

The Centipede Order Geophilomorpha in the Hawaiian Islands (Chilopoda)

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INTRODUCTION

The Hawaiian representatives of two of the four globally distributed orders of centipedes have recently been documented: Scolopendromorpha, with comments on the Scutigero-morpha (Shelley, 2000), and Lithobiomorpha (Zapparoli & Shelley, 2000). This contribution provides a corresponding review of the Geophilomorpha, the long, wormlike, epi-morphic chilopods with 14 antennomeres and at least 27 pedal segments and leg pairs. The most speciose chilopod order, it is also the most diverse in the Hawaiian islands. Our formerly limited knowledge of this fauna derived primarily from works by Silvestri (1904), Chamberlin (1920, 1926, 1930, 1953), Attems (1938a), Beardsley (1966), and Hoffman & Pereira (1991).

We studied 70 unpublished specimens from 10 different islands or atolls along with type material of *Nyctunguis bryanus* Chamberlin, *Honuaphilus alohanus* Chamberlin, and *Zelanion hawaiiensis* Chamberlin. Most of the unpublished material belongs to the Bishop Museum, Honolulu, and a few additional samples come from the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH). Except for the specimens identified as being from the latter, all material is deposited in the Bishop Museum. More Hawaiian samples undoubtedly exist in American repositories, but we have not attempted to record them during visits by one of us (RMS) to these institutions, and it is not possible to locate them now. We invite future students to issue supplements to our work as additional material is discovered.

Our investigations on Hawaiian Geophilomorpha here lead to the proposals of one new combination (*Marsikomerus bryanus* for *Nyctunguis bryanus*); and four new synonymies: one generic (*Honuaphilus* Chamberlin, 1926, under *Tuoba* Chamberlin, 1920) and three specific [*Marsikomerus pacificus* Attems, 1938, and *Lanonyx lanaius* Chamberlin, 1953, under *Marsikomerus bryanus*; and *Honuaphilus alohanus* under *Tuoba sydneynensis* (Pocock, 1891)]. Comprehensive study is recommended for the genera *Nesomerium* and *Fusichila*, both authored by Chamberlin (1953), and five nominal species: *Mecistocephalus spissus* Wood, *M. 'maxillaris'* (Gervais), *Fusichila waipaheenas* Chamberlin, *Nesomerium hawaiiense* Chamberlin, and *Zelanion hawaiiensis*. The genera *Tygarrup* Chamberlin and *Tuoba*; and the species *Tygarrup javanicus* Attems are reported from the islands for the first time; and new records from individual islands are listed for five other species.

For each species we present the following:

- a list of references (and synonyms) that includes the original description, the most important taxonomic references, particularly ones with meaningful illustrations,

and those pertaining to Pacific islands and the Hawaiian chain specifically; synonyms never used for Hawaiian records are not cited.

- an extended diagnosis based, as far as possible, on Hawaiian specimens, along with literature data and personal observations; only the inadequate original description is available for *N. hawaiiense*.
- published records and details of new localities from the Hawaiian archipelago.
- remarks on taxonomy, overall distribution, and status of the species in the Hawaiian islands.

We also provide a practical key and pertinent illustrations to all species of Geophilomorpha known from the Hawaiian archipelago, based as far as possible on characters that can be seen without clearing or dissecting specimens (Pereira, 2000; Foddai, Minelli & Pereira, 2002).

Family Mecistocephalidae

Tygarrup javanicus Attems

New state record

Mecistocephalus spissus: Attems, 1907: 95, figs. 8–9 [non *Mecistocephalus spissus* Wood, 1862].
Tygarrup javanicus Attems, 1929: 152; 1938b: 330, figs. 294–298; 1953: 143. Verhoeff, 1937a: 236; 1939: 87. Demange, 1981: 640, figs. 8–9. Titova, 1983: 151, figs. 14–17. Lewis & Rundle, 1988: 3, figs. 1–6. Christian, 1996: 110, fig. 6c. Wang & Mauriès, 1996: 89.

Diagnosis. Length varying up to 20 mm; number of leg-bearing segments 45, invariant; body tapering caudad; color dark yellow, without dark patches. Antennae with spearlike apical sensilla, club-like sensilla on both internal and external sides of antennomeres XIV. Head trapezoid, tapering caudad, ca. 1.4 times longer than wide. Frontal line rounded, convex caudad. Clypeus with one entire plagula; clypeal setae as follows: 1 pair on lateral parts of areolate clypeus, some pairs along anterior margin of plagula (2 pairs intermediate, ca. 5 pairs lateral), 1 pair on central part of plagula. Spiculum absent. Buccae without setae. Labral mid-piece longer than wide, with one tooth; each side-piece divided into two alae, anterior ala shorter than posterior ala along internal margin, posterior margin entire. Mandible without dentate lamellae, with ca. 6 pectinate lamellae; first lamella with ca. 5 teeth, intermediate lamella with ca. 10 teeth. First maxilla coxosternum divided mid-longitudinally, without lateral lappets, anterolateral corners virtually absent; telopodite with only one article, similar to coxal projection, without lappets. Second maxilla coxosternum not divided mid-longitudinally, without separate pleurites, posterior part not areolate, metameric pores opening close to lateral margins; pretarsus of telopodite pointed, not elongate, without comblike projections. Forcipular tergum narrower than that of first leg-bearing segment, coxosternum without chitin lines, cerrus absent; forcipular articles, from trochanteroprefemur to tarsungulum, with 1, 0, 1, and 0 teeth, respectively. Forcípules, when closed, extending beyond anterior margin of head. Poison calyx elongate, extending only to intermediate articles of forcípule. Sternal pores present in male only, in two paired subcircular areas. Sternal apodema present, not furcate. Sternum of ultimate leg-bearing segment shield-shaped, without posterior process. Each coxopleuron with ca. 15 ventral pores in adults, subcircular, opening independently, internalmost pores largest. Ultimate legs not sexually dimorphic, slender, covered with scattered setae; pretarsi reduced to short spines. A pair of anal pores present.

Occurrence in the Hawaiian Islands. Hawai‘i, O‘ahu.

Published records: None.

New records. HAWAII: Mauna Loa, Stainback Hwy, ‘*Metrosideros* to lower elevations’, 22 Jan 1974, J. Jacobi. O‘AHU: north end of Ko‘olau Mountains, 9 May 1964.

Remarks. The genus *Tygarrup* occurs primarily in southeast Asia, from the Himalayas through Indochinese Peninsula (Thailand, Laos, Cambodia, and Vietnam) to Java; it

also is found on the Seychelles and Mauritius Island in the Indian Ocean, and southern Japanese islands (Bonato *et al.*, 2003). It has not previously been recorded from the Hawaiian Islands. The species *T. javanicus* is mainly known from the Malay Peninsula and Java but also from the Seychelle Islands (Demange, 1981); introduced specimens have been found in two European localities, the Kew Gardens, London, England, and Vienna, Austria (Lewis & Rundle, 1988; Christian, 1996). In the Hawaiian islands *T. javanicus* is probably also a human introduction.

