a water-calabash. The sorcerer then had the owner of the soul in his power, and could levy blackmail on him as he pleased, for if he killed his *kakaola* he would go into a decline and soon die. (1891:72–73)

Pukui departs from this view of Hi'iaka and describes her as a healing goddess and "physician to the family of her sister Pele" (Pukui, Haertig, & Lee 1972:2:146), a role she frequently performs in the Pele–Hi'iaka cycle of myths (N. Emerson 1915).

Joseph Emerson claims that Kuamu was "an inferior demon in the form of man connected with the *Pele* family." He was also a messenger of ill will used by sorcerers. The following prayer was used to inflict his evilness on victims:

> O, Kuamu, go thou to Puhi,
> Enter him head and tail,
> Let him become your bread and meat,
> Return not back again until he is devoured of worms.
> The tabu is lifted. (Emerson 1892:21)

As noted earlier, Kuamu is sometimes regarded as an aspect of Kapo (Poepoe Collection n.d.:31).

Emerson also reports that Ka-moho-ali'i was another god who assisted sorcerers (1888:476), but he is more commonly depicted as a benevolent, helpful shark-god (Emerson 1892:9–10).

Kihe's notes provide fragments of a ceremony at a child's death: "Unihipile—child dies, hair thrown into Lua Pele—becomes a kino makane" (n.d.:569). According to Joseph Emerson, this is part of a ceremony to create an *unihipili*, a spirit used by sorcerers to execute their commands. The *kino makani* is a wind body, one of three aspects of the spirit, the others being sea and land. No mention is made by Emerson of Pele or her family being directly involved (1892:4).

CONCLUSION

This paper has attempted to reconstruct the traditional cult of Pele as it is described in the early literature on Hawai'i. Pele was a significant god (*akua*) as well as an important ancestral deity (*'aumakua*) to many Hawaiians on the island of Hawai'i. She was less important as an object of worship on the other islands, although the extensive mythology of the goddess was widespread throughout the archipelago. Early accounts indicate that she was generally regarded with fear, although those Hawaiians who traced their ancestry to her probably also regarded her with affection as a protective deity. The literature reveals at least 4 types of formal ritual leaders for Pele ceremonies: *kahuna pule*, who officiated at the *heiau* and Hale-ma'uma'u; *kāula*, who conducted ceremonies at Hale-ma'uma'u, and probably elsewhere; *kahu*, who assisted the ritual leaders by providing offerings and sometimes sacrificing them at the formal ceremonies; and *haka*, mediums who were possessed by the goddess or were able to communicate with her. In addition, many other people knew the appropriate rituals for various ceremonies to Pele. These ceremonies were held at various locations, such as the household; the hula *hālau*; tree-felling sites for canoe building; steam vents, craters, and paths within Pele's domain; active lava flows; *heiau*; and Hale-ma'uma'u. These ceremonies included curing ceremonies, requests for protection from lava flows, funeral ceremonies, daily household prayers, and prayers to request protection of the goddess during various activities. The offerings made to Pele during these ceremonies included pigs, *'awa*, fruits, vegetables, *kapa*, dogs, fish, fowl, flowers, and salt. Some writers claim humans were sacrificed to Pele, but the bulk of the literature does not mention such sacrifices. Certain members of Pele's family—especially her sister Kapo—were important deities in sorcery, but there is little evidence that Pele herself was significant in sorcery.

The religion of Pele was greatly altered by Christianity, but it was never destroyed. The major *heiau* fell into disuse and disappeared, along with the ceremonies performed in them, but private belief and worship of the goddess continued, especially in the volcano area. The literature of 19th century Hawai'i is replete with references to Pele worship (e.g., Hill 1856:264–67; Lyman 1929:6; Korn 1958:55; Emerson n.d.b; Brigham n.d.:20), and it has continued unabated to the present time (Nimmo 1986). However, modifications have occurred. For example, offerings of gin are frequently substituted for *'awa*, red cloth has replaced *kapa*, and red is now the color associated with Pele rather than white. Pele presently dominates ritual attention, whereas previously a variety of volcano gods received obeisance. The cult now has a much more dispersed group of followers: in the past, it was primarily localized in the volcano districts of Hawai'i Island, but today it draws adherents from throughout the Hawaiian Islands, crossing ethnic, racial, and economic divisions. The goddess has become an important focus for the Hawaiian Renaissance, the current revitalization of Hawaiian culture, and ceremonies are held for her by numerous people. Each year during the Merrie Monarch Hula Festival, special ceremonies are conducted for her by dancers at Kī-lau-ea (Bowman 1984). Another annual ceremony for Pele marks the beginning of Aloha Week on Hawai'i Island (The Sunday Star-Bulletin and Advertiser 1986:A-3), and recently special prayers were offered to the goddess at Kī-lau-ea as part of the concluding ceremonies of the "Year of the Hawaiian" (Clark & Tanji 1988:A-5). Some Hawaiians are currently fighting geothermal energy development in the volcano area in the belief that such development is a sacrilege against Pele (Pele Defense Fund 1988:A-10).

Undiminished by Westernization and modernization, Pele continues to attract a variety of followers in contemporary Hawai'i. For some, she is a living deity occasionally encountered throughout the islands. For others, she is an apotheosized ancestor to be worshipped with the rituals of tradition. Still others view her as the personification of the creative forces that gave birth to the Hawaiian Islands and the life upon them. She has survived the most difficult times and seems destined to become increasingly important in Hawai'i. It appears that Pele will be around for a very long time.

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Patterns of Protest: A Hawaiian Mat-Weaver's Response to 19th-Century Taxation and Change[1]

Roger G. Rose[2]

ABSTRACT

Hawaiians from Ni'ihau specialized in plaiting *makaloa* sedge mats valued throughout the archipelago for their flexibility and intricate geometric patterns worked in a technique called *pāwehe.* Such mats were luxury items acquired through taxation and tribute by the chiefly class, who used them as bed covers until *makaloa* mats were abandoned toward the end of the 19th century. One of the last examples created was presented to King Kalākaua in 1874 and incorporates a lengthy petition in the Hawaiian language, interwoven in the traditional *pāwehe* technique. It requests relief from burdensome taxes on animals and other oppressive conditions, dramatizing the plight of the Hawaiian commoner in a rapidly changing society.

BACKGROUND: PARAMETERS OF CHANGE

The 19th century was a time of profound change for the Hawaiian people. Within a very short time after Captain James Cook's discovery of the islands for the western world in 1778, every facet of Hawaiian culture was subjected to powerful forces of transformation. No matter how remote, no individual or part of the island chain was immune from outside pressures and the internal challenges of adaptation to western ways.

Hawaiian political and social life entered a new era in the decade after Cook. Following age-old patterns, only now taking advantage of his privileged access to European guns and advisors, a warrior chief named Kamehameha rose to preeminence on the island of Hawai'i and by 1795 had conquered the entire chain except for westernmost Kaua'i and dependent Ni'ihau, which capitulated in 1810. Thus unifying a loose aggregate of quasi-autonomous and fractious chiefdoms, Kamehameha the Great laid the foundations for the constitutional monarchy that emerged in the 1840s. Based on western precepts, the independent Kingdom of Hawai'i survived for half a century under the rule of his descendants until the nation he had established was overthrown and replaced by the Republic of Hawai'i in 1894. Annexation to the United States followed in 1898.

Paralleling these political changes, customary land tenure based on military conquest, political fealty, and economic tribute gave way during the mid-19th century to western-inspired land reforms and a monetary economy. Known as the Great *Māhele* (division) of 1848, the land reforms failed in the end to achieve their anticipated objective of providing fee simple lands to the average Hawaiian *maka'āinana,* or tenant-commoner; instead, large tracts of land passed

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from the hands of the chiefs to foreigners, especially as Hawaiians dwindled to a fraction of their precontact number. Ravaged by introduced diseases, the survivors sometimes resettled in villages away from their homesteads. Others were attracted to developing port towns where new opportunities for employment, including maritime adventure outside the kingdom, awaited. These and other factors helped hasten the process of land alienation and change.

The traditional religion and its underlying code of ritual and social behavior, or *kapu*, were repudiated soon after the death of Kamehameha in 1819, as a result of internal events. Congregationalist missionaries arrived from New England in 1820, followed by competing Catholics (1839), Mormons (1850), and other sects. As one consequence of American missionary activities the Hawaiian language was codified into written form, and a society formerly dependent on oral tradition for transmission of cultural values adopted mass education patterned on New England principles of classroom schooling. English began to replace Hawaiian as the language of instruction toward the end of the century, and the native tongue itself entered a long decline toward extinction.

Material culture and the arts underwent equally profound transformations during the century following Cook. The introduction of trade goods, western tools and technology, and new ideas and attitudes, stimulated some of the arts, such as wood carving and the manufacture of *kapa* (barkcloth). However, they flourished only to wither and die after a brief flowering, since they became irrelevant to the metamorphosed society. Other art forms, such as *hula* and featherworking, persisted, albeit in greatly modified form. Suppressed for a time by puritanical elements of the new order, *hula* reappeared publicly in the 1880s— one element of a revivalistic movement that, in re-energized form, is still very much in evidence today. Featherwork, too, was transformed but persists in the 20th century as a viable, contemporary folk art.

MAKALOA SEDGE MATS

This paper focuses on another material art unique to the Hawaiian Islands—the *makaloa* mat—and on a particular mat of historical significance. In the past, Hawaiians plaited a great variety of mats for sleep, clothing, the household, and other uses, such as canoe sails. Mats were made from a sedge called *makaloa*; *lau hala* (pandanus leaf); a bullrush (*Scirpus* sp.), called variously *'aka'akai* (O'ahu), *nānaku*, *naku*, or *kalahua* (Hawai'i), or *neki* (Kaua'i); and a few other materials (Buck 1957:113; Kamakau 1976:105; Malo 1951:49).

Cook saw such mats on reaching Kaua'i in February 1778 and pronounced them "both strong and fine and some are neatly coloured" (Beaglehole 1967:I:283). His companion, Captain James King, observed later from Kealakekua Bay: "Their Matts are superiour to the other Islands [to the south], both in fineness, & from the Variety of patterns in them, by working in Streaks of different Colours" (Beaglehole 1967:I:626). And surgeon David Samwell agreed: "They have a great Variety of Matts, some all white but most of them variegated with brown slips running the whole length of them and giving them a very beautiful appearance, these are worn by the Chiefs some times, while the more coarse and thick ones are laid on the floors of their Houses, and made into Sails for their canoes" (Beaglehole 1967:II:1187). Cook's men collected a number of mats, and at least three woven of *makaloa* sedge have survived in European museums (e.g., Barratt 1987:174,176,204; Henking 1957:381–82; Kaeppler 1978a:87, 1978b:12–13,59–60,140–41). The mat discussed here is a poignant mirror of the reactions of the Hawaiian people to the great metamorphosis that occurred during the century following Cook's arrival.

Makaloa mats, called *moena makaloa* or *moena Ni'ihau*, are so named because they were made from the *makaloa* sedge (*Cyperus laevigatus*), and primarily on Ni'ihau. This perennial sedge, formerly widespread in lowlands and marshy beaches throughout the islands, flourished especially along the fringes of Ni'ihau's dozen or so intermittent playa lakes, where it apparently was "semicultivated by the old Hawaiians in both fresh and brackish water bogs" (Degener

1946–57). The three largest lakes, concentrated on the low southern plain, are named Hālāli'i, Halulu, and Alieiki. Elsewhere, stands of *makaloa* are known from Kanahā Pond near Kahului on Maui, from Moloka'i, and from several places on Hawai'i and O'ahu as well as Kaua'i.

Ni'ihau is located 17.5 mi sw and in the lee of Kaua'i. Only 18 mi long by 6 wide, or about 72 sq mi, the island is 1,281 ft above sea level at Pānī'au Hill. Annual rainfall, measured at Ni'ihau Ranch headquarters at Ki'eki'e, ranges between 18 and 26 in. and is irregular and unpredictable, so the island has no permanent streams (Stearns 1947:3). Nevertheless, Ni'ihau was famous in the late 18th and early 19th centuries for its yams and produce, and "celebrated for the beautiful mats manufactured by its women" (Wilkes 1844:I:69). Because of its susceptibility to drought, the paper mulberry plant cultivated for barkcloth throughout Hawai'i and most of Polynesia did not flourish on this normally dry and windswept island; consequently, as anthropologist Peter H. Buck speculated, the people of Ni'ihau specialized in plaiting the *makaloa* sedge as a substitute source of fabric (*Honolulu Advertiser* 1944; *Honolulu Star-Bulletin* 1944).

Soft, flexible, and finely plaited, *makaloa* mats were prized far and wide as sleeping mats; Buck (1957:132) considered them to be "the finest sleeping mats in Polynesia." They were piled upon the coarser rush and pandanus mats (sometimes mixed with sweet-scented ferns and grasses) to make the traditional Hawaiian bed, or *hikie'e*—and later appeared as spreads on western-style bedsteads. (Actual bed coverings were usually of barkcloth, in historic times the distinctive *kapa moe* or "sleeping tapas" made from five or more sheets stitched together along one edge.) Ni'ihau mats were prized by the *ali'i*, or chiefly classes, and circulated throughout the archipelago as coveted articles of status and luxury. They figured among the produce collected as taxes at specified times of the year, and as *ho'okupu*, ceremonial tribute presented to chiefs and other dignitaries.

Most *makaloa* mats incorporate bands of variable twills for ornamentation into the body of the plain checkerwork plaiting. The finest were also decorated with red strips overlaid in intricate geometric patterns, parallel and zig-zag lines, and other motifs (e.g., Brigham 1906:78–83, figs. 77–83; Buck 1957:133–34, figs. 89–90). Such colored designs are called *pāwehe*, a generic term applied also to the decorative motifs stained onto gourds—another material arts specialty thought to be restricted to Ni'ihau and neighboring parts of Kaua'i. Hawaiians distinguished *makaloa* mats featuring overlaid *pāwehe* designs from those with decorative twills only, which they called *pākea*, or *moena makaloa pākea*. Having visited Ni'ihau in 1865, William T. Brigham (1892:65–66, 1903:15, 1915:13), later Bishop Museum curator, claimed that "those with colored patterns, moena pawehe, were seldom, if ever, made elsewhere." According to a tradition recorded in the early 20th century, *pāwehe* mats "were the finely patterned mats of Niihau, the kind that were designed by the supernatural woman Pahuihonu. It was she who taught them how to plait this kind of mat that is renowned to this day, a mat that is soothing to the skin. It can only be bought with much money" (Papiohuli 1913). The expression, "*Moena pāwehe o Ni'ihau* / Patterned mat of Ni'ihau," is a poetic reference to that island and its beautifully figured mats, "famed throughout the islands" (Pukui 1983:236).

AN INSCRIBED MAT

An obscure news item, discovered in the Hawaiian newspaper *Ka Nupepa Kuokoa* for 2 May 1874, has made it possible to document the origins of a unique *makaloa* mat preserved in Bishop Museum since 1891, but forgotten until recently (BPBM 2570; Fig. 1).

> A Patterned Mat
>
> Last Monday, Mr. G. S. Gay of Niihau gave King Kalakaua a beautifully designed mat plaited by Kalai, Niihau's most skillful woman in that particular

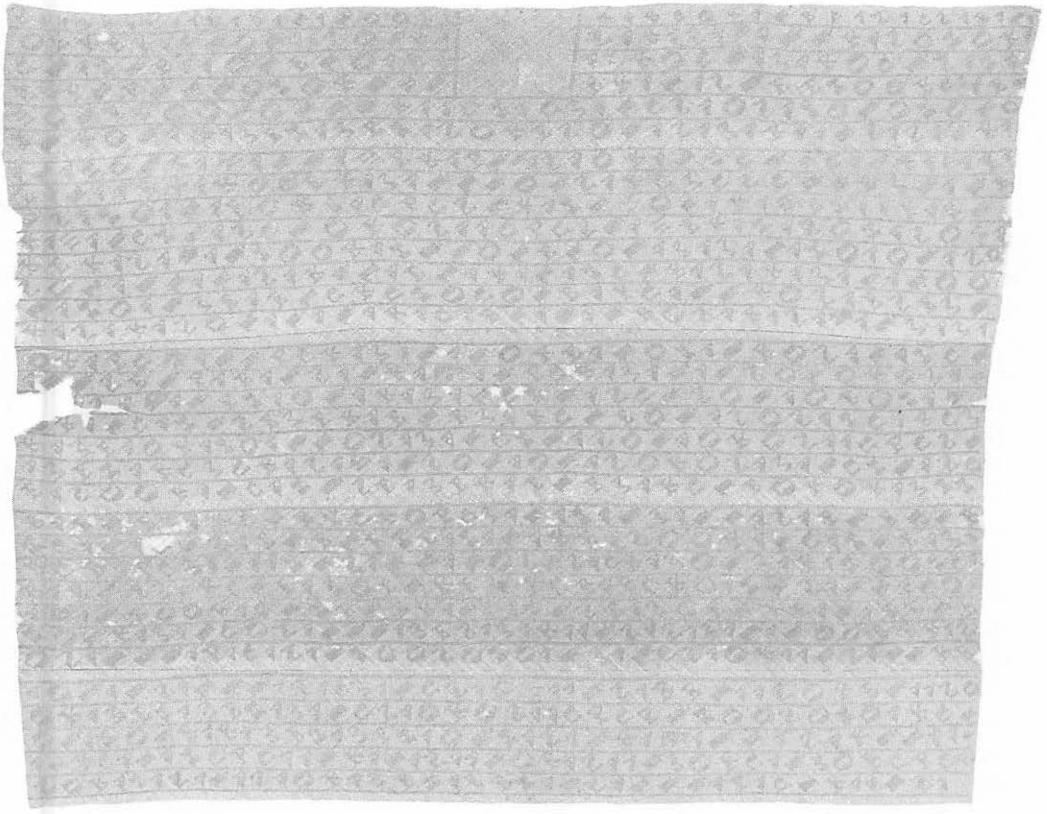

Fig. 1. Hawaiian *makaloa* sedge mat with petition to lift the tax on animals, presented to King Kalākaua in 1874. Text, beginning in lower left corner, has been photographed under ultraviolet light to reveal badly faded letters. (Composite photo by Christine Takata.)

> art. The mat was carefully plaited as it was intended for the late King but he is gone and so the gift is given to the present one. It is made with great skill for words are plaited into the meshes. It took eleven months to make. On the tenth month, the worker's husband died and she finished the article they had both labored on. It was sold to Mr. G. S. Gay and that was how the latter obtained it. These were the words plaited into it. . . . (Kuokoa 1874a)

The contemporary English-language *Hawaiian Gazette* (1874a) summarized the inscription "wrought in red letters" as "a petition, praying that the taxes may be removed on all animals, and for other changes in the laws." Worked in bold, block capitals using the traditional *pāwehe* technique, the lengthy appeal covering the entire front of the mat is, in itself, testimony to the perseverance of its Hawaiian makers.

Except for the inscription, the *makaloa* mat is indistinguishable from others in size, fineness, pliability, materials, manufacture, and technique (but not iconography) of decoration. It is plaited in diagonal check throughout from the flattened tubular stems of the *makaloa* sedge, whose widths of 2–3 mm yield a typical weave of 11 elements to the inch. The mat is rectangular but slightly irregular (probably stretched from hanging): 234 cm across the top, 213 cm at the bottom, 186 cm at the left edge, and 183 cm on the right. It is made in 5 horizontal panels, 31–44 cm wide, neatly joined where the plaiting is doubled in 2–3 cm seams and excess material trimmed away. Incidentally, adding a complete new set of wefts at one time like this, a general Polynesian technique, proves contrary to Buck's (1957:116) assertion that "in the Hawaiian technique, the new wefts are added singly by overlaying and doubling plaiting as an old weft needs extending; and no regular, continuous join can be observed."

In surviving mats, the glossy outer skin of the *makaloa* ranges through many shades of gold to a rich brown. On this mat the individual panels vary, some appearing lighter or darker overall than others, due in part to natural color variations of the material. The panels also fluoresce differentially under ultraviolet light, indicating that the waxy cuticles protecting the sedge stems may have degraded at different rates through exposure to light over time (Kronkright 1988). (The mat was apparently on continuous exhibition for at least a quarter of a century, first in the old Hawaiian National Museum from 1875 to 1891, then at Bishop Museum for a number of years afterwards.) Coloration within each panel is consistent, suggesting that the batches of raw material used in plaiting individual panels were somehow different: they may have been harvested at different seasons, have come from different sources, or have been subjected to different techniques of preparation or storage. Very little is known about the technology of *makaloa* mat-making and nothing has been recorded to account for these subtleties of appearance.

Now a faded reddish-brown, the letters of the inscription are formed from strips overlaid onto the front of the mat by a technique called *false embroidery* or *imbrication*. In this traditional *pāwehe* method, strips are inserted onto the foundation wefts and warps and folded over and reintroduced into the plait or cut off to form patterns of a solid color. Unable to determine whether *pāwehe* overlays were applied during the plaiting, Buck (1957:133–34) concluded in his analysis of mats in *Arts and Crafts of Hawaii* that "it is quite probable that the smaller motifs were added after the completion of the mat by pushing the colored wefts under crossing wefts." On this mat the letters were most likely added during the plaiting, and undoubtedly a prepared text was followed.

It is usually stated that the material used for *pāwehe* overlays comes from the protective sheaths that grow at the base of the *makaloa* sedge stems, which are naturally red when fresh but turn brown with age or long exposure to light (e.g., Brigham 1892:66, 1903:15, 1906:78, 1915:13; Neal 1965:86). Buck (1957:134) questioned this in his analysis of *makaloa* mats, since he had been informed by botanist Harold St. John "that the sheath of the *makaloa* sedge is not red and that the colored sheath must have been obtained from some other species of sedge." Studying this problem, St. John (1959:162) collected specimens on Ni'ihau in 1947 and 1949 at Lo'e Lake and identifed a related Cyperaceae, *Eleocharis calva* var. *australis*, as the plant bearing "the deep red basal sheaths . . . gathered by the native Hawaiians on Niihau and plaited to form ornamental geometrical patterns." St. John concluded that the plant, collected botanically on O'ahu and Ni'ihau as early as 1825, is an endemic variety of *E. calva* that occurs primarily in central and eastern North America. Though uncommon locally, it is "a lowland plant of fresh marshy habitats" up to 120 cm tall and known on Ni'ihau from "the edge of a small lake on the coastal plain bordering the mountainous upland" (St. John 1959:162). On O'ahu, it frequented cultivated lands, especially taro patches, where it was apparently a weed. Now rare on O'ahu, this *Eleocharis* "is well preserved on Niihau, and visible there for a few months after heavy southerly winter rains" (St. John 1959:162). It has also been collected on Kaho'olawe at Luakeālia Lalo.

On Ni'ihau the plant is called *tohetohe* or *kohekohe* (St. John 1959:159, 1982:2), a word applied throughout the islands to all species of *Eleocharis* whether native or introduced (Neal 1965:87; Pukui & Elbert 1971:146). An unpublished compilation of late-19th-century Hawaiian mat terms corroborates St. John's findings. It defines *moena pāwehe* as "a fine mat covered with designs, made with brown kohekohe grass; only made on Niihau," and clearly distinguishes *moena pākea*: "made of Makaloa grass like a rush, without any design, on Niihau and at Mokuleia, Oahu" (HEN nd:1:1252). In further support of St. John, the inscribed mat is mentioned in an unpublished historical catalogue of the Hawaiian National Museum prepared by curatrix Emma Metcalf Beckley (1882:13): "Moena Makaloa. Mat of fine rushes. The letters of the alphabet are outlined in weaving by using the reddish brown stem of another species of rush." Her following entry, a "Moena pakea," explains: "Rush mat made entirely of the same rushes as those of the groundwork of the former, but woven in different patterns. They are made of the Makaloa rush."

The inscribed mat, although preserved for over a century in public institutions, has never been discussed in the ethnographic literature. Buck (1957) was unaware of its historical significance or the fact that it had been presented to King Kalākaua. He considered it acculturated and therefore of little interest and thus ignored it in his analysis of mats in *Arts and Crafts of Hawaii.* Brigham (1892:67) merely listed it in his *Preliminary Catalogue of the Bernice Pauahi Bishop Museum* and in *Mat and Basket Weaving of the Ancient Hawaiians* (1906): "2570. 7 ft. x 6 ft. Lettered all over, but the rude letters almost faded out" (Brigham 1906:83). (The letters were deciphered and transcribed several years ago when the present author examined the mat while researching the history and collections of the Hawaiian National Museum.) Bishop Museum catalog records reveal only that the mat was acquired from the defunct National Museum in January 1891, in one of the first collections to be moved into the new Bishop Museum building (Rose 1980:51). Further research identified the mat in a manuscript "Inventory of Articles in the Government Museum" as item 209, "Large mat with interwoven inscription" (Inventory 1891).

Familiarly called the Government Museum, the Hawaiian National Museum was a short-lived precursor of Bishop Museum established by the legislature of 1874 in an attempt to preserve the kingdom's vanishing material heritage. It opened in mid-1875 under the stewardship of the Bureau of Public Instruction in Ali'iōlani Hale, a new government office building in central Honolulu. The mat was one of the inaugural exhibits in the fledgling museum and came from a small "curiosity" collection, including several portraits of Hawaiian and foreign royalty, moved across the street from 'Iolani Palace in preparation for the opening. The mat appears in an early inventory prepared by the first curator, Harvey Rexford Hitchcock (1876): "Mat, Niihau, with petition to the King worked in colors—Palace." Its history is not given, but the mat is listed on the receipt dated 23 September 1874: "1 Mat, called the Makaloa rec^{d} from Niihau" (Receipt 1874).

Reporting the presentation of the mat to King Kalākaua only five months before, the newspaper *Ko Hawaii Ponoi* (1874) noted that the weaver, Kala'i, came from Waimea on the island of Kaua'i. (In the past residents of Ni'ihau moved back and forth to the adjacent coasts of Kaua'i, particularly during times of drought.) A few days later *Kuokoa* (1874c) reported that the weaver—then nearly 80 years old—was living in 'A'ala, a district of Honolulu. The *Hawaiian Gazette* (1874b) added: "She is a very old woman, one of the few remaining links that connect the present generation with the time of Kamehameha I. She was twelve or fifteen years of age when she saw the old warrior King, and is now supposed to be nearly or quite eighty years old now." King Kalākaua apparently liked the work of "Niihau's most skillful woman in that particular art" (*Kuokoa* 1874a), for the *Hawaiian Gazette* remarked: "His Majesty has requested her to work two mats for the Philadelphia Centennial Exposition—one to show the American coat-of-arms and the other the British coat-of-arms, designs of which will be sent to her to copy. Should she execute the order, these will be very attractive specimens of Hawaiian handiwork" (*Hawaiian Gazette* 1874a; cf. *Kuokoa* 1874b). Kala'i declined, or was unable, to undertake the commission to help decorate the Hawaiian pavilion for the U. S. Centennial. Unfortunately, little more is known of her, except that her full name was apparently Kala'i-o-kamalino, a name that occurs regularly in some Ni'ihau family genealogies (Tava 1988).

Notwithstanding this sparse, but welcome, background, the assembled newspaper commentaries provide a few invaluable clues to the elusive record of *makaloa* mat-making. That a mat of this size and complexity could be made in 11 months is seemingly contrary to Brigham's (1892:66; cf. 1903:15, 1906:77, 1915:13) assertion in Bishop Museum's *Preliminary Catalogue*: "The fine mats can only be plaited while the sedge is young, hence the time of working is limited to a few months each year, and it is certain that the largest mats of this kind in this collection must have been in the makers hands seven or eight years." While possibly true of the very largest and most finely woven mats—such as a *kīhei* (cloak) in Bishop Museum said to have been worn by Kamehameha and which is about 20 by 10 ft and 25 wefts to the inch (Buck 1957:132)—this apparently was not a general rule applicable to all *makaloa* mats. The newspaper accounts do not elaborate on whether the 11 months included time to gather and prepare the *makaloa* sedge, or where and how the raw materials were acquired and worked—Ni'ihau, Kaua'i, or perhaps even O'ahu. That 2 persons—a husband and wife—worked on the mat together indicates that mat-making was not necessarily women's work exclusively. Lacking, unfortunately, are data on the actual division of labor, and whether the husband participated in the weaving itself.

George S. Gay, who presented the mat to King Kalākaua, belonged to the Sinclair-Gay-Robinson family that had purchased Ni'ihau from King Kamehameha V in 1864. A Ni'ihau resident, and an occasional visitor to the family home at Makaweli in the Waimea district of Kaua'i, Gay may have been acquainted with Kala'i or may have known of her reputation as a skilled weaver. Then about 21 years old, he was passing through Honolulu with his younger brother Charles to attend school in Boston, for which they embarked two weeks later on 11 May 1874. The elder Gay returned to Ni'ihau the following year and became resident manager of Ni'ihau Ranch, moving to California about 1891 (Gay 1981:14; *The Friend* 1874a, 1874b; *Pacific Commercial Advertiser* 1874b).

Although intended for another occasion, the mat with its petition nonetheless proved to be a timely gift, for 3 days after receiving it King Kalākaua convened the legislature of 1874. He had been elected to the throne only 10 weeks before, on 12 February 1874, following the death of King Lunalilo a month earlier. Kalākaua had just returned to Honolulu after a series of "royal progresses" to greet his subjects and learn their views on issues facing the kingdom. Presumably it was he who placed the mat in 'Iolani Palace, whence it was moved 5 months later to the Hawaiian National Museum.

THE INSCRIPTION

The petition is rendered entirely in archaic, Roman capital letters aligned diagonally with the weave and oriented toward the lower left corner of the mat (Fig. 2). Lacking spaces between words as well as punctuation, the inscription is difficult to read under ordinary light, especially where it is badly faded or worn. Except for 2 styles of *M* and other minor idiosyncrasies, the letter shapes are surprisingly consistent. All are angular block capitals with serifs, except for the *I*, which normally has a square dot to help distinguish it from the *L* and its weakly developed leg.

The letters are identical to those in the 1st alphabet and speller introduced by the American mission press in Honolulu in 1822 (*Missionary Album* 1969:101), which was used in island schools for many years. Beginning in 1829 the mission made concerted efforts to establish schools island-wide, and Hawaiians soon attained a remarkable degree of basic literacy as a result. By 1833 10 mission schools existed on Ni'ihau (Tabrah 1987:78). Although Lieutenant

Fig. 2. Detail of lettering on inscribed mat. Text beginning "E Kalani . . . " occurs at lower right corner of the rectangle at top center of mat. Note seam at center where 2 longitudinal panels are joined. Individual strands of *makaloa* sedge can be distinguished in this ultraviolet light photograph. (Photo by Christine Takata).

Charles Wilkes (1844:I:69) of the U. S. Exploring Expedition did not visit, he reported a decade later: "On this island there are two hundred children, about one-third of whom read: these are divided into twelve schools, under native teachers." Before the practice of tattooing was abandoned, similar letters were sometimes incorporated into tattoos, and words and names cut in the same block letters can still be observed on 19th-century petroglyphs scattered throughout the islands (e.g., Cox and Stasack 1970:53–58,64,80–93). Incorporating the written language into a *makaloa* mat is one more example of the creativity of the Hawaiian artisan, and a remarkable adaptation of a traditional decorative technique to an innovative purpose.

The letters on the mat are executed with a uniformity and skill that attest to the expert control of the weaver. They vary little in size from the normal 4–5 cm high by 3–3.5 cm wide, except for those of the very last line, which are only 3 cm high so as not to overlap onto the 2 cm border of double weave finishing the top edge of the mat. The letters are spaced about 1.5–2.5 cm apart; no attempt was made to align them in vertical columns, or to end lines at natural breaks, such as syllables and ends of words. Each line of letters is demarcated by strips 0.5–1.0 cm wide and spaced 4.5–5 cm apart, which are applied in the *pāwehe* technique using colored overlays that extend across the mat from edge to edge, like a sheet of ruled paper. Because of the difficulty in overlaying double sets of wefts and warps, there are no letters or lines on the seams joining the five individual panels, where the strips are about 7 cm apart.

The mat is divided into 29 full lines of text plus 4 interrupted lines at the top. The interrupted lines are separated into 2 equal "columns" by an open rectangle at the top center of the mat, 26 cm wide by 20 cm high, and outlined by the same overlaid strips that separate the lines of letters. The purpose of this open field is unclear but perhaps it had significance for the maker. Since it occurs near the finish of the mat it may mark, symbolically, the death of the husband after 10 months of joint labor.

Commencing at the lower left corner with the plaiting of the mat, the text reads from left to right and upward. From the end of the 3rd half-line at the top of the mat on the left, the text jumps across the rectangular gap and down 3 lines to the bottom of the right column; it then moves upward 2 more half-lines, returning to the extreme left margin of the mat. The last line, extending in 2 segments across the top of the mat, is narrower than the rest and the letters smaller and cramped. It seems the weaver ran out of space and did not wish to undo the double-weave border and commence another course of plaiting to accommodate the remaining text. Ironically, this compromise left no room for the last letter of her name.

Hawaiian mats after western contact sometimes carried simple messages but rarely, if ever, messages as extensive as this one. Brigham observed in 1906:

> After the islanders had learned to read, under the instruction of the American missionaries, the use of letters of the alphabet became common both in tatuing and mat decorating, and mats somewhat resembling the samplers of our grandmothers' days were woven. It soon became common to write affectionate greeting on mats intended as presents to friends, and I have seen a number of these. On sleeping mats I have seen embroidered the inscription "*Kuu ipo, kuu lei, kuu milimili e*" (My darling, my crown, my thing to be gazed upon). It is often difficult to decipher these mat inscriptions, as the technic prevents the use of curves, and the individual letters were of strange forms, and, like the ancient Greek inscriptions, there was not that separation between the words that a modern reader demands. (Brigham 1906:79–80)

Besides the petition, there is record of 1 other 19th-century mat with a lengthy inscription in Hawaiian. Because of its size and proportions, it may have been intended as an altar- or wall-hanging for a church.

> Some years ago a native brought to us a Niihau mat three fathoms in length and less than one in width, in which was wrought in red letters the Lord's prayer in Hawaiian. It was beautifully done, and must have cost him many months of labor. We engaged to take it at his price, but before he delivered it, he found a customer who offered him just double what he had valued it at. Such specimens are very rare, and of course valuable. If made by days' work, it would be valued at hundreds of dollars. (*Hawaiian Gazette* 1874a)

At the time of the mat's presentation to King Kalākaua, 2 Hawaiian newspapers printed the text of the petition in full. The versions in *Ko Hawaii Ponoi* (1874) and *Kuokoa* (1874a) vary in minutiae, but the latter is slightly more faithful (though not precisely identical) to the mat. For the sake of readability, *Kuokoa*'s version—including division of the block capitals into upper and lower case, separation of words, and punctuation—is generally followed here. Material in square brackets (mostly alternative syntax or missing letters and other minor lapses on the part of the weaver) does not appear on the mat but occurs in the newspaper versions; material in parentheses (mostly unintentional repetitions or alternative phraseology) occurs on the mat but not in the newspapers. The translation (HEN nd:1:2857) that follows is based on *Kuokoa*'s rendering of the text. A poetic expression of protest, the petition is composed in a literary style that employs various grammatical and syntactical constructions not used in contemporary conversational Hawaiian (Ashford-Hirano 1988).

No ka hanai ana o Kamehameha i nalii a pau i ka aina, a i ku ai ahupuaa, [a]i kalana, ai okana, ai moku, ai mokupun[i], oia hoi ka Kamehameha oihana i ka wa i lanakila ai o Kamehameha maluna o kona Aupuni. Hoonoho aku la oia i nalii a pau maluna o ka aina; kela ano keia ano o nalii a pau ana i hoonoho ai maluna o ka aina. Like hoi ka malu o nalii a me na makaainana malalo o ke kanawai hookahi; "Hele ka Luahine a moe i ke ala;" (Hele ka elemakule a moe i ke ala) ku ka puko a hina ilalo, ku ka (pu) maia a hina ilalo; —ninau ka Moi ma ka hoohuahualau i na elele: "Heaha la ke ano o ka luahi[n]e a me ka elemakule?—[He] puko, [he] pu maia?" Hai mai la na Elele i ke ano o ka luahine a me ka elemakule, o ko Kamehameha Kumukanawai no ia—oia no kona maluhia. No ka mea [he] (o ka) hoailona maluhia no ia o kona aupuni. O ka luahine [a] me ka elemakule oia no na hua kumukanawai. [Aole] e hao ia. Ka maluhia nui no ia o ko Hawaii nei Pae Aina i ka wa i puka mai ai. Noloko mai (o ka puwai i puka mai ai) o ke aloha i kona lahuikanaka [i puka mai ai]. Nolaila kau ae la ia i kona kanawai mamalahoa i mea e luku hou ole aku ai i kona enemi.

Nolaila lanakila [a]e la ka lahuikanaka malalo o ke kanawai hookahi i olelo ia, [he] mamalahoa, oia no ka maluhuia nui o kona aupuni, a me ka hanohano, hai na hoala no ke aupuni kahiko, (ia) [no] Kameha[meha] Ekahi. E ala ae kakou (e ka mailio) i na kumu nui i emi ai ka lahui Hawaii, a me ka pii ana o ka l[a]hui mua i ka wa kahiko ia Kamehameha no ke noi ana [a na] makaainana i ka Moi e hoololi i ka auhau maluna o na holoholona, pipi, lio, hoki, miula, hipa. Aole loa e koe kekahi o ia ano (i ka)—

E Kalani e:—E hookuu ae ia (m[a]kou ia) makou i na hana kanawai, i ka noho kauwa kuapaa ana malalo o na haku o ka lewa.

Nau na Kala[i]

Kamehameha provided for all the chiefs of the land thus establishing the *ahupua'a*, *kalana*, *okana* land sections and islands. That was what Kamehameha did when he stood at the head of his government.[3] He placed the chiefs over the lands; all kinds of chiefs settled on the land. Chiefs and commoners shared the peace under the one law, "Let the aged sleep on the highway unharmed; let the sugar canes grow till they fall over; let the bananas grow till they fall over." The king questioned his messengers to find out what they thought, "What are the old women and the old men like? Are they like the sugar cane and banana stalks?" They told him what they were like. That was Kamehameha's constitution—his peace. Peace was the symbol of his kingdom; the old women and old men, his constitution. There was no ruthless seizing. It brought peace to the Hawaiian Islands when it was issued. It was issued because of his love of the people. Therefore he laid down his Mamalahoa law that there be no more destruction of his foes.

Therefore the people became free under the one law called the Mamalahoa, the giver of the greatest peace in his kingdom, an honor that has come to us from an old kingdom, that of Kamehameha I. Let us rise to study the great cause for the decrease of the Hawaiian people, a large population in the olden

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[3] An alternative translation for the first 2 sentences, provided by an anonymous reviewer, reads: "In order for Kamehameha to feed all the chiefs from [off of] the land, he established chiefs of the *ahupua'a*, *kalana*, *'okana*, *moku*, and *mokupuni*. That was Kamehameha's business in the time when Kamehameha was victorious over his kingdom."

> days under Kamehameha, and to ask the king to change the taxes on animals, cattle, horses, asses, mules, and sheep and let none of them remain.
>
> O Heavenly One—release [us] from the burden of the law that keeps us slaves under masters from the sky.
>
> By me, Kala'i.

THE HAWAIIAN POLITY

The prevailing socioeconomic and political conditions that gave rise to this petition have been broadly outlined in the opening section of this paper. Allusions to cultural values and process, and specific complaints about the little-known subject of taxation of animals, require further elaboration, beginning with the petitioners' sentiments linking Kamehameha to the "old kingdom."

Kamehameha generally is credited with bringing peace and prosperity to the islands on gaining control at the beginning of the 19th century. As was custom, he used the system then in existence to redistribute conquered lands. After setting aside those desired for personal use, he awarded vast tracts to close kinsmen of his favored wife Ka'ahumanu. These relatives were also entrusted with critical political and economic offices (Sahlins 1981:57–58). Kamehameha made these allotments on a revocable basis, as in the past, but to a certain extent he allowed the heirs of deceased chiefs to remain on the lands he had previously granted them (Chinen 1958:6). Kamehameha's son Liholiho, who succeeded in 1819 as Kamehameha II, "made only a few changes in the distribution of lands, leaving the great majority of the lands with the chiefs who had been rewarded by his father" (Chinen 1958:6). This may have helped foster the sense of peace and stability under Kamehameha's "old kingdom," expressed so explicitly by the petitioners.

The potential for "ruthless seizing" that was an inevitable adjunct of the old system was not formally abolished until two decades after the death of Kamehameha, when the Hawaiian Declaration of Rights was enacted by the assembled council of chiefs in 1839. Often called the Magna Carta of Hawai'i, this founding document of civil rights proclaimed: "Protection is hereby secured to the persons of all the people, together with their lands, their building lots and all their property, and nothing whatever shall be taken from any individual, except by express provision of the laws" (cited in Kuykendall 1938:160). The Declaration of Rights also stipulated "that no chief may be able to oppress any subject, but that chiefs and people may enjoy the same protection under one and the same law." The Declaration of Rights was made a preamble to the nation's first formal constitution, promulgated by King Kamehameha III on 8 October 1840. It created a bicameral legislature and transformed the government from an absolute to a constitutional monarchy.

Kamehameha's famous Law of the Splintered Paddle, the *Māmalahoe* (or *Māmalahoa*) *Kānāwai*, stems from an incident that occurred early in his campaigns for conquest of the island of Hawai'i (Kuykendall 1938:33-34). According to one popular version, Kamehameha leaped from his canoe the moment it touched shore during a visit or plundering raid to Puna district about 1783 or 1784. Pursuing 2 fishermen, he slipped and caught his foot in a crevice in the lava; 1 of the men turned and struck the helpless Kamehameha on the head with his paddle so forcibly that the paddle splintered. Years later, the confrontation was commemorated in a celebrated law, designed to guarantee the safety of the highways to the innocent and the helpless. It is sometimes rendered: "Let the aged man go and sleep on the road-side, let the aged woman go and sleep on the road-side, and let no one injure or molest them" (Hopkins 1906:85). It is apparent that Kamehameha's law made a lasting impression on the *makaloa* petitioners.

The great population decrease cited by the petitioners, alarming already to the 1st generation of Hawaiians after Cook, was vividly documented by the earliest censuses and remained a constant source of concern throughout the 19th century. In his first speech as king, which opened the legislature in 1855, Kamehameha IV remarked, "The decrease of our population . . . is a subject, in comparison with which all others sink into insignificance" (Kuykendall 1953:69). King Kalākaua expressed precisely the same sentiment 19 years later in his own inaugural speech to the legislature of 1874: "The subject, however, that awakens my greatest solicitude is to increase my people, and to this point I desire to direct your earnest attention" (*Pacific Commercial Advertiser* 1874a). He recommended modification of the divorce law, continued attention to hygiene through the Board of Health, and special exemptions to those who rear large families. "*Ho'oulu Lāhui* Increase the Race" became one of Kalākaua's prime political slogans, as he continued throughout his reign to call for renewal of the Hawaiian population.

Alarm over the rate of population decrease was clearly justified. At Cook's arrival in 1778 Hawaiians numbered perhaps 250,000 to 400,000, with roughly 300,000 being the figure generally—though not unanimously (Stannard 1989)— accepted today. The 1st American missionary estimate in 1823 put the number at 142,050, while actual censuses of 1831–32 and 1835–36 recorded totals of 130,313 and 108,579 respectivley (Schmitt 1973:8). The 1st complete government census occurred in 1850, after which official counts taken at 6-year intervals show the following totals for the 19th century (after Schmitt 1977:25):

Year	Hawaiian/ part-Hawaiian	Total population
1850	—	84,165
1853	71,019	73,137
1860	66,984	69,800
1866	58,765	62,959
1872	51,531	56,897
1878	47,508	57,985
1884	44,232	80,578
1890	40,622	89,990
1896	39,504	109,020

Between 1850 and 1853 (when foreigners were enumerated separately), it is believed that Hawaiians and part-Hawaiians decreased by about 11,000 (Kuykendall 1953:37). In the 19-year interval between 1853 and 1872, when the *makaloa* petition was conceived, total loss in this category was 19,488 or roughly 1,000 per year—approximately 27% of the already reduced Hawaiian people in a single generaton. (The combined Hawaiian and foreign population reached its lowest point in about 1875 or 1876, but Hawaiians and part-Hawaiians continued to decrease, with sporadic fluctuations, to a low of 38,547 in 1910 [Schmitt 1977:25].) Besides introduced epidemic diseases to which Hawaiians had no natural immunity, reasons advanced for this staggering decline include "sterility and miscarriages caused by venereal diseases, abortion, infanticide, poor housing, inadequate sanitation and medical care, landlessness, alcohol, tobacco, and emigration" (Schmitt 1973:17). To these should be added a low birth rate and high infant mortality, especially in the years before 1880 when the Board of Health produced its landmark *Sanitary Instructions for Hawaiians* (Gibson 1880). It is little wonder the petitioners entreated their king: "Let us rise to study the great cause for the decrease of the Hawaiian people, a large population in the olden days under Kamehameha."

THE TAX SYSTEM

The tax on domestic animals, the primary concern of the petition, was among several means "nearest and most convenient" (Castle 1891:63) devised during the mid-19th century to garner revenues from the *maka'āinana* to pay expenses of the emerging Hawaiian government. In his recent book, *Working in Hawaii: A Labor History*, Edward D. Beechert (1985:26) distinguishes 3 stages of tax collection in 19th-century Hawai'i: "the period of ceremonial collections; secular collections after the overthrow of the traditional religion in 1819; and the centralization of tax collection, which by the 1830s had become personal taxation." Direct taxes on animals were instituted in the 1840s, as an element in the larger question of taxation that faced the kingdom and its subjects.

Under the system that existed during the time of Kamehameha, before abrogation of the old religion in 1819, the primary tax on the *maka'āinana* consisted of conscript labor and a produce tax. By custom, all land was apportioned by the ruling chiefs through subordinate chiefs down to the *konohiki*, a local headman who acted as a kind of supervisor-administrator. In return for use of the land and its resources, the tenant-commoner contributed specified amounts of labor to cultivation for the various layers of chiefs and *konohiki*, and assisted with labor-intensive projects, such as building and maintenance of fishponds, irrigation systems, and *heiau* (ceremonial structures). In addition, annual contributions were levied during certain times of the year, usually October or November during the *makahiki* festival, but the mode and manner varied somewhat on each island (Beechert 1985:26; Valeri 1985). Payments were made in agricultural produce, handcrafted articles consumed by the chiefs, and raw materials, such as feathers of certain forest birds used in the manufacture of luxury articles like feather helmets, capes, and cloaks (*'ahu'ula*). Sandalwood was added to the list of commodities in the early 19th century once its value in foreign trade had become established.

Other specialized payments or ritualized "gifts" called *ho'okupu* were also required from time to time, such as when the ruling chief or "king" traveled in the vicinity. These presentations were often arbitrary as well as burdensome. William Richards, a former missionary and influential advisor to the developing monarchy, commented to Lieutenant Wilkes of the U. S. Exploring Expedition in 1841: "If a sufficient amount of presents was not brought, the people were in danger of having their fields plundered by the marauding parties of the king's attendants" (Sahlins and Barrère 1973:25). Reverend Titus Coan, who labored in the Hilo and Puna districts of Hawai'i, wrote in 1847:

> A few chiefish companies passing in quick succession through a poor and remote district, act like swarms of locusts, devouring all sustenance, and leaving famine and starvation behind them. All this is done to make a display and to impress the people with the dignity and importance of the traveler. There is no form of oppression among Hawaiian chiefs and officers which has, on the whole, more pained and disgusted me than this. It is marked with pride, vanity and folly, and a careless, reckless disregard of the interests and happiness of the common people. (Armstrong, Chamberlain & Castle 1848:68)

Richards believed that "under the former kings . . . the royal tax was laid in accordance with a pretty regular system. It was annual, and was assessed by agents of the king appointed for the purpose, and was nearly the same every year" (Sahlins and Barrère 1973:24). The tax on an *'ili*, next in size to the smallest land division and more or less equivalent to the average tenant farm, consisted of 1 hog, 1 dog, 1 fishnet, 1 fishline, 1 cluster of feathers, and 20 tapas—part of which were "nearly square for bed cloths, and a part narrow and long for female dresses" (Sahlins and Barrère 1973:24).

Visiting in 1822–23, English missionary William Ellis (1831:IV:416) wrote: "There is no standing rule for the amount of rents or taxes, but they are regulated entirely by the caprice or necessities of their rulers." Retroactively, the legislature in 1842 did point out that formerly the government tax on a "common size farm" was "1 Fathom Swine, 40 Kapas, 40 Paus [*pā'ū*, women's skirts], 1 Dog, 80 Fathoms of fish line, and a fish-net 800 meshes in length" (Constitution and Laws 1842:196).

While the old system was still relatively intact, missionary Samuel Ruggles witnessed a tax-paying session on Kaua'i, evidently at Waimea during his first visit in June 1820. The mats he observed there probably were made of *makaloa* sedge but may have included ones of pandanus or other fibers. A part of the tribute, including "about 30 mats" and "upwards of 100 tappers [*kapa*], pieces of native cloth 8–10 feet square," was presented to the missionaries (Damon 1931:248). It was usual, according to Robert M. Kamins (1952:156) in his analysis of the tax system of Hawai'i, that "along the way . . . large portions of the tribute intended for the king often were diverted into the households and treasuries of the landlords, chiefs, and governors, so reducing the revenues of the central government and inducing the king to increase the levy upon the commoners." Ruggles described the scene as follows:

> The week past has been a busy time with the natives. The King's rent has been brought in from all parts of the Island and from Onehow [Ni'ihau], a small island to the westward. It consisted of hogs, dogs, mats, tappers, feathers, pearl fishhooks, calabashes and paddles. This rent is to go to Owhyhee [Hawai'i] as a present to the young King [Kamehameha II]. It was interesting to see the natives come, sometimes more than a hundred at a time, with their loads on their backs, and lay down their offerings at the feet of their great and good chief as they call him. (Damon 1931:247)

Abrogation of the old religion and its supporting *kapu* in 1819 destroyed the system of checks and balances on chiefly abuses and at the same time obviated the basic reason for the customary taxes. "No longer rationalized as an essential part of the political system," Beechert (1985:26) argued, "the continuing collections were, in effect, secularized. The net effect was to convert the political-religious system into a source of material wealth for the chiefs. The traditional tribute became a system of personal and property taxation." As one consequence of these changes, "an intense competition for status developed among the Hawaiian aristocracy. It took the form of ostentatious consumption of foreign luxury goods" (Sahlins 1985:141).

In essence, a dual system of taxation arose to pay for this new style of "celestial brilliance" (Sahlins 1985:141). The *konohiki* became a kind of central government employee, basically a tax collector, while the lesser chiefs intensified their traditional prerogatives of taxation—although without exercising their concomitant reponsibilities for managing the subsistence economy (Beechert 1985:27). The emerging central government, in the decades after the death of Kamehameha, began to levy annual taxes on various profitable activities—house building and clothes washing, for example—as well as a heavy tax on produce carried to developing markets in Honolulu and elsewhere (Sahlins and Barrère 1973:25). Not to be outdone, the lesser chiefs pushed to new heights their powers to tax the *maka'āinana* on their own respective parcels of land. As Beechert (1985:27) expressed it, "a veritable orgy of confiscation by the petty chiefs began. . . . To support their lavish spending, the chiefs impressed their populations into service to supply the income required. The Hawaiian *ali'i* had moved from a political economy which supported their prestige and political ambitions to an economy of conspicuous consumption." Such is the scene Sahlins (1985:155) depicts of prominent chiefs "disporting themselves in Chinese silk dressing gowns and European waistcoats, in chambers decorated with fine teak furniture and gilded mirrors, or at dinners served on solid-silver table settings, while the commoners progressively sank into an immiseration from which they have not yet recovered."

With loss of authority and restraints in the vacuum following Kamehameha's death, taxes levied on the *maka'āinana* by the petty chiefs could be devastating indeed. Observed William

Richards before the sweeping changes of 1839–40: "The oppressiveness of the system consisted mainly in the great number of lords over the same vassals some one of whom may be presumed to have disregarded all rule and justice and therefore scarcely none of the lower orders escaped the severest rigors of unrestrained tyranny" (Sahlins and Barrère 1973:26). As a consequence, "the common laborers did not themselves receive probably on an average more than one third of the avails of their labors, while the different orders of chiefs received the remaining two thirds" (Sahlins and Barrère 1973:23).

To rectify this oppression of the *maka'āinana*, a codified system of taxation was gradually implemented in conjunction with establishment of the constitutional monarchy between 1839 and 1846. Somewhat earlier, the 1st written law representing a direct tax levied on the *maka'āinana* had been enacted, when foreign merchants backed by American naval forces demanded payment for debts accumulated by the chiefs. The amount was set at 15,000 piculs of sandalwood valued nominally at $150,000 (Kuykendall 1938:92,434). According to the law, dated 27 December 1826, every able-bodied man was required to deliver half a picul (1 picul = 133⅓ lb) on or before 1 September 1827, or in lieu of sandalwood 4 Spanish dollars, or any valuable commodity of equivalent value; each woman was required to provide 1 mat, 6 by 12 ft, or *kapa* of equal value, or 1 Spanish dollar (Kuykendall 1938:92,434–35). (To ease the burden, each man was also permitted to cut half a picul of sandalwood for his own use.) Considerable sandalwood was amassed, but accounts were not settled, and the process was repeated 2 or 3 years later, as the sandalwood trade itself was coming to an end because of overcutting (Kuykendall 1938:92). The debt was not fully paid until 1843, but an important principle of taxation had been established.

Meanwhile, the emerging nation's first formal code of laws was proclaimed by King Kamehameha III on 5 January 1835. Essentially a penal code based on the Ten Commandments, it was followed by the Declaration of Rights previously mentioned and by the Laws of 1839 (revised in 1840), which constituted a civil code. These instruments, and the Constitution of 1840, established tax officers and procedures to regularize the collection of taxes and included provisions directly related to 3 kinds of taxation: a poll tax of 1 Spanish dollar on each man and graduated amounts on women and children; a land tax, or rent; and a labor tax requiring each man to work 6 days per month for his landlord and king plus up to 12 days for "important public work" if required (Constitution and Laws 1842:27).

Reflecting the gradual implantation of a monetary economy, the new taxes initially were collected in a combination of specie and produce. The poll tax was accepted in money—or arrowroot, cotton, sugar, nets, and other commodities, such as candlenuts, turmeric, fish, and coffee, at different times, in the "back part of the islands where money is difficult to be obtained" (Constitution and Laws 1842:24,86). The land tax was payable in produce, usually 1 swine, size dependent upon the farm but generally equivalent to 5–10 dollars. The labor taxes, modified in 1846 and 1848, were partly abolished in 1850, except as a penalty, when a school tax of 2 dollars a year was levied on all taxable males instead (Kuykendall 1938:352–53). Greatly disliked, the labor taxes gradually fell into disuse and were eventually replaced by a road tax in 1859 (Kamins 1952:158–59). Viewed as "unequal and unjust, bearing hard upon the poor natives" (Kamins 1952:161), the land tax was eliminated by proclamation of King Kamehameha III in 1851. A quaint anachronism, the poll tax survived in various forms into the mid-20th century (Kamins 1952:159).

Initially, the new laws provided also that taxes could be assessed by the governor of each island and by the subordinate chiefs (Beechert 1985:27–28). Provisions allowing dual and triple taxation were abolished in 1842 by the chiefs meeting at Lahaina as a legislature, whose aptly titled enactment "Burdens of the Lower Classes" restricted the powers of taxation to the central government. With the Laws of 1842, according to Beechert (1985:29), "the ancient system of social stratification and its economic base was abolished and a society based upon money values was put in its place." A tax law passed in 1841 clearly reflected this new philosophy: "Money is the standard by which all taxes and assessments are to be estimated, and it would be very well if all men would pay their taxes in money" (Constitution and Laws 1842:86). To prove the point, the legislature in 1846 made land taxes payable in money only (Statute Laws 1846:165). Labor taxes also could be commuted, at the daily rate of 12½ cents or on an annual basis. Although some continued to pay for a time in "arrow root, cotton, coffee—sugar—Turmeric, oil nuts, hogs &c at the market prices" (Sahlins and Barrère 1973:26), this practice was formally abolished in 1850 when all taxes, except labor, became payable "only in current coin of this kingdom" (Penal Code 1850:168).

Minister of Finance Edwin O. Hall rationalized the need for the new law in his report to the legislature of 1850:

> On account of the considerable increase in money, even in the remotest districts of the Kingdom, from the ready sale of the productions of the Islands, it is believed that the revenue would be increased and the people not be burdened, were the taxes now allowed to be paid in produce, required to be paid in money. Much loss which formerly accrued to the revenue from this source would thereby be prevented, and much trouble and vexation would be avoided. (Hall 1850:17)

The Treasury Board, created by the legislature in May 1842 (Constitution and Laws 1842:86), worked diligently to see that taxes were collected in money wherever possible—although in a bewildering assortment of circulating coins of the realm until a national currency could be established 40 years later. In sum, the requirements for payment of taxes in money only created a whole new set of problems for the *maka'āinana*, but at least the standardized tax codes lifted the oppressive uncertainties of the past and placed the average tenant-commoner on a theoretically equal footing with all other members of society.

THE TAX ON ANIMALS

The 1st direct tax on animals, the fundamental concern of the petitioners, was imposed by the legislature of 1843 and was a tax on dogs and cats. "All dogs and cats," the law stated, "shall be subject to an annual tax of one rial per head, payable to the tax-gatherer previously to the first of January of each year; otherwise they must be killed" (Laws 1843:4). The legislature in 1851 abolished the tax on cats but retained a "tax of one dollar on dogs" and stipulated stiff penalties for owners whose animals caused damage (Laws 1851:77).

Before the tax on cats was abolished, Minister of the Interior Gerrit P. Judd (1845:8) proposed to the legislature in 1845 to meet estimated government expenses of 80,000 dollars for the coming year, among other expedients, "by a tax on horses, mules and asses." Organic acts passed that year and in 1846 created administrative machinery of government, including a Department of Finance with control over foreign imposts and internal taxes. Article IV of the new internal tax code, later amended (Supplement to Statute Laws 1848:47), extended the laws to the beasts of the fields. All owners of "cattle, horses, mules, asses, cats and dogs" were required "on or before the first day of December, to file with the governor of the island in which they happen to be, a true statement of the number owned by them respectively attested" (Statute Laws 1846:169). Specifically, Sections VII–IX of the code called for a yearly tax of ½ dollar on all horses and mares; ¼ dollar on all mules and asses; 25 five cents on cattle; and 1 dollar per head on dogs and cats (Statute Laws 1846:170).

Assuming the ministerial portfolio of the nascent Department of Finance, G. P. Judd noted in his 1st annual legislative report that the new taxes would go into effect the following year.

"Being direct taxes," he cautioned, "they will at first prove onerous to the people and both expensive and uncertain in the collection" (Judd 1846:47). Admitting, the following year, that "taxes of the country are no doubt somewhat heavy," Judd (1847:6) further informed the legislature: "The tax on horses and mules, owing to some unaccountable neglect of the tax gatherers, has added to the revenue only $948.61. . . . Perhaps it would be wiser not to call for it at present, or to abolish it altogether, until the system of collecting taxes can be more perfectly organized throughout the kingdom."

Still in the process of organization, the government continued to encounter difficulties in collecting animal and other taxes. Again, Judd reported to the legislature of 1848:

> The Tax Officers justly complain that some of the sub-agents and Teachers of Schools, make a practice of assuming the ownership of lands, horses, dogs and other taxable property for the purpose of freeing their friends from taxation, and thereby defrauding revenue. This abuse of an immunity granted to them by law, should receive attention . . . if possible short of re-imposing the taxes from which the School Agents have been exempted. (Judd 1848:4)

Contrary to recommendations, the legislature imposed the chattel taxes on licensed teachers, and in 1855 moved to correct continuing abuses by authorizing "enumerators" to make "a faithful enumeration of all persons and animals in his district liable to be taxed, and to make a tax list of the same" (Laws 1855:22). With that, revenues from animal taxes became a regular and dependable source of income to the infant government, and a new category of expense to the Hawaiian *maka'āinana.*

There are few statistics documenting the number of horses and other animals in the kingdom at the time the new taxes were imposed. Horses were introduced from California in 1803 and imported in numbers during the 1820s and 1830s to work the cattle ranches developing on the island of Hawai'i. Cattle had been introduced by Captain George Vancouver in 1793, goats and sheep by Cook in 1778, and other European livestock by the early 19th century. Responding to a questionnaire circulated by Minister of Foreign Relations Robert C. Wyllie in 1846, missionaries throughout the islands reported that horses, as well as mules, donkeys, sheep, goats, and cattle, were plentiful and increasing. In his district, for example, Reverend Jonathan Green of Makawao, Maui, counted 16 mules and donkeys and 266 "horses, young and old, male and female. . . . More than half are mares. . . . Not a little complaint is made of damage done by horses. Some few of them are made to carry burdens, chiefly, however used only for pleasure" (Armstrong, Chamberlain & Castle 1848:22). Likewise, in the Honolulu area, Reverend Richard Armstrong estimated some 500 horses and 100 "mules and jackasses," and Reverend Peter Gulick of Waialua, O'ahu, reported "Horses three hundred and twenty-nine, mules eight, donkies thirty-four" (Armstrong, Chamberlain & Castle 1848:22–23). Five years later there were an estimated 11,700 horses on all the islands, as well as 10,200 sheep and 40,700 cattle, some 12,000 of which were wild cattle on the island of Hawai'i (Bishop 1852). This amounted to about 1 horse for every 6 Hawaiians, whether man, woman, or child.

The value of horses and other livestock at the time the animal taxes went into effect is of some interest. In upcountry Maui a horse was worth about 60 dollars, according to Reverend Green, in line with the average 60 dollars or range of 40–100 dollars reported for the kingdom. Mules were worth about 30 dollars but ranged from 10 to 50 dollars, while donkeys averaged a bit less than 20 dollars. Horned cattle brought 20 dollars a head but sheep and goats much less—goats about 50 cents and sheep perhaps 2 dollars (Armstrong, Chamberlain & Castle 1848:22–23). By comparison, ordinary unskilled laborers could earn 12½ cents to 25 cents per day, or about 5 dollars per month (Armstrong, Chamberlain & Castle 1848:79)—about the same rate at which road and labor taxes could be commuted. Carpenters and other skilled

Table 1. Animal tax revenues collected by the Hawaiian Bureau of Internal Taxes for the period 1847–58.*

Year**	Horses and mules***		Dogs and cats†		Total internal taxes
	$	%	$	%	$
1847	949	3.4	516	1.9	27,638
1848	1,519	3.1	807	1.6	49,304
1849	2,588	4.4	819	1.4	58,748
1850	2,745	5.6	700	1.4	48,818
1851	3,795	7.2	824	1.6	52,455
1852	3,464	9.1	2,531	6.6	38,118
1853	4,161	9.7	2,921	6.8	43,033
1854	5,311	11.8	3,346	7.4	45,058
1855	10,655	13.3	11,753	14.1	83,579
1856–58	18,995	14.8	14,746	11.0	134,306

* From reports of the minister of finance (Judd 1845, 1846, 1847, 1848; Finance Department 1848, 1849, 1850, 1851; Hall 1850; Judd 1851, 1853; Allen 1854, 1855, 1856; Kamehameha 1858).

** From 1847 through 1851 the fiscal year extended from 1 April to 31 March, converting during 1852 to a calendar basis; after 1856 the fiscal year reverted to 1 April–31 March biennium.

*** Mule taxes were listed separately beginning in 1855; they amounted to $478 in 1855 and $923 in 1856–58 biennium. Returns for 1855 include horse and mule taxes of $2,346 and dog taxes of $2,176 collected in 1854 but not received until 1855. Other similar variances exist in the totals because of changes in calculating the fiscal year, but overall trends are consistent.

† Dogs only after 1851.

craftsmen, some of whom were given special tax benefits, could earn considerably more. Except for the rate of 1 dollar on dogs (and cats until 1851), the tax on livestock was not disproportionately out of line with their value or the wages of unskilled laborers, provided, of course, they could find employment.

Most of the missionaries responding to Wyllie's questionnaire in 1847 concurred that a tax on animals was proper, if not absolutely necessary, to control what they considered a common nuisance. "The existence of large herds of cattle, horses, goats or sheep, is a great evil, and calls for a speedy remedy," they believed, citing damages caused by wild cattle and unrestrained livestock. "The owners grow rich at the expense of the poor agriculturalist. Their patch of potatoes is devoured in an hour and what has he left?" (Armstrong, Chamberlain & Castle 1848:92). Reverend Green of Makawao wanted "a heavy tax on horses and dogs," and Reverend David Lyman of Hilo believed "all large herds of cattle should be taxed." Edwin O. Hall, former secular agent with the mission and sometime minister of finance, urged: "Put a tax of $10 a year upon horses that are not in frequent use" (Armstrong, Chamberlain & Castle 1848:74,93). Reverend John Emerson of Waialua suggested: "Let every man keep four or six head of horned cattle and one horse gratis, and let all beyond that number be required to pay to the King a heavy tax—say one or two dollars per head annually, and horses a larger tax than cattle" (Armstong, Chamberlain & Castle 1848:75). Missionary views on the taxing of animals prevailed, and the legislature of 1856 passed a further levy of 10 dollars each on "entire horses two years old and upwards," apparently those designated for stud service (Laws 1856:48).

From inauguration of the new laws in 1847 until their revision in 1859, revenues from the animal taxes provided a steadily increasing source of income to the Hawaiian treasury (Table 1). Combined receipts from horses and mules rose from an initial 3–4% of the total annual revenues collected by the Bureau of Internal Taxes to nearly 15% at the end of the period; revenue from dogs (including cats until rescinded in 1851) grew from nearly 2% to a high of about 14%. At their peak in 1855, combined revenues from both sources amounted to 22,886 dollars or 27% of the kingdom's internal taxes of 83,579 dollars. During most of this period animal taxes provided a dependable, if not particularly large, proportion of the total, eventually growing to about 10% of annual government income derived from all sources, internal and external. The bulk came from custom house duties, followed by miscellaneous realizations, such as land rents and sales, license fees to the Bureau of Internal Commerce, and fines and penalties (Allen 1856; Walker 1874). During the later years of the reign of Kamehameha IV (1855–63), total government income normally averaged less than 300,000 dollars annually, excluding school and road taxes (Kuykendall 1953:176).

In 1859, a new and comprehensive civil code came into being, doubling the tax on animals except for the tax on dogs, which remained the same. Enacted when the "condition of the treasury was especially critical in 1856 and 1861" (Kuykendall 1853:176), the new rates created a heavy burden for the Hawaiian taxpayer. Section 481 of the revised internal code stipulated that:

> All horses more than two years old, male or female, shall be yearly taxed one dollar each. . . .
>
> All mules and asses, more than two years old, shall be yearly taxed half a dollar each.
>
> All dogs shall be yearly taxed one dollar each. (Civil Code 1859:105)

These revisions remained in effect with few modifications for more than 10 years. Some relief was granted when the legislature of 1870 lowered the annual tax on "horses, mares and colts" to 75 cents, but imposed an additional 10-cent fee for metal dog tags stamped with the year and number registering the animal by district (Laws 1870:54). Milking cattle and other domesticated animals not specifically mentioned in the Civil Code of 1859 were considered personal property and taxed according to prevailing rates ad valorem, usually 2% (Castle 1891:63).

The revised tax on animals brought significant revenues to the Hawaiian treasury, totaling some 870,000 dollars during the period 1860 through 1884 (Table 2). From doubling of the rate in 1859, to 1874 when the mat petition was presented to the king, animal taxes constituted roughly ½ to ⅓ of all revenues collected by the Bureau of Internal Taxes. During the 1862 biennium, when the new rates first went fully into effect, total internal tax revenues amounted to 133,237 dollars, of which 52,742 dollars or 39.6% came from the tax on horses alone; combined animal taxes from horses, mules, and dogs amounted to 49.9% of the internal tax. This percentage remained fairly consistent until the rate on horses was reduced by ¼ in 1870. Except for real estate taxes in 1874, revenues derived from the tax on horses were greater than that from any other internal category, which included personal property, polls, mules, dogs, carriages, and native seamen as well as real estate (cf. Thrum 1875).

Animal taxes thus paid a significant portion of the kingdom's operating expenses, which between 1860 and 1874 grew from about 680,000 to 1,000,000 dollars biennially (Schmitt 1977:619; Walker 1874). During much of this period government income from ordinary sources averaged more than 400,000 dollars annually (Kuykendall 1953:176). Of this some 40,000 dollars a year, or ⅒ of total revenues from all sources, internal and external, was derived from the direct tax on animals. As before, import duties continued to provide the bulk (Kamins 1952:164–65); however, customs receipts were not direct internal taxes, so they proved to be far less onerous on the Hawaiian people than were the combined animal taxes.

The tax on horses must have been a heavy burden on the average Hawaiian. A newspaper

Table 2. Animal tax revenues collected as internal taxes by the Hawaiian Treasury for the period 1860–84.*

Biennium**	Horses***		Mules		Dogs		Total internal taxes†
	$	%	$	%	$	%	$
1860	35,958	33.0	1,793	1.6	13,525	12.4	108,842
1862	52,742	39.6	2,691	2.0	11,018	8.3	133,237
1864	52,562	39.9	3,081	2.3	10,038	7.6	131,729
1866	60,296	40.0	4,265	2.8	12,016	8.0	150,662
1868	61,541	37.2	4,823	2.9	12,954	7.8	165,401
1870	60,027	36.0	5,110	3.1	15,430	9.3	166,507
1872	53,006	24.5	6,140	2.8	22,271	10.3	215,963
1874	50,088	24.2	6,073	2.9	19,555	9.5	206,723
1876	48,194	22.5	6,013	2.8	18,676	8.7	213,930
1878	47,564	14.4	3,053	0.9	16,465	5.0	331,163
1880	43,399	9.3	—		15,173	3.3	465,252
1882	42,819	7.2	—		13,965	2.3	595,973
1884	21,975	3.2	—		13,924	2.0	679,995

* From reports of the minister of finance (Gregg 1862; de Varigny 1864; Harris 1866; Phillips 1868; Mott Smith 1870, 1872; Nahaolelua 1874; Walker 1876; Kapena 1878; Kaai 1880; Walker 1882; Kapena 1884).

** For years 1 April to 31 March.

*** Incorporates "Stallion Tax" and "Stud Horse" fees through 1868, when receipts from these sources were no longer separately reported. Total receipts, until the taxes were rescinded in 1880, amounted to only $1,749.92.

† Does not include road and school taxes paid directly to the Bureau of Public Instruction.

report from rural O'ahu gives some idea, if tongue-in-cheek, of the very real dilemma that many Hawaiian families faced when the horse tax doubled from 50 cents to 1 dollar in 1859.

> At Waialua, on this island, the natives have begun to eat their horses, partly because they have nothing else that they can do with them, and no other place of their own but their stomachs in which to put them, and partly to avoid paying the tax of one dollar per head. Already several animals that were of no use during their lives, and were then utterly incapable of supporting a man, have helped after death to support whole families. A horse while living is not valued at one dollar a year in the shape of income tax, yet his flesh being put into that very appropriately named vessel, a harness cask, will keep a good sized household for a month. (*The Polynesian* 1859)

Why horses should account for such a high proportion of internal tax revenues seems to be the calculated result of government policy taking advantage of cultural values. Beyond their utility for cattle ranching and transportation, horses provided universal entertainment and were also numerous and, therefore, fair game to the revenue collector. As Kuykendall (1953:24) observed, "To the Hawaiians, the recreational aspect of horseback riding made the greatest appeal. They became enthusiastic and expert equestrians, and to an appreciable extent horseback riding took the place of swimming and surf-riding in the life of the people. Horse racing was early introduced and became a popular sport." Visiting in 1873, Charles Nordhoff (1874:102) found that "almost every one strong enough to ride has a horse; for the Hawaiians can not well live without horses." Moreover, "there are probably more horses than people on the Islands; and the native family is poor, indeed, which has not two or three hardy, rough, grass-fed ponies, easy to ride, sometimes tricky but more often quite trustworthy, and capable of living where a European donkey would die in disgust" (Nordhoff 1874:70).

Whether animal taxes had the desired effect of reducing the horse population cannot be readily substantiated. That the legislature, which "troubles itself chiefly about the horse and dog tax" (Nordhoff 1874:102), did try to impose controls is apparent. Nordhoff remarks, only partly in jest, of the situation that existed at the moment the mat-weavers were framing their petition:

> At a horse auction you see a singular collection of good and bad horses; and it is one of the jokes of the Islands to go to a horse auction and buy a horse for a quarter of a dollar. The Government has vainly tried to put a check to the reckless increase of horseflesh by laying a tax on these animals, and by impounding them if the tax is not paid. I was told of a planter who bought on one occasion fifty horses out of a pound, at twenty-five cents a head, and had them all shot and put into a manure pile. But if the horse is worth his tax it is pretty certain to be paid; and it is not easy to keep them off the pastures. (Nordhoff 1874:70)

What effects, if any, the mat petition had when presented to King Kalākaua is difficult to ascertain. By 1874, it is important to note, the Hawaiian economy "was at a standstill" (Beechert 1985:78). The sugar planters had had a bad year in 1872 with dim prospects for the next, sinking the whole nation and public generally into economic depression (Daws 1968:191; Kuykendall 1953:247). Citing falling customs receipts and "the rapid and steady decline of the native population," among other causes, Minister of Finance Paul Nahaolelua (1874:7) admitted to "a stationary condition of our material prosperity, and . . . in the last few years . . . a pause in the rapid progress." In light of such conditions, even Dowager Queen Emma, Kalākaua's chief rival for the throne in the 1874 campaign, was heard to promise: "if elected to take no salary repeal the horse tax roads tax and any other tax they want, and the great unwashed are whooping and yelling" (Daws 1968:198). That the direct tax on horses was decidedly unpopular among Hawaiians requires no further comment.

Kalākaua handily won the election, but he was unable to do much about "the great cause for the decrease of the Hawaiian people," which also troubled the petitioners. Although his sympathies in this regard were already well established (Kuykendall 1967:13), the government viewed the problem mostly in economic terms: a critical labor shortage would inhibit the development of sugar plantations, and as prosperity became more and more dependent on sugar export—particularly after the Reciprocity Treaty of 1874—so, too, would government revenues depend. Despite efforts by Kalākaua and others to "*Ho'oulu Lāhui* Increase the Race," the ultimate solution devolved to mass immigration of "cognate races" as cheap plantation labor. It was an implicit expectation that indentured labor, predominantly Japanese after 1885, would intermarry and augment the native population.

The plea "to change the taxes on animals, cattle, horse, asses, mules and sheep and let none of them remain" also met with mixed results. The legislature of 1876, convening in the very building where the mat petition was newly on display in the National Museum, did repeal the section of the animal tax dealing with mules and asses, which was relatively unproductive anyway (Laws 1876:145). Finally in 1882 the legislature eliminated the direct tax on horses almost as an afterthought while revising and consolidating assorted tax laws. Henceforth, horses "and all domesticated birds and animals not hereinbefore specifically taxed" were considered to be personal property and assessed ad valorem (Laws 1882:72).

Before the animal taxes were ameliorated and finally repealed, Minister of Finance J. S. Walker (1876:6) debated whether an apparent fall of revenues noted in 1876 was due to "an actual decrease of animals, or lack of diligence on the part of assessors and collectors." Reporting another "slight falling off in the Horse and Dog taxes" in 1882, Walker (1882:6) concluded, "While I have reasons for believing that there is a falling off in native horses I have equally good reasons for saying that dogs have not decreased." The ultimate effect on the royal treasury of the repeal of the direct tax on horses was even less clear. Comparing 1884 receipts to the previous tax period, Minister of Finance J. M. Kapena found "reason to believe their value as personal property more than covered the decreases shown." A contemporary analyst argued, however, "that the abolition of the tax on horses, they being transferred to personal property, did not produce a corresponding increase in the tax receipts from that source. On the contrary it probably operated simply to take off a portion of the taxes from the natives and Portuguese [after 1878] as the chief owners of horses" (Castle 1891:66–67).

Whether or not the net effect of transferring the direct tax on horses to personal property yielded any substantive benefits to the ordinary Hawaiian taxpayer, the fundamental plea of the mat petition had been achieved—at least symbolically. Ultimately, of course, the petitioners failed to obtain "release from the burden of the law that keeps us slaves under masters from the sky," but they did succeed, at least temporarily, in calling attention to the plight of the *maka'āinana*. While it may be argued that animal taxes were a trivial concern and insignificant burden overall, combined revenues from that source realized over a 35-year period amounted to more than 900,000 dollars extracted predominantly from the Hawaiian and part-Hawaiian community. In 1872, about the time the mat petition was created, animal taxes for the biennium totaled 81,417 dollars and represented a tax burden of $1.58 for every man, woman, and child of the Hawaiian and part-Hawaiian population of 51,531. Since the total tax per capita for the entire kingdom in 1875 was estimated by one source to be about $2.52 (Castle 1891:66), animal taxes were indeed a proportionately significant component of the tax burden borne by the mid-19th-century Hawaiian *maka'āinana*, Crude as this analysis may be, it provides some quantitative evidence of the average Hawaiian's contribution to the support of monarchical government. Inasmuch as a *makaloa* mat was also the vehicle for the protest, future lines of inquiry into the role of the material arts in the economic and cultural life of 19th-century Hawai'i are indicated.

THE DEMISE OF *MAKALOA* MAT-MAKING

It is doubtful that Kala'i, the weaver of the mat petition, lived to see any tangible results of her labors. Aged, she herself was apparently one of the last of Ni'ihau's master weavers, whose art was already headed toward extinction. There are a number of reasons for loss of this famed tradition: the change to a monetary economy, and specifically the laws of 1846 and 1850 requiring payment of taxes in money rather than produce; the comparatively low financial return in view of the difficulty and time required to complete a mat for sale; changing tastes, and loss of traditional as well as practical uses for Ni'ihau mats, especially in the latter 19th century; widespread decrease of the *makaloa* sedge through habitat destruction; a decline in the number of weavers on Ni'ihau caused by general population loss, compounded by conversion of the island to a private ranch in 1864 and total disruption of the lifestyle of those remaining.

Ni'ihau, small and drought-prone, was never very populous. After 2 days ashore in January 1778, a party of Cook's men "supposed, that there could not be more than five hundred people upon the island" (Cook & King 1784:II:218). Calculating from averages, Captain King later revised this figure upward to an equally implausible 10,000 (Cook & King 1784:III:129). The missionary censuses of 1831–32 and 1835–36 recorded 1,047 and 993 individuals respectively, while government figures in 1850, 1853, and 1860 indicate a fairly stable level of 714, 790, and 647 for those years (Schmitt 1977:11). Because of the shortage of fresh water, the new owners who purchased Ni'ihau from the king in 1864 developed an informal policy of limiting the population to only those needed to work the ranch. After 1866, when the census recorded 325 individuals, the population steadily dropped—to 233 in 1872, 177 in 1878, and a 19th-century low of 164 in 1896 (Schmitt 1977:11). At one point about 1880, according to one source, the island was "only occupied by Mr. Sinclair's servants and a mere handful of natives" (Bowser 1880:570).

It is impossible to know what percentage of the resident population was occupied in producing *makaloa* mats, but it is clear their numbers were severely reduced during the last half of the 19th century. For those who relocated to Kaua'i, or O'ahu and Maui, it is questionable to what extent either raw materials or incentives would have been available for them to continue their weaving tradition. It is interesting to note that about 1821 Queen Regent Ka'ahumanu, Kamehameha's widow and the ranking figure in government, carried away after a visit to Ni'ihau "expert mat weavers" and left them at Waialua on O'ahu (Kamakau 1961:253). What became of them is not recorded, but *moena pākea*, or *makaloa* mats without overlaid *pāwehe* designs were reportedly being made later at nearby Mokulē'ia (HEN n.d.:I:1252). A flourishing Ni'ihau mat-making tradition did not survive, but a poetic expression, "*Ka moena pāwehe o Mokulē'ia* / The patterned mat of Mokulē'ia" (Pukui 1983:160), may reflect this early-19th-century transplant.

Degradation of the natural habitat of the *makaloa* sedge on Ni'ihau also affected the mat-making industry, ultimately contributing to its demise. Because of their destructive grazing habits, goats put ashore by Captain Cook in 1778 proved disastrous to the island's fragile vegetation cover, causing erosion and filling of some of the intermittent lakes where the *makaloa* sedge grew. According to geologist Harold K. Stearns (1947:30), "feral goats in historic time ate so much of the vegetation that much of the deep red soil on the uplands, formed during the million years or more since the cessation of volcanism there, was washed into the lowlands, filling up Hawaiian fish ponds and many of the playas." These conditions, coupled with lack of attention, especially in the late 19th century, severely reduced the *makaloa* sedge. At their height by 1897, feral goats were exterminated early in the 20th century as the result of concentrated efforts (Forbes 1913:18; Judd 1932:8; Tabrah 1987:131).

Sheep, however, as well as competition from introduced plants, continued to threaten the remaining stands of *makaloa* (Degener 1946–57). Mainstay of Ni'ihau Ranch throughout much of its history, sheep numbered at least 10,000 and perhaps up to 35,000 or 40,000 during the latter 19th century (Bagot 1884:373; Lane 1888:437; Tabrah 1987:138,213; *Paradise of the Pacific* 1892). Visiting Ni'ihau in January 1912, John F. G. Stokes of Bishop Museum observed, "The areas of *Cyperus laevigatus* which used to be tended with some care are being crowded out by another species, as well as by sheep, except where [ranch manager] Mr. Robinson has protected it by fencing as of historical interest" (Forbes 1913:19). Stokes managed to collect *makaloa* at Ka'ali in the NW, and from the "swamp-like areas" near the S end "where various species of *cyperus* occur, including *C. laevigatus*, from which the old natives made their famous mats" (Forbes 1913:18). After a day on Ni'ihau in October 1929, Territorial Forester C. S. Judd (1932:9) commented, "There are natural ponds of brackish water in the south central portion and it was here that the makaloa rush throve before the sheep destroyed it and terminated the mat industry." Contrary to some reports (e.g., Tabrah 1987:15,136), however, the *makaloa* sedge did not become extinct. Ni'ihau Ranch is said to be still making some effort to protect the plant where it survives at Lake Halulu and elsewhere (Tava 1988).

The change to a monetary economy, and specifically the tax laws of 1846 and 1850 requiring payment in money rather than produce, was another major cause of the demise of mat-making. If not exactly flourishing, many of the traditional material arts were at least still being practiced when missionaries in 1847 responded to Minister of Foreign Relations R. C. Wyllie's questionnaire. Answers from his district by Reverend Coan of Hilo to the inquiry on native manufactures is typical: "kapas, mats, canoes, cordage, fishing nets, salt, and a few other things of less importance." On Maui, fellow missionaries reported "some native kapa and mats" from Wailuku, and "mats also, and ropes, &c., &c." from Makawao. Responses from the other islands were similar: from Honolulu, "brooms, mats, bonnets, hats, kapa, fish-nets, salt and the like"; from Waialua, "none, except of kapa"; and at Hanalei, Kaua'i, "those common to these islands, as kapa, mats, mat-bags, hats and bonnets, canoes, fish-nets, rope &c." (Armstong, Chamberlain & Castle 1848:15). The continuing manufacture of mats in most of the districts responding is of interest. It is not known what proportion was made from the *makaloa* sedge, but surely a large number. It is noteworthy that of nearly 150 Hawaiian mats and samplers preserved in Bishop Museum, the vast majority are of *makaloa*.

There are few eyewitness observations describing *makaloa* mats or mat-making. On first landfall off Ni'ihau, Cook was greeted by several canoes bringing "some small pigs and potatoes, and a good many yams and mats" (Cook & King 1784:II:213). The voyagers who followed, mostly seeking replenishments at this island so "famous for its yams, fruit, and mats" (Beechey 1831:I:234), rarely ventured ashore long enough to observe possible mat-making activities. One of the earliest was Gorham D. Gilman, a young Bostonian who visited in August 1845. Accompanied by a coffee planter from Kaua'i named Tobey, and Reverend Samuel Whitney of the mission station at Waimea, Gilman (1845:66) "called at several of the native houses in pursuit of Mats but found a very few, and for those they asked us exorbitant prices." Gilman (1845:69–70) estimated the population to be about 750 and, seeing no horses and only a few goats, next day visited a village of some 14 or 16 houses with a church and small Catholic chapel nearby.

> We found but few articles for trade, a few figured calabashes and mats, for which they were desirous of getting much more than we could get them for on Kauai or Oahu. The natives conducted us to a large cave where there was a very large mat in process of making for the use of some one of the nobility. It is several yards long, and the width in proportion, and will be a rich specimen of native work, the figures being neat and regularly worked in. (Gilman 1845:68)

The people of Ni'ihau relied on the sale of mats as one of their few sources of money, an increasingly necessary commodity as the 19th century wore on. Sometimes money was tight, or mats not always available for sale. In 1863, while King Kamehameha IV still owned Ni'ihau and had trouble collecting back rent, his land agent, J. Wahinekea, complained: "I went to Niihau to demand of the natives their rent for the fifth year. The natives said that there was no money to be had belonging to us now. I said how about mats, if you have any on hand let me take them and I will take them to the King, who will buy them. They replied, there are no mats made up now" (Tabrah 1987:89). That was in December; returning in March Wahinekea was able to collect only $21.50—but whether from the sale of mats is not stated.

Four years later, in July 1867, a visitor anchoring at Cook's Harbor with Captain Kinney of the *Nettie* found island produce awaiting on the shore and the "sharp Kanakas" ready to trade. Besides sweet potatoes, onions, and pineapples, he saw "those skillfully wrought and ornamented rush mats, the manufacture of which is peculiar to Niihau. They are pliable and elastic, and made of material that grows nowhere else [*sic*] on the Islands. We saw some as neatly plaited and as pliable as the best Panama hats. . . . We were struck with one ornamented with *red*" (La Paz 1867).

Only a decade later, decrying the loss of interest in mat-making throughout the islands, one of the Hawaiian newspapers took the opportunity to editorialize on this troubling response to changing times:

> In days past, Hawaiian women plaited mats of bull rushes, of lauhala and makaloa [sedge] which last made pawehe mats. Some women are still making them to cover their floors and beds, but the younger generation now growing up will not know these fine arts that will be useful in their homes. Most of the girls want to learn to sew or crochet. They are both good [arts] but they should not neglect mat making, that helps to keep the house clean. Let the young women combine the knowledge from their mothers with the new knowledge from the haoles [foreigners] and new teachers. Keep the hands occupied with work, the head with knowledge and the inner person with thought. Learn that which you have and reach out for the new.
>
> Let the grandmothers teach their grandchildren to plait mats, twist cords and sew. (*Ka Lahui Hawaii* 1877)

Clearly in decline by the 1880s, *makaloa* mat-making as a home industry seems to have disappeared within the next generation. As Brigham (1892:66; cf. 1903:15, 1915:13) first wrote in his *Preliminary Catalogue* in 1892, "these mats are still made, but the makers are fast dying out, and the younger generation of females does not take kindly to such continuous work." Undoubtedly, a few weavers continued to put their skills to occasional use, if not on Ni'ihau then at Waimea on Kaua'i and perhaps elsewhere sporadically in isolated areas into the 20th century. Brigham, for example, purchased for Bishop Museum in April 1901 a dozen mat samplers from Hannah Cook of Waimea, each a foot or two square and showing both twill and overlay designs in the *pāwehe* and *pākea* techniques (Accession 1901.08). Other than the inscribed mat created by Kala'i and her husband, these newly made samplers appear to be the only *makaloa* mats whose age and maker are documented.

