European Journal of Taxonomy 845: 101–131
https://doi.org/10.5852/ejt.2022.845.1957
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2022 · Shimizu A. *et al.*

Research article

urn:lsid:zoobank.org:pub:4A40954E-9BE5-4462-9845-F0A1BE825623

First records of the spider wasps *Ctenocerus* Dahlbom and *Paraclavelia* Haupt from Asia, with discussions on the systematics of Ctenocerinae (Hymenoptera: Pompilidae)

Akira SHIMIZU [1,*], Gavin BROAD [2], Jin YOSHIMURA [3] & James P. PITTS [4,*]

[1,3] Department of Biological Science, Tokyo Metropolitan University, Hachioji, Tokyo, 192-0397 Japan.
[1] Research Institute of Evolutionary Biology, Inc., Setagaya-ku, Tokyo, 158-0098 Japan.
[1,3] University Museum, the University of Tokyo, Bunkyo-ku, Tokyo, 113-0033 Japan.
[2] Natural History Museum, Cromwell Road SW7 5BD, London, UK.
[3] Shizuoka University, Hamamatsu, 432-8561 Japan.
[3] Department of International Health and Medical Anthropology, Institute of Tropical Medicine, Nagasaki University, Nagasaki, 852-8523 Japan.
[3] Marine Biosystems Research Center, Chiba University, Uchiura, Kamogawa, Chiba, 299-5502 Japan.
[4] Department of Biology, Utah State University, Logan, UT, 84322-5305 USA.

[*] Corresponding authors: aquilashimizu7@gmail.com and james.pitts@usu.edu
[2] Email: g.broad@nhm.ac.uk
[3] Email: yoshimura.jin@shizuoka.ac.jp

[1] urn:lsid:zoobank.org:author:F015CF83-2089-4DFF-AF69-535579E5307F
[2] urn:lsid:zoobank.org:D06689DE-526F-4CFA-8BEB-9FB38850754A
[3] urn:lsid:zoobank.org:author:B3B7F93C-2896-4DC5-B64D-1A37DF758927
[4] urn:lsid:zoobank.org:author:9B4EC38-0687-4650-9F0E-AF2324459E10

Abstract. We describe two new species of Ctenocerinae (Pompilidae) from Asia, i.e., *Ctenocerus srilankae* Shimizu sp. nov. from Sri Lanka and *Paraclavelia arabiae* Shimizu sp. nov. from Oman. These represent the first records of *Ctenocerus* Dahlbom, 1845 and *Paraclavelia* Haupt, 1930 in Asia. Two new combinations and a new synonymy are proposed: *Ctenocerus fasciatus* (Smith, 1851) (= *Micropteryx fasciata* Smith, 1851); *Paraclavelia decipiens* (Arnold, 1932) (= *Clavelia decipiens* Arnold, 1932); and *Ctenocerus* Dahlbom, 1845 (= *Euclavelia* Arnold, 1932). We discuss the difficulty of systematics of Ctenocerinae at generic level. The head and pronotal structures of *Ctenocerus* and *Paraclavelia* are presumably specialized for preying on trapdoor spiders. These structures are considered to have evolved independently of other unrelated parasitoid Pompilidae that have been confirmed or proposed to prey on trapdoor spiders. We also discuss the biogeographical distribution of these genera.

Keywords. *Clavelia*, convergence, *Parapompilus*, parasitoid, trapdoor spiders.

Shimizu A., Broad G., Yoshimura J. & Pitts J.P. 2022. First records of the spider wasps *Ctenocerus* Dahlbom and *Paraclavelia* Haupt from Asia, with discussions on the systematics of Ctenocerinae (Hymenoptera: Pompilidae). *European Journal of Taxonomy* 845: 101–131. https://doi.org/10.5852/ejt.2022.845.1957

Introduction

We dedicate this paper to the recently deceased Pompilidae taxonomists Michael C. Day, Raymond Wahis, and Marius Wasbauer.

The pompilid subfamily Claveliinae was first proposed by Haupt (1929) (type genus: *Clavelia* Lucas, 1851) for pompilids that had seemingly odd modifications of the head and pronotum: the vertex rises behind the ocelli before producing a sharp angle, and the pronotum is very long. Later, Haupt (1930) found further taxa with similar modifications, describing the South American genus *Lepidocnemis* Haupt, 1930 and the African genus *Paraclavelia* Haupt, 1930 and included these genera in Claveliinae. In his monograph of the African Claveliinae, Arnold (1932) recognized 11 genera, including *Clavelia* and *Paraclavelia*. Afterward, Arnold (1934) synonymized *Clavelia* with *Ctenocerus* Dahlbom, 1845. As a result, the subfamily name was changed from Claveliinae to Ctenocerinae Arnold, 1934 (see also Day 1981: 6).

Waichert *et al*. (2015) constructed a molecular phylogeny of Pompilidae Latreille, 1804 with global coverage, from Bayesian and maximum-likelihood analyses of four nuclear DNA markers. The resulting consensus tree showed that the sampled Ctenocerinae, including *Trichosalius* Arnold, 1934, *Paraclavelia*, and *Ctenocerus*, constituted the earliest diverging clade in the Pompilidae, sister to all other subfamilies.

When the first author, AS, visited the Natural History Museum, London in 2004, the late Mr M.C. Day, who had retired from the museum, introduced AS to the Pompilidae collection in the museum that he had been managing. At that time, he showed AS a female and three males of a species from Sri Lanka collected by K.V. Krombein (National Museum of Natural History, Washington D.C., USA) *et al.* and a female of another species from Oman, and stated that these were true Ctenocerinae from Asia (although Oman is a biogeographically complex country in the Middle East, straddling the Afrotropical, Indo-Malayan and Palaearctic realms). This surprised AS because *Ctenocerus* and *Paraclavelia* had been considered to be endemic to the African continent. In fact, Arnold (1932) stated that *Ctenocerus* was distributed in North Africa and the Ethiopian (now Afrotropical) Region, and *Paraclavelia* in the Ethiopian (= Afrotropical) Region. In 2019, AS visited the National Museum of Natural History, Washington D.C., USA and inspected the Pompilidae collection there. At that time, he found three female and five male specimens conspecific with the Sri Lankan species mentioned above. AS decided to study the Asian Ctenocerinae based on the above specimens borrowed from the two museums. The results led him the conclusion that both were undescribed species, with the Sri Lankan species belonging to *Ctenocerus* and the Arabian species belonging to *Paraclavelia*.

In this paper, we revise the generic characters of *Ctenocerus* and *Paraclavelia*, and describe two new species of both genera, which are recorded from Asia for the first time. We discuss the difficulty of systematics of Ctenocerinae at generic level. The head and pronotal structures of these wasps are presumably specialized for preying on trapdoor spiders (Araneae: Ctenizidae). These structures seem to have evolved independently of other unrelated parasitoid Pompilidae that have been confirmed or proposed to prey on trapdoor spiders. We also discuss the biogeographical distribution of these genera.

Material and methods

Morphological analysis

Specimens were photographed with a digital camera (Nikon Coolpix 4500 and MDC lens equipped with a stereo microscope Leitz TS and a transmitted light microscope Leitz Dialux). Photographs were stacked by using combineZM (Hadley 2008) and the final synthesized photographs were post-processed for contrast and brightness using Adobe Photoshop software.

The terminology of general morphology, including the wing veins and cells, follows Day (1988). In addition, the following term is used: antennocular line, the anterior margin of the frons from the antennal base to the eye in dorsal view.

Abbreviations of morphological terminologies

Fl or fl	=	flagellomere
FW	=	fore wing
HW	=	hind wing
LID	=	lower interocular distance
MID	=	middle interocular distance
OOcD	=	posterior ocellus-occipital carina distance
OOD	=	ocello-ocular distance
POD	=	postocellar distance
S1, 2, 3…	=	the first, second, third, … metasomal sterna
SMC1, 2, 3	=	the first, second and third submarginal cells of the fore wing
T1, 2, 3…	=	the first, second, third, … metasomal terga
TFD	=	transfacial distance (= head width)
UID	=	upper interocular distance

Abbreviations of repositories

ANIC	=	Australian National Insect Collection, Canberra, Australia
NHMUK	=	Natural History Museum, London, UK
NMNH	=	National Museum of Natural History, Washington D.C., USA
UMUT	=	University Museum, The University of Tokyo

Species of Ctenocerinae examined

We examined the following species (for detailed information on the specimens examined, including their repository collections, see Supp. file 1): *Ctenocerus flavicauda* (Arnold, 1932) (♀); *Ct. katangae* (Arnold, 1932) (♀); *Ct. klugi* Dahlbom, 1845 (♀, ♂); *Ct. lacteipennis* (Arnold, 1932) (♀, ♂); *Ct. robustus* (Arnold, 1932) (♀); *Ct. ramosus* Smith, 1865 (♀, ♂); *Ct. srilankae* Shimizu sp. nov. (♀, ♂), *Euclavelia fasciatus* (Smith, 1851) (here transferred to *Ctenocerus*) (♀, ♂); *Paraclavelia arabiae* Shimizu sp. nov. (♀); *Parac. caffer* (Kohl, 1886) (♀); *Parac. crudelis* (Smith, 1879) (♀, ♂); *Parac. katbergensis* Arnold, 1948 (♂) (there is a possibility that this species known only from the male is conspecific with *Parac. caffer* known only from the female); *Parac. marshalli* (Bingham, 1902) (♀, ♂); *Parac. rhodesiensis* Arnold, 1932 (♀, ♂); *Parac. somalica* Arnold, 1932 (♀); *Ct. decipiens* (Arnold, 1932) (here transferred to *Paraclavelia*) (♂); *Parapompilus argenteus* Arnold, 1932 (♀); *Parap. bicolor* (Smith, 1851) (♀); *Parap. brevipennis* (Fabricius, 1793) (♀); *Parap. bulawayoensis* Bischoff, 1913 (♀); *Parap. infernalis* Arnold, 1932 (♀, ♂); *Parap. iridipennis* (Cameron, 1904) (♀, ♂); *Parap. rufithrox* Arnold, 1932 (♀, ♂); and *Parap. zuluensis* Arnold, 1932 (♀).

In addition, we examined females of the following species of *Psorthaspis* Banks, 1912, *Entomobora* Gistel, 1857, and other genera that have the head and pronotum modified similarly to (but not exactly as) *Ctenocerus* and *Paraclavelia*: *Psorthaspis planata* (Fox, 1892), *Entomobora crassitarsis* (Costa, 1887), *Ctenostegus monstrosus* Evans, 1976, *Ctenos. tenellus* (Turner, 1910), and *Pedinpompilus* (*Pedinpompilus*) *salvatoris* (Kohl, 1913) (Pompilinae); and *Maurillus australis* Smith, 1855, and *Hypoferreola* sp. (probably "*Entypus*" *cephalotes* Saussure, 1867) (Pepsinae).

The label information on each specimen of these species is listed in Supp. file 1.

Results

Taxonomic account

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Pompilidae Latreille, 1804
Subfamily Ctenocerinae Arnold, 1934

Genus ***Ctenocerus*** Dahlbom, 1845

Ctenocerus Dahlbom, 1845: 456 (type species: *Ct. klugi* Dahlbom, 1845, ♂, Caffraria, South Africa (Dahlbom 1845, 1856), by monotypy).
Clavelia Lucas, 1851: 418, 421 (sensu Arnold 1932). [In part*]
Euclavelia Arnold, 1932: 112, figs 35–36. (type species: *Micropteryx fasciatus* Smith, 1851, original designation and monotypic.) **Syn. nov.**

Remarks

*In his monograph on the African Claveliinae (= Ctenocerinae), Arnold (1932, 1935) described the following species and subspecies of *Clavelia*, i.e., *Cl.* (*Protoclavelia*) *robusta* Arnold, 1932, ♀; *Cl.* (*Pr.*) *katangae* Arnold, 1932, ♀; *Cl.* (*Pr.*) *flavicauda* Arnold, 1932, ♀; *Cl.* (*Clavelia*) *ramosa ramosa* (Smith, 1865), ♀♂; *Cl.* (*Cl.*) *r. minor* Arnold, 1932, ♀♂; *Cl.* (*Cl.*) *lacteipennis* Arnold, 1932, ♂; *Cl.* (*Cl.*) *pennata* Bischoff, 1913, ♂; *Cl.* (*Cl.*) *capensis* Bischoff, 1913, ♂; *Cl.* (*Cl.*) *decipiens decipiens* Arnold, 1932, ♂; *Cl.* (*Cl.*) *decipiens pallidicornis* Arnold, 1932, ♂; *Cl.* (*Cl.*) *algoensis* Arnold, 1932, ♂; *Cl.* (*Cl.*) *pannosicornis* Aronod, 1932, ♂; *Cl.* (*Cl.*) *amplicornis* Arnold, 1932, ♂; *Cl.* (*Cl.*) *fuscipennis* Arnold, 1932, ♂; *Cl.* (*Cl.*) *croceicornis* Arnold, 1932, ♂; *Cl.* (*Cl.*) *auranticornis* Arnold, 1932, ♂; and *Cl.* (*Cl.*) *modesta* Arnold, 1935, ♀. Afterward, Arnold (1934) recognized *Clavelia* to be a junior synonym of *Ctenocerus*, as stated in the introduction. From our examination of females of four species (*Cl. robusta*, *Cl. katangae*, *Cl. flavicauda*, *Cl. ramosa*; see Supp. file 1) and Arnold's descriptions, it is apparent that all females of *Clavelia* sensu Arnold (1932, 1935) belong to *Cternocerus*. Hence, *Cl. robusta*, *Cl. katangae*, *Cl. flavicauda*, *Cl. ramosa*, and *Cl. modesta* should be transferred to *Ctenocerus*. The problems lie in the above species based only on the males. As far as being based on Arnold's (1932: fig. 10) description, *Clavelia algoensis* certainly belongs to *Ctenocerus* because the male has the frontal bridge (median longitudinal strip on lower frons connecting frons and clypeus on same plane). We examined two males of *Clavelia decipiens* (Supp. file 1) and found that the species should be transferred to *Paraclavelia*. We were not able to determine genera of the other species, because we were not able to examine male specimens of these species and Arnold's (1932) descriptions are insufficient for our generic identification.

