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

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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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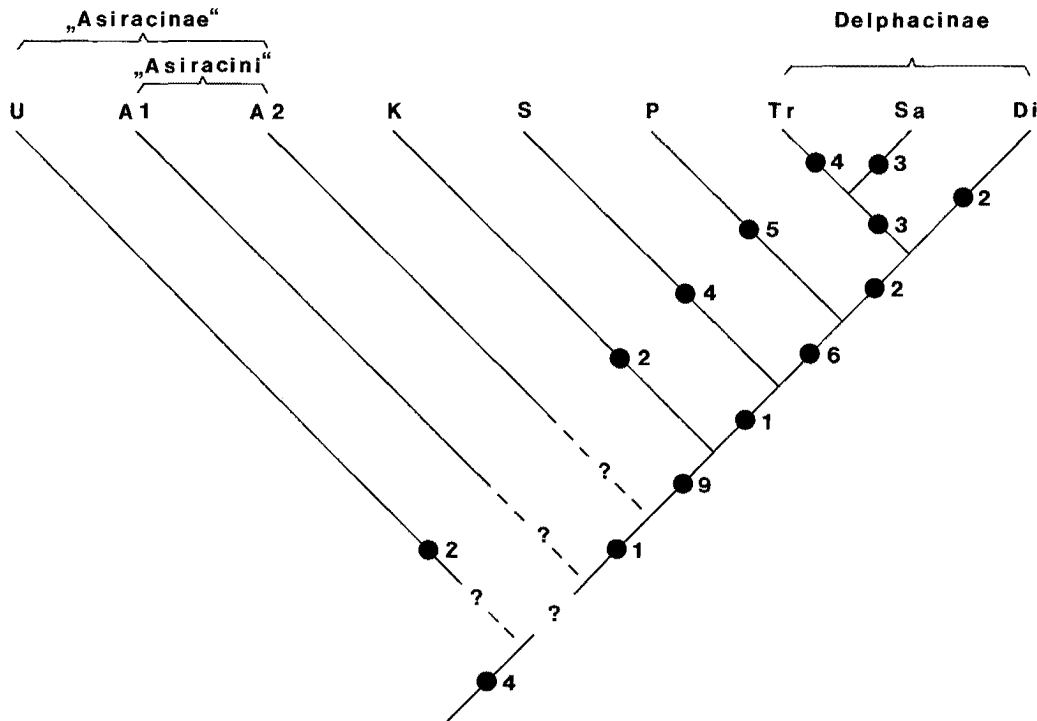
Fig. 1. Phylogenetic relationships within Delphacidae, modified after Asche (1985). Black spots: apomorphies, numbers refer to the total of apomorphies at each branch; quotation marks indicate paraphyly. Abbreviations: A1 = non-ugyopine Asiracinae without an oblique carina across genae; A2 = non-ugyopine 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.
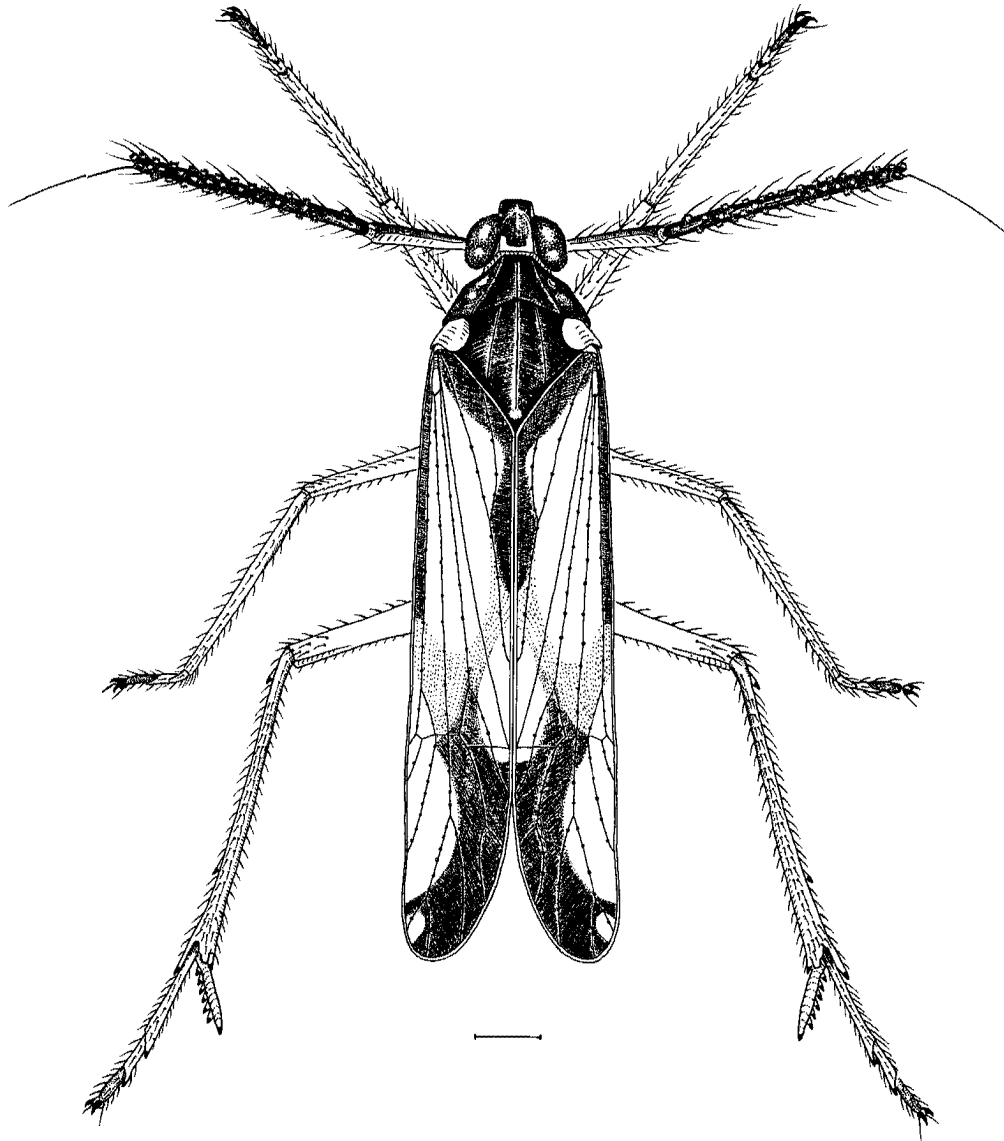
Fig. 2. *Vizcaya adornata* Asche, n. sp., habitus from dorsal, holotype ♂, Sulawesi. Scale: 0.5 mm.

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.