Mecistocephalus spissus Wood

Mecistocephalus spissus Wood, 1862: 43. Haase, 1887: 101. Attems, 1903: 213; 1929: 129, fig. 142; 1938a: 365; 1947: 96. Chamberlin, 1920: 63; 1926: 94; 1953: 77, 80. Takakuwa, 1942: 18, 22. Beardsley, 1966: 168. Nishida 1997: 195; 2002: 235.

Lamnonyx spissus: Cook, 1895: 61. Silvestri, 1904: 323, 326, pl. 11, figs. 5–7; 1919: 75, fig. 19.

Diagnosis. Length varying up to 70 mm; number of leg-bearing segments 45, invariant; body tapering caudad; color dark yellow-brown, without dark patches. Antennae with spearlike apical sensilla, clublike sensilla on internal and external sides of 5–7 distalmost antennomeres. Head trapezoid, tapering caudad, 1.7–1.8 times longer than wide. Frontal line rounded, convex caudad. Clypeus with two plagulae divided by mid-longitudinal areolate band, each plagula narrowing mediad; areolate clypeus without clypeal insulae; clypeal setae usually 3 pairs. Spiculum present. Buccae with setae on posterior halves only. Labral mid-piece longer than wide, with one tooth; each side-piece divided into two alae, anterior ala longer than the half of posterior ala along internal margin, posterior margin entire. Mandible without dentate lamellae, with ca. 8 pectinate lamellae; first lamella with ca. 7 teeth, intermediate lamella with 15–20 teeth. First maxilla coxosternum divided mid-longitudinally, without lappets, anterolateral corners subrectangular, slightly pointed; telopodite with only one article, similar to coxal projection, without lappets. Second maxilla coxosternum not divided mid-longitudinally, without separate pleurites; posterior part areolate, metameric pores opening close to lateral margins; pretarsus of telopodite pointed, not elongate, without comblike projections. Forcipular tergum narrower than that of first leg-bearing segment, coxosternum without chitin lines, cernus absent; forcipular articles, from trochanteroprefemur to tarsungulum, with 2, 1, 1, and 2 (1 dorsal, 1 ventral) teeth, respectively. Forcipules, when closed, extending beyond anterior margin of head. Poison calyx elongate, extending to distal part of trochanteroprefemur. Sternal pores absent. Sternal apodema present, not furcate. Sternum of ultimate leg-bearing segment shield-shaped, with swollen posterior process. Each coxopleuron with ca. 40 subcircular, ventral pores in adults. Ultimate legs not sexually dimorphic, slender, with scattered setae; pretarsi reduced to short spines. A pair of anal pores present.

Occurrence in the Hawaiian Islands. Hawai'i, Maui, Moloka'i, O'ahu, Kaua'i, Necker.

Published records. Hawai'i: Ka'u (Silvestri, 1904); Kilauea (Silvestri, 1919). Maui: Haleakalā (Silvestri, 1904, 1919). Moloka'i: island in general (Silvestri, 1904). O'ahu or Kaua'i: island in general (Wood, 1862; reported as O'ahu by Silvestri, 1904). Kaua'i: Halemanu (Silvestri, 1904). Necker: island in general (Chamberlin, 1926).

New records. **O'AHU:** Mt. Ka'ala, bog, 1225 m, 'ōhi'a litter and soil, 25 Oct 1996, N.L. Evenhuis. **KAUA'I:** island in general, Jul–Aug 1917, C.N. Forbes. **NECKER:** Summit Hill, in rock crevices, 22 Nov 2000, G.M. Nishida.

Remarks. *Mecistocephalus spissus* is apparently endemic to the Hawaiian Islands, where it is known from most of the major islands, primarily in mountainous regions. Other nominal species of *Mecistocephalus* that are anatomically similar to *M. spissus* occur in eastern Asia from Japan (Honshu) to the Philippines; their specific status await

evaluation, and some names may be placed in synonymy under *M. spissus*. This species has been erroneously reported from Himalayas, Myanmar, Sumatra, and Java based on misidentifications of specimens of *Tygarrup* spp. (Pocock, 1891a, 1894; Silvestri, 1895; Attems, 1907, 1930; Chamberlin, 1944a; Mittal & Dipta, 1977), some of which have been corrected (Silvestri, 1919; Attems, 1929; Attems, 1938b; Verhoeff, 1939; Chamberlin, 1953; Lewis & Rundle, 1988).

Mecistocephalus 'maxillaris' (Gervais)
sensu Silvestri

New island records

Lammonyx maxillaris: Silvestri, 1919: 61, fig. 9. [non *Geophilus maxillaris* Gervais, 1837].

Mecistocephalus maxillaris: Pemberton, 1925: 3, fig. 1. Illingworth, 1928: 42. Attems, 1929: 134, fig. 126; 1938a: 365. Brolemann, 1930: 81, figs. 58–66. Williams, 1931: 344. Adamson, 1932: 229. Silvestri, 1935: 132; 1939: 6. Chamberlin, 1930: 67; 1953: 78, 80. Demange & Pereira, 1985: 197, 198. Nishida, 1997: 195; 2002: 235. Foddai *et al.*, 2000: 64.

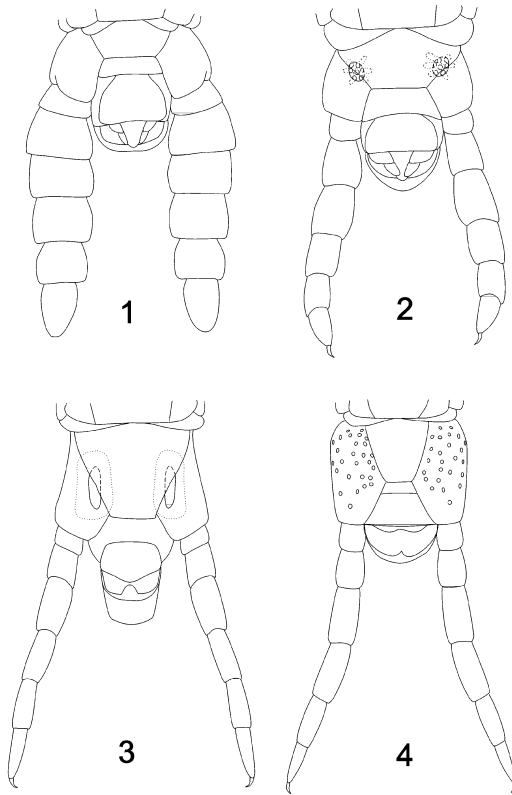
Diagnosis. Length varying up to 40 mm; number of leg-bearing segments 49, invariant; body tapering caudad; color yellow, without dark patches. Antennae with spearlike apical sensilla, clublike sensilla on both internal and external sides of 5–7 distalmost antennomeres. Head trapezoid, tapering caudad, 1.8–1.9 times longer than wide. Frontal line rounded, convex caudad. Clypeus with two plagulae divided by mid-longitudinal areolate band; areolate clypeus without insulae; clypeal setae usually 3–4 pairs. Spiculum present. Buccae with setae on posterior halves only. Labral mid-piece longer than wide, with one tooth; each side-piece divided into two alae, anterior ala as long as half of the posterior ala along internal margin, posterior margin entire. Mandible without dentate lamellae, with ca. 7 pectinate lamellae; first lamella with ca. 6 teeth, intermediate lamella with 10–15 teeth. First maxilla coxosternum divided mid-longitudinally, without lappets, anterolateral corners subrectangular, slightly pointed; telopodite with only one article, similar to coxal projection, without lappets. Second maxilla coxosternum not divided mid-longitudinally, without separate pleurites, posterior part areolate, metameric pores opening close to the lateral margins; pretarsus of telopodite pointed, not elongate, without comblike projections. Forcipular tergum narrower than that of first leg-bearing segment, coxosternum without chitin lines, cerrus absent; forcipular articles, from trochanteroprefemur to tarsungulum, with 2, 1, 1, and 2 (1 dorsal, 1 ventral) teeth, respectively. Forcípules, when closed, extending beyond anterior margin of head. Poison calyx elongate, extending to distal part of trochanteroprefemur. Sternal pores absent. Sternal apodema present, furcate, arms long, angle between them ca. 90°. Sternum of ultimate leg-bearing segment shield-shaped, usually with intermediate, weak, lateral constriction and rounded, posterior process. Each coxopleuron with ca. 40 subcircular, ventral pores in adults. Ultimate legs not sexually dimorphic, slender, with scattered setae; pretarsi reduced to short spines. A pair of anal pores present.