Diagnosis

Ctenocerus is distinguished from other genera of Pompilidae by the combination of the following features.

Both sexes

Clypeus distinctly narrower than LID (Figs 1A, F, J, 2E, G, I, 3D, 4A, D, G, 5D), rectangular or trapezoidal.

Female

Lower frons lateral to and ventral to antennal sockets deeply depressed, leaving median frontal bridge (Figs 1A, F, J, 2E, G, I, 3D, arrow). Clypeus lamelliform (flattened plate), usually truncate apically, its surface flat or slightly convex and polished, deeply and broadly depressed basilaterally. Scape

Fig. 1. Females of *Ctenocerus* Dahlbom, 1845. **A–E**. *C. robustus* (Arnold, 1932) (#14) (NHMUK). **F–I**. *C. klugi* Dahlbom, 1845 (#8) (NHMUK). **J–M**. *C. fasciatus* (Smith, 1851) (#3) (NHMUK). **A, F, J**. Head, anterior view, arrow indicates frontal bridge. **B, L**. Head and anterior part of mesosoma, dorsal view. **C, H**. Head and mesosoma, lateral view. **D, G, K**. Head and mesosoma, dorsolateral view. **E, M**. Posterior part of mesosoma and anterior part of metasoma, dorsal view. **I**. Wings. Numbers in parentheses after species names are specimen numbers in Supp. file 1. Scale bars = 1 mm.

compressed laterally, curved outward with lateral face concave (Figs 2B, 3E). Pronotum as long as or longer than mesoscutum at middle (Figs 1G, K–L, 3A); collar situated slightly below level of dorsum (Figs 1C, H, 2A, F, H, J, 3H); lateral face vertical, traversed by L-shaped groove (posterior part of streptaulus) (Figs 2H, 3H). Fore tibia with stout, decurved spine apicomesally (Figs 2C, 3F, arrow). All tarsal claw bifid. S2 with transverse groove (Fig. 3I).

Male

Vertex strongly convex and chevron-shaped above level of eye tops (Figs 4A, D, G, 5D). Lower frons with median frontal bridge, this being often narrow and slightly depressed below level of supra-antennal area (Figs 4A, D, G, 5D, arrow). Flagellomeres 1–10 uniramous (each flagellomere with lobe-like projection only basilaterally; Fig. 4B–C, J), biramous (each flagellomere with lobe-like projection both basilaterally and basimesally; Fig. 4D–E, H), or catenulate (cylindrical and connected with each other only by a hidden dorsal peduncle; Fig. 5H). Propodeum densely punctate, sometimes finely and transversely rugulose or minutely reticulate-rugulose, and covered with long pubescence (Figs 4K, 5B). Fore and mid tarsal claws bifid; hind tarsal claw bifid, or edentate, rectangularly bent subapically and their pair not very divergent.

Redescription (as a complement to Arnold's (1932) description, based on the type species)

Female

Measurements. Small to fairly large wasps, 9 to 22 mm in length.

Head. Usually slightly wider than high (Figs 1A, J, 2E, G, I, 3D) (narrower than high in *C. klugi* (Fig. 1F)). Vertex moderately to strongly convex above level of eye tops (Figs 1A, F, J, 2E, G, I, 3D) with surface fairly flattened; juncture of its anterior and posterior faces sharply or subacutely carinate medially (Figs 1D, G, K, 3E). Frons broad, half of this much broader than eye, usually polished; upper frons fairly flat. Frontal bridge various in width, e.g., very narrow and linear in the subgenus *Protoclavelia* Arnold, 1932 (Figs 1A, 2E) and broader than scape width in *C. klugi* (Fig. 1F), *C. fasciatus* (Fig. 1J) and *C. srilankae* sp. nov. (Fig. 3D). Malar space much shorter than half of fore tarsomere 1 thickness (Figs 2F, H, 3D). Mandible usually long and curved apically with small tooth subapically on inner margin (Figs 2G, I, 3D) (in *C. klugi* (Fig. 2M), very stout and strongly curved, laminated and polished anteriorly with broad outer rim on apical half, that being delimited from main part by deep groove). Maxillary palpus short, palpomeres 4–6 not much shorter or longer than palpomere 3. Gena, in dorsal view, variously developed but not swollen (Figs 1B, L, 3E). Ocelli forming an obtuse-angled triangle (Figs 1B, L, 3E, 4B, H, 5C). Occipital suture present only dorsally, its uppermost portion situated immediately below vertex crest (Fig. 1G, K).

Mesosoma. Pronotum with dorsum flattened medially, gradually sloping anteriorly, its lateral margin somewhat convex (Figs 1B, L, 3E); streptaulus absent medially; declivity short and gently sloping or practically absent because of continuous transition from dorsum to collar (Figs 1C, 2H); juncture of lateral face and dorsum usually bluntly carinate (Figs 1K, 2H, 3H) (broadly rounded in *C. klugi* (Fig. 1G)). Mesoscutum small (Figs 1K–L, 3A), flattened above; parapsides narrowly raised posterolaterally (Fig. 3B); parapsidal sulcus deeply impressed, divergent anteriorly. Scutellum flattened above, scarcely raised above level of mesoscutum (Fig. 1H). Metapostnotum variously developed (Figs 1E, H, M, 3B), sometimes short or linear medially. Propodeal dorsum gently convex or rather flattened longitudinally (Figs 1H, 2A, H, 3G–H) with stigma from anterior margin of propodeum by about twice its own length (Figs 1E, G, M, 3B); declivity rather flattened but not distinctly delimited from dorsum (Figs 1H, 2A, F, H, J, 3H), transversely rugose (Fig. 3B).

Wings. FW with three SMCs (Figs 1I, 3C). Pterostigma fairly long, its base much longer than cross-vein 2*r-rs*. Marginal cell lanceolate, acute at apex. Second abscissa of vein *M* (basal vein) curved. Last abscissa of vein *M* not attaining outer wing margin. Cross-vein *cu-a* originating distal to separation of vein *M+CuA*. HW cross-vein cu-a originating basal to (Figs 1I, 2J), at, or distal to fork of vein *M+CuA* (Figs 1C, 3C).

Legs. Fore tarsomeres 2–4 combined much shorter than fore tarsomere 1. Fore femur somewhat swollen, as thick as or thicker than mid femur (Figs 2A, F, 3H). Mid and hind femora with distinct basal ring. Mid tibia with short spines dorsally. Hind tibia with spines short or rudimentary dorsally (Figs 2K, 3J) and apically (Fig. 2L). Orbicula small, narrower than 0.6× width of tarsomere 5, with orbicular pecten

Fig. 2. Females of *Ctenocerus* Dahlbom, 1845. **A–D**. *C. fasciatus* (Smith, 1851) (#3) (NHMUK). **E–F**. *C. flavicauda* (Arnold, 1932) (#5) (NHMUK). **G–H**. *C. ramosus* Smith, 1865 (#16) (UMUT). **I–J**. *C. lacteipennis* (Arnold, 1932) (#12) (NHMUK). **K–L**. *C. robustus* (Arnold, 1932) (#14) (NHMUK). **M**. *C. klugi* Dahlbom, 1845 (#8) (NHMUK). **A, F, H, J**. Head and mesosoma, lateral view. **B**. Left scape, dorsolateral view. **C**. Right fore tibia, mesial view, arrow points to apicomesial spine on fore tibia. **D**. Apical part of metasoma, ventral view. **E, G, I**. Head, anterior view, arrow indicates frontal bridge. **K**. Left hind tibia, dorsal view. **L**. Apical part of left hind tibia, dorsal view. **M**. Mandible, anteroventral view. Numbers in parentheses after species names are specimen numbers in Supp. file 1. Scale bars: A–K, M = 1 mm; L = 0.5 mm.

consisting of short, fine, straight setulae. Tarsomere 5 with short, irregularly arranged spines or almost lacking spines beneath.

Metasoma. T1 usually petiolate (narrower immediately behind articulation than its width at articulation itself; Fig. 3A) or parallel-sided anteriorly (Fig. 1E, M). S6 not or slightly compressed laterally with (Figs 2D, 3I) or without median carina.

Male

Measurements. Much smaller and slenderer than female, 5.5 to 18 mm in length.

Head. Broader than long (Figs 4A, D, G, 5D). Juncture of anterior and posterior faces of vertex rounded (Figs 4B, E, H, 5C). Frons usually with numerous long erect setae; upper frons transversely convex; supra-antennal area not or only slightly produced anteriorly, not overhanging antennal radicle (Figs 4C, F, I, 5G). Clypeus with surface slightly convex. Malar space as long as or longer than half of fore tarsomere 1 thickness (Figs 4A, C–D, G, I, 5D). Scape short (Figs 4B–D, I–J, 5C, G), barrel-shaped unlike in female, sometimes with numerous setae, usually those on ventral side longer than elsewhere (Fig. 4I). In uni- or biramous flagellum, projection(s) on each flagellomere prolonged anteriorly, its outer face convex, inner face concave, both faces with short, dense spinules. Mandible short with small tooth subapically on inner margin (Fig. 4A, G). Occipital suture complete, its uppermost portion situated somewhat deep below vertex crest (Fig. 5B).

Mesosoma. Pronotum much shorter than mesoscutum medially (Figs 4H, 5A); collar situated deep below level of dorsum unlike in female (Figs 4C, F, I, 5G); streptaulus present (Fig. 5C); declivity vertical, flattened and polished (Figs 4C, F, I, 5G), its juncture with dorsum rounded; dorsum transversely convex and longitudinally declivous, usually gradually narrowing anteriorly (Figs 4E, H, 5C), truncate anteromedially with numerous long pubescence and setae, its juncture with lateral face rounded; L-shaped groove on lateral face obscure or absent (Figs 4C, F, 5G). Mesoscutum with parapsides narrowly reflexed posterolaterally (Fig. 5B). Disc of scutellum triangular (Figs 4K, 5B), scarcely or slightly raised above level of mesoscutum. Metanotum declivous. Metapostnotum longer than in female (Figs 4K, 5B). Propodeum with dorsum much longer than declivity (Figs 4C, 5F–G), parallel-sided (Fig. 5A–B) or gradually narrowing posteriorly; declivity not delimited from dorsum.

Wings. HW cross-vein cu-a originating usually at or distal to separation of vein *M+CuA* (Fig. 5E), confluent with vein *A*, forming long smooth arc, but occasionally short, almost straight and oblique, meeting vein *A* forming obtuse angle (Fig. 4C).

Legs. Apical margin of fore tibia with short, stout, decurved spine or lacking such spine mesally. Fore femur slender, thinner than mid femur (Figs 4C, I, 5G). Fore tarsomeres 2–4 combined as long as or shorter than fore tarsomere 1. Orbiculae of all legs similar to those of female or orbicula of hind leg remarkably small, its pecten absent. Fore and mid tarsal claws bifid; hind tarsal claw bifid, or edentate, rectangularly bent subapically and both claws parallel to each other or slightly divergent.

Metasoma. T1 not petiolate, gradually narrowing anteriorly. S2 without transverse groove. S6 with very small lateral hook posteriorly. Subgenital plate comparatively large, not compressed laterally (Fig. 5L).

Distribution

Africa (Palaearctic and Afrotropical Regions) and South Asia (Sri Lanka).

Ctenocerus srilankae Shimizu sp. nov.
urn:lsid:zoobank.org:act:E214E6F5-3193-41D1-91A3-FAAB02249E21
Figs 3, 5

Diagnosis

Female

Body and legs mostly black (Fig. 3A); head with longitudinal yellow streak along inner orbit (Fig. 3D); propodeum reddish brown (Fig. 3A–B); T1–5 with paired posterolateral patches of silvery pubescence; frontal bridge (Fig. 3D, arrow) much broader than pedicel width; and clypeus with apicolateral margin obliquely truncate.

Male

Body and legs mostly black (Fig. 5A) with pale yellow streaks on frons along inner orbit (Fig. 5D), upper gena along outer orbit (Fig. 5B–C) and posterior margin of pronotum, and pale-yellow spots on scutellum (Fig. 5A–B) and T7 apically; hind femur orange to reddish brown (Fig. 5A, F–G); T1–4 with posterior bands of silvery pubescence (Fig. 5A); flagellum catenulate (Fig. 5H); all tarsal claws bifid.