Heralding their demise, the *Directory and Hand-Book of the Kingdom of Hawaii* informed its readers as early as 1890 that Ni'ihau was "formerly noted for fine grass-woven mats" (Lane 1890:536). A San Francisco newspaper echoed 2 years later: "A fine grass . . . was formerly woven into 'Niihau mats'. . . . They are now very rare, and of late years the price, which formerly ranged from five to eleven dollars or so apiece, has advanced in an almost exorbitant degree since the industry was abandoned" (*Pacific Coast Commercial Record* 1892; reprinted in *Paradise of the Pacific* 1893). Honolulu's *Paradise of the Pacific* expressed like sentiments in 1899: "The handiwork of the natives in the making of a kind of mat is known all over the islands. They are called 'Niihau mats,' and bring large prices from the collectors of curios." Assessing the general state of Hawaiian mat-making in an article entitled "A Declining Industry," that same magazine suggested in 1903 that "extensive importation of cheap Chinese matting long ago discouraged the practice of the old art." Based on Brigham's writings it concluded: "Makaloa mats are still made on Niihau. . . . It would seem as though the small westernmost isle of the group is destined to be the spot where this interesting art is soon to be lost" (*Paradise of the Pacific* 1903; cf. 1908).

Quite correctly, Brigham (1906:77,81) noted in his treatise on Hawaiian mat-making in 1906 that "exact information is hard to obtain" on "this nearly obsolete mat." Believing that "a few old women still make the mats from the sedge which grows commonly enough along shores and in brackish marshes," he concluded that their "choicest mats are now very rare. . . . And another generation will have forgotten how to make *makaloa* mats" (Brigham 1906:2,77). Unfortunately, the prediction proved true. Although a journalist named Henry Dougherty supposed after a one-day visit in October 1929 that young girls "engage in Niihau reed-mat making" (Tabrah 1987:136), there is nothing to substantiate that the art was being practiced regularly. Except for the small samplers dating from the turn of the century, the mat petition presented to King Kalākaua in 1874 is among the last of the famous Ni'ihau mats to be made.

It is sadly appropriate that it also memorializes, in its way, the dying of a nation, whose struggling remnants prayed for release from burdensome taxes enslaving the Hawaiian people.

Today, there are said to be only one or two elderly women on Ni'ihau who retain some traditional knowledge of *makaloa* weaving. They no longer make the famed Ni'ihau mats, however, in part because of the scarcity of raw materials (Tava 1988; Wichman 1988). A lost art, *makaloa* weaving has only recently become a candidate for revival by a dedicated few of the current generation of students involved in perpetuating the material arts of Hawai'i.

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Extinction, Biogeography, and Human Exploitation of Birds on Tikopia and Anuta, Polynesian Outliers in the Solomon Islands[1]

David W. Steadman,[2] Dominique S. Pahlavan,[2] and Patrick V. Kirch[3]

ABSTRACT

We analyzed bird bones from prehistoric archaeological sites on Tikopia and Anuta, two small, isolated islands at the eastern edge of the Santa Cruz group of the Solomon Islands. Among the 468 identifiable bird bones from Tikopia are those of six species unknown there in modern times: *Puffinus lherminieri* (Audubon's Shearwater), *Papasula abbotti* (Abbott's Booby), *Sula sula* (Red-footed Booby), *Sterna fuscata* (Sooty Tern), *Megapodius freycinet* ("Scrub Fowl" or Common Megapode), and *Gallirallus philippensis* (Banded Rail). Among the 299 identifiable bird bones from Anuta are those of four species not previously recorded there: *Puffinus pacificus* (Wedge-tailed Shearwater), *Puffinus lherminieri* (Audubon's Shearwater), *Sula sula* (Red-footed Booby), and *Sterna fuscata* (Sooty Tern). Most, if not all, of these avifaunal losses are probably due to predation and habitat alteration by humans and introduced rats, dogs, and pigs. Knowledge of these losses is important for biogeography and evolution because it fills in gaps in the natural distributions of species. These findings are important culturally because they provide evidence of prehistoric use and over-exploitation of avian resources. The samples of bones from Tikopia and Anuta are readily compared because they are fairly similar in size and represent approximately the same interval of time (the past 3,000 years). Most of the differences in species composition between these samples are probably due to (1) random sampling effects (samples of bird bones in the hundreds are too small to represent thoroughly the avifauna of an island even as small as Tikopia or Anuta) and (2) the very small size of Anuta, which, combined with its great isolation, either is below the limit that can support a diverse land bird fauna or is such that its extremely small populations of birds would be highly vulnerable to environmental disruptions, whether or not these disruptions are human in origin.

INTRODUCTION

Faunal remains from archaeological sites are usually analyzed from a cultural rather than biological standpoint. Typically, the primary interest of faunal remains lies in what they reveal about the food habits of past peoples rather than in what they say about the animals themselves.

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To learn more about the natural (i.e., pre-human) distribution of birds in Oceania, DWS has obtained collections of bird bones from early archaeological sites on many islands, especially those of eastern Polynesia. Study of these bird bones has shown that numerous populations and entire species of birds have been lost in Polynesia since the time of human arrival, necessitating a reevaluation of the natural biogeography of Pacific birds (Steadman 1989a). The discovery of extinct birds is important to the archaeologist as well as the biologist because the bones of extinct species or populations, which often outnumber those of surviving birds, represent food sources that were exhausted by prehistoric peoples.

This paper is an analysis of the bird bones from archaeological excavations on the small islands of Tikopia and Anuta in the eastern Solomon Islands. The archaeology of these islands is well known (Kirch & Yen 1982; Kirch 1982, 1986a, 1986b; Kirch & Rosendahl 1973, 1976). Mammal bones from the Tikopia sites were reported by Flannery et al. (1988). Although bird bones from Tikopia have been studied more thoroughly than those of most Polynesian archaeological sites (Kirch & Yen 1982:275–284), initial examination of these bones was not done by specialists in avian osteology and was accomplished with a very limited collection of modern comparative skeletons. Previous to our study, bird bones from Anuta had not been identified to any taxonomic level beyond "bird" (Kirch & Rosendahl 1973:92–93). Herein we identify all diagnostic bird bones from all sites on both Tikopia and Anuta. The resulting data permit meaningful comparisons of the prehistoric status and exploitation of birds on these two islands.

MATERIALS AND METHODS

The bones were identified by DWS and DSP. PVK was responsible for the archaeological content of this paper. Identifications were based upon comparisons with modern skeletons of birds from the National Museum of Natural History (USNM), the University of Washington Burke Museum (UWBM), and the New York State Museum (NYSM). The bones from Tikopia and Anuta are housed in the Department of Zoology, Bishop Museum (BPBM). Other abbreviations used: AMNH = American Museum of Natural History; WSSE = Whitney South Sea Expedition; MNI = minimum number of individuals; NISP = number of identified specimens. Although we provide data for both MNI and NISP in the species accounts, we agree with Grayson (1984:62,63,90–92) that MNI values usually can be predicted from NISP values, and that the latter may be better indicators of relative abundance of species. Thus we use only NISP in the tables. Archaeological sediments on Tikopia and Anuta were sieved through screens of 0.25 in. mesh. Screens of this mesh size recover most bones of sea birds and large land birds, but recover few bones of small and medium-sized land birds. The Tikopia names for birds in the species accounts (in parentheses following the English names) are from Kirch and Yen (1982:283–284) and Firth (1985). The Anuta names for birds are from Feinberg (1977). Unless stated otherwise, the modern distributions of birds outside of Tikopia and Anuta are from Mayr (1945), duPont (1976), Hadden (1981), and Pratt, Bruner and Berrett (1987). Osteological nomenclature usually follows Baumel et al. (1979).

THE ISLANDS

Anuta and Tikopia are among the more isolated islands of eastern Melanesia. Politically, both islands are part of the Solomon Islands, and thus are usually grouped with the Santa Cruz Islands as the easternmost province (Te Motu Province) of the Solomon Islands. Geographically, however, Anuta and Tikopia are almost equidistant from Vanikoro in the Santa Cruz Islands and Vanua Lava in the Banks Islands (Fig. 1). Tikopia and Anuta, 137 km apart, are closer to each other than to any other occupied island. A small, uninhabited volcanic spire, Fatutaka (also called Fataka or Mitre Island), lies 32 km southeast of Anuta and can be seen from the latter during clear weather. When the winds are favorable, Anutans voyage by

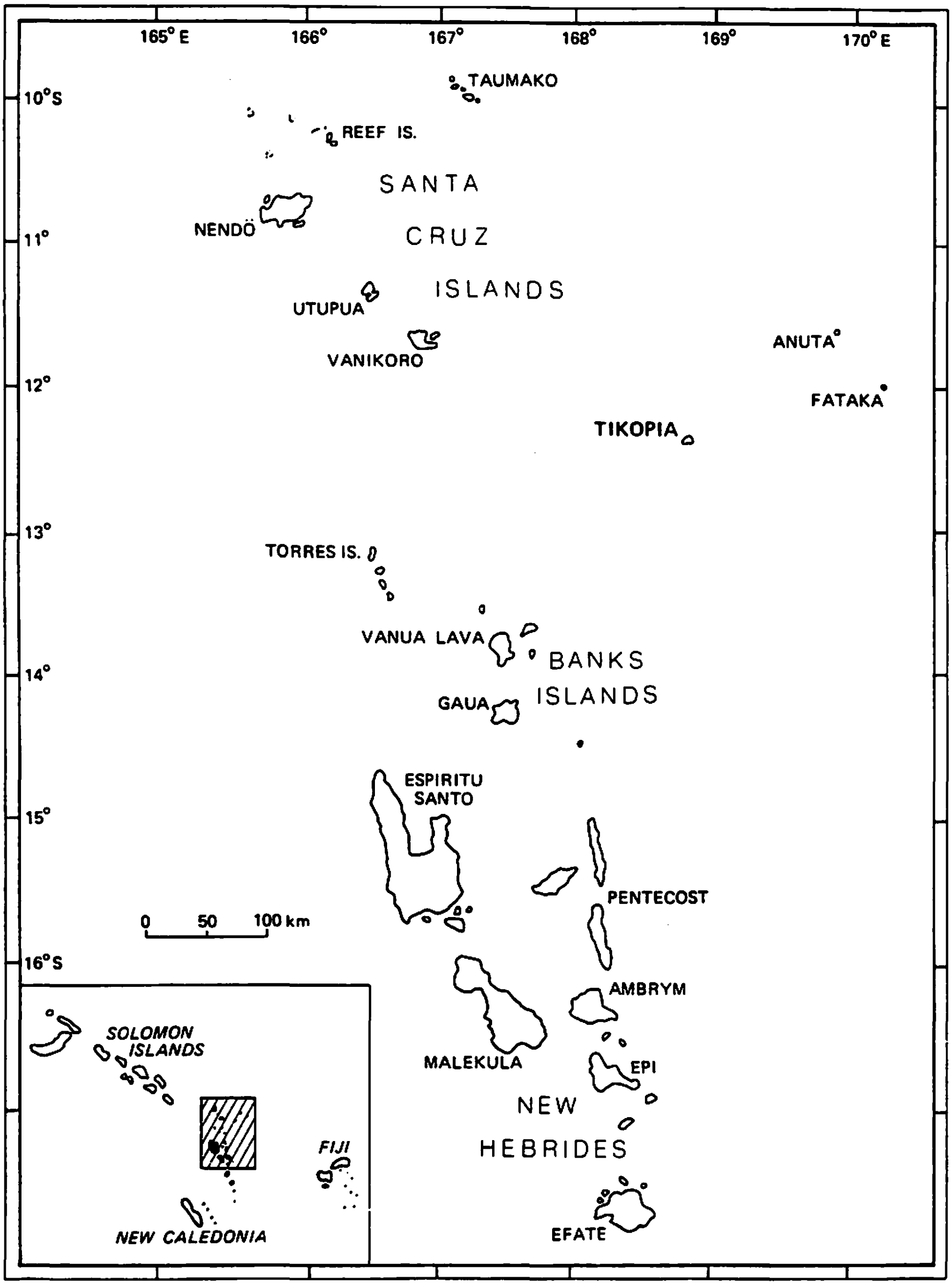

Fig. 1. Location of Tikopia and Anuta in relation to the Santa Cruz Islands and northern Vanuatu (= New Hebrides) (Kirch & Yen 1982:2).

outrigger to Fatutaka to gorge themselves on nesting sea birds and their eggs (Feinberg 1981:28,34). The birds of Fatutaka have never been surveyed, although Woodford (1916) mentioned that frigatebirds (*Fregata* sp.) nest there.

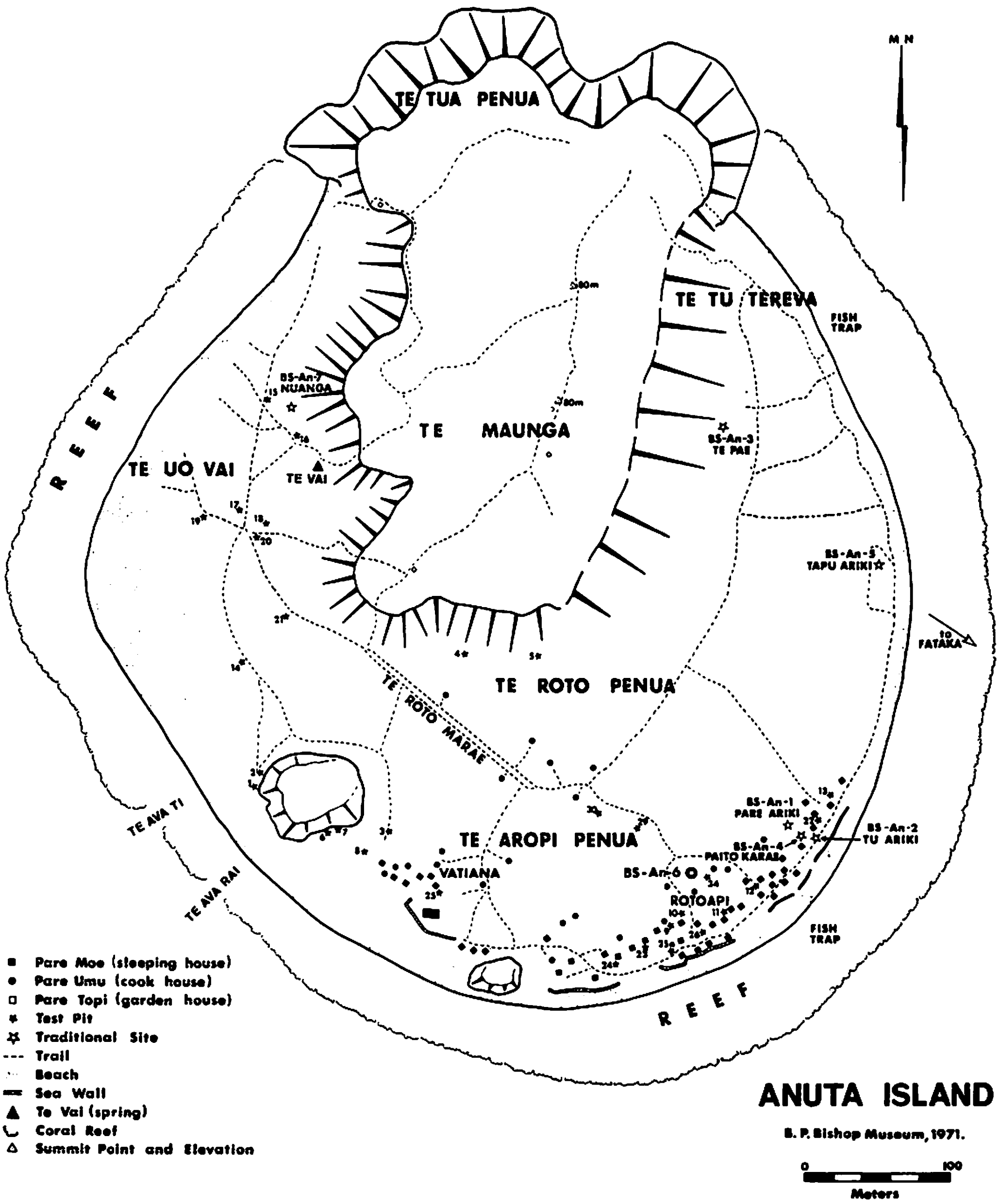

Fig. 2. Anuta Island, showing natural and cultural features, traditional sites, and excavation sites (Kirch & Rosendahl 1973:27).

Anuta (Fig. 2) is a diminutive "high" island with a total land area of only 40 ha (0.4 km^2) and a maximum elevation of 80 m above sea level. The island consists of the eroded remnant of an oceanic-type volcano. A fringing reef nearly encircles Anuta, except on the north where there are steep sea cliffs. The archaeological sites are located on the broad calcareous sand flat that accreted on the reef platform, especially on the south and west (Kirch & Rosendahl 1973: Fig. 1).

As might be expected on such a small island where the human population density is 432/km^2, the vegetation of Anuta is almost wholly anthropogenic. Yen (1973:122) described this managed vegetation in some detail and observed that "one conspicuous feature of the Anutan landscape is the lack of truly natural vegetation on any part of the island except the steep seaward cliffs of the mountain and the two southern promontories." Common Fairy-Terns (*Gygis alba*) and Brown Noddies (*Anous stolidus*) nest primarily on the crowns of large fruit trees (*Artocarpus*, *Burckella*) on the sandy flat and mountain slopes.

Tikopia (Fig. 3), with a land area of 4.6 km^2, is 11 times larger than Anuta although it too has a high population density (242 persons/km^2) and a largely anthropogenic landscape. The island consists of a remnant single-cone volcano (360 m above sea level) of late Pleistocene age. Faulting removed the southern rim of the volcano, exposing the central crater to the sea. Subsequently, the formation of a calcareous sand spit or tombolo separated this marine embayment from the sea, forming the island's present brackish water lake, which is frequented by Gray Ducks (*Anas superciliosa*). At the southwestern end of Tikopia a sandy flat has prograded across the fringing reef platform. This lowland calcareous plain contains extensive archaeological deposits, including the deep stratigraphic sequence of Sites TK-1, -35, and -36. Kirch and Yen (1982:79–85,346–349) described in detail these extensive geomorphological changes in the Tikopian landscape during the past 3,000 years.

The vegetation of Tikopia is thoroughly managed by the island's human population, with most of the land surface covered in a mosaic of orchard gardens and shifting cultivations (Kirch & Yen 1982:25–63). The dominance of arboriculture, rather than open field cropping, provides much habitat for birds such as the Rainbow Lorikeet (*Trichoglossus haematodus*), noisy flocks of which are commonly sighted in the crowns of sago palms (*Metroxylon salomonense*). Primary rainforest vegetation survives on the western coastal cliffs and on the steep cliffs rimming the inner slope of the crater lake. Difficult to climb by humans, these cliffs provide nesting habitats for boobies and noddies. Nonetheless, as Kirch and Yen (1982) extensively documented, most of the Tikopian landscape has been thoroughly modified through 3,000 years of human occupation.

The contemporary inhabitants of both islands are Polynesians, whose oral traditions indicate that their ancestors came from islands to the east, including 'Uvea, Futuna, Samoa, and Tonga. Culturally and linguistically, the people of Anuta and Tikopia are closely related and maintain regular inter-island contact through canoe-voyaging. Their languages are mutually intelligible, though distinct (Pawley 1967; Green 1971). The ethnography of Tikopia is meticulously described by Firth (1936, 1939, and other works) and that of Anuta by Firth (1954) and Feinberg (1981).

PREVIOUS ORNITHOLOGICAL STUDIES ON TIKOPIA AND ANUTA

There has never been a long-term study of the modern avifauna of Tikopia and Anuta. Our comparisons of the prehistoric and modern avifaunas would benefit greatly from a few weeks or months of intense ornithological survey on each island. A summary of modern records of birds on Tikopia and Anuta (Table 1) is based upon the references described below.

Members of the Whitney South Sea Expedition visited Anuta (which they called "Cherry Island" or "Anuda") on 8 February 1927 and Tikopia (called "Tucopia") on 11 and 12 February 1927 (Beck 1927:218–222; also see various WSSE publications in the Literature Cited). In spite of their great efforts, which yielded the only collection of birds ever made on Tikopia and the largest ever made on Anuta, the WSSE never compiled complete lists of species for either island. The specimens and field notes of the WSSE are housed in the Department of Ornithology, AMNH.

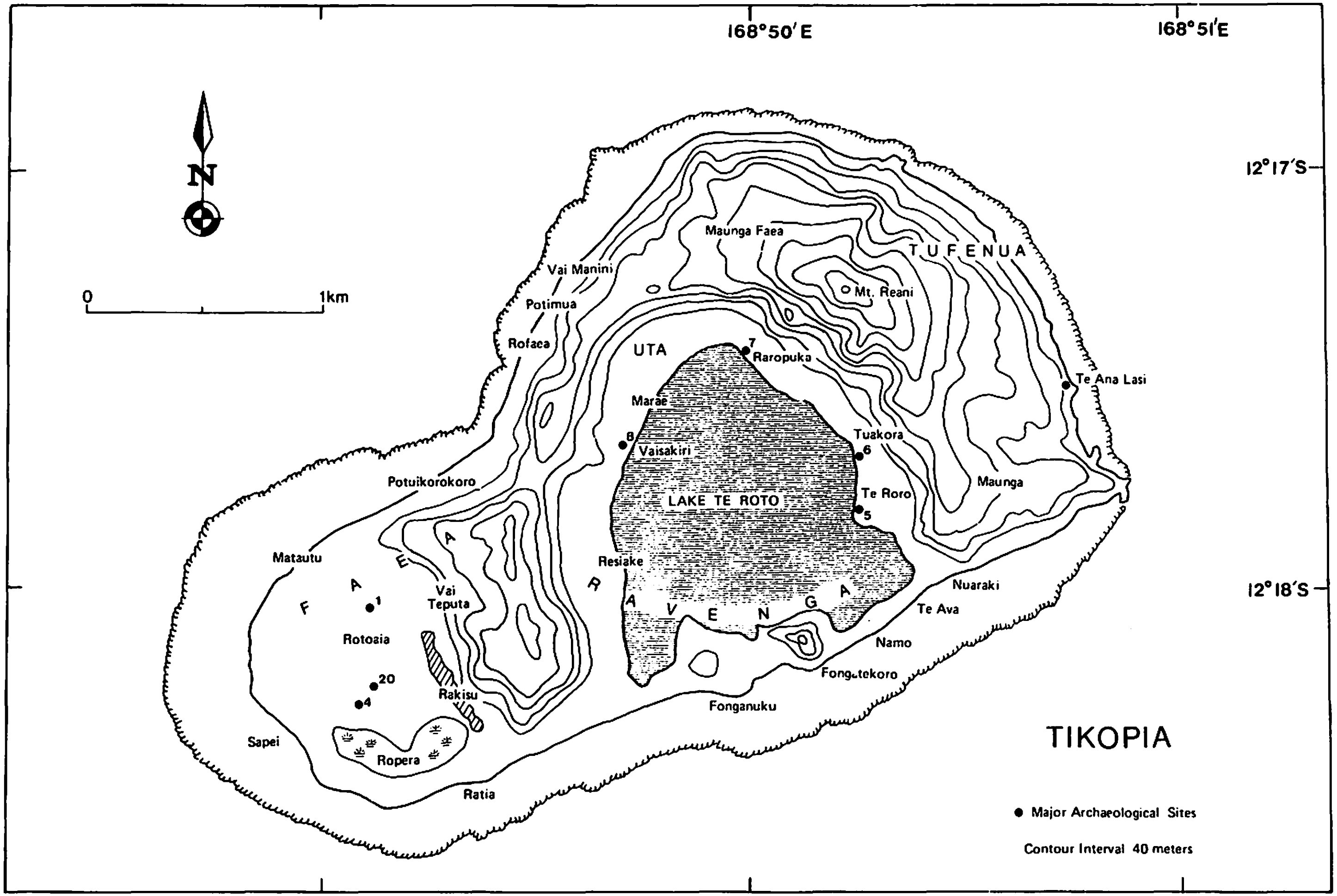

Fig. 3. Tikopia Island, showing natural and cultural features, traditional sites, and excavation sites (Kirch & Yen 1982:12).

Table 1. The birds of Tikopia and Anuta, Solomon Islands.

	Tikopia		Anuta	
	Modern record	Archaeo-logical record	Modern record	Archaeo-logical record
Sea birds				
Pterodroma rostrata (Tahiti Petrel)	X	X	—	—
* *Puffinus pacificus* (Wedge-tailed Shearwater)	?	X	—	X
Puffinus lherminieri (Audubon's Shearwater)	—	X	—	X
* *Phaethon rubricauda* (Red-tailed Tropicbird)	X	X	—	—
* *Phaethon lepturus* (White-tailed Tropicbird)	X	X	X	X
Papasula abbotti (Abbott's Booby)	—	X	—	—
Sula dactylatra (Masked Booby)	X	X	—	—
Sula leucogaster (Brown Booby)	X	X	X	X
Sula sula (Red-footed Booby)	—	X	—	X
Phalacrocorax melanoleucos (Little Pied Cormorant)	X	—	—	—
Fregata minor (Great Frigatebird)	?	X	X	X
Fregata ariel (Lesser Frigatebird)	?	X	—	X
Sterna fuscata (Sooty Tern)	—	X	—	X
Sterna lunata (M?) (Gray-backed Tern)	X	—	—	—
* *Anous stolidus* (Brown Noddy)	X	X	X	X
Anous minutus (Black Noddy)	X	X	X	X
* *Gygis alba* (Common Fairy-Tern)	X	—	X	—
Land birds				
Egretta sacra (Pacific Reef-Heron)	X	—	—	—
* *Anas superciliosa* (Gray Duck)	X	X	—	—
* *Pluvialis dominica* (M) (Pacific Golden Plover)	X	X	X	X
* *Charadrius mongolus* (M) (Mongolian Plover)	X	—	—	—
Heteroscelus incanus (M) (Wandering Tattler)	X	X	—	—
Numenius phaeopus (M) (Whimbrel)	?	—	—	—
Numenius tahitiensis (M) (Bristle-thighed Curlew)	X	X	—	—
Limosa lapponica (M) (Bar-tailed Godwit)	X	—	—	—

The Templeton Crocker Expedition of the California Academy of Sciences visited Anuta ("Anuda") on 15 July 1933, collecting two specimens of Black Noddy (*Anous minutus*) (Davidson 1934).

Sir Harry Luke visited Tikopia on 6 May 1941, making these observations of birds (Luke 1945:190,191): "Bosun birds [either *Phaethon lepturus* or *Phaethon rubricauda*] were flying about the cliffs . . . near the Christian village of Faea. . . . On the lake we saw some wild ducks [*Anas superciliosa*] . . . . Overhead flew pigeon [*Ducula pacifica*] and red and green parakeets [*Trichoglossus haematodus*]."

Kirch and Yen (1982:282–284) summarized the modern and prehistoric avifaunas of Tikopia. Their data on modern birds were based upon observations of R. Firth in 1928–29, 1952, and 1966, and their own observations in 1977 and 1978. The data of Kirch and Yen (1982, Table 41), combined with those of WSSE, yield a fairly complete picture of the modern avifauna of Tikopia, although uncertainties still exist. Information on the modern birds of Anuta remains less complete.

Table 1 continued

	Tikopia		Anuta	
	Modern record	Archaeo-logical record	Modern record	Archaeo-logical record
Arenaria interpres (M) (Ruddy Turnstone)	X	—	X	X
★ *Megapodius freycinet* (Common Megapode)	—	X	—	—
★ *Gallus gallus* (I) (Chicken)	X	X	X	X
Gallirallus philippensis (Banded Rail)	—	X	—	—
★ *Porphyrio porphyrio* (Purple Swamphen)	X	X	—	—
★ *Ducula pacifica* (Pacific Pigeon)	X	X	X	—
Trichoglossus haematodus (Rainbow Lorikeet)	X	—	—	—
Eudynamis taitensis (M) (Long-tailed Cuckoo)	X	X	X	X
Collocalia vanikorensis (Vanikoro Swiftlet)	X	—	—	—
Halycon chloris (Collared Kingfisher)	X	—	—	—
Aplonis tabuensis (Polynesian Starling)	X	X	—	—
Myzomela cardinalis (Cardinal Honeyeater)	X	—	—	—
Totals				
All species	27–31	25	11	14
All resident species	17–21	20	7	10
Resident sea birds	10–14	14	6	10
Resident land birds	7	6	1	0
Combined totals				
All species	36–37		16	
All resident species	26–27		12	
Resident sea birds	16–17		11	
Resident land birds	11		1	

★ = species reported from archaeological sites on Tikopia by Kirch and Yen (1982); I = introduced by man; M = migrant.

"Resident" totals exclude I, M. Combined totals = modern + archaeological.

ARCHAEOLOGICAL BACKGROUND

The archaeological investigation of Anuta was carried out by PVK and Paul Rosendahl in November-December 1971, as part of the first phase of the Southeast Solomon Islands Culture History Program of the Bishop Museum (Kirch & Rosendahl 1973, 1976; Green & Cresswell 1976). Prior to that study nothing was known of the island's archaeology or prehistory, and indeed, very little was on record of its ethnography (Firth 1954). A series of test excavations in the lowland calcareous flat revealed a large, stratified occupation site (AN-6), which was the focus of several larger excavations (Areas A to D). Site AN-6 yielded plainware Lapitoid ceramics and a large array of *Turbo*-shell fishhooks from the earliest occupation levels (Kirch & Rosendahl 1976). Radiocarbon dating suggested initial settlement of Anuta about 950 B.C. All of the bird bones analyzed herein are from Site AN-6.

Because the work on Anuta in 1971 had been limited essentially to test excavation, expanded excavations at AN-6 were planned as part of the 1977–78 phase of the Southeast Solomon

Islands Culture History Program. Two efforts by PVK to reach Anuta during this period were thwarted by heavy seas and shipping breakdowns, and no further archaeological study has been conducted. However, a reanalysis of the 1971 field data prompted Kirch (1982) to revise the stratigraphic sequence of Site AN-6, grouping the occupation strata into a series of chrono-stratigraphic zones. Zone E represents initial occupation of the island at ca. 950 B.C. Zone D represents continued occupation of Anuta by a pottery-making population during the first millennium B.C. Zone C is a massive deposit of largely sterile calcareous sand, which probably resulted from a major high-energy storm such as one of the cyclones that periodically lash the southeastern Solomon Islands. Anuta was evidently abandoned at about this time, perhaps as a result of the devastation of the island's fragile terrestrial ecosystem. Reoccupation of Anuta is indicated by Zone B deposits, with an earth oven dating to A.D. 580. Zone A is the extensive midden capping the AN-6 site, which is continuing to be deposited within the presently occupied village area. Until further excavations can be conducted on Anuta, this sequence appears to be the best interpretation of the 1971 test excavation results.

Tikopian archaeology was investigated by PVK in 1977 and 1978 as part of the second phase of the Southeast Solomon Islands Culture History Program (Kirch & Yen 1982; Kirch 1986a). Archaeological field strategy included a large series of test and transect excavations throughout the island, as well as intensive excavations at several key site localities. A total excavated area of 204 m^2 yielded a rich archaeological record with more than 5,000 artifacts and more than 35,000 vertebrate faunal remains. The faunal materials, dominated by fish bones, were analyzed by Kirch and Yen (1982:274–310), although identification of the avifaunal component was hampered by inadequate reference collections.

Tikopian prehistory can be subdivided into four cultural phases based on analysis of both artifactual and faunal materials (Kirch & Yen 1982:311–334). The Kiki phase (900–100 B.C.) began with initial colonization of the island by makers of a largely plainware, Lapitoid pottery. The Sinapupu phase (100 B.C.–1200 A.D.) is marked by the cessation of local pottery manufacture and by the importation of small quantities of exotic ceramics from Vanuatu to the south. The Tuakamali phase (1200–1800 A.D.) marks the arrival of immigrant populations of Polynesian speakers from the east. The Historic phase (post 1800 A.D.) marks the period of slight European influence. In some of the archaeological strata, it is difficult or impossible to distinguish between late Tuakamali and early Historic.

Most of the bird bones from Tikopia are from three localities (Tables 3, 4, 9). Virtually the entire prehistory of Tikopia is encapsulated within a deep stratigraphic sequence at the Sinapupu locality, including the arbitrary site designations TK-1, -35, and -36 (Kirch & Yen 1982:89–111). Individual strata in these excavations were combined into chrono-stratigraphic zones that can be correlated with the prehistoric cultural phases described above. The Kiki Site (TK-4) appears to represent the island's initial settlement locality, although its disturbed (gardened) upper Layer I also incorporates a very late prehistoric occupation component. The undisturbed Layer II of TK-4 contains materials dating exclusively to the early Kiki phase. Bird bones were also recovered from Sites TK-7, -8, -9, and -20 (Tables 5–8). TK-7 and -8 are midden deposits along the inner shore of the brackish water lake. TK-9 is a large rock shelter situated on the island's eastern coast. TK-20 is a major site of stone alignments in the Rotoaia area of western Tikopia. Sites TK-7, -8, -9, and -20 were occupied primarily or solely during the Tuakamali phase. Full details of all excavated sites are presented in Kirch and Yen (1982).

SPECIES ACCOUNTS

ORDER PROCELLARIIFORMES

FAMILY PROCELLARIIDAE

Pterodroma rostrata (Peale). Tahiti Petrel.

Material examined. TIKOPIA: NISP = 3, MNI = 2. Coracoid, BPBM 166358; humerus, BPBM 166068; ulna, BPBM 166286.

Remarks. This large petrel nests in the Marquesas, Society Islands, Solomon Islands, and New Caledonia (Murphy & Pennoyer 1952:20). The modern distribution is very localized within these island groups, although bones from archaeological sites in the Marquesas and Society Islands show that *Pterodroma rostrata* was previously more widespread. This is the first record from Tikopia. There are no records from Anuta. Kirch and Yen (1982:284) reported an unknown sea bird known to the Tikopia as *makatapa*. Firth (1985:230) listed the Tikopia *manu sina* as "?giant petrel." Perhaps one of these two names refers to *P. rostrata*.

The WSSE sighted individuals of Stejneger's Petrel, *P. longirostris* (Stejneger) and White-naped Petrel, *P. cervicalis* (Salvin), at sea 30 mi WSW of Tikopia on 13 February 1927 (Beck 1927:222). Neither of these species is known to nest in truly tropical waters. Because of the poor reliability of sight records of *Pterodroma*, we cannot be certain that these birds were identified accurately.

Pterodroma, species unknown. Indeterminate petrels.

Material examined. TIKOPIA: NISP = 2. Humerus, BPBM 166196; tarsometatarsus, BPBM 166118.

Remarks. These two specimens represent a large species of *Pterodroma*, but are too fragmentary for species-level identification. Because they may represent *P. rostrata*, these specimens yield no MNI and are not regarded as a distinct taxon in Table 1.

Puffinus pacificus (Gmelin). Wedge-tailed Shearwater (Tikopia *manu uri*).

Material examined. TIKOPIA: NISP = 1, MNI = 1. Humerus, BPBM 166240. ANUTA: NISP = 1, MNI = 1. Femur, BPBM 165699.

Remarks. The humerus from Tikopia is only tentatively referred to *Puffinus pacificus*, clearly being a species of *Puffinus* (rather than *Pterodroma*) in the size range of *Puffinus pacificus*. The distinctive femur from Anuta is confidently referred to *P. pacificus* because it is larger than the femur of *P. lherminieri* or *P. nativitatis* Streets. Moreover, the shaft of the femur is more curved than in any species of *Pterodroma*. The breeding distribution of *P. pacificus* includes virtually all island groups of the tropical Pacific (Murphy 1951: Fig. 1), although usually there are few nesting islands within any given island group. The only modern record of *P. pacificus* from the region is an unknown number seen 30 mi WSW of Tikopia on 13 February 1927 (Beck 1927:222). *Puffinus pacificus* is not known to nest on Tikopia today, although the Tikopia have a name (*manu uri*) for this species (Kirch & Yen 1982:283; Firth 1985:230), perhaps based upon birds seen at sea. The femur is the first record for Anuta.

Puffinus lherminieri Lesson. Audubon's Shearwater.

Material examined. TIKOPIA: NISP = 1, MNI = 1. Tibiotarsus, BPBM 181540. ANUTA: NISP = 35 (nearly all major skeletal elements represented), MNI =14. BPBM 165778–165780, 165782–165792, 165797, 165815, 165821, 165822, 165826, 165828–165830, 165860–165862, 165915, 165916, 165935, 165947, 165952, 165955, 165958, 165963, 165966, 165979.

Remarks. These are the first records of *Puffinus lherminieri* on Tikopia and Anuta. The nearest modern record for *P. lherminieri* is a sighting at sea 30 mi WSW of Tikopia on 13 February 1927 (Beck 1927:222). This small shearwater is very widespread in the tropical Pacific, although, like *P. pacificus*, the distribution within individual island groups is very discontinuous. Its bones are found commonly in Polynesian archaeological sites in the Marquesas, Society Islands, Cook Islands, and Tonga (Steadman 1989a).

Procellariidae, genus (?genera) and species unknown. Indeterminate petrels and/or shearwaters.

Material examined. TIKOPIA: NISP = 15, MNI = 0. Sternum, BPBM 166134; 2 scapula, BPBM 166082, 166237; humerus, BPBM 166083; 6 ulnae, BPBM 166128, 166165, 166259, 166324, 166325, 166377; carpometacarpus, BPBM 166084; femur, BPBM 166175; 3 tibiotarsi, BPBM 166136, 166185, 166186.

Remarks. These fragmentary specimens represent medium to large-sized species of *Pterodroma* and/or *Puffinus*.

ORDER PELECANIFORMES

FAMILY PHAETHONTIDAE

Phaethon rubricauda Boddaert. Red-tailed Tropicbird.

Material examined. TIKOPIA: NISP = 4, MNI = 2. Humerus, BPBM 166124; 3 carpometacarpi, BPBM 166075, 166210/166211, 166219.

Remarks. Kirch and Yen (1982:283) recorded *Phaethon rubricauda* for modern Tikopia, although a local name for it was not obtained. There are no records for Anuta. This large tropicbird is very widespread in the tropical Pacific and Indian oceans. Bones of *P. rubricauda* occur in Polynesian archaeological sites on Henderson Island (Schubel & Steadman 1989) and Mangaia (Steadman 1985).

Phaethon lepturus Daudin. White-tailed Tropicbird (Tikopia, Anuta *tavake*).

Material examined. TIKOPIA: NISP = 15, MNI = 6. Mandible, BPBM 166314; 3 coracoids, BPBM 166116, 181537, 181538; 4 humeri, BPBM 166177, 166203, 166326, 166376; 3 ulnae, BPBM 166168, 166357, 181491; carpometacarpus, BPBM 166197; 2 manus digit II phalanx 1, BPBM 166163, 166342; pelvis, BPBM 166248. ANUTA: NISP = 1, MNI = 1. Scapula, BPBM 165978.

Remarks. This small tropicbird, a symbol of the Kafika deities (Firth 1985:516), still occurs on Tikopia (Beck 1927:221; Kirch & Yen 1982:283) and Anuta (Beck 1927:218). It was nesting on Tikopia on 11 February 1927 (Beck 1927:221). *Phaethon lepturus* is very widespread in the tropical Pacific, Indian, and Atlantic oceans. Bones of *P. lepturus* occur in Polynesian archaeological sites on Henderson Island, the Marquesas, Huahine, Mangaia, and 'Eua (Steadman 1989a).

FAMILY SULIDAE

Papasula abbotti (Ridgway). Abbott's Booby.

Material examined. TIKOPIA: NISP = 2, MNI = 1. Coracoid, BPBM 166283; tarsometatarsus, BPBM 166234.

Remarks. The osteological, systematic, and biogeographical details of these specimens are discussed in Steadman, Schubel, and Pahlavan (1988). Tikopia is 6,400 km east of the only locality where *Papasula a. abbotti* survives (Christmas Island in the Indian Ocean). Bones of a distinctive, extinct subspecies of Abbott's Booby, *P. a. costelloi*, have been recovered from archaeological sites in the Marquesas (Steadman, Schubel & Pahlavan 1988), extending the former range of this endangered species an additional 4,800 km eastward into the Pacific. The Tikopian bones of *P. a. abbotti* are found only in the Kiki phase of Site TK-4, suggesting that this tree-nesting booby was extirpated very shortly (within a few decades to a few centuries) after the human colonization of Tikopia. There are no records of this species from Anuta.

Sula dactylatra Lesson. Masked Booby (Tikopia *mauakena*).

Material examined. TIKOPIA: NISP = 3, MNI = 2. Pterygoid, BPBM 181605; coracoid, BPBM 181599; humerus, BPBM 181598.

Remarks. *Sula dactylatra* still occurs on Tikopia today (Kirch & Yen 1982:283), although its nesting status is unknown. None of the sulid bones from Anuta was large enough to be of this species. There are no modern records of this species from Anuta. *Sula dactylatra* is widespread in the tropical Pacific and Indian oceans, although nesting islands are relatively few.

Sula leucogaster (Boddaert). Brown Booby (Tikopia *katoko*).

Material examined. TIKOPIA: NISP = 2, MNI = 2. Radius, BPBM 166241; tibiotarsus, BPBM 166182. ANUTA: NISP = 5, MNI = 2. Quadrate, BPBM 165971; sternum, BPBM 165874; coracoid, BPBM 165846; ulnare, BPBM 165909; tibiotarsus, BPBM 165720.

Remarks. The only modern record of *Sula leucogaster* from Tikopia is that of Kirch and Yen (1982:283). There is a sight record from Anuta on 8 February 1927 (Beck 1927:218). *Sula leucogaster* occurs in many localities scattered through the tropical Pacific, Indian, and Atlantic oceans.

Sula sula (Linnaeus). Red-footed Booby.

Material examined. TIKOPIA: NISP = 44 (nearly all major skeletal elements represented), MNI = 13. BPBM 166073, 166120, 166139, 166188, 166214, 166216–166218, 166233, 166239, 166242, 166243, 166249, 166250, 166262, 166273, 166284, 166294, 166328, 166352–166354, 166382, 166386–166398, 166415, 166416, 181547, 181559, 181585, 181588, 181592, 181593. ANUTA: NISP = 85 (nearly all major skeletal elements represented), MNI = 7. BPBM 165703, 165706, 165707, 165709–165712, 165718, 165743–165759, 165762, 165764–165774, 165793, 165845, 165848, 165850–165854, 165856–165858, 165872, 165873, 165879, 165880, 165887, 165891, 165892, 165895, 165898–165901, 165903, 165904, 165906, 165908, 165910–165912, 165923–165927, 165930, 165931, 165973, 165975, 165982, 165985, 165987, 165988, 165990–165992, 165994, 165996.

Remarks. There are no modern records of *Sula sula* from Tikopia or Anuta. This is the most common species of bird from the archaeological site on Anuta, and the second most common species from the Tikopian sites. Although *S. sula* is widespread in tropical oceans today, bones from archaeological sites on Henderson Island, the Marquesas, and Society Islands indicate that nesting populations have been removed from many islands within the Pacific range of the species (Steadman 1989a).

Sula, species unknown. Indeterminate boobies.

Material examined. TIKOPIA: NISP = 27 (nearly all major skeletal elements represented), MNI = 7. BPBM 166287, 166293, 166399, 166414, 181523, 181542, 181558, 181563, 181564, 181566, 181567, 181580–181584, 181587, 181589–181591, 181595, 181600–181602, 181641, 181642, 181648. ANUTA: NISP = 51 (nearly all major skeletal elements represented), MNI = 0. BPBM 165695, 165702, 165708, 165713–165717, 165719, 165727, 165760, 165761, 165763, 165775, 165794, 165816, 165847, 165849, 165855, 165868, 165875–165878, 165881–165886, 165888–165890, 165893, 165894, 165896, 165897, 165902, 165905, 165907, 165928, 165929, 165949–165951, 165972, 165974, 165993, 165995, 165997, 165998.

Remarks. These fragmentary specimens cannot be distinguished from the bones of *Sula sula* or *S. leucogaster.* They are too small to represent *S. dactylatra.*

FAMILY PHALACROCORACIDAE

Phalacrocorax melanoleucos (Vieillot). Little Pied Cormorant (Tikopia *manu fiti*).

Material examined. None.

Remarks. The WSSE collected two specimens of *Phalacrocorax melanoleucos* on Tikopia on 11–12 February 1927 (Amadon 1942) and saw about 10 other individuals (Beck 1927:219). This species is also listed for Tikopia by Kirch and Yen (1982:283) and Firth (1985:230). There are no records of this species from Anuta. Tikopia is the easternmost locality in the modern range of *P. melanoleucos*, which extends discontinuously through the Solomon Islands and New Caledonia to Australia, New Guinea, Indonesia, and Palau (Amadon 1942). The absence of its bones from archaeological sites might suggest that this small cormorant colonized Tikopia since the arrival of humans. This suggestion is supported by the apparent lack of differentiation between the Tikopia population and other populations except those on Rennell and New Zealand (Amadon 1942).

FAMILY FREGATIDAE

Fregata minor (Gmelin). Great Frigatebird (Tikopia *rofa*).

Material examined. TIKOPIA: NISP = 9, MNI = 3. Sternum, BPBM 166198; coracoid, BPBM 166220; scapula, BPBM 166298; 4 humeri, BPBM 166160, 166315, 181503, 181504; radius, BPBM 166316; manus digit II phalanx 1, BPBM 166069. ANUTA: NISP = 12, MNI = 5. 3 coracoids, BPBM 165698, 165731, 165732; scapula, BPBM 165831; 2 humeri, BPBM 165728, 165832; 2 ulnae, BPBM 165736, 165738; 3 radii, BPBM 165741, 165870, 165871; tibiotarsus, BPBM 165865.

Remarks. These specimens are larger than the bones of *Fregata ariel.* The WSSE collected one specimen of *F. minor* on Anuta on 8 February 1927 (Beck 1927:218). *Fregata minor* occurs in the South Atlantic and the tropical portions of the Pacific and Indian oceans.

Firth (1985:403) defined the Tikopia word *rofa* as *F. minor,* which "nests on Tikopia," thus providing the only record of *F. minor* for Tikopia. Firth (1985:203) defined *rofa kaute* as the "Wattled Frigate Bird (*F. aquila*)," which nests on Fatutaka. As *F. aquila* (Linnaeus) is usually regarded as a subspecific name for Atlantic populations of *F. minor,* we believe that Firth's *rofa kaute* is the male of *F. minor,* whose red throat patch would account for the name "Wattled Frigate Bird." Clark (1982) noted that the two Polynesian species of *Fregata* (*F. minor* and *F. ariel*) are not distinguished in any Polynesian language. We also have found this to be true on all Polynesian islands we have visited.

Fregata ariel (Gray). Lesser Frigatebird.

Material examined. TIKOPIA: NISP = 3, MNI = 1. Humerus, BPBM 166282; radius, BPBM 166115; carpometacarpus, BPBM 166080. ANUTA: NISP = 7, MNI = 2. Mandible, BPBM 165729; coracoid, BPBM 165730; scapula, BPBM 165733; 3 ulnae, BPBM 165737, 165739, 165740; carpometacarpus, BPBM 165986.

Remarks. These specimens are smaller than the bones of all individuals of *Fregata minor.* Although the bones listed above are the first records of *F. ariel* from either Tikopia or Anuta, modern sight records of *Fregata* have not been identified to species (Kirch & Yen 1982:283). Both species of *Fregata* wander far from roosting and nesting islands, especially during storms. Thus it is likely that both *F. ariel* and *F. minor* still visit (but probably do not nest on) both Tikopia and Anuta, which is why neither is counted among the extirpated species. *Fregata ariel* occurs locally through much of the tropical Pacific, Indian, and Atlantic oceans.

Fregata, species unknown. Indeterminate frigatebirds.

Material examined. ANUTA: NISP = 6. Mandible, BPBM 165735; 2 coracoids, BPBM 165961, 165970; scapula, BPBM 165936; 2 ulnae, BPBM 165734, 165735.

Remarks. These specimens fall into the range of size overlap between the bones of *Fregata minor* and *F. ariel*. The bones of female *F. minor* are consistently larger than any bones of *F. ariel*, while the bones of male *F. ariel* are always smaller than any bones of *F. minor*. The bones of male *F. minor* and female *F. ariel* are often impossible to distinguish.

FAMILY LARIDAE

SUBFAMILY STERNINAE

Sterna fuscata Linnaeus. Sooty Tern.

Material examined. TIKOPIA: NISP = 2, MNI = 1. Humerus, BPBM 166344; ulna, BPBM 166174. ANUTA: NISP = 4, MNI = 2. Maxilla, BPBM 165705; quadrate, BPBM 165932; scapula, BPBM 165934; ulna, BPBM 165818.

Remarks. We refer these specimens to *Sterna fuscata* rather than the similarly sized *Anous stolidus* because of these characters: quadrate—broader processus orbitalis quadrati, with a large basal foramen; rostrum—narrower and straighter; scapula—more dorso-ventrally compressed proximal portion of the blade; humerus—sharper apex of crista pectoralis, less pneumatic proximal end, larger fossae pneumotricipitalis, deeper fossa musculo brachialis, sharper caudal surface of proximal portion of shaft; ulna—larger overall, smaller cotyla dorsalis, larger papillae remigiales caudales, more elongate tuberculum carpale.

This is the first record from either Tikopia or Anuta for *Sterna fuscata*, which occurs locally throughout tropical oceans. Kirch and Yen (1982:283) and Clark (1982) listed the Tikopia name *tara* for *Sterna* sp., which could refer to either *S. fuscata* or *S. lunata*. Kirch and Yen (1982:283) also listed the name *rakia* for an unknown bird thought to be a tern. Clark (1982) identifies the Tikopia *rakia* as *Anous tenuirostris* (Temminck) (= *A. minutus*; see below). Firth (1985:230) listed the Tikopia *manu riki* as a general term for terns and *manu tai* as the Common Tern (*Sterna hirundo* Linnaeus), a migratory species not otherwise recorded for Tikopia.

Sterna lunata Peale. Gray-backed Tern.

Material examined. None.

Remarks. A single individual of *Sterna lunata* was collected just offshore of Tikopia on 11 February 1927 (Beck 1927:221). There is no evidence that *S. lunata* nests on Tikopia. There are no records of this species from Anuta. *Sterna lunata* occurs through much of the tropical Pacific.

Anous stolidus (Linnaeus). Brown Noddy (Tikopia *ngongo*).

Material examined. TIKOPIA: NISP = 135 (nearly all major skeletal elements represented), MNI = 38. BPBM 166070, 166079, 166086–166089, 166091–166093, 166095, 166098–166100, 166102, 166104–166108, 166110, 166111, 166113, 166117, 166121, 166122, 166133, 166135, 166137, 166138, 166141–166144, 166152–166156, 166158, 166164, 166167, 166169, 166170, 166172, 166173, 166176, 166178, 166179, 166189, 166191–166193, 166204, 166224, 166226, 166245–166247, 166252, 166256, 166257, 166271, 166272, 166279, 166280, 166289, 166292, 166296, 166308, 166309, 166321–166323, 166329, 166330, 166337, 166339, 166340, 166343, 166347–166351, 166361–166366, 166371, 166378–166380, 166385, 166400, 166402–166406, 166412, 166420–166422, 181493, 181497, 181507, 181530, 181532, 181541, 181543, 181565, 181568–181570, 181572, 181573, 181575, 181576, 181594, 181596, 181597, 181604, 181606, 181608, 181611, 181618, 181619, 181621, 181622, 181625, 181626, 181644, 181645. ANUTA: NISP = 44 (nearly all major skeletal elements represented), MNI = 12. BPBM 165697, 165700, 165704, 165722, 165724, 165776, 165777, 165781, 165795, 165796, 165798, 165799, 165800, 165801, 165803, 165804, 165809, 165819, 165820, 165833–165835, 165838, 165840, 165841, 165859, 165863, 165913, 165914, 165933, 165939, 165941–165944, 165953, 165954, 165956, 165959, 165960, 165967–165969, 165980.

Remarks. *Anous stolidus* is the best represented species in the archaeological record of Tikopia and the second most common archaeological species on Anuta. While species of *Anous* are rare in non-anthropogenic fossil sites on oceanic islands (Olson 1975, 1977; Olson & James 1982), bones of *Anous* spp. are common in Polynesian archaeological sites. As on Tikopia and Anuta, the pantropical *A. stolidus* usually outnumbers *A. minutus* in these situations. *Anous stolidus* was nesting on Tikopia on 11 February 1927 (Beck 1927:221) and was listed for Tikopia by Kirch and Yen (1982:283). This species is still eaten by the Tikopia and is sometimes kept as a pet. "A few" specimens of *A. stolidus* were collected on Anuta on 8 February 1927 (Beck 1927:218). The nesting requirements of *A. stolidus* are very versatile, which probably explains its high survivability on inhabited islands.

Anous minutus Boie. Black Noddy (Tikopia *rakia*).

Material examined. TIKOPIA: NISP = 35 (nearly all major skeletal elements represented), MNI = 15. BPBM 166078, 166085, 166090, 166094, 166096, 166097, 166157, 166171, 166202, 166346, 166381, 166408–166410, 166413, 166417, 166418, 166495, 181520, 181548, 181571, 181574, 181607, 181609, 181612–181617, 181620, 181624, 181631, 181637, 181639. ANUTA: NISP = 10, MNI = 4. Sternum, BPBM 165805; coracoid, BPBM 165701; 4 humeri, BPBM 165723, 165810, 165836, 165837; 4 ulnae, BPBM 165817, 165823, 165918, 165957.

Remarks. *Anous minutus* was nesting on Tikopia on 11 February 1927 (Beck 1927:221). "A few" specimens of *A. minutus* were taken on Anuta on 8 February 1927 (Beck 1927:218). Two others were collected on Anuta on 15 July 1933 by the Templeton Crocker Expedition (Davidson 1934). The bones reported here include most of those reported as *Gygis alba* by Kirch and Yen (1982:283). *Anous minutus* is widespread in the tropical Pacific and Indian oceans.

Gygis alba (Sparrman). Common Fairy-Tern (Tikopia *akiaki*).

Material examined. None.

Remarks. All of the bones reported by Kirch and Yen (1982:283) as *Gygis alba* are from indeterminate terns or *Anous minutus*. *Gygis alba* was nesting on Tikopia on 11 February 1927 (Beck 1927:221) and was listed for Tikopia by Kirch and Yen (1982:283). A few individuals of *G. alba* were seen on Anuta on 8 February 1927 (Beck 1927:218). *Gygis alba* is very widespread in tropical oceans. The lack of bones of *G. alba* from Tikopia and Anuta is puzzling. This small tern is found regularly in archaeological sites elsewhere in Polynesia. Like *Anous stolidus*, the plastic breeding requirements of *G. alba* probably explain its relatively high compatibility with human occupation.

Sterninae, genus (?genera) and species unknown. Indeterminate terns.

Material examined. TIKOPIA: NISP = 20, MNI = 2. 4 coracoids, BPBM 166109, 166221, 166260, 181521; 2 scapulae, BPBM 166103, 166401; furcula, BPBM 166411; 3 humeri, BPBM 166190, 166206, 166334; 6 ulnae, BPBM 166101, 166114, 166288, 166306, 166307, 166332; radius, BPBM 166407; carpometacarpus, BPBM 166129; manus digit II phalanx 1, BPBM 166341; tibiotarsus, BPBM 166130. ANUTA: NISP = 14, MNI = 0. 3 coracoids, BPBM 165802, 165938, 165962; 4 humeri, BPBM 165839, 165917, 165940, 165981; 2 radii, BPBM 165827, 165948; 2 carpometacarpi, BPBM 165825, 165983; manus digit II phalanx 1, BPBM 165984; 2 synsacra, BPBM 165725, 165842.

Remarks. Although much of this material probably represents *Anous stolidus* or *A. minutus*, the specimens are too fragmentary to identify even to genus.

ORDER CICONIIFORMES

FAMILY ARDEIDAE

Egretta sacra (Gmelin). Pacific Reef-Heron (Tikopia *keo*).

Material examined. None.

Remarks. The WSSE collected a male and female of *Egretta sacra* on Tikopia in February 1927 (Mayr & Amadon 1941). Kirch and Yen (1982:283) listed *E. sacra* for Tikopia. Firth (1985:182) stated that the Tikopia recognize the light (*keo kena*) and dark (*keo uri*) phases of this heron. *Egretta sacra* is found nearly throughout the tropical Pacific and may occur on Anuta, although there are no records. Clark (1982) noted *motuku* as another Tikopia name for *E. sacra*. *Motuku* is the widespread Polynesian cognate for *E. sacra*. *Keo* is cognate with *kao*, a widespread name for the Striated Heron, *Butorides* (*Ardeola*) *striata* (Linnaeus), a much smaller and more localized species unrecorded on Tikopia and Anuta. The scarcity or lack of bones of *Egretta sacra* in most Polynesian archaeological sites is because these "fishy" tasting birds were seldom eaten.

ORDER ANSERIFORMES

FAMILY ANATIDAE

Anas superciliosa Gmelin. Gray Duck (Tikopia *toroa*).

Material examined. TIKOPIA: NISP: 2, MNI = 1. Coracoid, BPBM 181519; scapula, BPBM 181518.

Remarks. The WSSE collected 13 specimens of *Anas superciliosa* on Tikopia on 11–12 February 1927 (Amadon 1943). At that time, the ducks were plentiful and had several broods of small young (Beck 1927:219). Luke (1945:191) also noted ducks on Te Roto ("the lake"), Tikopia in May 1941, as did Kirch and Yen (1982:283–284) in 1977–1978. There are no records from Anuta. The bones of *A. superciliosa* were from two test pits of the Tuakamali phase. Thus it may be that *A. superciliosa* colonized Tikopia only after the accretion of calcareous sands closed Te Roto from the sea. *Anas superciliosa* occurs in various fresh, brackish, and (rarely) salt water habitats from Indonesia, Australia, and New Guinea through much of Polynesia. The lack of differentiation of the oceanic populations and the lack of dated, early archaeological records from anywhere in Polynesia suggest that *A. superciliosa* is a recent colonizer of many islands, including Tikopia.

ORDER CHARADRIIFORMES

FAMILY CHARADRIIDAE

Pluvialis dominica (P.L.S. Müller). Lesser Golden-Plover (Tikopia, Anuta *turi*).

Material examined. TIKOPIA: NISP = 4, MNI = 4. Coracoid, BPBM 166254; 2 humeri, BPBM 166184, 166301; tarsometatarsus, BPBM 166251. ANUTA: NISP = 3, MNI = 1. 2 humeri, BPBM 165812, 165814; ulna, BPBM 165824.

Remarks. This migratory shorebird is common throughout Oceania. "Quite a lot" of *Pluvialis dominica* were seen on Tikopia on 11 February 1927 (Beck 1927:219). Kirch and Yen (1982:283) listed *P. dominica* for Tikopia, noting that modern Tikopia regard the bird as sacred. A single individual of *P. dominica* was seen on Anuta on 8 February 1927 (Beck 1927:218). We use the word *turi* for *P. dominica* somewhat cautiously because both Clark (1982) and Firth (1985:558) listed the Tikopia *turi* as a general term for migratory shorebirds.

Charadrius mongolus Pallas. Mongolian Plover.

Material examined. None.

Remarks. A "ring plover of some sort" was collected by the WSSE on the beach at Tikopia on 12 February 1927 in the company of one *Pluvialis dominica* and several *Arenaria interpres* (Beck 1927:283). Kirch and Yen (1982:283) listed "*Charadrius* sp. Plover *kiu*" as occurring today and in an archaeological context from Tikopia. We found no bones referable to *Charadrius*. The "ring plover" collected by the WSSE is a winter-plumage female of *C. mongolus* (AMNH 215556, examined by DWS in July 1988). This species breeds in northeastern Asia and winters in Micronesia and much of Melanesia. Tikopia is probably near the eastern limit of its regular winter range.

FAMILY SCOLOPACIDAE

Heteroscelus incanus (Gmelin). Wandering Tattler (Tikopia *turi vare*).

Material examined. TIKOPIA: NISP = 4, MNI = 4. 3 humeri, BPBM 166205, 166423, 181654; carpometacarpus, BPBM 166345.

Remarks. *Heteroscelus incanus* is very common and widespread in Oceania and undoubtedly occurs regularly today on Tikopia and Anuta. Nevertheless, the four bones from Tikopia are the only certain records for either island other than the definition of *turi vare* as the Tikopia word for *H. incanus* in Firth (1985:558).

Numenius phaeopus (Linnaeus). Whimbrel.

Material examined. None.

Remarks. An unknown number of probable *Numenius phaeopus* ("Hudsonian? Curlew") was seen on Tikopia on 11 February 1927 (Beck 1927:219). There are no specimens of *N. phaeopus* from Tikopia in AMNH. There are no records from Anuta. This large shorebird breeds at high northern latitudes, then migrates and winters through much of the tropical western Pacific, straying as far east as Tuvalu, Fiji, and Samoa.

Numenius tahitiensis (Gmelin). Bristle-thighed Curlew (Tikopia *kiu*).

Material examined. TIKOPIA: NISP = 2, MNI = 1. Cervical vertebra, BPBM 166331; humerus, BPBM 166302.

Remarks. These two specimens are larger than in *Numenius minutus* Gould and smaller than in *N. madagascariensis* (Linnaeus). They agree in size and other features with the cervical vertebra and humerus of *N. tahitiensis* but cannot be distinguished unequivocally from the similarly sized *N. phaeopus* (Linnaeus). The WSSE collected three females of *N. tahitiensis* on Tikopia on 11 and 12 February 1927 (Stickney 1943). Although there are no records of it from Anuta, *N. tahitiensis* is a widespread migrant and winter visitor in Polynesia and Melanesia, and probably visits Anuta at least occasionally. Kirch and Yen (1982:283) correlated the Tikopia name *kolili* with *Numenius* sp., which could be either *N. phaeopus* or *N. tahitiensis*. Firth (1985:191) identified *kolili* as the Common Sandpiper, *Actitis hypoleucos* (Linnaeus), a Eurasian migrant for which no other records exist from Tikopia or Anuta and which might be confused with *Heteroscelus incanus*.

Limosa lapponica (Linnaeus). Bar-tailed Godwit.

Material examined. None.

Remarks. The only record on Tikopia of *Limosa lapponica* is a female collected on 11 February 1927 by the WSSE (Stickney 1943). This migrant shorebird, relatively rare in the region covered here but more common to the west, has not been recorded from Anuta.

Arenaria interpres (Linnaeus). Ruddy Turnstone (Tikopia *turi fakataumako*).

Material examined. ANUTA: NISP = 1, MNI = 1. Coracoid, BPBM 165937.

Remarks. An unknown number of *Arenaria interpres* was seen on Tikopia on 11 February 1927; three others were seen on Anuta on 8 February 1927 (Beck 1927:218, 221). There are no specimens in AMNH. This distinctive shorebird, which breeds at high northern latitudes, migrates and winters through much of the tropical Pacific.

ORDER GALLIFORMES

FAMILY MEGAPODIIDAE

Megapodius freycinet Gaimard. "Scrub Fowl" or Common Megapode.

Material examined. TIKOPIA: NISP = 10, MNI = 4. Coracoid, BPBM 166317; radius, BPBM 166074; tibiotarsus, BPBM 166207; 3 tarsometatarsi, BPBM 166183, 166291, 166373; hallux, BPBM 181555; 2 pedal phalanges, BPBM 166126, 166338; claw, BPBM 166119.

Remarks. This is the first record of *Megapodius freycinet* for Tikopia. There are no records of it for Anuta. Green (1976:256) reported bones of megapodes (not identified to species) from Lapita sites in the Reef Islands, north of Santa Cruz (Nendo) Island. *Megapodius freycinet* has an extremely broad range (Amadon 1942), scattered from Indonesia, New Guinea, and northern Australia eastward to islands near Tikopia (Ureparapara, Gaua, and Valua in the Banks Islands and numerous islands in Vanuatu). *Megapodius freycinet* is widespread as well in the main group of the Solomon Islands. Considering the extinction/extirpation of various megapodes in Melanesia and Polynesia (see below), it is somewhat surprising that *M. freycinet* still survives on the Solomon Islands outlying atolls of Ontong Java and Sikaiana (Bayliss-Smith 1972), which have land areas of 9.5 km^2 and 1.3 km^2, respectively, roughly comparable to the areas of Tikopia and Anuta.

The only other extant species of *Megapodius* in Oceania are *M. pritchardi* G. R. Gray, a much smaller species confined to Niuafo'ou (Tonga) and *M. laperouse* Gaimard of Palau and the Marianas. Two extinct species of *Megapodius*, both larger than *M. freycinet*, are known from archaeological bones from Lifuka, Tonga (Steadman 1989a, b) and late Holocene fossils from New Caledonia (Balouet & Olson 1989). Also known from the late Holocene of New Caledonia is the extinct *Sylviornis neocaledoniae* Poplin, a truly giant megapode much larger than any species of *Megapodius* (Poplin, Mourer-Chauviré & Evin 1983, Poplin & Mourer-Chauviré 1985). Numerous 19th century records of megapodes (based upon eggs or sightings; mostly not determined to species) exist for Fiji, Tonga, and Samoa (Steadman 1989a, b). These records have generally been overlooked by modern authors because they were not included in the systematic review papers on megapodes by Mayr (1938) and Amadon (1942), which were based mainly on WSSE specimens.

Eight of the 10 bones of *M. freycinet* from Tikopia are from Layer II of Site TK-4, which Kirch and Yen (1982:326) regarded as the earliest human occupation of Tikopia. The ninth megapode bone is from lower strata of the Sinapupu phase of the Sinapupu locality, while the tenth is from Zone A_2 of Site TK-36, which includes a mixture of Kiki and Tuakamali phase sediments (Table 3). Thus, it is reasonable to suggest that *M. freycinet* became rare on Tikopia soon after the first arrival of people.

FAMILY PHASIANIDAE

Gallus gallus Linnaeus. Chicken (Tikopia, Anuta *kio*).

Material examined. TIKOPIA: NISP = 75 (nearly all major skeletal elements represented), MNI = 26. BPBM 166081, 166123, 166125, 166132, 166140, 166145–166151, 166159, 166166, 166187, 166194, 166195, 166199, 166201, 166208, 166209, 166212, 166213, 166215, 166235, 166258, 166267, 166269, 166270, 166274, 166277, 166290, 166299, 166300, 166304, 166311–166313, 166318–166320, 166355, 166356, 166359, 166360, 166367–166370, 166372, 166375, 166383, 166384, 181492, 181498, 181500, 181501, 181505, 181507, 181517, 181527, 181533, 181554, 181577, 181578, 181636, 181640, 181643, 181646, 181647, 181651–181653, 181655, 181656. ANUTA: NISP = 19 (most major skeletal elements represented), MNI = 6. BPBM 165696, 165721, 165726, 165742, 165806–165808, 165843, 165844, 165864, 165866, 165921, 165922, 165945, 165946, 165964, 165965, 165976, 165977.

Remarks. This well-known domesticate, which originated in Southeast Asia, accompanied prehistoric peoples nearly everywhere in Oceania. The bones from Tikopia and Anuta suggest that *Gallus gallus* was present on these islands since the time of initial Polynesian colonization. Kirch and Yen (1982:283) recorded *G. gallus* from Tikopia today; it exists on Anuta as well.

Galliformes, genus (?genera) and species unknown. Indeterminate galliform.

Material examined. TIKOPIA: NISP = 4. 3 humeri, BPBM 166200, 166297, 166303; pedal phalanx, BPBM 166222.

Remarks. These fragmentary specimens cannot be distinguished from the bones of *Megapodius* or *Gallus*.

ORDER GRUIFORMES

FAMILY RALLIDAE

Gallirallus philippensis (Linnaeus). Banded Rail.

Material examined. TIKOPIA: NISP = 5, MNI = 3. Humerus, BPBM 166327; 2 femora, BPBM 166131, 166310; 2 tibiotarsi, BPBM 166076, 166305.

Remarks. Among these bones are three that Kirch and Yen (1982:276,283) reported as "*Rallus*? or *Porzana*? Medium-sized Rail." The two fragmentary femora are only tentatively referred to *Gallirallus philippensis*. This rail is widespread in the southwest Pacific from New Guinea, Australia, and New Zealand east to Tonga, Samoa, and Niue. Because of its remarkable ability to colonize islands, which may result in multiple colonizations of a single island, the intraspecific variation of modern populations is complicated, with few discernible patterns (Schodde & de Naurois 1982). There are no modern records of *G. philippensis* from Tikopia or Anuta.

Porphyrio porphyrio (Linnaeus). Purple Swamphen (Tikopia *karae*).

Material examined. TIKOPIA: NISP = 31 (most major skeletal elements represented), MNI = 16. BPBM 166071, 166077, 166181, 166223, 166225, 166227, 166228, 166229, 166231, 166232, 166236, 166263, 166265, 166266, 166268, 166275, 166281, 166285, 166295, 166419, 181499, 181510, 181511, 181514, 181524, 181526, 181529, 181531, 181534, 181535, 181557.

Remarks. These specimens, although variable in size, agree with bones of *Porphyrio porphyrio* rather than those of the smaller, extinct *P. paepae* Steadman (currently known only from the Marquesas [Steadman 1988]), which is the only other Polynesian species of this genus outside of flightless forms from New Caledonia (Balouet & Olson 1989) and New Zealand. *Porphyrio porphyrio* was common on Tikopia on 11 February 1927 (Beck 1927:219) when the WSSE collected two males and two females (AMNH 216881-216884; examined by DWS in July 1988). Kirch and Yen (1982:283) also reported *P. porphyrio* from Tikopia today and in archaeological records. There are no certain records from Anuta, although Feinberg (1977) listed *karae* for Anuta, the word perhaps being borrowed from Tikopia. *Porphyrio porphyrio* occurs through warmer parts of Africa and Asia through Indonesia, New Guinea, Australia, and New Zealand, then east through the Pacific islands to Tonga, Samoa, and Niue.

ORDER COLUMBIFORMES

FAMILY COLUMBIDAE

Ducula pacifica (Gmelin). Pacific Pigeon (Tikopia, Anuta *rupe*).

Material examined. TIKOPIA: NISP = 5, MNI = 5. Coracoid, BPBM 166261; humerus, BPBM 181649; manus digit II phalanx 1, BPBM 181528; carpometacarpus, BPBM 166253; tarsometatarsus, BPBM 181627.

Remarks. *Ducula pacifica* is the only columbid recorded from Tikopia or Anuta. The WSSE collected *D. pacifica* on both islands in February 1927 (Amadon 1942). Luke (1945:191) recorded *D. pacifica* on Tikopia in May 1941, as did Kirch and Yen (1982:283) in 1977–1978. The *rupe* is traditionally regarded as an incarnation of the *Atua i Taumako*, an ancestral deity of the Taumako clan (Firth 1985:413).

The distribution of *D. pacifica* extends locally from the Bismarcks, Solomon Islands, and New Caledonia east to the Cook Islands. It is the only resident land bird known from Anuta, whether modern or prehistoric. With its remarkable ability to colonize small, remote islands, *D. pacifica* is an excellent example of a "supertramp" species (Diamond 1974, 1982). In Vanuatu, Diamond and Marshall (1977:727) listed *D. pacifica* among species "observed flying over open water between islands, or appearing as vagrants on islands where they did not maintain permanent populations." The lack of bones of *D. pacifica* from Anuta and the Kiki phase of Tikopia is compatible with the theory that this species of minimal geographic variation may be a relatively recent colonizer of these islands.

Mayr (1945:203) stated that the Green-winged Pigeon, *Chalcophaps indica* (Linnaeus), occurs "on all the [Santa Cruz] islands," although we cannot find any literature or specimens to verify this statement for either Tikopia or Anuta. Among the WSSE specimens of *C. indica* in AMNH, the localities nearest to Tikopia or Anuta are the islands of Utupua, Santa Cruz, Tinakula, and Fenualoa.

ORDER PSITTACIFORMES

FAMILY PSITTACIDAE

Trichoglossus haematodus (Linnaeus). Rainbow Lorikeet (Tikopia *sivi*).

Material examined. None.

Remarks. *Trichoglossus haematodus* was sighted but not collected on Tikopia in February 1927 (Beck 1927:219), May 1941 (Luke 1945:191), and 1977–78 (Kirch & Yen 1982:283). There are no records of this species from Anuta. This small, colorful parrot occurs from Indonesia to Vanuatu, reaching the eastern limit of its range on Tikopia. Clark (1982) listed the Tikopia *sivi* as *T. haematodus* and the Tikopia *lenga* for *Vini* (*Charmosyna*) *palmarum* (Gmelin), the latter not found on Tikopia. The Tikopia may know *V. palmarum* from their visits to Vanikoro, where this species does occur.

The nectarivorous Rainbow Lorikeet adapts well to arboriculture, which includes non-native flowering trees. This adaptability probably explains the survival of *T. haematodus* on Tikopia. Other nectarivorous, frugivorous, or insectivorous birds that tolerate arboriculture are *Ducula pacifica*, *Halcyon chloris*, *Aplonis tabuensis*, and *Myzomela cardinalis*.

ORDER CUCULIFORMES

FAMILY CUCULIDAE

Eudynamis taitensis (Sparrman). Long-tailed Cuckoo (Tikopia *kareva*, *kaareva*).

Material examined. TIKOPIA: NISP = 1, MNI = 1. Humerus, BPBM 181496. ANUTA: NISP = 1, MNI = 1. Humerus, BPBM 165867.

Remarks. The only modern record of *Eudynamis taitensis* for Tikopia is that of Kirch and Yen (1982:283). A specimen of *E. taitensis* was taken by WSSE on Anuta on 8 February 1927 (Bogert 1937). This cuckoo breeds only in New Zealand, then migrates and winters through most of Melanesia, Micronesia, and Polynesia. Many Tikopia, however, regard *E. taitensis* as indigenous to their island, where it is thought to be the embodiment of *Atua i te Uruao*, the God of the Woods (Firth 1985:167).

ORDER APODIFORMES

FAMILY APODIDAE

Collocalia vanikorensis (Quoy and Gaimard). Vanikoro Swiftlet (Tikopia *pakalili*).

Material examined. None.

Remarks. *Collocalia vanikorensis* occurs locally from Sulawesi to Vanuatu (Salomonsen 1983:88). The only record of *C. vanikorensis* on Tikopia is from Firth (1985:327), who stated that it nests in cliffs and is eaten by the Tikopia. There are no records from Anuta. This small swiftlet has been recorded from the nearby islands of Lomlom, Disappointment (Netepa), and Vanikoro (Mayr 1945:205), so its occurrence on Tikopia is plausible. There are no records of this species from Anuta. Because of the extreme difficulty in species-level systematics of *Collocalia* (Salomonsen 1983), specimens are needed to be certain that the species of *Collocalia* on Tikopia is not *C. spodiopygia* (Peale) or *C. esculenta* (Linnaeus), which also occur in the region.

Kirch and Yen (1982:284) listed the Pacific Swallow, *Hirundo tahitica* Gmelin, as occurring on Tikopia under the name *pakalili*. Because they did not list any species of *Collocalia*, we assume that the bird in question was in fact the superficially similar *C. vanikorensis*. Clark (1982) noted that the Polynesian names for *Hirundo tahitica* are always the same as those for *Collocalia*. Because *H. tahitica* has been recorded from nearby Lomlom, Santa Cruz Island, and Utupua (Mayr 1945:207), its occurrence on Tikopia is plausible and should be investigated further.

ORDER CORACIIFORMES

FAMILY ALCEDINIDAE

Halcyon chloris (Boddaert). Collared Kingfisher (Tikopia *sikotara*).

Material examined. None.

Remarks. The WSSE collected four specimens of *Halcyon chloris* on Tikopia on 11 and 12 February 1927, the plumage of which was too worn to determine to subspecies (Mayr 1931). Kirch and Yen (1982:283) included *H. chloris* among the modern birds of Tikopia. Kingfishers have not been reported from Anuta. The range of *H. chloris* extends from coastal Africa and Asia to Australia, New Zealand, and western Pacific islands east to Samoa and Tonga. Diamond, Gilpin and Mayr (1976) listed *H. chloris* as one of the long-distance "great speciators" of the Solomon Islands. Thus, its colonization of Tikopia is not extraordinary nor would it be surprising if the Tikopia form should prove to be an endemic subspecies.

ORDER PASSERIFORMES

FAMILY STURNIDAE

Aplonis tabuensis (Gmelin). Polynesian Starling (Tikopia *miti*).

Material examined. TIKOPIA: NISP = 2, MNI = 2. 2 humeri, BPBM 166264, 181539.

Remarks. These specimens agree in size and qualitative features with the smallest humeri in a series of fossils and skeletons of *Aplonis tabuensis* from 'Eua, Tonga. *Aplonis tabuensis* is near the western limit of its range on Tikopia, where it occurs as the endemic subspecies *A. tabuensis tucopiae* Mayr, collected on 11–12 February 1927 by WSSE (Mayr 1942). Kirch and Yen (1982:284) listed *A. tabuensis* among the modern birds of Tikopia. It is not known from Anuta. The distribution of *A. tabuensis* extends from the Santa Cruz group east to Fiji, Wallis and Futuna, Samoa, Tonga, and Niue. The occurrence of an endemic subspecies of *A. tabuensis* on Tikopia is interesting in light of the young geological age of the island, which has been dated as only ca. 80,000 years (Fryer 1974). Elsewhere, bones of *A. tabuensis* have been identified in Tonga from an archaeological site on Lifuka and a late Holocene paleontological site on 'Eua (Steadman 1989a,b).

FAMILY MELIPHAGIDAE

Myzomela cardinalis (Gmelin). Cardinal Honeyeater (Tikopia *lenga, malingi*).

Material examined. None.

Remarks. The WSSE collected a single specimen of *Myzomela cardinalis* on Tikopia on 11 February 1927, this being the holotype of an endemic subspecies *M. c. tucopiae* Mayr (Mayr 1932, 1937; Koopman 1957). Kirch and Yen (1982:284) listed *M. cardinalis* among both the modern and prehistoric birds of Tikopia. We found no bones of *M. cardinalis* or any other very small passerines in any of the archaeological material. The curious range of *M. cardinalis* consists of the Solomon Islands, Santa Cruz group, Vanuatu, and Samoa. It is not known from Anuta.

Kirch and Yen (1982:284) also reported bones of an unknown honeyeater, *Myzomela* sp. (local name *malingi*) from strata of the Kiki and Sinapupu phases on Tikopia. This unknown species was regarded by them as distinct from *M. cardinalis*, for which they recorded the name *lenga*. The name *malingi* probably refers to the female of *M. cardinalis*, which is mostly dark grayish olive above and yellowish olive below, whereas the male is entirely bright black and red (Pratt, Bruner & Berrett 1987, Plate 32). Perhaps *lenga* refers only to the male. Alternatively, Firth (1985:205) identified *lenga* as the Tikopia name for *Charmosyna margarethae* (= *Trichoglossus haematodus*). This should be investigated further, for the name *lenga* is a cognate with other western Polynesian names for small species of parrots (Clark 1982).

Table 2. Bird bones from Tikopia, arranged by cultural phase, designated by Kirch and Yen (1982).

	Phase					
Species	Kiki	Sinapupu	Tuakamali	Historic	Unknown*	Total
Sea birds						
Pterodroma rostrata (Tahiti Petrel)	1		1		1	3
Pterodroma sp. (unknown petrel)	1				1	2
Puffinus pacificus (Wedge-tailed Shearwater)	1					1
Puffinus lherminieri (Audubon's Shearwater)	1					1
Procellariidae sp. (unknown petrel/shearwater)	14				1	15
Phaethon rubricauda (Red-tailed Tropicbird)	4					4
Phaethon lepturus (White-tailed Tropicbird)	11	1	2		1	15
Papasula abbotti (Abbott's Booby)	2					2
Sula dactylatra (Masked Booby)				3		3
Sula leucogaster (Brown Booby)	1				1	2
Sula sula (Red-footed Booby)	11	3	25	4	1	44
Sula sp. (unknown booby)			11	16		27
Fregata minor (Great Frigatebird)	6			2	1	9
Fregata ariel (Lesser Frigatebird)	3					3
Sterna fuscata (Sooty Tern)	2					2
Anous stolidus (Brown Noddy)	88	4	13	23	7	135
Anous minutus (Black Noddy)	11	1	6	16	1	35
Sterninae sp. (unknown tern)	13		6	1		20
Land birds						
Anas superciliosa (Gray Duck)				2		2
Pluvialis dominica (Pacific Golden Plover)	2	1	1			4
Numenius tahitiensis (Bristle-thighed Curlew)	2					2
Heteroscelus incanus (Wandering Tattler)	3			1		4
Megapodius freycinet (Common Megapode)	8	1			1	10
Gallus gallus (Chicken)	36	4	7	15	13	75
Galliformes sp. (unknown galliform)	2		1		1	4
Gallirallus philippensis (Banded Rail)	4				1	5
Porphyrio porphyrio (Purple Swamphen)	8	8	12		3	31
Ducula pacifica (Pacific Pigeon)		2	1	2		5
Eudynamis taitensis (Long-tailed Cuckoo)	1					1
Aplonis tabuensis (Polynesian Starling)	1	1				2
Total bones	237	26	86	85	34	468
Minimum number of species	22	10	9	9	11	25

* Includes layer I of TK-4 (28 bones, mixed Kiki and Tuakamali) and layer I, zone A_2 of TK-36 (6 bones, mixed Tuakamali and Kiki).

Table 3. Bird bones from the Sinapupu locality, Tikopia (Sites TK-1, -35, -36; Test Pits 20, 47–49, 51, 52).

	Stratigraphic zone*							
	A_1	A_2	A_3	B_1	B_2	C_1	C_2	Total
Sea birds								
Pterodroma rostrata (Tahiti Petrel)		1						1
Puffinus pacificus (Wedge-tailed Shearwater)						1		1
Puffinus lherminieri (Audubon's Shearwater)						1		1
Procellariidae sp. (unknown petrel/shearwater)						1	2	3
Phaethon lepturus (White-tailed Tropicbird)		2		1		3	2	8
Sula leucogaster (Brown Booby)		1						1
Sula sula (Red-footed Booby)		4	4	2		1	2	13
Sula sp. (unknown booby)	1		8					9
Anous stolidus (Brown Noddy)		2	3	4		3	8	20
Anous minutus (Black Noddy)				1			2	3
Sterninae sp. (unknown tern)	1	2				1	1	5
Land birds								
Pluvialis dominica (Pacific Golden Plover)			1	1				2
Heteroscelus incanus (Wandering Tattler)							2	2
Megapodius freycinet (Common Megapode)		1			1			2
Gallus gallus (Chicken)	2	4	1	1	3	3	5	19
Galliformes sp. (unknown galliform)			1					1
Porphyrio porphyrio (Purple Swamphen)	1	4	7	5	2		6	25
Ducula pacifica (Pacific Pigeon)			1	1	1			3
Eudynamis taitensis (Long-tailed Cuckoo)							1	1
Aplonis tabuensis (Polynesian Starling)				1		1		2
Total bones	5	21	26	17	7	15	31	122
Minimum number of species	4	8	6	9	4	7	9	16

*Zones $A_1 - A_3$ = Tuakamali phase; zones B_1, B_2 = Sinapupu phase; zones C_1, C_2 = Kiki phase. A_2 contains some C_1–C_2 mixture in Site TK-36.

Table 4. Bird bones from Site TK–4, Tikopia.

	Layer*			
	I	II	II/III	Total
Sea birds				
Pterodroma rostrata (Tahiti Petrel)	1	1	—	2
Pterodroma sp. (unknown petrel)	1	1	—	2
Procellariidae sp. (unknown petrel/shearwater)	1	11	—	12
Phaethon rubricauda (Red-tailed Tropicbird)	—	4	—	4
Phaethon lepturus (White-tailed Tropicbird)	1	6	—	7
Papasula abbotti (Abbott's Booby)	—	2	—	2
Sula leucogaster (Brown Booby)	—	1	—	1
Sula sula (Red-footed Booby)	1	8	—	9
Fregata minor (Great Frigatebird)	1	6	—	7
Fregata ariel (Lesser Frigatebird)	—	3	—	3
Sterna fuscata (Sooty Tern)	—	2	—	2
Anous stolidus (Brown Noddy)	7	77	—	84
Anous minutus (Black Noddy)	1	9	—	10
Sterninae sp. (unknown tern)	—	11	—	11
Land birds				
Pluvialis dominica (Pacific Golden Plover)	—	2	—	2
Numenius tahitiensis (Bristle-thighed Curlew)	—	2	—	2
Heteroscelus incanus (Wandering Tattler)	—	1	—	1
Megapodius freycinet (Common Megapode)	—	8	—	8
Gallus gallus (Chicken)	11	27	1	39
Galliformes sp. (unknown galliform)	1	2	—	3
Gallirallus philippensis (Banded Rail)	1	4	—	5
Porphyrio porphyrio (Purple Swamphen)	1	2	—	3
Total bones	28	190	1	219
Minimum number of species	10	19	1	19

*Layer I = mixed Kiki and Tuakamali phases; layer II = Kiki phase; layer III = Kiki phase.

Table 5. Bird bones from Site TK–7, Tikopia.

	Layer*		
	II	III	Total
Sea birds			
Sula sula (Red-footed Booby)	17	1	18
Anous stolidus (Brown Noddy)	1	—	1
Total bones	18	1	19

*Layer II = Tuakamali phase; layer III = Sinapupu phase.

Table 6. Bird bones from Site TK–8, Tikopia.

	Layer*	
	I	Total
Sea birds		
Sula sp. (unknown booby)	1	1
Land birds		
Porphyrio porphyrio (Purple Swamphen)	1	1
Total bones	2	2

*Layer I = Tuakamali phase.

Table 7. Bird bones from Site TK–9, Tikopia.

	Layer*			
	I	I/II	III	Total
Sea birds				
Sula sp. (unknown booby)	—	1	—	1
Anous stolidus (Brown Noddy)	—	4	3	7
Anous minutus (Black Noddy)	4	2	—	6
Sterninae sp. (unknown tern)	—	2	1	3
Total bones	4	9	4	17

*All layers = Tuakamali phase.

Table 8. Bird bones from Site TK–20, Tikopia.

	Layer*	
	I	Total
Land birds		
Gallus gallus (Chicken)	2	2
Total bones	2	2

*Layer I = Tuakamali phase.

Table 9. Bird bones from the Ravenga coastal excavations, Tikopia.

	Test pit / Layer*													
	21	22		23	24	25	26	27	29	30	35		45	
	I	I	II	I	I	I	I	I	I	II	I	II	I&II	Total
Sea birds														
Sula dactylatra (Masked Booby)									1		2			3
Sula sula (Red-footed Booby)					4									4
Sula sp. (unknown booby)					9						5	1	1	16
Anous stolidus (Brown Noddy)					7				9		3	2	1	22
Anous minutus (Black Noddy)		1			2				11	2				16
Sterninae sp. (unknown tern)				1										1
Land birds														
Anas superciliosa (Gray Duck)			2											2
Heteroscelus incanus (Wandering Tattler)							1							1
Gallus gallus (Chicken)	1				3	3		2		2	1	2		14
Ducula pacifica (Pacific Pigeon)					1				1					2
Total bones	1	1	2	1	26	3	1	2	22	4	11	5	2	81
Minimum number of species	1	1	1	1	5	1	1	1	3	2	3	3	2	8

* All test pits and layers = Historic phase.

Table 10. Bird bones from the Faea coastal excavations, Tikopia.