Occurrence in the Hawaiian Islands. Hawai'i, Maui, Lāna'i, Midway.

Published records. Hawai'i: Hilo (Silvestri, 1919); Hāmākua, Kohala (Pemberton, 1925). Lāna'i: island in general (Illingworth, 1928).

New records. MAUI: Pu'unene, sugar cane, Dec 1927, E.H. Bryan; Ha'ikū, under stones, 20 Mar 1967, N.L.H. Krauss. MIDWAY: Sand I., litter under *Coccoloba* tree, 18 Dec 1997, G.M. Nishida; and Feb–May 1957, Y. Oshiro.

Remarks. The true identity of *Geophilus maxillaris* is inadequately known, its poor description (Gervais, 1837) being based upon specimens of uncertain origin collected in Paris and now lost; the name has been applied to different mecistocephalid species in all tropical regions. We provisionally follow the concept of Silvestri (1919), who redescribed the species based on specimens from the Hawaiian islands and other areas. In Hawai'i, *M. 'maxillaris'* is known from three major islands plus Midway and occurs in various habi-



Figs. 1–4. Ultimate leg-bearing segments, ventral views. **1.** *Orphnaeus brevilabiatius*. **2.** *Tuoba sydneyensis*. **3.** *Marsikomerus bryanus*. **4.** *Pachymerium ferrugineum*.

tats. Current knowledge of distribution is admittedly inadequate, but *M. 'maxillaris'* appears to be a widespread tropical geophilomorph (Chamberlin, 1953; Demange & Pereira, 1985; Foddai *et al.*, 2000) that was probably introduced into the Hawaiian archipelago (Chamberlin, 1930).

***Mecistocephalus waikaneus* Chamberlin New island records**

Mecistocephalus waikaneus Chamberlin, 1953: 81. Nishida, 1997: 195; 2002: 235.

Diagnosis. Length varying up to 30 mm; number of leg-bearing segments 49, invariant; body tapering caudad; color yellow, without dark patches. Antennae with spearlike apical sensilla, clublike sensilla on internal and external sides of 5–7 distalmost antennomeres. Head trapezoid, tapering caudad, 1.7–1.8 times longer than wide. Frontal line rounded, convex caudad. Clypeus with two plagulae divided by mid-longitudinal areolate band; areolate clypeus without insulae; clypeal setae usually

3–4 pairs. Spiculum present. Buccae with setae on posterior halves only. Labral mid-piece longer than wide, with one tooth; each labrum side-piece divided into two alae, anterior ala as long as the half of posterior ala along internal margin, posterior margin entire. Mandible without dentate lamellae, with ca. 7 pectinate lamellae; first lamella with ca. 6 teeth, intermediate lamella with 10–15 teeth. First maxilla coxosternum divided mid-longitudinally, without lappets, anterolateral corners subrectangular, slightly pointed; telopodite with only one article, similar to coxal projection, without lappets. Second maxilla coxosternum not divided mid-longitudinally, without separate pleurites, posterior part areolate, metameric pores opening close to lateral margins; pretarsus of telopodite pointed, not elongate, without comblike projections. Forcipular tergum narrower than that of first leg-bearing segment, coxosternum without chitin lines, cerus composed of 2 paramedian rows and 2 lateral groups of setae; forcipular articles, from trochanteroprefemur to tarsungulum, with 2, 1, 1, and 2 (1 dorsal, 1 ventral) teeth, respectively. Forcípules, when closed, extending beyond anterior margin of head. Poison calyx elongate, extending to distal part of trochanteroprefemur. Sternal pores absent. Sternal apodema present, furcate, arms very short. Sternum of ultimate leg-bearing segment shield-shaped, usually with intermediate, weak, lateral constriction and rounded, posterior process. Each coxopleuron with ca. 20 subcircular, ventral pores in adults. Ultimate legs not sexually dimorphic, slender, with scattered setae, dense short setae on ventral sides; pretarsi reduced to short spines. A pair of anal pores present.

Occurrence in the Hawaiian Islands. Hawai'i, Maui, O'ahu.

Published records. Hawai'i: Waikāne (Chamberlin, 1953).

New records. **HAWAII:** island in general, 0–305 m, exotic forest, 22 Jan 1974, J. Jacobi. **MAUI:** Kīpahulu valley, near sacred pools, 50–75 m, wet *Pandanus* & misc. tree litter, 28 May 1997, S.F. Swift. **O'AHU:** Honolulu, Makiki Hts Rd, 27 Jul 1964, T. Suman; Mānoa Trail head, litter, 30 Jan 1997, S.F. Swift; slopes of Mt. Tantalus, 10 Dec 1939, R.P. Currie (NMNH); Nu'uuanu Pali Dr, stream, Norfolk pine grove, 17 Feb 1985, V. & B. Roth.

Remarks. *Mecistocephalus waikaneus* also appears to be endemic to the Hawaiian chain, where it is known from three major islands, primarily in forested habitats. Other nominal species that are anatomically close to *M. waikaneus* occur in eastern and southern Asia, but their specific status await evaluation.

Family Schendylidae

Marsikomerus bryanus (Chamberlin)

Taxonomic changes, New island records

Nyctunguis bryanus Chamberlin, 1926: 92; 1953: 75. Attems, 1938a: 365, 369. Beardsley, 1966: 168. Nishida, 1997: 195; 2002: 236.

Marsikomerus pacificus Attems, 1938a: 372–374, figs. 1–6. Hoffman & Pereira, 1991: 48–52, figs. 1–37. Shelley, 2000: 39. Nishida, 2002: 236. **New Synonymy.**

Marsicomerus [sic] *pacificus*: Attems, 1947: 128.