Etymology

The species name is derived from its locality, Sri Lanka.

Type material

Holotype

SRI LANKA • ♀; "SRI LANKA: Tri. Dist. Tennamaravadi 18-v-1976" / "Collected by K. V. Krombein P. B. Karunaratne S. Karunaratne D. W. Balasooriyo"; NMNH.

Paratypes

SRI LANKA • 1 ♀, 1 ♂; Man. Dist., Kokmotte Bungalow, 0.5 mi NE of Wilpattu Natl. Park; 21–25 May 1976; K.V. Krombein, P.B. Karunaratne, S. Karunaratne and D.W. Balasooriyo leg.; NHMUK • 1♂; same collection data as for preceding; 22–25 May 1976; Malaise trap; NMNH • 1 ♀; Man. Dist., 0.5 mi NE of Kokmotte, Wilpattu Natl Park; 50–100 ft; 5–8 Oct. 1977; K.V. Krombein, P.B. Karunaratne, S. Karunaratne and D.W. Balasooriyo leg.; NMNH • 1 ♂; same collection data as for preceding; 22–23 Jan. 1977; Malaise trap; NMNH • 1 ♀; Anu. Dist., Padaviya; 180 ft; 18–19 May 1976; K.V. Krombein, P.B. Karunaratne, S. Karunaratne and D.W. Balasooriyo leg.; NMNH • 3 ♂♂; Anu. Dist., Padaviya, Irrigation Bungalow; 180 ft; 18 May 1976; Malaise trap; K.V. Krombein, P.B. Karunaratne, S. Karunaratne and D.W. Balasooriyo leg.; NMNH • 2 ♂♂; same collection data as for preceding; NHMUK.

Description (measurements of the holotype are given in parentheses.)

Female

Measurements. Length: body 9.1–14.3 (14.3) mm; FW 6.0–8.5 (8.5) mm.

Colouration. Body and legs dominantly black or reddish black (Fig. 3A, G). Frons with longitudinal yellow streak along inner orbit (Fig. 3D). Following reddish brown to dark rufous: clypeus apically (Fig. 3D), mandible, antenna, scutellum (disc sometimes reddish black (Fig. 3B)), metanotum, metapostnotum and propodeum dorsally, fore tibia ventroapically, all femora and tarsi apically (fore tarsomere 5 wholly reddish brown), tibial spurs, tarsal claws, S1 medially, and S2 anterior to and immediately posterior to transverse groove (Fig. 3I). Labrum and labio-maxillary complex orange brown (stipes and prementum dark brown). FW pale yellow (Fig. 3C); pterostigma yellowish brown; apical half of marginal cell, SMC3 except basally, SMC4, and discal cell 3 infuscate; HW transparent with yellowish tint, slightly infuscate apically.

Integument. Following with silvery white pubescence: frons around antennal socket (Fig. 3D), clypeus basilaterally, mandible basally, gena (Fig. 3E), thorax laterally (Fig. 3H) and ventrally, propodeum posterolaterally (Fig. 3B), all legs, T1–5 posterolaterally (dense and forming paired silvery patches (Fig. 3A)), T6 laterally, and S1–6 (Fig. 3I). Following with coppery pubescence: vertex medially, pronotal dorsum except posteriorly (Fig. 3E), scutum except anterolaterally and posterolaterally (Fig. 3B), scutellum, metasomal terga except for paired silvery patches and lateral margins, and S1 and S2 anteromedially (Fig. 3I). Setae on body scarce; vertex along inner orbit with a few fine, erect setae (Fig. 3D); apical margin of labrum, mandible, T6 and S5–6 with long erect bristles.

Head. 1.0–1.1 (1.1) × as broad as high. Vertex, frons, and mandible polished (Fig. 3D). Vertex strongly convex above level of eye tops. MID 0.65–0.66 (0.66) × TFD. Frons with median sulcus shortly impressed only on supra-antennal area. Antennocular line gently convex between eyes (Fig. 3E). Inner orbits convergent above and below (Fig. 3D). UID:MID:LID = 8.3–8.4 (8.4):10:8.7–9.2 (8.9). POD:OOD = 1:0.85–1.1 (1.1). OOcD /POD = 1.1–1.5 (1.5). Clypeus 1.4–1.8 (1.4) × as broad as long; apical rim not delimited from main part; apicolateral margin obliquely truncate; apical margin truncate or weakly emarginate. Gena, in dorsal view, roundly narrowing posteriorly (Fig. 3E), in profile, 0.5–0.6 (0.6) × as broad as eye, abruptly narrowing dorsally (Fig. 3H). Scape distinctly concave laterally (Fig. 3E). Scape:pedicel:fl1:fl2 =15–16 (15):2.1–2.8 (2.5):10: 9.1–9.4 (9.4). Fl1 2.8–3.1 (3.0) × as long as broad, 0.37–0.39 (0.37) × UID.

Mesosoma. Pronotum much longer than mesoscutum (Fig. 3A) with dorsum gently convex transversely and longitudinally; lateral margins slightly convex, roundly converging anteriorly (Fig. 3E); posterior margin subangulate medially (Fig. 3A). Mesoscutum depressed interiorly to parapsidal sulcus and along posterior margin (Fig. 3B). Disc of scutellum scarcely raised above level of mesoscutum. Metapostnotum 0.27–0.38 (0.27) × as long as metanotum at midline, shallowly and triangularly emarginate posteromedially. Propodeum with dorsum finely and transversely rugulose without median groove, its sides slightly convex in dorsal view (Fig. 3B); declivity rather flattened (Fig. 3H) but not delimited from dorsum, transversely or arcuately rugulose.

Legs. Mid tibiae with several short spines dorsally. Hind tibia lacking spines dorsally (Fig. 3J); apical outer margin with minute sparse spines. Longer spur of hind tibia 0.36–0.41 (0.38) × hind tarsomere 1.

Wings (Fig. 3C). FW marginal cell from wing tip by 0.83–0.87 (0.87) × its own length. SMC2:SMC3 = 1:0.97–1.5 (1.0) on vein *M*, 1:1.1–1.3 (1.2) on vein *Rs*. SMC2 0.63–0.69 (0.67) × as high as long, narrowed on vein *Rs* by 0.56–0.60 (0.58) × its length on vein *M*, receiving cross-vein *1m-cu* at its basal 0.37–0.43 (0.43). SMC3 0.65–1.0 (0.76) × as high as long, narrowed on vein *Rs* by 0.65–0.72 (0.68) × its length on vein *M*, receiving cross-vein *2m-cu* at its basal 0.44–0.52 (0.52), distant from outer wing margin by 1.7–2.4 (1.9) × its own length. Cross-vein *2rs-m* slightly curved, nearly vertical to vein *M*. Cross-vein *2m-cu* barely curved outward or bisinuate. Cross-vein *cu-a* originating distal to point of separation of vein *M+CuA* by more than its own length, curved outward. HW cross-vein *rs-m* nearly vertical or slightly oblique to vein *M*. Cross-vein *cu-a* originating posteriorly to point of separation of vein *M+CuA*.

Metasoma. T1 barely petiolate (Fig. 3A). S6 barely compressed laterally with short median carina posteriorly (Fig. 3I).

Male

Measurements. Length: body 7.4–5.8 mm; FW 4.5–5.8 mm.

Colouration. Body and legs mostly black (Fig. 5A); following pale yellow: longitudinal streaks on frons along inner orbit (Fig. 5D), upper gena along outer orbit and posterior margin of pronotum (Fig. 5B–C),

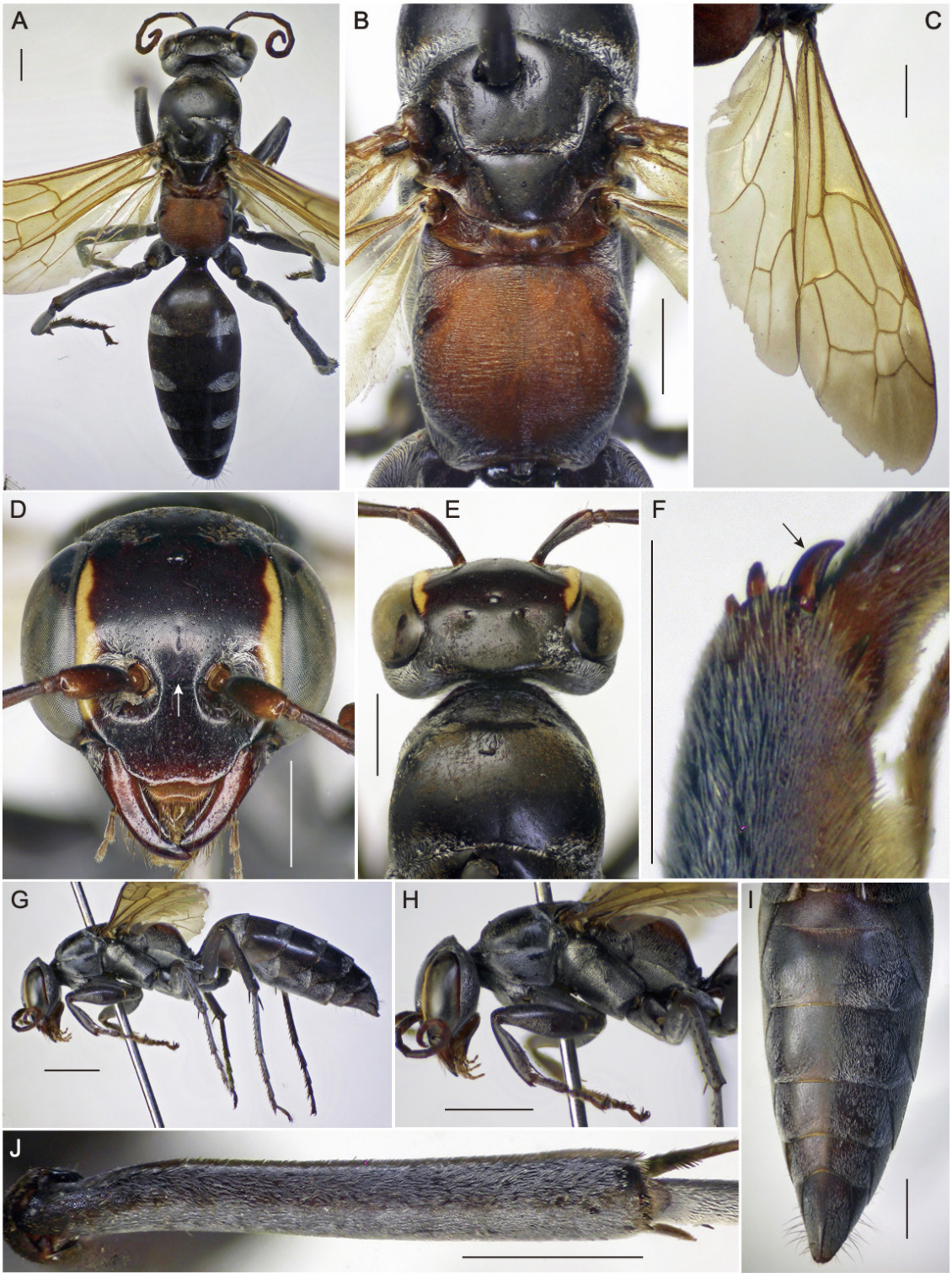


Fig. 3. *Ctenocerus srilankae* Shimizu sp. nov., holotype, ♀ (NMNH). **A**. Whole body, dorsal view. **B**. Posterior part of mesosoma, dorsal view. **C**. Right wings. **D**. Head, anterior view, arrow indicates frontal bridge. **E**. Head and pronotum, dorsal view. **F**. Apical part of left fore tibia, mesial view, arrow indicates apicomesial spine on fore tibia. **G**. Whole body, lateral view. **H**. Head and mesosoma, lateral view. **I**. Metasomal sterna 2–6, ventral view. **J**. Left hind tibia, dorsal view. Scale bars: A–E, I–J = 1 mm; F = 0.5 mm; G–H = 2 mm.

Fig. 4. Males of *Ctenocerus* Dahlbom, 1845. **A–C, J, L**. *C. lacteipennis* (Arnold, 1932) (#13) (NHMUK). **D–F, K**. *C. klugi* Dahlbom, 1845 (#11) (NHMUK). **G–I**. *C. ramosus* Smith, 1865 (#18) (UMUT). **A, D, G**. Head, anterior view, arrow indicates frontal bridge. **B, E, H**. Head and anterior part of mesosoma, dorsal view. **C, F, I**. Head and mesosoma, lateral view. **J**. Left flagellum, mesial view. **K**. Posterior part of mesosoma, dorsal view. **L**. Subgenital plate, ventral view. Numbers in parentheses after species names are specimen numbers in Supp. file 1. Scale bars: A–K = 1 mm; L = 0.5 mm.

spots on scutellum (Fig. 5A–B), fore coxa anteroapically, mid and hind coxae lateroapically, and T7 apically. Fore femur, tibia and mid femur apically, hind femur (Fig. 5G), sometimes hind tibia, all tarsi, and apical metasomal terga posteromedially orange to reddish brown. Fore tibial spur pale yellow; mid and hind tibial spurs light brown. Apical half of mandible reddish brown. Wings transparent with brownish tint, becoming iridescent depending on incident lighting angle (Fig. 5E); FW marginal cell anteriorly and outer wing margin slightly infuscate; pterostigma light brown.