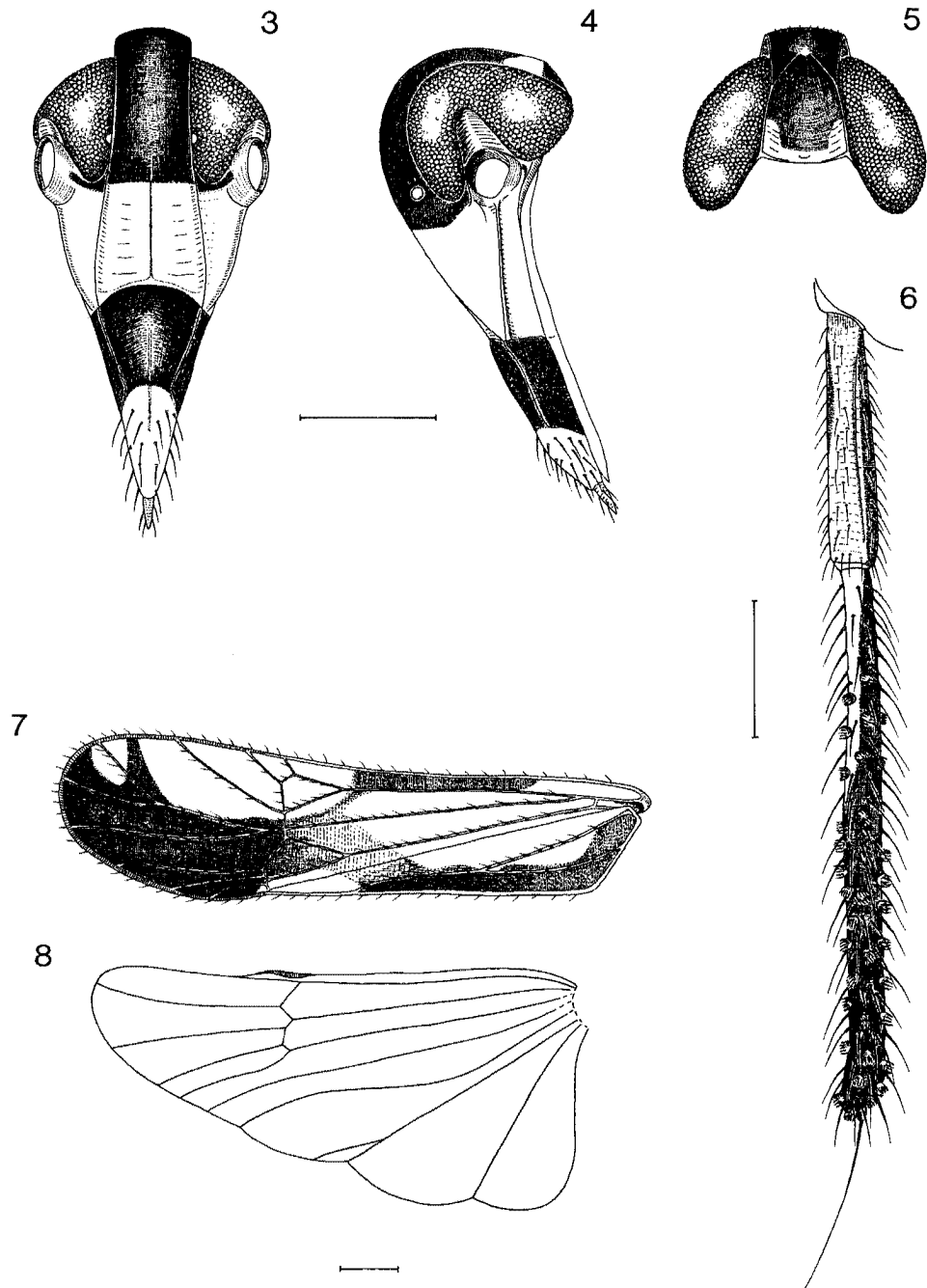
Figs. 3–8. *Vizcaya adornata* Asche, n. sp.: **3**, head, paratype ♀, frontal view; **4**, same, left lateral view; **5**, same, dorsal view; **6**, left antenna in frontal view, holotype ♂; **7**, left tegmen, paratype ♀; **8**, same, left hind wing. Scale: 0.5 mm.
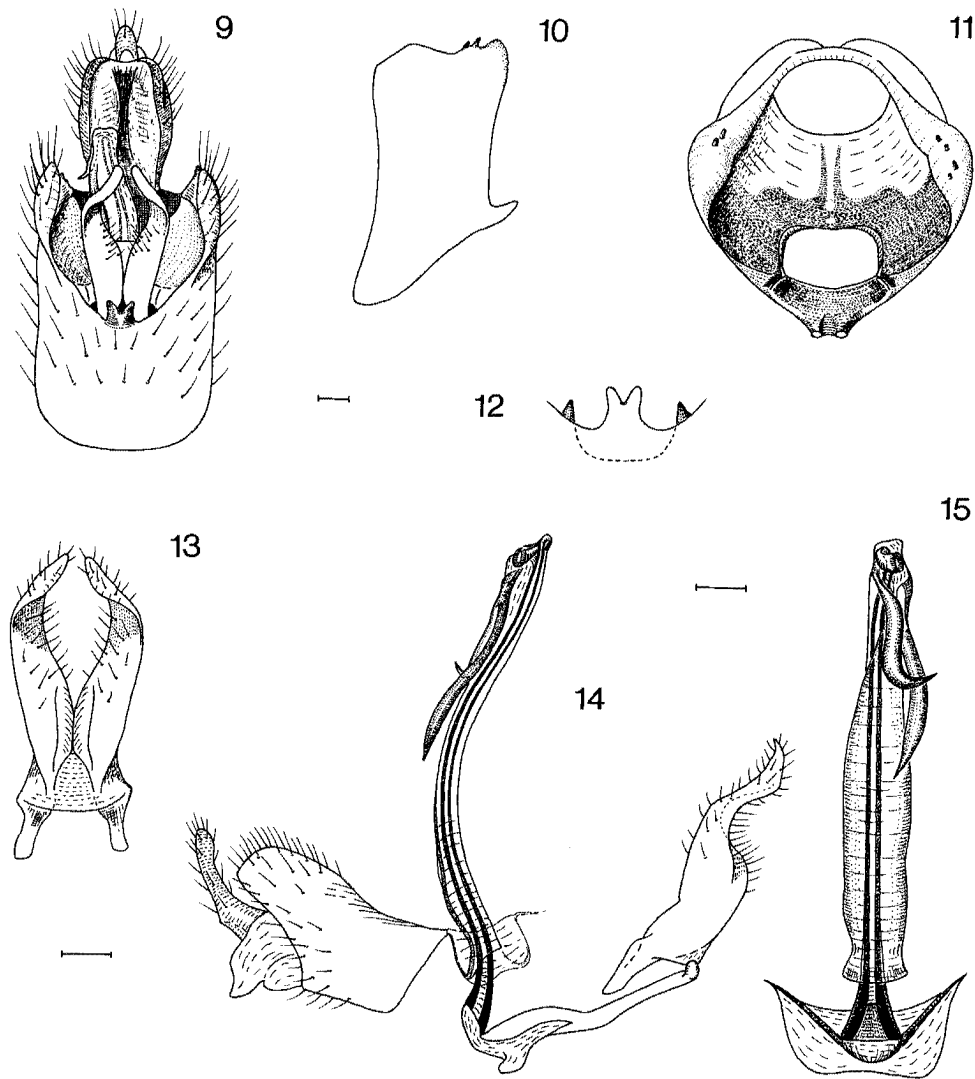
Figs. 9–15. *Vizcaya adornata* Asche, n. sp., male genitalia, holotype: **9**, genitalia in repose, ventrocaudal view; **10**, genital segment, left lateral view; **11**, genital segment, caudal view; **12**, median projection of ventrocaudal margin of genital segment, ventral view; **13**, parameres, ventral view; **14**, genitalia without genital segment, left lateral view; **15**, aedeagus, dorsal view. Scale: 0.1 mm.