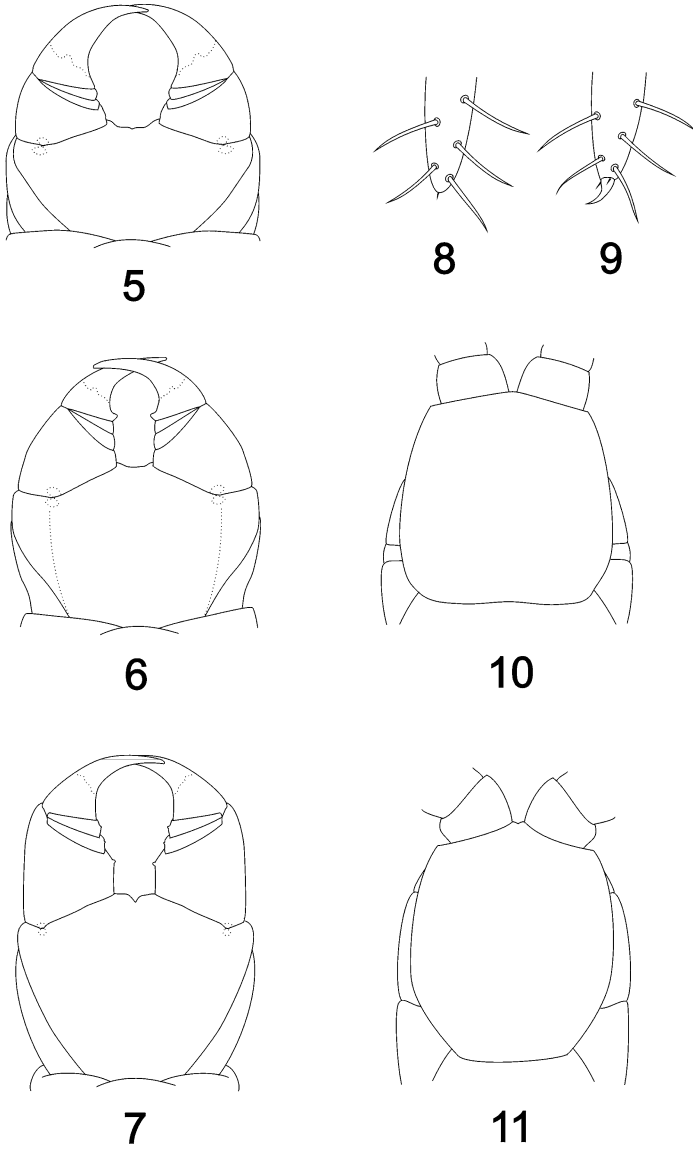
Marsukomerus [sic] *pacificus*: Chamberlin, 1953: 85.

Lanonyx lanaius Chamberlin, 1953: 75. **New Synonymy.**

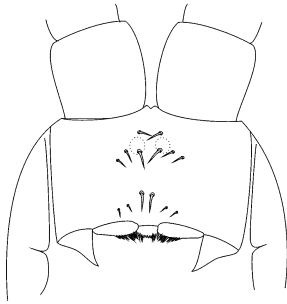
Marsikomerus lanaius: Hoffman & Pereira, 1991: 52–54, figs. 38–42. Shelley, 2000: 39. Nishida, 2002: 236.

Marsikomerus bryanus: this study. **New Combination.**

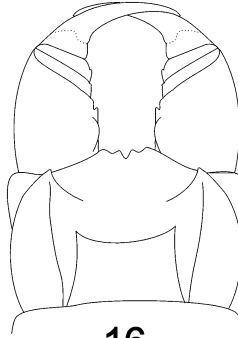
Diagnosis. Length varying up to 47 mm; number of leg-bearing segments 39–57 (but 45 and 55 not yet recorded); body tapering both anteriorly and caudad; color yellow to orange, sometimes with two paramedian subepithelial gray bands. Antennae with spearlike apical sensilla, clublike sensilla only on external sides of antennomeres XIV. Head subrectangular, 1.1–1.3 times longer than wide; anterior margin obtusely pointed. Frontal line absent. Clypeus homogeneously areolate; clypeal setae as follows: 1 pair anterior, 6–8 pairs on an intermediate band, 1 pair posterior. Labrum with ca. 13 teeth along central arc plus 3–5 teeth on each side. Mandible with one entire dentate lamella bearing 5–8



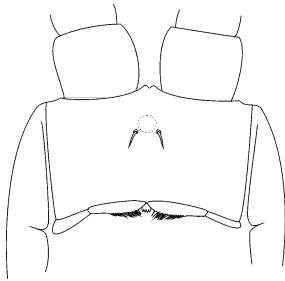
Figs. 5–7. Forcipular segments, ventral views. **5,** *Orphnaeus brevilabiatus*. **6,** *Tuoba sydneyensis*; **7,** *Marsikomerus bryanus*. **Figs. 8–9.** Tips of ultimate legs, ventral views. **8,** *Tygarrup javanicus*. **9,** *Marsikomerus bryanus*. **Figs. 10–11.** Heads, dorsal views. **10,** *Tuoba sydneyensis*. **11,** *Marsikomerus bryanus*.



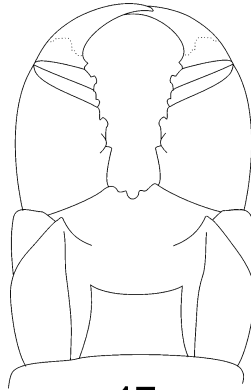
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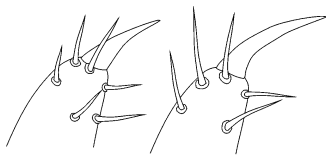
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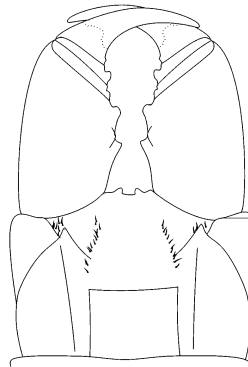


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teeth and one pectinate lamella. First maxilla coxosternum undivided, with pair of lateral lappets, anterolateral corners virtually absent; telopodite with two articles, larger than coxal projection, basal article with one external lappet. Second maxilla coxosternum not divided mid-longitudinally, with separate pleurites, metameric pores opening close to the posterior margin; pretarsus of telopodite pointed, elongate, with two rows of comblike projections. Forcipular tergum narrower than that of first leg-bearing segment, coxosternum without chitin lines; forcipular articles usually with one very small tooth apiece, that on trochanteroprefemur sometimes more developed. Forcípules, when closed, extending nearly to anterior margin of head. Poison calyx quite elongate, extending to intermediate articles of forcípule. Legs with anterior parunguis usually slightly longer than posterior parunguis, also with an additional, shorter, intermediate spine. Sternal pores present in both males and females in one median subcircular area. Sternum of ultimate leg-bearing segment trapezoid. Each coxopleuron with 1 ventral pore, subcircular in juveniles but longitudinally elongate in adults, females especially. Ultimate legs sexually dimorphic, very swollen in males but only weakly so in females, with scattered setae; dense short setae on ventral sides in males but only a few setae in females; pretarsi clawlike. Anal pores apparently absent.

Occurrence in the Hawaiian Islands. Hawai'i, Maui, Lāna'i, Moloka'i, O'ahu, Necker, Gardner Pinnacles.

Published records. Hawai'i: island in general (Chamberlin, 1953); Nā'ūhi Gulch (Attems, 1938a; see also Hoffman & Pereira, 1991). Lāna'i: Lāna'i Mts (Chamberlin, 1953). Necker: island in general (Chamberlin, 1926).