Integument. Body with silvery white pubescence, this being long and dense on lower frons (Fig. 5D), clypeus, scape below, pronotum anteriorly (Fig. 5C), pro- and mesopleura (Fig. 5G), metapostnotum laterally, and propodeum laterally (Fig. 5B); pubescence on T1–4 posterolaterally short but very dense, forming paired silvery patches, those appearing to be continuous medially depending on incident lighting angle (Fig. 5A); pubescence on propodeum posteromedially long, erect, and grey, directed forward or outward. T5 and 6 with coppery pubescence except posterolaterally. Coxae and trochanters covered with silvery white pubescence; remain of legs with silvery to sericeous pubescence. Vertex, lower frons, gena, pronotum, and propleuron with silvery white to grey setae, those on gena and propleuron in particular long and dense. Head, pro-, meso- and metanota, and mesopleuron finely and densely punctate (frons narrowly impunctate and polished at midline). Collar finely and transversely striate (Fig. 5C). Side of metanotum with several oblique striae. Metapostnotum also with several transverse striae, those being decurved posteromedially. Metapleuron and propodeum minutely reticulate-rugulose.

Head. Broad and rhomboid (Fig. 5D), 1.1–1.2 × as broad as high. Vertex strongly convex above level of eye tops, chevron-shaped. Frons with median sulcus very fine only below. MID 0.62–0.66 × as broad as head width. Antennocular line chevron-shaped between eyes (Fig. 5C). Inner orbits weakly emarginate above middle, as a whole divergent below (Fig. 5D). UID:MID:LID = 9.7–10.1:10:7.9–8.7. POD:OOD = 1:0.95–1.1. OOcD /POD = 0.80–1.2. Clypeus 1.5–2.0 × as wide as long, its surface broadly raised medially; lateral margin oblique, apicolateral corner broadly rounded; apical rim very narrow, smooth and polished, not depressed; apical margin almost straight. Labrum almost truncate apically. Scape short, its apicomesal corner pointed (Fig. 5C). Scape:pedicel:fl1:fl2 = 9.2–12:2.7–4.2:10:11–12. Fl1 1.4–2.1 × as long as wide, 0.28–0.34 × UID. Flagellomeres crenulate (Fig. 5H). Gena, in dorsal view, more strongly receding posteriorly than in female (Figs 5C vs 3E), in profile, 0.2–0.3 × as broad as eye. Uppermost part of occipital suture situated moderately deep below vertex crest (Fig. 5B).

Mesosoma. Pronotum with declivity almost vertical (Fig. 5G), somewhat concave; dorsum roundly narrowing anteriorly (Fig. 5C). Scutellum distinctly raised above level of mesoscutum (Fig. 5G). Metapostnotum 0.58–0.73 × as long as metanotum at midline, depressed below level of metanotum but on same plane as propodeal dorsum, constricted strongly in front of propodeal spiracle and slightly medially (Fig. 5B). Propodeum with dorsum transversely convex above without median groove, rather strongly narrowing posteriorly; declivity distinctly and transversely rugulose medially.

Legs. Mid and hind tibiae with several minute spines dorsally. Longer spur of hind tibia 0.44–0.52 × hind tarsomere 1. All tarsal claws bifid.

Wings (Fig. 5E). FW marginal cell from wing tip by 0.64–0.76 × its own length. SMC2:SMC3 = 1:0.79–1.0 on vein *M*, 1: 0.81–1.1 on vein *Rs*. SMC2 0.61–0.68 × as high as long, narrowed on vein *Rs* by 0.60–0.69 × its length on vein *M*, receiving cross-vein *1m-cu* at its basal 0.38–0.47. SMC3 0.69–0.85 × as high as long, narrowed on vein *Rs* by 0.62–0.74 × its length on vein *M*, receiving cross-vein *2m-cu* at its basal 0.47–0.63, from outer wing margin by 1.6–2.1 × its own length. Cross-vein *cu-a* originating distal to point of separation of vein *M+CuA* by less than its own length. HW cross-vein *cu-a* originating distinctly distal to point of separation of vein *M+CuA*.

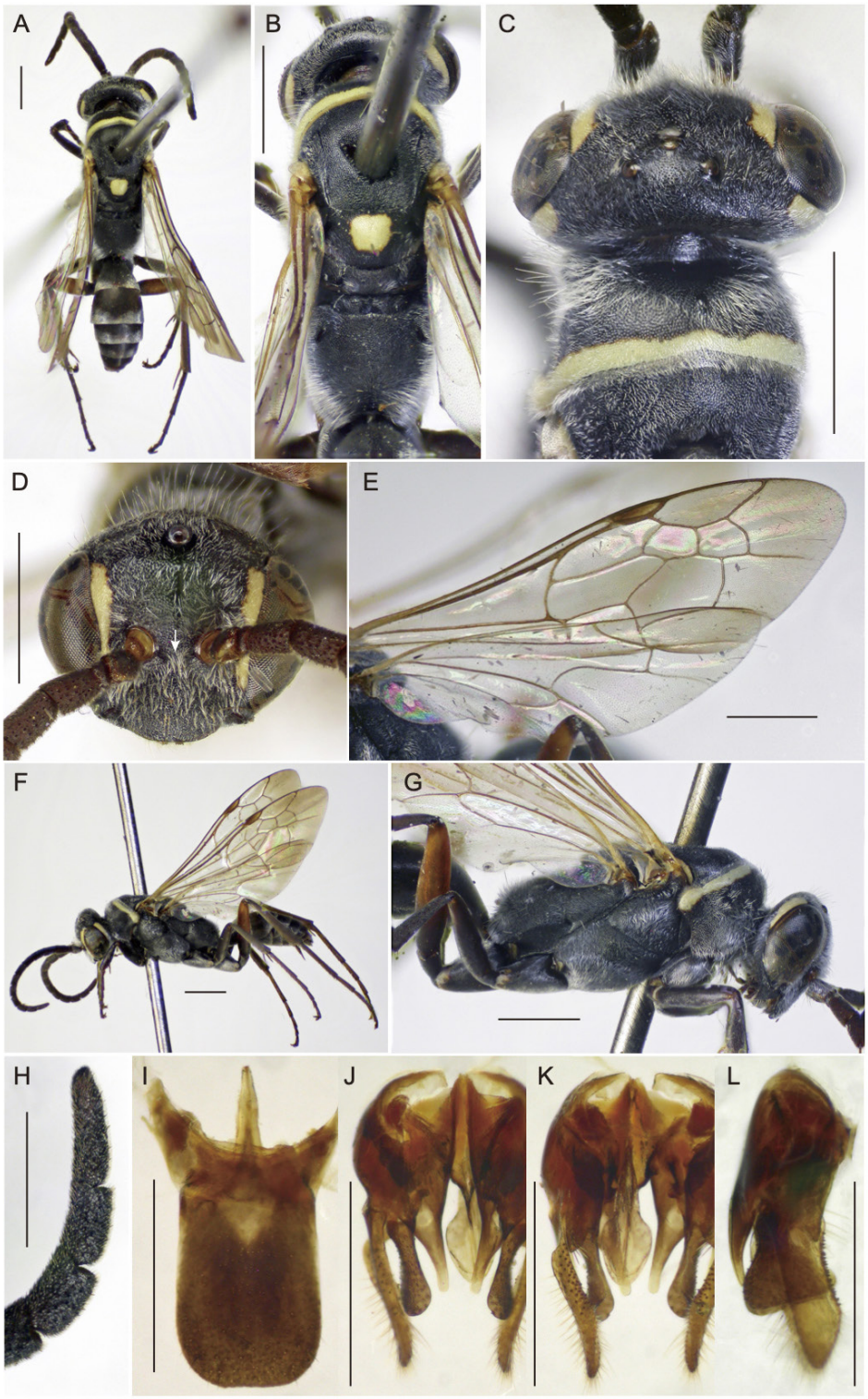


Fig. 5. *Ctenocerus srilankae* Shimizu sp. nov., paratype, ♂ (NHMUK). **A**. Whole body, dorsal view. **B**. Head and mesosoma, dorsoposterior view. **C**. Head and anterior part of mesosoma, dorsal view. **D**. Head, anterior view, arrow indicates frontal bridge. **E**. Left wings. **F**. Whole body, lateral view. **G**. Head and mesosoma, lateral view. **H**. Apical part of right flagellum, lateral view. **I**. Subgenital plate, ventral view. **J**. Genitalia, dorsal view. **K**. Same, ventral view. **L**. Right side of genitalia. Scale bars: A–G = 1 mm; H–L = 0.5 mm.

Metasoma. Somewhat compressed dorsoventrally. Subgenital plate roughly rectangular (Fig. 5I); lateral margins subparallel, roundly narrowing subapically, truncate at apex. Genitalia: paramere, in lateral view (Fig. 5L), parallel-sided and arcuate, with long, dense setae on dorsal margin and minute, dense spinules on ventral margin, extending far beyond apex of digitus volsellaris (Fig. 5J–K); digitus volsellaris, in lateral view (Fig. 5L), strongly broadened apically with apical margin truncate, extending beyond apex of parapenial lobe (Fig. 5J–K); basal hooklet double; parapenial lobe broadened basally, gradually narrowing apically into slender lobe, slightly extending beyond apex of aedeagus (Fig. 5J–K); aedeagus inverted-spade-shaped, ending with rounded apex.

Distribution

South Asia (Sri Lanka).

Genus ***Paraclavelia*** Haupt, 1930

Paraclavelia Haupt, 1930: 728 (type species: *Pompilus caffer* Kohl, 1886, by original designation and monobasic).

Clavelia – Arnold, 1932: 47 [*Cl. decipiens* Arnold, 1932 is transferred to *Paraclavelia* **comb. nov.**]

Diagnosis

This genus has most of the features of *Ctenocerus*, but differs from the latter in the following.

Female

Lower frons lateral to and ventral to antennal sockets deeply depressed, median area between antennal sockets steeply receding into lowermost transverse depression, hence frontal bridge absent (Figs 6A, D, G, J, 7D). Clypeus flat and polished with deep depression across whole width of its base, depression being broader laterally than medially. Pronotal collar usually situated slightly below level of dorsum (Figs 6C, F, I, L, 7H), but rather deeply depressed in *Parac. somalica* (Fig. 6N). Fore femur not swollen (Figs 6F, I, 7G).

Male

Supra-antennal area produced anteriorly into frontal ledge overhanging antennal radicle (Fig. 8C, F, I) Lowermost frons across its whole width depressed much below level of supra-antennal area, slightly below level of clypeus, lacking any trace of frontal bridge (Fig. 8A, D, G).

Description (as a complement to Haupt's (1930) description, based on the type species)

Female

Measurements. Small to fairly large wasps, 12 to 26 mm in length.

Head. Slightly wider than high. Vertex, in anterior view, moderately to strongly raised above level of eye tops (Figs 6A, D, G, J, 7D); juncture of anterior and posterior faces subacutely carinate medially (Figs 6B, E, K, 7B, E). Frons broad, its half much broader than eye, usually polished; surface of upper frons gently and longitudinally arched. Ocelli forming an obtuse-angled triangle (Figs 6B, E, H, J, 7E). Clypeus narrower than LID, lamelliform, its apical margin truncated, convex or concave (Figs 6A, D, G, J, 7D). Labrum small, partly concealed beneath clypeus, its apical margin truncate (Figs 6D, 7D). Malar space short (Figs 6C, F, I, L, 7H). Scape compressed laterally, curved outward with lateral face concave (Figs. 6B, E, K, P, 7E), mesal face usually with longitudinal carina (Fig. 6O, arrow). Mandible usually stout with anterior face flattened and polished (Figs 6A, D, 7D). Maxillary palpus short, palpomeres 4–6 not much shorter or longer than palpomere 3. Gena, in dorsal view, moderately developed but not swollen (Figs 6B, E, K, 7E). Occipital suture obsolete below, its uppermost portion situated immediately below vertex crest (Figs 6K, 7B).

Mesosoma. Pronotum as long as, or longer than mesoscutum at middle (Fig. 7B); streptaulus obsolete dorsally; declivity usually short, gently or steeply sloping (Figs 6C, F, I, L, 7H) (somewhat long and almost vertical in *Parac. somalica* (Fig. 6N)); dorsum flattened medially, gradually sloping anteriorly, its lateral margin slightly convex (Figs 6B, E, H, K, 7B, E); juncture of dorsum and lateral face bluntly carinate; lateral face vertical, traversed by L-shaped groove (posterior part of streptaulus) (Figs 6C, F, I, L, N, 7H) as in *Ctenocerus*. Mesoscutum flattened above with parapsides narrowly raised posterolaterally; parapsidal sulcus distinct (Fig. 7B), divergent anteriorly. Scutellum scarcely raised above level of mesoscutum (Figs 6C, 7H). Propodeal dorsum with stigma from anterior margin of propodeum twice its own length or more (Fig. 7B); surface with transverse rugae, those becoming stronger posteriorly; declivity flattened, sometimes delimited from dorsum by carina (one of rugae); surface arcuately or obliquely rugose.