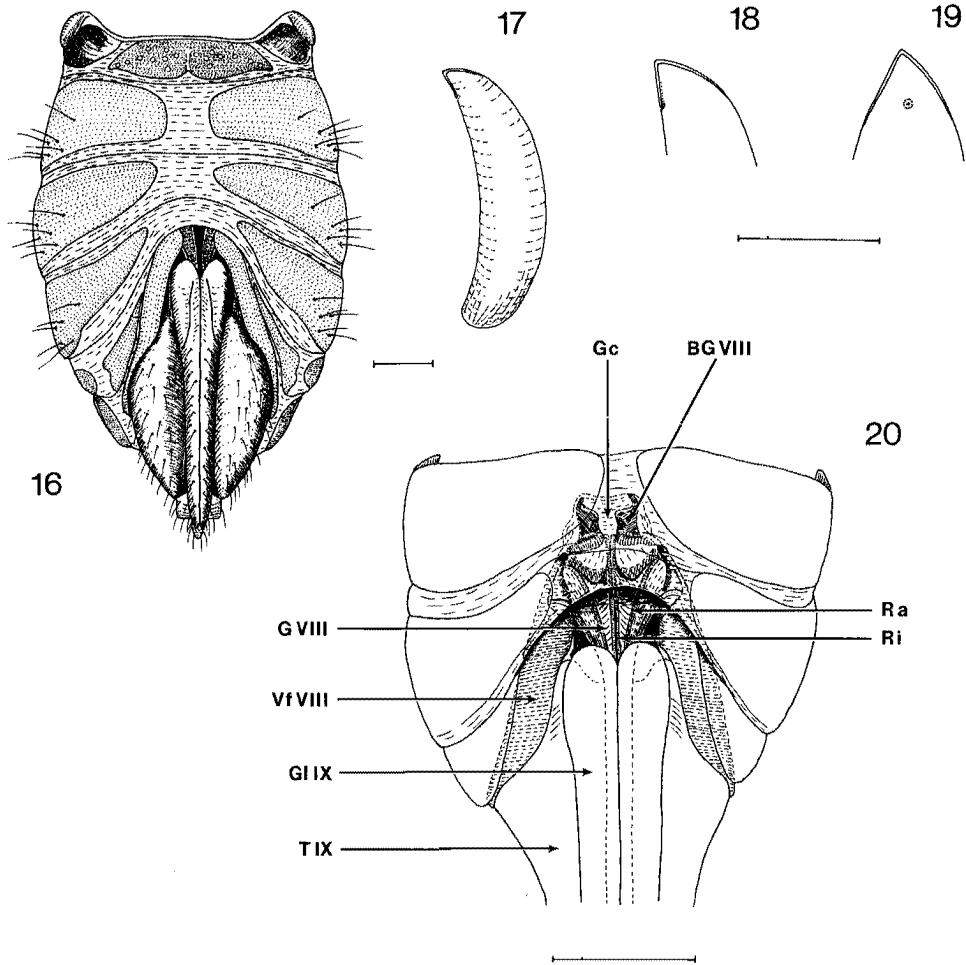
Figs. 16–20. *Vizcaya adornata* Asche, n. sp., female genitalia and egg, paratype: **16**, abdomen, ventral view; **17**, egg, note the relatively large size (same scale as abdomen); **18**, anterior pole of egg with micropyle, lateral view; **19**, anterior pole of egg, view onto micropyle; **20**, 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.
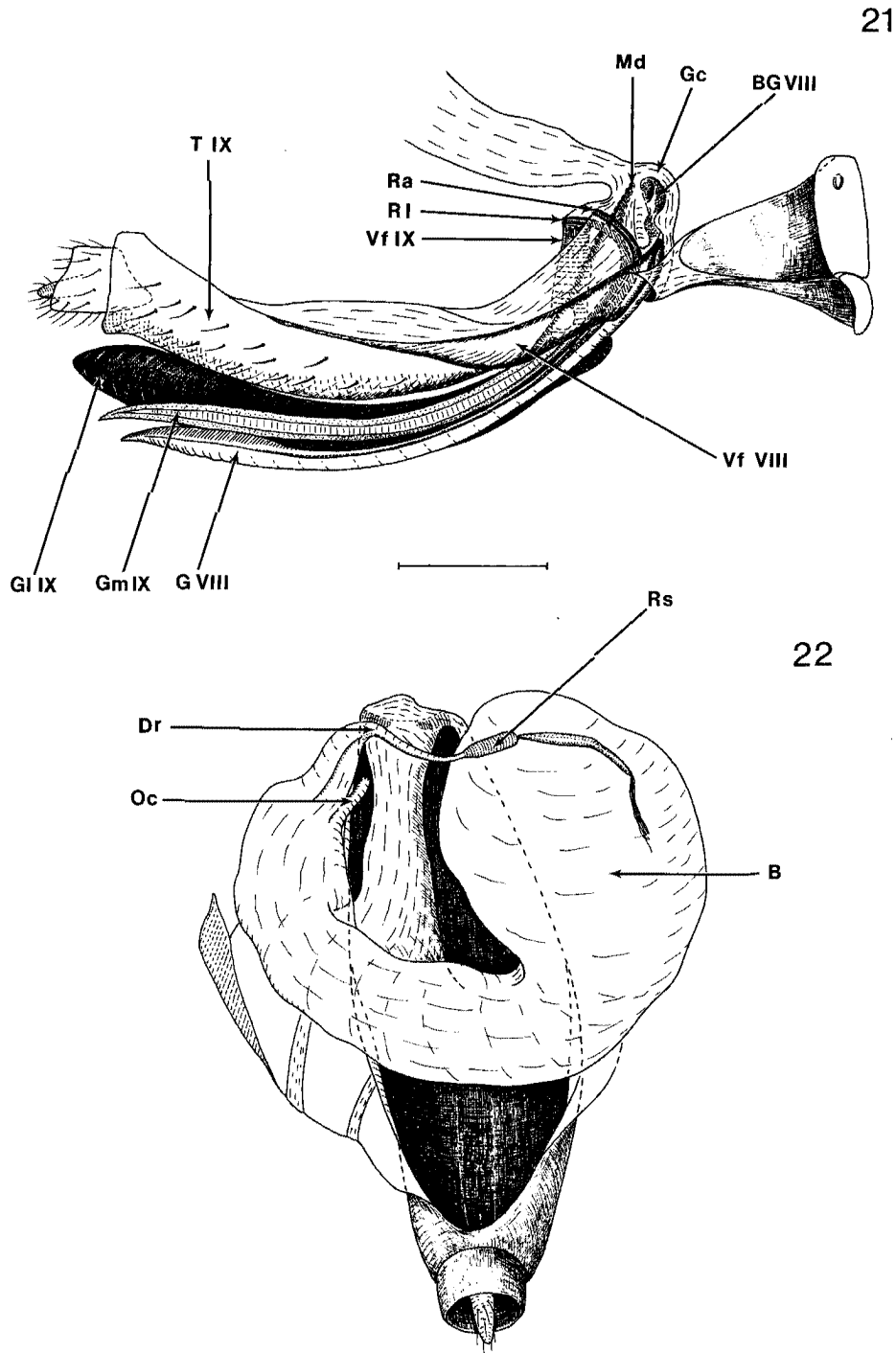
Figs. 21–22. *Vizcaya adornata* Asche, n. sp., female genitalia, paratype: **21**, ovipositor, right lateral view; **22**, internal ectodermal parts, dorsal view. Abbreviations: B = bursa copulatrix; Dr = ductus receptaculi; G VIII = gonapophyses VIII; Gc = genital chamber; Gl IX = lateral gonapophyses 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