New records. **HAWAI'I:** Honoka'a, Hāmākua Forest Reserve, caves, 600 m, 24 May 1972, F.G. Howarth (NMNH). **MAUI:** Honokawai, Kaulewelewe, 3000 ft, 2 Oct 1979, S.L. Montgomery; Ko'olau Forest Reserve, Itanawi Stream, 5000 ft, in dead fern frond, 8 Aug 1973, T.L. Casey; Haleakalā, 5500 ft, 27 May 1945, E.C. Zimmerman; Olinda, 1 May 1932, 5 May 1932, O. Bryant. **MOLOKA'I:** North of Hanalilolilo, 3725 ft, 13 Jul 1979, J. Jacobi, P. Higashino. **O'AHU:** Kīpapa, 18 Nov 1934, E.H. Bryan Jr.; Koala, moss, 21 Jun 1967, C.M. Yoshimoto; Wiliwilinui Ridge, 1800 ft, 8 Nov 1968, W.C. Gagné; Hale'au'au, 'ōhi'a lehua tree, under bark, 29 Nov 1925, W.H. Heinicke; Mt Tantalus, 19 Mar 1940, E.C. Zimmerman; Mt Ka'ala, 4000 ft, in moss on tree, 19 May 1966, C.M. Yoshimoto; Palikea, 20 Dec 1972, C.P. Hoyt. **GARDNER PINNACLES:** under rocks, 16 Dec 2000, G.M. Nishida.

Remarks. Two nominal species of *Marsikomerus* Attems have been recorded from the Hawaiian Islands (Hoffman & Pereira, 1991; Shelley, 2000): *M. pacificus*, proposed by Attems (1938a) for an adult female from the island of Hawai'i, and *M. lanaius* (described as *Lanonyx lanaius*) by Chamberlin (1953) for a subadult male from Lāna'i; no further specimens have been referred to either. Chamberlin (1926) previously proposed *Nyctunguis bryanus* for four specimens from Necker and later recorded it from the island of Hawai'i (Chamberlin, 1953); its true identity, however, was not clear. Based on our study of the holotype and one paratype of *N. bryanus*, 18 new individuals, and an evaluation of the redescription of the holotypes of *M. pacificus* and *M. lanaius* by Hoffman & Pereira (1991), we conclude that only one species is recognizable. All differences between the types of *N. bryanus*, *M. pacificus*, and *M. lanaius* reflect intraspecific variation, sexual dimorphism, and/or developmental changes. In particular, the condition of the forcípule

Figs. 12–13. Clypeuses, ventral views. **12.** *Pachymerium ferrugineum*. **13.** *Zelanion* sp. **Figs. 14–15.** Tips of second maxillary telopodites. **14.** *Pachymerium ferrugineum*. **15.** *Zelanion* sp. **Figs. 16–18.** Forcípular segments, dorsal views. **16.** *Tygarrup javanicus*. **17.** *Mecistocephalus spissus*. **18.** *Mecistocephalus waikaneus*.

lar trochanteroprefemur varies from the absence of a tooth to the presence of a minute one. Furthermore, we found that the original description of *N. bryanus* contains two errors that prevented subsequent authors from recognizing its true identity: the forcipular articles are described as 'unarmed', but small stout teeth are evident on the trochanteroprefemora of both the holotype and paratype; additionally, two 'coxal pits' are described on each coxopleuron, but the two type specimens (both females) actually exhibit a single elongate pore there, as is typical for this sex. We provisionally maintain *Marsikomerus* as distinct from *Nyctunguis* Chamberlin, 1914, but the taxonomic relationship between them deserves thorough evaluation. *Marsikomerus bryanus* also seems to be endemic to the Hawaiian Islands where it occurs primarily in forested montane environments. It is anatomically close to congeneric species in North America (the southeastern States and northern Mexico) (Hoffman & Pereira, 1991; Foddai, Pereira & Minelli, 2000), but minor differences exist, at least with *M. texanus* (Chamberlin, 1940), the best known continental species (see Crabill, 1961; Hoffman & Pereira, 1991).

Family Oryidae

Orphnaeus brevilabiatus Newport

Geophilus brevilabiatus Newport, 1845: 436.

Orphnaeus lividus Meinert, 1870: 19, pl. 2, figs. 6–11; 1886: 231.

Orphnaeus brevilabiatus: Haase, 1887: 111, pl. 6, figs. 117a–e. Pocock, 1894: 317; 1896: 40, pl. 3, figs. 14a–d. Attems, 1903: 201; 1914: 9, 18, 48, 61; 1928: 125; 1929: 112; 1938a: 365; 1947: 93. Chamberlin, 1914: 391; 1920: 38; 1939: 6; 1944b: 190; 1950: 136; 1953: 77. Swezey, 1926: 221. Adamson, 1932: 228. Silvestri, 1935: 132. Verhoeff, 1937b: 6. Chamberlin & Wang, 1952: 177. Wang, 1955: 15; 1956: 158; 1962: 87, figs. 1–4; 1963: 93. Lewis & Wranik, 1990: 67, figs. (3) 11–15. Shear & Peck, 1992: 2267. Golovatch, 1994: 159. Nishida, 1997: 195; 2002: 236. Foddai *et al.*, 2000: 112.

Orphnaeus bilabiatus [sic]: Chamberlin, 1913: 122.

Diagnosis. Length varying up to 90 mm (85 mm in Hawaiian specimens); number of leg-bearing segments 65 to 81 (73 to 79 in Hawaiian specimens); body tapering anteriorly and caudally; color yellow, with two paramedian subepithelial gray-green bands. Antennae with proximal parts flattened, with spearlike apical sensilla, clublike sensilla on external sides of some distalmost antennomeres and internal sides of articles XIV. Head oval, about as long as wide, anterior margin obtusely pointed. Frontal line absent. Clypeal setae: several tens. Labrum with several stout teeth. Mandible without dentate lamellae, with 4–5 pectinate lamellae. First maxilla coxosternum undivided, with pair of lateral lappets, anterolateral corners virtually absent; telopodite with only one article, larger than coxal projection, with one external lappet. Second maxilla coxosternum not divided mid-longitudinally, metameric pores opening close to posterior margin; pretarsus of telopodite pointed, not elongate, with one row of comblike projections. Forcipular tergum about as wide as that of first leg-bearing segment, coxosternum without chitin lines; forcipular articles without teeth. Forcípules, when closed, not extending beyond anterior margin of head. Poison calyx short, extending only to basal part of tarsungulum. Sternal pores arranged in two anterior and two posterior subcircular areas, number of pores roughly the same on anterior and posterior parts of trunk. Sternum of ultimate leg-bearing segment trapezoid, wider than long. Coxopleuron without pores. Ultimate legs sexually dimorphic, noticeably swollen in males but only weakly so in females; short setae on ventral side, denser in males than females; pretarsi absent. Anal pores apparently absent.

Occurrence in the Hawaiian Islands. O'ahu.

Published records. O'ahu: island in general (Meinert, 1870); Waimalu Valley (Swezey, 1926).

New records: None.