Wings. FW with three SMCs (Fig. 7C). Pterostigma as long as or longer than cross-vein 2*r*-*rs* at bottom. Marginal cell lanceolate, acute at apex. Second abscissa of vein *M* (basal vein) curved. Last abscissa of vein *M* not attaining outer wing margin. Discal cell 1 usually with indistinct membranous irregularity (fenestra) basally. Cross-vein *cu-a* originating distal to separation of vein *M+CuA*, oblique to vein *A*. HW cross-vein cu-a originating basal to, at (Fig. 7C), or distal to fork of vein *M+CuA*, confluent with vein *A*, forming smooth arc.

Legs. Apical margin of fore tibia usually with short, stout, decurved spine mesally (Figs 6M, 7F, arrow) (apical spines short, stout, but not decurved in *Parac. caffer*). Fore tarsomeres 2-4 combined much shorter than fore tarsomere 1. Mid and hind femora with distinct basal ring. Mid tibia with short spines dorsally. Hind tibia with spines short or rudimentary dorsally and latero- and dorsoapically (Fig. 7J). Tarsomere 5 with several short, irregularly arranged spines, one or two spines, or lacking spines beneath. Orbicula small, narrower than 0.6× width of tarsomere 5, with orbicular pecten consisting of a few rather strong, straight setulae, some of them being as long as, or longer than orbicula itself. All tarsal claws bifid.

Metasoma. T1 not petiolate, abruptly narrowing anteriorly or barely petiolate (Fig. 7A). S2 with transverse groove, this being sometimes fine and almost obsolete (Fig. 7I). S6 compressed laterally with or without median carina.

Male

Measurements. Much smaller and slenderer than female, 6–15 mm.

Head. Broader than long. Vertex strongly convex above level of eye tops, chevron-shaped (Fig. 8A, D, G); juncture of anterior and posterior faces broadly rounded (Fig. 8B, E, H). Frons with numerous long pubescence and setae. Clypeus distinctly narrower than LID (Fig. 8A, G), trapezoid or rectangular, its surface convex, covered with long pubescence and setae. Malar space longer than in female. Scape short (Fig. 8B, F, H–I), not compressed laterally, with numerous setae, those on ventral side longer and denser than elsewhere. Flagellum uni- or biramous (Fig. 8F, K), catenulate (Fig. 8J), or in a few species, basal and apical ends of each flagellomere contiguous all round (Arnold 1932: 67). Mandible short (Fig. 8A) with small tooth subapically on inner margin; anterior face flattened and polished. Occipital suture complete (Fig. 8E), its uppermost portion situated immediately or rather deeply below vertex crest.

Mesosoma. Pronotum shorter than mesoscutum at midline (Fig. 8E); collar situated deeply below level of dorsum (Fig. 8C, F, I); streptaulus present (Fig. 8E); declivity not short, flattened and vertical, its juncture with dorsum narrowly rounded; dorsum transversely convex and declivous, usually gradually narrowing anteriorly (Fig. 8B, E, H), truncate anteromedially, with numerous long pubescence and setae, its juncture with lateral vertical face rounded; L-shaped groove on lateral face sometime obscure.

Fig. 6. Females of *Paraclavelia* Haupt, 1930. **A–C, O–P**. *P. caffer* (Kohl, 1886) (#22) (NHMUK). **D–F**. *P. crudelis* (Smith, 1879) (#24) (NHMUK). **G–I**. *P. rhodesiensis* Arnold, 1832 (#33) (NHMUK). **J–M**. *P. marshalli* (Bingham, 1902) (#30) (NHMUK). **N**. *P. somalica* Arnold, 1932, holotype (#36) (NHMUK). **A, D, G, J**. Head, anterior view. **B, E, H, K**. Head and anterior part of mesosoma, dorsal view. **C, F, I, L, N**. Head and anterior part of mesosoma, lateral view. **M**. Apical part of left fore tibia, mesial view, arrow indicates apicomesial spine on fore tibia. **O**. Right scape, mesial view, arrow indicates longitudinal carina on mesial face of scape. **P**. Same, dorsolateral view. Numbers in parentheses after species names are specimen numbers in Supp. file 1. Scale bars: A–L = 1 mm; M = 0.2 mm; O–P = 0.5 mm. (N lacks a scale bar because of unavailable measurement data due to lack of access to the holotype.)

Mesoscutum with parapsides narrowly reflexed posterolaterally. Disc of scutellum triangular, slightly raised above level of mesoscutum. Metanotum declivous. Metapostnotum longer than in female. Propodeum densely punctate, sometimes finely and transversely rugulose or minutely reticulate-rugulose, and covered with long pubescence; dorsum much longer than declivity, parallel-sided, gradually sloping posteriorly; declivity not delimited from dorsum.

Wings. HW cross-vein cu-a originating usually at or distal to separation of vein *M+CuA*, confluent with vein *A*, forming long smooth arc.

Legs. Apical margin of fore tibia without short, stout, decurved spine mesally. Fore femur slender (Fig. 8F, I), thinner than mid femur. Fore tarsomeres 2–4 combined as long as or shorter than fore tarsomere 1. Fore, mid and hind orbiculae similar to those of female, or hind orbicula remarkably small, its pecten indistinct. Fore and mid tarsal claws bifid; hind tarsal claw bifid or edentate, rectangularly bent subapically, and both claws parallel to each other or slightly divergent .

Metasoma. T1 not petiolate, gradually narrowing anteriorly. S2 without transverse groove. S6 with small lateral hook posterolaterally. Subgenital plate comparatively large, not compressed laterally.

Distribution

Africa (Afrotropical Region) and the Arabian Peninsula (Oman).

Paraclavelia arabiae Shimizu sp. nov.
urn:lsid:zoobank.org:act:C089DF38-E7E2-48D2-90BF-7549FF207C63
Fig. 7

Diagnosis

Female

Body and legs predominantly black (Fig. 7A); clypeus (Fig. 7D), antenna (Fig. 7A, E), mandible and legs except coxae (Fig. 7G) reddish brown; T6 and S6 (Fig. 7I) orange brown. FW bifasciate (Fig. 7C), outer fascia very broad. L-shaped groove on pronotum laterally obsolete (Fig. 7H). FW discal cell 1 without irregularity in membrane basally. T1–3 with posterior silvery bands of short, dense, appressed pubescence (Fig. 7A). Scape without longitudinal carina on its mesal face. T1 barely petiolate. S2 with transverse groove fine and almost obsolete (Fig. 7I).

Etymology

The species name is derived from its locality, the Arabian Peninsula.

Type material

Holotype

OMAN • ♀; "OMAN Ayn Razat 9.iv.85 H. Hamer" [in handwriting]; NHMUK.

Description

Holotype female

Measurements. Length: body 9.4 mm; FW 5.9 mm.

Colouration. Body black (Fig. 7A). Following reddish brown: lower frons (Fig. 7D), including supra-antennal area below, clypeus, malar space, lower gena, antenna, mandible, pronotum anteriorly (Fig. 7B, E) and lateroventrally (Fig. 7H), apical margins of T3–5 and of S1–5 (Fig. 7I), and all legs excluding coxae (dark brown) (Fig. 7G–H). Labrum, labio-maxillary complex, T6 and S6 orange brown. FW

Fig. 7. *Paraclavelia arabiae* Shimizu sp. nov., holotype, ♀ (NHMUK). **A**. Whole body, dorsal view. **B**. Head and mesosoma, dorsal view. **C**. Right wings. **D**. Head, anterior view. **E**. Head and pronotum, dorsal view. **F**. Apical part of right fore tibia, mesial view, arrow indicates apicomesial spine on fore tibia. **G**. Whole body, lateral view. **H**. Head and mesosoma, lateral view. **I**. Metasoma, ventrolateral view. **J**. Right hind tibia, dorsal view. Scale bars: A–E, G–J = 1 mm; F = 0.5 mm.

transparent with two fasciae (Fig. 7C): inner fascia occupying on second abscissae of vein *M* and vein *Rs* (basal vein) and cross-vein *cu-a*, and apical half of clavus; outer fascia very broad, occupying marginal cell, SMC1 apically, SMCs 2 and 3, basal half of SMC4, distal ¾ of discal cell 2, discal cell 3, and subdiscal cell 2 except basally; outer wing margin slightly infuscate. HW transparent, broadly infuscate apical to cross-vein *rs-m*.

Integument. Head and pro-, meso- and metanota with minute dense punctures (sparser on clypeus). Pronotal collar with several transverse rugulae (Fig. 7E). Mesopleuron posteriorly and metapleuron finely and obliquely rugulose. Side of metanotum with several oblique striae. Metapostnotum with few undulating striae, lacking median depression. Propodeum with transverse rugulae (Fig. 7B), those becoming stronger posteriorly, lacking median groove. Most of integument with short, appressed silvery pubescence, dense on lower frons, clypeus basally, gena ventrally, thorax laterally and ventrally, disc of metanotum, propodeum posterolaterally, coxae, posterior third of T1, posterior fourth of T2, and T3 narrowly along posterior margin (Fig. 7A). Setae on body scarce; frons along inner orbit, labrum apically, mandible, propleuron, T6 and S2–6 with sparse setae.

Head. 0.96 × as broad as high. Vertex strongly convex above level of eye tops (Fig. 7D). Vertex and frons weakly polished. MID 0.65 × TFD. Frons with median sulcus short and faint only below. Antennocular line slightly inclined from antennal base to eye (Fig. 7E). Inner orbits subparallel but barely emarginate above middle (Fig. 7D). UID:MID:LID = 8.5:10:9.7. POD:OOD = 1:0.63. Clypeus 1.5 × as broad as long; anterior rim not depressed but smooth and polished; apical margin slightly convex. OOcD /POD = 0.94. Gena, in dorsal view, gradually narrowing posteriorly (Fig. 7E), in profile, 0.77 × as broad as eye, abruptly narrowing above (Fig. 7H). Scape flattened mesally (Fig. 7E). Scape:pedicel:fl1:fl2 = 12:3.2:10:8.5. Fl1 3.1 × as long as broad, 0.49 × UID.

Mesosoma. Pronotum with posterior margin subangulate medially (Fig. 7B). Metapostnotum 0.25 × as long as metanotum at midline, its posterior margin almost straight medially. Propodeum in dorsal view 1.1 × as broad as long; dorsum barely convex laterally in dorsal view (Fig. 7B), in profile roundly merging into declivity (Fig. 7H).

Legs. Mid tibia with few minute spines laterally. Hind tibia almost lacking spines dorsally (Fig. 7J) with spur 0.46 × as long as hind tarsomere 1.

Wings (Fig. 7C). FW marginal cell from wing tip by 0.65 × its own length. SMC2:SMC3 = 1:1.1 on vein *M*, 1:1.5 on vein *Rs*. SMC2 narrowed on vein *Rs* by 0.57 × its length on vein *M*, receiving cross-vein *1m-cu* at basal 0.45. SMC3 narrowed on vein *Rs* by 0.75 × its length on vein *M*, receiving cross-vein *2m-cu* at basal 0.53. Cross-veins *2rs-m* and *3rs-m* gently curved outwardly. Cross-vein *cu-a* slightly apical to point of separation of vein *M+CuA*, oblique but abruptly recurved near its terminal. Cross-vein *2m-cu* strongly curved near its origin. HW cross-vein *cu-a* originating at point of separation of vein *M+CuA*.

Metasoma. S6 somewhat compressed laterally with median carina only apically (Fig. 7I).

Male

Unknown.

Distribution

The southeastern Arabian Peninsula (Oman).

Key to the genera Ctenocerus Dahlbom, 1845 and Paraclavelia Haupt, 1930

(The key is not specific to the Asian species but applies to the African species.)

Females

1. Lower frons lateral to and ventral to antennal sockets deeply depressed, leaving frontal bridge (Figs 1A, F, J, 2E, G, I, 3D, arrow) this being continuous to clypeus on same plane; clypeus deeply and broadly depressed only basilaterally; fore femur swollen, thicker than mid femur (Figs 2A, F, H, J, 3H) ..... ***Ctenocerus*** Dahlbom, 1845
– Frontal bridge absent, i.e., lower frons deeply depressed lateral to antennal sockets and ventral to them across its whole width (Figs 6A, D, G, J, 7D); clypeus with deep depression across whole width of its base, depression being broader laterally than medially; fore femur not swollen (Figs 6F, I, 7H) ..... ***Paraclavelia*** Haupt, 1930

Males

1. Supra-antennal area of frons not or slightly produced anteriorly (Figs 4C, F, I, 5G); lower frons with frontal bridge (Figs 4A, D, G, 5D, arrow), this being sometimes narrow and slightly depressed below level of supra-antennal area unlike in female ..... ***Ctenocerus*** Dahlbom, 1845
– Supra-antennal area of frons produced into frontal ledge overhanging antennal radicle (Fig. 8C, F, I); frontal bridge absent (Fig. 8A, D, G), i.e., lowermost frons across its whole width depressed much below level of supra-antennal area and slightly below level of clypeus ... ***Paraclavelia*** Haupt, 1930

Based on these key characters, at least *Ct. decipiens*, which is known only from a male from South Africa, should be transferred to *Paraclavelia*. Examination of the males of this species has revealed that they bear the characteristics of *Paraclavelia*, i.e., the frons protruded over the antennal sockets (Fig. 8F) and lacking the frontal bridge (Fig. 8D), although the flagellum is biramous (Figs 8D–F, K). Moreover, the male of *Ct. srilankae* sp. nov. has the crenulate flagellum (Fig. 5H). Thus, the males of both *Ctenocerus* and *Paraclavelia* may have the flagellum uni- or biramous, or crenulate, as discussed below, invalidating this character as diagnostic for the genera as proposed by Arnold (1932).