	Test Pit / Layer*				
	3 I	6	16 VI	17 II	Total
Sea birds					
Fregata minor (Great Frigatebird)	2	—	—	—	2
Anous stolidus (Brown Noddy)	—	1	—	—	1
Land birds					
Porphyrio porphyrio (Purple Swamphen)	—	—	1	1	2
Gallus gallus (Chicken)	—	2	—	—	2
Total bones	2	3	1	1	7

*Test Pits 3, 6 = Historic phase; Test Pit 16, layer VI = Sinapupu phase; Test Pit 17, layer II = Tuakamali phase.

Table 11. Bird bones from Site AN-6, Anuta, Solomon Islands.

	Chrono-stratigraphic zone*						
	A	A/B	B/C	C/D	D	E	Total
Sea birds							
Puffinus pacificus (Wedge-tailed Shearwater)						1	1
Puffinus lherminieri (Audubon's Shearwater)		1	21	1		12	35
Phaethon lepturus (White-tailed Tropicbird)			1				1
Sula leucogaster (Brown Booby)	3		2				5
Sula sula (Red-footed Booby)	20	7	57			1	85
Sula sp. (unknown booby)	14	2	29		1	5	51
Fregata minor (Great Frigatebird)	3		8			1	12
Fregata ariel (Lesser Frigatebird)			7				7
Fregata sp. (unknown frigatebird)	1		4			1	6
Sterna fuscata (Sooty Tern)	1	2				1	4
Anous stolidus (Brown Noddy)	10	1	8		1	24	44
Anous minutus (Black Noddy)	3					7	10
Sterninae sp. (unknown tern)	4		4			6	14
Land birds							
Pluvialis dominica (Pacific Golden Plover)						3	3
Arenaria interpres (Ruddy Turnstone)						1	1
Gallus gallus (Chicken)	4		5	2	1	7	19
Eudynamis taitensis (Long-tailed Cuckoo)			1				1
Total bones	63	13	147	3	3	70	299
Minimum number of species	7	4	9	2	3	10	14

*A to E = youngest to oldest strata.

DISCUSSION

Bird Exploitation: Ethnographic Background

Ethnographic information on the exploitation of birds on Anuta and Tikopia is available from the works of Feinberg (1977, 1981), Firth (1936, 1939), Yen (1973), and from the field notes and observations by PVK on Anuta in 1971 and on Tikopia in 1977–78. On Anuta, hunting for birds is an occasional activity of men and boys. Such hunting is rather rare, and the contribution of avian flesh to the diet is limited. Over a 43-day period in 1971, the Notau family on Anuta caught nine birds with a total yield of 1.8 kg (Yen 1973:138). During the same period, approximately 34 kg of fish were obtained by the Notau household. Feinberg (1981:82) noted that only twice during his 11 months on Anuta were "enough birds captured for an island-wide distribution."

Birds are captured by the Anutans in two ways: (1) with a long-handled net (*te kupenga veu*) and (2) by hand (*tangotango*). The *kupenga veu* method can be practiced during the day in the vicinity of a nesting site but is most effective at dusk when birds return from foraging at sea. Yen (1973:117) remarked that such bird netting takes place on the slopes of the hill gardens, "for the seabirds also rest in the second growth of the gullies. The hunters usually take positions in the taro or manioc plots and entice the birds into the range of 3- to 4-meter-long poles with nets attached, by calling to them." A *kupenga veu* net observed by PVK had a diameter of 1.1 m, with a 5 cm mesh, and was attached to a bamboo pole 4.5 m long. The kinds of birds said to be caught with this net were *ngao* and *rakia*, names that probably refer to the Brown Noddy and Black Noddy, respectively.

The *tangotango* method is described by Feinberg (1981:34): the "procedure is to see a bird dozing in a tree, climb up behind it, grab it, and break its neck." A variation on the *tangotango* method is to use a noose on the end of a pole, which "is usually done with large species on the cliff face of the hill overlooking the sea."

Birds are exploited on Tikopia with very similar technology and levels of intensity as on Anuta. Firth (1939:60–61) wrote:

> Birds of a number of species exist, but again because of their religious affiliations [as lineage totems] very few of them are eaten. Even the pigeon, consumed by most Polynesians, is eaten only by members of a few kinship groups, and then rarely. The small swift (*Collocalia francica* [= *vanikorensis*]), a noddy, and a petrel are the only birds deliberately and periodically sought by netting. They are not regarded as the property of any individuals or groups, and the catch depends on personal skill and initiative. They are not an important element in the food supply.

On two or three occasions in 1977–78, PVK was served booby and Brown Noddy that had been netted from Tikopia's cliffs and baked in an earth oven. It was said that the small numbers of Gray Ducks found on the lake are the property of the chiefs of Ravenga district and may be taken only with their permission (Kirch & Yen 1982:21). In 1977–78, a teenage girl in Matautu Village kept a Brown Noddy as a pet. The bird had been taken as a fledgling and reared by the girl. It lived in a small, thatched birdhouse next to the girl's dwelling. The bird was free to fly about and usually went to sea during the day in search of food. It always returned to its house in the evening, however, no doubt enticed by the baked fish that the girl provided for it.

On both Anuta and Tikopia, the chicken is raised as a domestic species, living in and near the villages and fed primarily coconut gratings. These birds are normally consumed only for special feast occasions, while the eggs are not collected or eaten (except by resident archaeologists who found that two out of the three eggs they sampled were fertilized or rotten).

Aside from their use as food, frigatebirds provide large wing bones (humerus, ulna, radius) used to make traditional tattooing needles on both islands. The mid-shaft is beveled to form a chisel-like end that is finely serrated. The worked bone is then hafted onto a wooden shaft.

Extinction

The bones from Tikopia (Tables 3–10, summarized in Table 2) show that the following species have been lost since the arrival of people: Audubon's Shearwater, Abbott's Booby, Red-footed Booby, Sooty Tern, Common Megapode, and Banded Rail. From Anuta, the Wedge-tailed Shearwater, Audubon's Shearwater, Red-footed Booby, and Sooty Tern have been lost. We make no claim that these fossil records are complete; other species probably have been lost from these islands without the archaeological recovery of their bones. Based upon our studies elsewhere in Polynesia as well as continental zooarchaeological assemblages (Grayson 1984:132–151), samples of about 300 bones are not large enough to represent all species deposited at most archaeological sites.

We believe that human activities are responsible for the loss of birds on Tikopia and Anuta, although unequivocal proof of this is not possible. The clearing of forests for agriculture reduced the amount of indigenous habitat for native birds. Just as significant, each of the extirpated species is highly edible. Recovery of their bones from midden contexts strongly suggests that they were used for food. Rats and dogs also preyed on birds and must have been particularly harmful to ground-nesting species. Of the species lost from Tikopia and Anuta, all except Abbott's Booby and the Red-footed Booby nest on the ground. Today Abbott's Booby nests high in trees on its last remaining locality, Christmas Island in the Indian Ocean. The burning and felling of trees would have depleted its numbers in Tikopian forests. Eggs and nestlings of Abbott's Booby would have been easy prey for Tikopia who presumably, like other oceanic peoples, were excellent tree-climbers. Red-footed Boobies nest in low trees or bushes, usually from 1–3 m above the ground. Their loss can be attributed largely to predation from rats, dogs, and humans, with eggs and nestlings again being the most vulnerable.

The cultural sequence of Tikopia (Kirch & Yen 1982:311–334) consists of the Kiki phase (the first 800 years of occupation by pottery-makers), the Sinapupu phase, the Tuakamali phase, and the Historic phase. Strata of the Kiki phase greatly exceed those of the Sinapupu, Tuakamali, and Historic phases in total number of bird bones (237 versus 27, 86, and 86, respectively) and in species richness (27 versus 10, 9, and 9; Table 2). Even more than on Anuta (see below), the archaeological record on Tikopia suggests the loss of certain species soon after initial human colonization. The bones of three of the five extirpated species on Tikopia (Abbott's Booby, Sooty Tern, and Banded Rail) are confined to strata of the Kiki phase, which also yielded the only bones of seven of the nonextirpated species. Of the 10 bones of the Common Megapode, eight are from Kiki strata, one is from early Sinapupu strata of TK-35, and one is of unknown age. The Kiki phase was characterized by heavy predation on a great variety of birds, particularly petrel/shearwaters, tropicbirds, boobies, frigatebirds, shorebirds, terns, domestic chickens, megapodes, rails, and swamphens. Only for the Masked Booby, Red-footed Booby, Black Noddy, Gray Duck, Purple Swamphen, and Pacific Pigeon was predation during the later cultural phases as severe as during the Kiki.

On Tikopia, an avifauna fairly rich in species was quickly depleted by colonizing Polynesians. Elsewhere in Polynesia, this pattern of heavy predation on birds during first human contact has been documented also on Lifuka, Tonga (Steadman 1989b), much of eastern Polynesia (Steadman 1989a), Hawaii (James et al. 1987), and New Zealand (Anderson 1983, 1984; Cassells 1984). Bird losses of similar magnitude probably occurred on many other Pacific islands where no archaeological records of birds are currently available. Having evolved in the absence of predatory mammals, most island birds were probably very tame at first human contact, and thus were easily obtained by skilled Polynesian hunters. Even if these hunters became aware of the scarcity of certain species after decades or centuries of exploitation, they could do little to prevent predation by rats and dogs, or possible avian pathogens introduced with chickens. Moreover, these people were unlikely to alter their agricultural practices for the sake of preserving forest habitats for birds. By the end of the Kiki phase on Tikopia, it is likely that most of the island was under some form of managed vegetation. Hunting of birds continued throughout the prehistoric occupation of the island at a reduced intensity, as it does today. The steady but relatively low level of post-Kiki predation probably has prevented some of the extirpated species from recolonizing Tikopia, thereby maintaining an avifauna unable to recover to its pre-human level of richness.

Some strong patterns emerge when the bird bones from Anuta (Table 11) are analyzed according to the revised Anuta sequence (Kirch 1982). Zone E represents initial human colonization of Anuta beginning about 950 B.C., while Zone D is the continued occupation by this early pottery-making population. The sterile sands of Zone C represent the hypothesized cyclone and abandonment of the island, while Zone B is the reoccupation of Anuta by humans at ca. 600 A.D. Zones E and B/C both show high species richness and large numbers of bones (Table 11), which is exactly what might be expected to accompany human colonization events. There was an initial burst of predation on the Anuta avifauna (Zone E), followed by recovery of the avifauna while the island was unoccupied by humans (the time between Zones C/D and B/C), and then a second burst of predation (Zone B/C).

There are differences, however, between the two periods of greatest human predation on the birds of Anuta. Zone E is dominated by terns (37 of 64 bones), which are much scarcer in Zone B/C (12 of 120 bones). Boobies and frigatebirds are rare in Zone E (3 of 64 bones) but very common in Zone B/C (81 of 120 bones). The scarcity of boobies and frigatebirds in Zone E is difficult to explain unless Brown Noddies, which are so common in Zone E, are able to compete with the much larger boobies and frigatebirds for nesting sites. All of these species are highly edible. Only one of the four species lost from Anuta (Wedge-tailed Shearwater) is confined to Zone E. Bones of the other three extirpated species (Audubon's Shearwater, Red-footed Booby, Sooty Tern) are scattered nearly throughout the sequence, although the data suggest that predation on Audubon's Shearwater during Zone B/C may have been sufficient to prevent this species from surviving into Zone A. Unlike on Tikopia, the Anutan record is highly variable in the amount of time between arrival of people and loss of a particular species. In fact, the archaeological data suggest that two of the extirpated species (Red-footed Booby and Sooty Tern) might either still exist on Anuta in very low numbers or have been lost only decades ago. The asynchrony of island extinctions/extirpations, in spite of a probable heavy burst of early losses, occurred as well in Hawaii (Olson & James 1984; James et al. 1987), New Zealand (Anderson 1983, 1984), and eastern Polynesia (Steadman 1989a).

Biogeography

Cain and Galbraith (1956:100) stated that "thanks largely to the Whitney Expedition [WSSE] . . . the distribution and geographic variation of almost all the birds of the Solomon Islands are well known." The tireless rigor of the WSSE collectors was remarkable indeed, and for many of the hundreds of Pacific islands they visited the resident avifauna was represented completely in their specimens and field notes. Our studies have shown, however, that the WSSE information for Tikopia and Anuta probably was not complete for two reasons.

First is the very short period of time that WSSE spent ashore on the two islands (one day on Anuta, two days on Tikopia). Even on such small islands, a day or two is not enough time to survey the resident avifauna. We have been able to extract much supplemental information on the modern birds of Tikopia and Anuta from other sources, namely social anthropologists

(Feinberg 1977, 1981; Firth 1936, 1939), archaeologists (Kirch & Yen 1982), linguists (Clark 1982, Firth 1985), and government officials (Luke 1945). Throughout Oceania, such "non-ornithological" works often provide important information on birds. Regardless, our knowledge of the modern birdlife of Tikopia and Anuta would benefit from a few weeks of intense ornithological survey.

The second reason is that the natural distribution of Pacific island birds cannot be learned by studying only the birds alive today. A major wave of avian extinction has accompanied the human colonization of Polynesian islands during the past few millennia (Steadman 1989a). So many populations of land birds have been lost that biogeographic analyses based only upon the living fauna are likely to be misleading. On Tikopia and Anuta, rich archaeological records of birds allow us to evaluate the modern avifauna with historical perspective. Without the archaeological record, we would have little idea to what extent the birds of Tikopia and Anuta have been affected by human activities.

As mentioned earlier, at least six species have been lost from Tikopia since the arrival of people. From Anuta, at least four species have been lost. The loss of land birds includes the megapode and rail from Tikopia and no species from Anuta. Other land birds may have existed on Tikopia and Anuta only to be wiped out so rapidly by the first humans that their bones were not incorporated into the archaeological record, as is suggested in the "blitzkreig" model of continental extinction (Martin 1984).

Although the actual number of land birds that existed on these islands in pre-human times may have been greater, the archaeological record shows that the minimum natural land bird fauna of Tikopia was 11 species while that of Anuta was only one species, the "supertramp" Pacific Pigeon (Table 1). These numbers should be regarded as minimum values given that bones of passerines and other small birds are often not recovered from archaeological sites. This substantial difference in species richness probably is related to the smaller land area of Anuta. The modern number of species of birds on individual islands within the Solomon Islands/Vanuatu region is correlated positively with the island's area (Diamond & Mayr 1976, Diamond & Marshall 1977) and negatively with the island's distance from a large island (Diamond, Gilpin & Mayr 1976). The former relationship is most pronounced among islands that are much larger and/or much less isolated than Tikopia or Anuta. Except for Tikopia and Anuta, none of the data on numbers of species for the Solomon Islands or Vanuatu has been calibrated by studies of Holocene bone deposits. Until such information becomes available, we do not know how much extinction/extirpation has occurred in these island groups since the arrival of people.

With 11 species of land birds and an area of 4.6 km^2, Tikopia most closely resembles Ontong Java (9 species, 9.5 km^2) and Sikaiana (6 species, 1.3 km^2), two outlying atolls of the Solomon Islands. These two atolls are about as isolated (170 and 240 km, respectively) as Tikopia and Anuta from large islands with diverse avifaunas, although the nearest large islands to Ontong Java and Sikaiana are much larger and have more species than the "large" islands nearest to Tikopia and Anuta, which are 228 and 280 km from Vanikoro and 210 and 350 km from the Banks Islands. The effect of isolation can be appreciated further by noting that the seven islands in the main Solomon or Vanuatu groups with land areas of 2.4–8.9 km^2 (i.e., roughly similar in area to Tikopia) have from 13 to 38 species of land birds (Diamond & Mayr 1976: Table 1; Diamond & Marshall 1977: Appendix 1), compared with 11 for Tikopia.

The data for Anuta (one species, 0.4 km^2) also provide interesting comparisons. Fourteen islands in the Solomon Islands with smaller land areas than Anuta have from six to 22 species of land birds (Diamond & Mayr 1976: Table 1). Each of these islands is less isolated than Anuta by at least an order of magnitude. Long-term, uninterrupted survival of land bird populations may be very tenuous on islands of such a small size. For example, the land area of Anuta simply may be too small to sustain viable populations of many species. This makes sense intuitively because such a small island would be extremely vulnerable to environmental perturbations, whether natural or manmade. (Recall that strata of Zone C on Anuta are considered to represent a major storm that may have removed people as well as birds from the island.) Diamond (1983) reported the minimum land area needed to support various species of land birds in the New Guinea/Bismarck/Solomon Islands region. Although populations of certain birds (including species of *Halcyon* and *Aplonis*) exist regularly on islands even smaller than Anuta, Diamond (1983) was concerned with land-bridge islands close to rich source areas. Thus, his results are not especially applicable to Anuta or Tikopia, which never have been connected to another island and are relatively isolated. Although small islands near a major source area for new colonists may suffer prehistoric extinctions similar to those of isolated islands, the lost species are more likely to be replaced on nearby islands than on isolated islands such as Anuta or Tikopia.

To summarize, the large difference in number of land bird species between Tikopia (11 species) and Anuta (one species) suggests that the land area of Anuta may be so small that land bird populations are difficult to establish or maintain. If this is the case, then the effect of decreasing island area is very dramatic between the size of Tikopia (4.6 km^2) and Anuta (0.4 km^2), at least for relatively isolated islands in the western Pacific. However, we cannot rule out the possibility that at least some of the observed differences in species richness between Anuta and Tikopia are because bird bones from the earliest cultural levels are more representative of the actual pre-human species composition on Tikopia than on Anuta. On islands so small, the inclusion of a species in faunal remains may depend upon whether or not the first 50 years of cultural debris is deposited and recovered. For example, is the lack of flightless rails on both islands a true reflection of the natural absence of such species, or were flightless rails lost within the first decades of human occupation, leaving behind few or no bones? If the primary source of predation was rats rather than humans, then most of the bones of flightless rails and other ground-nesting birds would decompose on the humic forest floor rather than be preserved in the calcareous sands of cultural middens.

Alternatively, the young geological ages of Tikopia and Anuta (ca. 80,000 years) might suggest that endemic species of birds, including flightless rails, have never existed on these islands. Endemic subspecies of land birds do occur, however, on Tikopia (see species accounts of *Aplonis tabuensis* and *Myzomela cardinalis*). If the earliest excavated levels of the sites on Tikopia and Anuta truly represent the first decades of human occupation, if the bird bones from these strata truly represent all species present at first contact, and if the endemic species can be recognized osteologically, then the lack of flightless rails or other endemic species of birds on these islands is a natural phenomenon. This suggestion could be tested by screening (with sieves of 1/16 or 1/8 in. mesh) the oldest cultural strata on both islands, searching for the tiny bones that may tell us even more about the prehistoric birds of Tikopia and Anuta.

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Vizcayinae, a New Subfamily of Delphacidae with Revision of *Vizcaya* Muir (Homoptera: Fulgoroidea) — a Significant Phylogenetic Link

Manfred Asche[1]

ABSTRACT

A new subfamily of Delphacidae, the Vizcayinae, is established for the Oriental genus *Vizcaya* containing *V. bakeri* Muir from the Philippine Islands; *V. adornata*, n. sp., from Sulawesi; *V. orea*, n. sp., from Sumatra, Thailand, and Vietnam; *V. piccola*, n. sp., from Sarawak; and *V. vindaloa*, n. sp., from South India. The Vizcayinae links the evolutionary levels of Asiracinae and of the large monophyletic group of non-asiracine delphacids beginning with the level of the Kelisiinae. The significance of the Vizcayinae to the phylogeny of Delphacidae is discussed. Keys to the subfamilies and tribes of Delphacidae and to the species of *Vizcaya* are given.

INTRODUCTION

The planthopper family Delphacidae, with more than 2,000 described species, is the largest of the 20 recognized families of the Fulgoroidea. The phylogeny of the family has recently been studied (Asche 1985) and the family confirmed as monophyletic by several characters, of which the movable spur at the distal end of the posttibia is the most significant. This phylogenetic analysis also revealed several monophyletic groups within the Delphacidae, and consequently led to alterations of older classifications, e.g., Muir (1915), Haupt (1929), and Wagner (1963). The phylogenetic findings distinguished the following subgroups of Delphacidae: Asiracinae (with 2 tribes: Asiracini and Ugyopini), Kelisiinae, Stenocraninae, Plesiodelphacinae, and Delphacinae (with 3 tribes: Tropidocephalini, Saccharosydnini and Delphacini). The names for these taxa were partly in use in older classifications, but they now have a modified meaning. The phylogenetic relationships of the major subgroups within the Delphacidae concluded in Asche (1985) are shown in Fig. 1.

One of the main results of the 1985 study was the recognition of a substantial gap between the character display of the most primitive evolutionary level within the Delphacidae (the Asiracinae) and that of the next evolutionary level (the rest of Delphacidae; > 90% of all species). The morphological transformations from the asiracine-like configuration to the non-asiracine Delphacidae were complex and involved different organs, e.g., the male drumming organ, hind wing venation, and shape of the posttibial spur. The complete suite of corresponding derived characters was found to be present in the Kelisiinae, the most primitive group above the level of Asiracinae. These characters are also present in other delphacids, which were more

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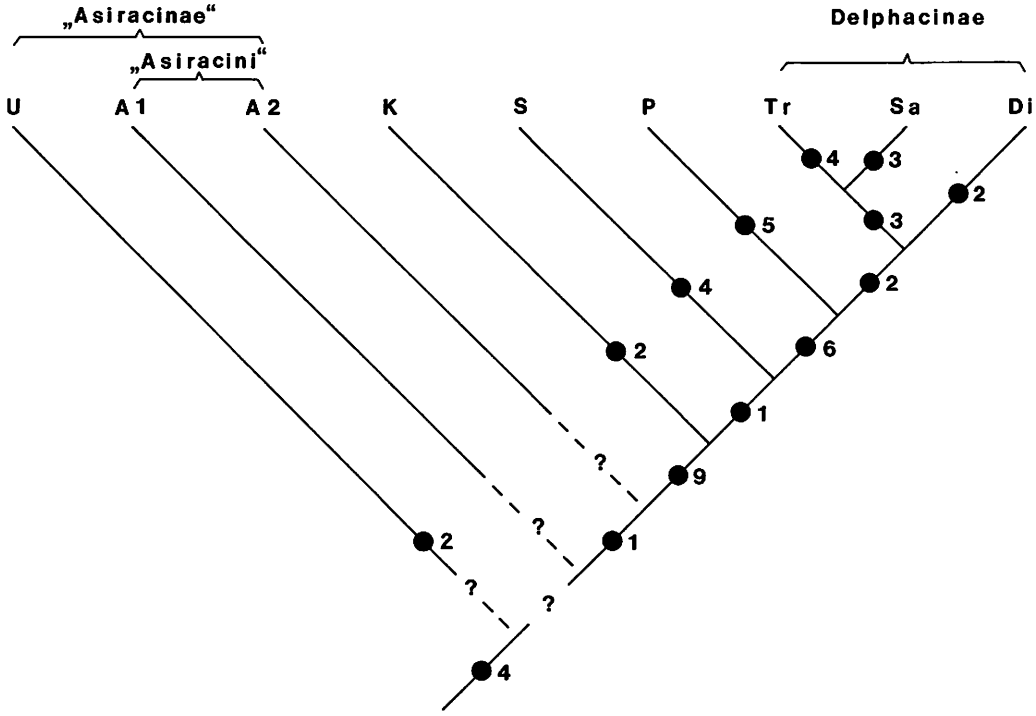


Fig. 1. Phylogenetic relationships within Delphacidae, modified after Asche (1985). Black spots: apomorphies, numbers refer to the total of apomorphies at each branch; quotation marks indicate paraphyly. Abbreviations: A1 = non-ugyopine Asiracinae without an oblique carina across genae, A2 = non-ugyopine Asiracinae with oblique carina across genae, Di = Delphacini (including the former Alohini, Megamelinae, Achorotilinae, Chlorioninae, Stirominae), K = Kelisiinae, P = Plesiodelphacinae, S = Stenocraninae, Sa = Saccharosydnini, Tr = Tropidocephalini (= Jassidaeinae), U = Ugyopini.

derived in other characters. The evolutionary transformation of these new acquisitions remained unclear since no transitional forms were known, though the existence of such forms in the evolutionary past of the non-asiracine delphacids had been postulated (Asche 1985: 120–39).

Recent studies on delphacids of the Oriental Region revealed that a group of species exists that displays a morphology between Asiracinae and the rest of the Delphacidae. This group contains the hitherto monotypic genus *Vizcaya* Muir with *V. bakeri* Muir from the Philippine Islands (Luzon) and the addition herein of 4 new species of *Vizcaya* from various parts of the Oriental Region west of Weber's Line. The shape of the posttibial spur (both sides convex, with conical teeth) led Muir (1917) to place *Vizcaya* in the tribe Alohini. However, by not dissecting the male genitalia Muir did not realize the phylogenetic value of this genus. Subsequently, the Alohini have been considered polyphyletic and form only a part of the highest derived group within the Delphacidae (Asche 1985:215–17), i.e., the group of taxa within the tribe Delphacini which is equipped with highly differentiated oviduct glands (for morphology see Strübing 1956a, b). According to its almost asiracine-like character display, it is very likely that *Vizcaya* lacks the apomorphic oviduct glands of modern delphacids. Conversely, a basal position of *Vizcaya* can be recognized within the Delphacidae, a phylogenetic ranking lower than the Kelisiinae, but higher than the Asiracinae. *Vizcaya* seems to link the 2 evolutionary levels of Asiracinae and the rest of the Delphacidae (see Discussion). By means of profound differences in several characters, this small group of species cannot be placed in any of the existing subfamilies without contradicting the current phylogenetic concept of these taxa, shown to be monophyletic with the exception of the Asiracinae (Asche 1985: 219–33). Consequently, the establishment of a new subfamily for the reception of *Vizcaya* appears justified.

Material from the following institutions were examined in this study: BMNH = British Museum (Natural History), London, England; BPBM = Bernice P. Bishop Museum, Honolulu, Hawai'i, U.S.A.; MNHN = Musée National d'Histoire Naturelle, Paris, France.

TAXONOMY

Key to the Subfamilies and Tribes of Delphacidae

1. Posttibial spur circular or quadrangular in cross section, without teeth on inner margin (Fig. 50); drumming organ in both sexes similarly shaped, males without elongate ventrocaudad apodemes of metapostnotum, without pronounced central part of 2nd abdominal tergite (Figs. 62–64) . . . . **Asiracinae** 2

Posttibial spur variously shaped, circular, triangular, or flat, quarter- to semicircular in cross section, normally with row of distinct teeth on inner margin (Figs. 51, 52); if teeth absent, spur flattened or triangular in cross section (not circular); drumming organ sexually dimorphic, males with elongate ventrocaudad apodemes of metapostnotum (Figs. 66, 69) and differentiated central part of 2nd abdominal tergite forming either continuous ellipsoid dome (Fig. 65), or with well-discriminated central plate (Fig. 68) 3

2(1). Posttibial spur quadrangular in cross section, with row of short bristles on each edge; median of 5 spines at distal end of basitarsus located distinctly basad of spinal row . . . . **Ugyopini**

Posttibial spur circular in cross section, hairs or bristles irregularly distributed over surface (Fig. 50); spines at distal end of basitarsus forming continuous row (Fig. 50) . . . . **Asiracini**

3(1). Hind wings with 5 veins from band of crossveins to posterior margin (Fig. 54); posttibial spur with solid conical teeth on inner margin (Fig. 51); male drumming organ with 1st and 2nd abdominal tergites ellipsoid, strongly convex, 2nd abdominal tergite without discriminated central plate, central depression present (Figs. 65–67) . . . . **Vizcayinae,** new subfamily

Hind wings with 4 veins from band of crossveins to posterior margin (Fig. 55); posttibial spur variously shaped, with or without teeth (Fig. 52); 2nd abdominal tergite of male drumming organ with distinctly separated central plate (Fig. 68) 4

4(3). Central sperm-conducting tube of aedeagus strongly sclerotized (as in Asiracinae and Vizcayinae; e.g., Figs. 71, 72), theca mostly membranous, or if sclerotized, then only in basal part of shaft 5

Central sperm-conducting tube of aedeagus membranous, theca mostly strongly sclerotized (Fig. 73) . . . . **Delphacinae** 7

5(4). Hind wing with veins M and Cu fused over most of their length; carinae of vertex forming inverted V; posttibial spur circular in cross section, with distinct conical teeth; 2nd abdominal sternite of male drumming organ with elongate, slender apodemes erect dorsad . . . (Neotropical) . . . . **Plesiodelphacinae**

Venation of hind wing, carination of vertex, and shape of posttibial spur different; 2nd abdominal sternite of male drumming organ with small shell-like or armlike apodemes directed caudad (not erect dorsad) 6

6(5). Posttibial spur solid, inner surface slightly concave, in cross section triangular with rounded edges, with distinct conical teeth on inner margin; mostly with black spot on gena; male genitalia with paired or single elongate rodlike processes from link between bases of aedeagus and anal segment (subanal processes). . . (Holarctic) . . . . **Kelisiinae**

Posttibial spur dilated, flattened, numerous small teeth with rectangular platelike base on inner margin; aedeagus with at least 1 curved, horn-shaped process arising from base or middle of theca, theca membranous distally; females with complete separation of copulatory and oviposition ducts (ditrysy) . . . . **Stenocraninae**

7(4). Distal spines of posttibia with 2 inner and 5 outer spines; aedeagus elastic, strongly elongate, in repose curled in membranous bag of diaphragm reaching far cephalad into the abdomen . . . . **Saccharosydnini**

Distal spines of posttibia with 2 inner and 3 outer spines; aedeagus different than above 8

8(7). Posttibial spur solid, triangular in cross section, inner surface slightly concave, without teeth; aedeagus and anal segment in close functional contact, aedeagus mostly integrated in ventral side of anal segment, base embraced by ventrolateral armlike processes of the anal segment; base of aedeagus twisted asymmetrically, at least 1 slender process arising from base; short lateral apodemes of the 1st abdominal sternite of male drumming organ bent ventrad . . . . **Tropidocephalini**

Posttibial spur variously shaped, solid or flattened, normally with teeth on inner margin (Fig. 52) (if without teeth, then aedeagus and male drumming organ different than in Tropidocephalini); base of aedeagus not strongly twisted, almost symmetrical (Fig. 73), diaphragm between base of aedeagus and anal segment differentiated in a distinct plate- or ringlike suspensorium; apodemes of 1st abdominal sternite of male drumming organ not bent ventrad but directed mediodorsad (Fig. 70) . . . . **Delphacini**

Vizcayinae, new subfamily

Diagnosis. Medium sized, slender delphacids with relatively long, slender legs and long, narrow tegmina. Head small, narrow in comparison to thorax, with well-developed compound eyes and ocelli. Vertex longer than wide, basal compartments ca. 2 × size of anterior, carinae on vertex weakly developed; frons narrow at apex, widening to frontoclypeal suture, height at least 2 × maximum width. Lateral carinae of frons and postclypeus prominent, median longitudinal carina mostly obliterated. Rostrum reaching anterior margin of postcoxae. Prominent oblique carina from lateral edge of frontoclypeal suture across genae to inferior margin of antennal base. Antennae with both segments elongate, the first segment (scape) depressed, the second (pedicel) terete with numerous sensory fields, which are irregularly arranged over the whole surface.

Pronotum and mesonotum tricarinate, carination obsolete. Posttibia laterally with 2, distally with 5 rigid spines, latter arranged in outer group of 3 long and inner group of 2 short spines. Postbasitarsus about ½ length of posttibia, 5 spines distally, median spine displaced proximad. Second posttarsal segment distally with 4 equally-shaped rigid spines forming a row. Pretarsus as in other Delphacidae (see Fennah 1945), claws and pads well developed. Posttibial spur in cross-section circular, distinct conical teeth on inner margin. Tegulae present. Tegmina elongate, conspicuously surpassing abdomen; basal cell between Cu and common stem of ScR+M weakly developed, subapical cells small. Hind wings with 5 independent veins from the line of cross-veins to apex.

Drumming organ sexually dimorphic: in females as in Asiracinae, in males 2nd abdominal tergite dilated, convex, with deep depression centrally; metapostnotum with pair of elongate apodemes directed caudad; 2nd abdominal sternite with pair of shell-like apodemes directed dorsocaudad. In nymphs numerous sensory pits on frons and vertex (> 18 in the last instar).

Male genitalia similar in construction to Asiracinae: central sperm-conducting tube of aedeagus strongly sclerotized, movable against theca; parameres clamp-like; anal segment hoodshaped; no distinguishable suspensorium. Distal part of aedeagus reduced to short rigid tube with apical phallotreme.

Female genitalia with long orthopteroid ovipositor; teeth on dorsal margin of median gonapophyses IX rudimentary; valvifers VIII long, slender. Eggs without distinguishable ringlike hatching suture around anterior pole; eggs large (about as long as ovipositor), micropyle subapically at anterior pole.

Type genus. *Vizcaya* Muir.

Remarks. The subfamily Vizcayinae is characterized by a unique combination of primitive characters (male and female genitalia, female drumming organ, hind wing venation, number and arrangement of sensory fields on antennae, number and arrangement of larval sensory pits, egg structure) and advanced characters found in the posttibial spur, male drumming organ, shape of head and antennae, and shape of the posttibial spur. For analysis of these characters and phylogenetic implications see Discussion.

Vizcaya Muir

Vizcaya Muir 1917:351. Type species: *Vizcaya bakeri* Muir, 1917; by monotypy.

Description. Head narrower than pronotum (0.7:1). Vertex medially 1.6–1.8 × longer than broad at base; lateral margins from base to middle of vertex slightly converging, then slightly diverging to frons; compartments of vertex shallowly concave, posterior compartments in middle line about 1.7 × longer than anterior; carinae limiting these cells faint or obsolete, mostly only anterior carinae of anterior compartment and short piece of median frontal carina present, together forming an inverted Y. Vertex rounding onto frons, transition smooth without median carina. Frons narrowest at transition to vertex, widest at frontoclypeal suture or slightly above suture; height of frons at least 2 × maximum width (2–2.5:1), higher than post- and anteclypeus together; area of frons convex at apex, then shallowly concave; lateral carinae prominent, slightly lamelliform, median carina obsolete or missing. Postclypeus convex, lateral carinae prominent, median carina obsolete. Anteclypeus convex without lateral carinae, median carina weak or missing. Oblique carina on genae prominent, genal areas laterad of carina shallowly concave, both sides forming blunt angle. Compound eyes in lateral view elongate, kidney-shaped, distinct incision medially above antennal base from inferior margin to about 1/2 the height of eye. Both antennal segments surpassing distance between anterior vertex and posterior tip of mesonotum; 1st segment depressed, slightly or conspicuously dilated and flattened (2.6–5 × as long as wide); 2nd segment terete, about 1.9–2.5 × longer than 1st, with >20 sensory fields irregularly distributed over whole surface, apicofrontal sensory field on slightly prominent conical base; antennal segments with numerous sturdy bristles. Pro- and mesonotum convex with smooth surface dorsally, tricarinate, carinae obsolete, partly extinct in some species, lateral carinae of pro- and mesonotum slightly diverging caudad; mesonotum medially about 3 × longer than pronotum. Tegmina long, narrow at base, widening distad of nodal line, about 3.6–4.3 × longer than maximum width; all specimens examined with base of M and ScR united into short common stem. Postbasitarsus about 2 × as long as 2nd and 3rd posttarsal segments together. Posttibial spur with 6–12 distinct conical teeth (including apical tooth), number of teeth individually varying. Coloration of head sharply contrasting dark and light: vertex (except for narrow yellowish portion at posterior margin) and superior 1/2 of frons dark brown or black, inferior 1/2 of frons and the genae yellowish, postclypeus and lorae dark brown or black, anteclypeus pale yellow.

Male genitalia. Caudal area of genital segment almost circular, diaphragm slightly sunken cephalad against margins of genital segment, parameres opening ovate; short, distally bilobate projection medially at ventrocaudal margin of genital segment; parameres slender, converging distally; aedeagus slender, elongate, slightly S-shaped, with rigid remnant of distal part bent left; slender, movable, spinelike process subapically on each side, spines in repose directed basad.

Female genitalia. Anterior bases of paired gonapophyses VIII with fingerlike projection directed cephalodorsad; median gonapophyses IX swordlike, distal 1/2 with minute teeth dorsally; bursa copulatrix voluminous, ductus receptaculi comparatively short.

Remarks. Muir (1917) placed *Vizcaya* in the Alohini referring to the shape of the posttibial spur and assigned it "nearest to *Proterosydne.*" However, the Alohini sensu Muir, which was only based on the possession of a dentated posttibial spur with both sides convex, has been shown to be polyphyletic, and the synonymy with the tribe Delphacini was established by Asche (1985). Closer relationships of *Vizcaya* to the monotypic Australian genus *Proterosydne* Kirkaldy, as suggested by Muir, could not be verified, since its type species, *Proterosydne arborea* Kirkaldy, clearly displays the morphological configuration of highly derived Delphacidae. Also, any affinities of *Vizcaya* to the SE Asian tropidocephaline genus *Lanaphora*, as referred to by Muir (1917), or to the neotropical genus *Burnilia* Muir & Giffard referred to by Metcalf (1943) by listing it as next genus after *Vizcaya* in his catalogue, are only superficial.

Externally, *Vizcaya* can be readily distinguished from other delphacid genera by an unique combination of characters. They are slender in appearance with long legs and long tegmina; the posttibial spur is convex on both sides with distinct conical teeth; the head is small and narrow with extremely elongate antennae; the transition of the vertex to frons is smooth and rounded. The coloration of the head possesses typically alternating dark and light portions.

Species of the genus *Vizcaya* are found only in South India and Southeast Asia.

Key to the Species of *Vizcaya* Muir

1. First antennal segment strongly compressed, dilated (Figs. 23, 32, 48); pro- and mesonotum orange or orange-brown 2

First antennal segment only slightly compressed, dilated (Figs. 6, 44); pro- and mesonotum dark brown or black 4

2(1). Tegmina about 3.6–3.8 × longer than maximum width, hyaline proximad of nodal line, no obvious color patterns except for small brownish suffusion around M at level of subapical cells and for small brown stripe between anal veins and inner margin 3

Tegmina long and narrow, about 4.3 × as long as wide, entirely brown except for narrow hyaline costal area (Fig. 24), coloration increasingly darker to apex . . . (Luzon I, Philippines) . . . . **Vizcaya bakeri** Muir

3(2). Tegmina with extended homogeneous brown area distad of nodal line, narrow band along apical margin, subapical inner margin hyaline without coloration (Fig. 49) . . . (S. India) . . . . **Vizcaya vindaloa, n. sp.**

Tegmina with broad brown band from nodal line to apex limited by the inner and apical margin, line drawn parallel to the branches of M, narrow parabolic area without brown coloration along the outer branch of M_1 (Fig. 33) . . . (Sumatra, Thailand, Vietnam) . . . . **Vizcaya orea, n. sp.**

4(1). Vertex, upper portion of frons, postclypeus, pro- and mesonotum black; tegmina proximad of nodal line with narrow brownish band between C and Sc+R ending well before anterior margin; distal part of tegmina with hyaline parabolic area along outer branch of M_1 small (Fig. 7); 2nd antennal segment 2.2 × longer than 1st, black except for narrow ventrobasal yellowish stripe . . . (Sulawesi) . . . . **Vizcaya adornata, n. sp.**

Vertex, superior frons, postclypeus, pro- and mesonotum chestnut brown to dark brown; tegmina proximad of nodal line with brown band between C and M reaching anterior margin, base of tegmina brownish; comparatively narrow brown band along inner and apical margin distad of nodal line; hyaline parabolic area large, surpassing inner branch of M_1 (Fig. 46); 2nd antennal segment 2.5 × longer than 1st, brownish on frontal, yellowish on caudal side . . . (Sarawak) . . . . **Vizcaya piccola, n. sp.**

Vizcaya adornata Asche, new species Figs. 2–22, 51, 65–67

Description. Comparatively small species: body length (from apex of vertex to tip of tegmina): male 4.9 mm (n=1); female 4.9 and 5.5 mm (n=2); 1st + 2nd antennal segments: male 2.3 mm, female 2.5 mm. Habitus, bodily proportions, general patterns of coloration (especially of the head) as in generic description. Coloration: vertex, superior part of frons, postclypeus and lorae, sides in front of and above compound eyes, pronotum and mesonotum except tip shiny black; other parts of head and tip of mesonotum ochraceous, black sides above eyes posteriorly interrupted by small pale yellowish marking; pale yellowish band forming broad U at posterior margin of vertex; 1st antennal segment orange, dorsal margin blackish, ventral margin from base to middle suffusely brownish; 2nd antennal segment orange at ventral base, otherwise dark brown to black, increasingly darker from base to tip; bristles of antennal segments orange to light brown; tegmina in clavus with brown stripe between anal veins and inner margin continuing to anterior margin of clavus; costal area proximad of nodal line brownish except for basal portion and portion laterad of outer subapical cell; granules on veins brown, bristles light brownish; veins of hind wings brown; posterior part of mesothorax, metathorax, and abdomen dark brown or blackish; legs pale yellow, last tarsal segments brownish. Carinae of vertex very fine, fading anteriorly. Frons 2.3 × higher than maximum width, widest slightly above frontoclypeal suture, median carina of frons only in inferior part faintly recognizable; median carina of post- and anteclypeus indistinct. First antennal segment slightly compressed, about 5 × longer than wide; 2nd antennal segment 2.2 × longer than 1st. Carination of pro- and mesonotum very fine but recognizable. Postbasitarsus 1.7 × longer than 2nd + 3rd posttarsal segments. Posttibial spur with 7 teeth (including apical tooth). Tegmina surpassing abdomen by about ⅓ of total length, 3.9 × longer than wide at maximum, widest slightly distad of nodal line, narrowest at basal ⅓. Drumming organ as in generic description.

Male genitalia. Genital segment (Figs. 9–11) ventrally 1.5 × longer than dorsally, laterodorsal edges slightly produced caudad, 2–4 short teeth subapically on dorsal margin; laterocaudal margins broadly rounded to diaphragm; 2 parallel slender stripes of stronger sclerotization forming forklike structure mediodorsad of opening for parameres; median projection of ventrocaudal margin of genital segment narrow, with V-shaped incision distally (Fig. 12); anal segment (Figs. 9, 14) about as long as parameres; parameres (Figs. 13, 14) in lateral view slightly S-shaped, somewhat dilated subapically, tapering to apex; aedeagus (Figs. 14, 15) slender, slightly depressed ventrodorsally, in lateral view slightly S-shaped; with 2 long, slender, movable, spinose processes subapically: longer process little less than ½ as long as theca, originating on left side, slightly curved to dorsal side; shorter process hook-shaped, originating on slender base on right side, in repose attached to dorsal side with tip pointing to left, little more than ½ the length of left process; connective between ventral side of membranous basal chamber and base of parameres, slightly compressed, bent in middle.

Female genitalia (Figs. 16, 20, 21–22). Generally as in generic description; valvifers VIII slightly dilated at level of anterior margin of lateral gonapophyses IX; median gonapophyses IX dorsally in distal half with row of very minute teeth.

Type data. Holotype ♂, INDONESIA: SULAWESI: Sulawesi Utara Prov, Dumoga-Bone National Park, Edward's subcamp, ca. 500 m, primary rainforest, at light, Project Wallace Expedition, 2.XII.1985 (M. Asche & H. Hoch). Paratypes: 1 ♀, same data as holotype; 1 ♀, INDONESIA: SULAWESI: Sulawesi Utara, E Kotamobagu, lakes region, hilltop behind PPA-bungalow, 1,000–1,200 m, primary montaneous rainforest, sweeping shrubs, Project Wallace Expedition, 21.XI.1985 (H. Hoch). Holotype and 1 paratype in BMNH; 1 paratype in BPBM.

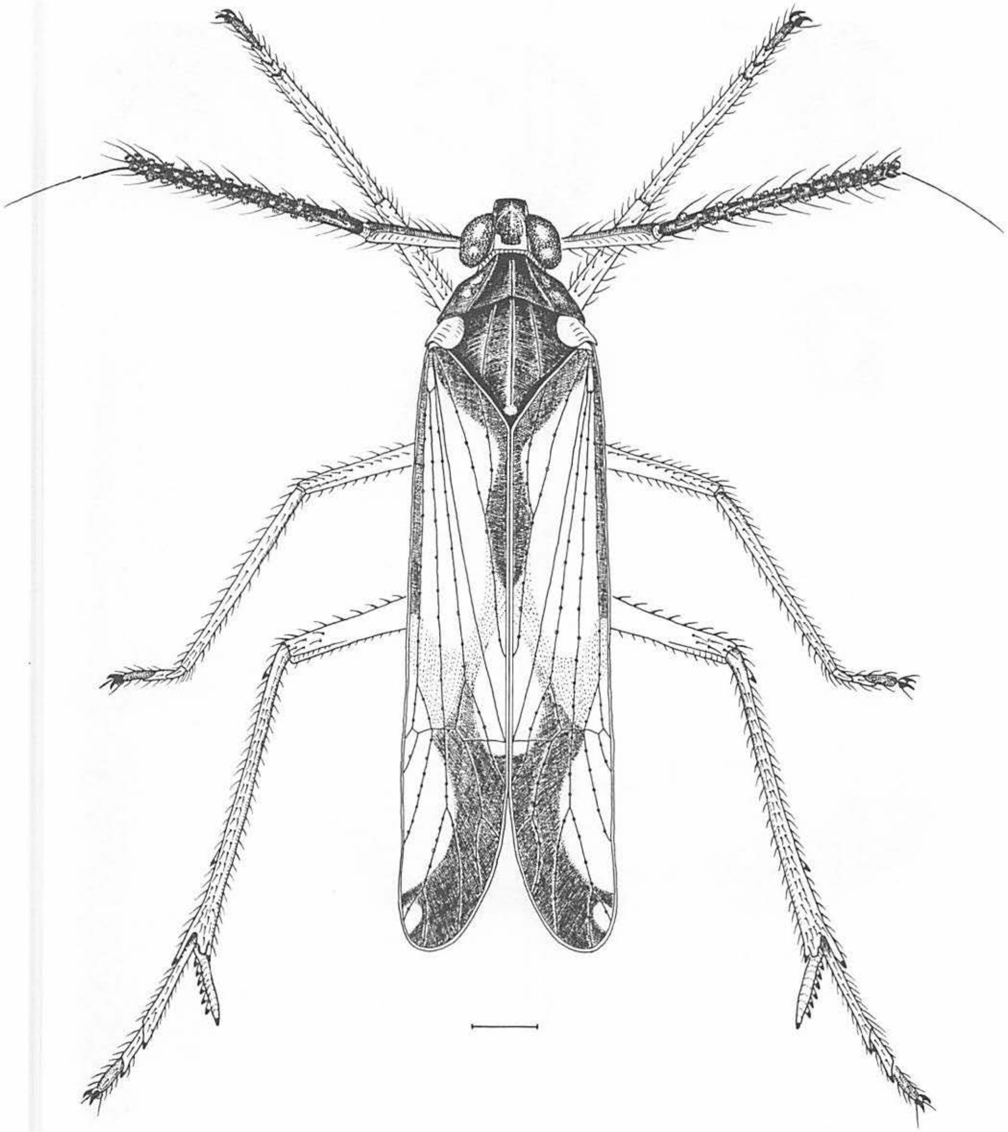
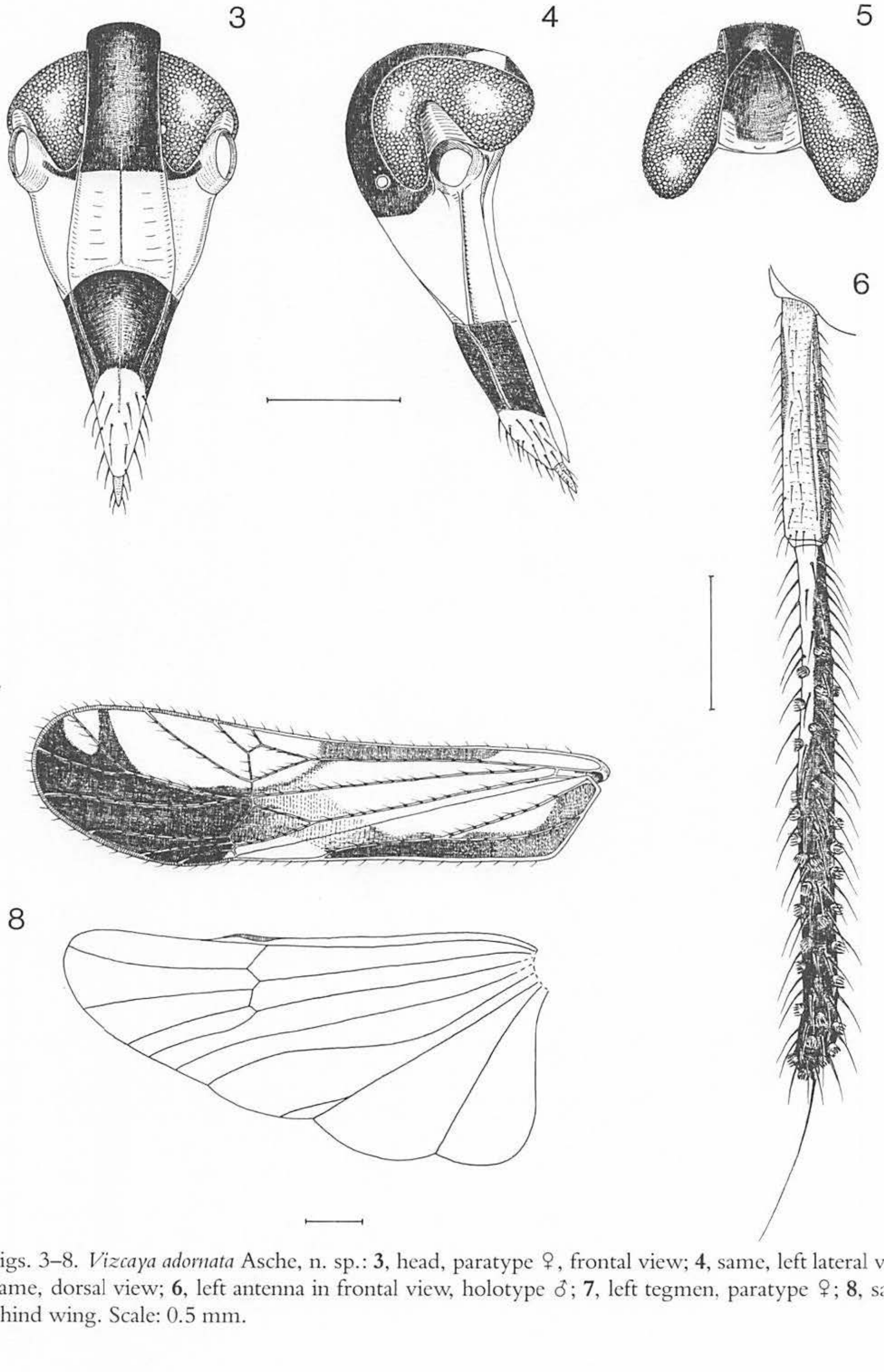
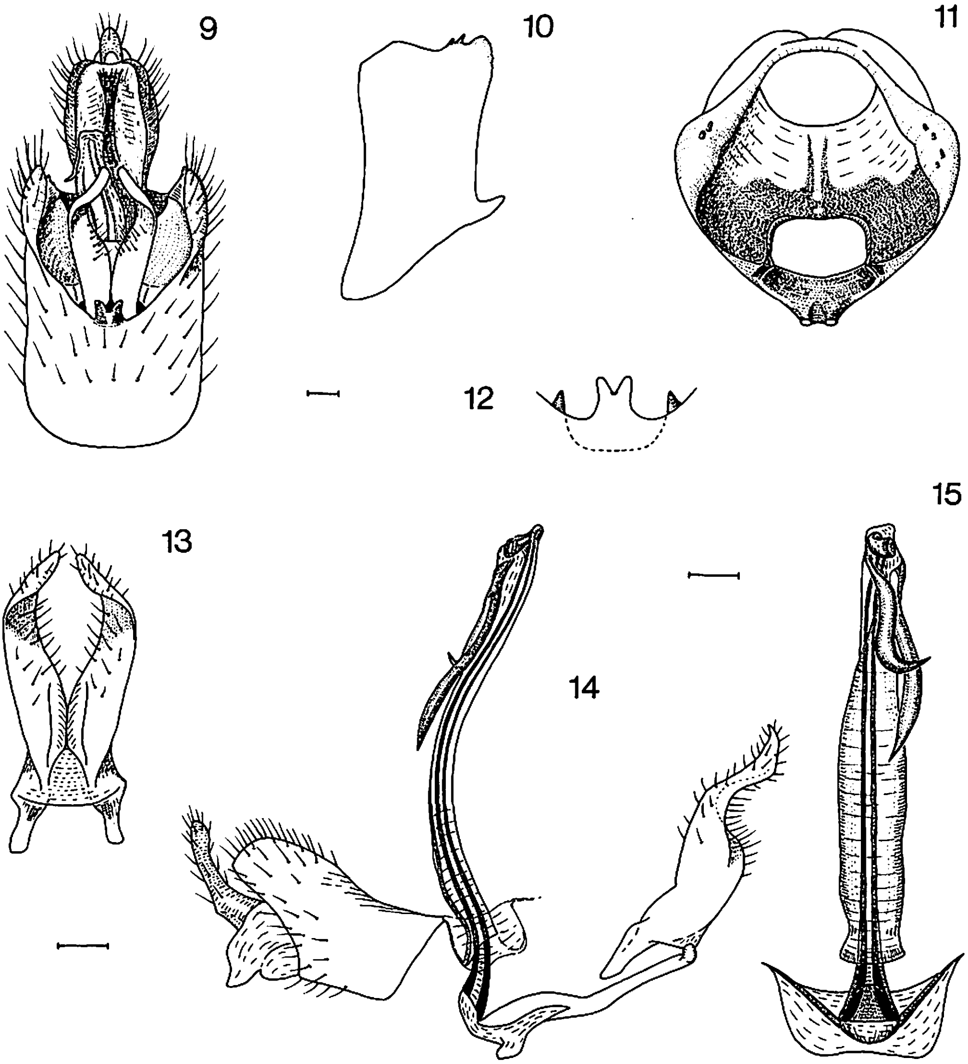


Fig. 2. *Vizcaya adornata* Asche, n. sp., habitus from dorsal, holotype ♂, Sulawesi. Scale: 0.5 mm.

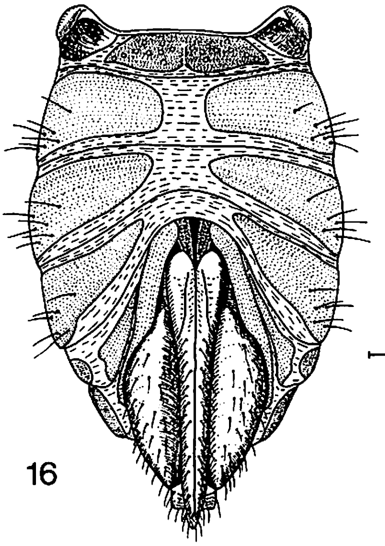
Remarks. In contrast to most other species of the genus, *Vizcaya adornata* is rather dark colored, with color patterns of head black (instead of brown), and thorax and abdomen black (instead of orange or brownish). In this aspect it resembles *V. piccola*, n. sp., from Borneo, but differs in body size as well as in form and proportions of the antennal segments. From the remaining species of this genus *V. adornata* is distinguished mainly by the color patterns of the tegmina (combination of a broad distal band and a stripe on each side proximad of nodal line), the proportions and coloration of the antennal segments, and by the shape of the male genitalia, especially the aedeagus (right spine short and hook-shaped). *V. adornata* is apparently endemic in Sulawesi.



Figs. 3–8. *Vizcaya adornata* Asche, n. sp.: **3**, head, paratype ♀, frontal view; **4**, same, left lateral view; **5**, same, dorsal view; **6**, left antenna in frontal view, holotype ♂; **7**, left tegmen, paratype ♀; **8**, same, left hind wing. Scale: 0.5 mm.



Figs. 9–15. *Vizcaya adornata* Asche, n. sp., male genitalia, holotype: **9**, genitalia in repose, ventrocaudal view; **10**, genital segment, left lateral view; **11**, genital segment, caudal view; **12**, median projection of ventrocaudal margin of genital segment, ventral view; **13**, parameres, ventral view; **14**, genitalia without genital segment, left lateral view; **15**, aedeagus, dorsal view. Scale: 0.1 mm.



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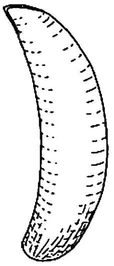

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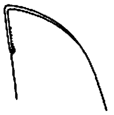

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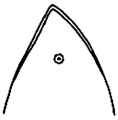

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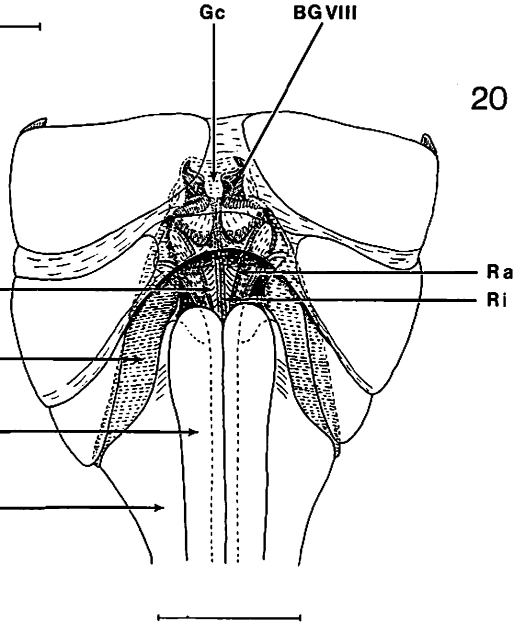

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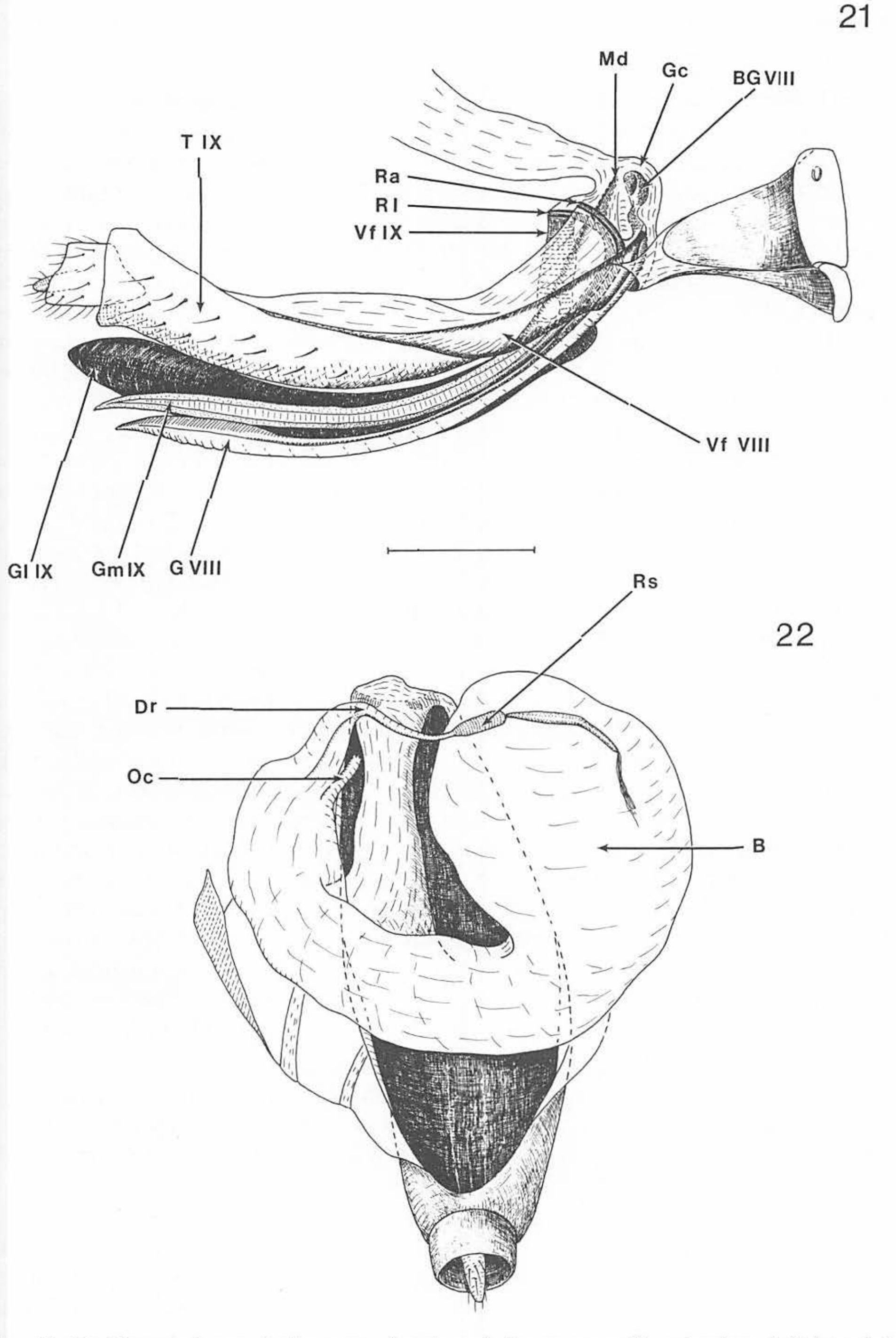
Figs. 16–20. *Vizcaya adornata* Asche, n. sp., female genitalia and egg, paratype: **16**, abdomen, ventral view; **17**, egg, note the relatively large size (same scale as abdomen); **18**, anterior pole of egg with micropyle, lateral view; **19**, anterior pole of egg, view onto micropyle; **20**, base of ovipositor, ventral view. Abbreviations: BG VIII = prolonged anterior base of gonapophyses VIII; G VIII = gonapophyses VIII; Gc = genital chamber; Gl IX = lateral gonapophyses IX; Ra = ramus anterior of gonapophyses VIII; Ri = ramus interior of gonapophyses VIII; T IX = abdominal tergite IX; Vf VIII = valvifer VIII. Scale: 0.1 mm.



Figs. 21–22. *Vizcaya adornata* Asche, n. sp., female genitalia, paratype: **21**, ovipositor, right lateral view; **22**, internal ectodermal parts, dorsal view. Abbreviations: B = bursa copulatrix; Dr = ductus receptaculi; G VIII = gonapophyses VIII; Gc = genital chamber; Gl IX = lateral gonapophyses IX; Gm IX = median gonapophyses IX; Md = mediodorsal process of gonapophyses IX; Oc = oviductus communis; Ra = ramus anterior of gonapophyses VIII; Rl = lateral ramus of median gonapophyses IX; Rs = receptaculum seminis; T IX = abdominal tergite IX; Vf VIII = valvifer VIII; Vf IX = valvifer IX. Scale: 0.1 mm.

Vizcaya bakeri Muir Figs. 23–31, 72

Vizcaya bakeri Muir, 1917:351.

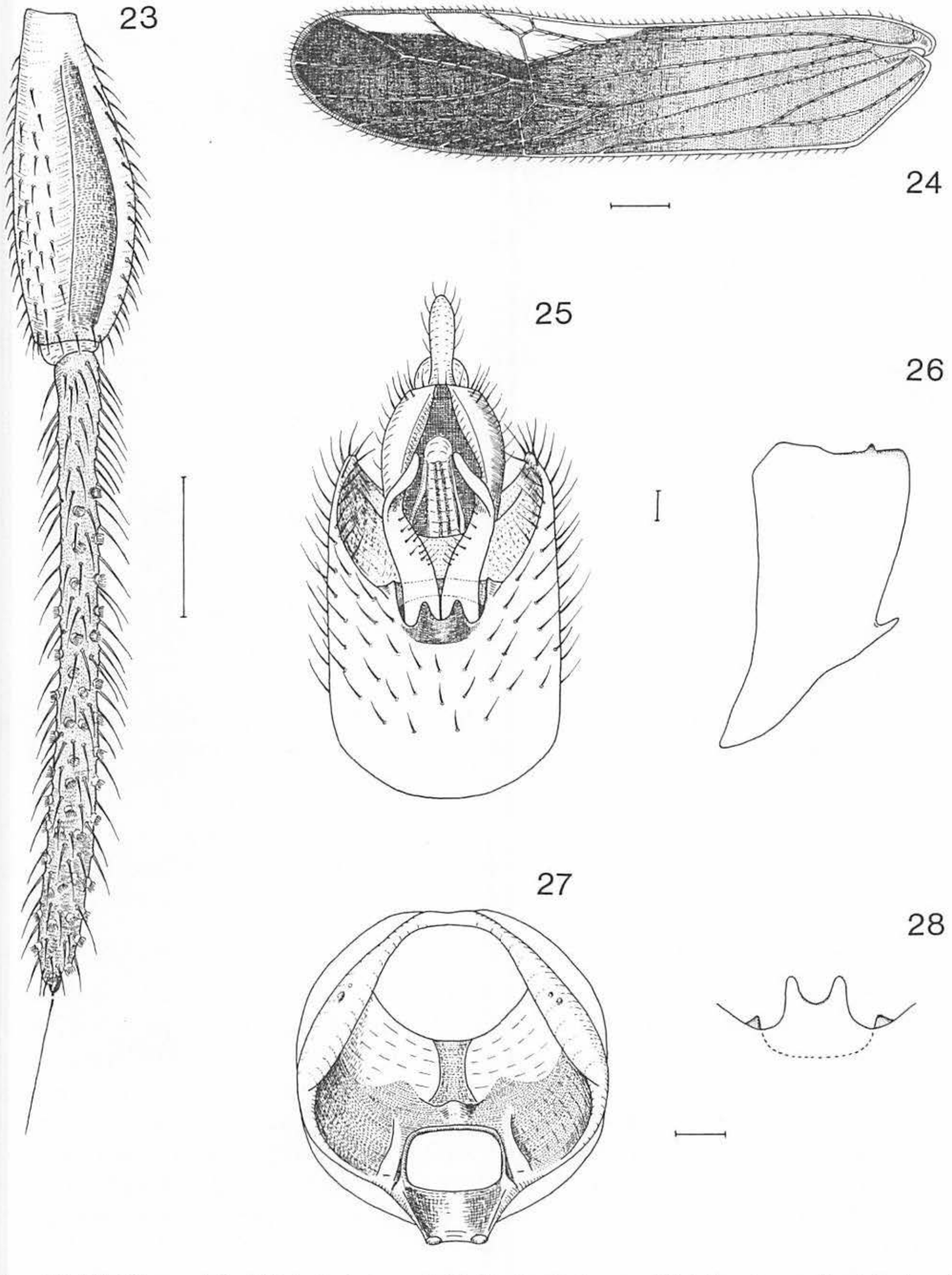
Description. In habitus and bodily proportions resembling *V. adornata*, but slightly larger; total length of male holotype (from apex of vertex to tip of tegmina): 5.7 mm; length of 1st + 2nd antennal segment: 2.8 mm. Coloration: vertex, superior portion of frons, postclypeus, lorae, sides in front and dorsad of compound eyes dark brown; inferior portion of frons, genae, anteclypeus, and triangular patches at posterior corners of vertex ochraceous; 1st antennal segment orange to light brown, dorsal and ventral margin dark brown; 2nd antennal segment brown, increasingly darker to apex; pro- and mesonotum orange to chestnut brown; tegmina, except hyaline costal area brown, color increasingly darker from base to apex, granules on veins brown, bristles stramineous; hind wings hyaline with brownish veins; posterior part of mesothorax, metathorax, and abdomen chestnut brown; legs pale yellow with 3rd tarsal segments brownish. Carinae of vertex faintly recognizable. Frons 2.5 × longer than maximum width, widest at frontoclypeal suture; frons in inferior ½ with very thin median carina, median carina of post- and anteclypeus obsolete. Surface of pronotum smooth, carinae absent; mesonotum with very fine carinae fading to posterior margin. First antennal segment strongly dilated, flattened, paddle-shaped, central area concave on both sides, margins rounded, widest in middle, 2.7 × longer than maximum width; 2nd antennal segment about 1.9 × longer than 1st. Proportions of posterior legs as in *V. adornata*. Posttibial spur in holotype asymmetrically dentated: 6 on left spur, 8 on right. Tegmina (Fig. 24) very long, slender: 4.3 × longer than maximum width; in tegmina 1st vein caudodistad of inner subapical cell (derived from Cu) forked distad of nodal line. Drumming organ as in generic description.

Male genitalia. Genital segment (Figs. 25–27) in lateral view trapezoid, in caudal view circular; ventrally about 1.5 × longer than dorsally; laterocaudal margins broadly rounded, laterodorsal angles slightly produced caudad, margin with 1–2 small teeth basad of these angles; median projection of ventrocaudal margin distally with broad U-shaped incision (Fig. 28); center of diaphragm dorsad of opening for parameres, with slightly reinforced sclerotization; parameres and anal segment similar to that in *V. adornata*, but parameres in lateral view continuously tapering without subapical dilation (Fig. 30); aedeagus (Figs. 30–31) slender, in lateral view slightly S-shaped, 2 slender movable spinose processes subapically on both sides: smaller spine on left side about ⅓ as long as theca, in repose directed basad with tip slightly curved dorsad, in dorsal view slightly dilated subapically; longer spine with bifurcate base on dorsal and right side, in repose directed basad, curved over right side of theca to ventral side, spine about 2 × as long as left one; connective compressed, straight, dorsal margin with small incision.

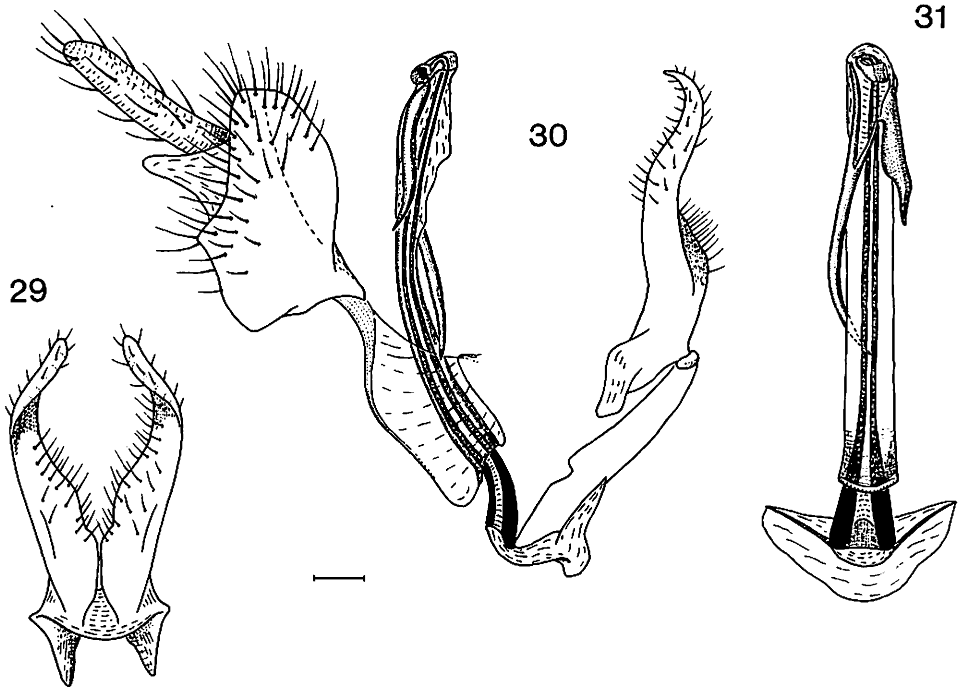
Female genitalia. Unknown.

Material examined. Holotype ♂, No. 4995, PHILIPPINE IS: LUZON I, on white printed label: "Imugin, N. Viscaya, Baker," on red label: "Type of (printed) *Viscaya* Muir" (handwritten by Muir), on red label: "Type of (printed) *V. bakeri* Muir" (handwritten by Muir), on white label: "*Viscaya bakeri* Muir, 1073" (handwritten by anonymous). Holotype in BPBM.

Remarks. According to Muir's (1917:352) indication in the original description of *V. bakeri*, a cotype female had been deposited in the Bureau of Science Collection in Manila. This specimen could not be located. *Vizcaya bakeri* can readily be distinguished from all other congeners by the proportions and coloration of the tegmina (the only species so far with such narrow and almost entirely brown tegmina), by the strongly dilated 1st antennal segment and by the shape and proportions of the movable spinose processes of the aedeagus (the longer spine with bifurcate base on dorsal side, then curved over the right to the ventral side). Within the genus, *V. bakeri* seems to have closer relationships to *V. orea*, n. sp., from Sumatra by means of certain congruences in the shape of the antennae and in the arrangement of the aedeagal



Figs. 23–28. *Vizcaya bakeri* Muir, holotype ♂, Philippine Is: Luzon: **23**, left antenna, frontal view; **24**, left tegmen; **25**, male genitalia, in repose, ventrocaudal view; **26**, same, genital segment, left lateral view; **27**, same, genital segment, caudal view; **28**, same, median projection of ventrocaudal margin of genital segment, ventral view. Scale: 0.5 mm, Figs. 23–24; 0.1 mm, Figs. 25–28.



Figs. 29–31. *Vizcaya bakeri* Muir, male genitalia, holotype: **29**, parameres, ventral view; **30**, genitalia without genital segment, left lateral view; **31**, aedeagus, dorsal view. Scale: 0.1 mm.

spines, rather than to *V. adornata* from Sulawesi. *V. bakeri* is only known from Luzon Island. A wider range of its distribution, at least in the Philippine Islands, is expected.

Vizcaya orea Asche, **new species** Figs. 32–43, 58–59

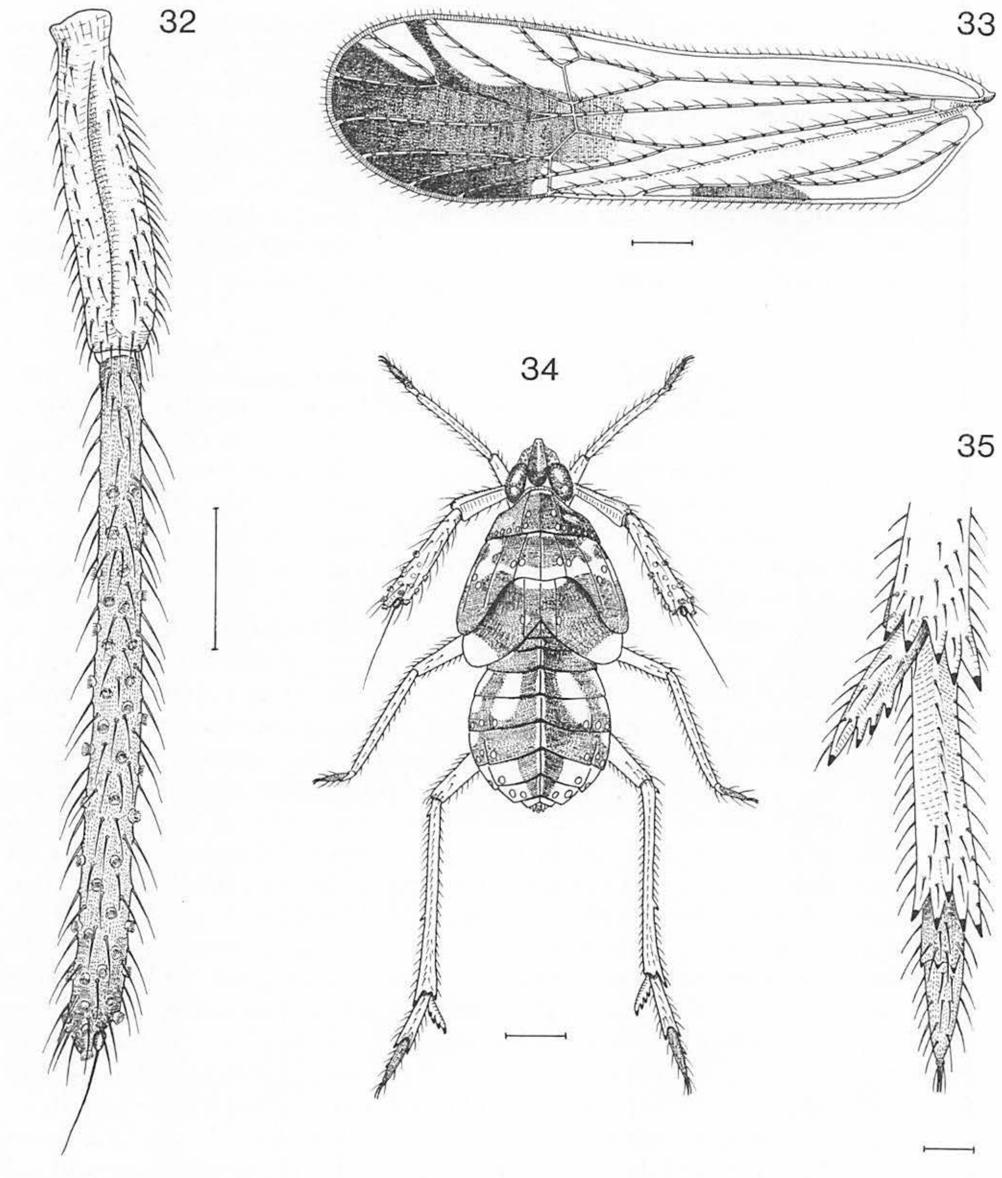
Description. *Adult.* In habitus, bodily proportions and coloration widely resembling *V. bakeri*; large species: total length of male (from apex of vertex to tip of tegmina): 5.7 and 5.8 mm (n = 2); female 6.2 mm (Vietnam, n = 1) and 6.3 mm (Thailand, n = 1); length of 1st + 2nd antennal segments in males: 2.5 mm; in females 2.8 mm. Coloration: head, antennae, thorax, abdomen, and legs generally as in *V. bakeri*, posterior part of vertex with continuous pale yellowish broad U-shaped marginal crossband (instead of light colored triangular corners in *V. bakeri*); tegmina with broad brown band distad of nodal line (Fig. 33) similar to pattern in *V. adornata*, hyaline parabolic area along outer branch of M_1 narrow, not surpassing level of M_1; almost entirely hyaline proximad of nodal line except for short brownish stripe between common stem of anal veins and inner margin and brownish suffusion between subapical cells. Carination of vertex, frons, post- and anteclypeus as in *V. adornata*; lateral carinae of pronotum only recognizable in anterior ½, fading posteriorly, medium carina of pronotum absent; carinae of mesonotum very fine but clearly recognizable. Frons 2.4 × longer than maximum width, widest at frontoclypeal suture. First antennal segment distinctly depressed and flattened, paddle-shaped as in *V. bakeri* but more slender, 4.45 × longer than maximum width; 2nd antennal segment 2 × as long as 1st. Proportions of posterior legs as in *V. adornata*. Posttibial spur with 9–11 teeth (including apical tooth), varying among individuals and on left and right sides. Drumming organ as in generic description.

Male genitalia. Generally similar to those of *V. bakeri*, differing in following characters: 3 short teeth each side of broadly rounded dorsocaudal margin of genital segment (Fig. 38); median part of diaphragm dorsad of opening for parameres reinforced by stronger sclerotized T-shaped structure (Fig. 38); median projection of ventrocaudal margin of genital segment short, comparatively wide, V-shaped incision distally (Figs. 39–40); aedeagus (Figs. 42, 43) long, slender, in lateral view only slightly S-shaped; as in *V. bakeri* with 2 unequally long and slender spinose processes subapically on left and dorsal side: left spine almost straight, tip only slightly curved dorsad, little longer than ⅓ total length of theca; dorsal spine about 2× as long as left one, in repose reaching almost ¾ length of theca basad, base bifurcate, in dorsal view tip curved to left side, slightly dilated subapically, tapering to apex.

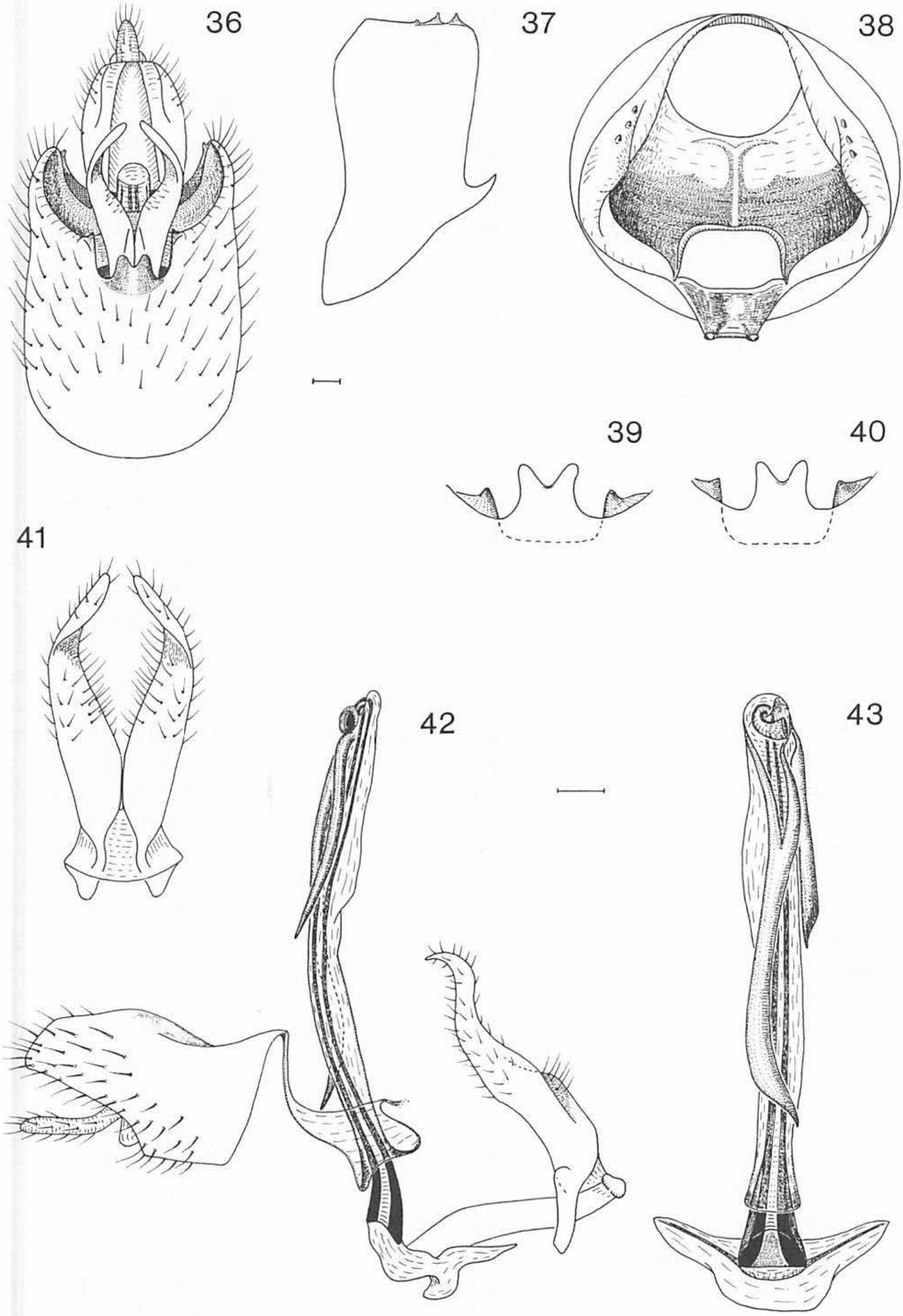
Female genitalia. As in *V. adornata*.

Nymph. Fourth instar, male (Figs. 34–35, 58–59). Total length (from apex of vertex to caudal end of abdomen): 2.65 mm; length of 1st + 2nd antennal segments: 1.25 mm. Coloration: ventral side, anterior part of vertex, frons below level of compound eyes, post- and anteclypeus, genae, rostrum, and legs pale yellow, last 2 tarsal segments brown; posterior part of vertex, superior part of frons, lateral areas in front of compound eyes brown; sides above eyes with dark brown spot; antennal segments orange to chestnut brown; pronotum brown except yellowish areas around median sensory pits; pads of forewings distally brown, pale yellow band and some scattered yellowish spots in anterior part across thorax; dorsal base and distal tips of hind wing pads pale yellow, otherwise brown; abdominal tergites chestnut brown, submarginally each side with yellowish longitudinal stripe beginning with tergites 4 and 5, stripe interrupted, homogeneously brown at tergite 6, stripe continuing over tergites 7 and 8; posterior margin of tergites 5 and 6 reddish; anterior angle of laterotergites pale yellow. Vertex medially 1.75× longer than wide at base, lateral margins strongly ridged, converging anteriorly, continuing as median frontal carinae; area of vertex deeply concave, without any compartments; median carinae of frons strongly elevated at transition vertex to frons, with area enclosed smooth, branching subapically to 2 fine, almost parallel median carinae; lateral margins of frons slightly convex, lamelliform; frons about 2× higher than maximum width, widest at level of antennae, area of frons concave, slightly ascending in middle to median carinae; carinae of post- and anteclypeus obsolete; oblique carina on genae prominent; 22 sensory pits laterad of median carinae on frons and vertex (11 on each side); sides in front of eyes each with 3 sensory pits; compound eyes depressed kidney-shaped with inferior incision weakly developed; 1st antennal segment paddle-shaped, 2.2× longer than maximum width, 2nd segment 2× as long as 1st, both segments with dense, long bristles, 2nd segment with 14–16 sensory fields irregularly arranged in distal portion. Pronotum and dorsal discs of fore- and hind wing pads tricarinate, carinae ridged, 2 weak carinae parallel to the outer margin on laterodorsal area of forewing pad. Pronotum with 14 sensory pits (7 each side), forewing pad with 8 (4 each side), and hind wing pad with 2 (1 each side). Abdomen ovate, strongly depressed, lateral margin sharp-edged, tergites strongly ridged medially, prominent sublateral carina parallel to outer margin from 5th to 8th tergite; abdominal tergites 1–4 without sensory pits, tergites 5–7 with 3, tergite 8 with 4 lateral sensory pits. Posttibia laterally with 2, distally with 5 rigid spines, 1.9× longer than posttarsi. Postbasitarsus 1.7× longer than 2nd + 3rd posttarsal segments, distally with 5 spines, median spine displaced proximad; last 2 tarsal segments compound, articulation (presumably fully developed in the 5th instar) indicated by 3 small rigid spines. Pretarsi small, claws present, pads indistinct. Posttibial spur with both sides convex, 4 conical teeth (including apical tooth).

Type data. Holotype ♂, INDONESIA: SUMATRA: Benkolen: Marang-Liwa, 1898 (Noualhier). 1♂, paratype, same data as holotype. Holotype and paratype in MNHN.



Figs. 32–35. *Vizcaya orea* Asche, n. sp.: **32**, left antenna, frontal view, ♀ from Thailand; **33**, left tegmen, holotype ♂, Sumatra; **34**, ♂ nymph, 4th instar, habitus in dorsal view, specimen from Thailand; **35**, same nymph, distal end of posttibia, posttarsi and posttibial spur. Scale: 0.5 mm, Figs. 32–34; 0.1 mm, Fig 35.



Figs. 36–43. *Vizcaya orea* Asche, n. sp., male genitalia, holotype (Fig. 40, paratype ♂, Sumatra): **36**, genitalia in repose, ventrocaudal view; **37**, genital segment, left lateral view; **38**, genital segment, caudal view; **39**, median projection of ventrocaudal margin of genital segment, ventral view; **40**, same, another specimen; **41**, parameres, ventral view; **42**, genitalia without genital segment, left lateral view; **43**, aedeagus, dorsal view. Scale: 0.1 mm.