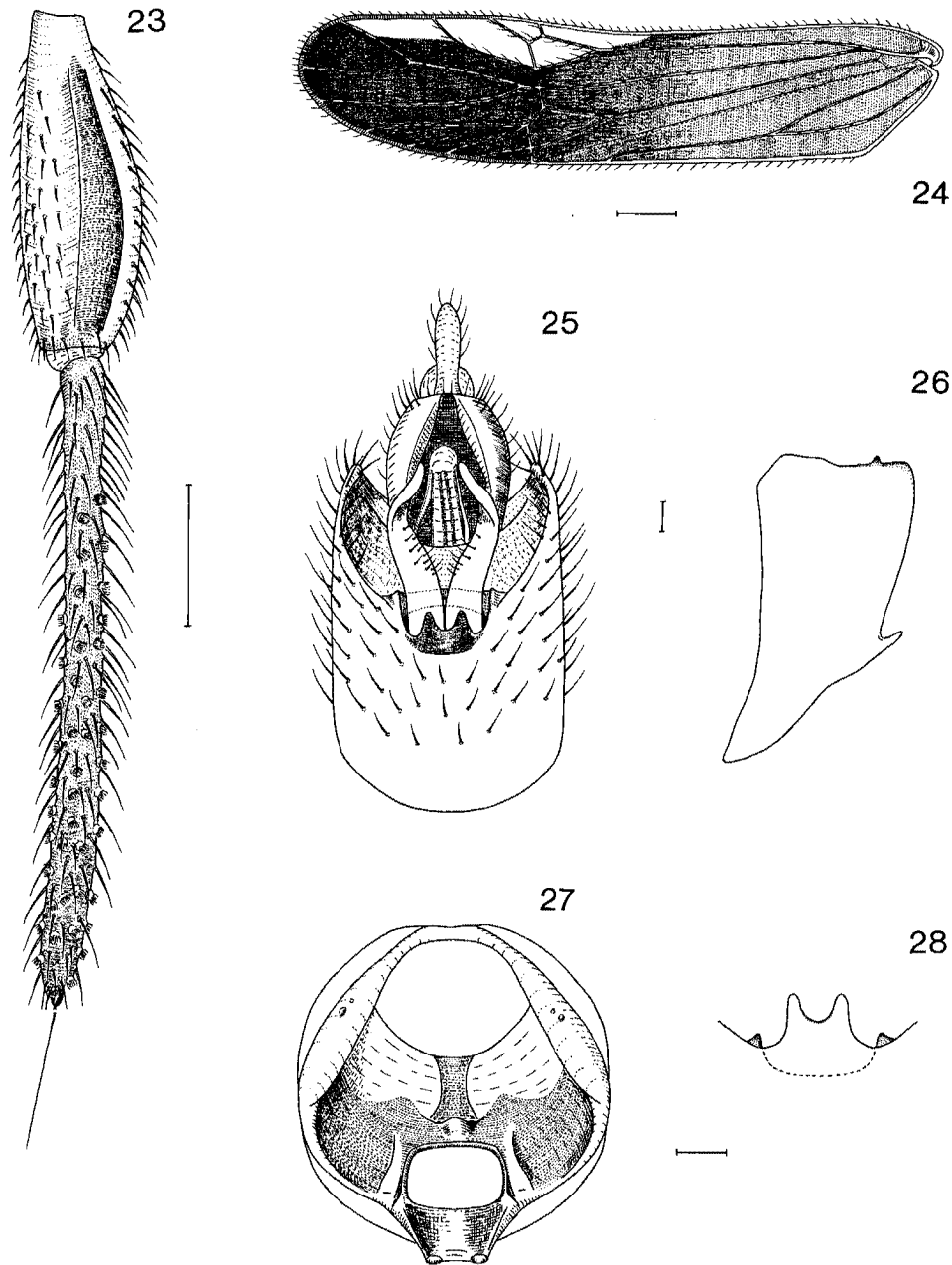
Figs. 23–28. *Vizcaya bakeri* Muir, holotype ♂, Philippine Is: Luzon: **23**, left antenna, frontal view; **24**, left tegmen; **25**, male genitalia, in repose, ventrocaudal view; **26**, same, genital segment, left lateral view; **27**, same, genital segment, caudal view; **28**, same, median projection of ventrocaudal margin of genital segment, ventral view. Scale: 0.5 mm, Figs. 23–24; 0.1 mm, Figs. 25–28.
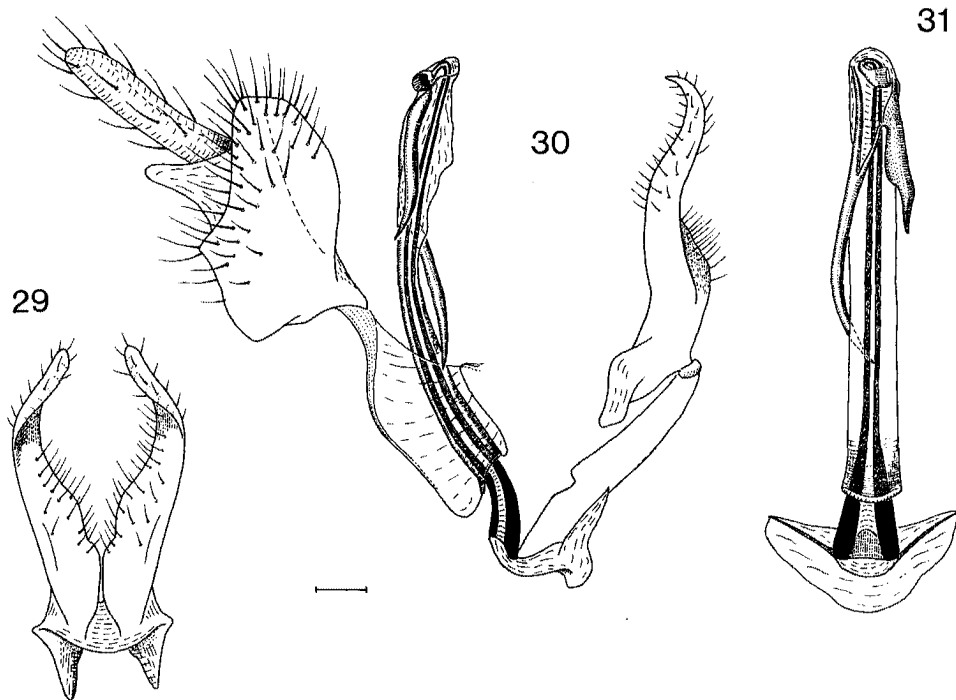
Figs. 29–31. *Vizcaya bakeri* Muir, male genitalia, holotype: **29**, parameres, ventral view; **30**, genitalia without genital segment, left lateral view; **31**, aedeagus, dorsal view. Scale: 0.1 mm.

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.