Here, we propose the following nomenclatural change:

Paraclavelia decipiens (Arnold, 1932) **comb. nov.**

Clavelia decipiens Arnold, 1932: 58, fig. 9.

Discussion

Difficulty of the taxonomy of Ctenocerinae at generic level

Arnold (1932) revised 11 genera of the African Ctenocerinae, which he classified into two tribes, Claveliini Arnold, 1932 (= Ctenocerini) and Psilotelini Arnold, 1932. Afterward, Arnold (1934: 399) rendered the monotypic genus *Stenoclavelia* Arnold, 1932 (Ctenocerini) invalid, because he found that *S. mirabilis* Arnold, 1932 belonged to *Cryptocheilus* Panzer, 1806. Furthermore, he created several new taxa of Cternocerinae, i.e., *Trichosalius*, *Paratrichosalius* Arnold, 1934 (as a subgenus of *Trichosalius*), *Masisia* Arnold, 1934, and *Hadropompilu***s** Arnold, 1934 (Arnold 1934); *Pezopompilus* Arnold, 1952 (Arnold 1952); and *Parapsilotelus* Arnold, 1960 (Arnold 1960). Here, we treat only the Claveliini consisting of three genera, *Ctenocerus* (= *Clavelia* in the sense of Arnold (1932)), *Paraclavelia*, and *Parapompilus* Smith, 1855, because they are considered to be closely related, at least morphologically.

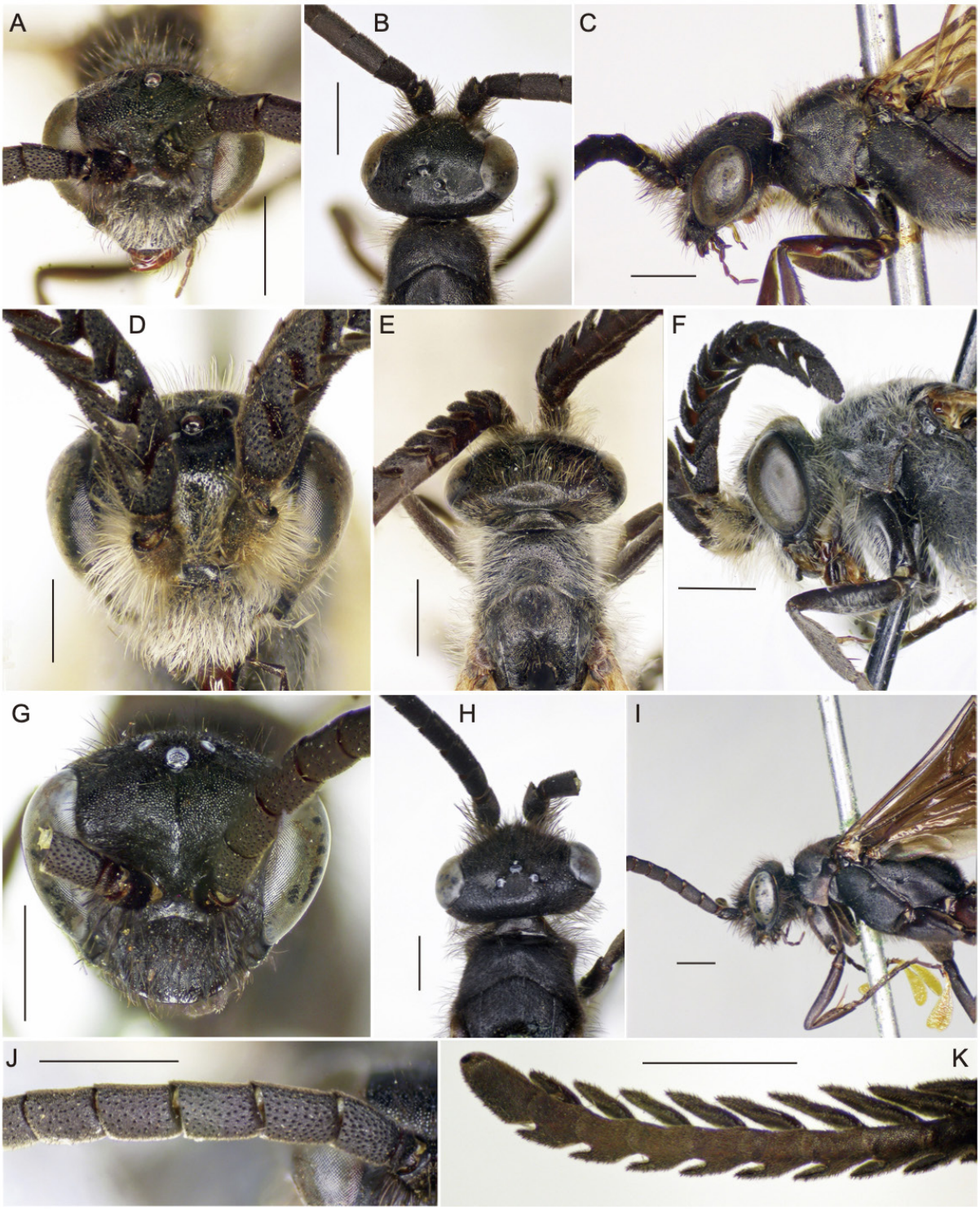


Fig. 8. Males of *Paraclavelia* Haupt, 1930. **A–C, J**. *P. katbergensis* Arnold, 1948 (#29) (NHMUK). **D–F, K**. *P. decipience* (Arnold, 1932) (#28) (UMUT). **G–I**. *P. crudelis* (Smith, 1879) (#26) (NHMUK). **A, D, G**. Head, anterior view. **B, E, H**. Head and anterior part of mesosoma, dorsal view. **C, F, I**. Head and mesosoma, lateral view. **J**. Right antenna, anterior view. **K**. Right flagellum, dorsal view. Numbers in parentheses after species names are specimen numbers in Supp. file 1. Scale bars = 1 mm.

Arnold (1932) described 14 species of *Clavelia*. He later synonymized *Clavelia* with *Ctenocerus*, and, therefore, establishing *Ctenocerus* as the senior synonym of *Clavelia* (Arnold 1934). As a result, Arnold (1934: 386) altered the subfamily name from Claveliinae to Ctenocerinae (see also Day 1981: 6).

At the Natural History Museum, London, AS compared female specimens identified as *Ct. klugi* (Fig. 1F–I) with one of the female syntype of *Euclavelia fasciatus* Arnold, 1932 (type species of *Euclavelia*) (Figs 1J–M, 2A–D) and concluded that *Euclavelia* should be regarded as a synonym of *Ctenocerus*, because both species share almost all diagnostic and generic characters of *Ctenocerus* listed above, although in *Ct. klugi*, T1 is not petiolate nor parallel-sided anteriorly. Arnold (1932) stated that the characters of *Pseudopedinaspis* Brauns, 1906 applied to *Euclavelia*, except that the wings of *Pseudopedinaspis* were remarkably reduced to small adnate flaps. As such, it may be better to treat *Pseudopedinaspis* also as a junior synonym for *Ctenocerus*. This genus, however, bears great modification in the mesosomal structure in accordance with the reduction of the wings. Thus, we leave the problem of the taxonomic position of *Pseudopedinaspis* to future studies.

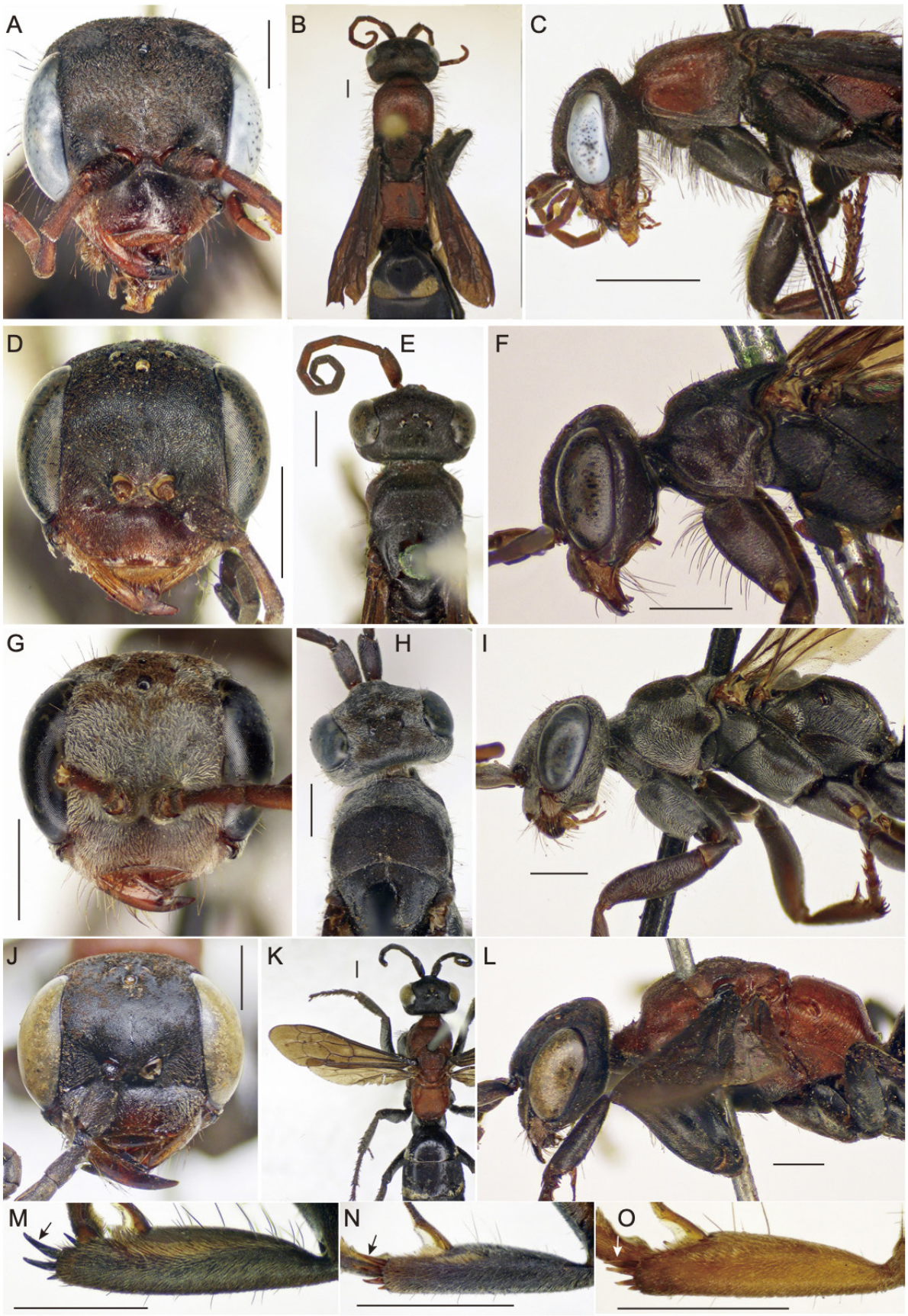
According to Arnold (1932), females of *Paraclavelia* are distinguishable from *Ctenocerus* by the clypeus being deeply depressed across the whole width of its base; hence, the lack of a frontal bridge. However, his distinction between the genera seems to be wrong in the males from the following situation: he succeeded in associating conspecific females and males in one species of *Ctenocerus* (*Ct. ramosus*) and two species of *Paraclavelia* (*Parac. crudelis* and *Parac. caffer*) (Arnold 1932); based on these associations, he considered that the male antenna of *Ctenocerus* was uni- or biramous, while that of *Paraclavelia* was crenulate, and used these different conditions to separate the males into the two genera. As stated above, however, in this study we conclude that these antennal conditions occur in both genera, which invalidates the characters Arnold (1932) used for genus-level recognition.