Additional specimens (non-type). THAILAND: Doi Suthep: 1 ♀, 1 ♂ 4th instar nymph, Chiangmai, 900 m, 14.XI.1957 (J.L. Gressitt) (BPBM). VIETNAM: 1 ♀, Ban Me Thuot, 500 m, 16–18.V.1960 (L.W. Quate) (BPBM).

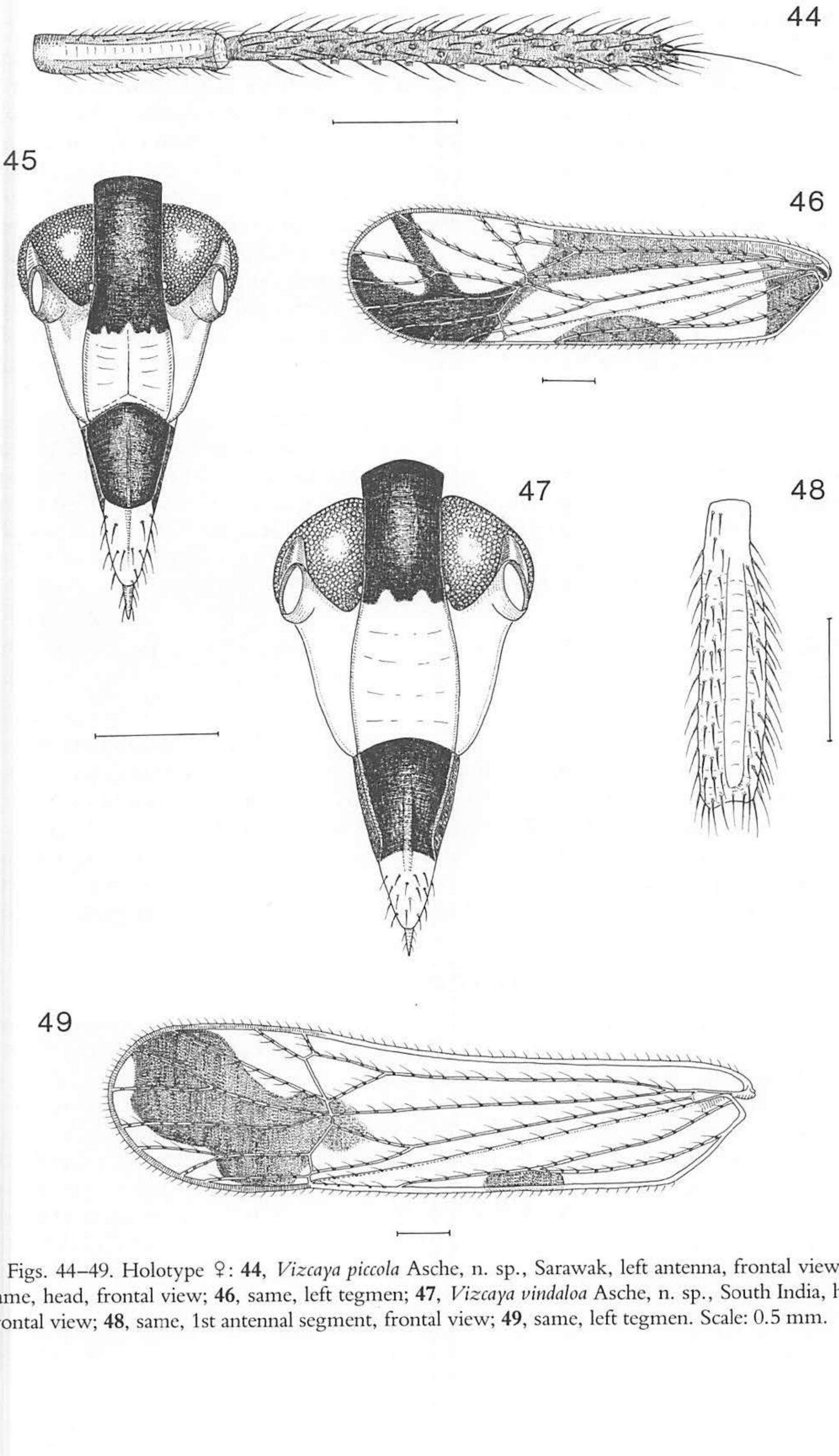
Remarks. *Vizcaya orea* is very similar to *V. bakeri*, especially in the male genitalia. Both species display a longer aedeagal spine, which arises with a bifurcate base subapically on the dorsal side. However, in *V. orea* this spine is located on the dorsal side reaching far basad, while in *V. bakeri* it is shorter and curved over the right to the ventral side. Moreover, the 2 species differ in the shape and color patterns of the tegmina (cf. Figs. 24 and 33). Female specimens from Thailand and Vietnam correspond well with the external characters of the males from Sumatra, and tentatively have been assigned to the same species. However, their conspecificity must still be proved by the examination of males from Thailand and Vietnam. Therefore the females are not included in the type material.

Vizcaya piccola Asche, **new species** Figs. 44–46, 54

Description. Male unknown. Female with bodily proportions and basic coloration as in *V. adornata*. Total length of female (from apex of vertex to tip of tegmina): 4.9 mm; length of 1st + 2nd antennal segments: 1.95 mm. Coloration: vertex, superior ⅔ of frons, postclypeus, lorae, sides in front of and above compound eyes, pro- and mesonotum, abdomen shiny dark brown; posterior parts of mesonotum, metanotum, and dorsal area of drumming organ reddish brown; posterior triangular corners of vertex, inferior frons, anteclypeus, and genae yellowish to stramineous; caudal tip of mesonotum creamy white; 1st antennal segment orange with dorsal and ventral margin brownish; 2nd antennal segment dark brown, bristles of antennae light brown; tegmina (Fig. 46) with color patterns as in *V. adornata*, but anterior area until level of junction of ScR+M homogeneously brown, area between C and M brown at outer side proximad of nodal line, semioval brown area in clavus along common stem of anal veins; distal part with dark brown band along inner apical margin, from this band narrow brown stripe leading diagonally to tip of Rs at outer subapical margin, enclosed hyaline parabolic area distinctly surpassing distal branches of M. Vertex with posterior carinae absent, median frontal carina only recognizable in inferior part, carinae of post- and anteclypeus obsolete; frons (Fig. 45) 2.4× higher than maximum width, area of frons in inferior part shallowly concave, otherwise convex, area of postclypeus strongly convex; 1st antennal segment (Fig. 44) relatively small, narrow: 4.1 × longer than broad, slightly compressed; 2nd antennal segment 2.5 × longer than 1st; medium carina of pro- and mesonotum absent, lateral carinae faint, fading to posterior margins; mesonotum strongly vaulted. Tegmina (Fig. 46) 3.6× longer than wide, widest distad of nodal line; M not passing the nodal line as straight vein, slightly displaced to inner margin. Proportions of posterior legs as in *V. adornata*. Posttibial spur with 6 teeth (including apical tooth). Female genitalia as in *V. adornata*, but valvifers VIII shorter in length, wider in middle.

Type data. Holotype ♀ (BPBM 14520), MALAYSIA: SARAWAK: Malang, Alpinia, 15.IX.1958 (J.L. Gressitt). Holotype in BPBM.

Remarks. *Vizcaya piccola* differs from the congeners by its small body size, the shape and proportions of the antennal segments, the slight displacement of M at the nodal line, the color patterns of the tegmina, and the small number (6) of teeth on the posttibial spur. It is more similar to *V. adornata* (dark coloration of pro- and mesonotum, 1st antennal segment only slightly compressed) than to the other species. However, its position in the genus can only be assessed by the finding of corresponding males. *V. piccola* is apparently endemic to Borneo.



Figs. 44–49. Holotype ♀: **44**, *Vizcaya piccola* Asche, n. sp., Sarawak, left antenna, frontal view; **45**, same, head, frontal view; **46**, same, left tegmen; **47**, *Vizcaya vindaloa* Asche, n. sp., South India, head, frontal view; **48**, same, 1st antennal segment, frontal view; **49**, same, left tegmen. Scale: 0.5 mm.

Vizcaya vindaloa Asche, new species Figs. 47–49

Description. Male unknown. Female similar in habitus and bodily proportion to *V. adornata.* Total length of female (from apex of vertex to tip of abdomen): 6.5 mm; length of 1st antennal segment: 1 mm; 2nd segment destroyed. Coloration: vertex, superior half of frons, postclypeus, lorae, sides in front of and above compound eyes shiny dark brown; inferior part of frons, anteclypeus, genae, 1st antennal segment and comparatively broad U-shaped sector at posterior margin of vertex orange-yellow, dorsal margin of 1st antennal segment brown, bristles yellowish; pro- and mesonotum orange, caudal tip of mesonotum creamy white; posterior parts of mesonotum, metanotum, and abdomen dark brown; tarsi of fore and middle legs brown, in hind leg only the 2nd and 3rd tarsal segments brown; tegmen hyaline proximad of nodal line, only small area in clavus between inner margin and junction of anal veins and suffusion between subapical cells brown; extended brown area distad of nodal line, hyaline marginal area at apex; no hyaline parabolic area along inner branch of M_1; veins and granules brownish, bristles yellowish.

Carinae on vertex faint, median carina of frons absent, median carina of post- and anteclypeus obsolete; frons (Fig. 47) 2.6 × higher than maximum width, widest at ⅓ its height from frontoclypeal suture. First antennal segment (Fig. 48) paddle-shaped, 4.4 × longer than broad, central area concave on both sides. Tegmina (Fig. 49) 3.8 × longer than wide, widest shortly distad of nodal line; M passing nodal line as straight vein. Proportions and dentation of posttibia as in *V. adornata.* Posttibial spur in female with 9 teeth (including apical tooth) on left, 12 teeth on right. Female genitalia as in *V. adornata*; valvifers VIII comparatively long, slender, no obvious dilation at base.

Type data. Holotype ♀, INDIA: TRAVANCORE: Thekkadi, Periyar Dam, 6–16.V.1937 (British Museum-Calcutta Museum Expedition to South India April-May 1937). Holotype in BMNH.

Remarks. *Vizcaya vindaloa* can readily be distinguished from the congeners by its large body size, the color patterns of the tegmina (distal part with extended brown area but with hyaline apical margin, proximal part largely hyaline) and the 3 brown tarsal segments of the fore and middle legs and the dark last 2 tarsal segments of the hind legs (in all other species, equally in all legs, only the last tarsal segment is darkened). Within *Vizcaya* it belongs to a group of species with paddle-shaped 1st antennal segment (*V. bakeri, V. orea*). However, any closer relationships can only be recognized after the finding of males. *V. vindaloa* is the only species known from outside of SE Asia.

DISCUSSION

A substantial gap in the character display between the plesiomorphic Asiracinae and the rest of Delphacidae has been recognized (Asche 1985). At that time 9 apomorphic characters were assessed that are absent in Asiracinae, but are present in the Kelisiinae, hitherto thought to be the most primitive group above the evolutionary level of Asiracinae (Fig. 1). These advanced characters are comprised of structures of the head and antennae, posttibial spur, hind legs, hind wings, sensory pits of nymphs, male genitalia, and male drumming organ. Accordingly, the non-asiracine Delphacidae formed a well-defined monophyletic group. The character analysis of Asche (1985) revealed a remarkable number of new acquisitions, which are assumed to have evolved with the transition from the evolutionary level of Asiracinae to the level of the rest of Delphacidae. With no transitional forms then known, such a significant gap between these levels left the sequence of evolutionary changes rather uncertain.

The genus *Vizcaya* represents an outstanding example of an evolutionary link, since *Vizcaya* species have retained some of the ancient characters inherited from Asiracinae, but have acquired part of the apomorphic characters formerly assumed to be displayed by the hypothetical ancestor species of all non-asiracine Delphacidae.

The following is an analysis of the character display of Vizcayinae in order to infer the phylogenetic position of this group.

Plesiomorphies of Vizcayinae

Vizcaya species possess the following asiracine-like characters here considered plesiomorphic:

1. Male genitalia

The anal segment (e.g., Figs. 9, 14) is rather long and ventrally concave, hoodlike, dorsally protecting the aedeagus. This is certainly a plesiomorphic configuration because it is common in Asiracinae and other Fulgoroidea (e.g., Cixiidae). In higher derived Delphacidae the anal segment can be highly differentiated and, in the majority of species, is equipped with spines or armlike projections.

The aedeagus is very similar to that of *Asiraca clavicornis* (Fabricius), and displays the same basic construction principle (Figs. 71–72). Its central sperm-conducting tube is strongly sclerotized and movable against the partly membranous theca. In higher derived Delphacidae starting with the Delphacinae, the central sperm-conducting tube is membranous, remnants of stronger sclerotization are only found at its basal part (Fig. 73).

The connection between the dorsal base of the aedeagus and the ventral base of the anal segment is formed by a continuation of the theca (no suspensorium as in Delphacini is differentiated).

The parameres (e.g., Fig. 13) are shaped like a pair of tongs. They are merely directed dorsad and not parallel to the diaphragm, but are rather directed caudad. The parameres function as claspers for embracing the base of the ovipositor during copulation. This form and function of the parameres is found in Asiracinae, but is modified in most of the more highly derived Delphacidae.

2. Female genitalia, eggs and oviposition

The long, sword-shaped orthopteroid ovipositor (Figs. 16, 20–21) and the internal ectodermal parts of the female genitalia (Fig. 22) of *Vizcaya* morphologically resemble the configuration found in *Asiraca* Latreille. The long and slender valvifers VIII are considered to be plesiomorphic (Wagner 1963). The dorsal margin of the median gonapophyses IX (= valvula II, see Müller 1942) are furnished with very minute, almost obsolete teeth, whereas in more derived Delphacidae a prominent row of teeth forming a sawlike structure is present.

This may suggest that the ovipositor of *Vizcaya* is not well suited to saw a slit into plant tissue as is the case in more derived Delphacidae (e.g., Delphacinae). Instead it may be used as a piercing tool as in Asiracinae. Accordingly, for *Vizcaya* a similar mode of oviposition as observed in *Asiraca clavicornis* seems very likely: *Asiraca* females insert the ovipositor into mostly soft stem plant tissue and lay a single egg with its anterior pole orientated toward the surface but fully covered by tissue. Then the female retracts the ovipositor and repeats laying more eggs in the same way at other spots.

It is also assumed that *Vizcaya* species do not protect their eggs after placing them in the plant tissue with wax (e.g., Stenocraninae), or with a laclike fluid that is produced in specialized oviduct glands, as in the majority of Delphacini. Corresponding secreting structures could not be found in *Vizcaya*.

The eggs of *Vizcaya* are relatively large in size (compare Figs. 17–18). The micropyle is located subapically at the anterior pole. No ringlike hatching-cap as obligate in all other Delphacidae above the level of Kelisiinae could be found. Presumably the nymphs of *Vizcaya* hatch through a small longitudinal slit at the anterior pole as in *Asiraca*. This mode has been considered to be a plesiomorphic character by Cobben (1965). In the swollen abdomen of a female of *Vizcaya adornata*, n. sp. from Sulawesi, only 8 fully developed eggs have been found, which indicates that only very few eggs can be laid at a time.

Also, in a random test of some Asiracinae a comparatively small number of developed eggs (of large size) ready for oviposition were found: 8–12 in the European *Asiraca clavicornis* (n = 6 females), 10–15 in *Ugyops kinbergi* Stal from Guam (n = 4 females), and 8–13 in *Melanesia* sp. from Sulawesi (n = 7 females) (Asche, unpublished data). However, in more highly derived Delphacidae such as species of the "advanced oviduct-gland-group" within the Delphacini, a considerably larger number of ripe eggs can be found that, compared to the size of the abdomen, are relatively smaller than in Asiracinae. In many species the eggs number 20–30, in some species even more (e.g., >40 in the European *Euides speciosa*; Asche, unpublished data). The development of only a few eggs at a time in *Vizcaya* corresponds well with the suggested behavior of single-egg-oviposition and is also considered a plesiomorphic character.

It may well be that the Delphacidae originally have been subjected to K-selection (sensu Southwood 1977) with few but large eggs, producing only few offspring in environments with comparatively low resource density. K-selected species are likely to adapt to only few or even 1 specific hostplant(s) which, in a given area, are normally not abundant but scattered (e.g., rainforest ecosystems). However, today, many of the higher derived Delphacidae are subject to r-selection with numerous eggs and offspring and live mostly in environments with high resource density such as grasslands. Many of these r-selected species are polyphagous and are very effectively attracted to human food crops like *Sogatella* Fennah spp. to rice (Asche & Wilson, in press) and *Perkinsiella* Kirkaldy spp. to sugarcane (Perkins 1903). This evolutionary change was possibly correlated with the anagenesis of the mode of oviposition and connected with the switch to habitats dominated by monocotyledons, mainly grasses, after the successful appearance of these plants in the Upper Cretaceous.

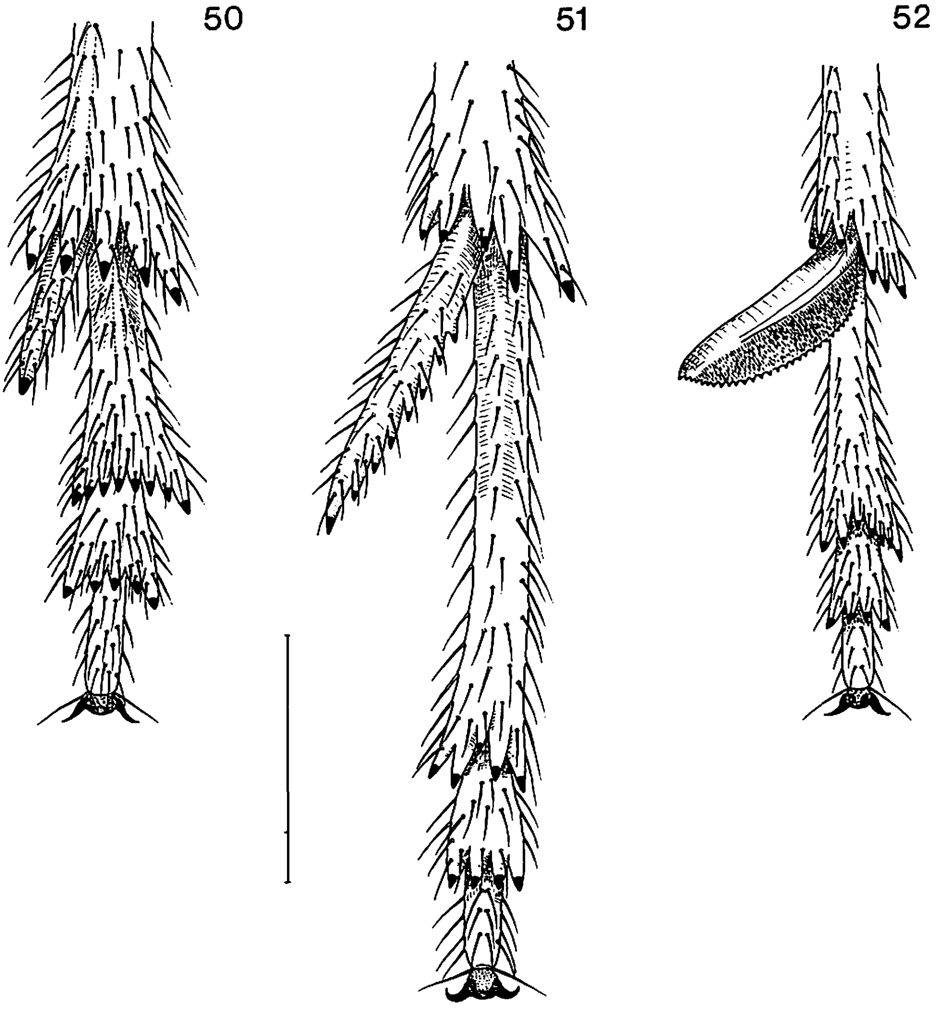
Today, approximately more than 80% of all Delphacidae feed on monocotyledons, where many of them are known to live in dense multi-species communities (e.g., Müller 1978). However, no hostplant of *Vizcaya* is known (*V. adornata* was collected at light in a lowland rainforest in Northern Sulawesi), whereas many species of Asiracinae live on ferns and dicotyledons, often trees (e.g., Fennah 1958), possibly a plesiomorphic association. The similarity in egg size and egg structures of *Vizcaya* with Asiracinae may suggest a similar mode of living (i.e., in a K-environment on shrubs or trees rather than on grasses).

3. Venation of the hind wing

The hind wings of *Vizcaya* show virtually the same venation as those of Asiracinae and many other Fulgoroidea, i.e., 5 independent veins lead from the band of crossveins to the distal margin (Figs. 8, 54), each of these veins may branch distally. The presence of the plesiomorphic condition of 5 veins in *Vizcaya* clearly indicates the position of this genus below the Kelisiinae, since the latter (and consistently all other non-asiracine Delphacidae) display the reduction of 1 of these veins (apparently the 3rd or 4th), thus only 4 total veins originate from that line of crossveins (Fig. 55). Moreover, in *Vizcaya* M and Cu are well separated from each other and include a comparatively broad cell as in Asiracinae (Fig. 8). In more highly derived Delphacidae M and Cu very much approach each other, the included cell becomes rather narrow (Fig. 55).

4. Sensory pits of the nymphs

The only *Vizcaya* nymph that could be studied so far is a 4th instar of apparently *V. orea*, n. sp., from Thailand (Figs. 34, 58–59). In this specimen the number and arrangement of larval sensory pits on the frons and vertex (22—11 on each side) are very similar to the plesio-

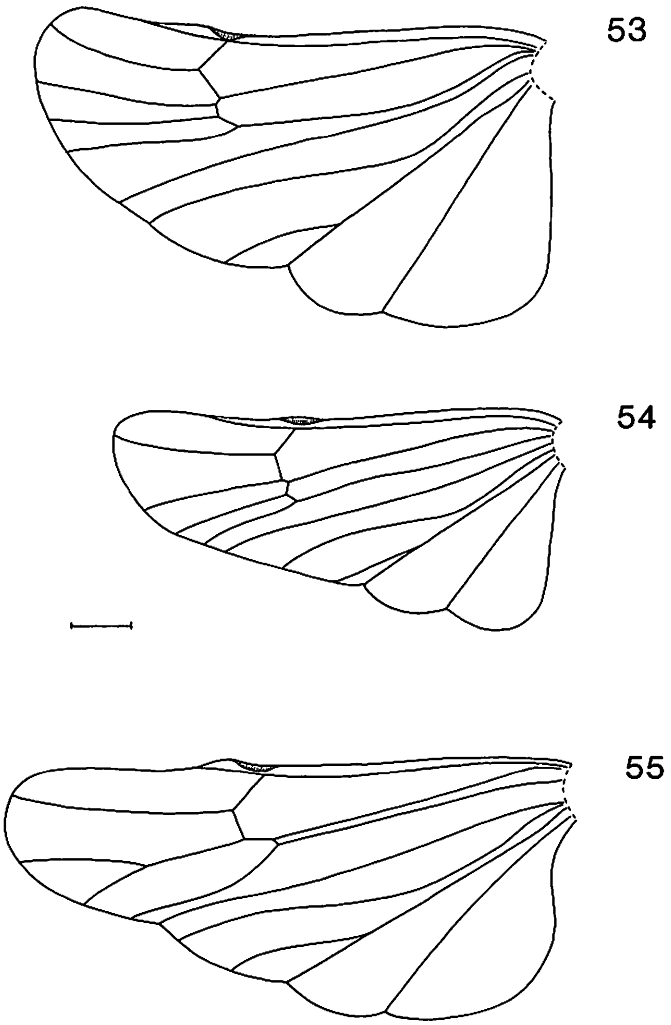


Figs. 50–52. Evolutionary trends in Delphacidae: morphological changes in the shape of distal end of posttibia, of the posttarsi and the posttibial spur: **50**, Asiracinae: *Asiraca clavicornis* (Fabricius), ♀, Romania; **51**, Vizcayinae: *Vizcaya adornata* Asche, n. sp., paratype ♀, Sulawesi; **52**, Delphacinae: *Peregrinus maidis* (Ashmead), ♀, Hongkong. Scale: 0.5 mm.

morphic configuration in Asiracinae. For example, the 5th instar nymph of *Asiraca clavicornis* possesses also 22 (Figs. 56–57), last instar nymphs of Ugyopini even many more (40–50+) sensory pits on frons and vertex (Asche 1985:455, Fig. 96).

In 5th instar nymphs of all other non-asiracine Delphacidae a constant number of only 18 (9 on each side) is present, always arranged in the same pattern (Figs. 60–61) (Asche 1985:134–35).

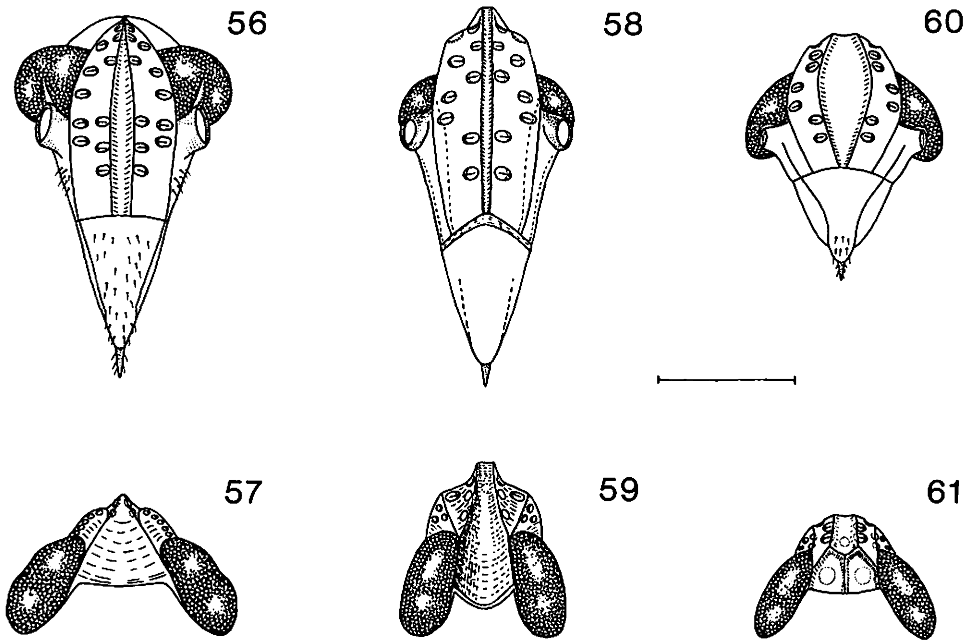
For the morphology of larval sensory pits in Delphacidae see Liebenberg (1956).



Figs. 53–55. Evolutionary trends in Delphacidae: morphological changes in the hind wing venation: **53**, Asiracinae: *Asiraca clavicornis* (Fabricius), ♀, Romania, 5 independent veins from line of crossveins to apex, cell between M and Cu wide; **54**, Vizcayinae: *Vizcaya piccola* Asche, n. sp., holotype ♀, Sarawak, venation as in Asiracinae; **55**, Delphacinae: *Peregrinus maidis* (Ashmead), ♀, Hongkong, 4 independent veins from line of crossveins to apex, cell between M and Cu narrow. Scale: 0.5 mm.

5. Antennal sensory fields

In *Vizcaya* the antennal sensory fields on the pedicel in juveniles and adults are numerous and irregularly arranged as in Asiracinae (e.g., Fig. 6). In this character, *Vizcaya* is evidently more primitive than Kelisiinae, which (as all other non-asiracine Delphacidae) show a reduction and stabilization of the number of sensory pits and their regular arrangement in rows or groups. The basic principle of arrangement of antennal sensory fields in taxa above *Vizcaya* seems to be 16 fields in 7 rows (if secondarily multiplied in adults of some species, this basic pattern is at least recognizable in the last instar nymphs).



Figs. 56–61. Evolutionary trends in Delphacidae: morphological changes in the head of nymphs, especially number and arrangement of sensory pits: **56**, **58**, **60**, frontal view; **57**, **59**, **61**, dorsal view. **56–57**, Asiracinae: *Asiraca clavicornis* (Fabricius), 5th instar, ♂, W. Germany, total 22 sensory pits on frons and vertex, 11 on each side; **58–59**, Vizcayinae: *Vizcaya orea* Asche, n. sp., 4th instar, ♂, Thailand, total 22 sensory pits on frons and vertex, 11 on each side; **60–61**, Delphacinae: *Chloriona* sp., 5th instar, ♂, W. Germany, total 18 sensory pits on frons and vertex, 9 on each side. Scale: 0.5 mm.

Nothing is known about the symbiont-configuration of *Vizcaya*; however, it is very likely that the basic configuration of a- and x-symbionts (as in Asiracinae and other Fulgoroidea, see Ermisch 1960; Müller 1940, 1949, 1962) is still retained. As far as was examined, it seems that in more highly derived Delphacidae these plesiomorphic symbionts get lost (symbiont "a" with the transition from Plesiodelphacinae- to Delphacinae-plateau, symbiont "x" with the transition from Tropidocephalini-Saccharosydnini- to Delphacini-plateau) or are replaced by other symbiont-types (e.g., "H+f" in Delphacini), respectively (Asche 1985).

Synapomorphies of Vizcayinae and the Rest of Non-Asiracine Delphacidae

The following characters are here interpreted as synapomorphies for all non-asiracine Delphacidae at the level of *Vizcaya* and above:

1. Male drumming organ
   While in Asiracinae and in all other Fulgoroidea checked for this character except a few Ommatidiotini (Issidae) (see Ossiannilsson 1949; Asche 1985), no obvious morphological differences in the sexes could be found, a striking sexual dimorphism in the drumming organ is present in *Vizcaya* and the rest of Delphacidae. Females of *Vizcaya* and all other non-asiracine Delphacidae retain the plesiomorphic configuration of Asiracinae. In males, however, the drumming organ has undergone major morphological alterations: (1) the 2nd

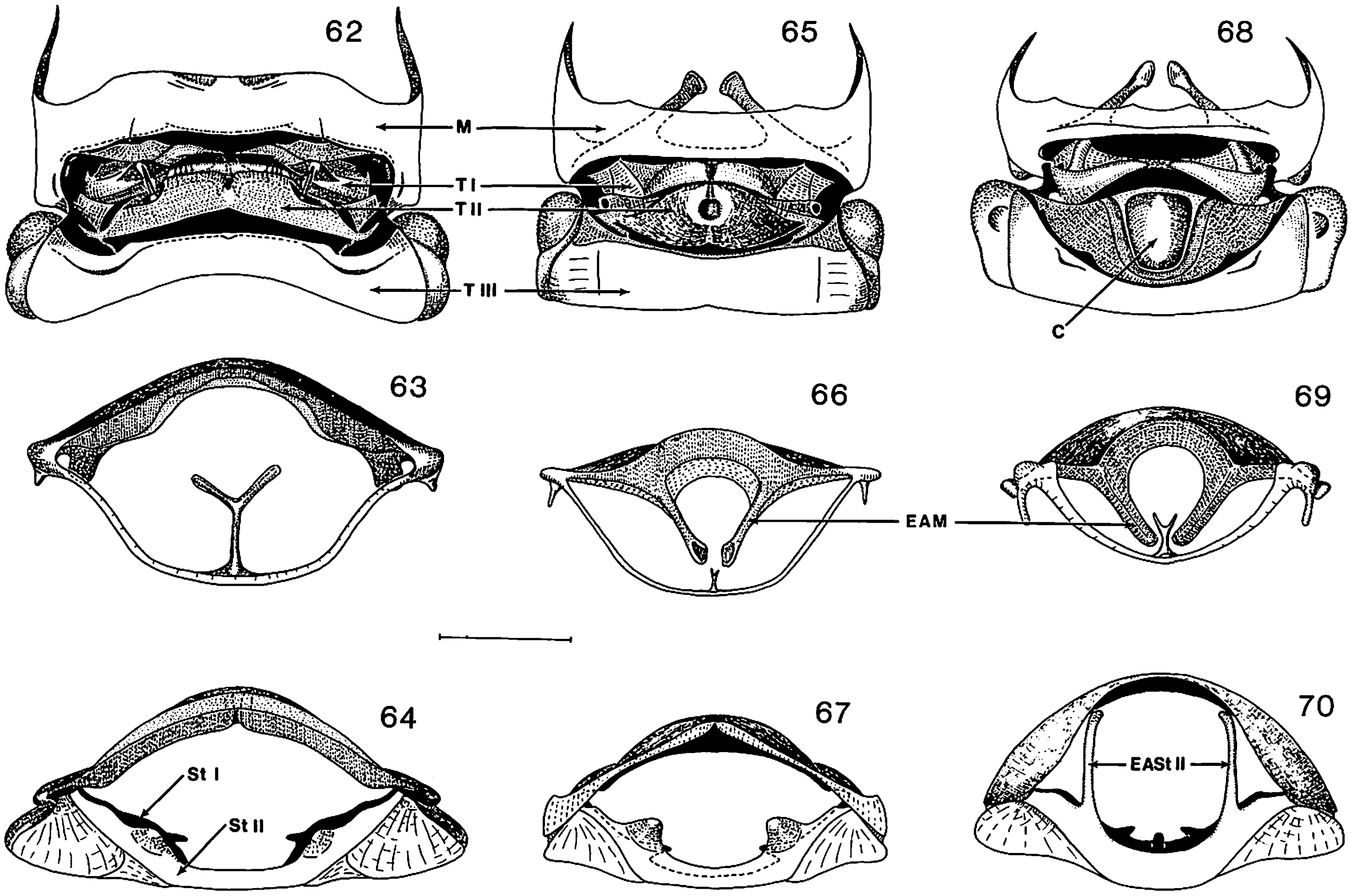
abdominal tergite is differentiated in a prominent plate system readily visible externally (cf. Figs. 62, 65) (character **2** in the following cladogram); (2) the metapostnotum (cf. Figs. 63, 66) has sent 2 long, slightly converging apodemes cephaloventrad as attachment places for a pair of strongly enlarged ventrolongitudinal muscles (Iadlm1 sensu Ossiannilsson 1949), which are connected to the center of the enlarged 2nd abdominal tergite (= character **3**); and (3) the 2nd abdominal sternite is furnished with a pair of shell-like projections slightly bent caudad (cf. Figs. 64, 67) and function as apodemes for a pair of enlarged dorsoventral muscles (Iavlm2 sensu Ossiannilsson 1949) (= character **4**).

2. Hind legs
   In *Vizcaya*, the number and arrangement of spines of posttibiae and posttarsi resemble the configuration of the rest of non-asiracine Delphacidae (cf. Figs. 50–52). The distal spines of the posttibiae are arranged in an inner group of 2 small spines and an outer group of 3 longer spines (= character **5**), whereas in *Asiraca* there is a continuous row of almost equally shaped spines. The number of lateral spines of the posttibiae is reduced to only 2, which is the general configuration of Delphacidae above the Asiracinae (= character **6**). Starting with *Vizcaya*, the distal spines of the postbasitarsus form 2 groups (= character **7**) and not a continuous row as in *Asiraca*.

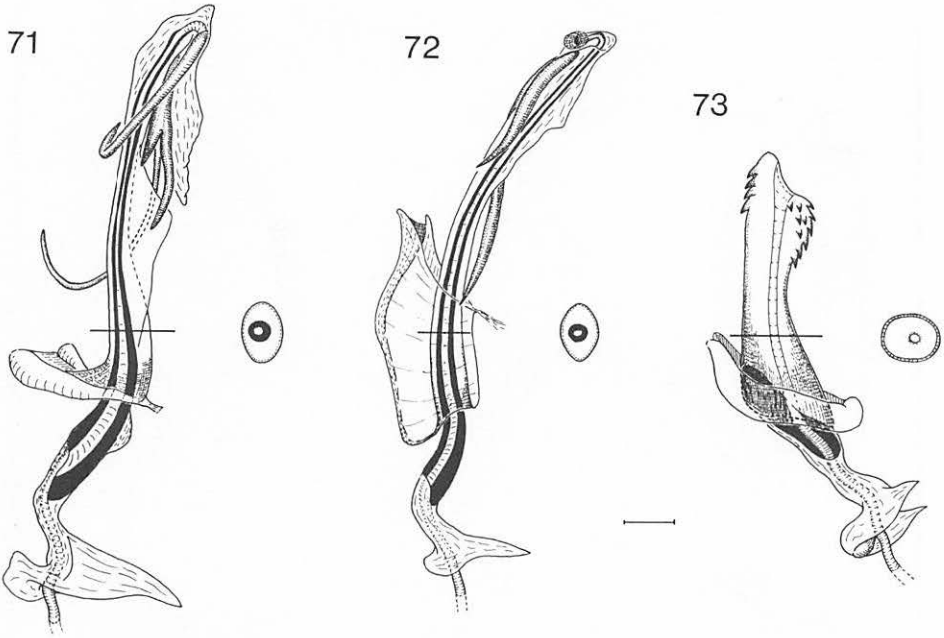
3. Posttibial spur
   The posttibial spur is the most important constitutive character of all Delphacidae. It is evidently derived from a once rigid spine out of a row of distal posttibial spines (Asche 1985:87–91). It is used as a support in jumping and has undergone a remarkable degree of differentiation within the family. However, the posttibial spur of Asiracinae is rather simple, almost still spinelike, in cross-section circular (Asiracini) or quadrangular (Ugyopini) and does not possess any teeth on the inner margin. The posttibial spur of adults and nymphs of *Vizcaya* is also spinelike or subulate, in cross-section, as in Asiracini, almost circular. However, as a new acquisition it bears a row of well-developed conical teeth on its inner margin (Figs. 35, 51) (= character **8**).

   It resembles the configuration found in Kelisiinae (although in cross-section the spur is not strictly convex on both sides), in Plesiodelphacinae, and in some Delphacini (e.g., in the species formerly placed in the polyphyletic "Alohini"). The development of conical teeth on a spinelike spur at the level of *Vizcaya* may mark the beginning of its transformation to different types of spurs such as are found in more highly derived Delphacidae. From this *Vizcaya*-configuration, the morphological variety of spur types, which all have undergone processes of flattening (Asche 1985), may have derived. It may well be that the *Vizcaya*-like posttibial spur of Kelisiinae, Plesiodelphacinae, and of some Delphacini (including the "Alohini") still represents a rather plesiomorphic stage. On the other hand, the posttibial spur seems able to undergo frequent morphological alterations in the course of adaptations to a special habitat. This seems to be the case at least in the "advanced oviduct-gland-group" within the Delphacini, which still represents more than 70% of all species. Therefore, it is equally conceivable that a similar *Vizcaya*-like posttibial spur might have evolved secondarily (and perhaps several times independently) on the base of an already advanced (flattened) spur. This might have been due to adaptations to different habitat types (e.g., switch from grass feeder to tree feeder or vice versa) or to other environmental changes that could have affected species such as during their colonization of oceanic islands (consider the large group of Pacific "Alohini" in the Hawaiian Islands; see Zimmerman 1948).

4. Genal carina
   Vizcaya species (nymphs and adults) display an oblique carina across the genae leading from the lateral edge of the frontoclypeal suture to the base of the antenna ending beneath or



Figs. 62–70. Evolutionary trends in Delphacidae: morphological changes in the male drumming organ: **62**, **65**, **68**, dorsal view; **63**, **66**, **69**, metapostnotum, caudal view; **64**, **67**, **70**, 1st and 2nd abdominal segments, caudal view. **62–64**, Asiracinae: *Asiraca clavicornis* (Fabricius), W. Germany. **65–67**, Vizcayinae, *Vizcaya adornata* Asche, n. sp., holotype. **68–70**, Delphacinae, *Aloha ipomoeae* Kirkaldy, Hawaiian Is: Oahu. Abbreviations: C = central plate of abdominal tergite II; EAM = elongate apodemes of the metapostnotum; EAStII = elongate apodemes of the 2nd abdominal sternite; M = metapostnotum; StI = 1st abdominal sternite; StII = 2nd abdominal sternite; TI–TIII = abdominal tergites I–III. Scale: 0.5 mm.



Figs. 71–73. Evolutionary trends in Delphacidae: morphological changes in the aedeagus: **71**, Asiracinae: *Asiraca clavicornis* (Fabricius), W. Germany, central sperm-conducting tube strongly sclerotized, see cross-section; **72**, Vizcayinae: *Vizcaya bakeri* Muir, holotype, Philippine Is: Luzon I, construction principle as in Asiracinae; **73**, Delphacinae: *Aloha ipomoeae* Kirkaldy, Hawaiian Is: Oahu, sperm-conducting tube membranous except for a small detached portion at base. Scale: 0.1 mm.

slightly in front of that base (Fig. 4). This configuration is also present in all other non-asiracine Delphacidae. A similar oblique carina is found in some of the Asiracini (5 genera). However, in contrast to *Vizcaya* and other non-asiracine Delphacidae, it ends distinctly caudad of the antennal base. In the rest of the Asiracini (the Neotropical genera *Tetrasteira* Muir, *Platysystatus* Muir, and *Equasystatus* Asche), and in all Ugyopini, such an oblique genal carina is missing, with high probability reflecting the plesiomorphic configuration within Delphacidae. As discussed in Asche (1985:227–33), the acquisition of an oblique carina across the genae has very likely occurred only once in the evolution of Delphacidae. Thus, the presence of such a carina can be interpreted as a synapomorphy for part of the Asiracini + the rest of Delphacidae (= character **1**). However, this assumption implies that the whole subfamily Asiracinae is paraphyletic—an unsatisfying situation that, due to the presence of mostly plesiomorphic characters, cannot be solved at present. The displacement of the genal carina from behind the antennal base to the inferior or anterior margin of that base is a synapomorphic character for all non-asiracine Delphacidae beginning with *Vizcaya* (= character **9**).

5. Aedeagus

In Asiracinae in repose, the distal part of the aedeagus is acutely bent to the base of the shaft, but is fully movable (also in taxa in which the distal part is shortened). Above the level of Asiracinae beginning with Vizcayinae, the distal part becomes a short tube with apical phallotrema, which is not movable against the shaft (Fig. 72). The transformation of a formerly movable distal part to a short rigid remnant can be considered as a synapomorphic character for all non-asiracine Delphacidae (= character **10**). At even higher evolutionary plateaus within the Delphacidae (above the Plesiodelphacinae [Asche 1985:176–80]) this remnant of the distal part is also reduced.

Several characters could be found emphasizing the monophyly of *Vizcaya* itself as well as the monophyly of the rest of non-asiracine Delphacidae starting with the level of Kelisiinae.

Autapomorphies of Vizcayinae

The following characters are here interpreted as autapomorphies for Vizcayinae:

1. Male drumming organ
   The special shape of the 2nd tergite of the male drumming organ (Fig. 65) (= character **11**). In *Vizcaya*, the dorsal plate system forms a more or less continuously vaulted ellipsoid dome with a deep central depression. In all other non-asiracine Delphacidae, a large central plate (without any depression) is clearly separated against the lateral plates of the tergite (Fig. 68). It seems likely that Vizcayinae—after the initial sexually dimorphic differentiation also found in other parts of the male drumming organ, characters shared with the rest of non-asiracine Delphacidae—has evolved its unique type of central region of the 2nd abdominal tergite, probably combined with a different mode of muscle attachment.
2. Vertex
   The transition of vertex to frons is entirely rounded and smooth; the carinae of the long and narrow vertex are inconspicuous, the anterior remnants of the carinae form an inverted V (Fig. 5) (= character **12**). A similar (but not identical) carination is found in Plesiodelphacinae; this is most likely the result of convergent evolution, especially since other more complex characters (e.g., the shape of the 2nd abdominal sternite of the male drumming organ and the hind wing venation) are considerably different.
3. Spine configuration of postbasitarsus
   The median of 5 distal spines of the postbasitarsus is conspicuously shifted proximad (Fig. 51) (= character **13**). Also in this character certain similarities to the configuration in Plesiodelphacinae as well as in Ugyopini are recognizable; however, significant differences in many other characters exclude a closer relationship of Vizcayinae to any of these groups. Again, the assumption of convergence seems likely which, of course, weakens the phylogenetic value of this character.
4. Antennae
   The antennal segments are strongly elongate with the basal segment compressed (e.g., Fig. 23). Elongate antennae are also present in many Asiracinae, but are not assumed to have characterized the common hypothetical ancestor species of non-asiracine Delphacidae for which relatively short and cylindrical antennal segments have been postulated (Asche 1985:137). Therefore, it seems likely that the elongate antennae of Vizcayinae are independently evolved (= character **14**).

Synapomorphies of Delphacidae Above the Level of Vizcayinae

All Delphacidae above the level of *Vizcaya* beginning with the Kelisiinae form a monophyletic group based on the following synapomorphic characters:

1. Aedeagus
   The sclerotized sperm-conducting tube and the theca are not movable against each other as in Asiracinae and *Vizcaya* (= character **15**).

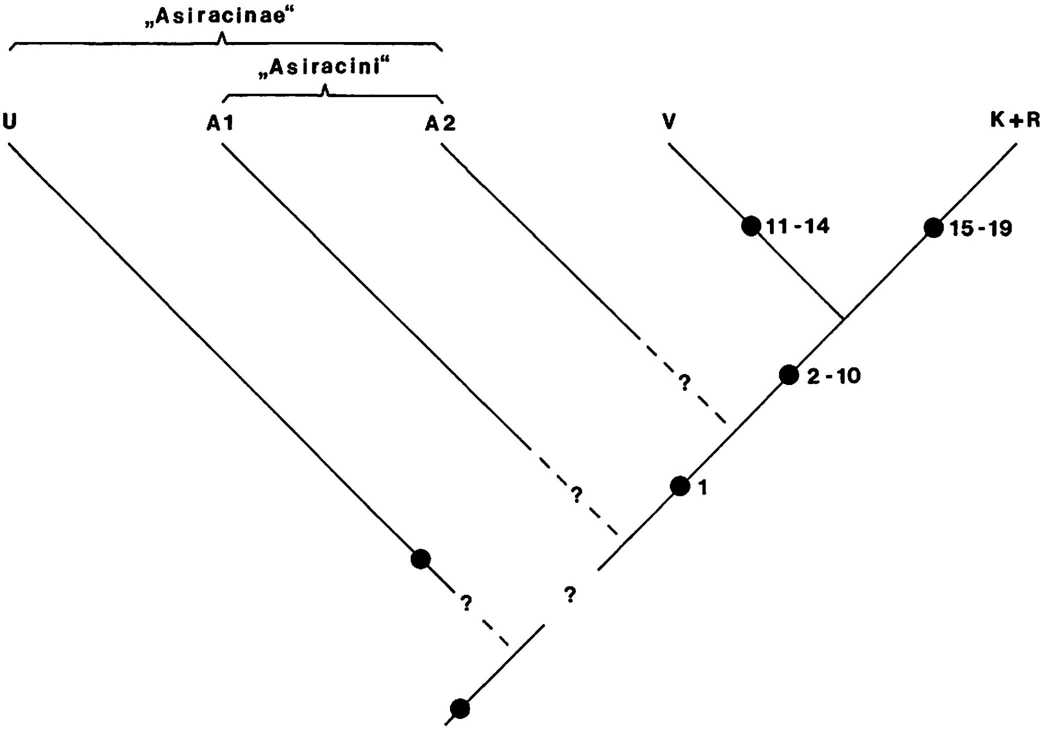


Fig. 74. Phylogenetic relationships of the Vizcayinae. Black spots: apomorphies, numbers refer to characters in text; quotation marks indicate paraphyly. Abbreviations: A1 = non-ugyopine Asiracinae without oblique carina across the genae, A2 = non-ugyopine Asiracinae with oblique carina across genae, K+R = Kelisiinae + rest of Delphacidae, U = Ugyopini, V = Vizcayinae.

2. Male drumming organ

   The 2nd abdominal tergite is differentiated into a distinguished central plate (Fig. 68) functioning as caudodorsal attachment for the paired ventrolongitudinal muscles, which attach to the apodemes of the metapostnotum (= character **16**).

3. Hind wing

   Out of the plesiomorphic set of 5 veins that arise from the line of crossveins (as in Asiracinae and *Vizcaya*), 1 vein is reduced (Fig. 55): only 4 veins lead from the line of cross-veins to the distal margin (= character **17**).

4. Larval sensory pits

   The number of sensory pits on the frons and vertex is reduced to a constant total of 18 (9 on each side); their arrangement is stabilized (Figs. 60–61) (= character **18**).

5. Antennal sensory fields

   The number of sensory fields on the pedicel is reduced to a total of 16. The sensory fields are regularly arranged in 7 groups (= character **19**). If the number of sensory fields and groups are secondarily multiplied, then the original number and arrangement can be recognized in the 5th instar nymph.

Conclusions

The analysis of characters has clearly demonstrated the high importance of *Vizcaya* to the phylogeny of Delphacidae. As shown above, *Vizcaya* has retained important plesiomorphic

Table 1. State of characters used in reconstructing phylogenetic relationships of Vizcayinae to other Delphacidae (cf. Fig. 74).

	Plesiomorphic state	Apomorphic state
1.	Oblique genal carina absent	Oblique genal carina present
2.	Male drumming organ: 2nd abdominal tergite without differentiated plate system	Male drumming organ: 2nd abdominal tergite with prominent plate system
3.	Male drumming organ: apodemes of metapostnotum shell-like, not elongate	Male drumming organ: apodemes of metapostnotum strongly elongate
4.	Male drumming organ: apodemes of 2nd abdominal sternite weakly developed, muscles Iavlm2 short	Male drumming organ: apodemes of 2nd abdominal sternite shell-like, projected caudad, muscles Iavlm2 enlarged
5.	Posttibia: distal spines form continuous row, spines equally shaped	Posttibia: distal spines form 2 groups (inner group: 2 small spines; outer group: 3 longer spines)
6.	Posttibia with 3 or more lateral spines	Posttibia with 2 lateral spines
7.	Postbasitarsus: distal spines form continuous row	Postbasitarsus: distal spines form 2 groups
8.	Posttibial spur without teeth on inner margin	Posttibial spur with a row of conical teeth on inner margin (if secondarily lost, spur flattened, not circular or quadrangular in cross-section)
9.	Genal carina leading from lateral frontoclypeal edge to posterior margin of antennal base or distinctly caudad of it	Genal carina leading from lateral frontoclypeal edge to inferior or anterior margin of antennal base
10.	Distal part of aedeagus movable against basal part (even if shortened)	Distal part of aedeagus reduced to short, rigid tube, not movable
11.	Male drumming organ: 2nd abdominal tergite without deep central depression	Male drumming organ: 2nd abdominal tergite with deep central depression
12.	Transition vertex-frons angular, carinae of vertex conspicuous, forming 2 large posterior and 1 small anterior compartment	Transition vertex-frons rounded, carinae of vertex inconspicuous, forming an inverse V, which includes a combined large posterior compartment, anterior compartment obsolete
13.	Postbasitarsus: median of distal spines (= 1st of outer group of homonomous spines) not significantly shifted proximad	Postbasitarsus: median of distal spines smaller than the others, displaced proximad
14.	Antennal segments cylindrical, but comparatively short, both segments equally shaped	Antennal segments conspicuously elongate, 1st segment compressed
15.	Aedeagus: sclerotized sperm-conducting part and theca over the whole length movable against each other	Aedeagus: sclerotized sperm-conducting part and theca at least in parts not movable against each other
16.	Male drumming organ: 2nd abdominal tergite without central plate	Male drumming organ: 2nd abdominal tergite with central plate
17.	Hind wing: 5 veins arise from line of crossveins	Hind wing: 4 veins arise from line of crossveins
18.	Larval sensory pits on frons and vertex: = >18, arrangement variable from group to group	Larval sensory pits on frons and vertex: number = 18 (9 on each side), arrangement in unique pattern
19.	Number of antennal sensory fields = >16, arrangement ± irregular without forming groups	Number of antennal sensory fields = 16, regularly arranged in 7 groups or rows (in some species secondarily multiplied, but basic pattern present in 5th instar nymph)

asiracine-like characters (aedeagus configuration, hind wing venation, eggs, number and arrangement of larval sensory pits, and antennal sensory fields), which indicates its comparatively basal position in the phylogenetic tree of Delphacidae. On the other hand, *Vizcaya* has acquired several complex advanced characters (male drumming organ, spine configuration of hind legs, posttibial spur, position of the oblique genal carina), which significantly elevates this group above the level of Asiracinae. However, these advanced characters are shared between *Vizcaya* and the rest of non-asiracine Delphacidae and are here interpreted as synapomorphies. Further, it could be demonstrated that *Vizcaya* has not (yet) acquired several advanced characters, which characterize the next evolutionary plateau (the Kelisiinae + rest).

The analysis revealed monophyly for all non-asiracine Delphacidae beginning with *Vizcaya*, monophyly for all Delphacidae above the level of *Vizcaya* beginning with the Kelisiinae, and monophyly for *Vizcaya* itself. It could be assessed that the position of *Vizcaya* in the phylogenetic tree ranks well above the level of Asiracinae but certainly below the level of Kelisiinae. The sequence of evolutionary changes from Asiracinae to Kelisiinae + rest is expressed in the cladogram (Fig. 74).

The cladogram shows that the Vizcayinae form the sister-group of all other non-asiracine Delphacidae. The Vizcayinae indeed mediate between the very primitive level of Asiracinae and the more highly derived level of Kelisiinae + rest. With this background, a subfamily rank for the group of *Vizcaya* seems adequate and justifiable.

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Cavernicolous Meenoplidae of the Genus *Phaconeura* (Homoptera: Fulgoroidea) from Australia[1]

Hannelore Hoch[2]

ABSTRACT

Recent investigations of limestone caves and lava tubes in tropical north Queensland have revealed the existence of a remarkably diverse cave-adapted arthropod fauna. Among the most diverse groups are the Fulgoroidea, represented by the families Cixiidae and Meenoplidae. Four new cave-dwelling meenoplid species of the genus *Phaconeura* are described from Queensland caves within the Chillagoe and Mitchell Palmer Karst: *minyamea*, n. sp., *mopamea*, n. sp., *crevicola*, n. sp., and *capricornia*, n. sp. Notes on their ecology and distribution are given, as well as a diagnosis and additional locality data for *P. pluto* from western Australia.

INTRODUCTION

Recent biological expeditions to study tropical north Queensland limestone caves and lava tubes (Howarth 1988; Stone 1988; Sullivan 1988) have shown that the cave-adapted arthropod fauna is much more diverse than had been assumed previously (Moore 1964; Hamilton-Smith 1967; Barr 1973). Among the most diverse groups found in the caves are the Fulgoroidea, represented by the families Cixiidae and Meenoplidae (Hoch & Howarth, 1989b). In the Cixiidae, 8 new cave-adapted species have been recognized in the genera *Undarana* (Hoch & Howarth 1989) and *Solonaima* (Hoch & Howarth, 1989a). Northern Queensland now has the highest concentration of cave-adapted Fulgoroidea in the world (Hoch & Asche 1988). Its outstanding position is corroborated by the finding of four new cavernicolous meenoplid species collected in limestone caves within the Tower Karst around Chillagoe (Mareebashire, Cape York Peninsula) and the Mitchell Palmer area, about 75 km to the north. Previously, only one cave-adapted meenoplid species was known from Australia: *Phaconeura pluto* Fennah, from Nambung National Park, Western Australia. Outside Australia, cave-adapted Meenoplidae are known only from Western Samoa (Hoch & Asche 1988) and the Canary Islands (Remane & Hoch 1988).

The 4 new cavernicolous meenoplid species described in this paper belong to *Phaconeura* Kirkaldy. The genus *Phaconeura* was established by Kirkaldy (1906:427) to accommodate Meenoplidae with a longitudinal median carina of the head. This genus is represented with 6 species and 1 subspecies in the epigean fauna of Australia: Queensland, New South Wales (Fennah 1963; Kirkaldy 1906; Woodward 1957).

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Characters discriminating the 4 new cavernicolous *Phaconeura* species are found in the degree of troglomorphy (morphological alterations in correlation to cave-adaptation, e.g., reduction of eyes, wings, and pigment) as well as in the configuration of the male genitalia, especially the aedeagus. Female genitalia seem to be less conspicuously differentiated among closely related species. The 4 new *Phaconeura* species are described, and notes on their ecology and distribution are given. A diagnosis and additional distribution data for *Phaconeura pluto* Fennah from Western Australia are also presented.

Specimens of the *Phaconeura* species described below are deposited in the following institutions and private collections: QM = Queensland Museum, Brisbane, Australia; BMNH = British Museum (Natural History), London, England; BPBM = Bernice P. Bishop Museum, Honolulu, Hawai'i, U.S.A.; AH = Private collection of M. Asche & H. Hoch, Marburg, F.R.G.

Measurements of body length were taken from specimens preserved in ethanol and equal the distance between apex of head and tip of abdomen. In the data given for the nymphs, arabic numerals refer to the number of specimens, roman numerals to the instar.

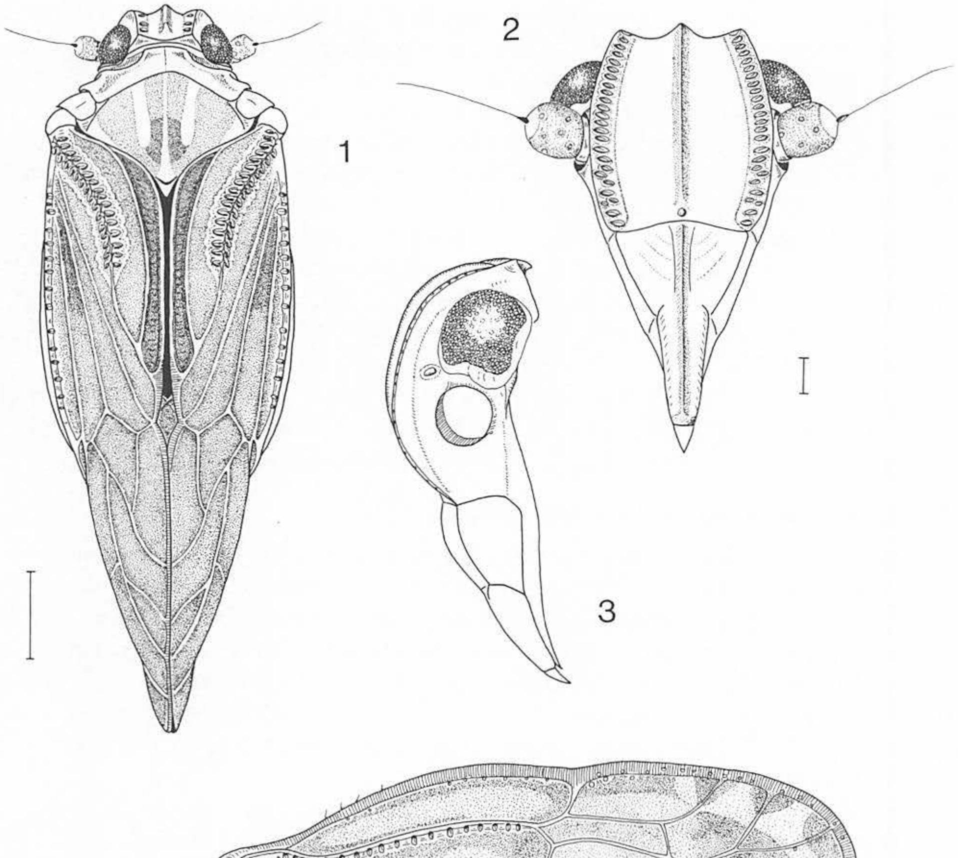
Phaconeura minyamea Hoch, **new species** Figs. 1–12

Description. Small meenoplids with tegmina steeply tectiform and a conspicuous color pattern: head and pronotum yellowish; lateral portions of mesonotum yellowish brown, with alternating brown and whitish longitudinal stripes laterad of median carina medially. Median carina and posterior margin of mesonotum whitish laterally. Intensity of brown pigment on mesonotum variable among individuals. Tegmina with venation whitish; cells brown with dark brown portions along margins, in anal cells and cells enclosed by Sc and M, and M and Cu, respectively. Wings infuscate with venation dark brown. Compound eyes red to reddish brown. Legs yellow.

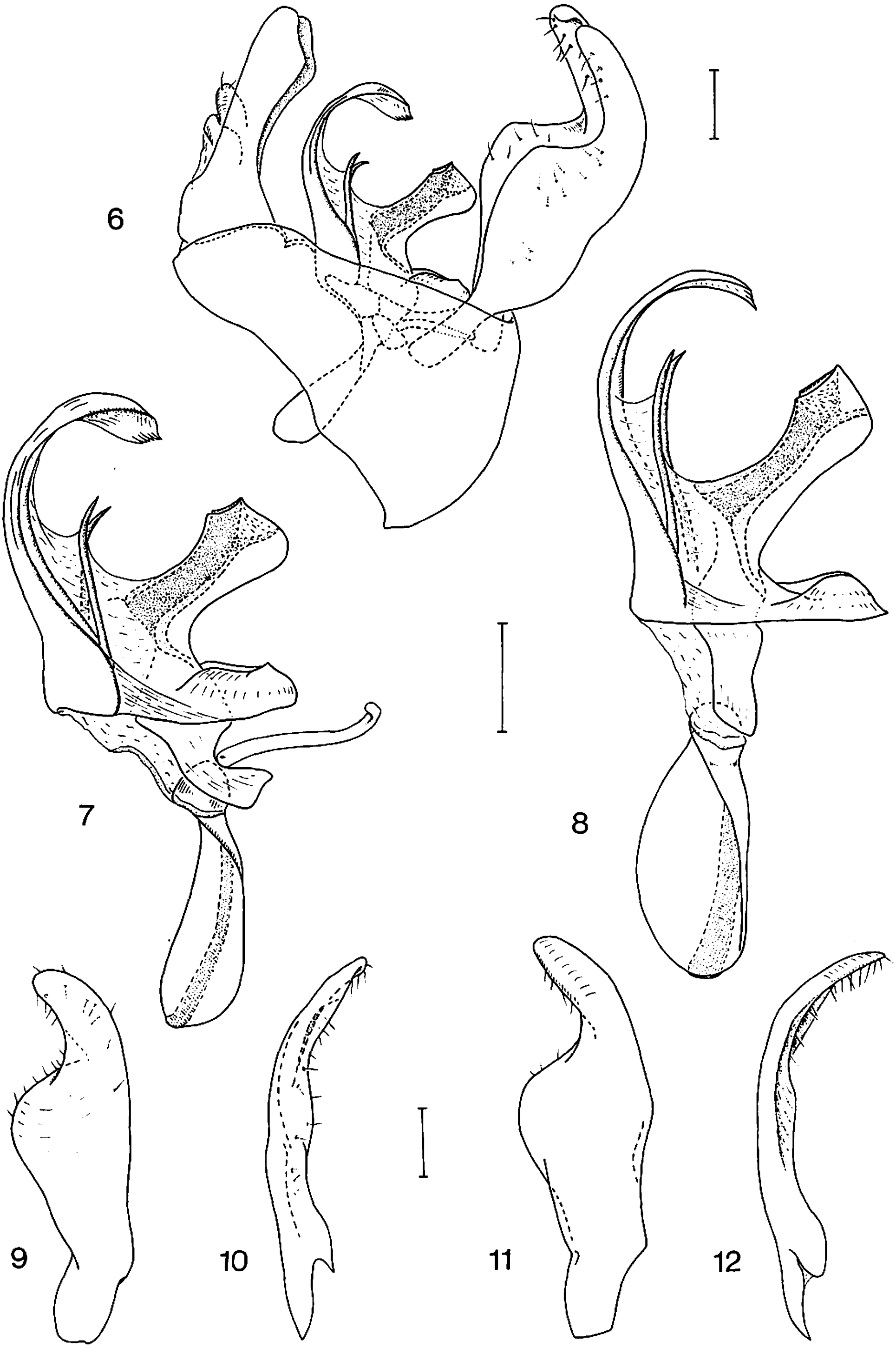
Compound eyes present, but slightly reduced in comparison to epigean *Phaconeura* species; lateral and median ocelli vestigial. Vertex broader at base than long medially (1.5:1), continuously rounded onto frons; posterolateral areolets small. Lateral margins of vertex and frons strongly ridged, directed laterad, continuous row of sensory pits reaching the frontoclypeal suture on each side. Sensory pits basad of antennal bases irregularly arranged (Fig. 2). Vertex and frons with distinct median carina vanishing just above median ocellus. Frons with lateral margins shallowly convex, widest at level of antennae; about as wide as long medially, medially slightly shorter than post- and anteclypeus together. Distinct interruption between lateral carinae of frons and clypeus at frontoclypeal suture. Median carina of ante- and postclypeus vestigial. Rostrum reaching posterior coxae. First antennal segment short, ringlike, 2nd antennal segment subcylindrical, length ca. 1.3 × width; antennal sense organs pustulate, some sensilla grouped in distinct circles irregular in number and arrangement. Pronotum with 3 rudimentary carinae, 1 median, 2 lateral, the latter 2 enclosing discoidal field behind each eye. Pronotum medially about ½ length of vertex, width 1.2 × maximum width of head. Posterior margin shallowly incised. Mesonotum with lateral portions oblique, tricarinate, median carina fairly distinct, lateral carinae vanishing. Tegmina as in epigean *Phaconeura* species, surpassing tip of abdomen by ca. ¼ their total length; 7 apical cells, venation as in Fig. 4. Arrangement of sensory pits on tegmen as in other *Kermesiinae*. Wings (Fig. 5) fully developed, as in epigean *Phaconeura* species. Posttibia distally with 7–8, postbasitarsus with 6–8, 2nd posttarsal segment with 6–7 spines in single row (sometimes variable within 1 individual). Postbasitarsus 0.7 × length of 2nd and 3rd posttarsal segments together. Claws and pads present.

Body length. MALE. 2.5–2.9 mm (2.65 ± 0.17 mm; $n = 7$). FEMALE. 2.7–3.0 mm (2.76 ± 0.15 mm; $n = 5$).

Male genitalia. Genital segment (Fig. 6) in lateral view with venter about 3 × longer than



Figs. 1–5. *Phaconeura minyamea*, n. sp.: **1,** habitus; **2,** head, ventral aspect; **3,** same, left lateral aspect (paratype ♂, Tea Tree Cave); **4,** tegmen; **5,** wing (♂, Queenslander Cave). Scale line: 0.5 mm, Figs. 1, 4–5; 0.1 mm, Figs. 2–3.



Figs. 6–12. *Phaconeura minyamea*, n. sp., male genitalia: **6,** genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect; **7,** aedeagus, left lateral aspect (paratype, Tea Tree Cave); **8,** same (specimen from Queenslander Cave); **9,** left paramere, maximum aspect; **10,** same, ventral aspect (paratype, Tea Tree Cave); **11,** left paramere, maximum aspect; **12,** same, ventral aspect (specimen from Queenslander Cave). Scale line: 0.1 mm.

dorsum; in caudal view figure-eight-shaped, as is characteristic for Meenoplidae. Anal segment in dorsal aspect longish ovate, apically shallowly incised; ventrocaudal lobes directed ventrad. Aedeagus (Figs. 7, 8) with sperm conducting part directed straight ventrad, ventral margin broadly rounded apically, phallotrema dorsally. Dorsad of sperm conducting part with unpaired process semicircularly curved ventrad, ending apically in compressed membranous flaglike velum with serrate distal margin. Shape of flaglike velum slightly variable among populations (see Remarks). Slender spine arises on each side of membrane connecting unpaired dorsal process with sperm conducting part, each spine slightly bent lateroventrad. Parameres (Figs. 9–12) longer than height of genital segment, in lateral aspect basal half dilated, distal part with a finger-shaped process, slightly variable among populations.

Female genitalia. As in other Meenoplidae strongly reduced; laterocaudal margin of ventral valvifer (*sensu* Woodward, 1957) produced as rounded lobe (ventral valvula *sensu* Woodward, 1957) bearing minute tip apically, which is directed mediocaudad.

Type data. Holotype ♂, AUSTRALIA: Queensland: Chillagoe, Tea Tree Area, Tea Tree Cave, 4.I.1989 (M. Asche, H. Hoch, F.G. Howarth) (QM). Paratypes. 3♂♂, 4♀♀, same data as holotype (QM, BPBM, BMNH, AH).

Non-type material. AUSTRALIA: Queensland: 2 ♂♂, Chillagoe, Queenslander Tower, Queenslander Cave, 5.VI.1985 (E. Carol, M. Irvin, F.D. Stone, J. Bresnan, V. Vlasoff) (QM, BPBM). 1♂, Chillagoe, Ryan's Creek Tower, Ryan's Creek Cave, 14.VI.1987 (Asche, Hoch) (AH). 1♀, Chillagoe, Mungana National Park, Carpentaria Tower, Carpentaria Cave, 12.VI.1987 (Asche, Hoch) (AH). Nymphs: 2 V, same data as holotype (QM).

Remarks. *Phaconeura minyamea* is readily distinguished from other members of the *smithi* group of species by the membranous, flaglike velum at the tip of the unpaired dorsal process of the aedeagus (Figs. 6–8). *P. minyamea* has fully developed tegmina and wings and is able to fly. It may well be capable of epigean dispersal, and thus may maintain a gene flow among populations from caves as far as 10 km apart. However, there is some variation in the shape of the velum among populations: in specimens from Tea Tree Area and Ryan's Creek Tower the "flag" is more conspicuously displayed than in specimens from Queenslander Tower. Whether this is due to the intraspecific variation of the specimens, or whether the populations from different towers are incipient species has to be determined by the examination of more material, and perhaps by applying biosystematic methods. The conspecifity of the Carpentaria Tower female with populations from the towers mentioned above, assumed preliminarily on the basis of the identical characteristic coloration of thorax and tegmina, can only be verified after the examination of associated males. Consequently, only specimens from Tea Tree Cave are designated as type material.

Etymology. Derived from the Australian aboriginal language, *minya* means "small," and *mea* means "eye."

Phaconeura mopamea Hoch, **new species** Figs 13–24

Description. Body and legs pale yellow; tegmina shallowly tectiform; tegmina and wings translucent, whitish, with venation pale yellow. In some specimens costal cell and anterior portion of cell enclosed by M and Cu slightly darker, pale brown (Figs. 13, 16, 18). Vertex slightly broader at base than long medially (1.2:1), continuously rounded onto frons; posterolateral areolets small. Compound eyes and median and lateral ocelli absent (Figs. 14, 15). Lateral margins of vertex and frons strongly ridged, directed laterad, each side bearing a row of oval sensory pits not reaching frontoclypeal suture. Vertex and upper portion of frons with distinct median carina, lower portion of frons and postclypeus smooth. Frons with lateral margins shallowly convex, broadest at level of antennae, about as wide as long medially, but medially slightly shorter than post- and anteclypeus together. Distinct interruption between lateral carinae of frons and clypeus at frontoclypeal suture. Lateral carinae of postclypeus distinctly present in upper ⅓, obsolete toward anteclypeus. Anteclypeus with blunt median carina. Rostrum elongate, slightly surpassing posterior coxae. First antennal segment short, ringlike, 2nd segment ovoid, length ca. 1.5 × width; antennal sense organs pustulate, some sensilla arranged in distinct circles, irregular in number and grouping. Pronotum with 3 indistinct carinae, 1 median and 2 lateral, latter 2 each enclosing discoidal field behind lateral margin of head. Pronotum slightly shorter than vertex medially, 1.8 × as wide as maximum width of head. Posterior margin shallowly incised. Mesonotum with 3 faint carinae; lateral portions shallowly oblique. Tegmina (Figs. 16, 18) reduced in length, 2.4–2.6 × longer than maximum width; in repose reaching (sometimes slightly surpassing) tip of abdomen; 5 apical cells; venation distad of nodal line individually variable (Fig. 13). Arrangement of sensory pits on tegmen as in *P. minyamea*. Wings (Figs. 17, 19) with anal cell vestigial. Posttibia distally with 7–8, postbasitarsus with 5–6, 2nd posttarsal segment distally with 4–5 spines in single row (individually asymmetrical); postbasitarsus 0.7 × length of 2nd and 3rd posttarsal segments together. Claws and pads present.

Body length. MALE. 2.2–2.8 mm (2.41±0.18 mm; n = 15). FEMALE. 2.5–3.2 mm (2.86±0.22 mm; n = 14).

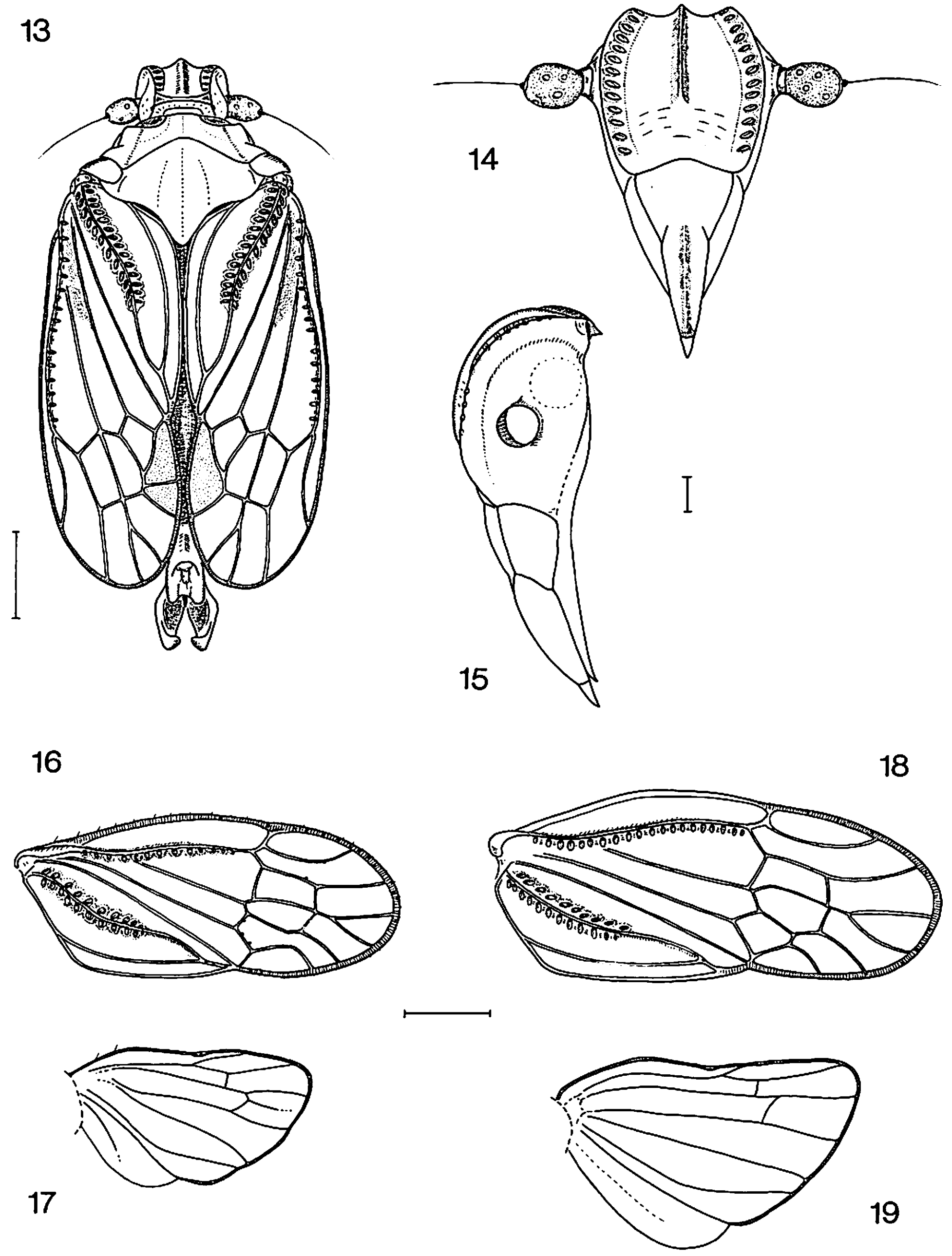
Male genitalia. Genital segment (Fig. 20) in lateral view with venter ca. 3 × longer than dorsum; in caudal view as in *P. minyamea*. Anal segment (Figs. 20–21) in dorsal aspect longish ovate, apically shallowly incised; ventrocaudal lobes with outline slightly variable among populations (see Remarks), bent ventrad. Aedeagus (Fig. 22) with sperm conducting part directed straight ventrad, phallotrema dorsally. Single process dorsad of sperm conducting part basally flat, apically tapering, bent ventrad. Slender spine, curved lateroventrad in apical portion, arises on each side from membrane connecting dorsal process with sperm conducting part. Parameres (Figs. 23–24) longer than height of genital segment, in lateral aspect basal ½ dilated, distal part with slender, finger-shaped process, curved dorsad; in ventral aspect inner margin smooth, shallowly convex.

Female genitalia. As described for *P. minyamea.*

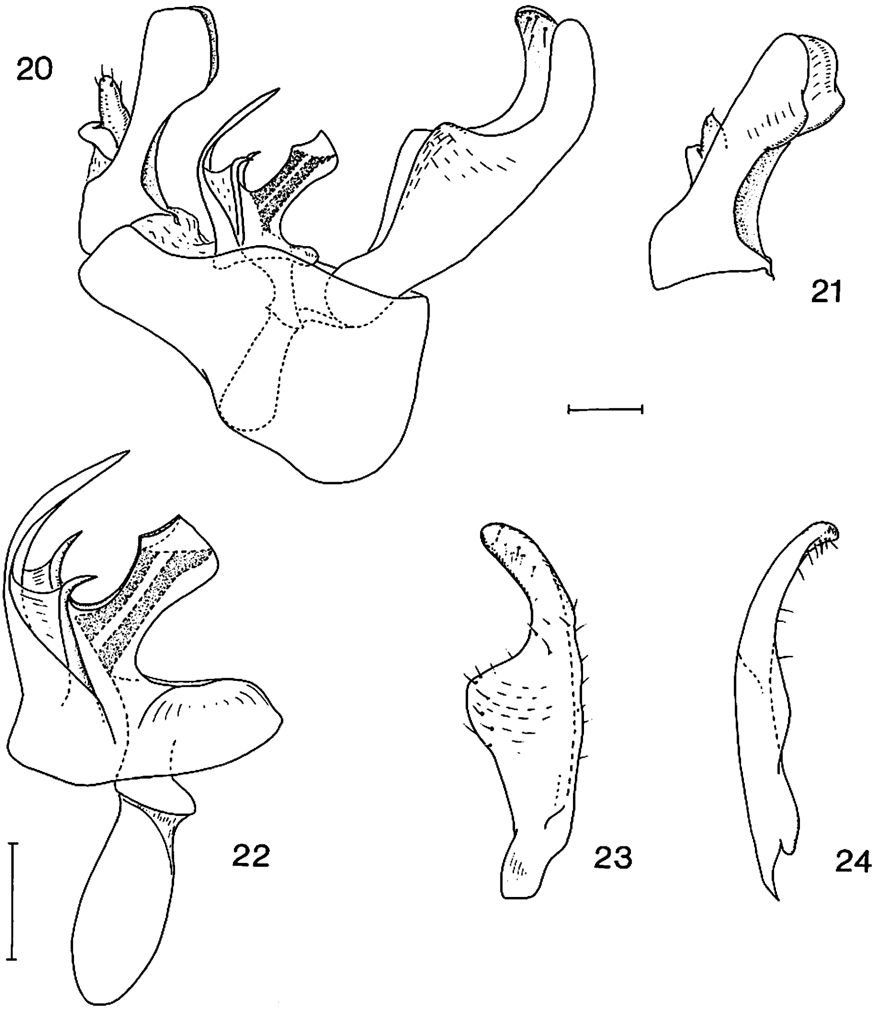
Type data. Holotype ♂, AUSTRALIA: Queensland: Chillagoe, Mungana National Park, Carpentaria Tower, Carpentaria Cave, 'Grand Canyon,' 28.V.1985 (F.G.Howarth) (QM). Paratypes: 4 ♂♂, 1 ♀, same data as holotype. 21 ♂♂, 19 ♀♀, same data as holotype except 12.VI.1987 (M. Asche, H. Hoch). 5 ♂♂, 1 ♀, same data as holotype, except 1.I.1989 (Asche, Hoch, Howarth). 1 ♂, same data as holotype except 20.VI.1984 (F.D. Stone). 6 ♂♂, same data as holotype except 3.VI.1985 (Stone, D. Irvin). 1 ♂, 1 ♀, same data as holotype except 11.VI.1986 (Howarth, S. Robson). 1 ♂, same data as holotype except 3.VI.1985, root room in 'Snake Pit' (Stone, Irvin). Paratypes in QM, BPBM, BMNH, AH.

Non-type material. AUSTRALIA: Queensland: 1 ♂, Chillagoe, Ryan Imperial Tower, Marachoo Cave, 23.VI.1984 (Howarth et al.). 2 ♂♂, Chillagoe, Markham Tower, Hercules Cave, 6.VI.1985 (Howarth et al.) (QM, BPBM). Nymphs. AUSTRALIA: Queensland: 1 V, Chillagoe, Carpentaria Tower, Carpentaria Cave, 20.VI.1984 (Stone). 1 II, 1 III, 5 IV, 6 V, same data except 3.VI.1985 (Stone, Irvin). 1 V, same data except 11.VI.1986 (Howarth, Robson). 2 IV, 1 V, same data except 12.VI.1987 (Asche, Hoch). 1 V, same data except 1.I.1989 (Asche, Hoch, Howarth) (QM, BPBM, AH).

Remarks. *P. mopamea* differs from the epigean species of the *P. smithi* group and from *P. minyamea* in characters that have undergone alterations during cave adaptation: complete reduction of compound eyes, ocelli, tegmina, wings, bodily pigment. It is distinguished from other



Figs. 13–19. *Phaconeura mopamea*, n. sp.: **13,** habitus; **14,** head, ventral aspect; **15,** same, left lateral aspect; **16,** tegmen; **17,** wing (paratype ♂, Carpentaria Cave); **18,** tegmen; **19,** wing (paratype ♀, Carpentaria Cave). Scale line: 0.5 mm, Figs. 13, 16–19; 0.1 mm, Figs. 14–15.



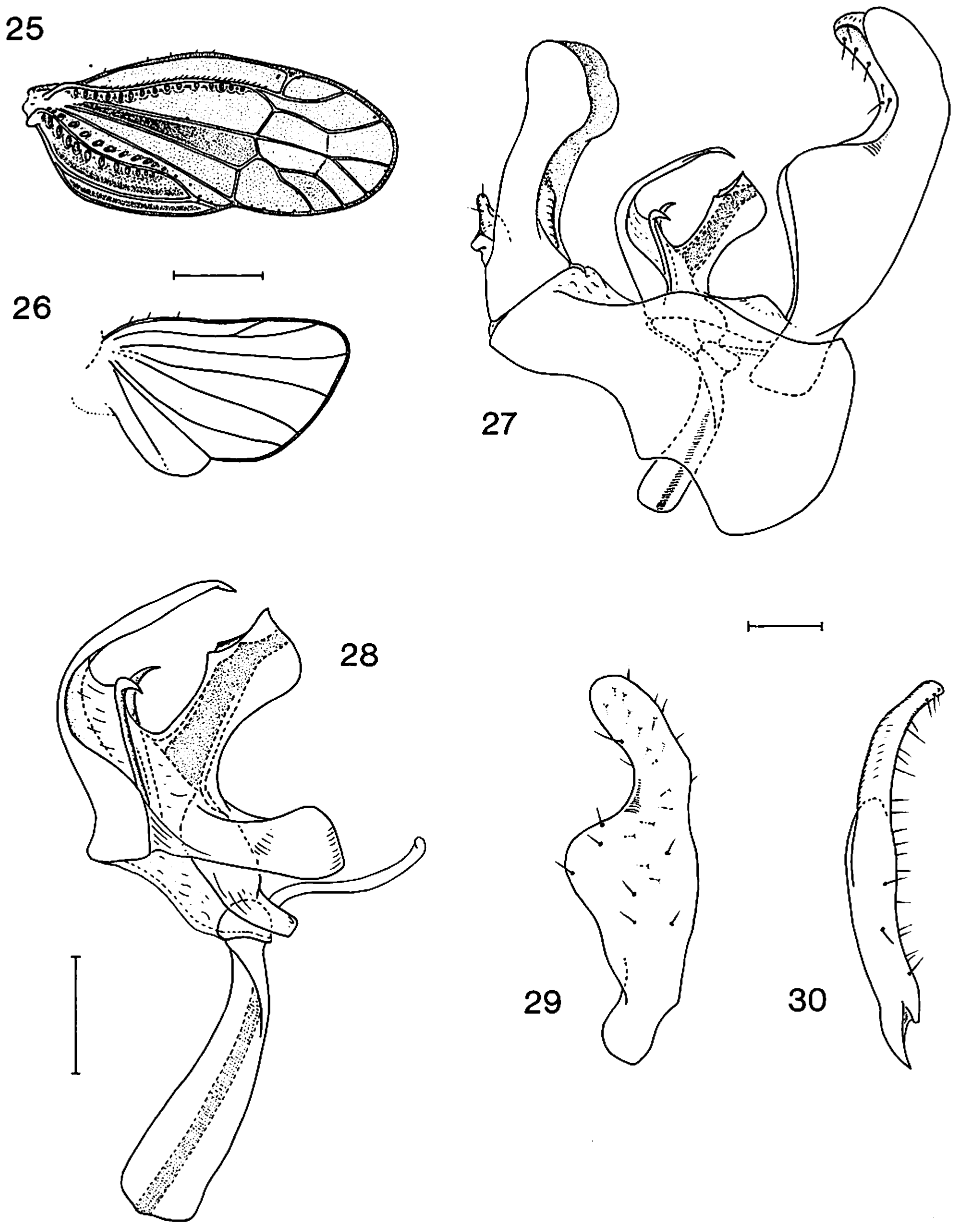
Figs. 20–24. *Phaconeura mopamea*, n. sp., male genitalia: **20,** genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect (paratype, Carpentaria Cave); **21,** anal segment, left lateral aspect (specimen from Marachoo Cave); **22,** aedeagus, left lateral aspect; **23,** left paramere, maximum aspect; **24,** same, ventral aspect (paratype, Carpentaria Cave). Scale line: 0.1 mm.

cave-adapted *Phaconeura* species by the characteristic shape of the aedeagus. Slight variation between populations from different but neighboring towers was found in the shape of the anal segment; whether this is of taxonomic significance can only be decided after the study of more material.

Etymology. Derived from the Australian aboriginal language, *mopa* means "no" or "none," and *mea* means "eye."

***Phaconeura crevicola* Hoch, new species** Figs. 25–30

Description. Body and legs pale yellow; tegmina shallowly tectiform; tegmina and wings translucent; tegmen (Fig. 25) with venation pale yellow, cells pale brown; anterior portion of



Figs. 25–30. *Phaconeura crevicola*, n. sp.: **25,** tegmen; **26,** wing. Male genitalia: **27,** genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect; **28,** aedeagus, left lateral aspect; **29,** left paramere, maximum aspect; **30,** same, ventral aspect (paratype ♂, Raindance Cave). Scale line: 0.5 mm, Figs. 25–26; 0.1 mm, Figs. 27–30.

cell enclosed by M and Cu as well as anal cells distinctly darker, brown. Wings (Fig. 26) hyaline. Structures and proportions of head, pro- and mesonotum as in *P. mopamea*. Tegmina length ca. 2.6 × their maximum width, in repose almost reaching tip of abdomen; 5 apical cells; venation distad of nodal line variable, crossveins partially vanishing. Arrangement of sensory pits as in *P. mopamea*. Wings without crossveins in distal part. Posttibia distally with 6–8, postbasitarsus with 5–6, and 2nd posttarsal segment with 3–5 spines in a row (variable within 1 individual). Proportions of posttarsal segments and structures of the pretarsi as in *P. mopamea*.

Body length. MALE. 2.6–3.0 mm (2.75 ± 0.19 mm; n = 4). FEMALE unknown.

Male genitalia. Genital and anal segments, parameres, and general structure of aedeagus (Fig. 27, 29–30) as in *P. mopamea*. Aedeagus (Fig. 27) with unpaired process dorsal of sperm conducting part bent ventrad almost 90 degrees, tip slightly bent basad.