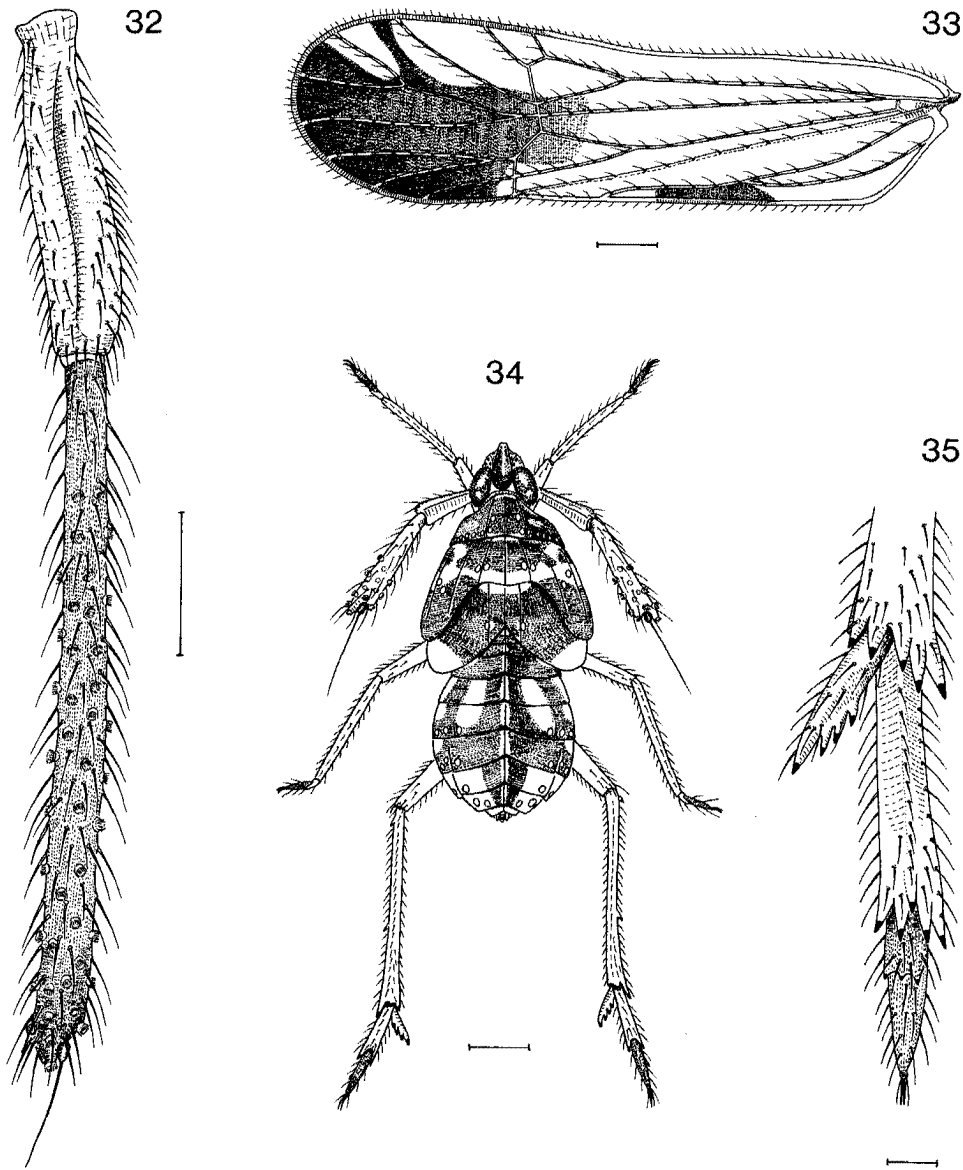
Figs. 32–35. *Vizcaya orea* Asche, n. sp.: **32**, left antenna, frontal view, ♀ from Thailand; **33**, left tegmen, holotype ♂, Sumatra; **34**, ♂ nymph, 4th instar, habitus in dorsal view, specimen from Thailand; **35**, same nymph, distal end of posttibia, posttarsi and posttibial spur. Scale: 0.5 mm, Figs. 32–34; 0.1 mm, Fig 35.
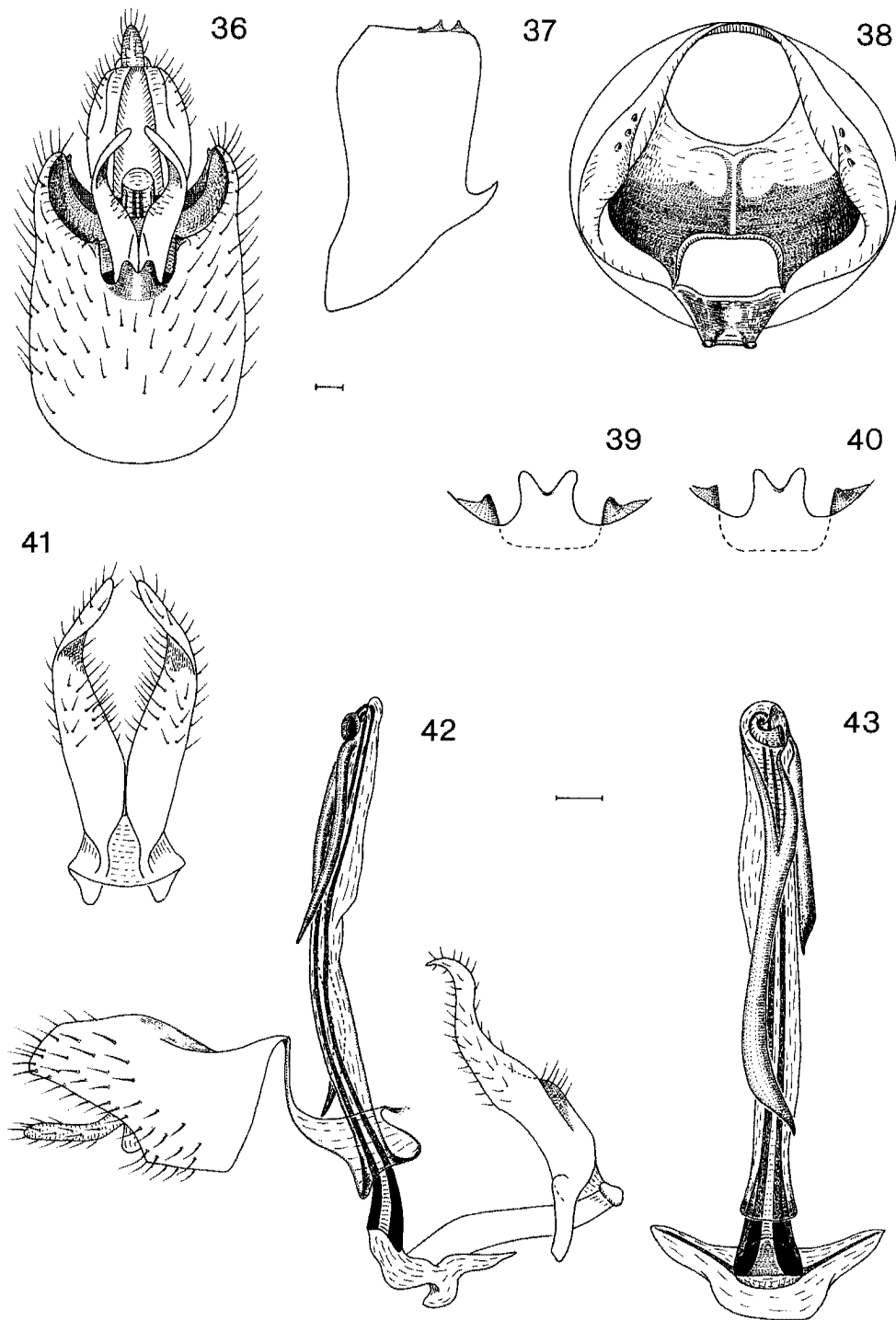
Figs. 36–43. *Vizcaya orea* Asche, n. sp., male genitalia, holotype (Fig. 40, paratype ♂, Sumatra): **36**, genitalia in repose, ventrocaudal view; **37**, genital segment, left lateral view; **38**, genital segment, caudal view; **39**, median projection of ventrocaudal margin of genital segment, ventral 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.