A further problem in the genera placed in Ctenocerini lies in the range and definition of *Parapompilus*. The taxonomic history of this genus is complicated. Arnold (1932) gave the following synonymy for *Parapompilus*:

Micropteryx Lepeletier, 1845 (type species: *Sphex brevipennis* Fabricius, 1793)
Lissocnemis Kohl, 1906 (type species: *Salius* (*Lissocnemis*) *irrasus* Kohl, 1906)
Cryptosalius Turner, 1917 (type species: *Pseudagenia rava* Bingham, 1896)
Dasyclavelia Haupt, 1929 (type species: *Pompilus namanus* Bischoff, 1913)

Lucas (1851: LXXV) created the genus *Clavelia* (type species: *Cl. pompiliformis* Lucas, 1851) based only on the holotype male from Boghar, Algeria (see also Lucas 1852: 425, pl. 8, ii). Smith (1855) proposed the name *Parapompilus* as a substitute for *Micropteryx* (see Arnold 1932: 89; Grünwaldt 1933), because *Micropteryx* was a pre-occupied name (see also Pate 1946). Pate (1946) proposed the genus *Marimba* Pate, 1946 as a new name for the African *Cryptosalius* in the sense of Arnold (1932), not of Turner (1917). According to Schultz (1905), Grünwaldt (1933), Day (pers. com.), and Wahis (pers. com.), *Cl. pompiliformis* is conspecific with *M. brevipennis* based only on the holotype male from Barbaria, Algeria. There is, thus, a great possibility that *Clavelia* becomes a senior synonym for *Parapompilus*. We, however, leave the name *Parapompilus* here because we have not examined types of the above taxa.

Parapompilus sensu Arnold (1932) has the head and pronotum less modified than do *Ctenocerus* and *Paraclavelia* in the female: the lower frons is more or less protruding anteriorly into a frontal ledge overhanging the antennal sockets and receding immediately below them (Fig. 9C, F, I, L); the clypeus is not flattened but convex (Fig. 9A, D, G, J) and is usually as long as LID (Fig. 9D, G, J), which feature is practically applicable to the male; the scape is not or barely curved outward (Fig. 9B, E, H, K); and the pronotal dorsum is not in a low position, i.e., the dorsum lying much above the level of the pronotal


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O

collar through the distinct declivity (Fig. 9F, I, L) (in *Parap. bicolor* and *Parap. brevipennis*, the dorsum lies only slightly above the level of the collar (Fig. 9C)). The genus is, however, diverse in the head and appendage structures: the clypeus is narrower than LID (e.g., *Parap. bicolor*, *Parap. brevipennis* (Fig. 9A)) or as broad as LID (e.g., *Parap. argenteus* (Fig. 9G), *Parap. bulawayoensis*, *Parap. infernalis*, *Parap. iridipennis* (Fig. 9D), *Parap. rufithrox* (Fig. 9J), *Parap. zuluensis*); the pronotum is longer than the mesoscutum (e.g., *Parap. argenteus* (Fig. 9H), *Parap. bicolor*, *Parap. brevipennis* (Fig. 9B), *Parap. bulawayoensis*, *Parap. rufithrox* (Fig. 9K)) or not (e.g., *Parap. infernalis*, *Parap. iridipennis* (Fig. 9E), *Parap. zuluensis*); the wings are strongly reduced (tip of FW not extending posterior margin of T2) (e.g., *Parap. bicolor*, *Parap. brevipennis* (Fig. 9B)) or not so reduced (e.g., *Parap. argenteus*, *Parap. bulawayoensis*, *Parap. infernalis*, *Parap. iridipennis*, *Parap. rufithrox* (Fig. 9K), *Parap. zuluensis*); two or three long, stout spines on the fore tibia apicomesally curved in *Parap. bicolor* (Fig. 9M) and *Parap. brevipennis* as in *Ctenocerus* and *Paraclavelia*, curved only apically in *Parap. argenteus* and *Parap. bulawayoensis* (Fig. 9N), and not curved in *Parap. infernalis*, *Parap. iridippenis* and *Parap. zuluensis* (Fig. 9O); and the fore femur is swollen (thicker than mid femur) (e.g., *Parap. argenteus* (Fig. 9I), *Parap. bicolor*, *Parap. brevipennis* (Fig. 9C), *Parap. bulawayoensis*, *Parap. rufithorax* (Fig. 9L)) or not (as thick as or thinner than mid femur) (e.g., *Parap. infernalis*, *Parap. irridipennis*, *Parap. zuluensis*). To revise this group, further studies, including the examination of the types (mostly deposited in the collections of South African Museum, Cape Town, South Africa and the Natural History Museum, London, UK) and molecular analyses, are needed.

Convergent evolution of morphological modifications in trap-door spider-preying Pompilidae

Ctenocerus and *Paraclavelia* share the following morphological features that seem to be associated with preying on trap-door spiders, as discussed below: (1) the vertex is raised far beyond the postocellar line (Figs 1F, J, 2G, I, 3D, 6A, D, G, J, 7D); (2) the frons is broad (half of MID much broader than eye); (3) the lower frons is deeply depressed lateral to and ventral to the antennal sockets, the depressions accommodating the antennal scape; (4) the clypeus is narrower than LID, lamelliform, usually truncate apically, its surface flat or slightly convex with a basal or basilateral depressions that are continuous to the lower frontal depression; (5) the scape is curved outward and concave on its lateral face (Figs 1L, 2B, 3E, 6B, E, K, P, 7E), which may fit in the frontal depression; (6) the pronotum is elongate (usually longer than the mesoscutum at the midline) (Figs 1K–L, 3A, 7B), flattened above and in a low position, i.e., the dorsum lying only slightly above the level of the collar (Figs 1C, H, 2A, F, H, J, 3H, 6C, F, I, L, 7H); and (7) the apical margin of the fore tibia has a stout curved spine mesally (Figs 2C, 3F, 6M, 7F).

The modifications in head and pronotal structures of *Ctenocerus* and *Paraclavelia* are very similar to those of the New World genus *Psorthaspis* (Pompilinae) (especially to *Ctenocerus* in having the frontal bridge). They share the above features 1–6 (Fig. 10A–D), although *Psorthaspis* does not have a stout curved spine on the fore tibia apicomesally (Fig. 10E). It is thus not surprising that Bradley (1944) placed *Psorthaspis* in Ctenocerini, Pompilinae [!].

Nothing is known about the biology of Ctenocerinae, except that *Paraclavelia caffer* was taken from the nest of a trapdoor spider, *Stasimopus robertsi* Hewitt, 1910 (Ctenizidae) (Arnold 1932). In contrast, the

Fig. 9 (previous page). Females of *Parapompilus* Smith, 1855. **A–C**. *P. brevipennis* (Fabricius, 1793) (#40) (NHMUK). **D–F**. *P. iridipennis* (Cameron, 1904) (#45) (NHMUK). **G–I**. *P. argenteus* Arnold, 1932 (#37) (NHMUK). **J–L**. *P. rufithorax* Arnold, 1932 (#47) (NHMUK). **M**. *P. bicolor* (Smith, 1851) (#38) (NHMUK). **N**. *P. bulawayoensis* (Bischoff, 1913) (#42) (NHMUK). **O**. *P. zuluensis* Arnold, 1932 (#49) (NHMUK). **A, D, G, J**. Head, anterior view. **B, K**. Head, mesosoma and anterior part of metasoma, dorsal view. **C, F, I, L**. Head and mesosoma, lateral view. **E, H**. Head and anterior part of mesosoma, dorsal view. **M–O**. Left fore tibia, mesial view, arrow indicates apicomesial spine on fore tibia. Numbers in parentheses after species names are specimen numbers in Supp. file 1. Scale bars = 1 mm.

North American species *Psorthaspis planata* is well known to behave as an ectoparasitoid of the trapdoor spider *Bothriocyrtum californicum* (O. Pickard-Cambridge, 1874), Ctenizidae (Jenks 1938). Behavioral observations by Jenks (1938) are summarized here. After detection of the burrow, the female wasp pounced on the trapdoor, raised it with her strong claws and supported it on her dorsum (Jenks 1938: 812, above figure; Shimizu *et al.* 2021: fig. 11) as she slipped through into the burrow to attack the spider. When unable to lift the flap sealed tightly with silk and mud, the wasp tore a hole in it with her powerful mandibles. In a 'furious rough-and-tumble fight', the wasp stung the spider into paralysis, laid an egg on the dorsum of the spider's abdomen posteromedially in a longitudinal position, and left the burrow without closing it.

Based on similarities in morphology with *Psorthaspis*, it is presumed that species of both *Paraclavelia* and *Ctenocerus* are also ectoparasitoids of trapdoor spiders living in subterranean burrows with lids. Arnold (1932: 48) thought similarly. The anteriorly flattened head of these genera, including the lamelliform clypeus and mandible, likely play an important role when the wasp locates and pries open the host-burrow lid as a lever and supports it. The elongate and dorsally flattened pronotum also must be employed in lifting and supporting the lid (Jenks 1938: 812, above figure; Shimizu *et al.* 2021: fig. 11). The stout curved spine of the fore tibia is suspected to function as a hook when the wasp lifts the trapdoor.

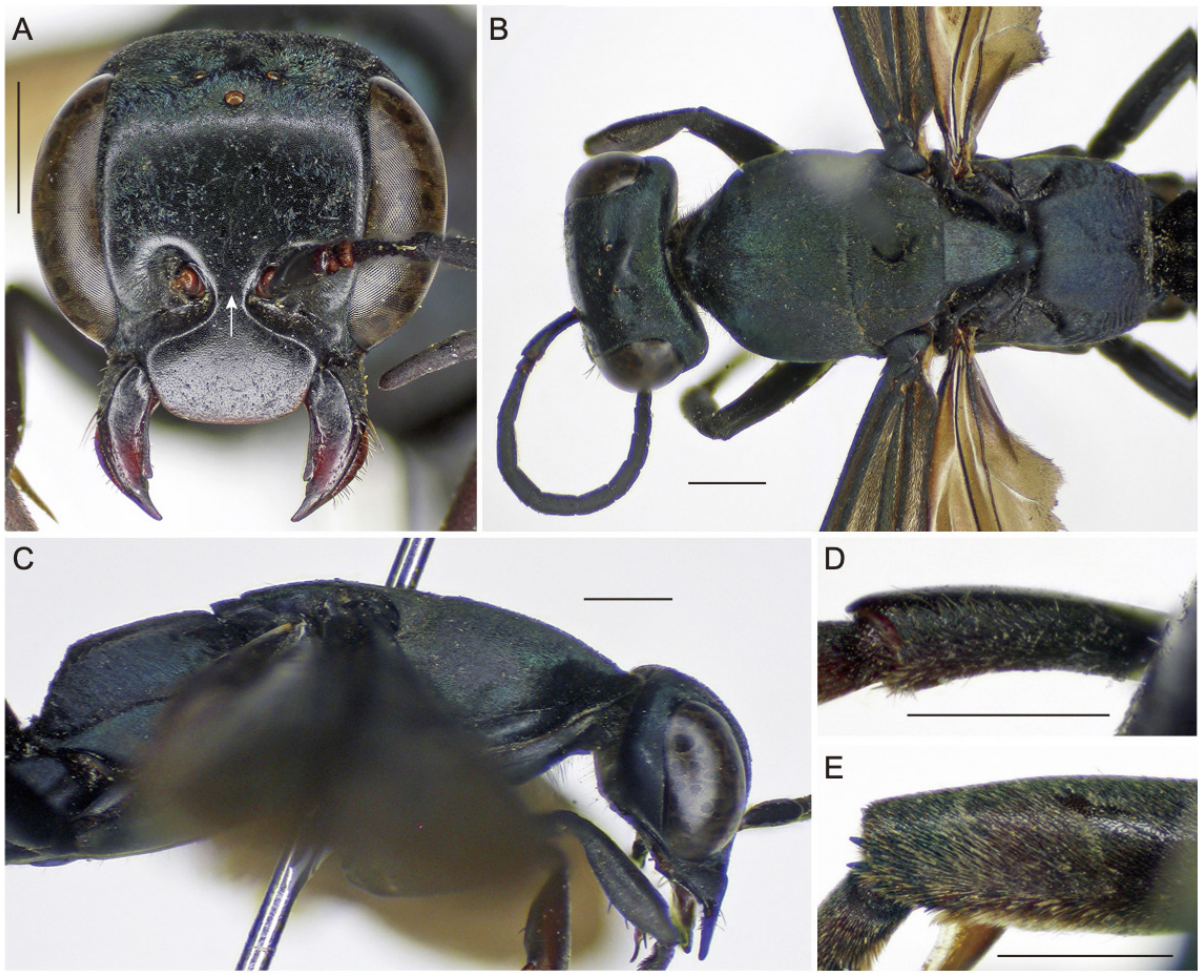


Fig. 10. Female of *Psorthaspis planata* (Fox, 1892) (#53) (UMUT). **A**. Head, anterior view, arrow indicates frontal bridge. **B**. Head and mesosoma, dorsal view. **C**. Head and mesosoma, lateral view. **D**. Left scape, dorsal view. **E**. Apical part of right fore tibia, mesial view. A number in parentheses after a species name is a specimen number in Supp. file 1. Scale bars: A–C = 1 mm; D–E = 0.5 mm.