Type data. Holotype ♂, AUSTRALIA: Queensland: Chillagoe, Rookwood Station, Katie Breen Tower, Raindance Cave, 5.I.1989 (M. Asche) (QM). Paratypes: 3 ♂♂, same data as holotype (QM, BPBM).

Remarks. *P. crevicola* is morphologically very close to *P. mopamea*, but differs in the coloration of the tegmina, which is considerably darker in *crevicola*, and in the shape of the unpaired dorsal process of the aedeagus.

Etymology. The name derives from the small crevices in the cave walls in which all 4 specimens were collected.

Phaconeura capricornia Hoch, **new species** Figs. 31–36

Description. Body and legs pale yellow; tegmina shallowly tectiform (Fig. 31); tegmina and wings translucent, tegmen with cells and venation pale yellow. Compound eyes and median and lateral ocelli absent. Former position of compound eyes faintly recognizable as indistinctly limited membranous area dorsal of antennae (Fig. 33). Vertex slightly broader at base than long medially (1.1:1), row of sensory pits on frons (Fig. 32) not as regular as in *mopamea* and *crevicola*: 3rd sensory pit above frontoclypeal suture placed slightly mediad. Otherwise proportions and carination of head and pronotum as in *mopamea* and *crevicola*. Mesonotum tricarinate with carinae vanishing, nearly planate. Tegmina (Fig. 34) reduced in length, ca. 2.3–2.4 × longer than maximum width, broadly rounded distally, in repose surpassing tip of abdomen by ca. ⅕ their length; venation distad of nodal line individually variable, crossveins partly vanishing, 4–5 apical cells. Wings (Fig. 35) without any crossveins. Posttibia distally with 6–7 (individually asymmetrical), postbasitarsus with 5, and 2nd posttarsal segment with 4 spines in a single row. Proportions of posttarsal segments and pretarsal structures as in *mopamea* and *crevicola*.

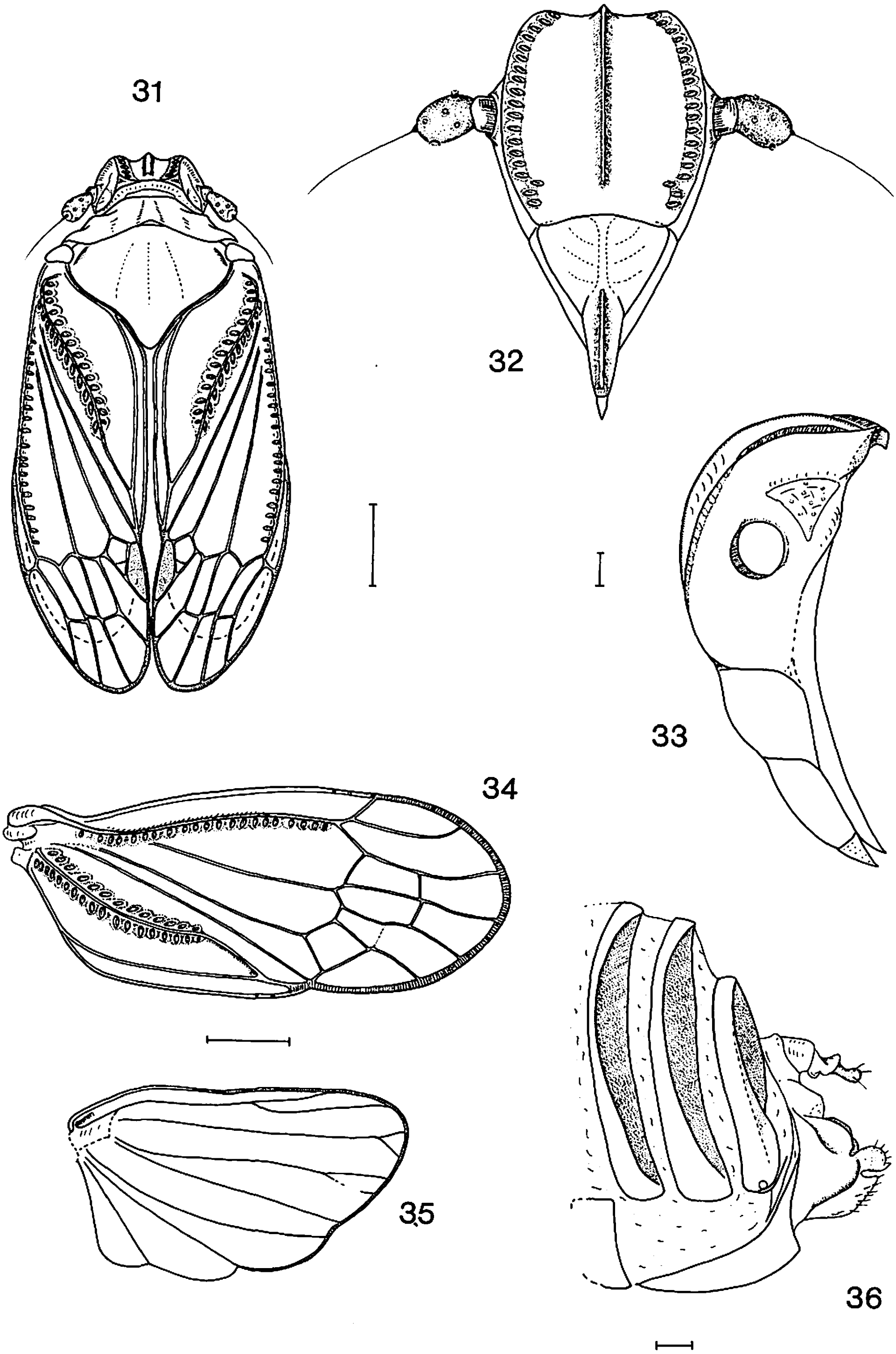
Body length. FEMALE. 2.7 mm (n = 2). MALE unknown.

Female genitalia (Fig. 36). As described for *minyamea*.

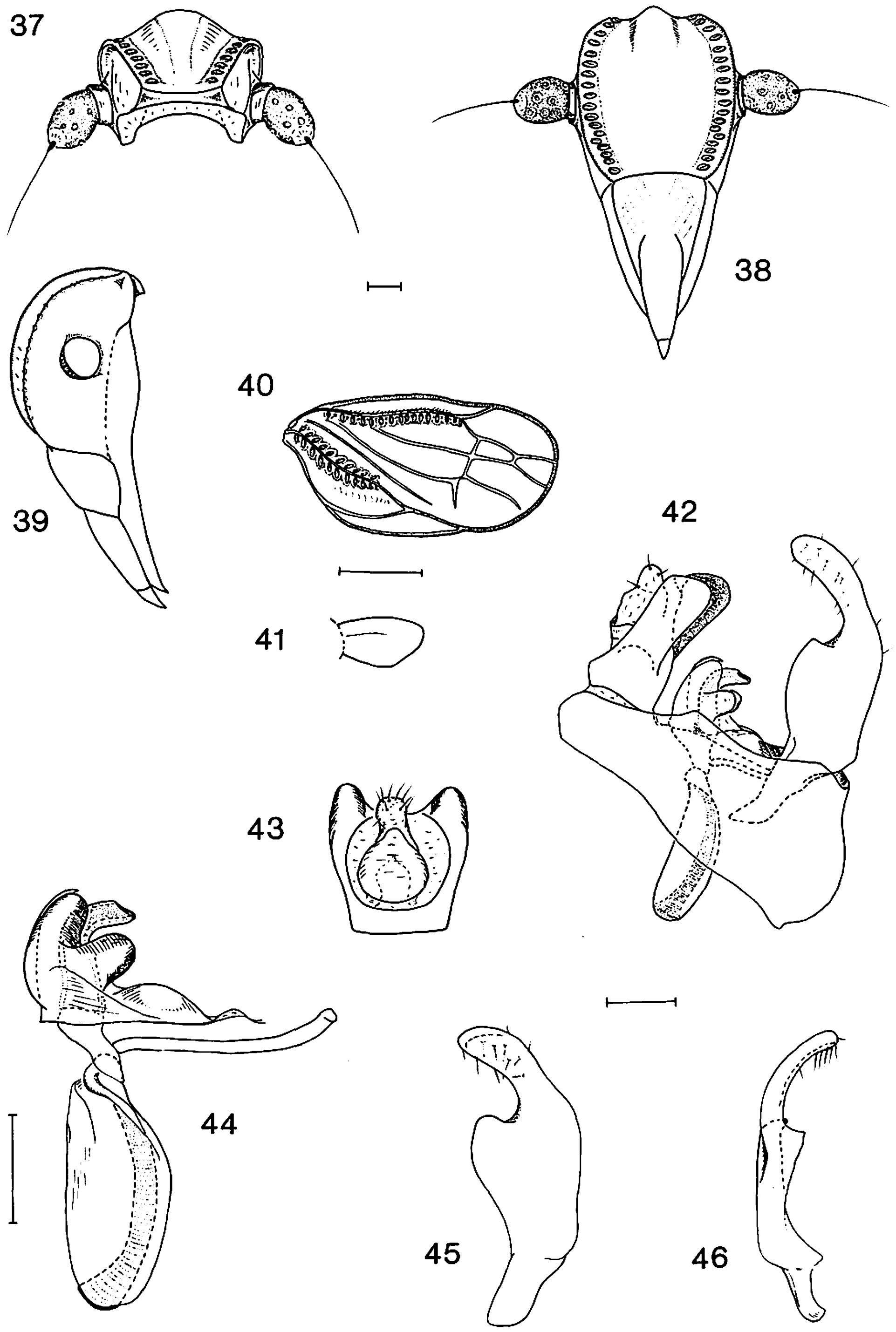
Type data. Holotype ♀, AUSTRALIA: Queensland: Cape York, Mt. Mulgrave Station, Capricorn Tower, Swiss Cheese Cave, 8.VI.1986 (F.G. Howarth, S. Robson) (QM). Paratypes: 1 ♀, same data as holotype (BPBM).

Remarks. Although *P. capricornia* resembles *mopamea* in habitus, it differs in structures of the head (the former position of the compound eyes recognizable as a membranous area; row of sensory pits on frons irregular) and in the venation of the tegmina, as well as in the degree and mode of their reduction.

Etymology. The species is named for the type locality in Capricorn Tower, in the Mitchell Palmer Karst.



Figs. 31–36. *Phaconeura capricornia*, n. sp.: **31,** habitus; **32,** head, ventral aspect; **33,** same, left lateral aspect (holotype ♀, Swiss Cheese Cave); **34,** tegmen; **35,** wing; **36,** female genitalia, left lateral aspect (paratype ♀, Swiss Cheese Cave). Scale line: 0.5 mm, Figs. 31, 34–35; 0.1 mm, Figs. 32–33, 36.



Figs. 37–46. *Phaconeura pluto* Fennah: **37,** head, dorsal aspect; **38,** same, ventral aspect; **39,** same, left lateral aspect; **40,** tegmen; **41,** wing. Male genitalia: **42,** genital segment, anal segment, aedeagus, parameres, *in situ*, left lateral aspect; **43,** anal segment, dorsal aspect; **44,** aedeagus, left lateral aspect; **45,** left paramere, maximum aspect; **46,** same, ventral aspect (specimen from Tick Cave). Scale line: 0.5 mm, Figs. 40–41; 0.1 mm, Figs. 37–39, 42–46.

Phaconeura pluto Fennah Figs. 37–46

Phaconeura pluto Fennah, 1973, Proc. Biol. Soc. Wash. 86(38): 444

Diagnosis. Small *Phaconeura* species (2.3–2.5 mm) with body, legs and tegmen white. Tegmen (Fig. 40) reduced in length, not covering tip of abdomen, venation variable and partly vanishing. Wings vestigial (Fig. 41). Compound eyes and ocelli absent. Median carina of vertex and frons absent (Figs. 37–39).

Male genitalia. Different from the other cave-dwelling *Phaconeura* species: anal segment (Figs. 42–43) short, ca. ½ length of parameres. Laterodistal lobes projected; caudal margin deeply excavated. Aedeagus (Fig. 44) short, stout, with 2 bulbous projections near base, directed ventrad; sperm conducting part curved ventrad distally, obliquely truncate apically; dorsally engulfed by an unpaired bulbous theca medially ridged on dorsal side; ridge forming short spine apically. Parameres (Figs. 45–46) finger-shaped distally, in ventral view with short tooth directed mediad at about ½ their total length.

Female genitalia. Strongly reduced, similar to those of *mopamea* and *capricornia*, with ventral valvula (*sensu* Woodward, 1957) distally rounded.

Material examined. AUSTRALIA: Western Australia: 1 ♂, 2 nymphs: 1 III, 2 V, Nambung National Park, near Cervantes, Tick Cave, 24.II.1974 (J. Lowry) (BMNH). 1 ♂, 1 ♀, Nambung National Park, Cadda Cave, 20.VIII.1973 (Lowry) (BMNH).

Remarks. The specimens examined of this species have been collected subsequently to the original description of *pluto* (Fennah 1973) and from two additional caves in the same area. Since no obvious morphological differences were found between the specimens from Tick and Cadda Caves and the description of *pluto* (specimens from Quandong Cave), conspecifity of the three populations is assumed.

DISCUSSION

The Karst areas around Chillagoe and at Mitchell Palmer belong to the same limestone band extending from SE of Chillagoe to the NNW, roughly parallel to the east coast of the Cape York Peninsula. The limestone was deposited in the late Silurian (416–434 my ago) as coral reefs, comparable to today's Barrier Reef and has since undergone various cycles of uplift and inundation with erosion leaving highly dissected cavernous limestone towers (Ford 1978). These towers stand up to 200 m above the surrounding plain, which was formed by massive alluvial deposits. This particular geologic situation may account for the virtual nonexistence of a mesocavernous rock system (MSS, *milieu souterrain superficielle*, *sensu* Juberthie 1983) that would allow an extensive underground dispersal of cave-adapted animals through cracks and crevices, resulting in a high degree of geographic isolation and speciation. The ages of the caves are estimated to range from at least 2 my to 5–10 my (Pearson 1982).

The new meenoplid species described in this paper were collected from different habitats within the cave environment: *minyamea* specimens were found within twilight and transition zones, as well as in the deep cave zone, while *mopamea*, *crevicola* and *capricornia* seem to be restricted to the deep cave zone where permanent darkness and stable conditions (constant temperature and relative humidity, close to saturation) prevail (Howarth 1988). Accordingly, the new species are ecologically classifiable as troglophilic (i.e., facultative cavernicolous [*minyamea*]) and troglobitic (i.e., obligate cavernicolous [*mopamea*, *crevicola* and *capricornia*]).

All 4 species were found feeding on roots of 1 or more unidentified host species, often on surfaces covered with soil deposits. Adults are much more closely associated with their host roots than are adult cavernicolous Cixiidae (Hoch & Asche 1988). Nymphs are assumed to be attended by ants, which would help explain the dispersal ability (Howarth, pers. comm. 1988), especially of troglobitic species like *mopamea*, which is found in different, although neighboring, towers (Figs. 47, 48).

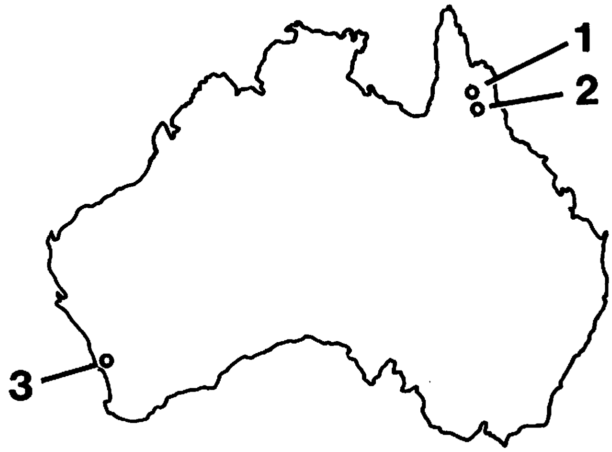


Fig. 47. Geographic distribution of cave-dwelling *Phaconeura* species in Australia. **1** = Mitchell Palmer Karst, N Queensland: *P. capricornia*; **2** = Chillagoe Karst (see Fig. 48); **3** = Nambung National Park, western Australia: *P. pluto*.

Three out of the 4 new species are represented by males, which in the general configuration of their genitalia are similar to *P. smithi* Woodward. *P. capricornia* is so far only known from 2 females, but on the basis of very similar external morphological features (e.g., proportions of head, venation of tegmina, general structures in the female genitalia) it is assumed to belong to the same group of species.

Whether these species represent a single evolutionary line that has invaded caves, with divergence occurring after the adaptation of a single ancestor, or whether they are descendants of different, but closely related epigean ancestor species, cannot be decided yet. Epigean species of the *P. smithi* group exist on the surface, but the morphological evidence has been not sufficient to determine a possible ancestor species.

Phaconeura pluto from Western Australia clearly represents a separate evolutionary line of cave invasion. Although externally similar to the troglobitic *Phaconeura* species of Queensland, it differs considerably by the configuration of the male genitalia. There is no evidence of close relationship to any of the known epigean *Phaconeura* species of Australia, instead *pluto* shares its particular configuration of the aedeagus with 2 undescribed *Phaconeura* species from New Guinea and Java (Asche, pers. comm., 1989). No information concerning the habitat of *pluto* has been published.

It is remarkable that in Australia, cave-adapted Meenoplidae have so far been found exclusively in limestone caves, whereas cave-adapted meenoplids from Samoa and the Canary Islands are known from lava tubes. However, the results of our recent investigations suggest that not only cave-adapted Cixiidae, but also cave-adapted Meenoplidae are far more common than was previously assumed. Thus, the lava tubes at Undara, 100 km south of the Chillagoe Karst, may yield potential for the existence of cave-adapted Meenoplidae. More research is needed to complete the biological survey of limestone caves and lava tubes in Queensland to determine the degree of speciation, the number of evolutionary lines of cave invasions, and patterns of distribution of cave animals.

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I express my sincere thanks to F. G. Howarth, Bishop Museum, Honolulu, and to Bro. N. Sullivan, Explorer's Club, New York, who helped to make my participation in the 1989 Chillagoe Caves Expedition possible. I also thank F. G. Howarth, M. Asche, Bishop Museum, and F. D. Stone, University of Hawaii, Hilo, for their help in the field and their valuable comments on the manuscript. M.R. Wilson, CAB International Institute of Entomology, London, also provided valuable suggestions. Members of the Chillagoe Caving Club (especially M. and D. Irvin) and of the Sydney Speleological Society (especially D., G., and T. Matts) provided not only hospitality and logistic support, but helped to keep up the unique spirit that made the Chillagoe Caves Expedition of 1989 an unforgettable one.

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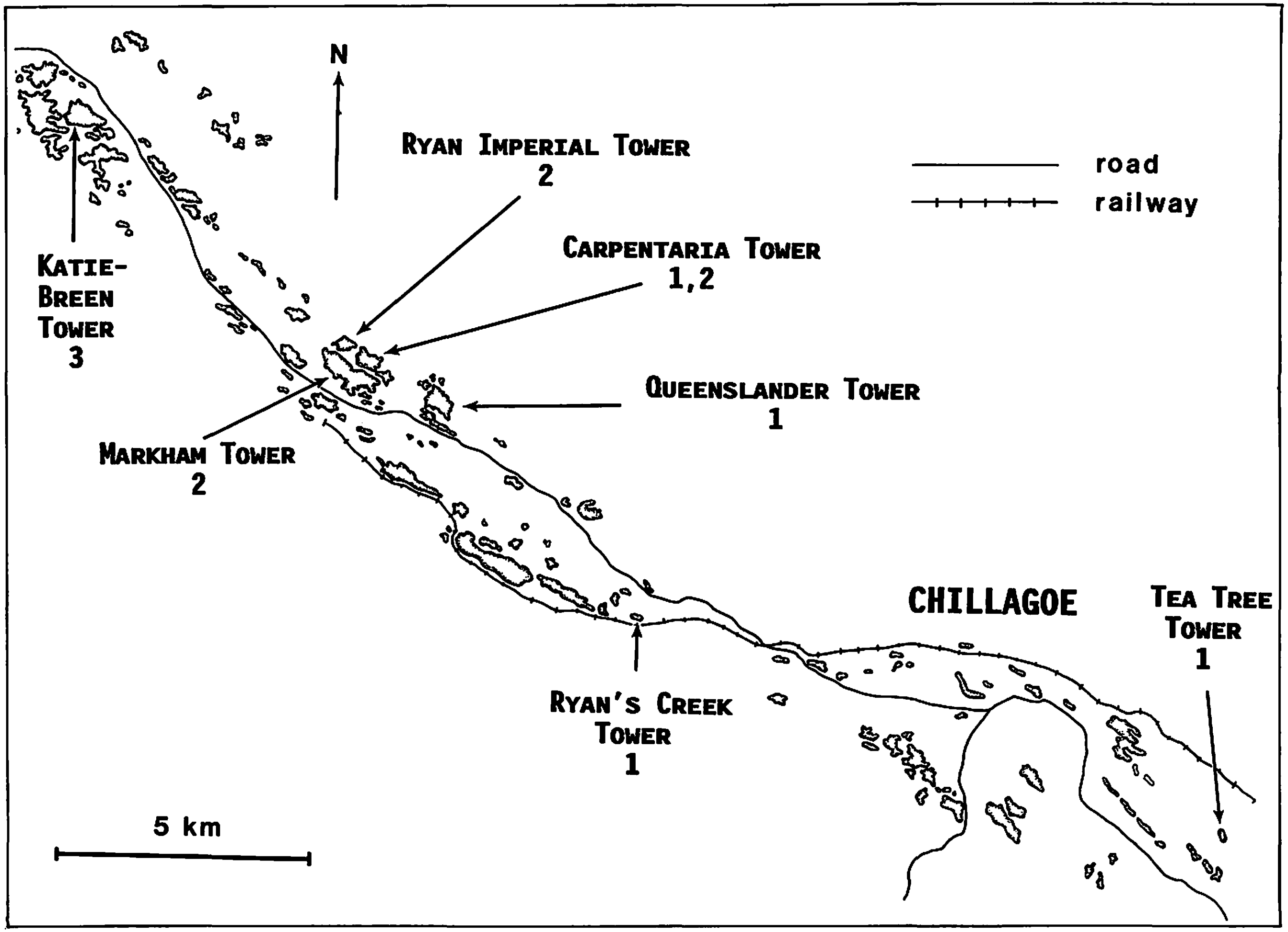

Fig. 48. Geographic distribution of cave-dwelling *Phaconeura* species in the Chillagoe Karst (map redrawn from Robinson 1982). **1**, *Phaconeura minyamea*; **2**, *Phaconeura mopamea*; **3**, *Phaconeura crevicola*.

Sosephena and *Trisephena,* Two New Genera from New Guinea with Tricarinate Frons (Homoptera: Flatidae)

John T. Medler[1]

ABSTRACT

Sosephena, new genus, is described for 2 new species *S. rinkela* and *S. binoba* from New Guinea. *Trisephena,* new genus, is described for 8 new species from New Guinea, as follows: *rubeola, trientor, imposita, lonessa, metrior, estrias, zestreya,* and *anomala.* Type species of the new genera are *S. rinkela* and *T. rubeola,* respectively. The tricarinate frons distinguishes the new genera from *Sephena.* Keys are provided to distinguish the new genera from related taxa and the species within the genera.

INTRODUCTION

My research on New Guinea Flatidae in the Bishop Museum collection, along with examination of specimens loaned by other major museums, has revealed many unnamed genera and species. Although Flatidae are found in all tropical and subtropical regions of the world, it is only in New Guinea and Australia that taxa show such a high proportion of uniformity in derived characters of the female ovipositor and spines on the hind legs.

This is one of a series of articles planned for publication on various complexes of genera and species in New Guinea. It is presented especially to describe unnamed species and to provide an inventory of the flatid fauna of New Guinea in relation to faunas of adjacent areas. The taxonomic research provides a scientific basis for reports of subsequent research on the biology and ecology of these insects.

Two new genera are erected here for undescribed species of Flatidae in New Guinea that have a strong tricarinate structure of the frons. The species are closely related to those with similar development of a tricarinate frons that have been described from Australia in the following genera: *Aflata* Melichar, *Burnix* Medler, *Euphanta* Melichar, *Euryphantia* Kirkaldy, and *Lesabes* Medler.

The metatibial spine formula in this *Trisephena* complex of genera ranges from 1:6 to 1:9, with the maximum number of spines recorded in *Aflata* (1:9:9).

The new taxa closely resemble *Sephena* Melichar in size, morphology, and general appearance. Also, the aedeagus has paired slender ventral processes, which arise apically and are elongated basally as far as the pygofer. Comparable ventral processes are absent in the Australian genera named above, except *Lesabes.*

The new species have a distinctive Cu vein pattern (Fig. 38). Vein Cu is displaced toward vein M from its usual position alongside the claval suture, resulting in the formation of a shallow

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triangular cell with its widest point at the oblique crossvein M_2–Cu. Vein Cu then angles back to meet the claval suture at the claval apex and continues to the apical margin giving rise to short branches, which terminate along the postclaval sutural margin.

The ovipositor has the same fingerlike development of valvulae III as reported by Medler (1985) in nearly all species of Flatidae in New Guinea and Australia. The anal segment is small and oval, and the lateral margins are often downturned.

METHODS

Descriptions of species are based on the type. Length was measured with a mm ruler. All other measurements were made with a binocular microscope eyepiece grid and converted to mm. Measurements from the holotype and allotype are cited in the following format. Length: overall from apex of head to apical margin of tegmen; vertex (v), pronotum (p), and mesonotum (m) along the dorsal midline; frons (f) along the midline from frontoclypeal suture to dorsal margin; tegmen (t) from origin of the basal stem to maximal apical margin; postclaval sutural margin (pcl) from tip of clavus to apex of the sutural angle, or to the midpoint of the arc if the sutural angle convex. Width: vertex (v) transversely along the posterior carina between its junction points with lateral carinae dorsad of the eyes; frons (f) at the maximal plane, usually but not always slightly above antennal insertions; tegmen (t) between costal and sutural margins at maximal point near the claval apex.

The hind leg spines are recorded by formula. Data are listed in sequence of (1) metatibial lateral spine, (2) metatibial apical spines, and (3) metatarsal basal segment apical spines (e.g., 1:6:8).

The following acronyms identify the depository museums that provided specimens used in the research: BPBM = Bishop Museum, Honolulu, HI, USA; AMNH = American Museum of Natural History, New York, NY, USA; BMNH = British Museum (Natural History), London, England; CAS = California Academy of Sciences, San Francisco, CA, USA; IRSN = Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; NCSU = North Carolina State University, Raleigh, NC, USA; PNGDPI = Department of Primary Industry, Konedobu, Papua New Guinea; RMHL = Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands.

SYSTEMATICS

Key to the *Trisephena* Complex of Genera of New Guinea and Australia

1. Disc of frons with 3 strongly raised carinae consisting of median longitudinal carina and 2 lateral carinae united dorsally into V- or U-shaped pattern; lateral margins of frons sharply carinate 3
Disc of frons with median longitudinal carina; tricarinate remnants, if present, extending no more than short distance from dorsal margin 2
2. Tegmen with 3 longitudinal veins (R, S, M) arising from basal stem . . . . ***Sephena*** auctorum
Tegmen with 2 longitudinal veins (R+S, M) arising from basal stem . . . . ***Sephena***
3. Fronto-clypeal suture truncate, or nearly so; color of tegmina not dark brown, otherwise variable 6
Fronto-clypeal suture strongly convex; tegmina brown or green 4
4. In frontal view, lateral margins of frons convexly narrowed to margin of clypeus. Tegmina green, with white zigzag line across disc . . . (Australia, monobasic) . . . . **Aflata**
Lateral margins of frons not evenly convex, flared outwardly above antennal insertions 5
5. Lateral carinae on disc of frons V-shaped. Specimen colored dark brown; tegmina with scattered dark pustules . . . . ***Euryphantia***

Lateral carinae on disc of frons U- or V-shaped. Specimen colored green ...... ***Euphanta***
6. Vertex shelflike, anterior margin slightly convex, clearly delimited by transverse carina arising from anterodorsal angles of genae . . . (Australia) 7
Not exactly as described above . . . (New Guinea) 8
7. Apex of tegmen obliquely truncate; precostal margin not pustulate; discal cell crossvein marked with red spot . . . (Monobasic) .... ***Lesabes***
Apex of tegmen convexly rounded, the costal and sutural angles of similar configuration; precostal margin pustulate . . . (Monobasic) .... ***Burnix***
8. Anterodorsal margin of head protruding well forward of genal angles; vertex strongly sulcate, median longitudinal suture depressed; crossveins of tegmina stramineous, contrasting with membrane color .... ***Sosephena*, n. gen.**
Anterodorsal margin of head formed by U-carinae of frons, truncate or nearly so. Narrow dorsal margin of frons separated from anterior margin of vertex by transverse carina arising from genal angles; tegmina crossveins red, or concolorous with unmarked membrane .... ***Trisephena*, n. gen.**

Genus ***Sosephena*** Medler, **new genus**

Type species. *Sosephena rinkela* Medler, here designated.

Diagnosis. Vertex wider than long, produced about ⅔ length of pronotum, surface uneven, medially sulcate, anterior margin bluntly acute, marginal carina extending from anterodorsal angle of genae. Ventral margin of frons transverse, lateral margins sharply carinate, elevated above flat disc, evenly convex from clypeus to dorsal margin, united dorsally with lateral margins of vertex, disc with 3 thickened longitudinal carinae, median carina nearly full length of frons, laterals extending about ¾ length, terminating ventrally at plane of antennal insertions, lateral carinae forming U-shaped dorsal margin, united with raised median carina. Genae anterodorsal margins acute, ocelli distinct. Pronotum anterior margin extended slightly anterad of eyes; disc with dimplelike depressions on each side of longitudinal median carina; lateral margins sharply carinate, postocular eminence raised, triangular, connected by ridge to lateroventral margin of paranotal lobe. Mesonotum with 3 longitudinal carinae, disc flat. Tegmina 2× longer than broad, apical margin broadly convex, 3 longitudinal veins (R, S, M) arising from basal stem, vein S branched apicad of M_1 fork; vein Cu diverging from claval suture toward vein M, forming a shallow triangular cell, number of crossveins moderate, pigmented giving tegmen barred appearance; Y-stem short. Hind leg spine formula 1:6.

Ovipositor modified, valvulae III fingerlike, not sclerotized, not suitable for piercing.

Length: 9.75–11.0 mm, females slightly longer and more robust than males.

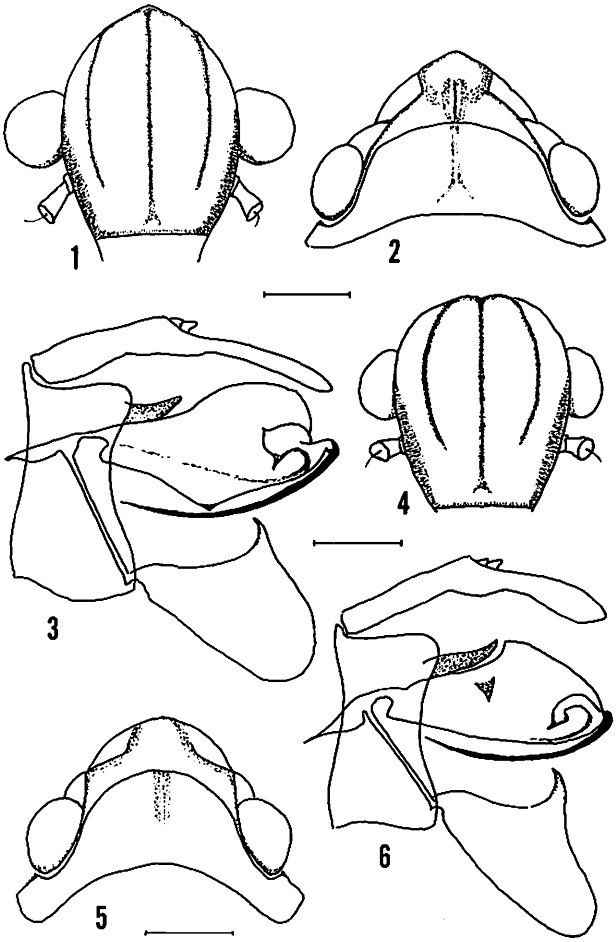
Distribution. Papua New Guinea.

Key to Species of *Sosephena*

Vertex margin produced acutely; disc sulcate, median longitudinal suture deeply impressed, usually narrowly bordered. Posterior spiral of aedeagus with triangular flange on basal margin .... ***rinkela*, n. sp.**
Vertex margin produced obtusely; dorsum depressed, not sulcate, median longitudinal suture shallow. Aedeagus with small triangular projection laterally near ventral margin .... ***binoba*, n. sp.**

Sosephena rinkela Medler, **new species** Figs. 1–3, 37–38

Description. Morphology of frons, vertex and pronotum conforming with generic diagnosis (Figs. 1–2). Narrow flattened ridge at base of vertex deeply bisected by longitudinal



Figs. 1–6. Holotype: **1**, *Sosephena rinkela,* frons; **2**, same, head; **3**, same, genitalia; **4**, *Sosephena binoba,* frons; **5**, same, head; **6**, same, genitalia. Scale = 0.5 mm.

suture, terminating in concave depression bordered by median segment of vertex transverse carina arising from anterodorsal angle of genae.

Morphology and venation of tegmen as in generic diagnosis (Figs. 37–38). Triangular cell formed by divergence of Cu from claval suture, Cu rejoining suture at claval apex, 4–5 terminal crossveins in postclaval sutural margin.

Color variable; holotype stramineous; allotype green, posterior margins of tegmen narrowly red including vein terminations; paratypes with wide array of faded colors from green or orange brown. Tegmen with conspicuous barred appearance due to crossveins bordered with red, orange, or yellow contrasting strongly against membrane. Veins, crossveins, and red margin colors exhibit considerable variation among specimens examined.

Holotype genitalia (Fig. 3).

Measurements (♂, ♀). From holotype and allotype. Length: overall 10.0, 11.0; v 0.75, 0.91; f 1.33, 1.49; p 0.54, 0.54; m 1.66, 1.66; t 8.30, 9.63; pcl 1.66, 2.49. Width: v 0.75, 0.91; f 1.04, 1.04; t 4.32, 4.98. Hind leg spine formula: 1:6:8; 1:6:9.

Type data. Holotype ♂ (BPBM 14,032), PAPUA NEW GUINEA: Morobe Prov: Lae, sea level, 26.VII.1955 (J.L. Gressitt); allotype ♀, Lae, 0–100 m, IX.1968 (N.L.H. Krauss). Both deposited in BPBM. Paratypes: PAPUA NEW GUINEA: Central Prov: ♂, Daradae, nr. Javarere, Musgrave Riv, 100 m, 3.X.1958 (Gressitt); ♂, Goilala, Loloipa, Owen Stanley Range, 1–15.II.1958 (W.W. Brandt); ♂, Tapini, 1,000–1,100 m, 18.V.1961 (J.L. & M. Gressitt); ♀, Tapini, 800–1,100 m, XI.1968, (Krauss) (BPBM). Eastern Highlands Prov: ♀, Arau, 40 km E of Kainantu, 1,400 m, 16.X.1959 (T.C. Maa); ♀, Kassam, 1,350 m, 48 km E of Kainantu, 7.XI.1959 (Maa) (BPBM); ♀, Sirasira, 14.V.1988, St. 029 (J. Van Stalle No. 27363) (IRSN). Madang Prov: ♀, Adelbert Mts, 800–1,000 m, 25.X.1958 (Gressitt); ♀, Dundi, 10.V.1988, St. 023 (Van Stalle No. 27363) (IRSN); 2♂, Saidor, Gabumi Vill, Finisterre Range, 24–30.VI.1958 (Brandt); ♀, Saidor, Sibog Vill, Finisterre Range, 6–16.VI.1958 (Brandt) (BPBM); ♀, Tapo Cr, 26 km SW Madang, 5° 24′S, 145° 38′E, 22.III.1987 (N.D. Penny); 2♀, Tapo Cr, 22.III.1987 (Penny) (CAS); ♀, Wanuma, 600–720 m, VIII.1968 (Krauss) (BPBM). Morobe Prov: ♀, Amingwiwa Mt (NW end), 1,000–1,500 m, 3.X.1970 (Gressitt); ♀, Bubia, Markham Val, 50 m, 20.IX.1955 (Gressitt); ♀, Bulem Riv, 64 km N of Lae, 30 m, 29.IV.1963 (J. Sedlacek); ♂, Bulolo, 10 km W, 780 m, 5–25.VIII.1967, malaise trap over stream (R. Straatman); ♀, Bulolo, 900 m, 29.III.1968 (P. Colman) (BPBM); ♀, Bulolo, Mt Busa, 950 m, 19.V.1988, St. 041 (Van Stalle No. 27363) (IRSN); ♂, ♀, Busa Riv, E of Lae, 100 m, 13–15.IX.1955 (Gressitt) (BPBM); ♂, 2♀, Finschhafen, 12–14.IV.1944, 11.V.1944 (E.S. Ross) (CAS); ♀, Finschhafen, Huon Pen, 50–150 m, 11.IV.1963 (Sedlacek); ♀, Kalolo, 750 m, 20–30, VIII.1966, malaise trap (G.A. Samuelson); ♀, Lae, Sirguawa Riv, 147° 10′E, 6° 45′S, 30 m, IV.1968 (O.R. Wilkes); ♀, Zenag-Lae Rd, 200 m, 17.I.1965, malaise trap (Sedlacek) (BPBM); ♀, Pindiu, Huon Pen, 3,000 ft (915 m), 13.VII.1964, 7th Archbold Exped. (H.M. Van Deusen) (AMNH); ♂, Tuwep, Selawaket Range, 1,350 m, 9.IX.1956, light trap (E.J. Ford, Jr.); ♂, Ulap, 800–1,000 m, IX.1968 (Krauss); ♂, Wau, 1,200 m, 22–30, VI.1962, light trap; ♀, 1,050 m, 7.I.1963; ♀, 1,090 m, 25.I.1963; ♀, 1,200 m, 1–3.X.1963 (Sedlacek); ♂, 1,200 m, 18.IV.1965; ♂, 1,250–1,800 m, 12.IX.1965; ♂, 900–1,100 m, 25.IX.1965 (J.& M. Sedlacek); ♀, Wau, Hospital Crk, 1,250 m, 17.V.1965, malaise trap (Sedlacek); ♀, Wau, 1,200–1,500 m, 30.IX.1965 (Sedlacek); ♀, Wau, 1,200 m, 18.I.1967 (Samuelson); ♂, Wau, 1,100–1,200 m, VI.1968 (Krauss); ♀, Wau, Mt Missim, 1,100–1,250 m, 14.VII.1971 (Sedlacek) (BPBM).

Collection data indicate that this species has a wide distribution in Papua New Guinea. It apparently is adapted to several different habitats; specimens were collected at elevations ranging from 0–1,800 m.

Sosephena binoba Medler, **new species** Figs. 4–6

Description. Morphology of frons, vertex, and pronotum conforming with generic diagnosis (Figs. 4–6). This species is closely similar to *rinkela*, but may be distinguished by the shape of the vertex that is less produced anteriorly, and the anterior margin tends to be convex rather than acute.

The genitalia (Fig. 6) differ from *rinkela* in structures of the aedeagus. A small triangular lateral projection originates close to dorsal margin at point below apex of dorsal process; in *rinkela* this triangular projection is absent.

Color green. Tegmen shape and venation similar to *rinkela*, barred appearance caused by orange-yellow crossveins contrasting with green membrane. Female tegmen posteriorly with narrow red margins, including pigmented vein terminations.

Measurements (♂, ♀). From holotype and allotype. Length: overall 9.75, 10.0; v 0.33, 0.33; f 1.20, 1.33; p 0.50, 0.54; m 1.49, 1.49; t 7.80, 8.13; pcl 1.99, 1.99. Width: v 0.79, 0.79; f 1.00, 1.00; t 4.15, 4.48. Hind leg spine formula: 1:6:7, 1:6:7.

Type data. Holotype ♂, PAPUA NEW GUINEA: Madang Prov: Nobonob Hill, 7 km NW Madang, 5° 10'S, 145° 45'E, 16.III.1987 (N.D. Penny); allotype ♀, Nobonob Hill, 7 km NW Madang, 5° 10'S, 145° 45'E, 21.III.1987 (Penny). Both deposited in CAS. Paratypes: PAPUA NEW GUINEA: Madang Prov: ♂, ♀, Nobonob Hill, 7 km NW Madang, 5° 10'S, 145° 45'E, 9.II.1987 (Penny) (CAS); ♂, Naru Riv, 31 km SW Madang, 5° 26'S, 145° 27'E, 3.III.1987 (Penny); ♀, Nobonob Hill, 7 km NW Madang, 5° 10'S, 145° 45'E, 13–14.II.1987 (Penny) (BPBM).

Distribution records limited to Madang Province; determinations confirmed by study of male genitalia of several specimens.

Genus ***Trisephena*** Medler, **new genus**

Type species. *Trisephena rubeola* Medler, n. sp., here designated.

Diagnosis. Dorsum of head short, wide, composed of frons and vertex; anterior margin formed by frontal U-carinae, narrow dorsal ledge of frons clearly delimited posteriorly from vertex by transverse carina arising from anterodorsal genal angles. Transverse carina either uninterrupted or medially broken to varying extent by longitudinal suture, V-notch, or shallow depression of vertex. Lateral margins of frons sharply carinate, elevated, evenly convex from clypeal margin to lateral margins of vertex, disc with 3 thickened longitudinal carinae, lateral carinae shorter than median carina, lateral carinae narrowly or broadly U-shaped, joined dorsally with median carina. Anterior and lateral margins of pronotum carinate, lateral margin extended beyond middle of eye, postocular eminence elevated, broadly triangular, margin extending as strong ridge to anteroventral margins of paranotal lobe. Mesonotum with 3 longitudinal carinae, disc flat.

Apical margin of tegmen obliquely truncate, shape of costal and sutural angles dissimilar, postclaval margin elevated; either 3 (R,S,M) or 2 (R+S,M) longitudinal veins arising from basal stem, vein R unbranched from base to weak R+C junction, vein S 5-branched, vein M strongly 4-branched, each branch forming several apical terminals, vein Cu oblique crossvein displacing Cu away from claval suture toward M_2 forming triangular cell; Cu and suture reunited at claval apex, Cu continuing toward apical margin as irregular submarginal vein with 5–6 branches terminating along postclaval sutural margin; Y-stem short. Tegmen of some species with scattered pustules, or heavy concentration of pustules basally in clavus and precostal marginal cell.

Color variable, tendency toward faded colors and sexual dimorphism, red colors more brilliant in females. Specimens with or without red spots and dashes, small red spots on lateral margins of frons and sides of pronotum, tegmina with thin red margins, variable sizes and frequencies of red spots and dashes on veins and membrane. Relatively small species, length 7.5–9.5 mm, females slightly larger than males.

Ovipositor modified, valvulae III fingerlike, not sclerotized, not suitable for piercing.

Distribution. Papua New Guinea, New Britain, Irian Jaya.

Key to Species of *Trisephena*

1. Anterior margin of vertex separated from dorsal surface of frons by unbroken transverse carina originating at genal angles. Tegmen with red spots, 2 longitudinal veins (R+S, M) arising from basal stem 2

Transverse carina delimiting anterior margin of vertex unbroken or interrupted medially by notch or depression; tegmen with or without red spots, 3 longitudinal veins (R, S, M) arising from basal stem 3

2. Apical margin of tegmen oblique, pcl margin convexly elevated; vein Cu and M_2 united by oblique crossvein . . . . ***zestreya*, n. sp.**
   Apical margin of tegmen elongate oval, pcl margin not elevated; apex of clavus midway between tip of scutellum and apex of tegmen; Cu and M_2 uniting in short stem, then dividing with noticeable gap between Cu and apex of clavus . . . . ***anomala*, n. sp.**
3. Tegmen without red spots, crossveins not outlined in red, or sparsely so. Transverse dorsal carina unbroken; frontal U-shaped carinae shallowly raised, dorsal margin with convex ledge anterior of vertex 4
   Frontal carinae wide, U-shaped, strongly raised. Tegmen with red spots, crossveins strongly red or outlined by red; transverse dorsal carina notched medially or interrupted by shallow depression 5
4. Overall length 7.5 mm; tegmina opaque white; ventrally directed process of aedeagus triangular, short (Fig. 21) . . . . ***estrias*, n. sp.**
   Overall length 9.0–9.5 mm; tegmina green; ventrally directed process of aedeagus slender, elongate (Fig. 24) . . . . ***metrior*, n. sp.**
5. Anterior margin of vertex truncate, interrupted medially by concave depression extending to frontal carinal margin . . . . ***lonessa*, n. sp.**
   Anterior margin of vertex angulate anterad, interrupted medially by depression or V-notch 6
6. Pronotum and frons not marked with small red dots; tegmen with sparse pattern of red crossveins. Dorsal basal process of aedeagus much enlarged apically (Fig. 15) . . . (New Britain) . . . . ***imposita*, n. sp.**
   Sides of pronotum and lateral margins of frons with numerous small red dots; tegmen usually heavily marked with red crossveins and spots; pustules prominent, especially in basal part of clavus and precostal margin 7
7. Posterodorsal angle of pygofer sharply pointed; posterior process of aedeagus circular (Fig. 9) . . . . ***rubeola*, n. sp.**
   Pygofer angle not pointed; posterior process of aedeagus straight or slightly curved, basally directed lateral process straight or downturned . . . . ***trientor*, n. sp.**

Trisephena rubeola Medler, **new species** Figs. 7–9, 35–36

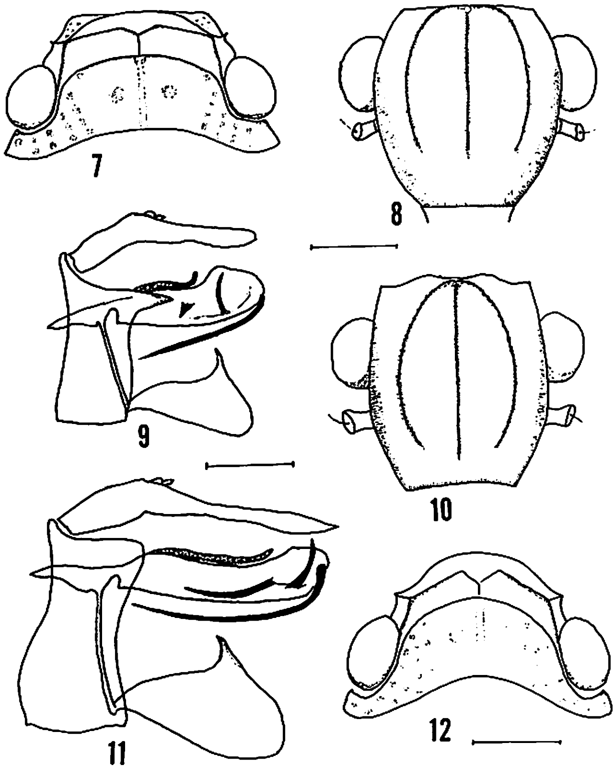
Description. Morphology of frons, vertex, and pronotum as in generic diagnosis (Fig. 7–8). In dorsal view, U-carina of frons forming anterior margin of head. Anterior margin of vertex delimited by slightly angulate transverse carina arising from anterodorsal angles of genae, median notch V-shaped. Pronotal lateral carina extended posteriorly nearly to raised triangular postocular eminence. Mesonotum tricarinate, disc flat. Tegmen whitish, translucent, apical margin obliquely truncate, postclaval sutural margin slightly raised (Fig. 36).

Coloration strongly red; sides and adjacent part of dorsum heavily marked with uniform red dots, disc unmarked except by red median longitudinal band that continues across mesonotum. Similar red spots also on frons in space between lateral margin and lateral arm of U-carina. Cells and crossveins of tegmina strongly marked with scattered red spots of variable size, most numerous on apical crossveins, vein terminations at margin red; scattered red pustules present, some pustules ivory, rimmed with red, pustules largest in size in base of clavus.

Coloration variable; pattern and color of markings variable; colors green, tawny, red orange; faded or bright.

Genitalia (Fig. 9). Posterodorsal angle of pygofer sharply pointed. This character state unique in the genus.

Measurements (♂, ♀). From holotype and allotype. Length: overall 9.0, 10.05; v 0.25, 0.29; f 1.16, 1.33; p 0.42, 0.46; m 1.66, 1.49; t 7.80, 8.30; pcl 1.83, 2.49. Width: v 0.83, 0.95; f 1.08, 1.33; t 3.65, 3.82. Hind leg spine formula: both 1:6:9.



Figs. 7–12. Holotype: **7**, *Trisephena rubeola*, head; **8**, same, frons; **9**, same, genitalia; **10**, *Trisephena trientor*, frons; **11**, same, genitalia; **12**, same, head. Scale = 0.5 mm.

Type data. Holotype ♂ (BPBM 14,033), allotype ♀, PAPUA NEW GUINEA: Eastern Highlands Prov: Kassam, 1,350 m, 48 km E of Kainantu, 7.XI.1959 (T.C. Maa). Both deposited in BPBM. Paratypes: PAPUA NEW GUINEA: Eastern Highlands Prov: ♂, ♀, Arau, 40 km E of Kainantu, 1,400 m, 16.X.1959 (Maa); ♂, ♀, Kassam, 48 km E of Kainantu, 1,350 m, 7.XI.1959 (Maa) (BPBM). East New Britain Prov: ♂, 2♀, Bainings, St. Paul's, Gazelle Pen, 350 m, 8–9.IX.1955 (Gressitt); ♀, Gaulim, Gazelle Pen, 130 m, 23–28.X.1962 (Sedlacek); ♂, ♀, Mt Sinewit, Gazelle Pen, 900 m, 7–16.XI.1962, malaise trap (Sedlacek) (BPBM). East Sepik Prov: ♂, Bainyik, S of Maprik, 150 m, 12.I.1960; ♀, 160 m, 29.XII.1959–17.I.1960 (Maa); 4♀, Wum, Upper Jimi Val, 840 m, 16–18.VII.1955 (Gressitt) (BPBM). Madang Prov: ♂, Bundi, 5° 45'S, 145° 15'E, 10–12.III.1987 (Penny) (CAS); ♀, Bundi, 1,300 m, 8.V.1988, St. 019, (Van Stalle No. 27363); ♀, Brahman Bundi, 700 m, 7.V.1988, St. 041, (Van Stalle No. 27363) (IRSN); ♀, Kurum, Karkar I, 0–100 m, VIII.1968, (Krauss) (BPBM); ♂, Naru Riv, 31 km SW Madang, 5° 26'S, 145° 27'E, 3.III.1987 (Penny); 2♂, 2♀, Nobonob Hill, 7 km NW Madang, 5° 10'S, 145° 45' E, 9–14.II.1987; ♂, ♀, 2–19.III.1987 (Penny) (CAS); ♀, Saidor, Sibog Vill, Finisterre Range, 27.V–5.VI.1958 (Brandt) (BPBM); 2♀, Tapo Crk, 26 km SW Madang, 5° 24'S, 145° 38'E, 23.II–15.II.1987 (Penny) (CAS); ♂, ♀, Wanuma, Adelbert Mts, 800–1,000 m, 24–25.X.1958 (Gressitt); 2♂, 3♀, Wanuma, 600–720 m, VIII.1968 (Krauss) (BPBM). Milne Bay Prov: ♀, Fergusson I, Mts between Agamoia and Ailuluai, 900 m, No. 4, 5–17.VI.1956, 5th Archbold Exped. (L.J. Brass) (AMNH). Morobe Prov: ♀, Bubia, IX.1949

(Krauss); 2♀, Busa Riv, E of Lae, 100 m, 14.X.1956 (Gressitt) (BPBM); ♂, Lae, Melambi Riv, Mirilunga Vill, 4,500 m, 29.XII.1956 (J.H. Ardley) (PNGDA); ♀, Lae, VII.1944 (F.E. Skinner); ♀, Lae, sea level, 26.VII.1955 (Gressitt) (BPBM); ♂, Umi Riv, Markham Vall, 480 m, No. 14, 24.XI.1959, 6th Archbold Exped. (Brass) (AMNH). Southern Highlands Prov: ♀, Korop, Upper Jimi Vall, 1,300 m, 12.VII.1955 (Gressitt) (BPBM). Western Highlands Prov: 2♂, ♀, Tsenga, Upper Jimi Vall, 14–15.VI.1955 (Gressitt) (BPBM). INDONESIA: IRIAN JAYA: ♂, Bodem, 11 km SE Oerberfaren, 100 m, 7–17.VII.1959 (Maa) (BPBM).

A ♀ specimen in the Bishop Museum from the Philippines: Mindanao, Agusan, 10 km SE Francisco, 14.XI.1959, L.W. Quate, may represent a valid extension of distribution to the Philippine Islands, or may only be a mislabeled specimen.

Trisephena trientor Medler, **new species** Figs. 10–12

Description. Morphology of frons, vertex, and pronotum as in generic diagnosis (Figs. 10, 12). Specimens closely resemble *rubeola* in red markings and angulate shape of vertex with median V-shaped notch, but differ in acute anterodorsal angle of genae and characters of the genitalia (Fig. 11). Heavily marked with red dotlike spots on pronotum; dark red brown median longitudinal band on pro- and mesonotum; red crossveins and spots on tegmina, large red spots on each side of discal cell crossvein, in next apicad tier of crossveins; and in Cu triangular cell. Tegmen pustulate, especially between S and M veins, in precostal margin, and base of clavus.

Measurements (♂, ♀). From holotype and allotype. Length: overall 8.5, 9.0; v 0.25, 0.25; f 1.20, 1.33; p 0.46, 0.50; m 1.41, 1.66; t 6.97, 7.64; pcl 2.16, 2.16. Width: v 0.79, 0.87; f 1.08, 1.20; t 3.32, 3.65. Hind leg spine formula: both 1:6:7.

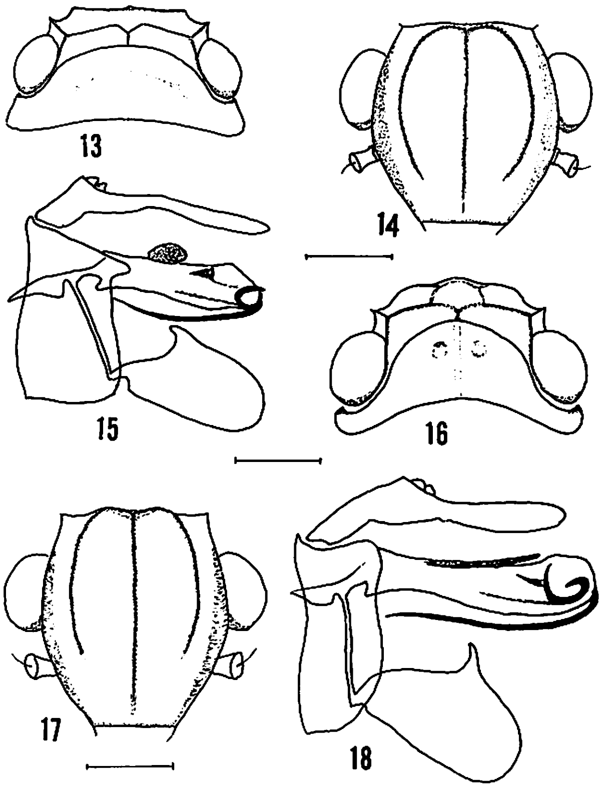
Type data. Holotype ♂ (BPBM 14,034), PAPUA NEW GUINEA: West Sepik Prov: Torricelli Mts, Mokai Vill, 750 m, 8–15.XII.1958 (W.W. Brandt); allotype ♀, Torricelli Mts, Mobitei, 750 m, 1.IV.1959 (Brandt). Both deposited in BPBM. Paratypes: PAPUA NEW GUINEA: East Sepik Prov: 2♂, ♀, Angoram, 20–30 m, 14–16.VIII.1969 (Gressitt) (BPBM); ♂, Maprik, 19.X.1957 (J. Smart) BM 1957–693 (BMNH). West Sepik Prov: ♂, Torricelli Mts, Mokai Vill, 750 m, 1–23.I.1958 (Brandt); ♀, Torricelli Mts, Mobitei, 750 m, 28.II–4.III.1959; 2♀, 1–15.IV.1959 (Brandt) (BPBM).

Trisephena imposita Medler, **new species** Figs. 13–15

Description. Morphology of frons, vertex, and pronotum as in generic diagnosis (Figs. 13–14). Head characters of this species are similar to *rubeola,* but specimens can be distinguished by distribution in New Britain, absence of red spots on frons and pronotum, and lack of median red spots on tegmina crossveins. Color stramineous, thin red lines on crossveins, margins of tegmina narrowly red. Genitalia (Fig. 15) are uniquely characterized by large dorsal process and circular posterior process of aedeagus.

Measurements (♂, ♀). From holotype and allotype. Length: overall 9.0, 9.0; v 0.21, 0.33; f 1.16, 1.25; p 0.42, 0.50; m 1.33, 1.33; t 7.14, 7.30; pcl 2.16, 1.99. Width: v 0.79, 0.83; f 1.08, 1.04; t 3.49, 3.65. Hind leg spine formula: both 1:6:7.

Type data. Holotype ♂ (BPBM 14,035), PAPUA NEW GUINEA: East New Britain Prov: Mt Sinewit, Gazelle Pen, 900 m, 14–16.XI.1962 (Sedlacek); allotype ♀, same date, but 7–16.XI.1962 (Sedlacek). Both deposited in BPBM. Paratypes: PAPUA NEW GUINEA: East New Britain Prov: ♀, Bainings, St. Paul's, Gazelle Pen, 350 m, 8.IX.1955 (Gressitt); ♂, Sio, N Coast, 600 m, 24.VII.1956 (Ford); ♂, Umboi I, 8 km WNW Lab Lab, 300 m, 8–19.II.1967 (G.A. & S.L. Samuelson, P.H. Colman) (BPBM). Morobe Prov: ♂, Buso, IX–XI.1979 (J. Martin) BM 1980–150 (BMNH).



Figs. 13–18. Holotype: **13**, *Trisephena imposita*, head; **14**, same, frons; **15**, same, genitalia; **16**, *Trisephena lonessa*, head; **17**, same, frons; **18**, same, genitalia. Scale = 0.5 mm.

Trisephena lonessa Medler, **new species** Figs. 16–18

Description. Morphology of frons, vertex, and pronotum (Figs. 16–17) are in agreement with the generic diagnosis except that median depression of vertex is the character state found in *Sosephena*. Tegmina heavily pustulate, most pustules red.

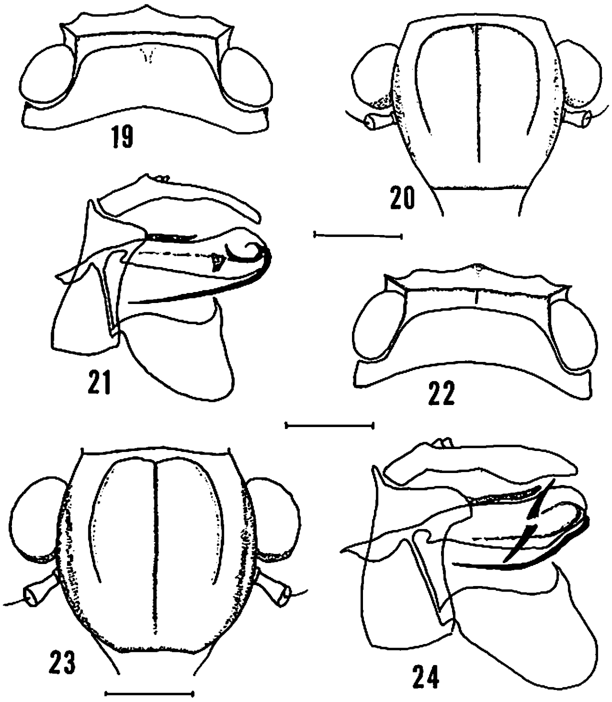
The species is represented by the unique holotype, which has distinctive genitalia (Fig. 18).

Measurements. From holotype. Length: overall 8.0; v 0.25; f 1.25; p 0.50; m 1.49; t 7.47; pcl 2.16. Width: v 0.83; f 1.08; t 3.32. Hind leg spine formula: 1:5:7.

Type data. Holotype ♂ (BPBM 14,036), PAPUA NEW GUINEA: West Sepik Prov: Eliptamin Vall, 1,200–1,350 m, 16–31.VII.1959 (W.W. Brandt). Deposited in BPBM.

Trisephena estrias Medler, **new species** Figs. 19–21

Description. Morphology of frons, vertex, and pronotum as in generic diagnosis (Figs. 19–20). Frontal carinae moderately raised on the disc, longitudinal median carina extending basad nearly full length of frons, dorsal portion of U-shaped carinae not sharply raised, slightly concave medially at junction with median carina, separated spatially from vertex by narrow shelflike convexity of frons. Transverse carina anteriorly delimiting margin of vertex extending straight, uninterrupted across dorsum, arising from convex anterodorsal margins of genae. Color light stramineous, membrane of tegmina semiopaque, without red markings.



Figs. 19–24. Holotype: **19**, *Trisephena estrias*, head; **20**, same, frons; **21**, same, genitalia; **22**, *Trisephena metrior*, head; **23**, same, frons; **24**, same, genitalia. Scale = 0.5 mm.

This species is closely related to *metrior*, but distinguished by different character states of the genitalia (Fig. 21).

Measurements. From paratype ♂. Length: overall 7.5; v 0.17; f 1.00; p 0.37; m 1.25; t 6.64; pcl 1.83. Width: v 0.79; f 1.00; t 3.32. Hind leg spine formula: 1:6:7.

Type data. Holotype ♂ (BPBM 14,038), PAPUA NEW GUINEA: Madang Prov: Wanuma, 600–720 m, VII.1968 (N.L.H. Krauss). Deposited in BPBM. The holotype tegmina are damaged. Paratypes: PAPUA NEW GUINEA: Western Prov: 2♂, Lk Murray, 8.XII.1972, white light (P.I. Imlay) (BPBM).

Trisephena metrior Medler, new species Figs. 22–24

Description. Morphology of frons, vertex, and pronotum as in generic diagnosis (Figs. 22–23), closely resembling *estrias*. Weakly defined U-carinae of frons meeting raised median carina at slight angle, separated from anterior margin of vertex by narrow convex dorsum of frons, anterior margin of vertex truncate, transverse carina arising at genae straight, uninterrupted medially. Head and body stramineous, tegmina green to faded dull green, red markings limited to oblique vein at widest part of Cu triangular cell and a few other crossveins.

This species is distinguished from *estrias* and other congeners by definitive character states of the genitalia (Fig. 24).

Measurements (♂, ♀). From holotype and allotype. Length: overall 9.0, 9.5; v 0.17, 0.17; f 1.16, 1.16; p 0.42, 0.42; m 1.49, 1.58; t 5.31, 7.97; pcl 1.83, 2.16. Width: v 0.83, 0.83; f 1.16, 1.16; t 3.49, 3.98. Hind leg spine formula: 1:6:6; 1:6:7.

Type data. Holotype ♂ (BPBM 14,037), PAPUA NEW GUINEA: East Sepik Prov: Bainyik, S of Maprik, 150 m, 4.I.1960 (T.C. Maa); allotype ♀, West Sepik Prov: Kumur, Upper Jimi Vall, 1,000 m, 13.VII.1955 (J.L. Gressitt). Both deposited in BPBM. Paratypes: PAPUA NEW GUINEA: East Sepik Prov: ♂, Bainyik, nr. Maprik, 225 m, 21.VI.1961 (Gressitt); ♀, Wagu, Upper Sepik, ½ way between Green & Yellow Riv, 180 m, 5.VII.1963 (Straatman); ♀, Wum, Upper Jimi Valley, 840 m, 18.VII.1955 (Gressitt) (BPBM). Western Highlands Prov: ♀, Baiyer Riv, 1,150 m, 17.X.1958, *Castanea*-like tree (Gressitt); ♀, Tsenga, Upper Jimi Vall, 1,200 m, 13.VII.1955 (Gressitt) (BPBM). INDONESIA: IRIAN JAYA: 3♂, Sabron, Cyclops Mts, Camp 2, 2,000 ft [610 m], VII.1936 (L.E. Cheesman) BM 1936–271 (BMNH).

Trisephena zestreya **Medler, new species** Figs. 25–26, 33–34

Description. Morphology of frons, vertex, and pronotum as in generic diagnosis (Figs. 25–26). This species is distinguished from other strongly red-spotted species in the genus by the straight anterior margin of vertex, elevated post-claval suture (Fig. 33), R+S venation (Fig. 34), and aedeagus basal process inconspicuous or absent (Fig. 27).

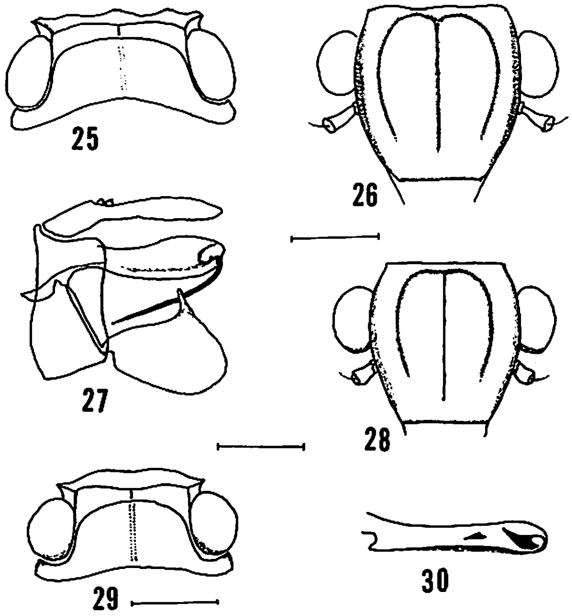
Measurements (♂, ♀). From holotype and allotype. Length: overall 8.0, 8.5; v 0.17, 0.17; f 1.00, 1.04; p 0.33, 0.33; m 1.33, 1.49; t 6.31, 6.97; pcl 1.99, 2.16. Width: v 0.79, 0.79; f 1.00, 1.04; t 5.82, 3.15. Hind leg spine formula: 1:7:8; 1:6:7.

Type data. Holotype ♂ (BPBM 14,039), PAPUA NEW GUINEA: Morobe Prov: Wau, 1,200 m, 2.V.1965 (J.& M. Sedlacek); allotype ♀, Wau, 1,100–1,200, VII.1968 (N.L.H. Krauss). Both deposited in BPBM. Paratypes: PAPUA NEW GUINEA: East Sepik Prov: ♀, Bainyik, S of Maprik, 150 m, 12.VI.1960 (Maa) (BPBM). Madang Prov: ♀, Nobonob Hill, 7 km NW Madang, 5° 10'S, 145° 45'E, 22.II.1987 (Penny) (CAS); ♀, Wanuma, Adelbert Mts, 800–1,000 m, 26.X.1958, grasses (Gressitt) (BPBM). Morobe Prov: ♂, Boana Mission, Huon Pen, 900 m, 4–5, IX.1956 (Ford); ♀, Wau, 1,200 m, 31.VII.1961 (Sedlacek); ♀, Wau, 1,200 m, 7.VI.1962 (Sedlacek); ♂, Wau, 1,100–1,200, VI.1968, on *Lantana camera*; ♀, VII.1968 (Krauss) (BPBM); ♀, Wau, 10 km S, 22.V.1988, St. 054 (Van Stalle No. 27363) (IRSN). West Sepik Prov: ♀, Torricelli Mts, Mobitei, 750 m, 16–31.III.1959 (Brandt) (BPBM). INDONESIA: IRIAN JAYA: 2♂, ♀, Araucaria Camp, 800 m, 11–19.III.1939 (Toxopeus); ♂, Bernhard Camp, 750 m, 27.III.1939 (Toxopeus); ♂, ♀, Rattan Camp, 1,200 m, 6.II.1939, 4.III.1939 (Toxopeus) [Netherlands Indies-America Exped.] (RNHL); ♀, Genjam, 40 km W of Hollandia, 100–200 m, 1–10.III.1960 (Maa); ♂, Hollandia area, W Sentani, Cyclops Mts, 150–250 m, 17.VI.1959 (Maa) (BPBM); ♀, Hollandia, Humboldt Bay, IV.1936 (Cheesman) BM 1936–271 (BMNH); ♀, Hollandia, rain forest clearing, 250 ft [75 m], ♀, 12.XII.1944, ♂, 18.I.1945, ♂, ♀, 7–9.II.1945, ♀, 19.III.1945, 2♂, 2♀, V.1945 (H. Hoogstraal) (NCSU); ♀, Ifar, E end Cyclops Mts, 150 m, 18.X.1957 (Gressitt); ♂, ♀, Ifar, Cyclops Mts, 300 m, 21.VI.1959 (Maa); 2♀, Ifar, 300–600 m, 20–22.VI.1959 (Maa); 2♂, Ifar, Cyclops Mts, 400–550 m, 23.VI.1959 (Maa) (BPBM); ♀, Mt. Lina, Cyclops Mts, 3,500 ft [1,070 m], III.1936 (Cheesman) BM 1936–271; ♂, Sabron, Cyclops Mts, Camp 2, 2,000 ft [610 m], VI.1936, 2♂, 4♀, VII.1936 (Cheesman) BM 1936–271 (BMNH); ♀, Waris, S of Hollandia, 450–500 m, 24–31.VII.1959 (Maa) (BPBM).

Widely distributed, with more numerous collection records in Irian Jaya than for other species in the genus.

Trisephena anomala **Medler, new species** Figs. 28–32

Description. Morphology of frons, vertex, and pronotum as in generic diagnosis (Figs. 28–29). The unique narrow convex shape apically of the tegmen (Fig. 32) differs from all



Figs. 25–30. Holotype: **25**, *Trisephena zestreya*, head; **26**, same, frons; **27**, same, genitalia; **28**, *Trisephena anomala*, frons; **29**, same, head; **30**, same, aedeagus. Scale = 0.5 mm.

congeners. Tegminal development of the R+S stem is shared with *zestreya*, along with scattered red spots and pustules. The union of veins M_2 and Cu to form a joint stem shown (Fig. 31) appears to be a venation pattern found only in this species. Holotype genitalia (Fig. 30) is disassociated aedeagus, which is only part available, other structures being lost.

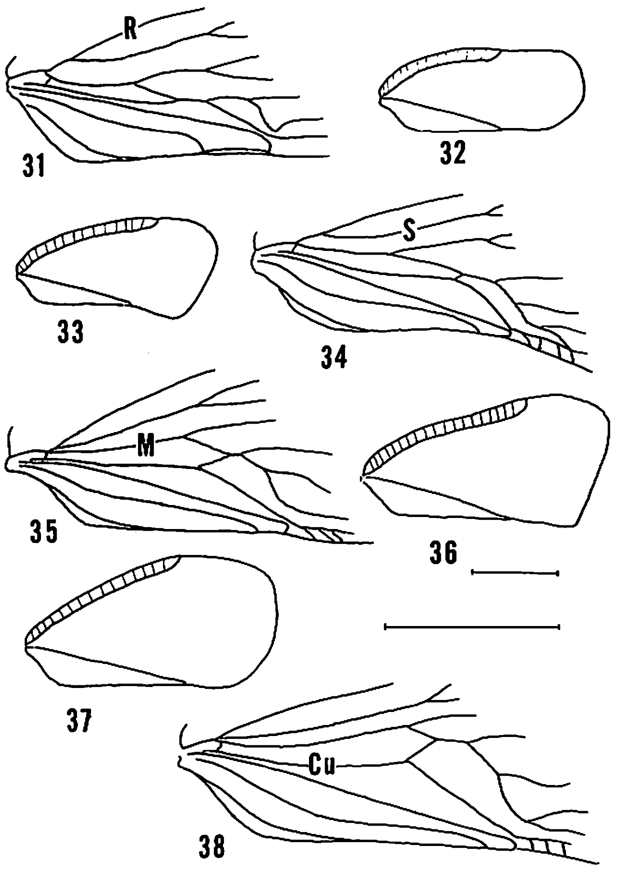
Measurements (♂, ♀). From holotype and allotype. Length: overall 8.0, 8.5; v 0.17, 0.17; f 0.91, 1.00; p 0.37, 0.37; m 1.33, 1.49; t 6.64, 7.47; pcl 1.66, 1.83. Width: v 0.66, 0.75; f 0.83, 1.00; t 2.52, 2.99. Hind leg spine formula: both 1:6:7.

Type data. Holotype ♂ (BPBM 14,040), PAPUA NEW GUINEA: East New Britain Prov: Mt Sinevit, Gazelle Pen, 900 m, 7–16.XI.1962 (J. Sedlacek); allotype ♀, Madang Prov: Wanuma, Adelbert Mts, 800–1,000 m, 23.X.1958, *Pipturus* (J. L. Gressitt). Both deposited in BPBM. The holotype tegmina are damaged; tegmen illustrations (Figs. 31–32) were taken from the allotype. Paratypes: PAPUA NEW GUINEA: East New Britain Prov: ♂, Mt Sinevit, Gazelle Pen, 900 m, 10.XI.1962, light trap (Sedlacek) (BPBM). Madang Prov: ♀, Kassam, 48 km E of Kainantu, 1,350 m, 7.XI.1959 (Maa); 2♀, Wanuma, Adelbert Mts, 800–1,000 m, 24–25.X.1958, *Pipturus* (Gressitt) (BPBM).

Taxonomic Notes on Australian Genera with Tricarinate Frons

Aflata Melichar (1902)

Type species. *Aflata stali* Melichar (1902), by monotypy. Lectotype ♀, Adelaide, designated by Medler (1986). Male genitalia illustrated by Fletcher (1979); other diagnostic features and generic key given by Fletcher (1988).



Figs. 31–38. Tegmen: **31**, *Trisephena anomala*, allotype, principal veins, R = radius; **32**, same, outline sketch; **33**, *Trisephena zestreya*, holotype, outline sketch; **34**, same, principal veins, S = sector; **35**, *Trisephena rubeola*, holotype, principal veins, M = media; **36**, same, outline sketch; **37**, *Sosephena rinkela*, allotype, outline sketch; **38**, same, principal veins, Cu = cubitus. Scale = 0.5 mm, Figs. 31, 34, 35, 38; 3.0 mm, Figs. 32, 33, 36, 37.

Burnix Medler (1988)

Type species. *Euphanta insignis* Lallemand (1935), by original designation. Lectotype ♂, Burnside, designated by Medler (1988). Male genitalia illustrated by Medler (1988).

Euphanta Melichar (1902)

Type species. *Poeciloptera munda* Walker (1851), by subsequent designation of Distant (1910). Holotype ♀, New Holland, reported in BMNH by Medler (1990). Diagnostic features and generic key given by Fletcher (1988). *Euphanta munda* (Walker) recorded in Papua New Guinea by Medler (1989), but all other name combinations of *Euphanta* in New Guinea synonymized with *Colgar* Kirkaldy by Medler (1989).

Euryphantia Kirkaldy (1906)

Type species. *Euryphantia cinerascens* Kirkaldy (1906), by original designation. Holotype ♀, Bundaberg, seen in BPBM by Medler (1987). Male genitalia illustrated by Fletcher (1980);

other diagnostic features and key given by Fletcher (1988). Recorded in Papua New Guinea by Medler (1989).

Lesabes Medler (1988)

Type species. *Neomelicharia handschini* Lallemand (1935), by original designation. Holotype ♀, Darwin, seen in Basel Natural History Museum by Medler (1988). Male genitalia illustrated by Medler (1988); other diagnostic features and distributions given by Medler (1988).

ACKNOWLEDGMENTS

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Dating of the Livraisons and Volumes of d'Orbigny's *Dictionnaire Universel d'Histoire Naturelle*

Neal L. Evenhuis[1]

ABSTRACT

Recent evidence of pagination, contents, and number of signatures per livraison of Charles d'Orbigny's 13–volume *Dictionnaire Universel d'Histoire Naturelle* is presented. Accurate completion dates of all the 13 volumes are also given.

In April 1839, a prospectus was sent to potential subscribers and libraries by the French publisher C. Renard of Paris announcing the forthcoming publication of the *Dictionnaire Universel d'Histoire Naturelle*, edited by Charles D. V. d'Orbigny. The prospectus offered the publication for sale by livraison and stated that the entire work would comprise 6–8 volumes in octavo and be issued in 120 livraisons. By the time the *Dictionnaire* was completed 10 years later, it consisted of 13 volumes and 150 livraisons.[2] A 2nd edition was published from 1867 to 1869 (see Stafleu & Cowan 1981 for details). Sherborn and Palmer (1899) and Iredale (1937) give information on reissues. According to the *Bibliographie de la France*, d'Orbigny co-authored, with M. de Wegmann, an abridged *Dictionnaire*, which appeared in 2 volumes, 1842–1844 in 80 livraisons. Copies of this *Dictionnaire* were not available for examination during this study.

As with other "Dictionnaires" published in the late 1700s and 1800s by French naturalists, this one was actually more of an encyclopedia of natural history terms and taxonomic names than a dictionary of definitions. Because the *Dictionnaire* lists numerous generic names of plants and animals, it takes on nomenclatural importance. Stafleu and Cowan (1981) mention that there are new botanical taxa described in the *Dictionnaire*; and there are many type designations for zoological genera throughout the 13 volumes, some of which are earlier than those generally accepted (see Evenhuis and Thompson 1990 for a list of the Diptera genera). The evident nomenclatural significance of this *Dictionnaire* necessitates finding the date of issue for each of the livraisons.

Previous works giving dates for the livraisons and volumes of the *Dictionnaire* include Sherborn and Palmer (1899), Iredale (1937), and Stafleu and Cowan (1981). Sherborn and Palmer's (1899) dates came primarily from the presentation dates of the *Dictionnaire*'s various livraisons at meetings of the Société Géologique de la France. They qualify the dates given for most of the livraisons in volumes 1–6 by their statement that actual publication dates may be months previous to the date of presentation to the Société. Stafleu and Cowan (1981) give dates of receipt for most (but not all) of the 13 volumes as recorded in the *Bibliographie de la France*

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[2] The Académie des Sciences, Paris lists receiving livraisons 150 and 151 on 5 November 1849. Livraison 151 contained the figure legends to the plates contained in the 3–volume atlas.

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(abbreviated hence forward as *BF*) but give no dates for the separate livraisons. Iredale (1937) points out that some livraisons were reviewed in the *Revue Zoologique de la Société Cuvierienne* from June 1839 to February 1847, often giving dates of publication earlier than those recorded in Sherborn and Palmer (1899). The reviews in the *Revue Zoologique*, in some cases, mention generic names, natural history terms entered in the *Dictionnaire*, or pagination. This allows some idea as to how many pages may make up a livraison and can give a more accurate date for nomenclatural actions such as type designations or proposals of new names that may have taken place in the *Dictionnaire*. Iredale (1937) presumes that either 48, 64, or 96 pages made up a livraison. Based on evidence supplied in the *BF* (see Table 2), the actual number of pages per livraison was generally 32, 48, 56, or 64. Sherborn and Palmer (1899) recommend that the dates of the completed volumes be used for dating because at that time the contents of each livraison were not known. Nomenclatural rules, however, necessitate that the earliest date possible be used, especially when one may wish to invoke the Law of Priority for homonymies or synonymies.

I have researched the listings of receipt for the livraisons of the *Dictionnaire* in the *BF* and the *Compte Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris* (*CR*), the dates of which are recorded in Table 2. Stafleu (1967) mentions that a date of receipt in the *BF* for a publication based in Paris can be taken as the actual publication date. That is not always the case with livraisons of the *Dictionnaire* because, in a few cases, the articles in the *Revue Zoologique* and receipt dates in the *CR* can precede the *BF* receipt date by as much as a few weeks or even a month or two. Some of the listings in the *BF* include the actual feuille (signature) numbers for a livraison or how many feuilles were received per livraison. Because each feuille in the *Dictionnaire* consisted of 8 pages and the feuilles are numbered at the bottom of each starting page, it is possible to calculate how many pages made up a particular livraison or group of livraisons that were mentioned by the *BF*. For those livraisons that were reviewed in the *Revue Zoologique*, which mentioned genera or other entries in the *Dictionnaire*, it is possible to estimate the minimal number of feuilles that included *at least* those entries mentioned in the *Revue Zoologique*. Pagination for those livraisons are in italics when it is possible that the actual pagination might be more or less than is listed.

Table 1 gives beginning and ending terms, pagination, and dating presently known for the volumes. The date given is when the last livraison of a particular volume was issued and not necessarily the date when the completed and bound volume was issued, which was probably later. Table 2 gives the details of contents, pagination, and dating for the livraisons. It is hoped that listing the beginning and ending entries for many of the livraisons will aid taxonomists in obtaining the earliest possible date for type designations or other nomenclatural actions found on those pages. For livraisons that were not recorded in the *BF*, *CR*, or listed in Stafleu and Cowan (1981), the dates given by Sherborn and Palmer (1899) should be used until further evidence of dating is discovered.

The author requests readers to supply him with any information they may have that will provide more accurate dating of these livraisons and fill gaps in data in Table 2.

ACKNOWLEDGMENTS

I thank the librarians and staff of the National Museum of Natural History, Washington, D.C., British Museum (Natural History), London, and University of Hawaii, Manoa, for their assistance and allowing me access to the journals consulted during this study; and the dipterists at the first two institutions for their continued encouragement throughout this project. Dr. F. Christian Thompson provided crucial information on various aspects of the *Dictionnaire* in the later stages of this project when I did not have access to it for reference.

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Table 1. Total pages, contents, and dates of receipt of volumes of the *Dictionnaire*.

Vol.	Contents	Pages	Date	Reference*
I	AAL—APHLOMIDÉES	232**+649	September 1841	I
II	APHODIE—BYZENUS	795	30 July 1842	SC
III	CAAMA—CLAVIGERE	744	7 July 1843	SC
IV	CLAVIJA—DICTYMÉNIE	752	20 May 1844	SP, CR
V	DICTYNES—GALENIA	768	22 March 1845	BF
VI	GALÉODE—HYSTRIX	792***	22 December 1845	CR
VII	IACARETINGA—MARTAGON	808	9 November 1846	CR
VIII	MARTE—OIDIUM	766	6 February 1847	SC
IX	OIE—PHORMIUM	776	17 July 1847	SC
X	PHORODESMA—REPTATION	760	27 December 1847	CR
XI	REPTILES—STELLIO	816	9 September 1848	SC
XII	STELLION—VANCOUVERIE	816	7 July 1849	SC
XIII	VANDE—ZYZEL	384	5 November 1849	CR

*Abbreviations: BF = *Bibliographie de la France*; CR = *Compte Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*; I = Iredale 1937; SC = Stafleu & Cowan 1981; SP = Sherborn & Palmer 1899.

**Discours préliminaire.

***This volume has 16 pages added (numbered as "176bis" to "191bis") in the entry "géographie, zoologique," which apparently had material added after the original feuilles had been printed.

Table 2. Contents, pagination, and dates of issue of livraisons of the *Dictionnaire*.

Vol.	Livr.	Feuilles	Pages	Contents (minimum)	Date	Reference[a]
I	1	1–3*[b]	1–48	AAL-ACCROISSEMENT (part)	29 June 1839	BF
	2	4–5*[b]	49–*80*	ACCROISSEMENT (concl.)-ACIDES (part)	August 1839	I
	3				[no date known]	
	4				16 March 1840	SP
	5				March 1840	I
	6				15 June 1840	SP
	7	20–25*[b]	*305*–400[c]	ALTERNANCE (concl.)-AMPOULAOU (part)	July 1840	I
	8	26–28*[b]	401–*448*	AMPOULAOU (concl.)-ANATOMIE (part)	August 1840	I
	9				2 November 1840	SP
	10	*33–34*[b]	*514–530*	ANIDIENS (concl.)-ANISOMELES (part)	23 November 1840	CR
	11				November 1840	I
	(12	?19–29	?145–232	?Discours	September 1841	I)[d]
	(12	?36–41*[b]	561–649	ANOMOTHECA-APHLOMIDÉES (plus 1 unnumbered page of errata)	September 1841	I)[d]
II	13	1–?	1–?	APHODIE-?	1 February 1841	SP
	14				5 April 1841	SP
	15	*12–13*	*177–200*	ARTHROSTIGMA-ASARCA (part)	6 September 1841	CR
	16	?–16*[b]	?–256[c]	?-ASTEROCHOETE (part)	8 November 1841	SP
	17	17–20*[b]	257–*320*	ASTEROCHOETE (concl.)-ATTAGIS (part)	November 1841	I
	18				24 January 1842	SP
	19				7 February 1842	SP
	20				21 March 1842	SP
	21				4 April 1842	SP
	22				16 May 1842	SP
	23				20 June 1842	SP
	24	46–50*[b]	*721*–795	BRAMIA (concl.)-BYZENUS (plus 1 unnumbered page of errata)	30 June 1842	BF
III	25	1–4*[b]	1–64	CAAMA-CALMARET (part)	22 August 1842	CR
	26	5–8*[b]	65–128	CALMARET (concl.)-CANTHARIDE (part)	1 September 1842	I
	27	9–11*[b]	129–176	CANTHARIDE (concl.)-CARNASSIERS (part)	10 October 1842	CR
	28	12–15*[b]	177–240	CARNASSIERS (concl.)-CAULINITES (part)	7 November 1842	CR
	29	16–19[b]	241–*296*	CAULINITES (concl.)-CERCOPITHEQUE (part)	November 1842	I
	30				2 January 1843	SP
	31				30 January 1843	CR

Vol.	Livr.	Feuilles	Pages	Contents (minimum)	Date	Reference[a]
	32				6 March 1843	SP
	33				10 April 1843	CR
	34				24 April 1843	CR
	35	?–43	?–688	?-CINCLODES (part)	29 May 1843	CR
	36	44–47[b]	689–744	CINCLODES (concl.)-CLAVIGERE	1 July 1843	BF
IV	37	1–?	1–?	CLAVIJA-?	31 July 1843	CR
	38	?–16	?–*128*	?-COMAROPHAGUS (part)	4 September 1843	CR
	39	17–?	*129*–?	COMAROPHAGUS (concl.)-?	2 October 1843	CR[e]
	40–41	?–38	?–*304*	?-COURLIS (part)	November 1843	I
	42	39–?	*305*–?	COURLIS (concl.)-?	26 December 1843	CR
	43–44				19 February 1844	SP, CR
	45				4 March 1844	SP, CR
	46				8 April 1844	CR
	47	?–88	?–704	?-DESCRIPTION (part)	29 April 1844	CR
	48	89–94	705–752	DESCRIPTION (concl.)-DICTYMENIE	20 May 1844	SP, CR[f]
V	49	1–?	1–?	DICTYNES-?	24 June 1844	CR
	50	?–16	?–*128*	?-DREPANOPHYLLE (part)	1 July 1844	CR
	51	17–?	*129*–?	DREPANOPHYLLE (concl.)-?	12 August 1844	CR[e]
	52				26 August 1844	CR
	53	?–*33*	?–*264*	?-ELEPHANT (part)	23 September 1844	CR[e]
	54				14 October 1844	CR
	55				18 November 1844	SP, CR
	56				16 December 1844	SP
	57				6 January 1845	SP, CR
	58				6 January 1845	SP, CR
	59	?–91	?–728	?-FROMENT (part)	17 February 1845	SP
	60	92–96	729–768	FROMENT (concl.)-GALENIA	22 March 1845	BF
VI[g]	61	1–?	1–?	GALÉODE-?	28 April 1845	CR
	62				19 May 1845	SP, CR
	63				[before 30 June 1845][h]	
	64				30 June 1845	CR
	65				23 July 1845	CR
	66–68				3 November 1845	SP
	69–70				3 November 1845	CR
	71				17 November 1845	SP
	72	?–99	?–792	?-HYSTRIX	22 December 1845	CR

Table 2. continued

Vol.	Livr.	Feuilles	Pages	Contents (minimum)	Date	Reference[a]
VII	73–74	1–?	1–?	IACARETINGA-?	29 December 1845	CR
	75				[no date known]	
	76				9 February 1846	CR
	77–78				16 March 1846	CR
	79–80				20 April 1846	CR
	81				4 May 1846	CR
	82				27 July 1846	CR
	83				17 August 1846	CR
	84	?–101	?–808	?-MARTAGON	31 August 1846	CR
VIII	85–86	1–?	1–?	MARTE-?	21 September 1846	CR
	87–88				19 October 1846	CR
	89–90				9 November 1846	CR
	91–92	?–80	?–640	?-NEZ (part)	14 December 1846	CR
	93[i]	81–84	641–672	NEZ (concl.)-NOTARCHE (part)	18 January 1847	CR
	94[i]	85–88	673–704	NOTARCHE (concl.)-NYMPHES (part)	18 January 1847	CR
	95[i]	89–92	705–736	NYMPHES (concl.)-OEIL (part)	6 February 1847	BF
	96[i]	93–96	737–766	OEIL (concl.)-OIDIUM	6 February 1847	BF
IX	97–98	1–?	1–?	OIE-?	February 1847	I
	99–100				29 March 1847	CR
	101–102				5 May 1847	CR
	103–104				24 May 1847	CR
	105–106	?–81	?–648	?-PERROQUET (part)	[no dates known]	
	107	82–89	649–712	PERROQUET (concl.)-PHALENITES (part)	17 July 1847	BF
	108	90–97	713–776	PHALENITES (concl.)-PHORMIUM	17 July 1847	BF
X	109–110	1–?	1–?	PHORODESMA-?	9 August 1847	CR
	111–112				6 September 1847	CR
	113–114				11 October 1847	CR
	115–116				25 October 1847	CR
	117–118				[no dates known]	
	119–120	?–96	?–760	?-REPTATION	27 December 1847	CR
XI	121–122	1–18	1–144	REPTILES-ROCCELLE (part)	10 January 1848	CR[j]
	123	19–26	145–200	ROCCELLE (concl.)-RONGEURS (part)	28 February 1848	CR[j]
	124	27–34	201–272	RONGEURS (concl.)-RUPPELLIE (part)	28 February 1848	CR[j]
	125–126	35–52	273–416	RUPPELLIE (concl.)-SCHIZASTER (part)	[no dates known]	
	127–132	53–102[b]	417–816	SCHIZASTER (concl.)-STELLIO	9 September 1848	BF
XII	133	1–8	1–64	STELLION-STROMBIDES	9 September 1848	BF
	134	9–16	65–128	STROMBIFORMIS-SYNCHRONISME (part)	9 September 1848	BF

Vol.	Livr.	Feuilles	Pages	Contents (minimum)	Date	Reference[a]
	135	17–24	129–192	SYNCHRONISME (part)-SYSTEME CRISTALLINS (part)	31 December 1848[k]	
	136	25–28	193–224	SYSTEME CRISTALLINS (part)	2 January 1849	CR
	137	29–*39*	225–*311*	SYSTEME CRISTALLINS	5 February 1849	CR
	?	*46–58*	*361–464*	TARET (concl.)-TERATOLOGIE (part)	2 January 1849	CR
	?	*60–66*	*479–522*	TERRAINS—GEOL.	26 March 1849	CR
	?–143	?–95	?–760	?-UNIO (part)	[no dates known]	
	144	96–102	761–816	UNIO (concl.)-VANCOUVERIE	7 July 1849	BF
XIII	145	1–7	1–56	VANDE-VEGETAUX, FOSSILES (part)	7 July 1849	BF
	146	9–16	57–128	VEGETAUX, FOSSILES (continued)	7 July 1849	BF
	147	17–24	129–192	VEGETAUX, FOSSILES (concl.)-VERONIQUE (part)	7 July 1849	BF
	148–149	25–?	193–?	VERONIQUE (concl.)-?	10 September 1849	CR
	150	?–48	?–384	?-ZYZEL	5 November 1849	CR

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[a] Abbreviations: BF = *Bibliographie de la France*; CR = *Compte Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris*; I = Iredale 1937; SP = Sherborn & Palmer 1899.