Remarks. *Orphnaeus brevilabiatus* is widely distributed in tropical regions (Haase, 1887; Attems, 1929; Foddai *et al.*, 2000). Within the Pacific area, it is known from the Solomon, Samoan, Fiji, Society, Marquesas, and Galápagos Islands; a comprehensive review exists in Foddai *et al.* (2000). In the Hawaiian Islands, the species is known only from two old records from O'ahu, where it is probably adventive.

Family Geophilidae

Tuoba sydneyensis (Pocock)

Name change, New island records

Geophilus sydneyensis Pocock, 1891b: 219. Attems, 1903: 262; 1914: 133; 1929: 326. Chamberlin, 1920: 54.

Necrophloeophagus sydneyensis: Pocock, 1901: 461.

Tuoba sydneyensis: Jones, 1998: 334, fig. 1–11.

Honuaphilus alohanus Chamberlin, 1926: 93; 1953: 85. Attems, 1938a: 365, 369. Butler, 1961: 380. Butler & Usinger, 1963a: 4; 1963b: 269. Beardsley, 1966: 179. Nishida, 1997: 195; 2002: 235.

New Synonymy.

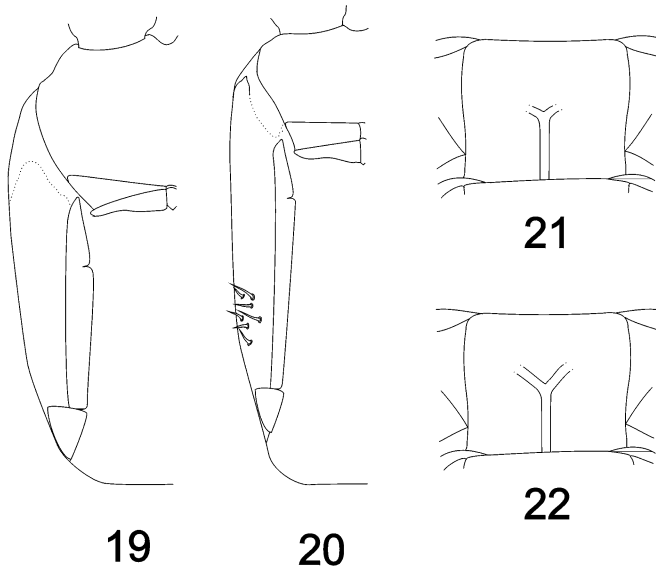
Diagnosis. Length varying up to 32 mm; number of leg-bearing segments 39–55 (43–47 in Hawaiian specimens); body tapering slightly anteriorly and caudad; color yellow-orange, without dark patches. Antennae 4–5 times longer than head, with spearlike apical sensilla, clublike sensilla on both internal and external sides of articles XIV; antennomeres II–XIV ca. 2 times longer than wide. Head subrectangular, about as long as wide; anterior margin obtusely pointed. Frontal line absent. Clypeus homogeneously areolate except for posterior, marginal, inareolate band. Clypeal setae: 1 pair anterior and ca. 6 pairs posterior. Each bucca with two anterior setae. Labral mid-piece wider than long, with 7–9 teeth; each side-piece entire, with 2–3 teeth on medial parts. Mandible without dentate lamellae, with one pectinate lamella. First maxilla coxosternum undivided, with pair of small lateral lappets, anterolateral corners virtually absent; telopodite with two articles, larger than coxal projection, basal article with one short external lappet. Second maxilla coxosternum not divided mid-longitudinally, metameric pores opening close to posterior margin; pretarsus of telopodite short but pointed. Forcipular tergum approximately as wide as that of first leg-bearing segment, coxosternum with almost complete chitin lines; forcipular articles, from trochanteroprefemur to tarsungulum, with 0, 0, 0, and 1 teeth respectively. Forcipules, when closed, extending nearly to anterior margin of head. Poison calyx short, extending to distal part of trochanteroprefemur. Legs with anterior parunguis longer than posterior parunguis. Sternal pores on posterior bands on anterior segments, in two paired subcircular areas on posterior ones. Carpophagus structure present on anteriormost segments, sacculus about half as wide as sternum. Sternum of ultimate leg-bearing segment trapezoid. Each coxopleuron with ca. 30 pores in adults, all opening in one pit on ventral side. Ultimate legs sexually dimorphic, swollen in males but slender in females, with scattered setae, dense short setae on ventral side in both sexes; pretarsi clawlike. A pair of anal pores present.

Occurrence in the Hawaiian Islands. Moloka'i, Laysan, Pearl and Hermes Reef, Midway, Kure.

Published records. Laysan: island in general (Chamberlin, 1926). Pearl and Hermes Reef: island in general (Chamberlin, 1926). Kure: island in general (as 'Ocean I', Chamberlin, 1926).

New records. **MOLOKA'I:** Kamiloloa, 3200 ft, rotten *Pipturus*, 19 Dec 1925, O.H. Swezey. **LAYSAN:** island in general, litter in coconut grove, 10 May 1985, W. Gagné. **PEARL AND HERMES REEF:** South-East Island, in soil, 13 Dec 1970, J.L. Gressitt. **MIDWAY:** Eastern Island, under driftwood on beach, May 1997, G.M. Nishida.

Remarks. We place *H. alohanus*, considered 'species inquirenda' by Attems (1938a),



Figs. 19–20. Right buccae, ventral views. **19,** *Tygarrup javanicus*. **20,** *Mecistocephalus spissus*.
Figs. 21–22. Sterna of 10th leg-bearing segments, ventral views. **21,** *Mecistocephalus waikaneus*. **22,** *Mecistocephalus 'maxillaris'*.

in synonymy under *T. sydneyensis* based on examinations of three syntypes of the former (from Laysan and Johnston islands; see Chamberlin, 1926) and 20 additional Hawaiian specimens. The monotypic genus *Honuaphilus* Chamberlin, 1926 therefore falls in synonymy under *Tuoba* Chamberlin, 1920 (**New Synonymy**). The original diagnosis of *Honuaphilus* and the original description of *H. alohanus* contain two relevant errors: a 'well-defined median clypeal area' is characterized, but the clypeus is actually uniformly areolate aside from a posterior marginal band; additionally, the first maxillary coxal projections are described as longer than the telopodites, but they actually are shorter. Hawaiian specimens do not differ anatomically from individuals of *T. sydneyensis* from Australia, New Caledonia, New Britain, and the Solomon Islands (Jones, 1998). The deletion of *Honuaphilus* from the Hawaiian centipede fauna is offset by the addition of *Tuoba*, a widely ranging genus in the Australian region that also occurs in the Americas, Africa, SE Asia, and the Mediterranean basin (Foddai *et al.*, 2000). *Tuoba sydneyensis* occurs primarily in littoral habitats and is a beach-dwelling species throughout its range (Chamberlin, 1953; Jones, 1998); thus, it may have reached the Hawaiian Islands without human assistance.

***Nesomerium hawaiiense* Chamberlin**

Nesomerium hawaiiense Chamberlin, 1953: 84. Nishida, 1997: 195; 2002: 235.