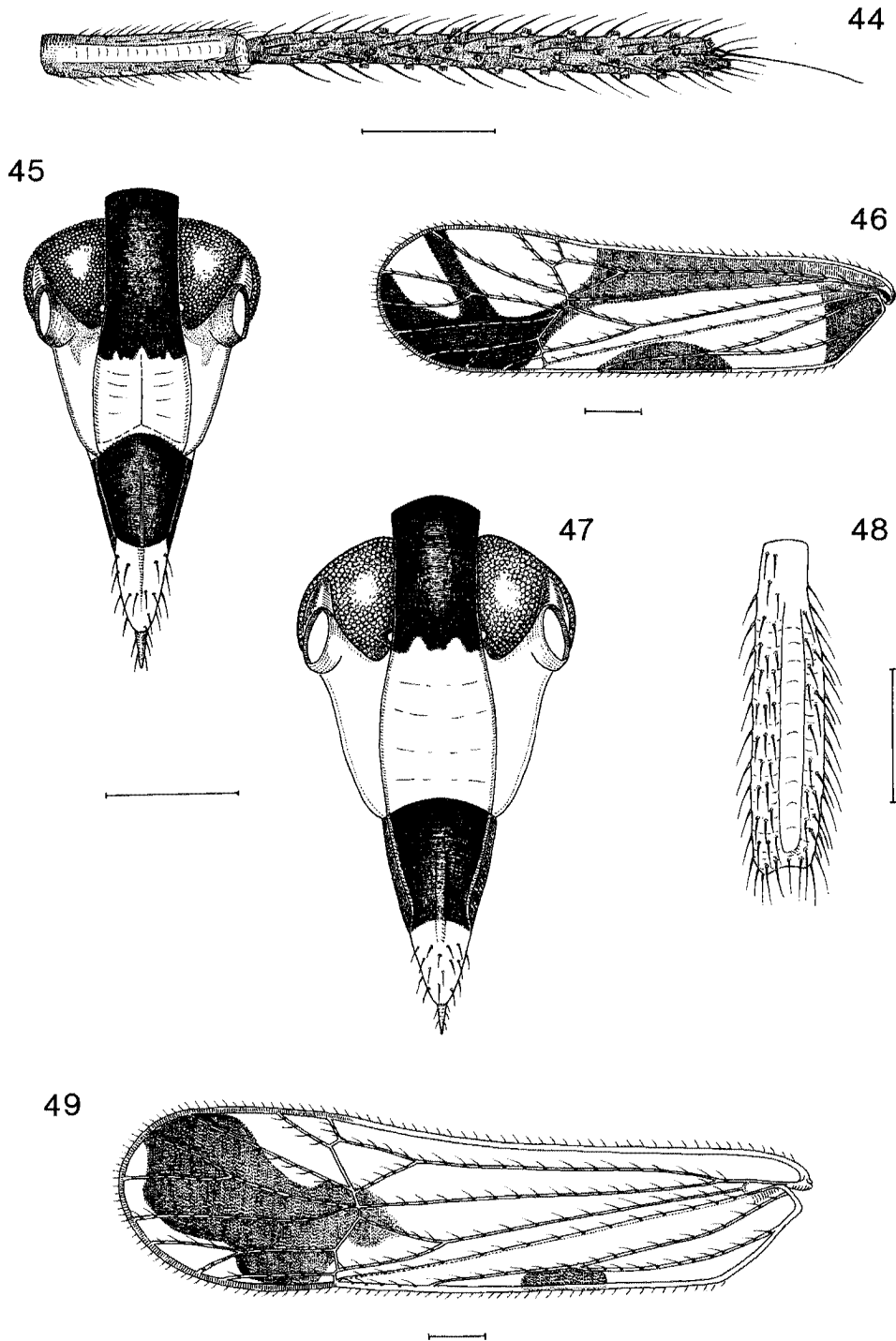
Vizcaya piccola Asche, new species   Figs. 44–46, 54

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. ador-nata*. 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-
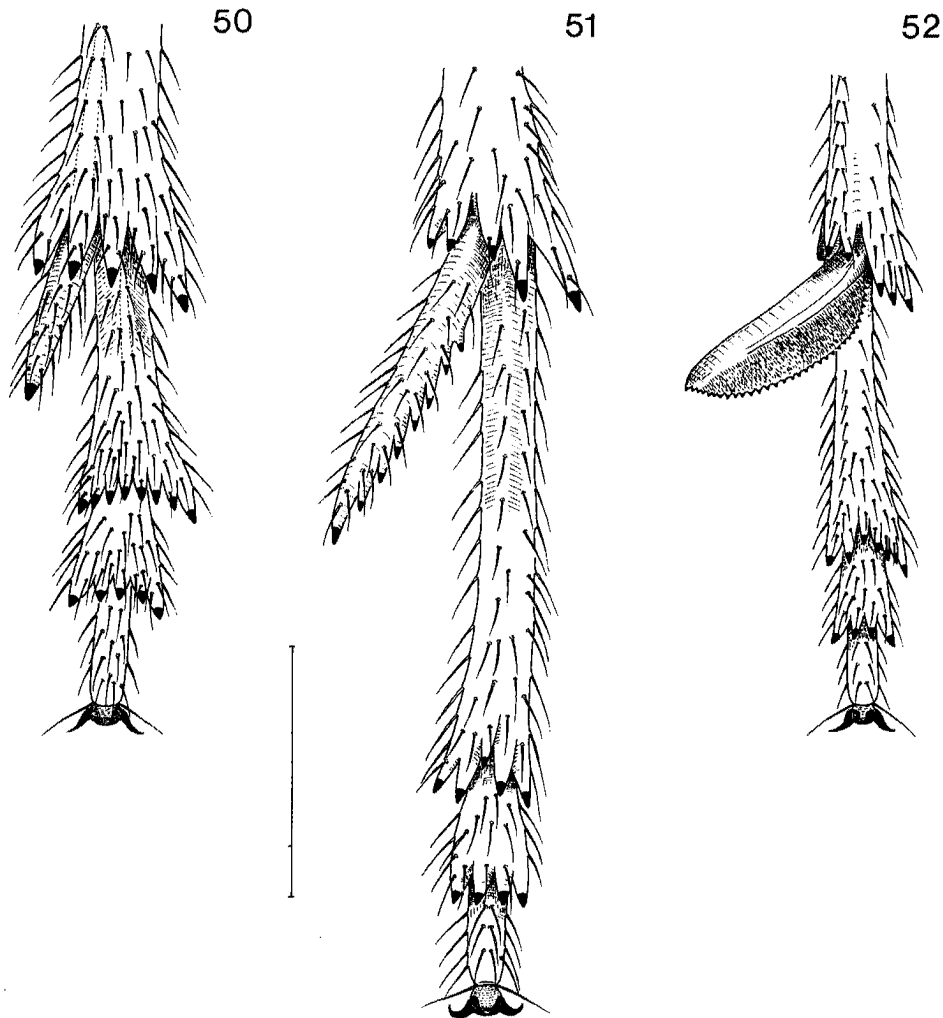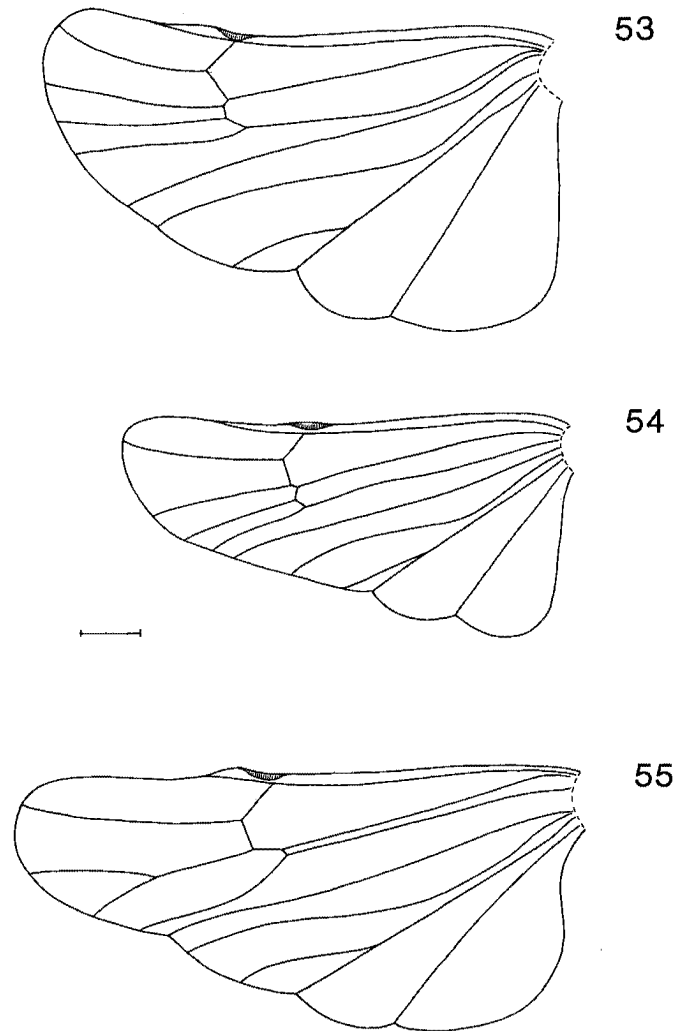
Figs. 50–52. Evolutionary trends in Delphacidae: morphological changes in the shape of distal end of posttibia, of the posttarsi and the posttibial spur: **50**, Asiracinae: *Asiraca clavicornis* (Fabricius), ♀, Romania; **51**, Vizcayinae: *Vizcaya adornata* Asche, n. sp., paratype ♀, Sulawesi; **52**, 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).
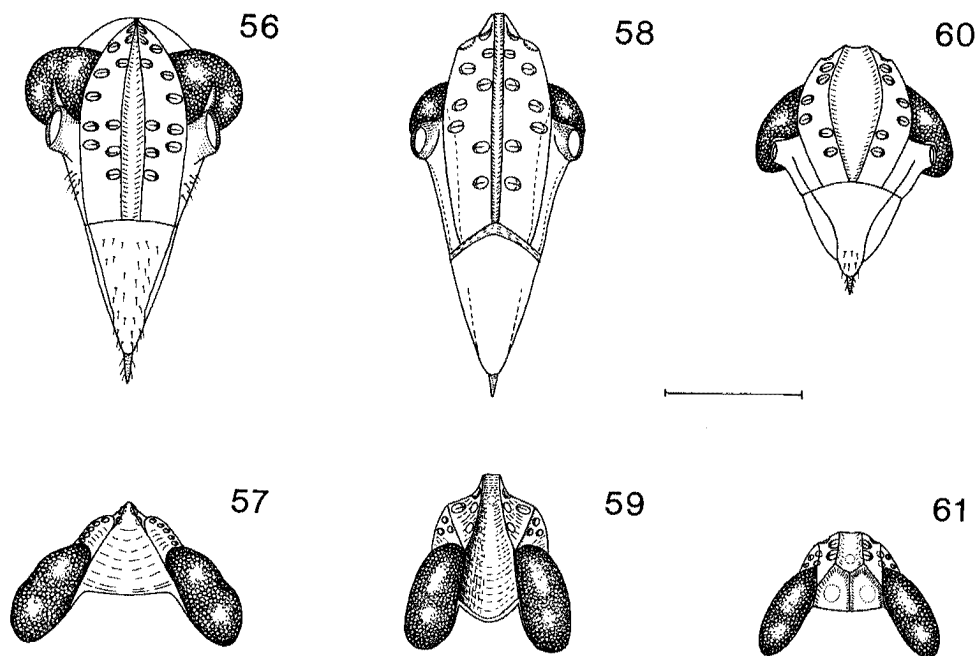