[b] Includes feuille numbers marked with an asterisk (*) (e.g., 28, 28*, 29, 29*, etc.).

[c] Following page begins with different typeface and size, and boldface is used for class abbreviations; this is assumed to indicate separation of livraisons.

[d] There is no indication whether this livraison contains the Discours or the Dictionnaire text; contents of previous feuilles in this volume lends strong support to it being the last feuille of the Discours; *BF* received this livraison on 18 December 1841 stating that it contained 11 feuilles; Sherborn and Palmer (1899) record the Société Géologique de France as receiving it on 8 November 1841. I have listed the probable contents of the livraisons for both possible cases (i.e., Discours and text) based on the size of 11 fueilles.

[e] Information on the contents of these livraisons are given in the *Revue Zoologique*.

[f] *BF* received this livraison on 1 June 1844 giving the feuille information.

[g] This volume has 16 pages added (numbered as "176bis" to "191bis") in the entry "géographie zoologique," which apparently had material added after the original feuilles had been printed.

[h] Sherborn and Palmer (1899) record the Société Géologique de France as having received this livraison on 3 November 1845. Because all the livraisons were issued in order and livraison 64 was received by the Académie des Sciences, Paris on 30 June 1845, it can be safely concluded that livraison 63 was issued before 30 June 1845.

[i] *BF* states that feuilles 81–96 were received on 6 February 1847 for livraisons 95–96 at 4 feuilles each; since 8 pages made up each feuille, it is assumed that "93" rather than "95" was intended and that each livraison had 32 pages.

[j] Information on the feuille numbers received are provided in the *BF*.

[k] *CR* records the receipt of feuilles 25–28 (livraison 136) of volume XII on 2 January 1849. Livraison 135 was issued sometime between 9 September 1848 and 2 January 1849. Without any evidence of an issue or receipt date in *BF* or *CR*, the last day of 1848 is assumed to be the date of issue until a better date can be obtained.

Type Designations of Genus-group Names of Diptera Given in d'Orbigny's *Dictionnaire Universel d'Histoire Naturelle*

Neal L. Evenhuis[1] and F. Christian Thompson[2]

ABSTRACT

Previously overlooked valid type designations for 37 genus-group names of flies (Diptera) found in the *Dictionnaire Universel d'Historie Naturelle* are listed herein. One previously overlooked new species-group name, *Sphecomyia boscii* Demarest (Syrphidae), was also found. The *Dictionnaire* is described and its significance evaluated. A taxonomic index to all the Diptera names in the *Dictionnaire* is provided.

INTRODUCTION

Upon researching nomenclatural information for a database of generic typifications of all Diptera genus-group names (to be published elsewhere), we discovered a number of type designations earlier than those recorded in other regional Diptera catalogs, which appear in various volumes of Charles V. D. d'Orbigny's *Dictionnaire Universel d'Histoire Naturelle* (for further details and dates of the separate volumes and livraisons, see Evenhuis 1990). Some coleopterists (e.g., Barber & Bridwell 1940; Arnett 1950; Blackwelder 1952) have previously noted numerous type designations given in the *Dictionnaire* for beetle genera; however, it appears that only 2 dipterists had previously noted type designations (1 genus each) from this *Dictionnaire*.[3]

General Remarks on the *Dictionnaire*

This 13-volume work (with an additional 3-volume atlas), originally issued in 150 separate livraisons from 1839 to 1849, is one of a group of comprehensive works produced in the first half of the 19th century (see Table 2) when Paris was the center of study for the natural sciences. While contemporary dictionaries and encyclopediae are considered as only secondary sources of information, listing summaries of work produced elsewhere, these early French works contain much original research. Unfortunately, the alphabetical arrangement of information in these works makes retrieval by taxon cumbersome. To retrieve all the information on taxa in a particular group, one must know all the names to look under or must read the work from cover to cover. Because of this difficulty, modern workers on Diptera have ignored some of these works.

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[3] Since submittal of this manuscript, the *Catalog of the Diptera of the Australasian and Oceanian Regions* has been published, which incorporates many of the designations reported here.

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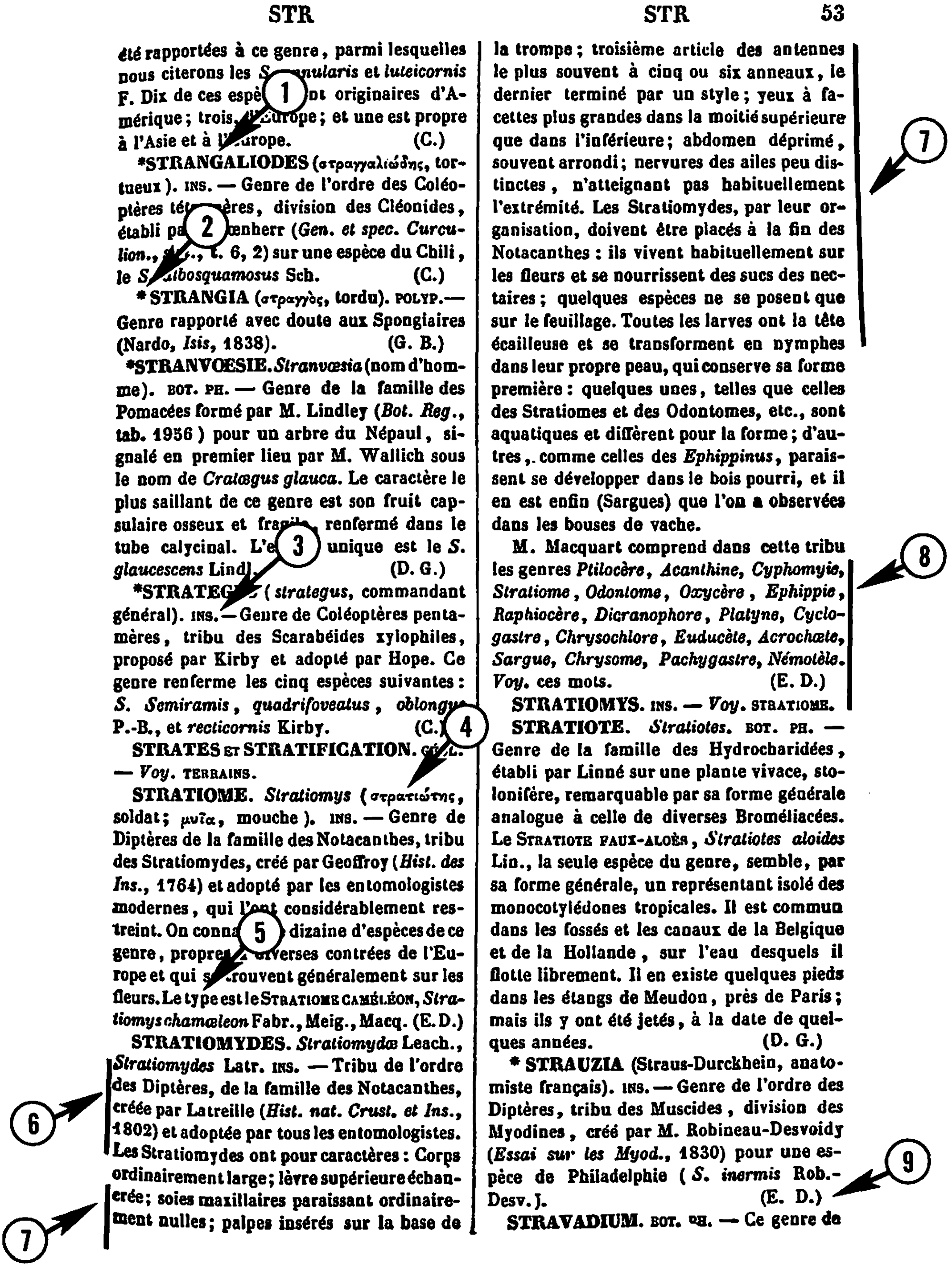

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été rapportées à ce genre, parmi lesquelles nous citerons les *S. annularis* et *luteicornis* F. Dix de ces espèces sont originaires d'Amérique; trois d'Europe; et une est propre à l'Asie et à l'Europe. (C.)

***STRANGALIODES** (στραγγαλιώδης, tortueux). ins. — Genre de l'ordre des Coléoptères tétramères, division des Cléonides, établi par Schœnherr (*Gen. et spec. Curculion.*, syn., t. 6, 2) sur une espèce du Chili, le *S. albosquamosus* Sch. (C.)

*** STRANGIA** (στραγγὸς, tordu). polyp.— Genre rapporté avec doute aux Spongiaires (Nardo, *Isis*, 1838). (G. B.)

***STRANVŒSIE.** *Stranvœsia* (nom d'homme). bot. ph. — Genre de la famille des Pomacées formé par M. Lindley (*Bot. Reg.*, tab. 1956) pour un arbre du Népaul, signalé en premier lieu par M. Wallich sous le nom de *Cratœgus glauca*. Le caractère le plus saillant de ce genre est son fruit capsulaire osseux et fragile, renfermé dans le tube calycinal. L'espèce unique est le *S. glaucescens* Lindl. (D. G.)

***STRATEGUS** (*strategus*, commandant général). ins. — Genre de Coléoptères pentamères, tribu des Scarabéides xylophiles, proposé par Kirby et adopté par Hope. Ce genre renferme les cinq espèces suivantes: *S. Semiramis*, *quadrifoveatus*, *oblongus* P.-B., et *recticornis* Kirby. (C.)

STRATES et **STRATIFICATION.** géol. — *Voy.* terrains.

STRATIOME. *Stratiomys* (στρατιώτης, soldat; μυῖα, mouche). ins. — Genre de Diptères de la famille des Notacanthes, tribu des Stratiomydes, créé par Geoffroy (*Hist. des Ins.*, 1764) et adopté par les entomologistes modernes, qui l'ont considérablement restreint. On connaît une dizaine d'espèces de ce genre, propres aux diverses contrées de l'Europe et qui se trouvent généralement sur les fleurs. Le type est le Stratiome caméléon, *Stratiomys chamæleon* Fabr., Meig., Macq. (E. D.)

STRATIOMYDES. *Stratiomydæ* Leach., *Stratiomydes* Latr. ins. — Tribu de l'ordre des Diptères, de la famille des Notacanthes, créée par Latreille (*Hist. nat. Crust. et Ins.*, 1802) et adoptée par tous les entomologistes. Les Stratiomydes ont pour caractères: Corps ordinairement large; lèvre supérieure échancrée; soies maxillaires paraissant ordinairement nulles; palpes insérés sur la base de la trompe; troisième article des antennes le plus souvent à cinq ou six anneaux, le dernier terminé par un style; yeux à facettes plus grandes dans la moitié supérieure que dans l'inférieure; abdomen déprimé, souvent arrondi; nervures des ailes peu distinctes, n'atteignant pas habituellement l'extrémité. Les Stratiomydes, par leur organisation, doivent être placés à la fin des Notacanthes: ils vivent habituellement sur les fleurs et se nourrissent des sucs des nectaires; quelques espèces ne se posent que sur le feuillage. Toutes les larves ont la tête écailleuse et se transforment en nymphes dans leur propre peau, qui conserve sa forme première: quelques unes, telles que celles des Stratiomes et des Odontomes, etc., sont aquatiques et diffèrent pour la forme; d'autres, comme celles des *Ephippinus*, paraissent se développer dans le bois pourri, et il en est enfin (Sargues) que l'on a observées dans les bouses de vache.

M. Macquart comprend dans cette tribu les genres *Ptilocère*, *Acanthine*, *Cyphomyie*, *Stratiome*, *Odontome*, *Oxycère*, *Ephippie*, *Raphiocère*, *Dicranophore*, *Platyne*, *Cyclogastre*, *Chrysochlore*, *Euducèle*, *Acrochæte*, *Sargue*, *Chrysome*, *Pachygastre*, *Némotèle*. *Voy.* ces mots. (E. D.)

STRATIOMYS. ins. — *Voy.* stratiome.

STRATIOTE. *Stratiotes*. bot. ph. — Genre de la famille des Hydrocharidées, établi par Linné sur une plante vivace, stolonifère, remarquable par sa forme générale analogue à celle de diverses Broméliacées. Le Stratiote faux-aloès, *Stratiotes aloides* Lin., la seule espèce du genre, semble, par sa forme générale, un représentant isolé des monocotylédones tropicales. Il est commun dans les fossés et les canaux de la Belgique et de la Hollande, sur l'eau desquels il flotte librement. Il en existe quelques pieds dans les étangs de Meudon, près de Paris; mais ils y ont été jetés, à la date de quelques années. (D. G.)

*** STRAUZIA** (Straus-Durckheim, anatomiste français). ins. — Genre de l'ordre des Diptères, tribu des Muscides, division des Myodines, créé par M. Robineau-Desvoidy (*Essai sur les Myod.*, 1830) pour une espèce de Philadelphie (*S. inermis* Rob.-Desv.). (E. D.)

STRAVADIUM. bot. ph. — Ce genre de

Fig. 1. Facsimile page of d'Orbigny's *Dictionnaire* (vol. 12) showing format of entries and examples of author's initials. 1 = scientific name; 2 = asterisk denoting entry not listed in previous "Dictionnaires"; 3 = abbreviation of major taxon to which entry belongs; 4 = derivation of name (etymology); 5 = type designation; 6 = taxonomic category to which the entry belongs and who proposed the name; 7 = diagnostic characters for the group the name represents; 8 = list of commonly included taxa; 9 = author's initials. In this case "E.D." = Eugène Desmarest.

Each volume of d'Orbigny's *Dictionnaire* is separately paginated and contains textual explanations for various natural history terms and taxonomic names. Each term is a separate entry and has its own author (indicated at the end of each entry by the author's initials in parentheses; see list below for the authors responsible for the Diptera genera). The entries in the *Dictionnaire* are set in boldface type. Terms not included in previous "dictionnaires" are prefaced with an asterisk. Terms that are not taxonomic names, and a few common taxa, are given longer treatises than the usual entry. For example, under the term "Description," there is a 5-page discourse on what should be included in taxonomic descriptions [although written in 1844, the advice is more than applicable today as many currently published descriptions do not meet these recommended standards!]. Many generic names of Diptera are included in the *Dictionnaire* (though not all of those that were known at that time), especially those proposed by French taxonomists. Some taxa are listed alphabetically under the scientific name, others under the French vernacular. For valid taxonomic names, an entry begins with the derivation of the name (etymology), followed by an abbreviation indicating the major taxon to which the name belongs (e.g., "INS" for insects), then the category (order, family, tribe, genus or species), who proposed the name, the diagnostic characters for the group the name represents, and ends with either a type designation or a list of common included taxa. Of the type designations noted, some are the earliest validly published for those particular genera. For invalid taxonomic names, there is a cross reference to the valid name. Most taxonomic entries are indexed under the scientific name, but some commonly known taxa are found under the colloquial name. An example of a page of the *Dictionnaire* is given in Fig. 1.

For the most part, the type designations given in the *Dictionnaire* are based on a common species of each genus, and usually a species that could be found in the environs of Paris or elsewhere in France. In many cases, basing the genus-group name on such a commonly found type species results in a stabilized concept of that particular genus, but in a few cases the type-species designation poses a taxonomic problem with regard to current or traditional generic concepts. The *Dictionnaire* records 189 type designations for Diptera genera. Listed below are the 37 earliest recorded valid type designations for Diptera genera found in the *Dictionnaire*. Type designations proposed in the *Dictionnaire* for 2 genus-group names, *Scatomyza* and *Stylia*, had been recorded previously in the literature, but are included in the list below for the sake of completeness.

Authorship of the Diptera Entries

The author's initials listed below represent those persons responsible in the *Dictionnaire* for the various Diptera genera listed in volumes I-XIII. As with the other authors in the *Dictionnaire*, the initals used and the form of noting the author's name or initials are not always consistent (see Stafleu & Cowan [1981] for a list of the botany authors' initials—variations are not listed), for example, often an author's surname will be spelled out after a long treatise (such as "Desmarest" for "Nycteribia"), but abbreviated as initials for the typical shorter entries.

C. = Chevrolat (only with Duponchel for *Apiocera*; otherwise, primarily Coleoptera entries)
D. = P. Duponchel
E. D. = E. Desmarest
J. = A. Jussieu (only for *Limnobia*, *Limnophila*, *Psilomyia*; otherwise, primarily botany entries) [Also uses "Ad. J." for botany entries.]
L., H. L. = P. H. Lucas
M. = C. Montagné (only *Sciomyza*; otherwise, primarily botany entries)
P.G. = P. Gervais (only *Braula*; otherwise, primarily botany entries)

P. Duponchel was responsible for the Diptera, Lepidoptera, and Coleoptera names (the last coauthored with Chevrolat) in volumes I-VI (1839–1846). Duponchel's death in 1846 must have disrupted authorship plans because no author's initials are listed for many Diptera and Lepidoptera entries in the next 2 volumes (Chevrolat's initials are continued for Coleoptera entries). In volume VII, of all the Diptera entries, only 2 (*Limnobia* and *Limnophila*) have the author's initials (in this case "J." for A. Jussieu, who was primarily responsible for the phanerogam botany entries). The remainder of the entries in volume VII are without initials and responsibility must be attributed to Charles d'Orbigny as editor of the *Dictionnaire*, though it is possible this was not his intention (he lists his initials for other items within the *Dictionnaire* spanning geology, botany, mammalogy, ornithology, mineralogy, and entomology [the last restricted to family name entries]). In volume VIII, P. H. Lucas (on p. 505) started to take over Duponchel's responsiblities (i.e., Lepidoptera and Diptera genera; Chevrolat continued to deal with the Coleoptera entries), but there are 4 entries authored by E. Desmarest (*Myopa*, *Nycteribia*, *Oedemagena*, and *Oestrus*), and a few have no author's initials. Volume IX is almost all Lucas for Diptera (except no initials for *Olina*). Volume X Diptera entries waffle between Lucas and no initials and Jussieu's initial is given for *Psilomyia*. In volume XI Lucas ended his work with Diptera genera on page 454 with *Scotioptera* and E. Desmarest took over on page 530 with *Selachops* and continues through volume XIII as the sole responsible author for Diptera entries. In volume XI there is one odd authorship (C. Montagné for *Sciomyza*). Montagné was primarily responsible for cryptogam botany entries. Some of these anomalies in the author's initals may, of course, be printer's errors.

Methodology of Research on the Diptera Names in the *Dictionnaire*

Names of taxa are important, because without them communication about concepts is impossible. To be useful a name must be precise, always being used to denote the same concept. We have been working to establish the correct and complete set of such names for Diptera. These names are indexed in the existing regional catalogs, or what we now prefer to call databases (Thompson & Knutson 1987). In building our databases (Evenhuis 1989; Thompson, in prep.), we encountered numerous problems. For example, there is the problem of omission of information most often resulting from overlooked data. What authors write has usually been found to be correct. However, sometimes in checking information provided by author A, we discovered data overlooked by author B. Just how much critical data, especially that found in the early taxonomic and nomenclatural literature, has been overlooked by workers on Diptera systematics is difficult to estimate, but we believe it to be significant, if not in quantity, then in quality.

The only way to determine what and how much data has been overlooked is to undertake a comprehensive and systematic search of the literature rather than the traditional narrow, retrospective one. Many authors restrict their searches of earlier literature to verification of what previous authors have cited. Thus, some names remain forgotten because subsequent authors dealt only with those names their predecessors dealt with (see Thompson & Torp 1986). Only a few workers have used a different approach. Sherborn, in compiling data for his *Index Animalium* (1902, 1922–1932, 1932–1933), searched all of the earlier literature systematically for all zoological names for the years 1758–1850; the search took 31 years to complete. We are implementing such an approach for Diptera names. Unfortunately, modern realities of the continuous and speedy publication of taxonomic results and investigations do not allow us the luxury Sherborn had of postponing publication results for decades while accumulating data.

We have consulted the various regional Diptera catalogs and Sherborn's bibliographies (1902:xi–lvi; 1922:xv–cxxxi; 1923:cxxxiii–cxxxvi; 1925:cxxxvii–cxxxix) to identify nomenclatural and taxonomic works that needed to be checked and from which to generate lists of type designations and other data to be verified (see Tables 1 and 2). We then scanned these works from the 1st page to the last, entering all nomenclatural information dealing with Diptera into a database.

For this paper each of us systematically scanned the pages of the *Dictionnaire Universel d'Histoire Naturelle* for all Diptera names from volume I to volume XIII (a total of 9,626 pages). After finishing the initial scan, both authors' lists were checked against each other and omissions (less than 1% error factor) added to each. The resulting list consisted of 857 names of Diptera taxa (see Appendix). These names were then entered into a database enabling a check of the type designations of genera in the *Dictionnaire* against other earlier and contemporary type designations already entered into the database (Table 1). This check resulted in 37 valid designations in the *Dictionnaire* that were earlier than previously recorded. We then referred to existing regional Diptera catalogs for ancillary information and the most recent treatment of each genus listed below, and finally to the original description of each genus-group name to determine originally included species and nomenclatural availability. Only one genus (*Boisduvalia*) was not found in any previous regional catalog.

The Principle of Type Species for Genus-group Names as Interpreted Herein

The concept of tying names to objects (nomenclatural types) arose naturally from Aristotelean philosophy, requiring that all members of a group conform to a type (*eidos*) and that such groups were static concepts. Cuvier and other French zoologists after the French revolution exemplified this typological approach to systematics. Hence, it was only natural for them to refer to the "type" of a group. Some French workers went so far as to use the term "Type" as a taxonomic category (between Subkingdom and Class; e.g., Blainville [Appel 1980]). With the gradual shift to evolutionary thought and its recognition of variation and change over time, the typological approach to classification largely disappeared; however, the problem of deciding what names to apply to groups remained. For this reason, nomenclatural types are essential.

The 1st real code of zoological nomenclature (Strickland 1842) based a number of its provisions (3–5, 7) on the concept of a genus-group name having a type species. The problem even with such a code is that one needs to be able to distinguish when a worker in those days was designating a nomenclatural type versus merely indicating the *eidos* of a group. The functional difference between these approaches is that nomenclatural types are invariant, once selected they do not change; whereas morphological types may change if subsequent workers believe another "type" better reflects the *eidos*. Likewise, morphological types need not be restricted to only those taxa known to the original author of the concept. Hence, typologists frequently selected taxa as "types" that were common or local. These types may not have been known to the original author when describing the genus-group name, thus are ineligible as nomenclatural types. Furthermore, typologists frequently used expressions that did not include the word "type," but instead such wordings as "principal species," "premier species," or "tête la genre."

No accurate historical analysis of typification has been written, but one can be pieced together (Méquignon 1932; Blackwelder 1952, 1967; Mayr, Linsley & Usinger 1953; Farber 1976). All mention the difficulty among workers in recognizing nomenclatural types and distinguishing them from morphological types. To aid in separating between the typological approach to classification (morphological types) and the fixation of names (nomenclatural types), the I.C.Z.N. Code (International Commission on Zoological Nomenclature 1985) demands that the action of "'designation' in relation to fixation of a type species must be rigidly construed" [Art. 67(c)] and specifically excludes certain formulations. For our work on subsequent designations, we have interpreted this section of the Code to mean that an available type designation needs 2 components: the use of the word "type" in conjunction with an eligible nominal species. Specifically, we do not consider formulations such as "genus X established for species A" or "X was erected for species A" to be valid designations. These statements are

Table 1. Sources for subsequent type designations of Diptera genus-group names.

A. General Sources:

Year(s)	Author	Short title	Available designations
1810	Latrielle	Consid. Gener. Ins.	104
1824–1839	Curtis	British Entomology	106
1839–1849	d'Orbigny	Dict. Univ. Hist. Nat.	177
1840	Westwood	Intr. Mod. Class. Ins.	353
1840	Blanchard	Hist. Nat. Anim. Artic.	80
1845	Blanchard	Hist. Ins.	23
1845–1848*	Blanchard	In: Cuvier, Le Règne Animal (Disciples' Ed.)	218

B. Specialized Sources (Diptera only):

Year(s)	Author	Short title	Available designations
1826–1834	Macquart	Ins. Dipt. nord Fr.	9
1834–1835	Macquart	Hist. Nat. Ins. Dipt.	18
1838	Zetterstedt	Ins. Lappon., Dipt.	6
1838–1855	Macquart	Dipt. Exot. Nouv. ou peu Conn.	38
1842–1860	Zetterstadt	Dipt. Scand	85
1844	Rondani	Ord. Sist. Gen. Ital. Dipt.	26
1859	Chenu	Encycl. Hist. Nat. (Anneles)	28

* Plates dated from Cowan (1976).

Table 2. French *Dictionnaires* and *Encyclopédies* of the early 19th century.

Years	Author(s)	Title
1789–1832	Olivier, Latreille, Lepeletier, Serville, Guérin-Méneville	Encyclopédie Methodique. 196 vols. Vols. 4–10, Histoire Naturelle, Insectes
1803–1804	Soc. Nat. et Agric.	Nouveau Dictionnaire d'Histoire Naturelles... 1st Ed. 24 vols.
1804–1806, 1816	Cuvier	Dictionnaire des Sciences Naturelles. 1st Ed. 7 vols.
1816–1819	Soc. Nat. et Agric.	Nouveau Dictionnaire d'Histoire Naturelles... 2nd Ed. 36 vols.
1816–1830	Duméril	Dictionnaire des Sciences Naturelles. 2nd Ed. 61 vols.
1822–1831	Bory	Dictionnaire Classique d'Histoire Naturelle. 17 vols.
1833–1839	Guérin-Méneville	Dictionnaire Pittoresque d'Histoire Naturelle. 9 vols.
1837–1845	Drapiez	Dictionnaire Classique des Sciences Naturelles. 11 vols.
1839–1849	d'Orbigny	Dictionnaire Universel d'Histoire Naturelle. 13 vols.
1842–1844	d'Orbigny	Dictionnaire Abrégée d'Histoire Naturelle. 2 vols.
1850–1861	Chenu	Encyclopédie d'Histoire Naturelle. 7 vols.

ambiguous as it is unclear whether they are simple statements of the existence of a single included species or valid typifications.

The earliest currently accepted source of subsequent designations for type species of genus-group names in insects is Latreille (1810). Other early sources for subsequent typifications of Diptera genus group names analyzed by us are listed in Table 1.

Type Designations for Diptera Genera Given in the *Dictionnaire*

The following are the 37 genus-group names that have valid type designations given for them in the *Dictionnaire* and are the earliest yet known. Specialists may wish to apply to the International Commission for Zoological Nomenclature to set aside designations listed here that are found to change current or traditional generic concepts to the point that they unnecessarily disrupt taxonomic stability in that particular group. The citation of author of each designation below follows this format: author of designation, editor of the *Dictionnaire*, volume number of *Dictionnaire*, page number of designation, and date of designation (dating following evidence given in Evenhuis [1990]), e.g., Duponchel *in* d'Orbigny (1:29 [29 June 1839]). Appendix 1 lists all the Diptera names recorded in the *Dictionnaire* and gives the volume, page number, and any type species listing or list of included species.

ACANTHINA Wiedemann

Acanthina Wiedemann, 1830:50. Type species: *Acanthina elongata* Wiedemann, 1830, by designation of Duponchel *in* d'Orbigny (1:29 [29 June 1839]).

Family. Stratiomyidae.

Remarks. James (1973) listed the same type species as designated by Brauer (1882:86). *Acanthina* is preoccupied by Fischer, 1807. The current valid name for this genus is *Acanthinomyia* Hunter.

ACEMYA Robineau-Desvoidy

Acemya Robineau-Desvoidy, 1830:202. Type species: *Acemya oblonga* Robineau-Desvoidy, 1830 (as *Tachina*) [= *Tachina acuticornis* Meigen, 1824], by designation of Desmarest *in* d'Orbigny (12:318 [2 January 1849]).

Family. Tachinidae.

Remarks. Herting (1984) listed the type species of *Acemya* as *Acemyia subrotunda* Robineau-Desvoidy, 1830 [= *Tachina acuticornis* Meigen, 1824], by designation of Rondani (1856:75). Despite the generic orthography in Herting (1984), the correct spelling for this genus is *Acemya*. Macquart's (1834b:267) spelling of *Acemyia* is either an incorrect subsequent spelling or an unjustified emendation.

ACINIA Robineau-Desvoidy

Acinia Robineau-Desvoidy, 1830:775. Type species: *Acinia javeae* Robineau-Desvoidy, 1830, by designation of Duponchel *in* d'Orbigny (1:85 [between August 1839 and 16 March 1840]).

Family. Tephritidae.

Remarks. Foote (1984:70) gave Rondani (1871) as the earliest type designation of *Acinia*. Duponchel designates the type as "*Acinia corniculata* Fabricius ou l'*A. javeae* Rob.-Desv.," the "ou" in our opinion being merely a statement of synonymy following Macquart (1835:469).

ATOMOSIA Macquart

Atomosia Macquart, 1838:73 [1839:189]. Type species: *Atomosia annulipes* Macquart, 1838, by designation of Duponchel *in* d'Orbigny (2:309–10 [November 1841]).

Family. Asilidae.

Remarks. Oldroyd (1975) listed the type species of *Atomosia* as *Atomosia incisuralis* Macquart, 1838, designated by Coquillett (1910:512). *Atomosia annulipes* was placed in the genus *Aphestia* Schiner by Martin and Papavero (1970). Acceptance of Duponchel's designation would change the current generic concepts of *Atomosia* and *Aphestia*. Application to I.C.Z.N. to suppress the designation by Duponchel may be warranted in this case.

BACCHIS Robineau-Desvoidy

Bacchis Robineau-Desvoidy, 1830:803. Type species: *Bacchis cellarum* Robineau-Desvoidy, 1830, by designation of Duponchel *in* d'Orbigny (2:409 [before 30 June 1842]).

Family. Sphaeroceridae.

Remarks. Papp (1984) treated *Bacchis* as a *nomen dubium* and stated, incorrectly, that "no type species has been designated." *Bacchis cellarum* was also listed by Papp as a *nomen dubium*, probably because the type of *cellarum* is lost or destroyed. Until the identity of the type species, *cellarum*, can be ascertained, *Bacchis* must be considered an unrecognizable genus in Sphaeroceridae.

BENGALIA Robineau-Desvoidy

Bengalia Robineau-Desvoidy, 1830:425. Type species: *Bengalia testacea* Robineau-Desvoidy, 1830 [= *Musca torosa* Wiedemann, 1819], by designation of Duponchel *in* d'Orbigny (2:542 [before 30 June 1842]).

Family. Calliphoridae.

Remarks. Pont (1980b) listed the type species of *Bengalia* as *Bengalia labiata* Robineau-Desvoidy, 1830, by designation of Townsend (1916:6). *Bengalia torosa* (Wiedemann) is currently considered a member of *Bengalia*, hence there is no change in generic concept.

BLONDELIA Robineau-Desvoidy

Blondelia Robineau-Desvoidy, 1830:122. Type species: *Blondelia nitida* Robineau-Desvoidy, 1830 [= *Tachina nigripes* Fallén, 1820], by designation of Duponchel *in* d'Orbigny (2:609 [before 30 June 1842]).

Family. Tachinidae.

Remarks. The previous earliest type designation for *Blondelia* was by Coquillett (1910:515), in which he designated *Tachina nigripes* Fallén. Robineau-Desvoidy's (1830) original description of *Blondelia* includes 4 species, none of which is *Tachina nigripes*. Thus, Coquillett's designation is invalid. Sabrosky and Arnaud (1965:1039) noted the invalidity of Coquillett's (1910) designation, but desired to retain it for reasons of stability and universality. The earliest known valid designation for *Blondelia* at that time was that of Townsend (1916:6), in which he designated *Blondelia pallidipalpis* Robineau-Desvoidy. Sabrosky and Arnaud stated that *B. pallidipalpis* is a *nomen dubium*. To retain Coquillett's (1910) designation, suspension of I.C.Z.N. rules would be required. Herting (1984) listed *Blondelia nitida* as a junior synonym of *B. nigripes* (Fallén), thus acceptance of Duponchel's designation upholds the traditional generic concept of *Blondelia* and suspension of I.C.Z.N. rules is no longer required to retain stability of nomenclature.

BOISDUVALIA Robineau-Desvoidy

Boisduvalia Robineau-Desvoidy, 1830:730. Type species: *Boisduvalia rutilans* Robineau-Desvoidy, 1830, by designation of Duponchel *in* d'Orbigny (2:638 [before 30 June 1842]).

Family. Unknown, probably Platystomatidae.

Remarks. *Boisduvalia* has not been treated in any modern Diptera catalog. Robineau-Desvoidy (1830) included *Boisduvalia* in his family Phytomydae, tribe Myodinae, next to *Rivellia*, and included 5 species (1 Oriental, 2 Afrotropical, 2 patria ignota). Loew (1873:18) considered

Boisduvalia a junior synonym of *Rivellia*. Wulp (1896:181) considered the genus to be distinct. Hendel (1914:169) designated *rutilans* as the type species of *Boisduvalia* and suggested that the genus was a tephritid related to *Speniscomyia* Bezzi and *Pseudospheniscus* Hendel. As with the genus, none of Robineau-Desvoidy's originally included species has been treated in any of the modern Diptera catalogs. Macquart (1835:437), however, placed *rutilans* in the genus *Ortalis*.

CARICEA Robineau-Desvoidy

Caricea Robineau-Desvoidy, 1830:530. Type species: *Caricea communis* Robineau-Desvoidy, 1830 [= *Musca tigrina* Fabricius, 1775], by designation of Duponchel *in* d'Orbigny (3:172 [10 October 1842]).

Family. Muscidae.

Remarks. Huckett (1965) and Pont (1972, 1977, 1980a) listed the type species of *Caricea* as *Caricea communis* Robineau-Desvoidy, designated by Hennig (1961:519). Pont (1986) listed an earlier type designation by Stein (1908:11) of *Caricea erythrocera* Robineau-Desvoidy, 1830, which placed *Caricea* as a senior synonym of *Lispocephala* Pokorny. The discovery in this study of Duponchel's designation of *C. communis* returns *Caricea* to junior synonymy under *Coenosia* Meigen, resurrecting *Lispocephala* to a valid genus once again.

CHELIGASTER Macquart

Cheligaster Macquart, 1835:479. Type species: *Musca putris* Linnaeus, 1758 (as *Cheligaster*, by designation of Duponchel *in* d'Orbigny (3:453 [before 29 May 1843]).

Family. Sepsidae.

Remarks. Zuska and Pont (1984) listed the same type species by designation of Coquillett (1910:522). *Cheligaster* is currently considered a junior synonym of *Themira* Robineau-Desvoidy.

CLELIA Robineau-Desvoidy

Clelia Robineau-Desvoidy, 1830:255. Type species: *Clelia agilis* Robineau-Desvoidy [= *Tachina tetraptera* Meigen, 1824], 1830, by designation of Duponchel *in* d'Orbigny (4:4 [31 July 1843]).

Family. Tachinidae.

Remarks. Herting (1984:174) listed *Clelia* with the same type species by designation of Robineau-Desvoidy (1863 (2):61). *Clelia* is preoccupied by Fitzinger, 1826, and is currently considered a junior subjective synonym of *Leucostoma* Meigen, 1803.

CYPHOMYIA Wiedemann

Cyphomyia Wiedemann, 1819:54. Type species: *Stratiomys cyanea* Fabricius, 1794, by designation of Duponchel *in* d'Orbigny (4:548 [before 29 April 1844]).

Family. Stratiomyidae.

Remarks. Rozkosny and Nartshuk (1988) listed *Cyphomyia* with the type species *Cyphomyia auriflamma* Wiedemann, 1819, by designation of Blanchard *in* Auduoin et al. (1847:plate 172bis). James (1973) listed *auriflamma* as the type species by designation of Brauer (1882). *Stratiomys cyanea* (Fabricius) is currently considered a member of *Cyphomyia*, hence acceptance of Duponchel's designation would not change the present generic concept.

DIABASIS Macquart

Diabasis Macquart, 1834a:207. Type species: *Tabanus bicinctus* Fabricius, 1805, by designation of Duponchel *in* d'Orbigny (4:717 [20 May 1844]).

Family. Tabanidae.

Remarks. Both Philip (1965) and Fairchild (1971) listed the same type species by designation of Coquillett (1910:532). *Diabasis* is preoccupied by Hoffmansegg, 1817, and Desmarest, 1823. The current valid name for this genus is *Diachlorus* Osten Sacken.

DICTENIDIA Brullé

Dictenidia Brullé, 1833:399. Type species: *Tipula bimaculata* Linneaus, 1758, by designation of Duponchel *in* d'Orbigny (4:752 [20 May 1844]).

Family. Tipulidae.

Remarks. Alexander and Alexander (1973) gave the same type species as designated by monotypy. A check of the original description of *Dictenidia* shows the originally included species to be "*Tipula Bimaculata*, Lin.; Fab.; et *Paludosa*, Fab.," hence *bimaculata* is not the type species by monotypy.

DUFOURIA Robineau-Desvoidy

Dufouria Robineau-Desvoidy, 1830:257. Type species: *Dufouria aperta* Robineau-Desvoidy, 1830 [= *Tachina chalybeata* Meigen], by designation of Duponchel *in* d'Orbigny (5:144 [either 12 August 1844 or 26 August 1844]).

Family. Tachinidae.

Remarks. Herting (1984) listed *Dufouria* with the same type species by designation of Robineau-Desvoidy (1863 (2):68).

EXOPROSOPA Macquart

Exoprosopa Macquart, 1840:35 [1841:313]. Type species: *Exoprosopa audouinii* Macquart, 1840, by designation of Duponchel *in* d'Orbigny (5:545 [before 17 February 1845]).

Family. Bombyliidae.

Remarks. Previous regional catalogs (Painter & Painter 1965; Bowden 1975, 1980; Painter, Painter & Hall 1978; Zaitzev 1989) listed the type species of *Exoprosopa* as *Anthrax pandora* Fabricius, 1805, by designation of Coquillett (1910:544). *Exoprosopa audouinii* is currently considered a member of the pantropical genus *Ligyra* Newman. Acceptance of Duponchel's (1845) designation would considerably change the long-established generic concept of the worldwide genus *Exoprosopa*. *Exoprosopa* would become a senior synonym of *Ligyra*; and those species previously attributed to *Exoprosopa* would take the next available name, *Litorhynchus* Macquart, which has had a confused nomenclatural and taxonomic history. Application has been made (Evenhuis & Greathead 1989) to the I.C.Z.N. to suppress the designation by Duponchel *in* d'Orbigny (1845) in favor of the one by Coquillett (1910).

FORELLIA Robineau-Desvoidy

Forellia Robineau-Desvoidy, 1830:760. Type species: *Forellia onopordi* Robineau-Desvoidy, 1830 [= *Musca artemesiae* Fabricius, 1794], by designation of Duponchel *in* d'Orbigny (5:676 [on or before 17 February 1845]).

Family. Tephritidae.

Remarks. Foote (1984) listed the type species of *Forellia* as *Musca artemesiae* Fabricius, 1794, by designation of Coquillett (1910:545). At first glance, this designation would be invalid because *Musca artemesiae* was not one of the originally included species. A check of Coquillett (1910) shows that he placed *onopordi* Robineau-Desvoidy in synonymy with *artemesiae*, which validates the designation of *onopordi* as type species. *Forellia* is currently considered a junior synonym of *Trypeta* Meigen.

GERON Meigen

Geron Meigen, 1820:223. Type species: *Geron gibbosus* Meigen, 1820 [=*Bombylius gibbosus* Olivier, 1789], by designation of Duponchel *in* d'Orbigny (6:206 [before 22 December 1845]).

Family. Bombyliidae.

Remarks. Painter and Painter (1965), Bowden (1975, 1980), Painter, Painter and Hall (1978), and Zaitzev (1989) list the same type species as designated by Rondani (1856:165).

GRAPHOMYA Robineau-Desvoidy

Graphomya Robineau-Desvoidy, 1830:257. Type species: *Musca maculata* Fabricius, 1830, by designation of Duponchel *in* d'Orbigny (6:305 [before 22 December 1845]).

Family. Muscidae.

Remarks. Pont (1986:162; 1989:687) gave the same type species by designation of Westwood (1840:141). Unfortunately, Westwood's designation is not valid because he cited 2 species as the type ("*M. maculata* Fab., and *meditabunda* F. Pz. 44. 23., is the type of *Graphomya* R. D.").

GYMNOSTYLIA Macquart

Gymnostylia Macquart, 1835:216. Type species: *Macromya depressa* Robineau-Desvoidy, 1830, by designation of Duponchel *in* d'Orbigny (6:439 [before 22 December1845]).

Family. Tachinidae.

Remarks. Guimarães (1971) listed the same type species as designated by Townsend (1916:7). *Gymnostylia* is an objective junior synonym of the Neotropical genus *Macromya* Robineau-Desvoidy.

HOPLISTES Macquart

Hoplistes Macquart, 1834a:253. Type species: *Sargus bispinosus* Wiedemann, 1830, by designation of Duponchel *in* d'Orbigny (6:676 [before 22 December 1845]).

Family. Stratiomyidae.

Remarks. James (1973:22) listed Macquart (1834a) as having originally designated *Sargus bispinosus* Wiedemann as type species. A check of the original description and originally included 3 species (*bispinosus*, *hortulanus*, and *pomaceus*) shows that there is no evidence to indicate that Macquart designated any one of these 3 as type species.

HYDRELLIA Robineau-Desvoidy

Hydrellia Robineau-Desvoidy, 1830:790. Type species: *Hydrellia communis* Robineau-Desvoidy, 1830 (in synonymy with *Notiphila griseola* Fallén), by designation of Duponchel *in* d'Orbigny (6:743 [22 December 1845]).

Family. Ephydridae.

Remarks. Cogan (1984) listed the type species of *Hydrellia* as *Hydrellia aurifacies* Robineau-Desvoidy, 1830, by designation of Coquillett (1910:553). *Hydrellia communis* is currently considered a member of the genus *Hydrellia*, hence there is no change in generic concept.

MALLOPHORA Macquart

Mallophora Macquart, 1834a:300. Type species: *Asilus infernalis* Wiedemann, 1821 (as *Mallophora*), by designation of d'Orbigny (7:609 [before 31 August 1846]).

Family. Asilidae.

Remarks. Martin and Papavero (1970) listed the type species of *Mallophora* as *Asilus bomboides* Wiedemann, 1821, by designation of Coquillett (1910:565). *Asilus infernalis* is currently considered a member of the genus *Mallophora*, hence there is no change in generic concept. D'Orbigny, as editor of the *Dictionnaire*, is considered the responsible author for this entry because there are no author's initials.

MEIGENIA Robineau-Desvoidy

Meigenia Robineau-Desvoidy, 1830:198. Type species: *Meigenia cylindrica* Robineau-Desvoidy, 1830 (as *Tachina*), by designation of Desmarest *in* d'Orbigny (12:318 [2 January 1849]).

Family. Tachinidae.

Remarks. Herting (1984) listed the type of *Meigenia* as *Meigenia floralis* Robineau-Desvoidy, 1830, by designation of Robineau-Desvoidy (1863 (1):1065). *Meigenia cylindrica* is currently considered a member of the genus *Meigenia*, hence there is no change in generic concept.

MICROPALPUS Macquart

Micropalpus Macquart, 1834a:316. Type species: *Tachina vulpina* Fallén, 1810, by designation of d'Orbigny (8:200 [before 14 December 1846]).

Family. Tachinidae.

Remarks. Herting (1984:96) listed the same type species as designated by Rondani (1856:63). *Micropalpus* is currently considered a junior synonym of *Linnaemya* Robineau-Desvoidy, 1830.

NEMOPODA Robineau-Desvoidy

Nemopoda Robineau-Desvoidy, 1830:743. Type species: *Nemopoda putris* Robineau-Desvoidy, 1830 [= *Sepsis nitidula* Fallén, 1820], by designation of d'Orbigny (8:611 [14 December 1846]).

Family. Sepsidae.

Remarks. Zuska and Pont (1984) listed the same type species as designated by Rondani (1874:170, 178). D'Orbigny, the editor of the *Dictionnaire*, is considered responsible for this designation because no author's initials are listed for this entry.

SCATOMYZA Fallén

Scatomyza Fallén, 1810:15. Type species: *Musca scybalaria* Linneaus, 1758, by designation of Lucas *in* d'Orbigny (11:411 [between 28 February and 9 September 1848]).

Family. Scathophagidae.

Remarks. Vockeroth (1965) had previously listed this type designation and was followed recently by Gorodkov (1986).

SENOMETOPIA Macquart

Senometopia Macquart, 1834b:296. Type species: *Sturmia atropivora* Robineau-Desvoidy, 1830, by designation of Desmarest *in* d'Orbigny (11:552 [9 September 1848]).

Family. Tachinidae.

Remarks. Herting (1984) listed the type species of *Senometopia* as *Carcelia aurifrons* Robineau-Desvoidy, 1830, by designation of Townsend (1916:8). Acceptance of Desmarest's designation would result in considerable changes in generic concepts. *Sturmia atropivora* is currently considered a member of the genus *Zygobothria* Mik (B. K. Cantrell & R. W. Crosskey, in litt.). Because of a further type designation for *Sturmia* by Desmarest (see below), *Senometopia* would become a junior objective synonym of *Sturmia*, which becomes a senior synonym of *Zygobothria*. The next available name for species previously attributed to *Senometopia* is *Eocarcelia* Townsend. Application to the I.C.Z.N. for suppression of Desmarest's (1848) designation in favor of Townsend's (1916) designation may be warranted to maintain stability of taxonomy and usage.

SITAREA Robineau-Desvoidy

Sitarea Robineau-Desvoidy, 1830:763. Type species: *Sitaea scorzonerae* Robineau-Desvoidy, 1830, by designation of Desmarest *in* d'Orbigny (11:643 [9 September 1848]).

Family. Tephritidae.

Remarks. Foote (1984) listed the same type species as designated by Coquillett (1910:606). *Sitarea* has been placed as a junior synonym of *Orellia* Robineau-Desvoidy by White (1986).

SMIDTIA Robineau-Desvoidy

Smidtia Robineau-Desvoidy, 1830:183. Type species: *Smidtia vernalis* Robineau-Desvoidy, 1830 [= *Tachina conspersa* Meigen, 1824], by designation of Desmarest *in* d'Orbigny (11:649 [9 September 1848]).

Family. Tachinidae.

Remarks. Herting (1984) listed the same type species as designated by Robineau-Desvoidy (1863 (1):294).

STACHYNIA Macquart

Stachynia Macquart, 1835:36. Type species: *Myopa gemina* Wiedemann *in* Meigen 1824 [= *Conops aculeata* Linneaus, 1761], by designation of Desmarest *in* d'Orbigny (11:798 [9 September 1848]).

Family. Conopidae.

Remarks. *Stachynia* was originally proposed (unnecessarily) as a replacement name of *Dalmannia* Robineau-Desvoidy, 1830. Chvála and Smith (1988) list *Stachynia* as a junior objective synonym of *Dalmannia* with the type species as "*Myopa punctata* Fabricius, 1794 (aut.)," as a result of *punctata* being designated as the type species of *Dalmannia* by Rondani (1856:59). The earlier designation of *Myopa gemina* by Desmarest for *Stachynia* results in the type species of *Dalmannia* also being *gemina*. *Myopa gemina* is currently considered a member of the genus *Dalmannia*, hence no change in generic concept should result with the acceptance of the change in type species noted here.

STEVENIA Robineau-Desvoidy

Stevenia Robineau-Desvoidy, 1830:220. Type species: *Stevenia tomentosa* Robineau-Desvoidy, 1830 [= *Musca atramentaria* Meigen, 1826], by designation of Desmarest *in* d'Orbigny (12:32 [9 September 1848]).

Family. Rhinophoridae.

Remarks. Crosskey (1977) listed the same type species as designated by Robineau-Desvoidy (1863 (2):378).

STURMIA Robineau-Desvoidy

Sturmia Robineau-Desvoidy, 1830:171. Type species: *Sturmia atropivora* Robineau-Desvoidy, 1830, by designation of Desmarest *in* d'Orbigny (12:77 [9 September 1848]).

Family. Tachinidae.

Remarks. Herting (1984) listed the type species of *Sturmia* as *Sturmia vanessae* Robineau-Desvoidy, 1830 [= *Tachina bella* Meigen, 1824], by designation of Robineau-Desvoidy (1863 (1):888). Acceptance of Desmarest's designation would result in considerable changes in generic concepts (see *Senometopia* above). The next available name for species previously attributed to *Sturmia* (*sensu* Herting) is *Oodigaster* Macquart. Application to I.C.Z.N. for suppression of Desmarest's designation may be necessary to maintain stability of taxonomy and usage.

STYLIA Robineau-Desvoidy

Stylia Robineau-Desvoidy, 1830:754. Type species: *Stylia maculata* Robineau-Desvoidy, 1830, by designation of Desmarest *in* d'Orbigny (12:78 [9 September 1848]).

Family. Tephritidae.

Remarks. Hardy (1977) listed the same type species and designation by Desmarest, but also lists a later designation by Hering (1954:167) of *Stylia bidentis* and states erroneously that *Stylia* Robineau-Desvoidy is preoccupied by *Stylia* Desmarest. If Desmarest's designation is accepted, *Stylia* would have to be considered an unrecognized genus because the type species, *S. maculata*, is destroyed (Foote & Blanc 1979) and no other specimens of this species are known. If application is made to I.C.Z.N. to suppress Desmarest's (1848) designation in favor of Hering's (1954) designation, then *Stylia* would become a senior synonym of *Dioxyna* Frey, 1945 (see White 1986). Acceptance of Desmarest's designation is desirable from the standpoint of stability of taxonomy and common usage (I. M. White, in litt.).

WINTHEMIA Robineau-Desvoidy

Winthemia Robineau-Desvoidy, 1830:178. Type species: *Musca quadripustulata* Fabricius, 1794 (as "*W. quadripustulata* Rob.-Desv., Fabr, Pall., Meig."), by designation of Desmarest *in* d'Orbigny (13:301 [between 10 September and 5 November 1849]).

Family. Tachinidae.

Remarks. Herting (1984:38), following his mentor Mesnil (1949:80), accepted the statement in Robineau-Desvoidy (1830:173) "Ce genre se rapporte au *Musca quadripustulata* de Fabricius" as evidence of an original designation. Herting's interpretation was followed recently by Cantrell and Crosskey (1989). Robineau-Desvoidy's statement is ambiguous and we do not consider it an original designation. Though one might attribute a genus to a species, that does not necessarily imply that the species so indicated is also the type of that genus . Robineau-Desvoidy (1863 (1):207) subsequently designated *Tachina variegata* Meigen, 1824, as the type species, the action of which was followed by Sabrosky and Arnaud (1965:1089), Guimarães (1971:195), and Cantrell (1989); however, Desmarest's designation predates Robineau-Desvoidy's (1863) designation and is of the same species as Robineau-Desvoidy's (1830) alleged "designation."

XYPHOSIA Robineau-Desvoidy

Xyphosia Robineau-Desvoidy, 1830:762. Type species: *Xyphosia cirsiorum* Robineau-Desvoidy, 1830 [= *Musca miliaria* Schrank, 1781], by designation of Desmarest *in* d'Orbigny (13:332 [on or before 5 November 1849]).

Family. Tephritidae.

Remarks. Hardy (1977) and Foote (1984) listed the type species of *Xyphosia* as *Musca miliaria* Schrank, 1781, by designation of Rondani (1870:8). Rondani's designation, however, is invalid because *Musca miliaria* Schrank is not one of the species originally included in *Xyphosia* by Robineau-Desvoidy (1830). A later designation by Rondani (1871:4) of *miliaria* was done with *cirsiorum* in synonymy. *Xyphosia cirsiorum* is currently considered synonymous with *miliaria* Schrank (see Foote 1984), hence there is no change in generic concept with acceptance of this type-species designation.

ZENAIS Robineau-Desvoidy

Zenais Robineau-Desvoidy, 1830:148. Type species: *Zenais silvestris* Robineau-Desvoidy, 1830, by designation of Desmarest *in* d'Orbigny (13:346 [5 November 1849]).

Family. Tachinidae.

Remarks. Herting (1984) listed the type species for *Zenais* as *Zenais fera* Robineau-Desvoidy, 1830, by designation of Robineau-Desvoidy (1863 (1):912). *Zenais silvestris* is not listed in Herting's (1984) Palearctic tachinid catalog, presumably because it was among the 1,000 species-group names that he could not place to genus. If that is so, then acceptance of Desmarest's designation would result in *Zenais* having to be considered an unrecognizable genus. Currently, *Zenais* is considered a junior synonym of *Meigenia* Robineau-Desvoidy.

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APPENDIX 1

Index of Diptera Names in the *Dictionnaire Universel d'Histoire Naturelle*

All Diptera names from family group to genus group mentioned in the *Dictionnaire* are listed below. They are listed within their currently known familial placement. Queried familial placements are listed as such. Unplaceable family/ordinal group names are listed at the beginning of the appendix. Genus-group entries are placed in italics; family-group names are in plain roman text. If a type species was designated in the *Dictionnaire*, the species and wording as stated in the *Dictionnaire* are placed here in quotes; otherwise a brief statement of included species is mentioned. If only one species was listed, whether monotypy was implied or not, it is listed here in parentheses. Numbers in brackets following the indexed entry refer to volume and page in the *Dictionnaire*.

Antennaires: Family/Ordinal group entry. Ordinal group name [1: 572].
Anthomyzides: Family/Ordinal group entry [1: 595].
Anthophilae: Family/Ordinal group entry [1: 597].
Anthraciens: Family/Ordinal group entry [1:601].
Antliata: Family/Ordinal group entry [1: 631].
Aploceres: Family/Ordinal group entry [2: 13].
Aricinae: Family/Ordinal group entry [2: 134].
Armentariae: Family/Ordinal group entry [2: 141].
Astoma: Family/Ordinal group entry [2: 264].
Athericeres: Family/Ordinal group entry [2: 290].
Bibionites: Family/Ordinal group entry [2: 564].
Bombomydes: Family/Ordinal group entry [2: 643].
Brachocera: Family/Ordinal group entry [2: 704].
Brachyceratae: Family/Ordinal group entry [2: 706].
Calypteratae: Family/Ordinal group entry [3: 82].
Cephalopsides: Family/Ordinal group entry [3: 276].
Cephalopsites: Family/Ordinal group entry [3: 276].
Chetoloxes: Family/Ordinal group entry [3: 474].
Chorelleae: Family/Ordinal group entry [3: 624].
Coprobies: Family/Ordinal group entry [4: 200].
Coriaceae: Family/Ordinal group entry: = Puparies [4: 238].
Creophilae: Family/Ordinal group entry [4: 333].
Dichaetes: Family/Ordinal group entry [4: 739].
Diptera: Family/Ordinal group entry [5: 62].
Dufouridae: Family/Ordinal group entry [5: 143].
Entomobies: Family/Ordinal group entry [5: 333].
Entomocera: Family/Ordinal group entry [5: 333].
Faunidae: Family/Ordinal group entry [5: 572].
Geomyzides: Family/Ordinal group entry [6: 195].
Halterata: Family/Ordinal group entry: = Diptera [6: 464].
Mouche: Family/Ordinal group entry. General write-up [8: 370].
Musciphoreae: Family/Ordinal group entry [8: 448].
Myodaires: Family/Ordinal group entry [8: 506].
Myopariae: Family/Ordinal group entry [8: 519].
Nematoceres: Family/Ordinal group entry. Cross reference [8: 606].
Nemocera: Family/Ordinal group entry [8: 609].
Notacantha: Family/Ordinal group entry [8: 672].
Palomydeae: Family/Ordinal group entry [9: 427].
Phytomidae: Family/Ordinal group entry [10: 133].
Pupipara: Family/Ordinal group entry [10: 640].
Sericoceres: Family/Ordinal group entry [11: 560].
Tanystoma: Family/Ordinal group entry [12: 343].
Terrestres: Family/Ordinal group entry [12: 523].
Vagantes: Family/Ordinal group entry [12: 806].
Viviparae: Family/Ordinal group entry [13: 261].
Zoomyae: Family/Ordinal group entry [13: 365].

Acroceridae

Acrocera: (Type—"*A. globulus* Latr. (*Syrphus globulus* Panz.)") [1: 97].
Astomella: (Type—"*Ast. curviventris*") [2: 264].
Cyrtides: Family/Ordinal group entry: = Vesiculeux [4: 558].
Cyrtus: (Type—"*acephalus (Acrocera gibba* Fabr.)") [4: 558].
Eriosoma: One species mentioned (*calida*). No designation [5: 402].
Henops: = *Ogcodes* [6: 536].
Ogcodes: Three species mentioned. No designation [8: 765].
Panops: Three species mentioned. No designation [9: 445].
Philopota: One species mentioned (*conica*). No designation [9: 738].
Vesiculosa: Family/Ordinal group entry [13: 211].

Agromyzidae

Agromyza: Genus group entry [1: 198].
Odontocera: Five species mentioned. No designation [8: 722].
Phytomyza: Seven species mentioned. No designation [10: 133].

Agromyzidae?

Cnemacantha: One species mentioned (*muscaria*). No designation [4: 28].

Anisopodidae

Mycetobia: No species mentioned [8: 453].
Rhyphus: Three species mentioned. No designation [11: 132].

Anthomyiidae

Adia: = *Chortophila* Macquart [1: 131].
Aegeria: = *Hylemyia* Macquart [1: 139].
Anthomyia: (Type—"*Musca pluvialis* Linne") [1: 595].
Anthomyides: Family/Ordinal group entry [1: 594].
Atomogaster: (Type—"*Anthomyia triquetra* de Meigen") [2: 309].
Chlorina: Two species mentioned. No designation [3: 606].
Chortophila: Genus group entry [3: 627].
Cuculla: Three species mentioned. No designation [4: 447].
Delia: One species mentioned (*chorea*). No designation [4: 659].
Egeria: One species mentioned (*sylvatica*). No designation [5: 218].
Egle: One species mentioned (*vulgaris*). No designation [5: 219].
Hydrophoria: (Type—"*H. conica* (*Minca* id. Fallen, *H. tibialis*? R.-D.)") [6: 760].
Hydrotaea: Divided into three groups, with type species for each [6: 763].
Hylemyia: One species mentioned (*strenua*). No designation. "place en tête de ce genre." [6: 773].
Myopina: (Type—"*Musca myopina* Fall. (*Myopina reflexa* Rob.-Desv.)") [8: 520].
Zabia: One species mentioned (*longipes*). No designation [13: 339].
Zaphne: No species mentioned [13: 343].

Anthomyiidae?

Chloe: One species mentioned (*sylvicola*). No designation [3: 602].

Anthomyzidae

Leptomyza: One species mentioned (*frontalis*). No designation [7: 311].

Apioceridae

Apiocera: Two species mentioned. No designation [2: 7].

Asilidae

Acnephalum: "nous ne citerons que celle qu'il appelle *A. Olivieri*, et qui a ete trouvée dans L'le de Paxos par Olivier." [1: 88].
Apoclea: No designation [2: 22].
Asilici: Family/Ordinal group entry [2: 218].
Asilitae: Family/Ordinal group entry [2: 218].
Asilus: (Type—"*Asilus crabroniformis* de Linne") [2: 218].
Atomosia: (Type—"*Atomosia annulipes*") [2: 309].
Atractia: (Type—"*Asilus psilogaster* de Wiedemann") [2: 310].
Ceraturgus: Three species mentioned. No designation [3: 294].
Chalcidimorpha: One species mentioned (*fulvipes*). No designation [4: 595].
Craspedia: Two species mentioned. No designation [4: 322].
Damalis: (Type—"*Damalis myops* Fab.") [4: 595].
Dasypogon: (Type—"*Dasypogon punctatus* Meig.") [4: 612].
Dasypogonites: Family/Ordinal group entry [4: 613].
Dioctria: (Type—"*D. rufipes* Meig. (*Asilus* id. Deg.)") [5: 38].
Discocephala: One species mentioned (*rufiventris*). No designation [5: 76].
Dolichodes: One species mentioned (*ferruginea*). No designation [5: 97].
Erax: One species mentioned (*nodicornis*). No designation [5: 384].
Gonypes: Two species mentioned. No designation [6: 277].
Hoplistomerus [as "*Hoplistomera*"]: (Type—"*Laphria serripes* Fabr.") [6: 676].
Laphria: One species mentioned (*aurea*). No designation [7: 243].
Laxenecera: Two species mentioned. No designation [7: 263].
Lecania: Two species mentioned. No designation [7: 265].
Lophonotus: No species mentioned [7: 440].
Mallophora: (Type—"*M. infernalis*") [7: 609].
Megapoda: One species mentioned (*cyanea*). No designation [8: 58].
Ommatius: Five species mentioned. No designation [9: 100].
Phoneus: One species mentioned (*servillei*). No designation [9: 756].
Rhopalogaster: (Type—"*Rhopalogaster longicornis* Macq.") [11: 123].
Senobasis: No species mentioned [11: 551].
Senoprosopis: No species mentioned [11: 552].
Tapinocera: No species mentioned [12: 345].
Trupanea: No species mentioned [12: 710].

Asteiidae

Asteia: Two species mentioned. No designation [2: 247].
Leiomyza: One species mentioned (*glabriuscula*). No designation [7: 279].

Athericidae

Atherix: No designation [2: 292].
Styrex: = *Atherix*. No species mentioned [12: 85].

Aulacigastridae

Aulacigaster: One species mentioned (*rufitarsis*). No designation [2: 334].

Bibionidae

Bibio: Two species mentioned. No designation [2: 563].
Bibionidae: Family/Ordinal group entry [2: 563].
Dilophus: (Type—"*Dilophus vulgaris*") [5: 18].
Eupeitenus: One species mentioned (*ater*). No designation [5: 500].
Hirtea: No species mentioned. Cross reference [6: 653].
Penthetria: Two species mentioned. No designation [9: 575].

Bombyliidae

Amictus: Two species mentioned. No designation [1: 351].
Anthraciens: Family/Ordinal group entry [1: 601].
Anthrax: (Type—"*hottenotota* Fabricius (= entoure & *circumdata* Hoffmansegg)") [1: 603].
Apatomyza: No species mentioned [1: 640].
Bombyliari: Family/Ordinal group entry [2: 644].
Bombyliarii: Family/Ordinal group entry [2: 644].
Bombylides: Family/Ordinal group entry [2: 644].
Bombyliites: Family/Ordinal group entry [2: 645].
Bombylius: Not a valid designation; applied to an unnamed subgroup [2: 644].
Callostoma: (Type—"*Callostoma fuscipennis*") [3: 63].
Comptosia: One species mentioned (*fascipennis*). No designation [4: 164].
Corsomyza: (Type—"*Cors. pennipes* de Wiedemann") [4: 257].
Cyclorhynchus: One species mentioned (*testaceus*). No designation [4: 500].
Cyllenia: Three species mentioned. No designation [4: 515].
Dasypalpus: One species mentioned (*capensis*). No designation [4: 611].
Enica: One species mentioned (*longirostris*). No designation [5: 324].
Eniconevra: One species mentioned (*fuscipennis*). No designation [5: 325].
Exoptata [as "*Exaptata*"]: One species mentioned (*anthracoides*). No designation [5: 540].
Exoprosopa: (Type—"*Exop. Audouinii*") [5: 545].
Geron: (Type—"*Geron gibbosus* Hoffm.") [6: 206].
Lepidophora: One species mentioned (*aegeriiformis*). No designation [7: 292].
Litorhynchus: Three species mentioned. No designation [7: 410].
Lomatia: (Type—"*L. lateralis*") [7: 428].
Mulio: Two species mentioned. No designation [8: 424].
Ogcodocera: One species mentioned (*dimidiata*). No designation [8: 765].
Phthiria: No species mentioned [10: 12].
Ploas: Four species mentioned. No designation [10: 276].
Sphaerogaster: No species mentioned [11: 731].
Spogostylum: Genus group entry [11: 777].
Stygia: (Type—"*S. lateralis* Meigen") [12: 77].
Stygidium: Genus group entry [12: 77].
Systropus: One species mentioned (*macilentus*). No designation [12: 312].
Thlipsomyza: One species mentioned (*compressa*). No designation [12: 558].
Tomomyza: Genus group entry [12: 600].
Toxophora: Three species mentioned. No designation [12: 624].
Usia: (Type—"*Usia aenea* Latr.") [12: 800].
Xestomyza [as "*Xestomysa*"]: Two species mentioned. No designation [13: 316].

Braulidae

Braula: One species mentioned (*caeca*). No designation [2: 728].

Calliphoridae

Amenia: Two species mentioned. No designation [1: 348].
Calliphora [as "*Calliphore*"]: (Type—"*Musca vomitaria* de Linne") [3: 56].
Chrysomyia: Genus group entry [3: 658].
Cosmina: Three species mentioned. No designation [4: 268].
Idia: (Type—"*I. fasciata* Meig.") [7: 16].
Lucilia: (Type—"*Lucilia caesar*") [7: 457].
Metopia: Genus group entry [8: 186].
Nitellia: One species mentioned (*lanio*). No designation [10: 373].
Ochromyia: Four species mentioned. No designation [8: 713].
Onesia: Three species mentioned. No designation [9: 111].
Pollenia: (Type—"*Pollenia rudis* Rob.-Desv.") [10: 373].
Rhynchomya: Three species mentioned. No designation [11: 129].
Silbomyia: No species mentioned [11: 604].

Cecidomyiidae

Anarete: One species mentioned (*pini*). No designation [1: 427].
Brachyneura: One species mentioned (*fusco-grisea*). No designation [2: 710].
Campylomyza: Two species mentioned. No designation [3: 110].
Catocha: One species mentioned (*latipes*). No designation [3: 236].
Cecidomyia: No designation [3: 247].
Cecidomytes: Family/Ordinal group entry [3: 248]
Cordyla: One species mentioned (*fusca*). No designation [4: 235].

Dasyneura: Two species mentioned. No designation [4: 611].
Lasioptera: One species mentioned (*albipennis*). No designation [7: 249].
Lestremia: Two species mentioned. No designation [7: 320].
Macropeza: One species mentioned (*albitarsis*). No designation [7: 547].

Celyphidae

Celyphus: Two species mentioned. No designation [3: 257].
Cryptogastres: Family/Ordinal group entry [4: 431].

Ceratopogonidae

Ceratopogon: One species mentioned. No designation [3: 292].
Culicoides: One species mentioned (*pulicaris*). No designation [4: 460].
Serromyia: = *Prosonomyia* [11: 574].
Sphaeromias: No species mentioned [11: 731].

Chamaemyiidae

Estelia: Three species mentioned. No designation [5: 452].
Leucopis: (Type—"*Leucopis grisecla*") [7: 323].
Ochthiphila: Seven species mentioned. No designation [8: 714].

Chaoboridae

Corethra: One species mentioned (*plumicornis*). No designation [4: 238].

Chironomidae

Chironomites: Family/Ordinal group entry [3: 594].
Chironomus: Genus group entry [3: 594].
Tanypus: (Type—"*T. nebulosus* Meig.") [12: 343].

Chloropidae

Camarota: (Type—"*Camarota flavitarsis* Meig.") [3: 88].
Chlorops: (Type—"*Chlorops gracilis* Meig.") [3: 609].
Elachiptera: (Type—"*Chlorops brevipennis* de Meigen") [5: 221].
Eurhina. Two species mentioned. No designation [5: 512].
Gymnopoda: One species mentioned (*tomentosa*). No designation [6: 438].
Homalura: (Type—"*Homalura tarsata* Meigen") [6: 672].
Oscinis: Several species mentioned. No designation [9: 233].
Siphonella: (Type—"*S. oscinina* Macq., Fall. (*Chlorops nitida* Meig.)") [11: 633].

Chloropidae?

Heramyia [as "*Heramya*"]: Two species mentioned. No designation [6: 550].
Myrmemorpha: One species mentioned (*brachyptera*). No designation [8: 548].
Therina: One species mentioned (*femorata*). No designation [12: 554].

Chyromyidae

Chyromya: One species mentioned (*fenestrarum*). No designation [3: 664].

Clusiidae

Heteronevra [as "*Heteroneura*"]: One species mentioned (*nubila*). No designation [6: 600].

Coelopidae

Coelopa: One species mentioned. No designation. *Psalidomyia* given as a synonym [4: 76].

Conopidae

Conops: (Type—"*Conops macrocephala* Lin.") [4: 191].
Conopsaires: Family/Ordinal group entry [4: 191].
Conopsides: Family/Ordinal group entry: = *Conopsaires* [4: 191].
Conopsites: Family/Ordinal group entry: = *Conopsaires* [4: 191].
Dalmannia: One species mentioned (*punctata*). No designation [4: 594].
Myopa: Three species described. No designation [8: 519].
Sicus: No species mentioned [11: 595].
Stachynia: (Type—"*S. gemina* Wied., Rob.-Desv., Macq") [11: 798].
Stylogaster: One species mentioned (*stylatus*). No designation [12: 81].
Zodion: (Type—"*Zodion cinereum* Meig. (= *conopsoides* Latr., *pedicellatum* Rob.-Desv.") [13: 360].

Culicidae

Aedes: One species mentioned (*cinereus*). No designation [1: 138].
Anopheles: Three species mentioned. No designation [1: 563].
Culex: Genus group entry [4: 309].
Culicides: Family/Ordinal group entry [4: 458].
Culicii: Family/Ordinal group entry: = "Culicides" [4: 460].

Diastatidae

Campichaeta: One species mentioned (*rufipes*). No designation [3: 107].
Diastata: (Type—"*Diastata anus* Meig.") [4: 731].

Diopsidae

Diopsideae: Family/Ordinal group entry [5: 42].
Diopsis: (Type—"*Diopsis ichneumonea* Linn.") [5: 42].

Dixidae

Dixa: (Type—"*Dixa aestivalis*") [5: 92].

Dolichopodidae

Anglearia [as "*Angleuria*"]: One species mentioned (*antennata*). No designation [1: 501].
Argyra. Two species mentioned. No designation [2: 127].
Chrysosoma: Two species mentioned. No designation [3: 661].
Chrysotus: (Type—"*Chry. neglectus* Meig.") [3: 661].
Diaphorus [as "*Diaphora*"]: (Type—"*Diaphora Hoffmanseggii*") [4: 729].
Dolichopoda: Family/Ordinal group entry [5: 98].
Dolichopus: Invalid designation of *Dolichopus ungulatus* Latr. [5: 98].
Hydrophorus: One species mentioned (*jaculus*). No designation [6: 760].
Medeterus: One species mentioned (*regius*). No designation [8: 44].
Orthochile: (Type—"*Ortochile nigro-caerulea* Latr.") [9: 213].
Porphyrops: Five species mentioned. No designation [10: 438].
Psilopus: (Type—"*Psilopus platypterus* Fab. (= *tipularius* Fall.)") [10: 599].
Rhaphium [as "*Raphium*"]: Eight species mentioned. No designation [10: 722].
Sybistroma: (Type—"*S. nodicornis* Meigen") [12: 101].

Drosophilidae

Drosophila: (Type—"*Musca cellaris* Linn.") [5: 137].
Gitona: One species mentioned (*bistigma*). No designation [6: 224].
Stegana: Two species mentioned. No designation [11: 809].
Zygothrica [as "*Zygotricha*"]: No species mentioned [13: 384].

Dryomyzidae

Dryomyza: One species mentioned (*flaveola*). No designation [5: 140].
Dryope: = *Dryomyza* [5: 140].

Eginiidae

Eginia: One species mentioned (*cylindrica*). No designation [5: 218].

Empididae

Acromyia: *Hybos* [1: 101].
Aplomera: (Type—"*Gayi*") [2: 15].
Atelestus: One species mentioned (*sylvicola*). No designation [2: 286].
Brachystoma: Two species mentioned. No designation [2: 716].
Brachystoma: Family/Ordinal group entry [2: 716].
Clinocera: One species mentioned (*nigra*). No designation [4: 10].
Cyrtoma: (Type—"*Cyrtoma nigra* Meig. (*Empis palicaria* Fallen)") [4: 560].
Drapetis: (Type—"*Drapetis exilis* Meig.") [5: 126].
Elaphropeza: (Type—"*Hemerodromia ephippiata* de Meigen") [5: 228].
Empides: Family/Ordinal group entry [5: 293].
Empis: One species mentioned (*opaca*). No designation [5: 294].
Eriogaster: One species mentioned (*laniventris*). No designation [5: 400].
Euthyneura: One species mentioned (*myrtilli*). No designation [5: 532].
Gloma: One species mentioned (*fuscipennis*). No designation [6: 236].
Heleodromia: One species mentioned (*immaculata*). No designation [6: 500].
Hemerodromia: (Type—"*Hemerodromia monostigma*") [6: 528].
Hilara: Two species mentioned. No designation [6: 615].
Hybos: (Type—"*Hybos funebris* Meig.") [6: 722].
Hybotidae: Family/Ordinal group entry [6: 722].
Hydrodromia: Two species mentioned. No designation [6: 748].
Leptopeza: One species mentioned (*flavipes*). No designation [7: 312].
Microphorus: No species mentioned [8: 201].
Ocydromia: Four species mentioned. No designation [8: 717].
Oedalea: Two species mentioned. No designation [8: 729].
Pachymerina: Four species mentioned. No designation [9: 387].
Paramesia: Two species mentioned. No designation [9: 479].
Platypalpus: Seven species mentioned. No designation [10: 258].
Rhamphomyia [as "*Rhampiomyia*"]: Six species mentioned. No designation [11: 87].
Sicus: No species mentioned [11: 595].
Tachydromia: (Type—"*T. fuscipennis* Fall.") [12: 319].
Tachydromiae: Family/Ordinal group entry [12: 319].
Tachypeza: No species mentioned [12: 320].
Trichina: No species mentioned [12: 649].
Wiedmannia: = *Empis* [13: 299].
Xiphidicera: One species mentioned (*rufipes*). No designation [13: 317].

Ephydridae

Coenia: (Type—"*Coenia palustris* (*Ephydra* id. Meig.)"). *Caricola* Robineau-Desvoidy given as a synonym [4: 78].

Dichaeta: One species mentioned (*caudata*). No designation [4: 739].

Discocerina: One species mentioned (*pusilla*). No designation [5: 77].

Discomyza: (Type—"*Discomyza incurva* Meig. (*Psilopa* id. Fall.)") [5: 78].

Dryxo: One species mentioned (*lipsoides*). No designation [5: 142].

Ephydra: (Type—"*Ephydra annulata* Meig.") [5: 353].

Gymnopa: One species mentioned (*subsultans*). No designation [6: 437].

Hydrellia: (Type—"*Hydrellia griseola* Fall. (*communis* R.-D.)") [6: 743].

Hydrina: One species mentioned (*nitida*). No designation [6: 743].

Mosillus: No species mentioned [8: 370].

Notiphila [as "*Nothiphila*"]: No species mentioned [8: 674].

Ochthera: Two species mentioned. No designation [8: 713].

Teichomyza: One species mentioned (*fusca*). No designation [12: 439].

Telmatobia: No species mentioned [12: 445].

Trimerina: Two species mentioned. No designation [12: 678].

Fanniidae

Aminta: One species mentioned (*floralis*). No designation [1: 354].

Fannia: One species mentioned (*saltatrix*). No designation [5: 558].

Glossinidae

Glossina: One species mentioned (*longipalpis*). No designation [*longipalpis* = *Nemothina palpalis* R.-D.] [6: 237].

Helcomyzidae

Actora: One species mentioned (*aestuum*). No designation [1: 115].

Heleomyzidae

Herbina: Two species mentioned. No designation [6: 557].

Heteromyza: (Type—"*H. atricornis* Meig.") [6: 600].

Helomyzidae

Helomyza: Two species mentioned. No designation [6: 523].

Hippoboscidae

Anapera: Two species mentioned. No designation [1: 426].

Craterina: = *Stenopteryx* [4: 327].

Haemobora: One species mentioned (*pallipes*). No designation [6: 452].

Hippobosca: No designation [6: 618].

Leptotaena: (Type—"*Leptonema Cervi*") [7: 315].

Melophagus: Genus group entry [8: 108].

Nycteribia: Genus group entry [8: 697].

Olfersia: No species mentioned [9: 82].

Ornithobia: One species mentioned (*pallida*). No designation [9: 200].

Ornithomyia: Two species mentioned. No designation. [9: 202].

Phthiromyiae: Family/Ordinal group entry [10: 13].

Stenopteryx [as "*Stenepteryx*"]: (Type—"*S. hirudinis* Leach") [12: 6].

Strebla: One species mentioned (*vespertilionis*). No designation [12: 54].

Stylidia: No species mentioned [12: 79].

Lauxaniidae

Lauxania: One species mentioned (*lupulina*). No designation [7: 260].

Lauxanides: Family/Ordinal group entry [7: 260].

Pachycerina: (Type—"*Pachyc. seticornis*") [9: 382].

Pteredontia: One species mentioned (*flavipes*). No designation [10: 608].

Sapromyza: Seven species mentioned. No designation [11: 353].

Suillia: Genus group entry [12: 90].

Sylvia: No species mentioned [12: 103].

Trigonometopus: One species mentioned (*frontalis*). No designation [12: 673].

Lauxaniidae?

Teremyia: One species mentioned (*laticornis*). No designation [12: 473].

Terenia: No species mentioned [12: 473].

Lonchaeidae

Lonchaea: (Type—"*L. chorea*") [7: 432].

Lonchopteridae

Lonchoptera: (Type—"*L. lutea*") [7: 433].

Megamerinidae

Lissa: One species mentioned (*loxocerina*). No designation [7: 404].

Lissodema: = *Lissa* [7: 404].

Micropezidae

Calobata: Three species mentioned. No designation [3: 65].
Ceyx: Genus group entry [3: 362].
Micropeza: (Type—"*Micropeza punctum* Latr.") [8: 201].
Taeniaptera: One species mentioned (*trivittata*). No designation [12: 322].

Muscidae

Ardoptera: (Type—"*Hem. irrorata* de Meigen") [2: 99].
Azelia: One species mentioned (*gentilis*). No designation [2: 393].
Azelidae: Family/Ordinal group entry [2: 393].
Byomya: Three species mentioned. No designation [2: 789].
Byomya [as "*Bryomya*"]: Three species mentioned. No designation [8: 372].
Caricea: (Type—"*Caricea communis*") [3: 172].
Coenosia: (Type—"*Coenosia tigrina* Meig. (= *quadrum* Fall., *communis* R. D.)") [4: 79].
Curtonevra: Divided into four groups. No designation [4: 472].
Drymeia: One species mentioned (*obscura* Meig.) (= *Musca hamata* Fall.). No designation [5: 138].
Eriphia: No species mentioned [5: 403].
Euphemia: One species mentioned (*pratensis*). No designation [5: 502].
Fellaea: One species mentioned (*fera*). No designation [5: 584].
Graphomyia [as "*Graphomya*"]: (Type—"*Musca maculata* Fabr.") [6: 305].
Haematobia: (Type—"*H. stimulans* (*Stomoxis* id. Meig.)") [6: 453].
Limnophora: One species mentioned (*palustris*). No designation [7: 380].
Lispe: (Type—"*L. tentaculata*") [7: 404].
Musca: Cross reference [8: 443].
Musca: Seven species mentioned. No designation [8: 372].
Musciae: Family/Ordinal group entry [8: 448].
Muscides: Family/Ordinal group entry [8: 446].
Ophyra: (Type—"*Oph. leucostoma*") [9: 138].
Plaxemyia. Two species mentioned. No designation. [8: 372].
Selachops: No species mentioned [11: 530].
Sphora: No species mentioned [11: 727].
Sphora: One species mentioned (*nigricans*). No designation [8: 372].
Spilogaster: (Type—"*S. uliginosa* Mac., Fall. Meig. (*Rohrella punctata* Rob.-Desv.)") [11: 762].
Stagnia: Two species mentioned. No designation [11: 800].
Stomoxys: (Type—"*Stomoxys calcitrans*") [12: 51].

Muscidae?

Dasyphora: One species mentioned. No designation [4: 612].

Mycetophilidae

Asindulum: (Type—"*Asindulum nigrum* de Latreille") [2: 220].
Bolitophila: Two species mentioned. No designation [2: 641].
Ceroplatus: Two species mentioned. No designation [3: 340].
Gnoriste [as "*Gnorista*"]: One species mentioned (*apicalis*). No designation [6: 251].
Leia: Two species mentioned. No designation [7: 277].
Macrocera: (Type—"*M. lutea*") [7: 543].
Macronevra: One species mentioned (*winthemii*). No designation [7: 546].
Mycetophila: Four species mentioned. No designation [8: 453].
Mycetophilides: Family/Ordinal group entry [8: 454].
Pachypalpus: (Type—"*Pachyp. ater* (*Mycetophila anomala*)") [9: 388].
Platyura: Genus group entry [10: 263].
Sciophila. Six species mentioned. No designation [11: 435].

Mydidae

Cephalocera: (Type—"*C. longirostris*") [3: 271].
Mydas: (Type—"*Mydas giganteus*") [8: 497].
Mydasii: Family/Ordinal group entry [8: 497].

Nemestrinidae

Colax: One species mentioned (*macula*). No designation [4: 86].
Fallenia: One species mentioned (*fasciata*). No designation [5: 557].
Hirmoneura: (Type—"H. *obscura* de Meigen") [6: 635].
Nemestrinidae: Family/Ordinal group entry [8: 608].
Nemestrinus [as "*Nemestrina*"]: One species mentioned (*reticulata*). No designation [8: 608].
Trichophthalma: No species mentioned [12: 657].
Trichopsidea: No species mentioned [12: 657].

Neriidae

Longina: (Type—"*L. abdominalis*") [7: 437].
Nerius: Two species mentioned. No designation [8: 626].

Oestridae

Cephalemyia: One species mentioned (*ovis*). No designation [3: 270].
Cephenemyia: (Type—"*Cephenemyia trompe*") [3: 280].
Chylivorae: Family/Ordinal group entry [3: 663].
Cuterebra: Several species cited. No designation [4: 473].
Hypoderma: Two species mentioned. No designation [6: 786].
Oedemagena: One species mentioned (*tarandi*). No designation [8: 729].

Oestrides: Family/Ordinal group entry [8: 762].
Oestrus. Six species described. No designation [8: 760].
Trypoderma: = *Cuterebra*. No species mentioned [12: 712].

Opomyzidae

Opomyza: Two species mentioned. No designation [9: 141].

Otitidae

Amethysa: One species mentioned (*fasciata*). No designation [1: 349].
Blainvillia: Two species mentioned. No designation [2: 590].
Cephalia: Two species mentioned. No designation [3: 270].
Ceroxys: Two species mentioned. No designation [3: 342].
Delphinia: One species mentioned (*thoracica*). No designation [4: 662].
Dorycera: (Type—"*Musca* no 25 de Geoffroy (*Dorycera graminum* Meigen, *Oscinis thamnicolara* Rob.-Desv.)") [5: 118].
Eniconevra: (Type—"*fenestralis*") [5: 325].
Nothacanthina: One species mentioned (*bispinosa*). No designation [8: 672].
Ortalis: One species mentioned (*cerasi*). No designation [9: 212].
Otites: Genus group entry [9: 242].
Tetanops: Two species mentioned. No designation [12: 526].

Otitidae/Platystomatidae

Dicromyia: One species mentioned (*brasiliensis*). No designation. [4: 750]
Eurypalpus: One species mentioned (*testaceus*). No designation. [5: 523]

Otitidae?

Cleitamia: One species mentioned (*astrolabei*). No designation [4: 3].
Stylophora: One species mentioned (*zonata*). No designation [12: 81].