Diagnosis (based only on the original description). Length 45 mm; number of leg-bearing segments 69. Head subrectangular, 1.2–1.3 times longer than wide. Frontal line absent. Clypeus with one median clypeal area; clypeal setae, 1 pair located within median clypeal area. Labrum with mid-piece wider than long, with 10–12 long teeth; side-pieces almost reciprocally in touch anterior to mid-piece, entire, with teeth on medial parts. Mandible with 3–4 pectinate lamellae. First maxilla coxosternum and telopodite without lappets. Second maxilla coxosternum not divided mid-longitudinally; pretarsus of telopodite pointed. Forcipular coxosternum without chitin lines; forcipular articles, from trochanteroprefemur to tarsungulum, with 1, 1, 1, and 1 teeth, respectively. Forcípules, when closed, extending beyond anterior margin of head. Sternal pores on posterior bands. Sternum of ultimate leg-bearing segment trapezoid. Each coxopleuron with 1 ventral pore. Ultimate legs swollen in males except for two distalmost articles (unknown in female); pretarsi absent.

Occurrence in the Hawaiian Islands. Unknown.

Published records. Hawaiian Islands in general (Chamberlin, 1953).

New records: None.

Remarks. The genus *Nesomerium* and the species *N. hawaiiense* were proposed for only one individual; no others have subsequently been referred to either taxon. The original description is inadequate, and the validity and taxonomic placement of these putative endemic taxa await assessment. Chamberlin (1953) originally assigned them to the Geophilidae, but the described structure of the mandibles conflicts with the condition in this family and suggests that this placement is incorrect.

Pachymerium ferrugineum (Koch)

New island records

Geophilus ferrugineus Koch, 1835: pl. 2; 1847: 187.

Pachymerium ferrugineum: Verhoeff, 1924: 415. Attems, 1929, 215, fig. 202–203, 205; 1938a: 365, 369, 370. Brolemann, 1930: 134, fig. 185–192. Chamberlin, 1953: 83. Wang, 1956: 158. Nishida, 1997: 195; 2002: 235.

Diagnosis. Length varying up to 50 mm; number of leg-bearing segments 41 to 57 (43 in a Hawaiian female); body tapering caudad; color yellow-orange, without dark patches. Antennae with spearlike apical sensilla, clublike sensilla on internal and external sides of antennomeres XIV. Head subrectangular, 1.3–1.4 times longer than wide, anterior margin straight. Frontal line absent. Clypeus with two paired clypeal areas and two paired, pigmented, weakly areolate areas close to posterior margin; clypeal setae: 1 pair anterior, 2–3 pairs intermediate (1 pair within clypeal areas), usually 1 pair posterior. Labral mid-piece wider than long, with 5–7 stout teeth and ca. 3 pairs of fimbriae external to teeth; each side-piece entire, with ca. 15 fimbriae on medial parts. Mandible without dentate lamellae, with one pectinate lamella. First maxilla coxosternum undivided, with pair of lateral lappets, anterolateral corners virtually absent; telopodite with two articles, larger than coxal projection; one external lappet on each article. Second maxilla coxosternum not divided mid-longitudinally, metameric pores opening close to posterior margin; pretarsus of telopodite pointed, not elongate. Forcípular tergum noticeably narrower than that of first leg-bearing segment, coxosternum with incomplete chitin lines; forcípular articles, from trochanteroprefemur to tarsungulum, with 1, 0 (or 1), 0, and 1 teeth, respectively. Forcípules, when closed, extending beyond anterior margin of head. Poison calyx short, extending to distal part of trochanteroprefemur. Sternal pores mainly in two postero-lateral groups, coalescent in anteriormost and ultimate segments; also located on two anterolateral groups, coalescent on ultimate segments. Carpophagus structure absent. Sternum of ultimate leg-bearing segment trapezoid. Each coxopleuron with ca. 30 subcircular pores in adults, opening independently on ventral and lateral sides of coxopleuron. Ultimate legs sexually dimorphic, swollen in males but slender in females, with scattered setae; dense short setae on ventral sides in males, only a few setae in females; pretarsi clawlike. A pair of anal pores present.

Occurrence in the Hawaiian Islands. O'ahu, Kaua'i.

Published records. O'ahu: Honolulu (Attems, 1938a).

New records. KAUA'I: island in general, 13 May 1969.

Remarks. *Pachymerium ferrugineum*, considered native to Europe, is now known to occur widely across the Holarctic Region (Attems, 1929; Eason, 1964); within the Pacific area it is known from Taiwan (Wang, 1956) and Easter Island (Verhoeff, 1924). In the Hawaiian Islands *P. ferrugineum* is known only from a couple of records of probably adventive specimens (Attems, 1938a; Chamberlin, 1953).

***Zelanion hawaiiensis* Chamberlin**

Zelanion hawaiiensis Chamberlin, 1953: 82–83. Nishida, 1997: 195; 2002: 235.

Diagnosis. Length 28 mm; number of leg-bearing segments 39; body tapering caudad; color brown, without dark patches. Head subrectangular, longer than wide. Frontal line not evident. Clypeus with one median clypeal area; clypeal setae: 1 pair close to postero-external margins of clypeal area, none in latter. Labral mid-piece with ca. 4 teeth; side-pieces almost reciprocally in touch anterior to mid-piece; side-pieces entire, with fimbriae on medial parts. Mandible without dentate lamellae, with one pectinate lamella. First maxilla coxosternum not divided mid-longitudinally, without lappets, antero-lateral corners virtually absent; telopodite with two articles, larger than coxal projection, basal article with one external lappet. Second maxilla coxosternum divided mid-longitudinally by faint suture, metameric pores opening close to posterior margin; pretarsus of telopodite pointed, elongate, without comblike projections. Forcipular tergum noticeably narrower than that of first leg-bearing segment, coxosternum without chitin lines; forcipular articles, from trochanteroprefemur to tarsungulum, with 1, 1, 1, and 1 teeth, respectively. Forcípules, when closed, extending beyond anterior margin of head. Poison calyx short, extending to intermediate articles of forcípule. Sternal pores a few, close to the posterior margin of sterna. Carphogus structure absent. Sternum of ultimate leg-bearing segment trapezoid. Each coxopleuron with 15 subcircular pores in adults, all opening independently on ventral and lateral sides of coxopleuron. Ultimate legs swollen in males, unknown in females; dense short setae on ventral sides in males, unknown in females; pretarsi clawlike. A pair of anal pores present.

Occurrence in the Hawaiian Islands. Hawai'i.

Published records. Hawai'i: island in general (Chamberlin, 1953).

New records: None.

Remarks. *Zelanion hawaiiensis* was proposed for one individual from an unspecified locality on the Island of Hawai'i; no other specimens have subsequently been referred to the species. From the original description, *Z. hawaiiensis* is anatomically close to *Z. antipodum* (Pocock, 1891) from New Zealand and Australia (Archev, 1936), but it may differ in the pattern of the clypeal setae and other minor details (Chamberlin, 1953). Consequently, the validity and status of this presumed Hawaiian endemic also awaits assessment (Nishida, 1997, 2002). The one known specimen was likely adventive from Australia or New Zealand, the area to which the genus is otherwise limited.