Figs. 56–61. Evolutionary trends in Delphacidae: morphological changes in the head of nymphs, especially number and arrangement of sensory pits: **56**, **58**, **60**, frontal view; **57**, **59**, **61**, dorsal view. **56–57**, Asiracinae: *Asiraca clavicornis* (Fabricius), 5th instar, ♂, W. Germany, 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
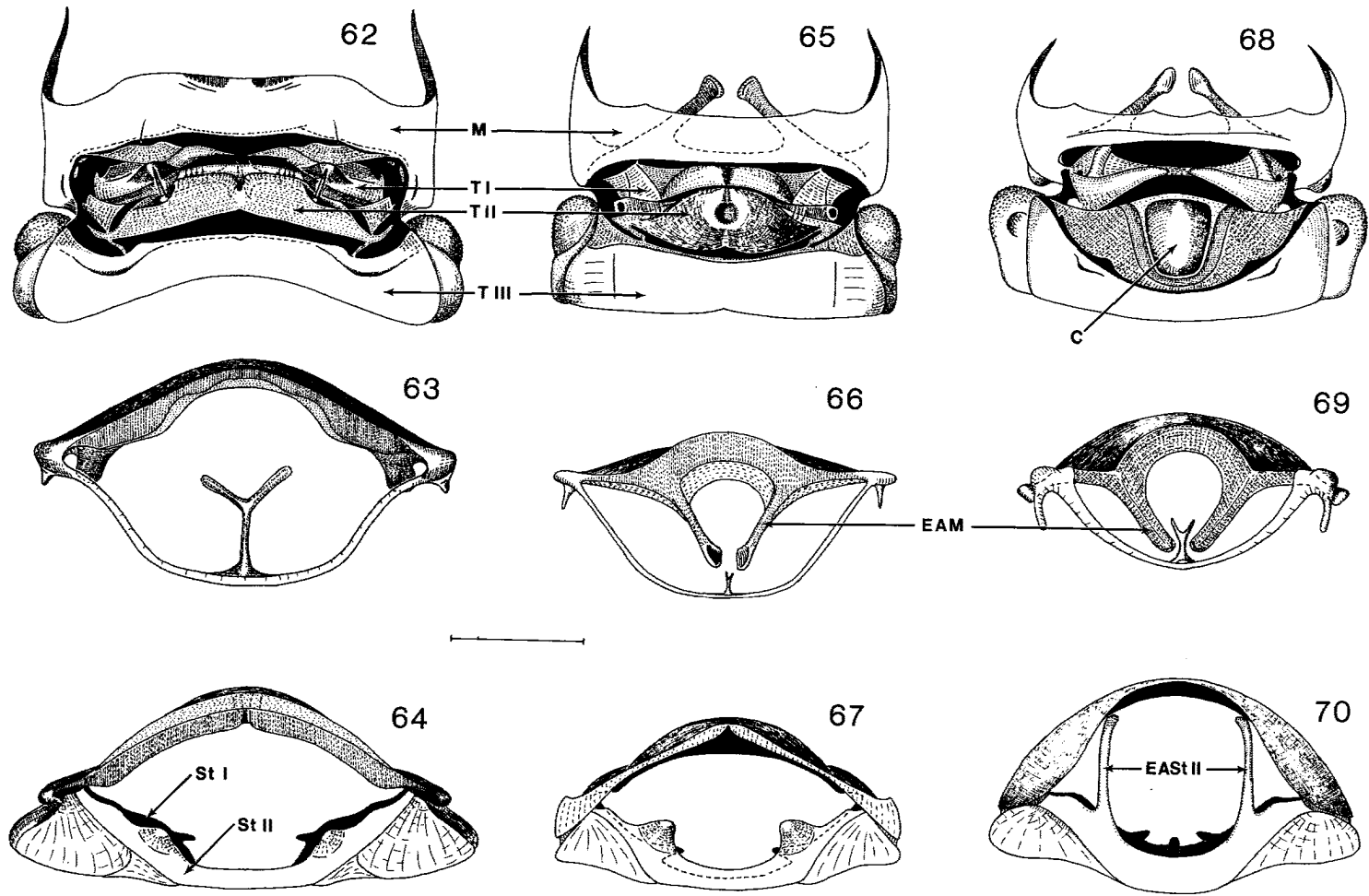
Figs. 62–70. Evolutionary trends in Delphacidae: morphological changes in the male drumming organ: **62, 65, 68,** dorsal view; **63, 66, 69,** metapostnotum, caudal view; **64, 67, 70,** 1st and 2nd abdominal segments, caudal view. **62–64,** Asiracinae: *Asiraca clavicornis* (Fabricius), W. Germany. **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.