Pallopteridae

Toxoneura [as "*Toxonevra*"]: Genus group entry [12: 624].

Pantophthalmidae

Acanthomera: (Type—"*A. picta*") [1: 33].
Rhaphiorhynchus [as "*Raphiorhynchus*"]: (Type—"*Raph. planiventris* Wied.") [10: 721].

Phoridae

Conicera: One species mentioned (*atra*). No designation [4: 177].
Gymnophora: One species mentioned (*armata*). No designation [6: 437].
Phora: Five species mentioned. No designation [9: 773].
Trineura: = *Phora*: No species mentioned [12: 679].
Trineura [as "*Trinevra*"]: Cross reference [12: 680].

Piophilidae

Chyliza: Invalid designation of *Chy. leptogaster* Fall., ou *Sargus scutellatus* Fabr. [3: 663].
Piophila: Genus group entry [10: 209].
Thyreophora: Three species mentioned. No designation [12: 570].
Tyrophaga: No species mentioned [12: 751].

Pipunculidae

Atelenevra: (Type—"*A. velutina* . . . ou *Pipunculus spurius*") [2: 283].
Chalarus: = *Atelenevra*. No species mentioned [3: 369].
Pipunculus: Four species mentioned. No designation [10: 217].

Platypezidae

Callomyia: (Type—"*C. elegans* Meig.") [3: 62].
Platypeza: Four species mentioned. No designation [10: 258].
Platypezinae: Family/Ordinal group entry [10: 258].

Platystomatidae

Achias: (Type—"*A. oculatus* Fabricius") [1: 71].
Boisduvalia: (Type—"*B. rutilans*") [2: 637].
Hesyquillia: Two species mentioned. No designation [6: 594].
Loxonevra: One species mentioned (*decora*). No designation [7: 455].
Platystoma: (Type—"*Platystoma seminationis* Latr. (*Dictya* id. Fab.)") [10: 262].
Rivellia: Three species mentioned. No designation [11: 139].
Timia: Two species mentioned. No designation [12: 586].
Ulidia: (Type—"*Ulidia demandata* Meig.") [12: 753].
Ulidiai: Family/Ordinal group entry [12: 753].

Platystomatidae?

Clidonia: One species mentioned (*basalis*). No designation [4: 9].

Psilidae

Dasyna: Two species mentioned. No designation [4: 611].

Loxocera: (Type—"*L. ichneumonea*") [7: 455].
Platystyla: (Type—"*Plat. Hoffmanseggii*") [10: 262].
Psilomyia: Four species mentioned. No designation [10: 598].

Psychodidae

Nemopalpus [as "*Nemapalpus*"]: (Type—"*N. flavus*") [8: 605].
Psychoda: Three species mentioned. No designation [10: 605].
Sycorax: Cross reference to *Psychoda* [12: 102].
Tinearia: = *Psychoda*. No species mentioned [12: 588].
Trichoptera: = *Psychoda*. No species mentioned [12: 657].

Ptychopteridae

Bittacomorpha: One species mentioned (*clavipes*). No designation [2: 585].
Ptychoptera: One species mentioned (*contaminata*). No designation [10: 623].

Rhagionidae

Chrysopila: Genus group entry [3: 659].
Leptides: Family/Ordinal group entry [7: 307].
Leptis: One species mentioned (*strigosa*). No designation [7: 308].
Spania: One species mentioned (*nigra*). No designation [11: 708].

Rhagionidae?

Dasyomma: (Type—"*Dasyomma coerulea*") [4: 611].

Rhinophoridae

Melanophora: Genus group entry [8: 70].

Rhinophoridae?

Clytho: Two species mentioned. No designation [4: 25].

Richardiidae

Chlorophora: One species mentioned (*liturata*). No designation [3: 609].
Setellia: One species mentioned (*afra*). No designation [11: 585].

Ropalomeridae

Ropalomera: Two species mentioned. No designation [11: 206].

Sarcophagidae

Agria: One species mentioned (*affinis*). No designation [1: 196].
Araba: One species mentioned (*leucocephala*). No designation [2: 51].
Cynomya: (Type—"*C. mortuorum*") [4: 542].
Diaugia: One species mentioned (*angustata*). No designation [4: 734].
Miltogramma: (Type—"*Miltogramma fasciata*") [8: 220].
Phrissopodia: Two species mentioned. No designation [10: 8].
Sarcophaga: Six species mentioned. No designation [11: 356].
Theria: One species mentioned (*palpalis*). No designation [12: 554].

Scathophagidae

Acolaste: No species mentioned [1: 89].
Amina: One species mentioned (*parisiensis*). No designation [1: 354].
Amina: (Type—"*Amina parisiensis*") [11: 411].
Cleigastra: (Type—"*Cleigastra apicalis* Macq., *Cordylura* ud. Meig.") [4: 3].
Cordylura: (Type—"*Cordylura pubera* Fall.") [4: 236].
Cordylurides: Family/Ordinal group entry [4: 236].
Cordylurites: Family/Ordinal group entry [4: 236].
Delina: Two species mentioned. No designation [4: 659].
Scathophaga [as "*Scatophaga*"]: Two subgenera given with type species [11: 411].
Scatomyza: = *Scatophaga*: No species mentioned [11: 410].
Scatomyza: (Type—"*Scatom. scybalaria*") [11: 411].

Scathophagidae?

Tomella: No species mentioned [12: 600].
Volusia: One species mentioned (*nitida*). No designation [13: 276].

Scatopsidae

Arthria: One species mentioned (*analis*). No designation [2: 172].
Aspites: One species mentioned (*beroliensis*). No designation [2: 240].
Scatopse [as "*Scathopse*"]: (Type—"*Scatopse notata* Meig. (*S. albipennis* Fab.)") [11: 411].

Scenopinidae

Athrichia: = *Scenopinus* [2: 294].
Scenopinii: Family/Ordinal group entry [11: 412].
Scenopinus: One species mentioned (*fenestralis*). No designation [11: 412].

Sciaridae

Molobrus: (Type—"*Tipula Thomae*") [8: 302].
Zygoneura: One species mentioned (*sciarina*). No designation [13: 383].

Sciomyzidae

Chetocera: One species mentioned (*claripennis*). No designation [3: 472].
Dictya: No species mentioned. Cross reference [4: 752].
Dyctya [as "*Dyctia*"]: One species mentioned (*claripennis*). No designation. Notes that Robineau-Desvoidy "re-established" the genus [5: 150].
Graphomyzina: One species mentioned (*elegans*). No designation [6: 305].
Hydromya: Two species mentioned. No designation [6: 754].
Retellia: (Type—"*Ret. claro punctata*") [11: 82].
Sciomyza: Five species mentioned. No designation [11: 435].
Sepedon: (Type—"*S. sphegeus* Fabr. (*S. palustris* Latr., *rufipes* Fabr.)") [11: 552].
Tetanocera: (Type—"*T. ferruginea* Fall.") [12: 525].
Thais: No species mentioned [12: 542].
Thecomyia: One species mentioned (*longicornis*). No designation [12: 550].

Sciomyzidae?

Arina: One species mentioned (*obscura*). No designation [2: 135].
Cylidria: One species mentioned (*femorata*). No designation [4: 512].
Scotimyza: (Type—"*Scotim. fuscipennis* Macq."). [11: 454]

Sepsidae

Anisophysa: Two species mentioned. No designation [1: 539].
Cheligaster: (Type—"*Cheligaster putris*") [3: 453].
Enicopus: (Type—"*Sepsis annulipes* de Meigen") [5: 325].
Nemopoda: (Type—"*N. cylindrica* (. . . *putris* R. D., *nitida* Fall. . . .)") [8: 611].
Orygma: One species mentioned (*luctuosa*). No designation [9: 230].
Sepsidae: Family/Ordinal group entry [11: 557].
Sepsis: (Type—"*S. cynipsea* Fall.") [11: 557].

Simuliidae

Atractocera: = *Simulium*. No designation [2: 311].
Simulides: Family/Ordinal group entry [11: 619].
Simulium: (Type—"*S. reptans* Latr.") [11: 619].

Sphaeroceridae

Apterina: One species mentioned (*pedestris*). No designation [2: 42].
Borborites: Family/Ordinal group entry [2: 654].
Borborus: Three species mentioned. No designation [2: 654].
Ceroptera: One species mentioned (*rufitarsis*). No designation [3: 341].
Crumomya: One species mentioned (*glacialis*). No designation [4: 378].
Heteroptera: One species mentioned (*pusilla*). No designation [6: 602].
Olina: Genus group entry [9: 84].
Sphaerocera: Two species mentioned. No designation [11: 729].
Sphaeroceridae: Family/Ordinal group entry [11: 730].

Sphaeroceridae?

Bacchis: (Type—"*B. cellarum*") [2: 409].
Coprina: One species mentioned (*bovina*). No designation [4: 199].
Fimetia: One species mentioned (*cadaverina*). No designation [5: 634].

Stratiomyidae

Acanthina: (Type—"*A. elongata* Wiedemann") [1: 29].
Acrochaeta: (Type—"*A. fasciata*") [1: 98].
Actina: = *Beris* [1: 108].
Basentidema: One species mentioned (*syrphoides*). No designation [2: 486].
Beris: No designation [2: 549].
Chiromyza: (Type—"*Chiromyza vittata*") [3: 591].
Chrysochlora: Genus group entry [3: 652].
Chrysomyia: Genus group entry [3: 658].
Clitellaria: = *Ephippium* [4: 12].
Cyclogaster: Two species mentioned. No designation [4: 495].
Cyphomyia: (Type—"*Cyph. cyanea* Wiedm. (*Stratiomys* id Fabr.)") [4: 548].
Dicranophora: (Type—"*Dicranophora furcifera* (*Sargus* id. Wiedm.)") [4: 749].
Ephippium: (Type—"*Ephippium thoracicum* Latr.") [5: 352].
Exochostoma: Family/Ordinal group entry [5: 544].
Hermetia: (Type—"*Hermetia illucens* Latr. (*Musca leucopa* Linn.)") [6: 575].
Hoplistes: (Type—"*Sargus bispinosus* Wiedm.") [6: 676].
Nemotelus: (Type—"*Nemotelus pantherinus* Macq. (. . . *uliginosus* Latr., *marginatus* Fab.") [8: 612].
Odontomyia: One species mentioned (*viridula*). No designation [8: 723].
Oxycera: Eight species mentioned. No designation [9: 364].
Pachygaster: Two species mentioned. No designation [9: 385].
Platyna: (Type—"*Plat. hastata* Wied.") [10: 254].
Ptilocera: (Type—"*P. quadridentata* Wied.") [10: 619].
Raphiocera: (Type—"*Raph. armata* Macq. (*Sargus* id. Wied.)") [10: 720].
Sargus: One species (*cuprarius*) mentioned. No designation [11: 362].
Stratiomydae: Family/Ordinal group entry [12: 53].
Stratiomys: (Type—"*Stratiomys chamaeleon* Fabr.") [12: 53].
Thorasena: No species mentioned [12: 560].

Vappo: = *Pachygaster* [13: 5].
Xenomorpha: No species mentioned [13: 313].

Syrphidae

Aphritis: (Type—"*Aph. apiformis*") [2: 3].
Ascia: One species mentioned (*podagricus*). No designation [2: 209].
Baccha: One species mentioned (*elongata*). No designation [2: 409].
Brachyopa: Two species mentioned. No designation [2: 710].
Brachypalpus [as "*Brachypa*"]: Vernacular is given as "Brachypalpe" as well as the derivation [2: 710].
Callicera: One species mentioned (*aenea*). No designation [3: 51].
Cenogaster: = *Volucella* [3: 259].
Ceratophya: Three species mentioned. No designation [3: 291].
Ceria: Three species mentioned. No designation [3: 334].
Cheilosia: One species mentioned (*vidua*). No designation [3: 438].
Chrysogaster: Genus group entry [3: 653].
Chrysotoxum: Genus group entry [3: 661].
Chymophila: One species mentioned (*splendens*). No designation [3: 663].
Criorhina: (Type—"*Cr. apicata* Macq.") [4: 344].
Didea: One species mentioned (*fasciata*). No designation [5: 6].
Dimeraspis: One species mentioned (*podagra*). No designation [5: 18].
Doros: Three species mentioned. No designation [5: 115].
Eristalis: No species mentioned [5: 405].
Eumerus: One species mentioned (*grandis*). No designation [5: 495].
Graptomyza: (Type—"*Grapt. ventralis*") [6: 307].
Helophilus [as "*Elophilus*"]: One species mentioned (*pendula*). No designation [5: 280].
Merodon: Genus group entry [8: 149].
Milesia: Several species mentioned. No designation [8: 214].
Mixogaster: One species mentioned (*conopsoides*). No designation [8: 252].
Mixtemyia: One species mentioned (*quadrifasciata*). No designation [8: 252].
Ocyptamus: Two species mentioned. No designation [8: 718].
Orthonevra: Two species mentioned. No designation [9: 215].
Palpada: No designation [5: 405].
Palpada: (Type—"*Palp. scutellata*") [9: 428].
Paragus: One species mentioned (*bicolor*). No designation [9: 478].
Pelecocera: (Type—"*Pelec. tricincta* Hoffm.") [9: 548].
Pipiza: Six species mentioned. No designation [10: 216].
Platynochaetus: One species mentioned (*setosus*). No designation [10: 255].
Psarus: Two species mentioned. No designation [10: 588].
Psilota: (Type—"*Philota anthracina*"). [10: 599].
Rhingia: Two species mentioned. No designation [11: 91].
Senogaster: One species mentioned (*caerulescens*). No designation [11: 551].
Sericomyia: One species mentioned (*mussitans*). No designation [11: 561].
Spazigaster: One species mentioned (*apennini*). No designation [11: 720].
Sphaerophoria: (Type—"*S. scripta* (*Scaeva menthastri* Fall.)") [11: 732].
Sphecomyia: One species mentioned (*boscii*). No designation. *Sphecomyia boscii*, new species-group name [11: 737].
Sphegina: One species mentioned (*craipes*). No designation [11: 743].
Spilomyia: No species mentioned [11: 763].
Syritta: One species mentioned (*pipicus*). No designation [12: 135].
Syrphidae: Family/Ordinal group entry [12: 135].
Syrphus: Three species mentioned. No designation [12: 135].
Temnocera: One species mentioned (*violacea*). No designation [12: 446]
Temnostoma: No species mentioned [12: 447].
Triglyphus: No species mentioned [12: 668].
Tropidia: Three species mentioned. No designation [12: 704].
Volucella: One species mentioned (*bombylans*). No designation [13: 276].
Xylota: (Type—"*Xylota ignava* Meig.") [13: 331].

Tabanidae

Acanthocera: (Type—"*A. longicornis* Macquart (*Tabanus longicornis* Fabricius)") [1: 30].
Chrysopites: Family/Ordinal group entry [3: 660].
Chrysops: (Type—"*Chrysops caecutiens* Meig.") [3: 660].
Chrysopsis: = *Chrysops* [3: 660].
Diabasis: (Type—"*Diabasis bicinctus* (*Tabanus* id. Fabr.)") [4: 717].
Dichelacera: One species mentioned (*immaculata*). No designation [4: 739].
Dicrania: One species mentioned (*cervus*). No designation [4: 748].
Ectenopsis: One species mentioned (*vulpecula*). No designation [5: 204].
Erodiorhynchus: One species mentioned (*eristaloides*). No designation [5: 407].
Haematopota: (Type—"*Haematopota pluvialis* (*Tabanus* id. Linn.)") [6: 454].
Lepiselaga: Three species mentioned. No designation [7: 304].
Pangonia: One species mentioned (*maculata*). No designation [9: 441].

Rhinomyza: (Type—"*Rhinomyza fusca* Wied.") [11: 107].

Selasoma: No species mentioned [11: 534].

Silvius: (Type—"*S. vituli*") [11: 615].

Tabanii: Family/Ordinal group entry [12: 313].

Tabanus: Invalid designation of *T. morio* Latr. . . . et *T. cervicornis* Fabr. . . . *T. aurocinctus* Fab. [12: 344].

Tabanus: Cross reference [12: 313].

Tanyglossa: = *Pangonia*. No species mentioned [12: 342].

Tachinidae

Acemya [as "*Acemyia*"]: No species mentioned [1: 61].

Acemya: (Type—"*T. oblonga*") [12: 318].

Actia: = *Thryptocera* Macquart [1: 107].

Albinia: One species mentioned (*buccalis*). No designation [1: 245].

Alophora: Two species mentioned. No designation [1: 293].

Amedea: Family/Ordinal group entry [1: 346].

Aphria: Two species mentioned. No designation [2: 3].

Aplomya: One species mentioned (*zonata*). No designation [2: 15].

Argyritis: No species mentioned [2: 128].

Aria: One species mentioned (*fulvicrus*). No designation [2: 134].

Aricia: Two species mentioned. No designation [2: 133].

Athrycia: Two species mentioned. No designation [2: 294].

Belvoisia: One species mentioned (*bicincta*). No designation [2: 540].

Bengalia: (Type—"*B. testacea*") [2: 542].

Besseria: One species mentioned (*reflexa*). No designation [2: 555].

Billaea: One species mentioned (*grisea*). No designation [2: 573].

Blainvillia: One species mentioned (*palpata*). No designation [2: 590].

Blondelia: (Type—"*B. nitida*") [2: 609].

Bonnellia: Three species mentioned. No designation [2: 648].

Bonnetia: Two species mentioned. No designation [2: 649].

Brachelia: One species mentioned (*westermanni*). No designation [2: 700].

Carcelia: One species mentioned (*amaena*). No designation [3: 164].

Cassidaemyia: (Type—"*C. clausa* Macq.") [3: 209].

Catilia: One species mentioned (*nitida*). No designation [3: 234].

Ceranthia: Two species mentioned. No designation [3: 285].

Ceromya: One species mentioned (*erythrocera*). No designation [3: 338].

Chrysosoma: One species mentioned (*viridis*). No designation [3: 661].

Cistogaster: (Type—"*Cist. globosa* Macq., *Gymnosoma* id. Meig."). *Pallasia* R.-D. given as a synonym [3: 722].

Clairvillia: One species mentioned (*pusilla*). No designation [3: 734].

Clelia: (Type—"*Clelia agilis* Rob.-Desv.") [4: 4].

Clytia: One species mentioned (*continua*). No designation [4: 27].

Crameria: One species mentioned (*oestroidea*). No designation [4: 316].

Curtocera: One species mentioned (*bicincta*). No designation. *Duvaucelia* Robineau-Desvoidy given as a synonym. [4: 472].

Dejeania: Two species mentioned. No designation [4: 657].

Dexia: One species mentioned (*rustica*). No designation [4: 715].

Dexiariae: Family/Ordinal group entry [4: 716].

Diaphania: One species mentioned (*testacea*). No designation [4: 728].

Dinera: One species mentioned (*crista*) (= *imperatoriae*). No designation [5: 31].

Dionaea: Two species mentioned. No designation [5: 41].

Dufouria: (Type—"*aperta*") [5: 143].

Dumerilia: One species mentioned (*rubida*). No designation [5: 145].

Duvaucelia: One species mentioned (*bicincta*). No designation [5: 149].

Duvaucelia: = *Curtocera*. No species mentioned [4: 472].

Echinomyia: (Type—"*Musca grossa* Linn.") [5: 190].

Elomyia: One species mentioned (*nebulosa*). No designation [5: 279].

Elophoria: One species mentioned (*myoidea*). No designation [5: 280].

Erebia: One species mentioned (*tremula*). No designation [5: 385].

Eriothrix: One species mentioned (*lateralis*). No designation [5: 403].

Ernestia: One species mentioned (*microcera*). No designation [5: 406].

Ervia: One species mentioned (*triquestra*). No designation [5: 414].

Erycia: One species mentioned (*grisea*). No designation [5: 416].

Erycinae: Family/Ordinal group entry [5: 417].

Erynnia: One species mentioned (*nitida*). No designation [5: 418].

Estheria: One species mentioned (*imperatoria*). No designation [5: 453].

Eurygaster: One species mentioned (*rustica*). No designation [5: 519].

Exorista: (Type—"*Musca larvarum* de Linne") [5: 545].

Fabricia: One species mentioned (*fer* Meig.) (= *rotundata*). No designation [5: 548].

Faurella: One species mentioned (*meridionalis*). No designation [5: 572].

Fausta: One species mentioned (*nigra*). No designation [5: 573].

Feburia: One species mentioned (*rapida*). No designation [5: 575].

Feria: Two species mentioned. No designation [5: 602].

Fischeria: One species mentioned (*bicolor*). No designation [5: 635].
Freroea: One species mentioned (*gagatea*). No designation [5: 721].
Germaria: One species mentioned (*latifrons*). No designation [6: 204].
Gigamyia: (Type—"*Stomoxis gigantea* Wiedm.") [6: 216].
Gonia: Two species mentioned. No designation [6: 267].
Guerinia: Invalid designation of *T. pallipalpis* [12: 318].
Gymnochaeta: = *Chrysosoma* [6: 435].
Gymnosoma: (Type—"*Gymnosoma rotundata* Meig.") [6: 439].
Gymnostylia: (Type—"*G. depressa*"): = *Macromyia, Harrisia & Leschenaultia* R.-D [6: 439].
Harrisia: Two species mentioned. No designation [6: 493].
Hebia: One species mentioned (*flavipes*). No designation [6: 496].
Helina: One species mentioned (*euphemoidea*). No designation [6: 516].
Hemyda: Three species mentioned. No designation [6: 535].
Hyalomyia: (Type—"*H. atropurpurea* R.D. (*Phasia* id. Meig.)") [6: 721].
Hystricia: Three species mentioned. No designation [6: 792].
Lophosia [as "*Lophasia*"]: One species mentioned (*fasciata*). No designation [7: 441].
Masicera: Genus group entry [8: 23].
Meigenia: (Type—"*T. cylindrica*") [12: 318].
Micropalpus: (Type—"*Micropalpus vulpinus*") [8: 200].
Myobia: Two species mentioned. No designation [8: 505].
Nemoraea: Two species mentioned. No designation [8: 611].
Ocyptera: Seven species mentioned. No designation [8: 719].
Omalogaster: Four species mentioned. No designation [9: 92].
Pallasia: = *Cistogaster*. No species mentioned [9: 417].
Phania: Seven species mentioned. No designation [9: 721].
Phasia: Five species mentioned. No designation [9: 724].
Prosena: Three species mentioned. No designation [10: 561].
Ptilocera: Four species mentioned. No designation [10: 619].
Ramphina: Two species mentioned. No designation [10: 709].
Rutilia: Three species mentioned. No designation [11: 278].
Scotioptera: Two species mentioned. No designation [11: 454].
Senometopia: (Type—"*S. atropivora*") [11: 552].
Sericocera: One species mentioned (*leucozona*) (= *abdominalis & nigrina*). No designation [11: 560].
Servillia: One species mentioned (*ursina*). No designation [11: 578].
Siphona: (Type—"*S. geniculata* Meig.") [11: 633].
Smidtia: (Type—"*S. vernalis* Rob.-Desv.") [11: 649].
Sophia: = *Scotioptera*: No species mentioned [11: 683].
Spallanzania: No species mentioned [11: 708].
Stevenia: (Type—"*S. tomentosa* Rob.-Desv.") [12: 32].
Strongygaster [as "*Strongylogaster*"]: One species mentioned (*globula*). No designation [12: 65].
Sturmia: (Type—"*S. atropivora* Rob.-Desv.") [12: 77].
Tachina: Invalid designation of *Tachina larvarum* Meig., Lin., Fabr. [12: 317].
Tachinariae: Family/Ordinal group entry [12: 317].
Thelaira: One species mentioned (*abdominalis*). No designation [12: 550].
Thelida: One species mentioned (*filiformis*). No designation [12: 550].
Themira: Two species mentioned. No designation [12: 552].
Theresia: One species mentioned (*tandree*). No designation [12: 553].
Thryptocera: (Type—"*T. setipennis* Fallen") [12: 564].
Triarthria: No species mentioned [12: 643].
Trichodura: No species mentioned [12: 654].
Trichopoda: One species mentioned (*formosa*). No designation [12: 657].
Trichoprosopus: No species mentioned [12: 657].
Trixa: (Type—"*T. caerulescens* Meig.") [12: 693].
Uramyia: One species mentioned (*producta*). No designation [12: 764].
Voria: One species mentioned (*latifrons*). No designation [13: 282].
Voria: (Type—"*Tachina latifrons*") [12: 318].
Wagneria: One species mentioned (*gagatea*). No designation [13: 288].
Wahlbergia: No species mentioned [13: 288].
Weberia: One species mentioned (*appendiculata*). No designation. [13: 293]
Winthemia: (Type—"*W. quadripustulata*") [13: 301].
Xysta: One species mentioned (*gagatea*). No designation [13: 334].
Zaida: Three species mentioned. No designation [13: 340].
Zaira: No species mentioned [13: 340].
Zelia: One species mentioned (*analis*). No designation [13: 345].
Zenais: (Type—"*Z. silvestris*") [13: 346].
Zeuxia: One species mentioned (*cinerea*). No designation [13: 350].
Zophomyia: (Type—"*Zophomyia temula* Scop.") [13: 377].

Tanypezidae

Tanypeza: One species mentioned (*longimana*). No designation [12: 343].

Tephritidae

Acinia: (Type—"*Acinia corniculata* Fabricius, ou l'*A. Javeae* Rob. Desv.") [1: 85].

Blephariptera: Two species mentioned. No designation [2: 606].

Bractrocera [as "*Bractocera*"]: One species mentioned (*longicornis*). No designation. Credits name to Guérin, not Macquart [2: 415].

Ceratitis: Stated as monotypic: Three species mentioned. *Petalophora* Macquart given as a synonym [3: 288].

Dacus: Invalid designation of *Dacus oleae* Meig. [4: 574].

Dasyneura: One species mentioned (*zonata*). No designation [4: 611].

Ensina: One species mentioned (*sonchi*). No designation [5: 330].

Forellia: (Type—"*Forellia onopordi*") [5: 676].

Herina: Two species mentioned. No designation [6: 559].

Senopterina: One species mentioned (*brevipes*). No designation [11: 552].

Sitarea: (Type—"*S. scorzonerae* Rob.-Desv. -*Musca Doronici?* DeGeer") [11: 643].

Sphenella: One species mentioned (*linariae*). No designation [11: 744].

Strauzia: One species mentioned (*inermis*). No designation [12: 53].

Stylia: (Type—"*S. maculata* Robineau-Desvoidy") [12: 78].

Tephritidae: Family/Ordinal group entry [12: 455].

Tephritis: (Type—"*T. artemisiae* Fab.") [12: 455].

Terellia: (Type—"*T. pallens* Meig.") [12: 472].

Trupanea: *Trypeta*: No species mentioned [12: 710].

Trypeta: *Tephritis*: No species mentioned [12: 711].

Urellia: Two species mentioned. No designation [12: 790].

Urophora: One species mentioned (*cardui*) (= *reaumurii*). No designation [12: 793].

Vidalia: One species mentioned (*impressifrons*). No designation [13: 220].

Xyphosia: (Type—"*Xyphosia cirsiorum*") [13: 332].

Tethinidae

Tethina: No species mentioned [12: 526].

Thaumaleidae

Thaumalea: No species mentioned [12: 546].

Therevidae

Ruppellia: (Type—"*Rupp. semiflava* Wied.") [11: 272].

Thereva: Invalid designation of *T. nobilitata* et *plebeia* Latr. [12: 554].

Tipulidae

Anisomera: One species mentioned (*nigra*). No designation [1: 537].

Aporosa: Two species mentioned. No designation [2: 33].

Cerozodia: Genus group entry [3: 342].

Chenesia: One species mentioned (*castanea*). No designation [3: 469].

Chionea [as "*Chione*"]: One species mentioned (*araneoides*). No designation [3: 588].

Ctenogyna: No species mentioned [4: 443].

Ctenophora: (Type—"*Ctenophora pectinicornis* Meig. (*Tipula* id. Linn.)") [4: 444].

Cylindrotoma: (Type—"*Cylind. distinctissima* (*Limnobia* id. Meig.)") [4: 514].

Dicranomyia: No species mentioned [4: 749].

Dictenidia: (Type—"*Tipula bimaculata* de Linne") [4: 752].

Dolichopeza: One species mentioned (*sylvicola*). No designation [5: 98].

Enchocera [as "Enchocere"]: = *Xiphocere* [5: 302].

Eriocera: One species mentioned (*nigra*). No designation [5: 398].

Erioptera: Two species mentioned. No designation [5: 401].

Eriopteryx: = *Erioptera* [5: 401].

Geranomyia: One species mentioned (*unicolor*). No designation [6: 201].

Glochina: One species mentioned (*sericata*). No designation [6: 235].

Gonomyia: = *Limnobia* [6: 275].

Gynoplistia: Two species mentioned. No designation [6: 441].

Hexatoma: One species mentioned (*bimaculata*). No designation [6: 613].

Idioptera: One species mentioned (*maculata*). No designation [7: 17].

Limnobia: One species mentioned (*lutea*). No designation [7: 379].

Limnophila: One species mentioned (*picta*). No designation [7: 380].

Megistocera: One species mentioned (*filipes*). No designation [8: 63].

Nematocera: = *Hexatoma*. Cross reference [8: 606].

Nephrotoma: One species mentioned (*dorsalis*). No designation [8: 620].

Ozodicera: One species mentioned (*ochracea*). No designation [9: 377].

Pachyrhina [as "*Pachyrina*"]: Four species mentioned. No designation [9: 389].

Pedicia: (Type—"*Pedicia rivosa* Lat.") [9: 533].

Polymera: Two species mentioned. No designation [10: 387].

Rhamphidia [as "*Ramphidia*"]: Two species mentioned. No designation [10: 709].

Rhipidia: One species mentioned (*maculata*). No designation [11: 110].

Siagona: No species mentioned [11: 593].

Styringomia: Genus group entry [12: 85].

Symplecta: Two species mentioned. No designation [12: 123].

Synapha: One species mentioned (*fasciata*). No designation [12: 126].

Tanyptera: No species mentioned [12: 343].

Tipula: Two species mentioned. No designation [12: 592].

Tipulariae: Family/Ordinal group entry [12: 591].

Tricyphosia: No species mentioned [12: 663].

Ula: One species mentioned (*mollissima*). No designation [12: 752].

Unomyia: = *Limnobia*. No species mentioned [12: 762].

Xiphocera: One species mentioned (*percheronii*). No designation [13: 318].

Xiphura: Notes on synonymy with *Ctenophora* [13: 320].

Trichoceridae

Trichocera: Two species mentioned. No designation [12: 651].

Vermileonidae

Vermileo: One species mentioned (*degeerii*) (= *vermileo*). No designation [13: 186].

Xylophagidae

Coenomyia: Two species mentioned. No designation [4: 78].

Pachystomus: (Type—"*Pachyst. syrphoides* Lat. (*Rhagio* id. Panz.)") [9: 391].

Sicarii: Family/Ordinal group entry [11: 595].

Sicus: No species mentioned [11: 595].

Subula: (Type—"*S. marginata* Meg.") [12: 86].

Xylophagii: Family/Ordinal group entry [13: 329].

Xylophagus: Two species mentioned. No designation [13: 324].

Hispinae of the New Guinea-Solomons Area. II. Tribe Coelaenomenoderini (Coleoptera: Chrysomelidae)[1]

J. L. Gressitt and G. A. Samuelson[2]

ABSTRACT

Five genera of Coelaenomenoderini are found in the area studied, including 1 new genus, *Bulolispa*, with 2 new species. *Cyperispa* has 8 species or subspecies of which 4 are described as new; *Heterrhachispa* remains with its single species; *Enischnispa* has 6 species or subspecies of which 2 are new; and *Pharangispa* has 8 of which 5 are new. All taxa are keyed and all new taxa are illustrated.

INTRODUCTION

The tribe Coelaenomenoderini Weise (1911) is distributed throughout the Old World tropics and is limited in the Pacific to the Papuan area, viz., New Guinea and nearby archipelagos, northern Queensland, and the Solomon Islands. Weise (1911) and Würmli (1975) keyed the genera. The tribe contains 9 genera and 1 subgenus, including 1 new genus added herein. Five genera with 25 species and subspecies are listed for the area.

This paper covers all the Coelaenomenoderini recorded for the Papuan area and adds those specimens that accumulated in Bishop Museum since the previous reports by Gressitt (1957, 1960, 1963). Nearly all the specimens were obtained through Bishop Museum fieldwork, mostly in Papua New Guinea and the Solomon Islands. Additional specimens treated herein were borrowed from other collections, which are identified by their codens in the Material Examined sections. Holotypes of all the new taxa are deposited in Bishop Museum. Citations without codens indicate Bishop Museum as the depository; however, parts of series may be distributed to other institutions. Depositories are identified as follows: ANIC = Australian National Insect Collection, Canberra; BMNH = British Museum (Natural History), London; BPBM = Bishop Museum, Honolulu; CASC = California Academy of Sciences, San Francisco; HSIC = Ministry of Natural Resources, Honiara; KONE = Department of Primary Industry, Konedobu; MNHN = Museum National d'Histoire Naturelle, Paris; USNM = National Museum of Natural History, Washington, D.C.; ZSMC = Zoologische Staatssammlung, München.

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In new species or subspecies proposed herein, the holotype and allotype descriptions are restricted to only the individual being described.

Measurements of body length and body breadth are rounded to the nearest 0.05 mm; other measurements are rounded to the nearest 0.01 mm.

SYSTEMATICS

All 5 genera treated herein are restricted to the Papuan area.

Key to Papuan Genera of Coelaenomenoderini

1. Antenna with less than 11 segments 2
   Antenna with 11 segments . . . . ***Cyperispa***

2(1). Antenna with 8 segments (8th sometimes suggestive of 3 segments); elytral costae subuniform or alternate interstices more strongly raised than others 3
   Antenna with 6 segments; 4th, 7th, and 8th elytral interstices much more strongly costate than others . . . . ***Heterrhachispa***

3(2). Elytral costae not uniform, alternate interstices more prominent than others; lateral margin of elytron not flattened; last antennal segment without conspicuous pits 4
   Elytral costae uniform, feeble; lateral margin of elytron expanded, flat, well visible from above; last antennal segment with numerous large sensory pits . . . . ***Pharangispa***

4(3). Prothorax slightly constricted preapically, slightly broadened apically; 6th elytral interstice very prominent, hiding lateral margin in dorsal view . . . . ***Enischnispa***
   Prothorax nearly straight at side, slightly narrowed at apex, not collared; 7th elytral interstice prominent but not completely hiding margin . . . . ***Bulolispa*, n.gen.**

Genus *Cyperispa* Gressitt

Cyperispa Gressitt, 1957, Nova Guinea, n. s. 8(2):268 (type species: *Cyperispa hypolytri* Gressitt; Solomon Is); 1960, Pac. Insects 2(1):66.—Würmli, 1975, Entomol. Arb. Mus. Frey 26:40, 44.

Key to Species of *Cyperispa*

1. Posterolateral portion of pronotum with large oblique depression; elytron largely pale, usually with dark transverse band, sometimes entirely pale, or with dark apical region 2
   Posterolateral portion of pronotum with 2 depressions separated by distinct ridge; elytron and basal ½ of pronotum black; body length 6.9–7.6 mm . . . . ***hypolytri***

2(1). Body length to 5.0 mm, commonly around 4.5 mm 3
   Body length >5.0 mm, nearly always over 5.25 mm 6

3(2). Elytron largely pale but with dark transverse band preapically, broadest behind middle 4
   Elytron entirely pale, broadest at middle; body length 4.1 mm . . . . ***lungae*, n. sp.**

4(3). Pronotum almost impunctate on central portion, median line not carinate behind middle 5
   Pronotum with some punctures on central portion, median line carinate behind middle; elytral dark band not prolonged posteriorly along suture; body length 4.3 mm . . . . ***s. scleriae***

5(4). Elytron with dark band prolonged posteriorly and narrowly along suture; body length 3.95–4.2 mm . . . . ***s. malaitensis***
   Elytron with dark band not prolonged posteriorly; body length 4.5–5.15 mm . . . . ***s. gelae*, n. subsp.**

6(2). Elytron with dark band across middle 7
   Elytron with dark region apically, obliquely extending forward at suture almost to middle of elytron; body length 5.0–6.2 mm . . . . ***palmarum*, n. sp.**

7(6). Elytral dark band relatively broad, about 0.50–0.54 × as long as elytron; abdominal sterna sometimes black; body length 5.8–6.6 mm . . . . ***t. thoracostachyi***

Elytral dark band relatively narrow, about 0.42–0.43 × as long as elytron; abdominal sterna never black; body length 5.2–6.0 mm . . . . ***t. kolombangara*, n. subsp.**

Cyperispa hypolytri Gressitt Fig. 5A

Cyperispa hypolytri Gressitt, 1957, Nova Guinea, n. s. 8(2):268, figs. 19a, c, d, e (Guadalcanal; BPBM); 1960, Pac. Insects 2(1):66, 67.

Material examined. None additional to type series.

Distribution. Solomon Islands (Guadalcanal).

Cyperispa scleriae scleriae Gressitt Fig. 4A

Cyperispa scleriae Gressitt, 1957, Nova Guinea, n. s. 8(2):268, 271 (Guadalcanal; BPBM); 1960, Pac. Insects 2(1):67, 68.

Material examined. None additional to type series.

Distribution. Solomon Islands (Guadalcanal).

Remarks. The holotype is male (teneral), not female as originally indicated.

Cyperispa scleriae malaitensis Gressitt Fig. 4B

Cyperispa scleriae malaitensis Gressitt, 1960, Pac. Insects 2(1):67, 68 (Malaita; BPBM).

Material examined. None additional to type series.

Distribution. Solomon Islands (Malaita).

Remarks. The sex of the holotype was not originally indicated; it is male.

Cyperispa scleriae gelae Gressitt, **new subspecies** Figs. 1A, 4C, 5B

MALE (holotype). Testaceous; antenna black, with pitchy brown on segments 1, 2, and 11; elytron with band from just behind middle to top of apical declivity, produced forward at suture in triangle reaching slightly anterior to middle. Body length 4.75 mm; breadth 1.55 mm.

Head not quite as broad as prothorax (24:25), smooth above; interantennal process blunt, hardly reaching middle of scape. *Antenna* not quite ½ as long as body, moderately stout; scape and pedicel subequal; $3 > 1 + 2$ and subequal to $4 + 5$; $4 = 11$. *Prothorax* longer than broad (27:25), widest near apex, constricted near base; disc largely smooth, punctured and hairy near apex, a few punctures at center and laterobasal depression. *Elytron* distinctly widened posteriorly, widest in 3rd ¼; disc regularly seriate-punctate with alternate interstices stronger. *Venter* largely impunctate on thorax, finely punctured on abdomen. *Legs* smooth.

FEMALE (allotype). Antenna not quite ⅖ as long as body. Body length 5.0 mm; breadth 1.85 mm.

PARATYPES. Body length 4.5–5.15 mm; breadth 1.5–1.65 mm.

Type data. Holotype ♂ (BPBM 14,583) and allotype ♀ (BPBM) SOLOMON IS: Florida Group: Nggela I: Haleta, 1–10 m, 2–5.x.1964, long sedge [*Thoracostachyum*?] nr sago swamp (R. Straatman); paratopotypes: 10, same data; 2, same data, except 2–3.x.1964, long sedges nr sago swamp. Some BPBM paratypes deposited in ANIC, BMNH, HSIC, USNM, ZSMC.

Remarks. Differs from *s. scleriae* in being larger and relatively broader, with a wider dark band on elytra.

Cyperispa thoracostachyi thoracostachyi Gressitt Fig. 5C

Cyperispa thoracostachyi Gressitt, 1960, Pac. Insects 2(1):66, 67 (Malaita; BPBM).

Material examined. None additional to type series.

Distribution. Solomon Islands (Malaita).

Remarks. The sex of the holotype was not originally indicated; it is female.

Cyperispa thoracostachyi kolombangara Gressitt, **new subspecies** Figs. 1C, 4D, 5D

MALE (holotype). Pale castaneous; antenna pitchy in middle, quite pale on last 2 segments; elytron with broad black band on middle ⅓. Body length 6.0 mm; breadth 1.95 mm.

Head smooth above; interantennal process stout. *Antenna* over ½ as long as body. *Prothorax* slightly longer than broad, broadest just before apex; disc punctured, with erect hairs on anterior ⅓, few punctures on rest. *Elytron* regularly punctate-striate, alternate interstices slightly stronger.

FEMALE (allotype). Color paler. Antenna ½ as long as body. Body length 5.3 mm; breadth 1.9 mm.

PARATYPES. Most reddish, often elytron paler than pronotum. Body length 5.2 mm; breadth 1.8–2.3 mm.

Type data. Holotype ♂ (BPBM 14,584), SOLOMON IS: New Georgia Group: Kolombangara I: S slope, nr Kukundu, 200 m, 9.vii.1959, on sedge #3512 (J. L. Gressitt); allotype ♀ (BPBM), Iriri, 100 m, 3.vii.1964 (J. & M. Sedlacek); 1 paratopotype, same data as holotype, except 300 m, on sedge #3510 (Gressitt); 35 paratypes, same data as allotype; 7, same loc., 100 m, 30.vi.1964, palm, *Pandanus* (Sedlaceks); 12, same loc., 100–250 m, 1.vii.1964, palm, *Pandanus* [some without host label] (Sedlaceks). Some BPBM paratypes deposited in ANIC, BMNH, CASC, HSIC, KONE, MNHN, USNM, ZSMC.

Remarks. Differs from *t. thoracostachyi* Gressitt in being slightly smaller, more reddish, with the elytral band narrowed and nearly transverse anteriorly and the elytron more pubescent.

Cyperispa lungae Gressitt, **new species** Figs. 1B, 5E

FEMALE (holotype). Testaceous, ochraceous on pronotum and basal ½ of elytron; antenna red-pitchy, paler distally and still paler on segments 1–2. Body length 4.1 mm; breadth 1.35 mm.

Head as broad as prothorax, smooth above; interantennal process obtuse, not reaching middle of scape. *Antenna* ½ as long as body, slender in middle; segment 3 = 4 + 5, much longer than 1 + 2, all longer than 4. *Prothorax* slightly longer than broad (25:22), strongly constricted near base, widest near apex; disc largely smooth, undulating at side, punctures in depressions and 3 at center; hairy and punctured in 3 preapical depressions. *Elytron* slender, widest in middle, hairy, punctures largely alternating in paired rows; interstices weak. *Venter* finely punctured on abdomen. *Legs* smooth.

Type data. Holotype ♀ (BPBM 14,585), SOLOMON IS: Guadalcanal I: Lunga River bridge, 3.ix.1960, "light trap" (C.W. O'Brien).

Remarks. Differs from *s. scleriae* in having elytron unicolorous, more slender postmedially, more broadly margined in middle with punctures staggered (zigzag) within double rows.

Cyperispa palmarum Gressitt, **new species** Figs. 1D, 4E, 5F

MALE (holotype). Ochraceous, with antenna dusky from dense black hairs except on segments 1, 2, and 11; elytron with posterior ⅖ blackish brown, dark area extending forward along suture to just anterior to middle; abdomen slightly pitchy. Body length 5.55 mm; breadth 1.9 mm.

Head nearly as broad as prothorax (28:29), smooth above; interantennal process blunt, not reaching middle of scape. *Antenna* slightly over ½ as long as body, appearing stout because of dense hairs; segment 3 much longer than 1 + 2, distinctly shorter than 4 + 5 and distinctly longer than 10 + 11. *Prothorax* just longer than broad (30:29), constricted near base, widest ⅓ from apex; disc punctured, hairy on anterior ⅓, smooth with few punctures behind middle. *Elytron* distinctly widened behind middle, widest in 3rd ¼; disc evenly seriate punctate, interstices almost uniform. *Venter* feebly punctured, stronger on side of prothorax. *Legs* short, fairly smooth.

FEMALE (allotype). Body length 6.2 mm; breadth 2.25 mm.

PARATYPES. Body length 5.0–6.8 mm; breadth 1.9–2.4 mm.

Type data. Holotype ♂ (BPBM 14,586) and allotype ♀ (BPBM), SOLOMON IS: Santa Isabel I: Tatamba, 1–50 m, 1.ix.1964, on tall palms, also pinnate palms (R. Straatman); paratopotypes: 4, same data; 3, same data, except tall, small palm [*Ptychosperma*?]; 11, same loc., 0–50 m, 3.ix.1964, small pinnate palm, rattans, fan leaf palm (Straatman); 1, same data, except 6.ix.1964, tall palms; paratypes: 2, Ovi Vill, nr Tatamba, 16.ix.1964, sago palm, *Metroxylon* (Straatman); 1, Togilava Riv, 0–50 m, 6.ix.1964, tall palm (Straatman). Some BPBM paratypes deposited in ANIC, BMNH, CASC, HSIC, USNM, ZSMC.

Remarks. Differs from *hypolytri* Gressitt in having the pronotum entirely pale and the elytron pale with a pitchy posterior area, and in having the pronotum smoother and more flattened.

Genus ***Heterrhachispa*** Gressitt

Heterrhachispa Gressitt, 1957, Nova Guinea, n. s. 8(2):272 (type species: *H. kurandae* Gressitt; Queensland); 1960, Pac. Insects 2(1): 69.—Würmli, 1975, Entomol. Arb. Mus. Frey 26:41, 44.

Remarks. This monotypic genus has Papuan affinities. It appears to be restricted to northern Queensland, Australia.

Heterrhachispa kurandae Gressitt Fig. 5G

Heterrhachispa kurandae Gressitt, 1957, Nova Guinea, n. s. 8(2):273, fig. 20a; 1960, Pac. Insects 2(1):69.

Material examined. None additional to holotype.

Distribution. Australia (northern Queensland).

Genus ***Enischnispa*** Gressitt

Enischnispa Gressitt, 1957, Nova Guinea, n. s. 8(2):274 (type species: *E. calamivora* Gressitt; New Ireland); 1960, Pac. Insects 2(1):69; 1963, ibid. 5(3):662.—Würmli, 1975, Entomol. Arb. Mus. Frey 26:42, 45.

Key to Species of *Enischnispa*

1. Elytral puncture rows 3 and 4 merged into 1 row along more than middle ⅓; dorsum largely or entirely blackish 2
Elytral puncture rows 3 and 4 complete throughout, punctures may be crowded, more or less irregular along middle; dorsum largely blackish or not 3
2(1). Elytron in postmedian portion with interstice 2 much more strongly raised than 3; tarsi reddish; body length 3.5–4.25 mm . . . (NE New Guinea) . . . . ***rattana***

Elytron in postmedian portion with interstice 3 a little more strongly raised than 2; tarsi nearly black; body length 4.25 mm . . . (SE New Guinea: Vogelkop) . . . . ***daemonoropa***

3(1). Body length <3.5 mm; elytral disc at least narrowly pale, postmedian area briefly darkened 4

Body length >3.5 mm; dorsum largely blackish, preapex of elytron with brief yellow streaks on interstices 2 and 4; elytron more or less slender, 4.6 × as long as broad; elytral interstices 2, 4, 6 strongly raised, lacking high transverse interspaces between punctures; body length 4.3 mm . . . (SE New Guinea) . . . . ***palmicola***

4(3). Elytron relatively stout: <4.5 × as long as broad; elytral postmedian dark area usually not reaching suture 5

Elytron relatively slender: 4.7–5.0 × as long as broad; elytral postmedian dark area more or less reaching narrowly darkened suture; elytral apex more or less sinuate or angular because of prominent interstices; body length 2.85–3.05 mm . . . (SE New Guinea) . . . . ***calamella*, n. sp.**

5(4). Elytral suture pale or narrowly pale pitchy for most of length; venter pale; pronotum with 2 impunctate areas medially, slightly before and behind middle; elytral apex rounded; body length 3.15–3.5 mm . . . (New Ireland) . . . . ***c. calamivora***

Elytral suture darkened narrowly; venter usually dark; pronotum with impunctate areas larger, more connected, more or less T-shaped; elytral apex blunt, more or less subtruncate at extremity; body length 2.7–3.15 mm . . . (NE and SE New Guinea) . . . . ***c. papuana*, n. subsp.**

Enischnispa calamivora calamivora Gressitt Figs. 4F, 5H

Enischnispa calamivora Gressitt, 1957, Nova Guinea, n. s. 8(2):275, figs. 20 b, c (New Ireland; BPBM); 1960, Pac. Insects 2(1):69, 70; 1963, ibid. 5(3):662 (part).

Material examined. None additional to type series.

Distribution. Bismarck Archipelago (New Ireland).

Enischnispa calamivora papuana Samuelson, **new subspecies** Figs. 2A, 4G, 5I

MALE (holotype). Body surfaces largely dark fuscous to piceous, elytron ochraceous along inner disc from base to preapex; elytral suture narrowly darkened, postmedian dark band invading ochraceous area but not reaching suture; antenna reddish fuscous; legs reddish fuscous to piceous. Body length 2.95 mm; breadth 1.0 mm.

Head just as broad as prothorax; interantennal process somewhat rounded in profile, carinate behind; occiput and vertex rather closely punctate, punctures deep, interspaces smooth, shining. *Antenna* not quite ½ as long as body; scape turgid, thicker than pedicel, pedicel as long as scape; segment 3 shorter than 1 + 2, 4–5 gradually decreasing in length, 7 = 4, 8 slightly longer than preceding 4. *Prothorax* slightly longer than broad (34:32); side convex along middle, briefly constricted subapically, gradually narrowed to prebasal constriction; disc deeply punctured, with slightly swollen impunctate area across middle, another area medially on basal ½. *Scutellum* smooth, briefly depressed before apex. *Elytron* about 4.45 × as long as broad, very gradually broadened to preapex, then rounded to subtruncate extremity; posthumeral area gently constricted; disc deeply and more or less regularly punctate, tending to form rows in pairs, separated by costae on 2nd, 4th, and 6th interstices, the last most strongly developed. *Venter* smooth to deeply punctate; prothoracic intercoxal piece flattened, bearing pair of large punctures; metasternum with median area impunctate, otherwise punctate; abdomen more closely punctate on apical 3 sternites. *Legs* with 1st pair much larger than others.

FEMALE (allotype). Similar to holotype. Antenna slightly over 1/3 as long as body. Body length 2.7 mm; breadth 0.85 mm.

PARATYPES. Similar to above. One specimen teneral and generally paler. Body length 2.85–3.15 mm; breadth 0.95–1.05 mm.

Type data. Holotype ♂ (BPBM 14,587) and allotype ♀ (BPBM), PAPUA NEW GUINEA (NE New Guinea): East Sepik Prov: Bainyik nr Maprik, 225 m, 21.vi.1961, slender leaf rotan (J.L.& M. Gressitt); 1 paratopotype, same data but 150 m; 1 paratype, Morobe Prov: Bubia, Markham Vall, 50 m, 17.ix.1955, screw palm (Gressitt); paratypes, PAPUA NEW GUINEA (SE New Guinea): Western Prov: 4, Oriomo Gov't Stn, 26–28.x.1960, palm (Gressitt); 1, same loc., 28.x.1960, *Calamus*, Gressitt. Some BPBM paratypes deposited in ANIC, BMNH.

Remarks. Differs from *c. calamivora* in having the elytron more narrowly pale along inner disc and apex of the elytron more irregular, subtruncate. Specimens from the different sectors of New Guinea are fairly uniform in general facies. The specimens from Bainyik and Oriomo were treated (the latter questionably) as the nominate subspecies by Gressitt (1963:662).

Enischnispa daemonoropa Gressitt Fig. 5J

Enischnispa daemonoropa Gressitt, 1963, Pac. Insects 5(3):662, 664 (New Guinea; BPBM).

Material examined. None additional to type series.

Distribution. New Guinea (SW) (S Vogelkop area).

Remarks. The sex of the holotype is female, not male as originally indicated.

Enischnispa rattana Gressitt Figs. 4H, 5K

Enischnispa rattana Gressitt, 1960, Pac. Insects 2(1):69, 70, fig. 18e (New Guinea; BPBM).

Material examined. None additional to type series.

Distribution. New Guinea (NE).

Remarks. The sex of the holotype was not indicated originally; it is male.

Enischnispa palmicola Gressitt Fig. 5L

Enischnispa palmicola Gressitt, 1963, Pac. Insects 5(3):662, fig. 31b (New Guinea; BPBM).

Material examined. None additional to type series.

Distribution. New Guinea (SE).

Enischnispa calamella Gressitt, **new species** Figs. 2B, 4I

MALE (holotype). Dorsum largely dark reddish fuscous, inner elytral disc with linear ochraceous area interrupted behind middle by fuscescent band, suture narrowly fuscous; antenna orangish, last 2 segments fuscescent to fuscous; venter dark fuscous; legs pale, yellow-testaceous. Body length 3.0 mm; breadth 0.90 mm.

Head barely broader than prothorax (31:30); eye large; occiput punctured; interantennal process subtriangular, ridged medially above, reaching to middle of scape. *Antenna* almost ½ as long as body; pedicel as long as scape; segment 3 shorter than 1 + 2, 4–6 gradually decreasing in length; 8 with suggestion of divisions, distinctly longer than preceding 3. *Prothorax* slightly longer than broad (31:30), subcylindrical, narrowed at base, slightly collared; disc deeply punctured, with cross-shaped smooth area occupying ¾ of discal length, a few punctures at center. *Scutellum* smooth, with some minute punctures. *Elytron* slightly broadened posteriorly, slightly constricted at end of basal ⅕; disc grossly and evenly punctured, 2nd interstice more prominent postmedially, 4th more prominent anteriorly, 6th prominent throughout. *Venter*: metasternum smooth, shining, sparsely punctulate except anterolaterally where punctures are deep; abdomen rather deeply and closely punctate. *Legs* fairly smooth.

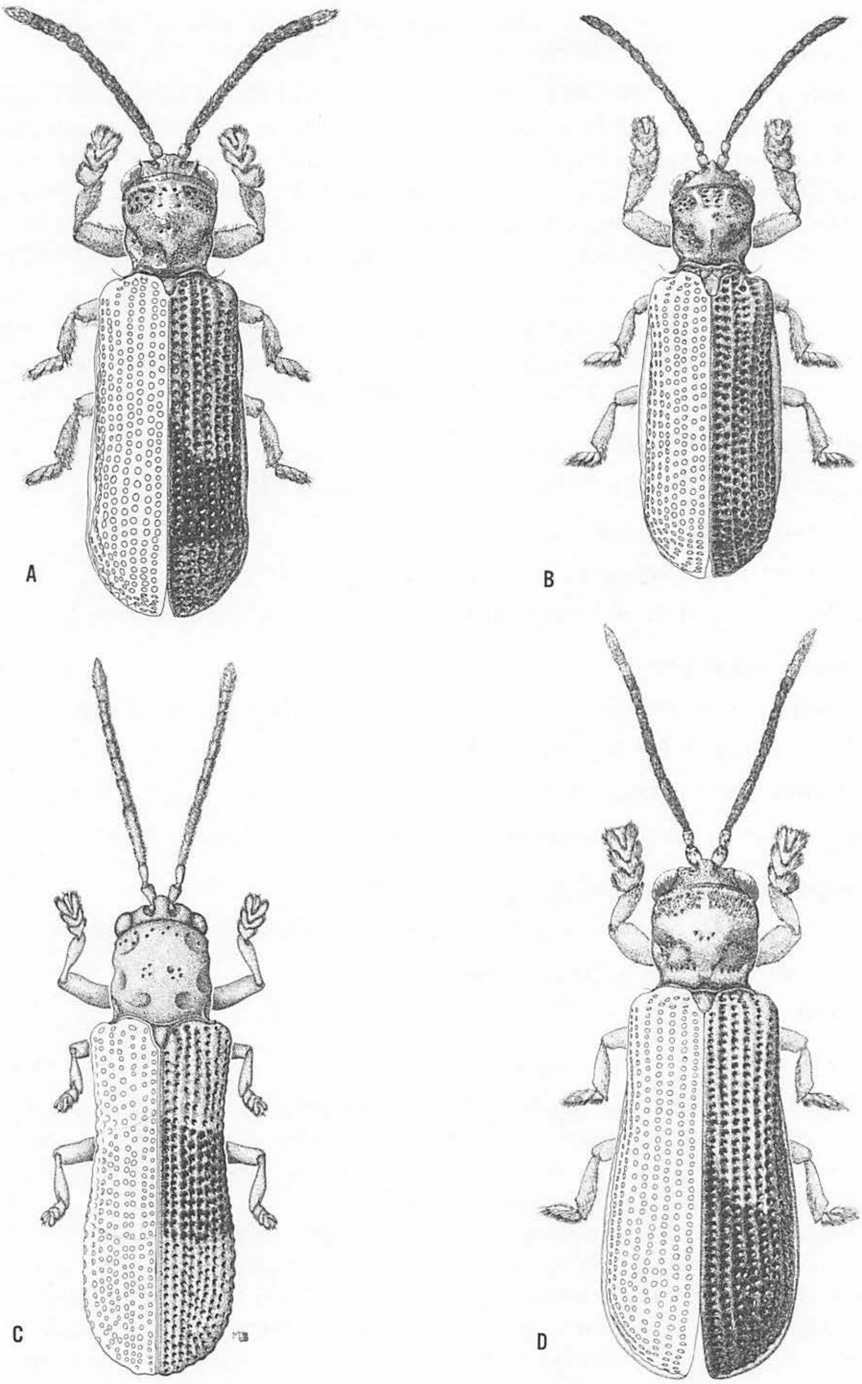

Fig. 1. Dorsal view: **A,** *Cyperispa scleriae gelae*, paratype, 4.8 mm; **B,** *C. lungae*, holotype, 4.1 mm; **C,** *C. thoracostachyi kolombangara*, paratype, 5.7 mm; **D,** *C. palmarum*, paratype, 6.4 mm. Figures not to same scale.

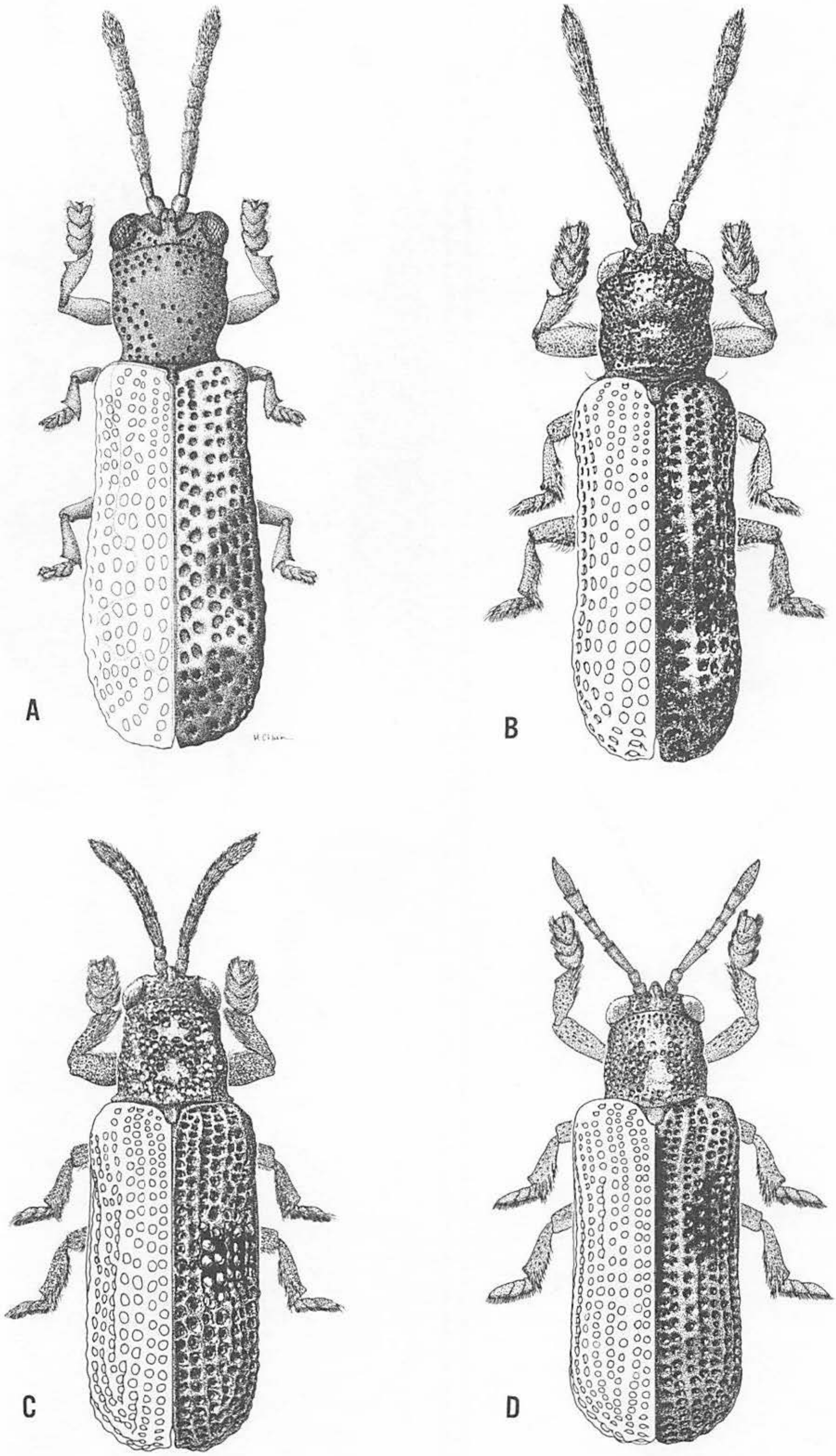

Fig. 2. Dorsal view: **A,** *Enischnispa calamivora papuana*, allotype, 2.7 mm; **B,** *E. calamella*, paratype, 3.0 mm; **C,** *Bulolispa bimaculata*, paratype, 3.9 mm; **D,** *B. sublineata*, holotype, 3.75 mm. Figures not to same scale.

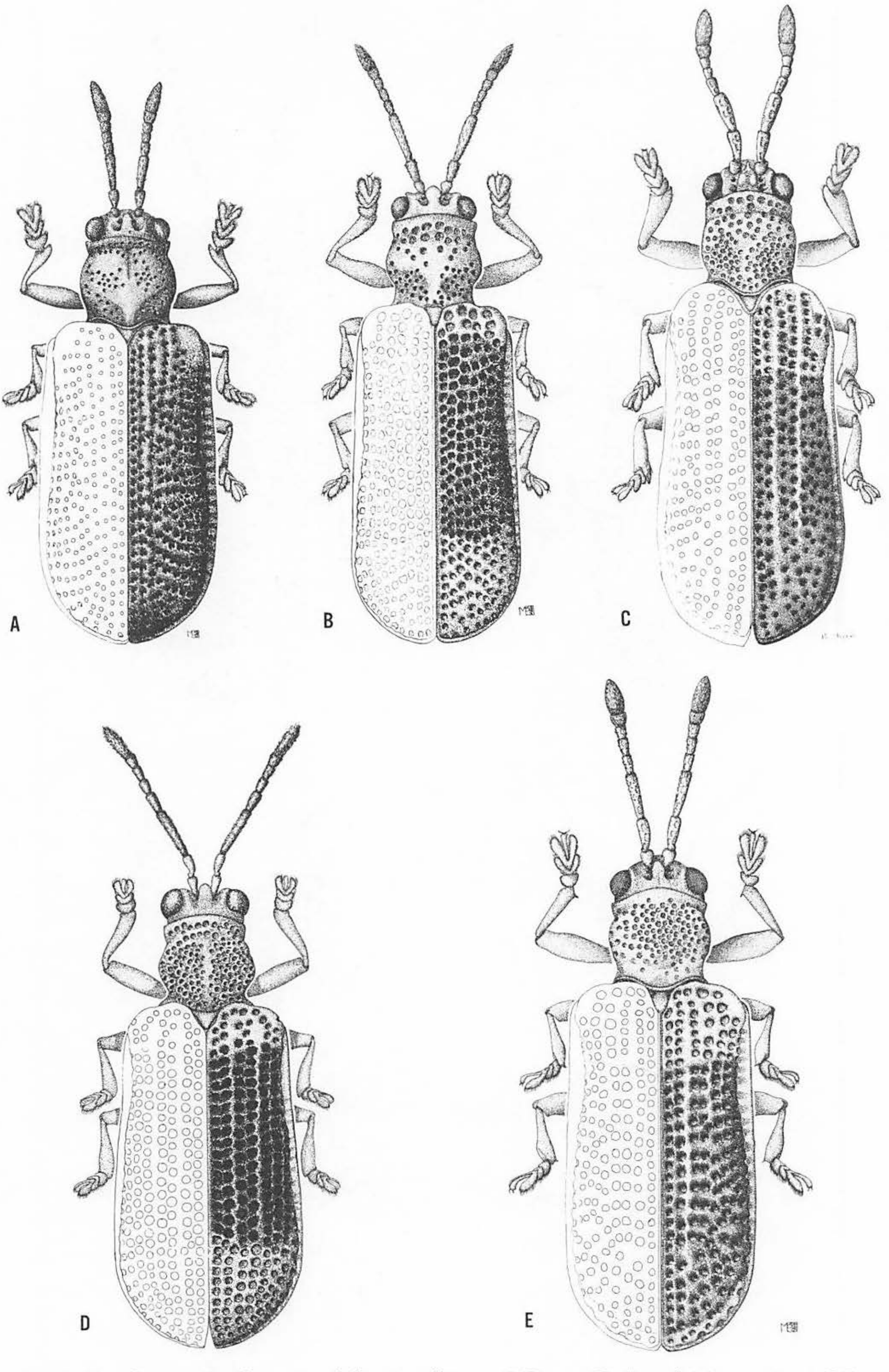

Fig. 3. Dorsal view: **A,** *Pharangispa heliconiae*, allotype, 5.85 mm; **B,** *P. a. alpiniae*, paratype, 5.7 mm; **C,** *P. a. bella*, holotype, 5.65 mm; **D,** *P. a. georgiana*, paratype, 6.05 mm; **E,** *P. a. marginata*, holotype, 6.55 mm. Figures not to same scale.

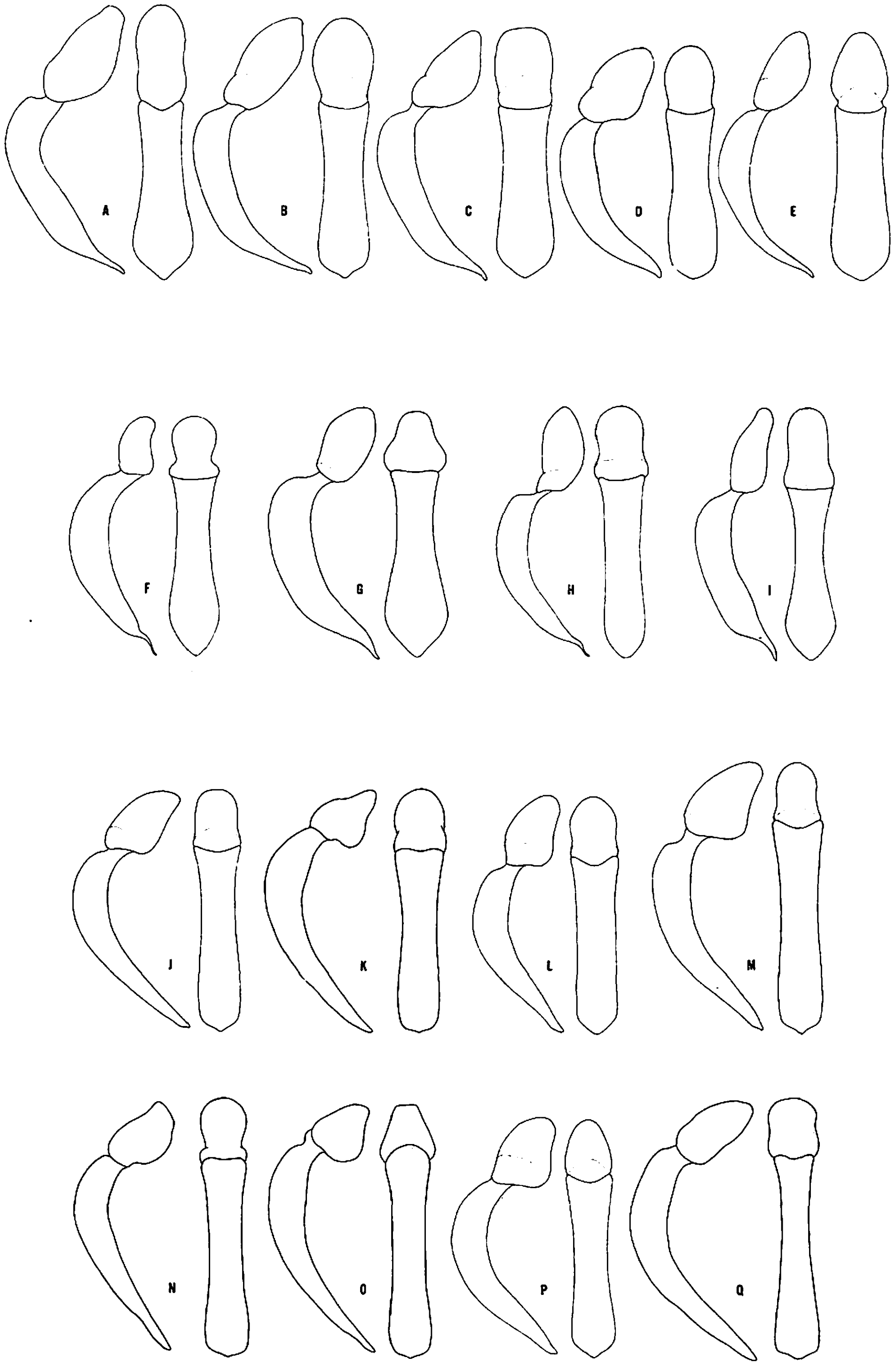

Fig. 4. Aedeagus, lateral and dorsal views: **A,** *Cyperispa s. scleriae,* holotype; **B,** *C. s. malaitensis,* paratype; **C,** *C. s. gelae,* holotype; **D,** *C. thoracostachyi kolombangara,* paratype; **E,** *C. palmarum,* holotype; **F,** *Enischnispa c. calamivora,* paratype; **G,** *E. c. papuana,* holotype; **H,** *E. rattana,* paratype; **I,** *E. calamella,* holotype; **J,** *Pharangispa purpureipennis*; **K,** *P. heliconiae,* paratype; **L,** *P. cristobala*; **M,** *P. fasciata*; **N,** *P. a. alpiniae,* paratype; **O,** *P. a. bella,* holotype; **P,** *P. a. georgiana,* holotype; **Q,** *P. a. marginata,* holotype. Figures not to same scale.

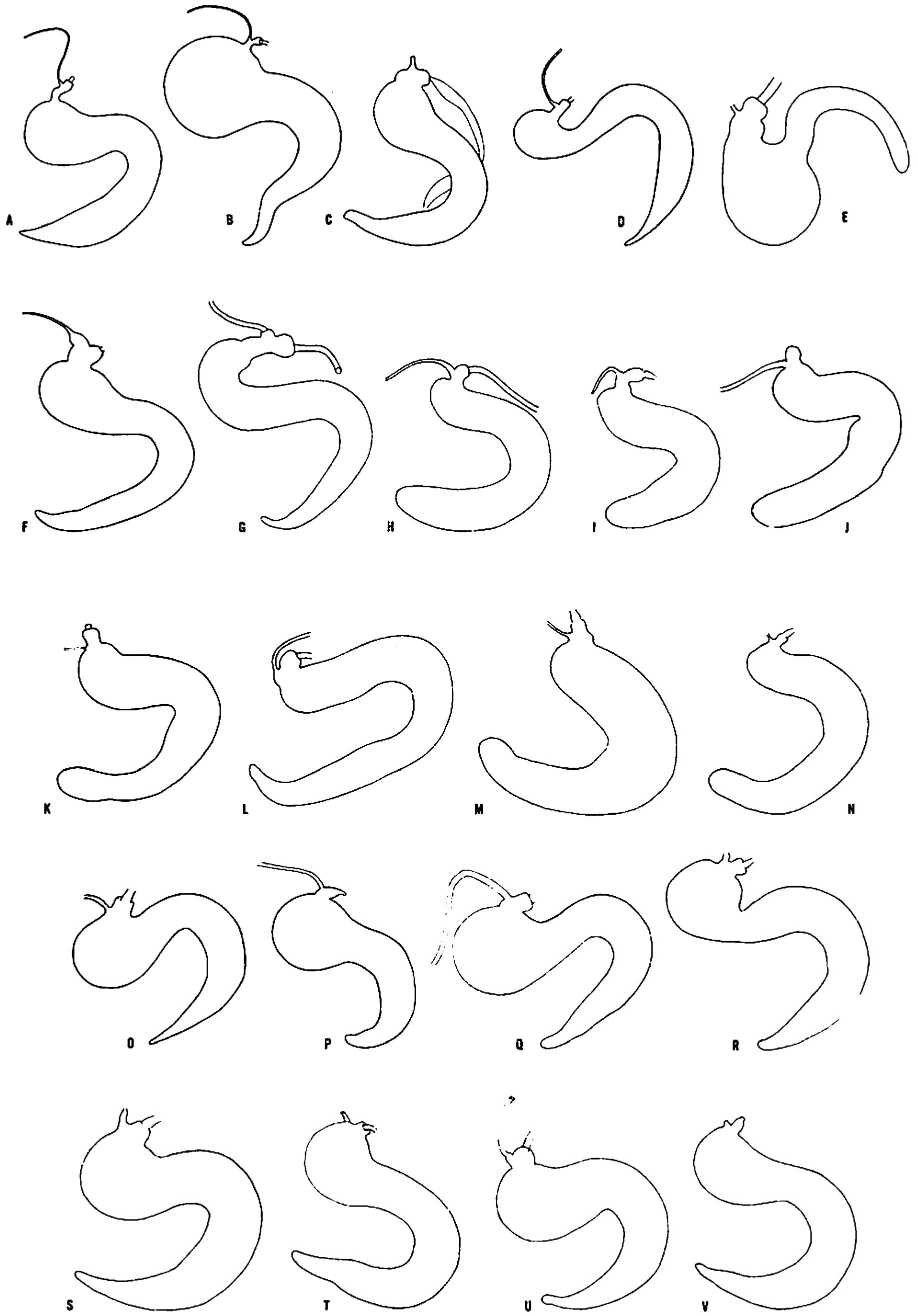

Fig. 5. Spermatheca, lateral view: **A**, *Cyperispa hypolytri*, paratype; **B**, *C. scleriaegelae*, allotype; **C**, *C. t. thoracostachyi*; **D**, *C. t. kolombangara*, paratype; **E**, *C. lungae*, holotype; **F**, *C. palmarum*, allotype; **G**, *Heterrhachispa kurandae*, holotype; **H**, *Enischnispa c. calamivora*, allotype; **I**, *E. c. papuana*, allotype; **J**, *E. daemonoropa*, paratype; **K**, *E. rattana*, paratype; **L**, *E. palmicola*, holotype; **M**, *Bulolispa bimaculata*, paratype; **N**, *B. sublineata*, holotype; **O**, *Pharangispa purpureipennis*; **P**, *P. heliconiae*, allotype; **Q**, *P. cristobala*; **R**, *P. fasciata*; **S**, *P. a. alpiniae*, allotype; **T**, *P. a. bella*, allotype; **U**, *P. a. georgiana*, allotype; **V**, *P. a. marginata*, allotype. Figures not to same scale.

PARATYPES. Body length 2.9–3.0 mm; breadth 0.85–0.90 mm.

Type data. Holotype ♂ (BPBM 14,588), PAPUA NEW GUINEA (SE New Guinea): Brown Riv nr Port Moresby, 10 m, 5.xi.1960, on rattan (J.L. Gressitt); 5 paratopotypes, same data.

Remarks. Differs from *c. calamivora* Gressitt in having the prothorax more cylindrical and with discal impunctate areas larger and elytron more angular posteriorly. The Brown River specimens were questionably assigned to *c. calamivora* by Gressitt (1963:662). The type series appears to be represented by males only.

Genus ***Bulolispa*** Gressitt & Samuelson, **new genus**

Head short, frons very short, transverse; antenna short, of 8 segments, segment 3 roughly subequal to 1 + 2 or 8; prothorax as long as broad, side nearly straight, not constricted preapically, rugose-punctate; scutellum subtriangular; elytron strongly and regularly punctured, interstices irregularly raised and sublateral, carinae quite prominent (7th strongest) but not completely hiding lateral margin in dorsal view.

Type species. *Bulolispa bimaculata* Gressitt, n. sp.

Etymology. *Bulolispa* = placename Bulolo + *Hispa*. Gender feminine.

Distribution. Lower montane New Guinea (NE).

Remarks. Differs from *Enischnispa* by being a little less narrow, less opaque, with the prothorax even at the side, not constricted preapically, and the sublateral elytral carina involving the 7th interstice instead of 6th.

Key to Species of *Bulolispa*

1. Pronotum with 2 smooth areas, before and behind center, well separated; elytron with black spot at middle not touching suture or margin; body length 3.65–3.9 mm . . . . ***bimaculata*, n. sp.**

   Pronotum with 2 smooth areas nearly joined, each about as long as broad; elytron with suture black on most of basal ¾, part of extreme base black, longitudinal black area anterior to middle continued anteriorly on side to below humerus; body length 3.75 mm . . . . ***sublineata*, n. sp.**

Bulolispa bimaculata Gressitt, **new species** Figs. 2C, 5M

FEMALE (holotype). Pale orange-testaceous, shiny, hyaline, eye pitchy brown, elytron with subrounded black spot occupying less than central ⅓ of disc and not touching suture or submarginal costa. Body length 3.65 mm; breadth 1.30.

Head short; eye large, hardly extending beyond lateral margin of prothorax; occiput coarsely punctured; interantennal process subtriangular above, barely ½ as long as scape; frons extremely short, much broader than long. *Antenna* just over ⅓ as long as body, gradually thickened distally to middle of 8th (last) segment, apex suddenly acute; scape barely longer than pedicel, both together slightly shorter than segment 3; 3 slightly shorter than 4 + 5 or 8; relative lengths of segments (1/100ths mm): 12:11:24:16:14:12:12:25. *Prothorax* just as long as broad (at basal breadth), slightly longer than broad, slightly narrower at apex than at base, straight at side; disc coarsely rugose-punctate, with short, irregular smooth area just anterior to center and smaller narrow one just behind center. *Scutellum* triangular, depressed medially. *Elytron* slightly constricted at end of basal ⅕, slightly broadened posteriorly, widest well behind middle, broadly rounded behind; disc with 9 rows of strong punctures except near base and apex, costae uneven, 2nd and 4th strong, 7th strongest. *Venter* strongly punctured, posterior part of metasternum smooth. *Legs* very short, moderately punctured.

PARATYPE. Elytral black spot smaller, broader than long. Body length 3.90 mm; breadth 1.40 mm.

Type data. Holotype ♀ (BPBM 14,589), PAPUA NEW GUINEA (NE New Guinea): Morobe Prov, Bulolo Riv, 800 m [date 31.i.1963 lined out on label] (J. Sedlacek); paratype ♀, Wau, 1,200 m, 1.xii.1965, MVL [Hg-vapor lamp] (Sedlacek).

Remarks. Differs from *Enischnispa rattana* Gressitt in being shorter, pale hyaline instead of opaque, with less of pronotal disc smooth, and without constrictions of prothorax.

Bulolispa sublineata Samuelson, **new species** Figs. 2D, 5N

FEMALE (holotype). Pale orange-testaceous, hyaline; eye golden brown to pitchy; elytron marked with black on inner part of extreme base, most of basal ¾ of suture, and sublongitudinal area of disc anterior to middle extending forward along lateral margin to below humerus. Body length 3.75 mm; breadth 1.35 mm.

Head with eye projecting slightly beyond side of prothorax; occiput punctured, depressed each side behind antennal insertions; interantennal process subtriangular, blunt, ⅗ as long as scape; frons transverse. *Antenna* ⅓ as long as body; scape and pedicel subequal, together slightly shorter than segment 3; 3 slightly shorter than 4 + 5 or 8; relative lengths of segments (1/100ths mm): 12:12:26:14:14:14:12:30. *Prothorax* just as long as basal broad, slightly convex at side, widest behind middle, narrowed toward base and anterior to middle, cylindrical apically; disc coarsely and closely punctured, impunctate areas before and behind middle, slightly grooved medially. *Scutellum* slightly concave. *Elytron* slightly wider near apex than base, nearly straight at side, conjointly rounded apically; disc with punctures strong and regular; interstices subequal, 2nd and 7th stronger, the latter not quite hiding part of lateral margin from above. *Venter* rather strongly punctate except posterior part of metasternum. *Legs* finely punctate.

Type data. Holotype ♂ (BPBM 14,590), PAPUA NEW GUINEA (NE New Guinea): Eastern Highlands Prov: Okasa nr Okapa, 1,400 m, 17.i.1963 (J. & M. Sedlacek).

Remarks. Differs from *bimaculata*, n. sp., in having the antenna slightly more slender and less pubescent, prothorax less parallel-sided, narrowed anteriorly, with larger smooth areas on top of disc, and elytron with suture largely dark and discal mark farther forward and longer.

Genus *Pharangispa* Maulik

Pharangispa Maulik, 1929, Bull. Entomol. Res. 20(2):233 (type species: *P. purpureipennis* Maulik; Solomon Is).—Gressitt, 1957, Nova Guinea, n. s. 8(2):268, 275; 1960, Pac. Insects 2(1):70.—Würmli, 1975, Entomol. Arb. Mus. Frey 26:41, 44.

Key to Species of *Pharangispa*

1. Pronotal disc generally closely and coarsely punctate centrally; elytral disc partly pale 2

Pronotal disc sparsely punctate to largely impunctate centrally, partly smooth; elytral disc entirely dark purplish (only lateral margin more or less dark reddish); body length 5.25–6.0 mm . . . (Santa Isabel I) . . . . ***heliconiae*, n. sp.**

2(1). Elytral dark markings attaining scutellum; elytral margin not distinctly broadened postbasally: breadths of margin at basal ⅕ and middle subequal 3

Elytral dark markings not attaining scutellum; elytral margin slightly broadened along basal ⅕, distinctly broader than at middle 4

3(2). Elytral dark region covering much of disc, extending to pale lateral margin; body length 4.65–6.3 mm . . . (Guadalcanal I, Santa Isabel I) . . . . ***purpureipennis***

Elytral dark region confined to inner ½ of disc; body length 4.3–5.15 mm . . . (San Cristobal I, Malaita I) . . . . ***cristobala***

4(2). Elytral apex pale over apical ⅕ or more 5
Elytral apex or preapex dark (apical part of lateral margin dark or narrowly pale) 7
5(4). Elytral dark area a transverse band confined mainly to apical region, not extending anteriorly into basal ⅓; body length 5.4–6.2 mm . . . (Bougainville I) . . . . ***fasciata***
Elytral dark area more extensive than transverse band, extending anteriorly into basal ⅓ or more 6
6(5). Elytral interstices 2 and 4 not costate, each in low zigzag pattern; body length 4.4–6.3 mm . . . (Malaita I) . . . . ***alpiniae*, n. sp.**
Elytral interstices 2 and 4 weakly costate; body length 5.25–6.5 mm . . . (New Georgia Group) . . . . ***a. georgiana*, n. subsp.**
7(4). Elytral margin dark proximal to dark discal area including apical portion; body length 4.9–6.8 mm . . . (Santa Isabel I) . . . . ***a. bella*, n. subsp.**
Elytral margin entirely pale; body length 5.5–6.65 mm . . . (Florida Group, Choiseul I, Guadalcanal I) . . . . ***a. marginata*, n. subsp.**

Pharangispa purpureipennis Maulik Figs. 4J, 5O

Pharangispa purpureipennis Maulik, 1929, Bull. Entomol. Res. 20(2):276, figs. 1, 4 (Guadalcanal I, Ysabel I; BMNH).—Gressitt, 1957, Nova Guinea n. s. 8(2):276, figs. 21a, c (Guadalcanal I).

Material examined. SOLOMON IS: Guadalcanal I: 7, Bettikama, ix.1960 (W. W. Brandt); 1, Kiwi Ck, 2.xii.1944 (H. E. Milliron) (CASC); 1, Mt Austen, 300 m, 1.xi.1980, *Alpinia* (J. L. Gressitt); 1, Nalimbu Riv, 29 km SE of Honiara, 5.vi.1960 (C. W. O'Brien); 1, Poha, 20 m, 10 km E of Honiara, 25.ix.1964, *Heliconia* (R. Straatman); 16, Roroni, 10 m, 35 km E of Honiara, 10, 11, 18.v.1964, ginger (Straatman); 1, Tadhimboko, 0–100 m, xi.1972 (N.L.H. Krauss); 68, Tathimanhi, 15.v.1960, feeding on under surface of leaf of "karo" = native name (O'Brien); 2, Tenaru Riv, 25 m, 15.ix.1957, *Alpinia* (Gressitt); 3, Tenaru, 10–50 m, 3,14,24.v.1964, ginger (Straatman, J. Sedlacek); 3, Tenaru Ck, 10–50 m, 7.v.1964, ginger (Straatman). Some BPBM specimens deposited in ANIC, CASC, HSIC, KONE, MNHN, USNM, ZSMC.

Distribution. Solomon Islands (Guadalcanal I, Santa Isabel I).

Remarks. Specimens from the islands of Malaita and New Georgia cited in Gressitt (1960:70) are *a. alpiniae*, n. sp., and *a. georgiana*, n. subsp., respectively.

Pharangispa heliconiae Gressitt, **new species** Figs. 3A, 4K, 5P

MALE (holotype). Castaneous, tinged pitchy; elytron purplish, tinged castaneous; antenna pitchy reddish on segments 1–2, pitchy black on remainder. Body length 5.5 mm; breadth 2.25 mm.

Head narrower than prothorax, smooth, finely grooved medially on occiput; interantennal process low, almost flat at apex, not reaching middle of scape. *Antenna* short, almost ⅓ as long as body; pedicel longer than scape; segment 3 longer than 1 + 2 or 8; relative lengths of segments (1/100ths mm): 16:20:44:18:14:12:12:38. *Prothorax* slightly longer than broad, constricted near base, convex at side just behind middle, slightly narrowed between middle and apex; disc convex, large central smooth area somewhat uneven, finely punctured on side of disc and apical ¼. *Scutellum* smooth. *Elytron* over 3 × as long as broad, strongly and regularly punctured, 2nd interstice from suture barely stronger than others; lateral margin fairly flat, narrower apically. *Venter* largely smooth and impunctate. *Legs* fairly slender, smooth.

FEMALE (allotype). Slightly darker than holotype; pronotal disc with more punctures anterolaterally, fine median line anteriorly; antenna 2/7 as long as body; relative lengths of segments (1/100ths mm): 16:24:42:16:14:14:12:32. Body length 5.85 mm; breadth 2.4 mm.

PARATYPES. Pronotal disc more closely punctate in the paratype male illustrated; the others with the pronotal disc slightly to conspicuously more impunctate centrally. Body length 5.25–6.0 mm; breadth 2.15–2.45 mm.

Type data. Holotype ♂ (BPBM 14,591) and allotype ♀ (BPBM), SOLOMON IS: Santa Isabel I: Hageulu, 600–650 m, 10.ix.1964, on *Heliconia* (R. Straatman); 3 paratopotypes, same data. BPBM paratype deposited in BMNH.

Remarks. Differs from *purpureipennis* Maulik in being flatter with shorter antenna, having a much smoother pronotum, and an almost entirely purple elytron.

Pharangispa cristobala Gressitt Figs. 4L, 5Q

Pharangispa cristobala Gressitt, 1957, Nova Guinea, n. s. 8(2):276, 278 (San Cristobal; CASC); 1960, Pac. Insects 2(1):71.