Deletions

Mecistocephalidae

***Fusichila waipaheenas* Chamberlin**

The monotypic genus *Fusichila* Chamberlin and the species *F. waipaheenas* were pro-

posed for one individual from Kaua'i (Waipahe'e) and were based on anomalous features of the labrum. The original description suggests that the specimen is a juvenile *Mecistocephalus* Newport with an abnormally developed labrum, so the validities of these presumed endemic Hawaiian taxa are suspect.

***Mecistocephalus tridens* Chamberlin**

Chamberlin (1922) proposed this species for specimens found at Honolulu in soil imported from Java (see also Chamberlin, 1953). There is no evidence that the species has become established, so we do not regard *M. tridens* as a component of the Hawaiian fauna.

Geophilidae

***Sepedonophilus hodites* Chamberlin**

Chamberlin (1940) proposed this species for a male found at Honolulu in soil imported from Australia. There is no evidence that it has become established, so we do not regard *S. hodites* as a component of the Hawaiian fauna.

Key to the Geophilomorpha of the Hawaiian Islands

1. Coxopleura of the ultimate legs without pores (Fig. 1); forcipules without teeth (Fig. 5)..... *Orphnaeus brevilabiatus*
- Coxopleura of the ultimate legs with pores (Figs. 2–4); forcipules with teeth (Figs. 6–7)..... 2
2. Coxopleura of the ultimate legs with one large ventral pore or pit apiece (Figs. 2–3) 3
- Each coxopleuron of the ultimate legs with many independent ventral pores (Fig. 4) 5
3. Ultimate legs without apical claws (Fig. 8); more than 60 pairs of legs *Nesomerium hawaiiense*
- Ultimate legs with apical claws (Fig. 9); less than 60 pairs of legs 4
4. Forcipular tarsungulum with a basal tooth, remaining articles without teeth, coxosternum with chitin lines (Fig. 6); length of head subequal to maximum width (Fig. 10) *Tuoba sydneyensis*
- Forcipular tarsungulum without a basal tooth, remaining articles with or without teeth, coxosternum without chitin lines (Fig. 7); length of head greater than maximum width (Fig. 11) *Marsikomerus bryanus*
5. Ultimate legs with apical claws (Fig. 9) 6
- Ultimate legs without apical claws (Fig. 8) 7
6. Clypeus with two paired clypeal areas (Fig. 12); pretarsus of second maxillary telopodite not elongate (Fig. 14)..... *Pachymerium ferrugineum*
- Clypeus with one median clypeal area (Fig. 13); pretarsus of second maxillary telopodite elongate (Fig. 15) *Zelanion hawaiiense*
7. 45 pairs of legs 8
- 49 pairs of legs 9
8. Forcipular trochanteroprefemur with one tooth (Fig. 16); buccae (i.e., cephalic pleurites) without spicula (Fig. 19) *Tygarrup javanicus*
- Forcipular trochanteroprefemur with two teeth (Fig. 17); buccae with spicula (Fig. 20)..... *Mecistocephalus spissus*
9. Forcipular cerrus with two paramedian rows and two lateral groups of setae (Fig. 18); anterior arms of sternal apodema very short (Fig. 21) *Mecistocephalus waikaneus*
- Forcipular cerrus absent (Fig. 17); anterior arms of sternal apodema long (Fig. 22)..... *Mecistocephalus 'maxillaris'*

Table 1. Occurrences of Hawaiian Geophilomorpha by Island.

	HA	MA	LA	MO	OA	KA	NE	GP	LY	PH	MY	KU	UN
<i>Tygarrup javanicus</i>	x				x								
<i>Mecistocephalus spissus</i>	x	x		x	x	x	x						
<i>Mecistocephalus 'maxillaris'</i>	x	x	x								x		
<i>Mecistocephalus waikaneus</i>	x	x			x								
<i>Marsikomerus bryanus</i>	x	x	x	x	x		x	x					
<i>Orphnaeus brevilabiatus</i>					x								
<i>Tuoba sydneyensis</i>				x					x	x	x	x	
<i>Nesomerium hawaiiense</i>													x
<i>Pachymerium ferrugineum</i>					x	x							
<i>Zelanon hawaiiensis</i>	x												
number of species	6	4	2	3	6	2	2	1	1	1	2	1	1

HA = Hawai'i; MA = Maui; LA = Lāna'i; MO = Moloka'i; OA = O'ahu; KA = Kaua'i; NE = Necker; GP = Gardner Pinnacles' LY = Laysan; PH = Pearl & Hermes Reef; MY - Midway; KU = Kure; UN = Unknown.

DISCUSSION

The known Hawaiian geophilomorph centipede fauna consists of 4 families, 8 genera, and 10 species: 4 genera and 4 species in the Geophilidae, 2 genera and 4 species in the Mecistocephalidae, and 1 genus and species apiece in the Schendylidae and Oryidae. We consider four of these species, less than half of the fauna, to be indigenous: *Mecistocephalus spissus*, *M. waikaneus*, *Marsikomerus bryanus*, and *Tuoba sydneyensis*. Pending further investigations on their taxonomic statuses and positions, three of these are regarded as Hawaiian endemics: two exhibiting East Asian affinities (*Mecistocephalus spissus* and *M. waikaneus*) and one related to the North American fauna (*Marsikomerus bryanus*). Five species are considered human importations: two are widespread in the tropics (*Mecistocephalus 'maxillaris'* and *O. brevilabiatus*), one is native to SE Asia (*Tygarrup javanicus*), one is probably native to Australia or New Zealand (*Z. hawaiiensis*), and one has a European origin (*P. ferrugineum*). *Nesomerium hawaiiense* is apparently endemic to the Hawaiian islands, but its status is questionable. Before the present study, three genera and eight species were regarded as endemic to the Hawaiian chain and neighboring oceanic islands, too high a figure for a group in which genera and species with restricted ranges are uncommon, whereas dispersed taxa are frequently encountered. Our conclusion that probably no genus and only three or four species are endemic is more compatible with knowledge of global geophilomorph occurrences.

Within the archipelago, species diversity increases from west to east, thus correlating with island size rather than age (Table 1): six species have been recorded from Hawai'i and O'ahu; four from Maui; three from Moloka'i; two each from Lāna'i, Kaua'i, Necker, and Midway; and one each from Gardner Pinnacles, Laysan, Pearl and Hermes Reef, and Kure. Regarding putative indigenous species, three apiece occur on Hawai'i, Maui, Moloka'i, and O'ahu, two occupy Necker, and one each inhabits Lāna'i, Kaua'i, Gardner Pinnacles, Laysan, Pearl and Hermes Reef, Midway, and Kure. Introduced species dominate on the Island of Hawai'i and O'ahu (three each), while one adventive is known from Maui, Lāna'i, Kaua'i, and Midway. The indigenous geophilomorphs occur on more islands/atolls than the introductions; consequently, *Marsikomerus bryanus* is known from seven islands/atolls, *Mecistocephalus spissus* from six, *Tuoba sydneyensis*

from five, and *Mecistocephalus waikaneus* from three. Of the putatively introduced species, *Mecistocephalus 'maxillaris'* occurs on four islands/atolls, *Tygarrup javanicus* and *P. ferrugineum* on two, and the other three species on one island apiece. The fact that *N. hawaiiense* has been recorded only once further suggests that it is allochthonous rather than indigenous.

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