Fig. 11. Various taxa of the *Entomobora*-morphotype. **A–B**. *Entomobora crassitarsis* (Costa, 1887) (Pompilinae) (#56) (UMUT). **C**. *Austroclavelia venator* Evans, 1972, holotype (Pepsinae) (AUSTRALIA: Morialta, Mt Lofty Hills, South Australia; ANIC). **D–E**. *Maurillus australis* Smith, 1855, holotype (Pepsinae) (#59) (NHMUK). **F–G**. *Hypoferreola* sp. (probably "*Entypus*" *cephalotes* Saussure, 1867) (Pepsinae) (#58) (NHMUK), arrow in F indicates frontal bridge. **H–I**. *Ctenostegus monstrosus* Evans, 1976 (Pompilinae) (#54) (NHMUK). **J–K**. *C. tenellus* (Turner, 1910) (Pompilinae) (#55) (NHMUK), arrow in J indicates frontal bridge. **L–M**. *Pedinpompilus* (*Pedinpompilus*) *salvatoris* (Kohl, 1913) (Pompilinae) (#60) (NHMUK). **A, C–D, F, H, J, L**. Head, anterior view. **B, E, G, I, K, M**. Head and anterior part of mesosoma, lateral view. Numbers in parentheses after species names are specimen numbers in Supp. file 1. (C–E, Shimizu *et al*. 2021.) Scale bars = 1 mm.

Based on the molecular phylogenetic trees constructed by Waichert *et al.* (2015: fig. 1) and by Rodriguez *et al.* (2016), *Ctenocerus* and *Paraclavelia* are the earliest diverging clade of Pompilidae, while *Psorthaspis* is placed in the large Pompilinae clade. Thus, the modified head and pronotal structures shared between Ctenocerinae (*Ctenocerus* and *Paraclavelia*) and *Psorthaspis* appear to have evolved independently through convergence. When the wasps attempt to open burrow lids, the spider hooks its first pair of legs onto the edge of the flap opposite its hinge and maintains its closure (Janvier 1930). Thus, the wasps face physical resistance before opening the burrow lid; hence the lid opening is of critical importance for the wasps (Iwata 1976; Shimizu *et al.* 2021). This seems to have resulted in a convergent evolution of the head and pronotal specialization in the parasitoid Pompilidae preying on trapdoor spiders (Shimizu *et al.* 2021). In fact, another pompiline genus, *Entomobora*, which is known to parasitize trapdoor spiders of the genera *Nemesia* Audouin, 1826 (Nemesiidae), *Ummidia* Thorell, 1875 (Halonoproctidae) and *Cteniza* Latreille, 1829 (Ctenizidae) (Ferton 1897, 1901, 1905; Gros 1983, 2004; see also Shimizu *et al.* 2021), bears the highly modified head and pronotum very similar to those of *Paraclavelia*, *Ctenocerus*, and *Psorthaspis*. The characters shared by *Entomobora* and the three genera are: (1) the clypeus narrower than LID, flattened with a basal or basilateral depressions that are continuous to the lower frontal depression (Fig. 11A); (2) the frons broad (half of MID broader than eye); (3) the lower frons deeply depressed lateral to and ventral to the antennal sockets; and (4) the scape curved outward, and flattened or concave laterally (Fig. 11B). The pronotal structure of *Entomobora* is, however, different from that of *Paraclavelia*, *Ctenocerus* and *Psorthaspis*: the dorsum is truncate anteriorly with a deep, almost vertical declivity; hence, the neck region lies deeply below the level of the pronotal dorsum (Fig. 11B) (Shimizu *et al*. 2021). Such *Entomobora*-like modifications (the *Entomobora*-morphotype) is also found in the Australian *Austroclavelia* Evans, 1972 (Fig. 11C) and *Maurillus* Smith, 1855 (Fig. 11D–E), and the South American *Hypoferreola* Ashmead, 1902 (Fig. 11F–G) (*Lepidocnemis* Haupt, 1930 and *Abernessia* Arlé, 1947 are probably synonyms of *Hypoferreola*, all belonging to Pepsinae), the Australian *Ctenostegus tenellus* species group Evans, 1976 of *Ctenostegus* Haupt, 1930 (e.g., *C. monstrosus* (Fig. 11H–I), *C. tenellus* (Fig. 11J–K)), and the European *Pedinpompilus* (*Pedinpompilus*) *salvatoris* (Fig. 11L–M) (all belonging to Pompilinae), although other subgenera of *Pedinpompilus* Wolf, 1961 do not bear any modifications in the head and pronotum (see Wolf 1961). (Note: the frontal bridge of *Hypoferreola* (Fig. 11F, arrow) and *Ctenostegus tenellus* (Fig. 11J, arrow) are the same as that of *Ctenocerus* and *Psorthaspis*.) The fact that strikingly similar morphological specializations are found in unrelated taxa of different subfamilies, genera, or subgenera implies that the selection pressure for attacking trapdoor spiders, which can potentially make lethal counterattacks on the wasps, has been intense, and, thus, such morphotypes of specialization may have evolved rapidly and independently. Based on our new molecular phylogenetic analysis, we are preparing a separate paper on the evolutionary processes of these morphotypes for the above taxa.

Distribution of *Ctenocerus* and *Paraclavelia* outside the African continent

We here reported two new species of *Ctenocerus* and *Paraclavelia* from Sri Lanka and Oman, respectively. The new localities indicate that these genera are not endemic to the African continent. The molecular phylogeny of the whole Pompilidae (Waichert *et al.* 2015) shows that the diversification of spider wasps (Pompilidae) took place in the Tertiary. If this data is correct, there is a high possibility that species of these genera dispersed from Africa to the Arabian Peninsula and South Asia after the Gondwanan breakup. We may expect new species of these genera in West to South Asia, including the Indian subcontinent.

Acknowledgements

Some of the ideas in this paper are based on the personal notes from the recently deceased Raymond Wahis and Michael C. Day. We sincerely acknowledge their contributions. We thank R. Wahis for the gift of variable specimens identified by himself and J. Rodriguez (CSIRO, Acton, Australia) for her

examination of the holotype of *Austroclavelia venator* and providing its photograph. We also thank curators at the NMNH for the examination of specimens, and A. Harris (Otago Museum, Dunedin, New Zealand) and two anonymous reviewers for critically reviewing the manuscript and making important suggestions. This research was supported by the Utah Agricultural Experiment Station, Utah State University, and approved as journal paper number 9567. This work was supported, in part, by a US National Science Foundation grant DEB-1555905.

Competing financial interests

The authors declare no competing financial interests.

References

Arnold G. 1932. The Psammocharidae of the Ethiopian region. Part 2. Subfamily Claveliinae, Haupt. *Annals of the Transvaal Museum* 15: 41–122.

Arnold G. 1934. The Psammocharidae of the Ethiopian region. Part 3. Subfamily Macromerinae Haupt. *Annals of the Transvaal Museum* 15: 283–399.

Arnold G. 1935. Scientific results of the Vernaylang Kalahari Expedition, March to September, 1930. Sphegidae and Psammocharidae. *Annals of the Transvaal Museum* 16 (4): 497–505.

Arnold G. 1952. New species of African Hymenoptera. No. 10. *Occasional Papers of the National Museum of Southern Rhodesia* 2 (17): 460–493.

Arnold G. 1960. Mission zoologique de l'I.R.S.A.C. en Afrique orientale. (P. Basilewsky et N. Leleup, 1957). XXXII. Hymenoptera Pompilidae. *Annales du Musée royal du Congo belge (Sér. 8°)* 81: 437–445.

Bradley J.C. 1944. A preliminary revision of the Pompilinae of the Americas exclusive of the tribe Pompilini (Hymenoptera: Pompilidae). *Transactions of the American Entomological Society* 70: 23–157.

Dahlbom A.G. 1845. *Hymenoptera Europaea praecipue Borealia ... per familias, genera, species et varietates disposita atque descripta. Vol. 3*. Lund.

Dahlbom A.G. 1856. Note sur le genre *Ctenocerus* Dahlb. *Annales de la Société entomologique de France* (3) 4: 345–348.

Day M.C. 1981. A revision of *Pompilus* Fabricius (Hymenoptera: Pompilidae), with further nomenclatural and biological considerations. *Bulletin of the British Museum (Natural History), Entomological Series* 42: 1–42.
Available from https://www.biodiversitylibrary.org/page/2247124 [accessed 16 Sep. 2022].

Day M.C. 1988. Spider wasps. Hymenoptera: Pompilidae. *Handbooks for the Identification of British Insects* 6 (4): 1–60.

Ferton C. 1897. Nouvelles observations sur l'instinct des pompilides (Hyménoptères). *Actes de la Société linnéenne de Bordeaux* 52: 101–132.

Ferton C. 1901. Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs avec la description de quelques espèces. *Annales de la Société entomologique de France* 70: 83–148.

Ferton C. 1905. Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs. *Annales de la Société entomologique de France* 74: 56–104.

Gros E. 1983. Note sur la biologie de quelques Pompilides (3e partie). *L'entomologiste* 39: 125–136.

Gros E. 2004. Notes comportementales sur 23 espèces de Pompilides de la faune franco-ibérique (Hymenoptera, Pompilidae). *Bulletin de la Société entomologique de France* 109: 387–408.
https://doi.org/10.3406/bsef.2004.16144

Grünwaldt W. 1933. Die Claveliinen-Gattung *Euclavelia* Arn. (Hym. Psamm.). *Entomologiske Meddelelser* 18: 252–258.

Hadley A. 2008. CombineZM.

Haupt H. 1929. Weiterer Ausbau meines Systems der Psammocharidae. Mit Beschreibung neuer Gattungen und Arten. *Mitteilungen aus dem Zoologischen Museum in Berlin* 15: 107–197.

Haupt H. 1930. Die Einordnung der mir bekannten Psammocharidae mit 2 Cubitalzellen in mein System. *Mitteilungen aus dem Zoologischen Museum in Berlin* 16: 673–797.

Iwata K. 1976. *Evolution of Instinct. Comparative Ethology of Hymenoptera.* Amerind Publishing, New Delhi. (English translation of "Honnô no Shinka", 1971).

Janvier H. (Claude-Joseph, F.) 1930. Recherches biologiques sur les prédateurs du Chili. *Annales des Sciences naturelles, Zoologie* 13: 235–354.

Jenks G.E. 1938. Marvels of metamorphosis. A scientific "G-man" pursues rare trapdoor spider parasites for three years with a spade and a candid camera. *The National Geographic Magazine* 74: 807–828.

Lucas H. 1851. (Communication.) *Bulletin de la Société entomologique de France* (2) 9: LXXV. Available from https://www.biodiversitylibrary.org/item/40400#page/805/mode/1up [accessed 16 Sep. 2022].

Lucas H. 1852. Description et figure d'un nouveau genre d'hyménoptères de la famille des fouisseurs, qui habite les possessions françaises du nord de l'Afrique. *Annales de la Société entomologique de France* (2) 10: 417–425.
Available from https://www.biodiversitylibrary.org/item/34969#page/423/mode/1up [accessed 16 Sep. 2022].

Pate V.S.L. 1946. The generic names of the spider wasps (Psammocharidae *olim* Pompilidae) and their type species (Hymenoptera: Aculeata). *Transactions of the American Entomological Society* 72: 65–137.

Rodriguez J., Pitts J.P., Florez J.A., Bond J.E. & von Dohlen C.D. 2016. Molecular phylogeny of Pompilinae (Hymenoptera: Pompilidae): evidence for rapid diversification and host shifts in spider wasps. *Molecular Phylogenetics and Evolution* 94: 55–64. https://doi.org/10.1016/j.ympev.2015.08.014

Schultz W.A. 1905. *Hymenopteren-Studien.* Wilhelm Engelmann, Leipzig.

Shimizu A., Pitts J.P., Rodriguez J., Wahis R. & Yoshimura J. 2021. Systematics and convergent evolution in three Australian genera of Pepsinae spider wasps (Hymenoptera: Pompilidae). *Austral Entomology* 50: 301–316. https://doi.org/10.1111/aen.12530

Smith F. 1851. *List of the British Animals in the Collection of the British Museum, Part 6, Hymenoptera Aculeata*. London. https://doi.org/10.5962/bhl.title.1582

Smith F. 1855. *Catalogue of Hymenopterous Insects in the Collection of the British Museum, Part 3. Mutillidae and Pompilidae.* London. https://doi.org/10.5962/bhl.title.20858

Turner R.E. 1917. New species of Hymenoptera in the British Museum. *Transactions of the Entomological Society of London* 50: 53–84. https://doi.org/10.1111/j.1365-2311.1917.tb01402.x

Waichert C., Rodriguez J., Wasbauer M.S., von Dohlen C.D. & Pitts J.P. 2015. Molecular phylogeny and systematics of spider wasps (Hymenoptera: Pompilidae): redefining subfamily boundaries and the origin of the family. *Zoological Journal of the Linnean Society* 175: 271–287. https://doi.org/10.1111/zoj.12272

Wolf H. 1961. Beitrag zur Kenntnis der Gattungen *Pedinaspis* Kohl 1885 und *Evagetes* Lepeletier 1845 (Hym. Pompilidae). *Opuscula Entomologica* 26: 67–90.

Manuscript received: 11 Mar. 2022
Manuscript accepted: 2 September 2022
Published on: 26 October 2022
Topic editor: Tony Robillard
Desk editor: Pepe Fernández

Supplementary file

Supp. file 1. List of the specimens examined, except for holotypes and paratypes of *Ctenocerus srilankae* Shimizu sp. nov. and *Paraclavelia arabiae* Shimizu sp. nov., with their label information and specimen depositories. Abbreviations of repositories: NHMUK = Natural History Museum, London, UK; UMUT = University Museum, The University of Tokyo, Tokyo, Japan.
https://doi.org/10.5852/ejt.2022.845.1957.7923