Material examined. SOLOMON IS: San Cristobal I: 3, Kira-Kira, 0–50 m, 9.xi.1964, Zingiberaceae, banana (R. Straatman); 9, Wairahu Riv, 100 m, 9–15.v.1964, *Heliconia*, ginger (J. Sedlacek); 1, same data but *Heliconia*, rattan; 3, same loc., 100–400 m, 9–15.v.1964 (Sedlacek). Malaita I: 1, Dala, 50 m, 9–14.vi.1964 (J. & M. Sedlacek). New to Malaita. Some BPBM specimens deposited in ANIC, BMNH, HSIC, KONE, MNHN, USNM, ZSMC.

Distribution. Solomon Islands (San Cristobal I, Malaita I).

Pharangispa fasciata Gressitt Figs. 4M, 5R

Pharangispa fasciata Gressitt, 1957, Nova Guinea, n. s. 8(2):276, 278 (Bougainville; BMNH); 1960, Pac. Insects 2(1):70.

Material examined. PAPUA NEW GUINEA: North Solomon Is Prov: Bougainville I: 1, Kukugai Vill, 150 m, xi.1960 (W.W. Brandt); 1, without locality, iii.1968 Zingiberaceae [no further data].

Distribution. Papua New Guinea: Solomon Islands (Bougainville I).

Remarks. This is the only banded species that has the dark area including the elytral lateral margin.

Pharangispa alpiniae alpiniae Samuelson, **new species** Figs. 3B, 4N, 5S

MALE (holotype). Orange-testaceous except antenna and much of elytron; antenna with scape and pedicel pitchy orange, segments 3–6 dark red-fuscous, 7–8 blackish with fine silvery pubescence; elytral dark area with bluish tinge, occupying disc from about basal 1/12 to apical 1/4; anterior border of dark area convex across both elytra, forming brief angular emargination at suture; posterior border of dark area oblique, longest at suture; lateral margin pale. Body length 5.4 mm; breadth 2.15 mm.

Head not quite as broad as prothorax; interantennal process short, rounded, less than 1/2 as long as scape; postantennal area briefly depressed; vertex smooth. *Antenna* short, not quite 3/10 as long as body; segments 7–8 moderately thickened, heavy; scape short, pyriform, pedicel longer than scape, segment 3 longest, longer than 1 + 2 or 8, 8 = 1 + 2; relative lengths of segments (1/100ths mm): 20:28:54:24:22:16:20:48. *Prothorax* slightly longer than broad; side convex along middle, briefly constricted preapically, gradually narrowed posteriorly to prebasal constriction; disc subevenly convex, prebasal area slightly impressed sublaterally; surface bearing large and small deep punctures commonly 3 × as large as interspaces, median area narrowly impunctate along finely impressed line. *Scutellum* smooth. *Elytron* about 3.75 × as long as broad; side very gradually broadened to preapex; posthumeral region weakly constricted; lateral margin broadest postbasally, gradually narrowed to apex; disc strongly and regularly punctured; puncture rows 1 + 2 and 3 + 4 paired, 2nd interstice dividing them somewhat raised, irregular, not distinctly costate. *Venter* smooth to alutaceous. *Legs* more or less smooth.

FEMALE (allotype). Similar to holotype but antennal segments more uniformly pitchy, with 7–8 not as blackish. Body length 5.8 mm; breadth 2.3 mm.

PARATYPES. Body length 4.4–6.3 mm; breadth 1.7–2.5 mm.

Type data. Holotype ♂ (BPBM 14,592) and allotype ♀ (BPBM), SOLOMON IS: Malaita I: Dala, 50 m, 8–14.vi.1964, ginger (J.& M. Sedlacek); paratopotypes: 7, same data; 8, same loc., 4.vi.1964, ginger (R. Straatman); 1, same data but on large rotan; 17, same loc., 50 m, 6–8, 9–14, 15.vi.1964 (Sedlaceks); 9, same loc., 20.vi.1964, ginger (Straatman); paratypes: 1, 12 km E of Dala, 300 m, 17.vi.1964 (J. Sedlacek); 17, Nuna Lava, 25 km NE of Dala, 200 m, 16.vi.1964 (Sedlacek); 29, same loc., [vi.1964], *Heliconia* (Straatman); 1, same data, but on *Freycinetia*; 12, Auki, 2–20 m, 21.viii.1957, *Alpinia*, #3034 (J. L. Gressitt); 1, same loc., 2–20 m, 22.ix.1957 (Gressitt); 6 (+ exuviae and pupa), same loc., 2–20 m, 2, 3.x.1957, *Alpinia* (Gressitt); 33, 3 km N of Auki, 30 m, 2.vi.1964, ginger [some without host label] (Sedlaceks); 15, same data but on coconut palm; 44, same loc., 1 m, 5.vi.1964 (Sedlaceks); 8, Tangtalau-Kwalo, 200–350 m, 24.ix.1957, *Alpinia* (Gressitt); 3, Tangtalau, 150–200 m, 200 m, 25, 26.ix.1957, *Alpinia* [some without host label] (Gressitt); 2, Auki-Tangtalau, 25–200 m, 26.ix.1957, *Alpinia* (Gressitt); 3, E of Kwalo (E of Auki), 350 m, 28, 29.ix.1957 (Gressitt); 7, Andalimu-Ngarafata (SW of Fiu Riv), 1–10 m, 19.ix.1957, *Alpinia* (Gressitt); 1, Dupi, 2.x.1957, *Alpinia* (Gressitt). Some BPBM paratypes deposited in ANIC, BMNH, CASC, HSIC, KONE, MNHN, USNM, ZSMC.

Remarks. The *alpiniae* complex is allied to *fasciata* Gressitt; all subspecies differ from *fasciata* in having the elytral dark area more extensive and the spermatheca with receptacle less constricted and more closed in outline. All of the subspecies have the spermathecal outline fairly consistent. Specimens of the nominate *alpiniae* tend to have the dark elytral marking fairly uniform, but in some the anterior pale area is deeper, occupying about the basal ⅕; the anterior border of the dark area has the sutural emargination in almost all; the posterior border is usually oblique and longest at suture, but in some it is transverse or rarely inversely oblique. In a few specimens, all the flagellar antennal segments are black, but the scape and pedicel are always much paler, usually orange-testaceous.

Pharangispa alpiniae bella Samuelson, **new subspecies** Figs. 3C, 4O, 5T

MALE (holotype). Orange-testaceous except antenna and most of elytron; antenna with segments 1–6 pitchy orange-fuscous, 7–8 blackish with fine silvery pubescence; elytron pale across basal ¼, lateral margin pale to slightly behind middle, remainder blackish with blue lustre; anterior border of dark elytral area transverse; epipleuron darkened apically. Body length 5.65 mm; breadth 2.25 mm.

Head not as broad as prothorax; interantennal process rounded, about ½ as long as scape; occiput deeply impressed above eye. *Antenna* not quite ⅖ as long as body; scape very short and robust, pedicel over 2 × as long as scape, segment 3 = 8, 7–8 moderately thickened; relative lengths of segments (100ths mm): 16:34:44:26:18:16:18:44. *Prothorax* slightly longer than broad (60:56); side convex along middle, briefly constricted preapically, more gradually narrowed behind to prebasal constriction; disc subevenly convex, broadly and shallowly depressed posterolaterally, surface closely punctate centrally, punctures mostly 3 × as large as interspaces; preapical area with some large punctures, some about 2 × as large as central ones. *Scutellum* smooth. *Elytron* about 4.2 × as long as broad; side fairly straight, gradually broadened to preapex; posthumeral area gradually constricted; lateral margin broadest basally, gradually narrowed to apex; discal punctures more or less regular, deep, with puncture rows 1 + 2 and 3 + 4 paired, closely fitting, divided by slightly swollen interstices (2nd and 4th); puncture rows 5 + 6 also paired; transverse interspaces commonly raised, delimiting associated pairs of punctures on apical ½. *Venter* smooth to alutaceous. *Legs* more or less smooth.

FEMALE (allotype). Similar to holotype. Antennal segments dark fuscous, distinctly thickened as in male; relative lengths of segments (1/100ths mm): 20:36:50:24:20:17:17:41. Body length 6.0 mm; breadth 2.5 mm.

PARATYPES. Body length 4.9–6.8 mm; breadth 2.05–3.0 mm.

Type data. Holotype ♂ (BPBM 14,593) and allotype ♀ (BPBM), SOLOMON IS: Santa Isabel I: Tatamba, 0–50 m, 27.viii.1964, ginger (R. Straatman); paratopotypes: 19, same data; 1, same loc., 7/1.1963, #3323 (M. McQuillan) (HSIC); 7, same loc., 0–50 m, 28.viii.1964, Zingiberaceae "common everywhere, not *Heliconia*" (Straatman); 9, same loc., 0–50 m, 3,5,14.x.1964, pinnate small palm, rattans, fan leaf palm, Zingiberaceae, *Heliconia* (Straatman); paratypes: 3, Hageulu, 500–650 m, 2–13.ix.1964, *Pandanus* with narrow leaf (Straatman); 9, same loc., 600–650 m, 10,11.ix.1964, ginger, *Heliconia*, tall sp. of ginger [11.ix only] (Straatman); 6, Holibara, 400–600, 550 m, 21,22.viii.1964, banana, *Heliconia*, ginger (Straatman); 11, Kolotuve, 15,16.vi.1960 (C.W. O'Brien); 1, Ovi Vill, nr Tatamba, 16.ix.1964 (Straatman); 3, Sukapisu, 900 m, 19.vi.1960 (O'Brien); 4, Tanatahi Riv, 0–50 m, 4.ix.1964, ginger (Straatman); 1, Thathaje, [no date], *Alpinia* (B.C. Stone?); 3, Togilava Riv, 0–50 m, 6.ix.1964, Zingiberaceae (Straatman). Some BPBM paratypes deposited in ANIC, BMNH, CASC, HSIC, KONE, MNHN, USNM, ZSMC.

Remarks. This is the only subspecies in the *alpiniae* complex that has the entire apical area of the elytron dark.

Pharangispa alpiniae georgiana Samuelson, **new subspecies** Figs. 3D, 4P, 5U

MALE (holotype). Orange-testaceous except antenna and most of elytron; antenna pitchy reddish fuscous, scape and pedicel slightly paler, orangish; elytron with dark area occupying most of disc from basal 1/6 to apical 3/10; lateral margin completely pale; dark elytral area blackish with violaceous lustre, anterior border slightly oblique, shortest at suture, posterior border transverse. Body length 5.55 mm; breadth 2.25 mm.

Head not as broad as prothorax; interantennal process rounded, almost 1/2 as long as scape; postantennal area briefly impressed; vertex largely smooth. *Antenna* 2/5 as long as body; scape short but more than 1/2 as long as pedicel; segment 3 shorter than 7 + 8, 7–8 slightly thickened; relative lengths of segments (1/100ths mm): 16:26:50:26:20:22:22:47. *Prothorax* as broad as long; side convex along middle, briefly constricted preapically, gradually narrowed to prebasal constriction; disc subevenly convex, somewhat flattened anteriorly, slightly and broadly impressed posterolaterally, discal punctures large and deep centrally, commonly 3 × as large as interspaces, some punctures larger anteriorly. *Scutellum* smooth. *Elytron* about 3.85 × as long as broad; side rather straight, gradually broadened to preapex; posthumerus gently constricted postbasally; lateral margin broadest basally, continued slightly narrower to preapex, narrowed to apex; disc strongly and deeply punctured, puncture rows 1 + 2 and 3 + 4 paired, 2nd interstice slightly swollen, weakly costate; 4th interstice also somewhat costate. *Venter* and *legs* mostly smooth.

FEMALE (allotype). Pale areas more yellowish than orangish; elytron with dark area more jagged on anterior border, oblique (shortest at suture) on posterior border; pale elytral base slightly shorter than in holotype. Relative lengths of antennal segments (1/100ths mm): 20:26:48:24:20:18:18:43. Body length 5.7 mm; breadth 2.25 mm.

PARATYPES. Body length 5.25–6.5 mm; breadth 2.25–2.7 mm.

Type data. Holotype ♂ (BPBM 14,594) and allotype ♀ (BPBM), SOLOMON IS: New Georgia Group: New Georgia I: Munda, 1–30 m, 19.viii.1959, ginger (J. L. Gressitt); paratopotypes: 4, same data; 19, same loc., 1–30 m, 15, 20.vii.1959, ginger, [1 labelled #3516] (Gressitt); paratypes: Kolombangara I: 9 [without loc.], 0–40 m, 30 m, 1–1,000 m, 23.i–13.ii.1964, *Heliconia* [some without host label] (P. Shanahan); 8, Iriri, 2 m, 100–250 m, 29.vi.1964, 1.vii.1964, palm, *Pandanus* (J.& M. Sedlacek). Some BPBM paratypes deposited in ANIC, BMNH, CASC, HSIC, KONE, MNHN, USNM, ZSMC.

Remarks. Similar to nominate *alpiniae*, n. sp., in having the preapical area of the elytron pale, but it differs by having the elytral interstices more swollen and the apex of aedeagus more angulate. The elytral dark area varies slightly in the anterior and posterior margins; either may be transverse or oblique.

Pharangispa alpiniae marginata Samuelson, **new subspecies** Figs. 3E, 4Q, 5V

MALE (holotype). Orange-testaceous except antenna and most of elytron; antenna with segments 1–6 slightly darker pitchy orange, 7–8 dark fuscous with silvery pubescence; elytron pale on basal ¼, remainder, except lateral margin, blackish with bluish lustre; dark elytral area truncate on anterior border, lateral margin entirely pale. Body length 6.55 mm; breadth 2.65 mm.

Head narrower than prothorax; interantennal process rounded, about ½ as long as scape; postantennal area deeply impressed each side; vertex mostly smooth. *Antenna* nearly ⅖ as long as body; scape short, about ½ as long as pedicel; segment 3 = 4 + 5, 7–8 moderately thickened; relative lengths of segments (1/100ths mm): 21:38:56:30:26:20:22:46. *Prothorax* slightly longer than broad (67:64); side convex along middle, briefly constricted preapically, more gradually narrowed to prebasal constriction; disc subevenly convex, shallowly impressed posterolaterally; discal punctures close, deep, commonly 3 × as large as interspaces; anterior punctures somewhat larger than central ones. *Scutellum* smooth. *Elytron* about 3.8 × as long as broad; side rather straight, gradually broadened to preapex; posthumeral area gradually constricted; lateral margin broadest basally, gradually narrowed to apex; disc strongly and regularly punctured; puncture rows 1 + 2 and 3 + 4 paired, 2nd interstice slightly swollen and weakly costate. *Venter* and *legs* mostly smooth.

FEMALE (allotype). Similar to holotype, antenna slightly darker, segments 7–8 not as thickened. Relative lengths of antennal segments (1/100ths mm):18:30:49:26:23:22:18:43. Body length 5.9 mm; breadth 2.5 mm.

PARATYPES. Body length 5.5–6.65 mm; breadth 2.3–2.8 mm.

Type data. Holotype ♂ (BPBM 14,595), SOLOMON IS: Florida Group: Nggela I: Haleta, 100 m, 13.x.1964, *Heliconia* (R. Straatman); allotype ♀ (BPBM), Choiseul I: Kitipi Riv, 80 m, 17.iii.1964, *Heliconia* (P. Shanahan); paratopotypes, Nggela I: 5, same data as holotype; 13, same loc., 0–50 m, 0–300 m, 2–3, 4.x.1964, ginger, *Heliconia*, banana (Straatman); 6, same loc., 0–50 m, 0–100 m, 200–250 m, 6,7,10,15.x.1964, [1 labelled *Heliconia*] (Straatman); paratypes: Small Nggela I: 6, Hanavaivine, 15.ix.1960, feeding on "karo" [= native name] (C.W. O'Brien); 1, Dende, 17.ix.1960 (O'Brien); Choiseul I: 9, Malangona, 100 m, 20.iii.1964, *Heliconia* (Shanahan); 6, same loc., 20 m, 30 m, 22,23.iii.1964, *Heliconia* (Shanahan); Guadalcanal I: 1, Lunga Riv (bridge), 4.ix.1960 (O'Brien). Some BPBM paratypes deposited in ANIC, BMNH, CASC, HSIC, KONE, MNHN, USNM, ZSMC.

Remarks. Similar to *a. bella*, n. subsp., in having the preapical area of the elytron dark and the apex of the aedeagus angulate; it differs from *a. bella* by having the elytral margin completely pale to the apex, and by having the elytral interstices slightly less prominent. The pale elytral margin is distinct for its entire length in most specimens; several have the preapical region stained with fuscous; 1 specimen has the margin completely dark apically.

Checklist of Papuan Coelaenomenoderini

Cyperispa Gressitt
  hypolytri Gressitt
  scleriae scleriae Gressitt
  scleriae malaitensis Gressitt
  scleriae gelae Gressitt, n. subsp.
  thoracostachyi thoracostachyi Gressitt
  thoracostachyi kolombangara Gressitt, n. subsp.
  lungae Gressitt, n. sp.
  palmarum Gressitt, n. sp.

- *Heterrhachispa* Gressitt
  - *kurandae* Gressitt
- *Enischnispa* Gressitt
  - *calamivora calamivora* Gressitt
  - *calamivora papuana* Samuelson, n. subsp.
  - *daemonoropa* Gressitt
  - *rattana* Gressitt
  - *palmicola* Gressitt
  - *calamella* Gressitt, n. sp.
- *Bulolispa* Gressitt & Samuelson, n. gen.
  - *bimaculata* Gressitt, n. sp.
  - *sublineata* Samuelson, n. sp.
- *Pharangispa* Gressitt
  - *purpureipennis* Maulik
  - *heliconiae* Gressitt, n. sp.
  - *cristobala* Gressitt
  - *fasciata* Gressitt
  - *alpiniae alpiniae* Samuelson, n. sp.
  - *alpiniae bella* Samuelson, n. subsp.
  - *alpiniae georgiana* Samuelson, n. subsp.
  - *alpiniae marginata* Samuelson, n. subsp.

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Fauna of Thai Caves. II. New Entomobryoidea Collembola from Chiang Dao Cave, Thailand[1]

Louis Deharveng[2]

ABSTRACT

Four new species of Entomobryoidea collected in Chiang Dao cave, northern Thailand, are described and illustrated: *Troglopedetes leclerci*, n.sp., *Pseudosinella chiangdaoensis*, n.sp., *Coecobrya guanophila*, n.sp., and *C. similis*, n.sp.

INTRODUCTION

Large collections of Collembola were made in Tham Chiang Dao (Tham = cave in Thai) during the speleo-scientific expeditions of the "Association Pyrénéenne de Spéléologie" in Thailand, particularly in 1985. Dr. Fred Stone also collected some collembological material from the same cave studied here.

Collembola are represented by at least 10 species in Tham Chiang Dao, of which only *Troglopedetes fredstonei* Deharveng has already been described. The present paper deals with 4 new species of Entomobryoidea *Troglopedetes leclerci*, n.sp., *Pseudosinella chiangdaoensis*, n.sp., *Coecobrya guanophila*, n.sp., and *Coecobrya similis*, n.sp. Two additional species (*Coecobrya* sp. and *Troglopedetes* sp.) were also found in one occasion in the cave, but the material is not sufficient for a full description.

The following abbreviations are used: abd. = abdominal segment; ant. = antennal segment; th. = thoracic segment. Numbering and morphology of labial basal setae follow Gisin (1967).

Holotypes are deposited in Museum National d'Histoire Naturelle, Paris, France (MNHN); paratypes are deposited in the following collections: Bishop Museum, Honolulu, Hawai'i (BPBM); Biology Department, Chiang Mai University, Chiang Mai, Thailand (BDCM) and Laboratoire d'Ecologie des Invertébrés Terrestres, Université Paul Sabatier, Toulouse, France (LEITT).

SYSTEMATICS

Troglopedetes leclerci Deharveng, **new species** Figs. 1–6

Length: 0.7–1mm. Color: white, with spot of blue pigment on each eye. Antenna 2–2.5 × as long as cephalic diagonal (Fig. 1). Ant. ratio in μm: 54:93:72:(84 + 84) (1 male), 75:138:120:(129 + 111) (1 female); ant. I, II with a few scales; ant.IV subdivided into 2 subsegments, without apical bulb. Eyes 3 + 3, small. Clypeolabral formula ?,4/5,5,4. Four prelabral setae ciliated. Outer maxillary ramus with 1 papillated seta, 1 basal seta, 2 sublobal hairs. Setae of labial basis as M1M2REL1l2; M1 to L1 subequal, ciliated; l2 reduced to smooth, short, large

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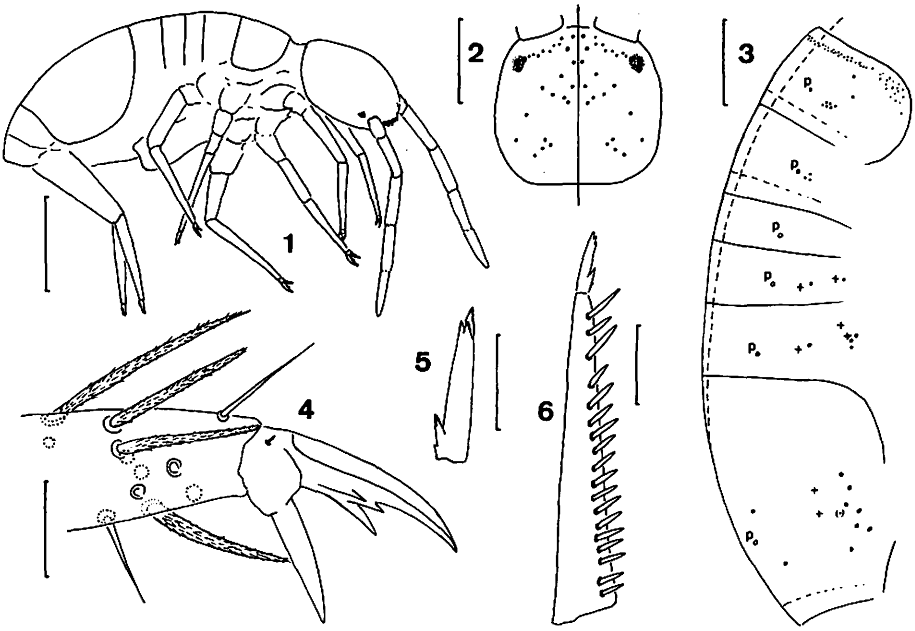


Figs. 1–6. *Troglopedetes leclerci* Deharveng, n.sp. (p: = pseudopora; + = trichobothria): **1**, habitus; **2**, dorsal cephalic macrochaetotaxy; **3**, macrochaetotaxy of tergites; **4**, apex of tibiotarsus and praetarsus of leg III; **5**, mucro, ventral view; **6**, mucrodens, lateral view. Scales: 250 μm, Fig. 1; 100 μm, Figs. 2–3; 50 μm, Fig. 6; 25 μm, Fig. 5; 10 μm, Fig. 4.

spine. Legs devoid of scales. Unguis slightly elongated, rather strong unpaired tooth at basal ½ and pair of unequal teeth at basal ⅓ of inner side of claw (Fig. 4). Trochanteral organ of LIII with 5 to 9 smooth, straight, unequal setae. Tenent hair pointed or feebly capitate, slightly shorter than inner side of claw. Ventral tube with 6 + 6 setae on lateral flaps (4 + 4 smooth distal, 2 + 2 rough, more proximal), 3 + 3 large, rough, anterior setae, about 30 posterior, medium-sized setae, rough except 2 smooth, straight distal ones. Macrochaetae present on body with following pattern: 7,4/6 + 2,3/0,1,1,2 (Figs. 2, 3). Other dorsal setae: short to medium, smooth, thin, pointed (probably s-setae) and short, ordinary ciliated setae; body otherwise covered with rounded scales. Manubrium scaled ventrally, with many subequal ciliated setae dorsally, leaving median glabrous streak; 3–4 + 3–4 ciliated dorsodistal setae; no smooth setae on lateral border. Dens (Fig. 6) slightly tapering, ventrally scaled, with 2 dorsal rows of spines throughout, spines of external row larger, less sclerotized than those of internal row; short and long ciliated setae present only along dorsal side of dens. Mucro elongate, 4 main blunt teeth and additional minute tooth at base of basal tooth (Fig. 5).

Type data. Holotype ♂, THAILAND: Changwat Chiang Mai: Amphoe Chiang Dao, Tham Chiang Dao, "réseau guano," on walls, 10.VII.1985 (P. Leclerc) (TC45) (MNHN). Paratypes: THAILAND: 1 ♀, 1 juv., topotypic, "réseau guano," on walls, 10.VII.1985 (P. Leclerc) (TC45); 1 juv., topotypic, "réseau guano," G8 station, 10.VII.1985 (P. Leclerc) (TC46); 1 ♀, topotypic, "réseau supérieur," S5 station, 7.VII.1985 (L. Deharveng) (TC25); 1 ♀, topotypic, "réseau supérieur," 25.XII.1980 (L. Deharveng) (THA110). One paratype in BDCM; 4 paratypes in LEITT.

Etymology. We are pleased to name this species for Philippe Leclerc, who made large collections of Collembola with us in Tham Chiang Dao.

Relationships. *Troglopedetes leclerci* belongs to the same group as *T. fredstonei*, previously described from Tham Chiang Dao. It is easily distinguished from *fredstonei* by its smaller size, shorter antennae and legs, different macrochaetotaxic pattern, and presence of 3 + 3 pigmented eyes. These 2 species differ from all other described *Troglopedetes* by the following combination of characters: 4th antennal segment subdivided into 2 subsegments; 2 rows of spines on the dens; mucro devoid of basal denticulations.

Troglopedetes sp.

One young specimen of a 3rd species of this genus was collected in Tham Chiang Dao, near the entrance, in roots and soil. It differs from all known Thai species of the genus by its mucro being devoid of a basal tooth and by a larger number of macrochaetae on the tergites.

Pseudosinella chiangdaoensis Deharveng, **new species** Figs. 7–14

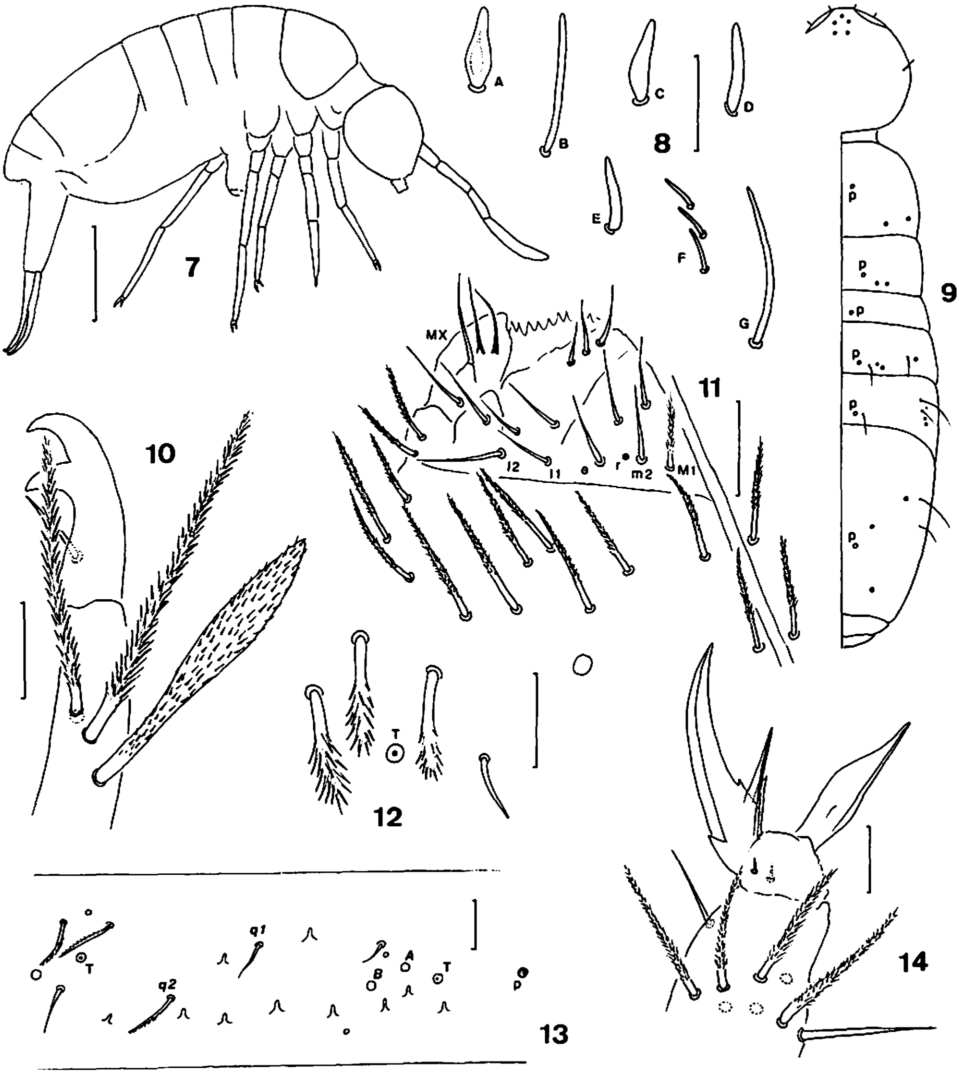
Length: 1–1.2 mm. Color: entirely white. No eyes. Antenna ca. 2 × as long as cephalic diagonal; ant. ratios in μm: 62:100:99:195 (Fig. 7). Antennae devoid of scales, with 6 types of setae: 1) ordinary ciliated setae, medium to long, on all segments; some long and thin, perpendicular to integument on ant.II; 2) smooth, straight, thin ordinary setae, medium sized, perpendicular to integument on ant.IV, ventrally on ant.I; 3) short, smooth, thin microchaetae at bases of ant.I (4) and ant.II (4); 4) subcylindrical, medium sized s-setae, numerous on ant.II, III, and IV; some thicker and shorter (Figs. 8B, G), absent on ant.I; 5) short, thick s-setae, a few on ant.I (ventrally), II, III, and IV (Figs. 8A, C, D, E); 6) short, thin s-setae, ventrally on ant.I, a few on dorsodistal part of ant.II, on apical part of ant.III, some on ant.IV.

Ant.III organ with 2 internal s-setae of type 5, in small alveoli; guard setae mixed with type 4 and type 6 setae. One pseudopore at apex of ant.III. Prelabral setae ciliated. Labral formula ?,4/5,5,4. Labial formula M1m2rel1l2; m2, e, and l2 very slightly rough; r reduced to extremely minute seta with large base (Fig. 11). Outer maxillary ramus with 1 thin papillated seta, 1 basal seta, and 2 sublobal hairs as long and thin as papillated seta; venter head with scales and some ordinary ciliated setae (Fig. 11).

Legs without scales. Unguis elongated, small unpaired tooth at basal 37–40% and pair of pointed, long, unequal proximal teeth; 2 very small dorsobasal teeth also present; unguiculus rather thin, with 1 or 2 very small external teeth; pretarsal setae very short (Fig. 14). Tibiotarsal tenent hairs thin, pointed, 1 on each tibiotarsus; smooth ventrodistal seta of tibiotarsus III nearly as long as adjacent ciliated setae (Fig. 14). Trochanteral organ with 8 thin, smooth, straight setae (1 specimen examined). Ventral tube with 6 + 6 laterodistal setae (5 + 5 rough, 1 + 1 ciliated), 6 + 6 long ciliated anterior setae, 2 + 2 smooth medium posterior setae. Tenaculum with 4 + 4 teeth and 1 large ciliated seta. Manubrium with 2 + 2 ventrodistal ciliated setae and at least 5–6 + 5–6 dorsodistal ciliated setae; dorsum with numerous ciliated subequal setae, without smooth setae, each side with longitudinal row of smaller, thinner ciliated setae. Dens rather short, with ventral scales and rows of ciliated setae (1 internal row and 2 external rows; setae more numerous and rows not distinguishable at base). Distal nonannulated part of dens more than 2 × mucro; mucro strong, bidentate, with large basal seta (Fig. 10). Macrochaetae on body with following pattern: R000/22/0201 + 2 (Fig. 9). Chaetotaxy of abd.II: -ABq1q2 (Fig. 13). On abd.IV seta "s" is absent (Fig. 12).

Type data. Holotype ♀, THAILAND: Changwat Chiang Mai: Amphoe Chiang Dao, Tham Chiang Dao "réseau supérieur"; 31.VII.1985 (P. Leclerc) (TC55) (MNHN). Paratypes: THAILAND: 2 ex., topotypic, "réseau supérieur"; 10.VII.1985 (L. Deharveng) (TC36) (LEITT).

Relationships. *Pseudosinella chiangdaoensis*, n.sp., is the first species of this genus described



Figs. 7–14. *Pseudosinella chiangdaoensis* Deharveng, n.sp. (p = pseudopora): **7,** habitus; **8,** different types of setae (see text) on ant.I (E,F), ant.II (A,D,G) and ant.III (B,C); **9,** schematic dorsal macrochaetotaxy; **10,** apex of mucrodens; **11,** labium base, outer maxillary ramus (MX) and part of ventral chaetotaxy of head; **12,** trichobothrial complex of abd.IV (left side); **13,** chaetotaxy of abd.II (left side; ʌ = scales; T = trichobothria); **14,** apex of tibiotarsus and praetarsus of leg III. Scales: 250 μm, Fig. 7; 25 μm, Fig. 11; 10 μm, Figs. 8,10,12–14.

from Thailand. Its macrochaetotaxic pattern is different from that of any of its congeners. In Thailand, *Pseudosinella* seem to be restricted mainly to cave environments, where they are not common. They may be relict species, but the reason for their limitation to caves, as well as their taxonomic relationships, are not clear.

Genus **Coecobrya** Yosii, **new status**

Sinella (Coecobrya) Yosii, 1956, Jap. J. Zool., 11(5): 622; type species *Sinella (Coecobrya) akiyoshiana* Yosii, 1956, l.c., by original designation.

Table 1. Characters of the *Sinella-Coecobrya* complex.

	Sinella*	Coecobrya*	Sinella**	Coecobrya**
Subapical organ of ant. IV	absent***	present	absent*** or present	
Ant.II organ	absent	present	absent or present	
Ventral tube setae	numerous	fewer	variable	
Dens and manubrium smooth dorsal setae	absent	present	absent or present	
Mucro	bidentate or falcate		bidentate	falcate

* Sensu Yosii 1964.
** Sensu mihi.
*** Dubious statement.

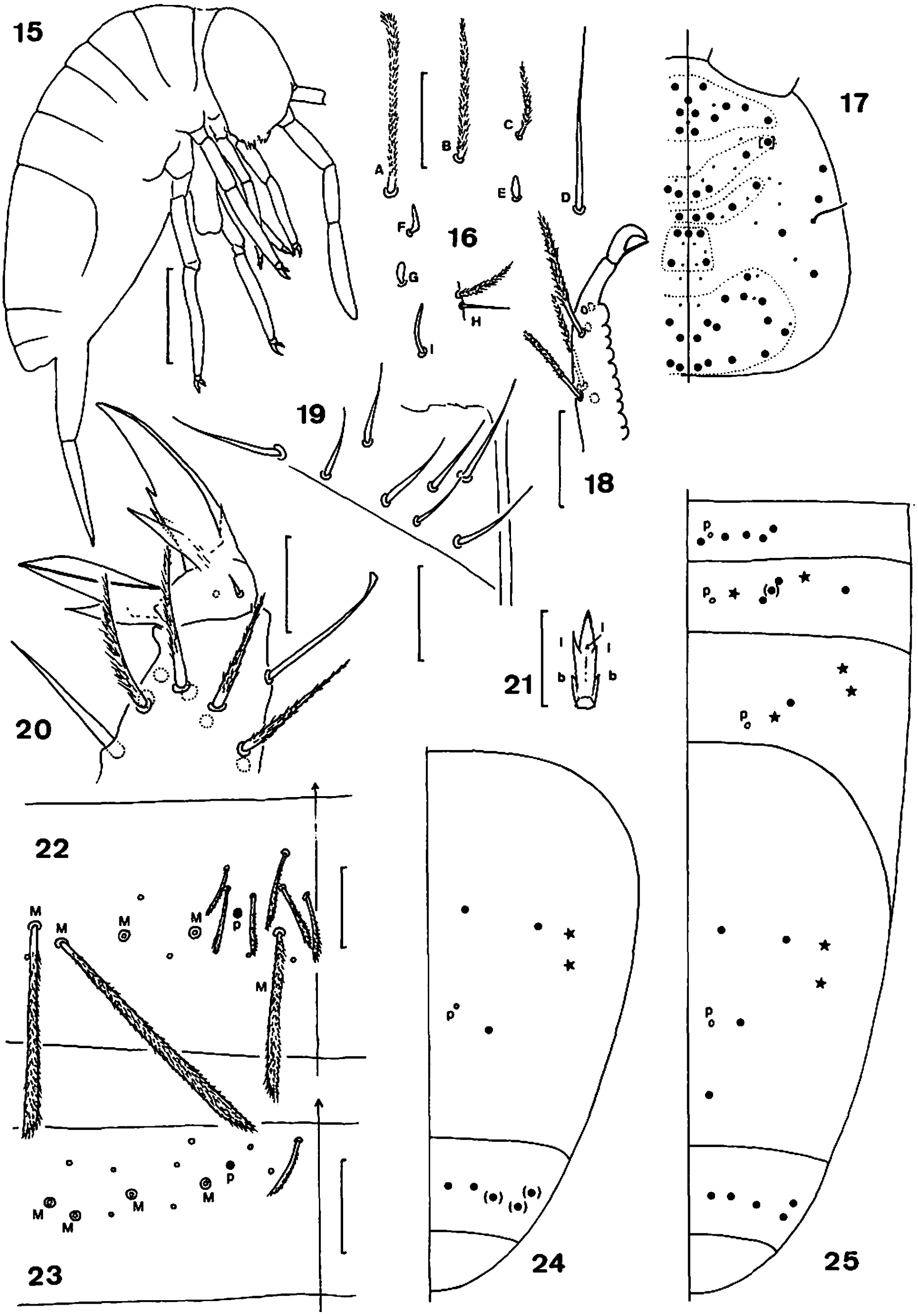
Yosii (1956) separates *Coecobrya* from *Sinella* by the presence in the former of only 1 smooth seta on tibiotarsus III and a falciform mucro. From the study of American species, Christiansen (1960) considered this difference only specific. Yosii (1964) follows Christiansen on this point; he proposed in the same paper a new set of sharp differential characters (Table 1), which I checked in all Thai species at hand. The 2 species described below would belong to *Coecobrya* sensu Yosii 1964, whereas several undescribed species of central and northern Thailand have characters both of *Sinella* sensu Yosii (dens and manubrium setae) and *Coecobrya* sensu Yosii (antennae and ventral tube). A better taxonomic and biogeographical consistency is obtained by considering the form of the mucro as the basic differential character between *Coecobrya* (falcate mucro) and *Sinella* (bidentate mucro): in this case, all Thai species come in *Coecobrya*, whereas all American except the probably introduced *C. caeca* (Christiansen and Bellinger, 1980) come in *Sinella*. On these grounds, I adopt here this new conception and, considering the number and diversity of species belonging to either 2 genera, I raise *Coecobrya* to generic status. Incidentally, the form of mucro has been described for all known species, which is not the case for the differential characters proposed by Yosii (1964). Many undescribed *Coecobrya* of different evolutionary lines are present in soils and in caves in Thailand. *Sinella* is absent in our samples.

Coecobrya guanophila Deharveng, **new species** Figs. 15–19, 21, 22, 25

Length: 0.9–1.2 mm. Color: entirely white. No eyes. Antennae about ½ as long as body. Ant. ratio in μm: 81:150:126:243 (Fig. 15). Antennal setae of 6 types: 1) Ciliated, medium to long setae; apically pointed (Figs. 16B, C, H), except sometimes 1–(2) large ones on dorsal side of ant.I and ant.II (Fig. 16A). 2) Smooth straight setae, inserted perpendicular to integument; either long (3 internal, 1 ventro-external on ant.I, 2 ventral, 3 internal on ant.II, 1 ventrodistal on ant.III, Fig. 16D), or rather short (numerous on ant.IV, Fig. 16H). 3) Smooth, short microchaetae at bases of antennal segments (at least 4 on ant.I, 4 on ant.II, ?0 on ant.III, none on ant.IV). 4) Subcylindrical, rather thin s-setae; numerous, mainly on dorsal side of ant.IV, also present on ant.II, III and ventrally on ant.IV (Fig. 16I). 5) Thick, short s-setae on ant.II (1 external, 1 internal, Fig. 16E) and ant.III (1 ventral, 3 external, 1 internal, Fig. 16F), apparently none on ant.I, IV. 6) Short, thin ordinary or s-setae inserted not perpendicular to integument, on ant.I, II (ventrally), and on ant.III, IV.

Ant.III organ with 2 very small, thick, internal sensillae (Fig. 16G), not hidden in integumental fold, guard-setae not different from other s-setae of segment. No apical bulb on ant.IV.

Clypeolabral formula ?,4/5,5,4. Four prelabral setae smooth. External differentiated seta of



Figs. 15–25. *Coecobrya guanophila* Deharveng, n.sp. (Figs. 15–19,21,22,25). *Coecobrya similis* Deharveng, n.sp. (Figs. 20,23,24) (p = pseudopora; M = macrochaeta; stars = trichobothria): **15**, habitus; **16**, different types of setae (see text) on ant.II (A, B, C, D, E), ant.III (F, G) and ant.IV (H, I); **17**, schematic dorsal macrochaetotaxy of head (small dots = short setae; groups of setae are surrounded by dotted lines); **18**, apex of mucrodens; **19**, labium base; **20**, apex of tibiotarsus and praetarsus of leg III; **21**, claw, ventral view (i = unpaired tooth; l = lateral unequal teeth; b = dorsobasal teeth); **22,23**, chaetotaxy of abd.I (left side); **24**, schematic macrochaetotaxy of abd. tergites IV–V; **25**, schematic macrochaetotaxy of abd. tergites I–V. Scales: 250 μm, Fig. 15; 25 μm, Figs. 18–19, 21–23; 10 μm, Figs. 16, 20.

labial palp well developed, curved. Setae of labial base smooth (Fig. 19). Outer maxillary ramus with 1 papillated seta, 1 basal seta, 3 sublobal hairs. Ventral side of head with numerous smooth setae and ciliated setae.

Dorsal macrochaetotaxic pattern: 15, 6–8, 8, 5, 20–26/ numerous on th.II-III/5, 2–3, 1, 1 + 3; on abd.II some specimens have 2 + 2, others have 3 + 3 macrochaetae; on abd.V, generally 5 + 5 macrochaetae, with some variability (Figs. 17, 22, 25). Pseudopora of abd.IV rather variable in position.

Unguis not elongate, with unpaired tooth at basal 50–60 % of inner side, 2 proximal unequal inner teeth and 1 pair dorsobasal subequal teeth (Fig. 21). Unguiculus with strong external tooth. One tenent hair on each tibiotarsus, smooth, thin, not capitate on TI and TII, capitate on TIII. Tibiotarsus III with only 1 smooth ventral seta distally. Each tibiotarsus has strong ciliated ventrobasal macrochaeta. Trochanteral organ with 12 smooth setae, some relatively long, others very short. Tenaculum with 4 + 4 teeth and 1 strong rough seta. Ventral tube with 7 + 7 smooth setae, little swelling on lateral flaps, 1 + 1 smooth posterior setae and 6 + 6 ciliated anterior setae. Manubrium with numerous, medium sized, ciliated setae on dorsal and ventral sides, containing 6–7 + 6–7 smooth dorsal setae, rather long, inserted perpendicular to integument. Dorsodistal setae 2 + 2, with 2 + 2 pseudopora nearby. Dens with numerous, rather long, ciliated setae, 1 dorsobasal smooth, rather long, seta. Mucro falciform, strongly curved, with 1 straight basal seta; distal nonannulated part of dens subequal to length of mucro (Fig. 18).

Type data. Holotype ♀, THAILAND: Changwat Chiang Mai: Amphoe Chiang Dao, Tham Chiang Dao, "réseau guano," 16.VII.1985 (P.Leclerc) (TC47) (MNHN). Paratypes: THAILAND: 9 ex., topotypic, "réseau guano," 16.VII.1985 (P. Leclerc) (TC47); 1 ex., topotypic, 25.XII.1980 (Deharveng) (THA110); 13 ex., topotypic, VIII.1981 (F. Stone) (5253, 5254); numerous ex., topotypic, 2.VII.1985 to 31.VII.1985 (L.Deharveng) (TC18, 21, 22, 25, 26, 27, 29, 32, 38, 40); numerous ex., same data (P. Leclerc) (TC44, 45, 57); 1 ex., topotypic, 5.VII.1986 (F.Stone) (TCD 102C). Five paratypes in MNHN; 10 paratypes in BPBM; 4 paratypes in BDCM; numerous paratypes in LEITT.

Etymology. The name of the species refers to its abundance in humid guano deposits in caves.

Relationships. *Coecobrya guanophila* comes near *C. caeca* (Schött) as redescribed by Christiansen and Bellinger (1980). The macrochaetotaxic pattern of abd.I-III is the same. The main difference is the number of smooth or very finely striate ventral setae on tibiotarsus III, which is only 1 in *C. guanophila*; they are several in *C. caeca*.

According to Yosii (1956), the Japanese cave species *C. dubiosa* Yosii and *C. guanophila* have similar macrochaetotaxic patterns, except in the presence of 2 + 2 posterior macrochaetae on abd.IV in the former instead of 1 + 1 in *C. guanophila*. *Coecobrya dubiosa* should also be devoid of smooth ventral seta on tibiotarsus III, a character which has yet to be checked. At least the distal smooth seta seems to be a constant feature in *Coecobrya*.

Coecobrya similis Deharveng, **new species** Figs. 20, 23, 24

Length: 0.55–0.95 mm. Color: entirely white. No eyes. Antennae about ½ as long as body. Ant. ratio in μm: 39:60:60:114. Antennal setae of 6 types as in *C. guanophila*: type 1 apically pointed except sometimes 1–2 large setae on dorsal side of ant.II, rarely of ant.I; type 2 either long (some on ant.I, ant.II and ant.III), or rather short (numerous on ant.IV); type 3 with at least 4 on ant.I, 3 on ant.II, ?0 on ant.III, none on ant.IV; type 4 as in *guanophila*; type 5 on ant.II (at least 1) and ant.III (several), apparently none on ant.I and ant.IV; type 6 as in *guanophila*.

Ant.III organ with 2 very small thick internal sensillae, similar to type 5, not hidden in integumental fold, guard setae not different from other type 4 s-setae of segment. No apical bulb on ant.IV.

Clypeolabral formula ?,4/5,5,4. Four prelabral setae smooth. External differentiated seta of labial palp well developed. Setae of the labial base smooth. Outer maxillary ramus with 1 papillated seta, 1 basal seta, 3 sublobal hairs. Ventral side of head with numerous smooth, ciliated setae.

Dorsal macrochaetotaxic pattern illustrated in Figs. 23, 24: 15,6–8,8,5,20–26/numerous on th.II-III/4,2–3,1,1 + 2; macrochaetae on abd.V variable in number, feebly differentiated from large mesochaetae. Pseudopora on abd.IV variable in position.

Unguis not elongate, with unpaired tooth at basal 50–60% of inner side, 2 proximal unequal inner teeth, 1 pair dorsobasal subequal teeth; unguiculus with strong external tooth; 1 tenent hair on each tibiotarsus, smooth, thin, pointed on TI and TII, capitate on TIII; tibiotarsus III with only 1 smooth ventral seta distally (Fig. 20). All tibiotarsi have 1 or 2 broad ciliated ventrobasal macrochaeta. Trochanteral organ with 9–12 smooth setae, some relatively long, others very short. Ventral tube with 6 + 6 smooth setae, slight swelling on lateral flaps, 1 + 1 smooth posterior setae, 5–6 + 5–6 ciliated anterior setae. Tenaculum with 4 + 4 teeth and 1 strong ciliated seta. Manubrium with numerous, medium-sized ciliated setae on dorsal and ventral side containing 6–7 + 6–7 smooth dorsal setae, rather long, inserted perpendicular to integument. Dorsodistal setae 2 + 2, with 2 + 2 pseudopora nearby. Dens with numerous, rather long, ciliated setae, 2 dorsobasal smooth, rather long, setae. Mucro falciform, with straight basal seta. Distal nonannulated part of dens subequal to length of mucro.

Type data. Holotype ♀, THAILAND: Changwat Chiang Mai: Amphoe Chiang Dao, Ban Tham, 500 m, forest soil, 17.XII.1980, berlese extractor (L. Deharveng) (THA13) (MNHN). Paratypes: THAILAND: numerous ex., topotypic, 500m, forest litter and soil, 17.XII.1980, berlese extractor (L. Deharveng) (THA10,11,12,13). Three paratypes in MNHN; 8 paratypes in BPBM; 8 paratypes in BDCM; numerous paratypes in LEITT.

Other material examined. THAILAND: 3 ex., Changwat Chiang Mai, Amphoe Chiang Dao, Tham Chiang Dao, roots and soil near entrance, dark zone, 25.XII.1980 (L.Deharveng) (THA 108) (LEITT).

Observations. *Coecobrya similis* is frequent in the forest litter outside Tham Chiang Dao; the few specimens found in the cave were just at the entrance and should be considered trogloxenes.

Relationships. Morphological differences between *C.guanophila* and *C. similis*, which are otherwise very similar, are summarized below:

	guanophila	*similis*
Body size in mm	0.9–1.2	0.55–0.95
Macrochaetae on abd.I	5 + 5	4 + 4
Macrochaetae on abd.IV	4 + 4	3 + 3
Smooth dorsobasal setae on dens	1	2

Coecobrya sp.

One specimen of a 3rd species of *Coecobrya* was collected in Tham Sia Dao, a small fossil cave, which develops only a few meters from the "réseau Touristes" of Tham Chiang Dao. This new species is not closely related to *C. guanophila* or *C. similis*. In particular, its macrochaetotaxic pattern is rather different on abdominal tergites (5,3,1,1 + 5).

ACKNOWLEDGMENTS

I wish to thank National Research Council of Thailand for giving permission and support to collect fauna in the Chiang Dao area.

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Fauna of Thai Caves. III. Two New Cavernicolous Species of *Arrhopalites* from Thailand (Insecta: Collembola)[1]

Pierre Nayrolles[2]

ABSTRACT

Two new species of *Arrhopalites* from Chiang Dao cave, northern Thailand, *A. chiangdaoensis* and *A. anulifer*, are described and illustrated.

INTRODUCTION

During the Thai 81 and Thai-Maros 85 expeditions, extensive faunal collections were carried out in Chiang Dao cave, a large underground system of the Chiang Mai Province. Symphypleona Collembolans were represented by 2 new species of *Arrhopalites*, which are described in this paper. They are the 1st species of this genus recorded from Thailand.

The following abbreviations are used: abd. = abdominal segment; ant. = antennal segment.

Holotypes are deposited in Museum National d'Histoire Naturelle, Paris, France (MNHN); paratypes are deposited in the following collections: Bishop Museum, Honolulu, Hawai'i (BPBM); Biology Department, Chiang Mai University, Chiang Mai, Thailand (BDCM); and Laboratoire d'Ecologie des Invertébrés Terrestres, Université Paul Sabatier, Toulouse, France (LEITT).

SYSTEMATICS

Arrhopalites chiangdaoensis Nayrolles, **new species** Figs. 1–7

Description. *Body length.* ♀: 0.6 mm; ♂: 0.5 mm. *Color.* White, or more or less reddish, particularly head (preserved in alcohol). *Antennae.* Relative lengths of antennal segments I:II:III:IV = 1:2:3.1:8. Ant. III with papilla in basal ½ (Fig. 6). Ant. III organ with usual 2 rods. Ant. IV distinctly subdivided into 5 subsegments, basal subsegment ca. 1.2× longer than terminal one. *Head.* Eyes 1 + 1 unpigmented. Only thin ordinary setae present. *Legs* (Figs. 2–4). Tibiotarsal chaetotaxy as in table 1 (nomenclature follows Nayrolles 1988). Like *Arrhopalites terricola*, V ai and particularly V pi of 2nd and 3rd pairs of legs shifted toward base. Claws slender, without tunica, each with distinct inner tooth. Inner lamella of unguiculus more developed on hind legs than on 1st and 2nd legs. Unguiculus of all legs without tooth, with long apical needle, distinctly longer than tip of claw. *Tenaculum* (Fig. 5). With tridentate rami, small, club-shaped appendage at base of each ramus, 2 setae at tip of pars anterior. *Furca* (Fig. 1). Ratio dens/mucro 1.7; manubrium with 5 + 5 dorsal setae. Chaetotaxy of dentes as in table 4; same as *A. pygmaeus* (Wankel). Ventral setae of dentes: 3,2,1 . . . 1. Mucro serrated on both sides, without apical swelling. *Small abd.* Anal setae thin, smooth, median setae of upper anal

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flap (a0) not forked. Subanal appendage (Fig. 7) split into 2 more or less unequal serrated branches.

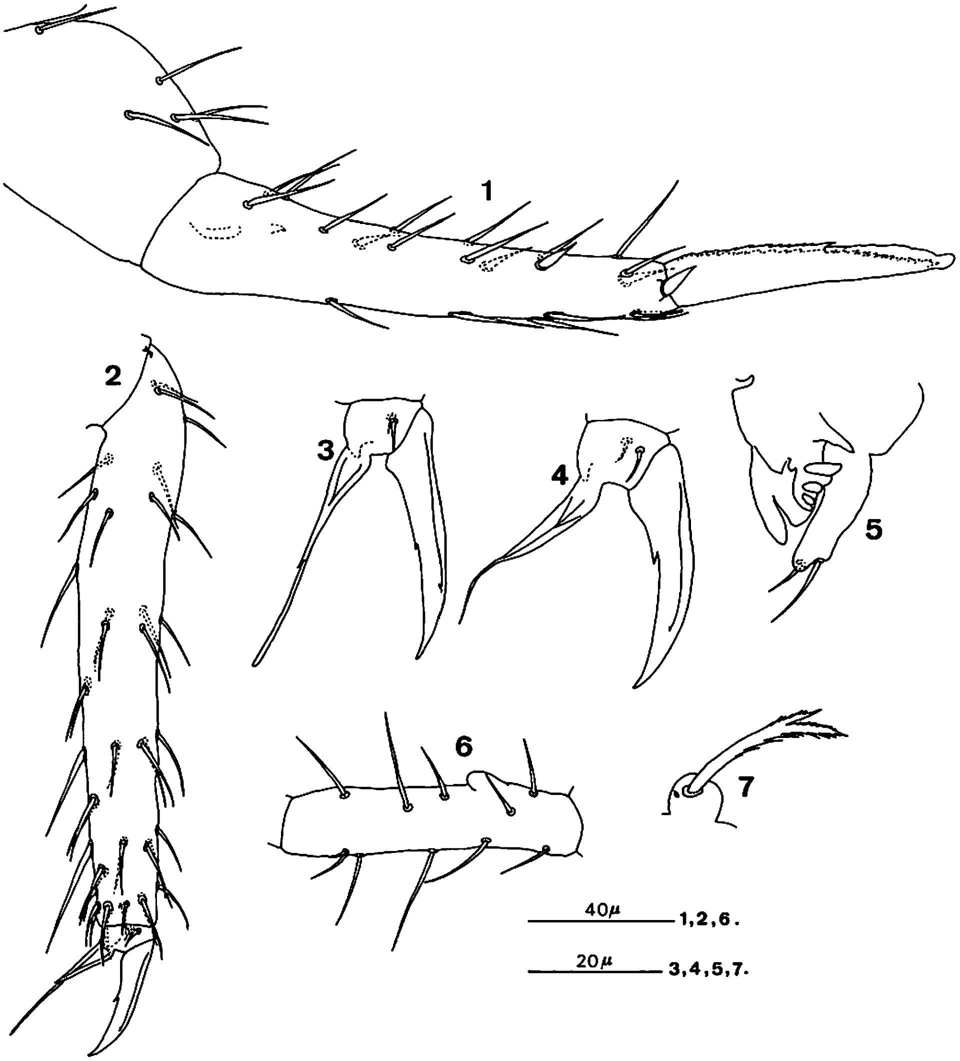
Type data. Holotype ♀ and 1 paratype ♀, THAILAND: Changwat Chiang Mai: Amphoe Chiang Dao, Tham Chiang Dao, "réseau actif," trap, 25.XII.1980 (Deharveng) (THA 104b). Other paratypes: 2 ♀, 1 ♂, 1 juv., same station, "réseau supérieur," 25.XII.1980, (Deharveng) (THA 110). 13, same station, VII.1985 (Deharveng): "réseau touriste," 2 ♀ (TC 19); "réseau guano," 1 ♀ (TC 32); "réseau supérieur," 6 ♀, 1 ♂, 3 juv. (TC 25, TC 26, TC 27, TC 84). Holotype in MNHN, Paris; 2 paratypes in BPBM; 2 paratypes in BDCM; 13 paratypes in LEITT.

Remarks. On account of its characters (ant. III with a papilla on its basal half and a long apical needle on the empodial appendage of the hind legs), *Arrhopalites chiangdaoensis*, n. sp., seems close to the group of European species established by Cassagnau and Delamare Deboutteville (1953), which includes *furcatus* Stach, *ornatus* Stach, and *elegans* Cassagnau & Delamare. The differential characters of these species are given by Selga (1963). *Arrhopalites chiangdaoensis* and *elegans* differ from the other 2 species by their subanal appendage split into 2 serrated branches (subanal appendage with 2 smooth branches in *furcatus*, abundantly branched in *ornatus*). Differences between *elegans* and *chiangdaoensis* are weak: *elegans* has 1 inner tooth on the unguiculus of forelegs and the claws of hindlegs are thick, while *chiangdaoensis* has its unguiculus of the forelegs without a tooth and the claws of hindlegs are relatively slender; this last character can be considered as a troglomorphic one. A North American species: *hirtus* Christiansen has also ant. III with a papilla and all empodial appendages each with a long apical needle; nevertheless, seta e6 of the dens is absent and subanal appendage is deeply serrated in *hirtus*, while e6 is present and subanal appendage is simply split in 2 serrated branches in *chiangdaoensis*.

Arrhopalites anulifer Nayrolles, **new species** Figs. 8–14

Description. *Body length.* ♀: 0.6–0.7 mm. *Color.* White (preserved in alcohol). *Antennae.* Relative lengths of antennal segments I-IV = 1:1.9:3.6:7.1. Ant. III without prominent papilla, with circular area devoid of integumentary granulation in basal ½. Ant. III organ with usual 2 rods. Ant. IV (Fig. 10) more or less subdivided into 6 subsegments (sometimes 5 subsegments when 2 basal ones are fused). One or several rings more or less marked (generally 2) between subsegments. *Head.* Eyes 1 + 1 unpigmented. Vertical setae spiny except 3 setae of median row (like *Arrhopalites nivalis* Yosii). *Legs* (Figs. 11–13). Tibiotarsal chaetotaxy as in table 2. Claws of forelegs longer, more slender than those of 2nd and especially 3rd pair of legs; claws of leg III more curved. Fine tunica dorsally on the claws of median and hind legs; tunica absent on the claws of forelegs. Inner tooth on claws of all legs. All unguiculus with distinct tooth (smaller on 3rd pair of legs than on 1st and 2nd); apical needle longer than tip of claw. *Tenaculum.* Normal with 2 setae at tip of pars anterior. *Furca* (Figs. 8–9). Ratio dens/mucro 1.5; manubrium with 5 + 5 dorsal setae. Chaetotaxy of dentes as in table 4; ventral setae of dentes: 3,2,2,1,1; mucro serrated on both sides, rounded at tip. *Small abd.* (Fig. 14). Upper anal flap bears 7 (3–1–3) large, winged setae (a0,a1,a2,a3) alternating with 3 slender setae. Each lateral flap with 3 large winged setae (ai1,ai2,ai3) alternating with slender setae. Upper anal flap with 3 + 3 spinose processes: 1 + 1 small dorsal, 2 + 2 large lateral. One small female has only 2 + 2 spinose processes on upper anal flap, 1 of large spinose processes, most ventral one, wanting. Subanal appendage in side view straight, gradually narrowing toward tip; straight in dorsal view, equally thick throughout length, weakly denticulated at tip.

Type data. Holotype ♀ and 1 paratype ♀, THAILAND: Changwat Chiang Mai: Amphoe

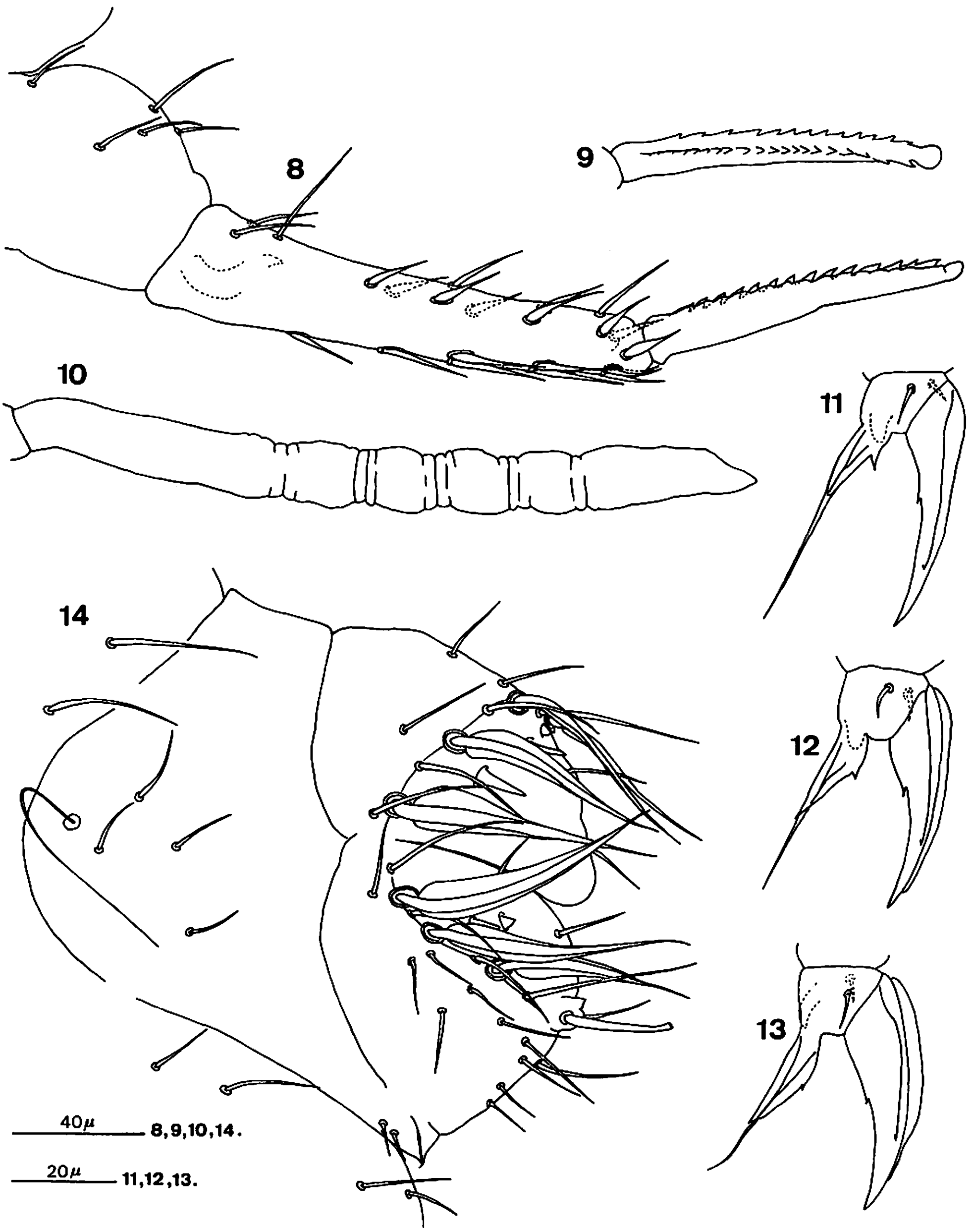


Figs. 1–7. *Arrhopalites chiangdaoensis*, n. sp.: **1,** furca, external view; **2,** tibiotarsus of leg II, anterior view; **3,** praetarsus of leg I, anterior view; **4,** praetarsus of leg III, anterior view; **5,** tenaculum, right side view; **6,** right ant. III; **7,** subanal appendage.

Chiang Dao, Doi Chiang Dao, 1,720 m, shaft P1, −22 m, 12.VII.1985 (J.P. Besson) (DC 14). Holotype in MNHN, Paris; paratype in LEITT.

Other material examined. THAILAND: Changwat Chiang Mai: 1 juv., Amphoe Chiang Dao, Tham Chiang Dao, 25.XII.1980, "réseau supérieur," (L.Deharveng) (THA 110); 1 ♀, same station, 6.VII.1985, "réseau touriste," (Deharveng) (TC 19); 2 ♀, same station, 7.VII.1985, "réseau supérieur," (Deharveng) (TC 27); 9 ♀, 11 juv., forest near Ban Tham Chiang Dao, decaying wood, 17.XII.1980, (Deharveng) (THA 5). Three ex. in BPBM; 3 ex. in collection of BDCM; 18 ex. in LEITT.

Etymology. The specific epithet, *anulifer* is from the Latin *anulus* = ring, with reference to the rings between subsegments of ant. IV.



Figs. 8–14. *Arrhopalites anulifer*, n. sp.: **8,** furca, external view; **9,** mucro, dorsal view; **10,** left ant. IV; **11,** praetarsus of leg I, anterior view; **12,** praetarsus of leg II, anterior view; **13,** praetarsus of leg III, anterior view; **14,** small abd., left side view.

Discussion. The presence of spinose processes on the anal flaps links *Arrhopalites anulifer*, n. sp., to the *coecus* group. On account of its ant. IV subdivided with rings between the subsegments, its lack of a ventral spine at the tip of the dens, and particularly its 3 + 3 spinose processes on the upper anal flap, *anulifer*, n. sp., seems very close to *antrobius* Yosii (redescribed by Yosii 1967). They can be separated by the characters in table 3.

Ecology and Feeding of *Arrhopalites chiangdaoensis* and *A. anulifer*

Arrhopalites chiangdaoensis was found only in the cave whereas *anulifer* has been met also in a shaft 22 m deep and in decaying wood in the forest.

The observation of the digestive tube of *chiangdaoensis* shows that this species ingests clay; only 1 female had myceliae mixed with clay. The digestive tubes of some individuals had unusual contents. One female had fragments of Collembola (2 mandibules, 1 claw, labium); 3 females and 1 juvenile had pieces of scales, probably from Tineoidea (Lepidoptera), which are abundant in the cave; 1 female had 1 piece of scale and some setae of *Sinella* (Collembola present in the same sample). Thus, *chiangdaoensis* seems to be polyphagous; the scales of Tineoidea in the digestive tube might be connected with eating moth cadavers.

One individual of *A. anulifer* had clay in its digestive tube; 1 female had myceliae and a labium of an unidentified Collembola. All others had myceliae or nothing (lacking of digestive contents connected with the molt).

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Table 1. Tibiotarsal chaetotaxy of *Arrhopalites chiangdaoensis*, n.sp.

	P1	P2	P3
Primary setae			
Wanting setae of whorls	0	Vp	Vp
Setae K	–	–	–
Setae FP	+	+	+
Secondary setae			
Fundamental setae (Vai & Vpi)	+	+	+
Setae FS	–	–	FSa
Present setae of interwhorls	–	–	–
Oval organs	–	–	–
Specially shaped setae	–	–	–
Variable setae	Vai frequently wanting (1 case for 2)	Sometimes Vai wanting	–

Table 2. Tibiotarsal chaetotaxy of *Arrhopalites anulifer,* n.sp.

	P1	P2	P3
Primary setae			
Wanting setae of whorls	0	Vp	Vp
Setae K	–	–	–
Setae FP	+	+	+
Secondary setae			
Fundamental setae (Vai & Vpi)	+	+	+
Setae FS	–	–	FSa
Present setae of interwhorls	–	–	–
Oval organs	–	–	–
Specially shaped setae	–	–	–
Variable setae	–	–	–

Table 3. Differences between *Arrhopalites antrobius* and *Arrhopalites anulifer,* n.sp.

A. antriobius	*A. anulifer,* n. sp.
Most ventral spinose process of upper anal flap small	Most ventral spinose process of upper anal flap large
Ventral setae of dentes: 3,2,1,1,1	Ventral setae of dentes: 3,2,2,1,1
Dorsal setae of dentes: 1 basal + 4	Dorsal setae of dentes: 1 basal + 3
Mucro not rounded at tip	Mucro rounded at tip
1 setae on pars anterior of tenaculum	2 setae on pars anterior of tenaculum

Table 4. Dental chaetotaxy of *Arrhopalites chiangdaoensis,* n. sp., and *Arrhopalites anulifer,* n. sp. (nomenclature follows Christiansen & Bellinger 1981).

	e2	e3	e4–5	e6	e7	e8–9	id3	l1	l2–3	l4	ve1	ve2–4	ve5
A. chiangdaoensis	+	s	+	+	+	–	+	s	s	–	+	+	–
A. anulifer	s	s	s	–	+	–	–	s	s	(s)	+	+	+

Additions to the Genus *Ochyrotica* Walsingham, 1891, in Southeast Asia (Lepidoptera: Pterophoridae: Agdistinae)

C. Gielis[1]

ABSTRACT

Ochyrotica taiwanica, n. sp., is described from Taiwan. New distribution data are given for *O. borneoica*, *O. yanoi*, *O. toxopeusi*, and *O. breviapex*.

INTRODUCTION

Since recent publications on the genus *Ochyrotica* Walsingham, 1891 (Arenberger & Gielis 1988; Arenberger 1988; Gielis 1988), new material has become available for study. The insects involved originate from China (Hainan, Taiwan), the Philippine Islands, and New Guinea (Irian Jaya and Papua New Guinea). Most specimens belong to the *O. connexiva* and *O. concursa* groups, which have been recently revised. The *O. cretosa/buergersi* group, which has a more Indo-Australian distribution, is still under study.

MATERIALS AND METHODS

Material was examined from the following institutions: Bishop Museum (BPBM), Honolulu, Hawai'i, USA; National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., USA; Zoologisk Museum (ZMUC), University of Copenhagen, Copenhagen, Denmark. Specimens without abdomens are denoted with the abbreviation w.a. Material in the author's collection is abbreviated CG.

Ochyrotica taiwanica Gielis, **new species** Figs. 1–3

MALE (Fig. 1). Wingspan 15 mm. Forewings snow white, pattern golden to dark brown, continuous band along costal and dorsal margins. Costal margin darker. Costal margin narrowed at ⅓ of wing length, widened at ⅔. Dorsal band rather narrow basally, widened at ⅓, but not reaching costal band. Widening at ⅔ reaches costal margin. Two small longitudinal lines and wavy transverse line of brown scales in distal field. Some pronounced iridescent scales between longitudinal small lines. Apex prolonged, acute, tornus rounded. Fringes brown, with dark basal fringe-line. Hind wings brown, some darkening near apex and anal angle. Thorax snow white with costal and dorsal continuation of forewing markings. Head with grey-brown bifid scales (characteristic of genus). Palpae slender, greyish white. Frons white. Antennae brown, short ciliate, approximately 0.5 forewing length. Abdominal segments 2, 4, 6, and 7 snow white; segments 1 and 5 dark brown; segment 3 brown, with dorsolateral white line. Hind legs dark brown, some white scales near bases of spur pairs.

Genitalia (Figs. 2–3). Valvae symmetrical, rounded. Sacculus with sharp-angled widening in ⅓ of valvae. Saccular process consisting of spined blotch and stout thornlike process distal

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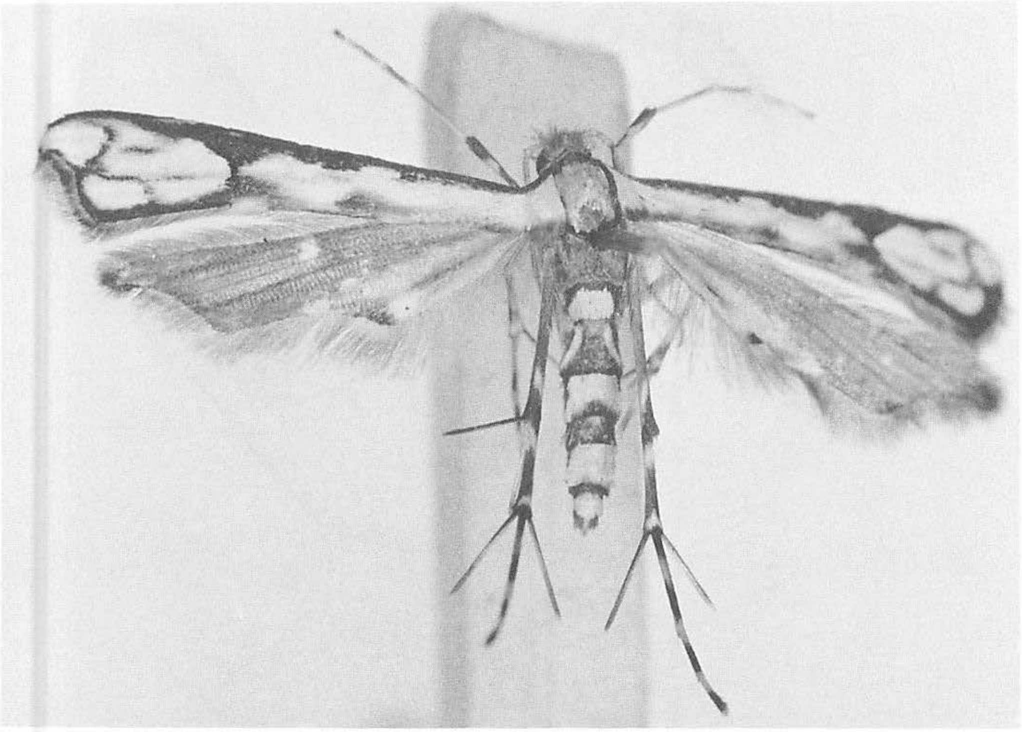


Fig. 1. *Ochyrotica taiwanica*, n. sp., holotype.

of blotch in middle of valvae. Tegumen simple, rather small. Uncus stout. Vinculum narrow. Juxta small with pair of short anellus arms. Aedeagus straight, stout, end acutely pointed. Cornuti distal in bundle of parallel small spines.

Flight period. November.

FEMALE. Unknown.

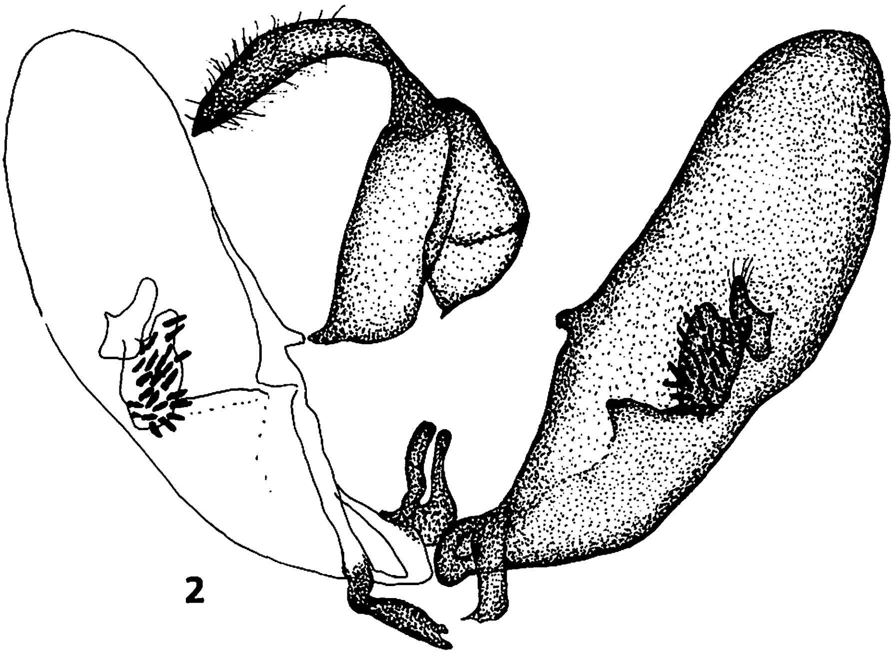
Type data. Holotype ♂, [TAIWAN]: Taihoku [now Taipei], 17.xi.1932, S. Issiki, genitalia CG 1948 (USNM).

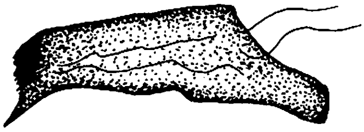
Distribution. Known only from type locality.

Remarks. This species closely resembles the holotype of *O. connexiva* (Walsingham). Since the male of that species is unknown, it is essential to consider the differences.

Table 1. Comparison of *Ochyrotica connexiva* and *Ochyrotica taiwanica*.

	O. connexiva	*O. taiwanica*
Costal and dorsal forewing markings	touch twice	touch once
Forewing transverse markings in distal white field	angulate	sinuous
Forewing longitudinal markings in distal white field	not pronounced	pronounced
Hind wing apical and anal angles	concolorous	darkened





Figs. 2–3. *Ochyrotica taiwanica*: **2**, male genitalia; **3**, aedeagus.

Ochyrotica borneoica Gielis, 1988

Ochyrotica borneoica Gielis in Arenberger & Gielis, 1988:279.

Material examined. PHILIPPINE IS: Tawi Tawi: 5♂♂, 20♀♀, 1 w.a., Tarawakan, North of Batu Batu, 22.x.–13.xi.1961, Noona Dan. Exp. (ZMUC, CG); Balabac: 2♂♂, Dalawan Bay, 7–10.x.1961, Noona Dan. Exp. (ZMUC).

Distribution. Indonesia: Borneo (Kalimantan); Philippine Is: Tawi Tawi: Balabac.

Remarks. The distribution of this species appears not to be restricted to the island of Borneo as originally assumed. This revised distribution confirms that the identity of *Ochyrotica* "species 1" from the island of Sumatra is uncertain (Arenberger & Gielis, 1988:284).

Ochyrotica yanoi Arenberger, 1988

Ochyrotica yanoi Arenberger, 1988:276–79; Gielis, 1989:69.

Material examined. [PEOPLES REPUBLIC OF CHINA]: Hainan [I], 1♂, xi.1942, S. Issiki; Hainan: 2 w.a., Hudibasi, xi.1942, S. Issiki; [TAIWAN]: 1♀, Taihoku [now Taipei], 23.xi.1932, S. Issiki (all USNM).

Distribution. Japan: Ryukyu Is: Okinawa; China: Hainan I; Taiwan; Vietnam: Tonkin.

Remarks. The distributional gap between the Vietnamese and Japanese occurrences has been closed, at least partly, by the recognition of specimens from Hainan and Taiwan.

Ochyrotica breviapex Gielis, 1989

Ochyrotica breviapex Gielis, 1989:69–72.

Material examined. PAPUA NEW GUINEA: Morobe Prov: 5♂♂, 16♀♀, Wau, Wau Ecol. Inst., 1,200 m, 12–24.vii, 25–31.vii, 1–10.viii, and 23–31.viii.1983, S. E. & P. M. Miller, secondary montane forest/U.V. light trap and Malaise trap (USNM); 62 specimens, Wau, 1,200–1,250 m, 8.i.1962, 19–31.i.1967, 20.v.1965, 22.v.1965, 26.v.1965, 27.v.1965, 28.v.1965, 3.vi.1965, 9.vi.1965, 11.vi.1965, 14.vi.1965, 19.vi.1965, 22.vi.1965, 24.vi.1965, 26.vi.1965, 7.vii.1961, 8.vii.1961, 25.vii.1961, 26.vii.1961, 2.viii.1961, 4.viii.1961, 11.viii.1965, 17.viii.1961, 22.viii.1961, 25.viii.1965, 30.viii.1965, 8.ix.1961, 11.xi.1961, Malaise trap (J. Sedlacek; J. L. Gressitt & J. Sedlacek; R. Straatman) (BPBM); Southern Highlands Prov: 1♂, N of Mendi, 1,800 m, 8.x.1958, light trap, Gressitt (BPBM); SOLOMON IS: Guadalcanal: 1 w.a., Kiwi Crk, 18.ix.1944, H. E. Milliron (BPBM); PHILIPPINE IS: Mindanao: 1♂, Agusan, Esperanza, 4–11.xi.1959, light trap, C. M. Yoshimoto (BPBM); Mindanao: 1♂, Bukidnon, Mt. Katanlad, 1,250 m, 4–9.xii.1959, light trap, L. W. Quate (BPBM); Misamis Or.: 1♀, Hindangon, 20 km S of Gingoor, 600–700 m, 20–24.iv.[19]60, Torrevillas (BPBM).

Distribution. Indonesia: Borneo (Kalimantan); Papua New Guinea: Wau, Mendi; Philippine Is: Misamis Oriental: Mindanao; Solomon Is: Guadalcanal.

Remarks. This species appears to occur not only in the Indonesian Archipelago and New Guinea but also in the Philippine Islands.

Ochyrotica toxopeusi Gielis, 1988

Ochyrotica toxopeusi Gielis, 1988:285–86.

Material examined. INDONESIA: New Guinea: [Irian Jaya]: 1♀, Nabire, S of Geelvink Bay, 0–20 m, 6.vii.1962, Gressitt (BPBM).

Distribution. Indonesia: Sulawesi, Irian Jaya.

Remarks. With the material presently examined, the species seems to have an extension of its distribution toward the Australian faunal elements.

ACKNOWLEDGMENTS

I thank Dr. S. E. Miller (BPBM), Dr. D. R. Davis (USNM) and Mr. O. Karsholt (ZMUC) for loans of material, which made this publication possible; Dr. Miller for correcting the English text; and Mrs. B. van de Sant for typing the manuscript.

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A New Species of the Genus *Chelocoris* from Vietnam (Hemiptera: Phymatidae: Carcinocorinae)

Nicholas A. Kormilev[1]

ABSTRACT

The new phymatid, *Chelocoris vietnamensis*, n. sp., (Hemiptera: Carcinocorinae) is described and represents the 1st record of the genus from Vietnam. A diagnosis and figure of the pronotum and scutellum are provided to help distinguish this species from the closely related *C. spinosulus* from India.

INTRODUCTION

Through the kind offices of Dr. Scott E. Miller, chairman of the Department of Entomology, Bishop Museum, Honolulu, Hawai'i, I had the privilege to study a small lot of Oriental Phymatidae, for which I express my sincere gratitude.

In this lot, comprising the subfamilies Macrocephalinae and Carcinocorinae, 1 specimen represents a new species of the genus *Chelocoris* Bianchi, 1899, which is described below.

The genus *Chelocoris* Bianchi is distributed in mountainous areas of northern Pakistan, Kashmir, northern India, Tibet, Nepal, Bhutan, southwest China, and now is known from Vietnam.

Chelocoris vietnamensis Kormilev, **new species** Fig. 1

FEMALE. Elongate ovate. Head, forelobe of pronotum, corium, femora, and tibiae with dense, spiculoid, setigerous granulations, and with a few longer spines. Lateral borders of pronotum, scutellum, and connexiva denticulate.

Head. Longer along median line than width across eyes (25:21); clypeus narrow, as long as antenniferous tubercles, with 1 long and 2 short spines; 3 spines between eyes, middle one longest; ocelli nearer to eyes than to hind border of head. Bucculae with 2 flaps. Antennas short, 1.26 × as long as width of head across eyes. Relative lengths and widths of antennal segments I-IV are 6(4):3(2):5(3):12.5(4.5). Relative lengths of labial segments I-III are 15:9:7.

Thorax. Pronotum shorter along median line than maximum width across lateral angles (40:65). Anterior border truncate; anterior angles with 2 (1+1) strong, setigerous spines; 2 (1+1) similar spines at middle of anterolateral borders; 2 (1+1) slightly smaller spines in front of median pit of forelobe, a few smaller spines on disk between spiculoid, setigerous granulations. Anterolateral borders slightly convex, denticulate; interlobal depression clearly visible. Hind disk with fine, dense punctures; anterolateral borders of hind lobe with a few spiculoid, setigerous granulations of different length; lateral angles cut out or truncate; posterolateral border rimmed, denticulate; hind border truncate; hind angles minute. Hind disk with 3 longitudinal depressions, 1 medially, 2 sublaterally. Carinae arising from hind border of forelobe, straight, divergent, reaching hind angles. Scutellum longer than basal width (32:22),

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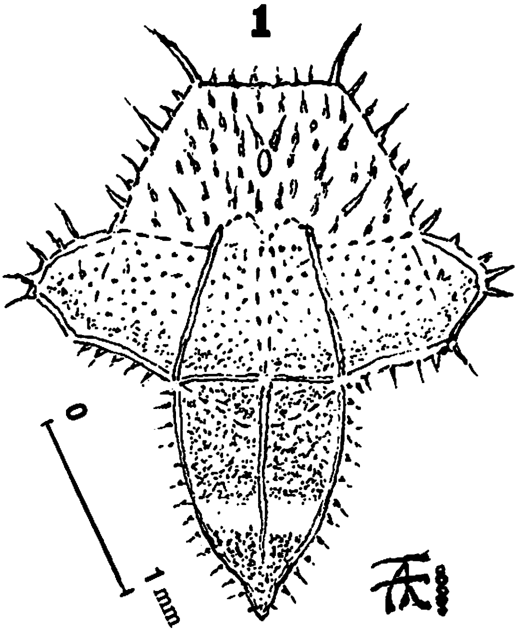

Fig. 1. *Chelocoris vietnamensis*, n.sp., ♀, dorsal aspect of pronotum and scutellum.

constricted before tip; lateral borders rimmed, denticulate; disk finely punctured; median carina thin, not reaching tip of scutellum. Hemelytra slightly longer than abdomen; corium reaching hind border of connexivum V; corium with setigerous granulation. Membrane with simple veins, not branched; one closed cell, formed by Cu + PCu, reaching almost to middle of membrane; another, formed by PCu + A, reaching tip of scutellum. *Pleurae.* Propleurae with spiculoid, setigerous granulations, fore border with spines of different sizes. Other pleurae with round granulations. *Legs.* Fore femora longer than their maximum width (38:12.5), covered with setigerous granulations. Fore tibiae with very fine setigerous granulations; middle and hind tibiae with erect setae.

Abdomen. Rhomboid, shorter than maximum width (80:85); anterolateral and posterolateral borders slightly convex; hind border rounded. Lateral borders with sparse, spiculoid, setigerous granulations. Venter with round granulations.

Coloration. Head pale yellow; pronotum yellow on fore lobe, orange on hind lobe, infuscate along hind border; scutellum brown with transverse, subapical, yellow band; corium whitish with orange veins, infuscate at tip; abdomen pale yellow, dark brown transverse bands across segments IV and V, except on posteroexterior portion of connexivum V; ventral side yellow to orange, lateral angles of abdomen dark brown; legs yellow to orange.

Measurements. Total length 6.10 mm; width of pronotum 2.60 mm; width of abdomen 3.40 mm.

Type data. Holotype ♀, VIETNAM: 39 km S of Djiring, 810 m, 29.IV.1960, L. W. Quate (BPBM 14,568). Deposited in the Bishop Museum, Honolulu, Hawai'i.

Remarks. *Chelocoris vietnamensis*, n. sp., is related to *C. spinosulus* Kormilev (1962) from Almora, northwest India, but the head and fore lobe of pronotum are much more densely covered with spiculoid, setigerous granulations; the scutellum is constricted before apex; and the lateral borders of scutellum and abdomen are denticulate (only finely and densely serrate on *C. spinosulus*).

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