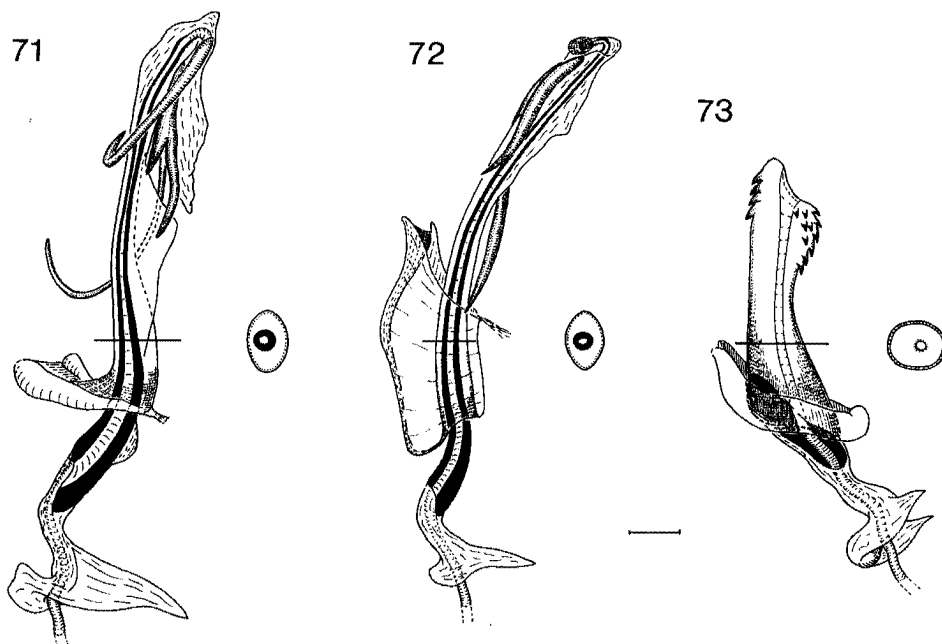
Figs. 71–73. Evolutionary trends in Delphacidae: morphological changes in the aedeagus: **71,** Asiracinae: *Asiraca clavicornis* (Fabricius), W. Germany, central sperm-conducting tube strongly sclerotized, see cross-section; **72,** Vizcayinae: *Vizcaya bakeri* Muir, holotype, Philippine Is: Luzon I, 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**).
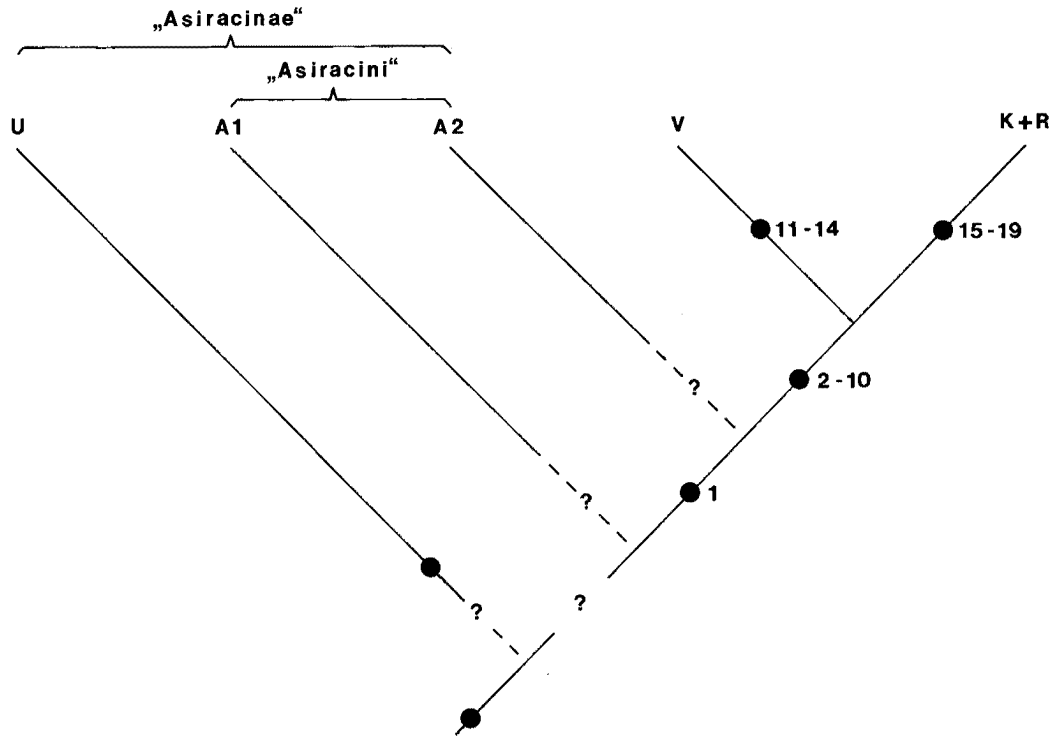
Fig. 74. Phylogenetic relationships of the Vizcayinae. Black spots: apomorphies, numbers refer to characters in text; quotation marks indicate paraphyly. Abbreviations: A1 = non–ugyopine Asiracinae without oblique carina across the genae, A2 = non–ugyopine Asiracinae with oblique carina across genae, 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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