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COVER IMAGES

FRONT COVER: Figure 1 in Kavanaugh and Cueva-Dabkoski, p. 494: *Cyclosomus inustus* Andrewes, adult male feeding on a small fly (photograph reproduced from Wang et al. 2017 with permission of Liang-Jong Wang).

COVER DESIGN

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Ruellia eriocalyx (Acanthaceae, Ruellieae), a Pyrophytic Species from Central Brazil

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***Ruellia eriocalyx*, a name in use for a species in central Brazil was never validly published. We publish this name and provide a morphological description, photographs of specimens, ecological data, a preliminary conservation assessment, discussion of its putative relatives, and a list of materials studied.**

KEYWORDS: Valid publication, morphological description, conservation

With more than 350 species and a worldwide distribution, monophyletic *Ruellia* L. is one of the largest and most widely distributed genera of Acanthaceae (Tripp and Darbyshire 2017; Manzitto-Tripp et al. 2022). In the New World, species range from the north-central United States to Uruguay and central Argentina. During research for a sectional classification of the ca. 275 species of *Ruellia* in the New World (Manzitto-Tripp and Daniel, in prep.) numerous taxonomic and nomenclatural issues became evident; most of these are to be discussed and/or resolved in that study. Here, we effect publication of a name, *Ruellia eriocalyx*, which has been in wide usage for a Brazilian species but never validly published.

Glaziou (1911) published a new species of *Ruellia* from Brazil and provided a name, an indication of its status ("n. sp. ?"), a very brief description, a locality, a single collection (with collector and number), list of herbaria, months (presumably referring to collection and flowering time), and a common name. Unfortunately, his "protologue" does not effect valid publication of the name, "R. eriocalyx," that he used according to Article 38.2 (Ex. 3) of the International Code of Nomenclature for Algae, Fungi, and Plants (Turland et al. 2018). Glaziou's (1911) indication of "Herbacé, fl. bleues" does not qualify as a validating description or diagnosis because he employed this same brief description to multiple species of *Ruellia* (both new and previously described ones) in his account of plants from central Brazil. Nevertheless, this "name" has been used for a distinctive Brazilian species on both herbarium specimens and in scientific documents (e.g., Vilar 2009). Most attributions of the name have been cited as "Ruellia eriocalyx Glaziou ex Wasshausen." Wasshausen was aware that the name had not been validly published by Glaziou, and he annotated numerous specimens with this authorship; however, he did not publish the name (Dieter Wasshausen, pers. comm.).

Ruellia eriocalyx Glaziou ex T.F. Daniel, E. Tripp & C. Ezcurra

BRAZIL. **Goiás**: "Entre As Antas et Pedro Gardinha" (fide protologue), "dans les campos queimados" (fide holotype), 30 VIII 1894 (flr), *A. Glaziou 21877a* (holotype: P-image!; isotype: K!). Figure 1.

Perennial herbs to 10 cm tall from a stout vertical caudex, sometimes appearing subcaulescent; roots thick (but not fusiform-tuberous), numerous. Young stems ± densely pubescent with whitish trichomes. Leaves ± congested, green, sessile to subsessile, blades ovate-elliptic to elliptic to linear-elliptic to oblanceolate to obovate, 6–50 mm long, 1.5–13 mm wide, 1.8–11.6 (-17) times longer than wide, surfaces ± densely pubescent with whitish trichomes. Reduced dichasia (1-flowered), borne in axils of leaves, 1 per axil. Bracteoles absent or inconspicuous (if present, not observed). Flowers pedicellate, pedicels (2.5–) 7–42 mm long, pubescent like stems; calyces deeply 5-lobed, 11–23 mm long, externally pubescent like leaves, lobes subulate to lance-subulate, subequal in length; corolla purplish, infundibuliform, (30–) 40–56 mm long, externally pubescent, tube 23–36 mm long, narrow proximal portion subcylindric and ± abruptly expanded at apex into a ± broadly conical throat, 7–16 mm long, throat 14–27 mm long, longer than narrow proximal portion of tube, widest at mouth, limb 26–39 mm in diameter, lobes of limb 7–15 mm long, 7–16 mm wide; stamens included in corolla throat, longer pair 10–14 mm long, shorter pair 6.5–8.5 mm long; style 18–26 mm long, stigma lobes unequal, l lobe 1.5–2.6 mm long, other lobe 0.4–0.8 mm long. Capsules elliptic, 9–11 mm long.

Phenology. Flowering: June-November; fruiting: September.

Distribution and habitat. Central Brazil in the Distrito Federal and the state of Goiás. Plants occur in recently burned cerrado, campo sujo, campo limpo, and campo rupestre at elevations from 975 to 1110 meters.

Local name. "Flor do fogo" (*Glaziou 21887a*; Vilar 2009).

Uses. Vilar (2009) noted that plants are used locally for medicinal purposes.

Conservation. Based on the collections cited below, the species has an Extent of Occurrence (EOO) of 3,475 sq. km and an Area of Occupancy (AOO; 2 km cell width) of 36 sq. km (IUCN 2022). Within the EOO plants are known from three areas (i.e., three subpopulations): a nickel-mining region 8 to 15 km NNE of the city of Niquelandia in north-central Goiás, a region ca. 165 km to the south in the Distrito Federal (just south of Brasília), and a locale ca. 23 km west of Brasília in the western Distrito Federal. Plants in Goiás would appear to be threatened by the severe habitat destruction resulting from extensive mining activities there. Plants occurring south of Brasília in the Distrito Federal are known from three contiguous protected areas (Reserva Ecológica do IBGE, Fazenda Água Limpa [FAL], and Estação Ecológica do Jardim Botânico de Brasília). Most collections of the species have been made in these protected areas, and plants there would not appear to be under threat. The single collection (*Irwin & Soderstrom 5984*) made ca. 25 km west of these preserves is from along a major highway in a region comprising a mixture of native vegetation, agricultural lands, and housing/businesses. Natural areas in this region would appear to be threatened by anthropogenic development. Thus, there appear to be two locations (in Goiás and in the western portion of the Distrito Federal), each constituting a threatened subpopulation. The degree of isolation of the subpopulations is not known, but the population is potentially severely fragmented (condition a) because no collections have been made between them. Using IUCN (2022) criteria for Geographic Range (B), a preliminary conservation assessment of Endangered (EN) is proposed, based on either the EOO or the AOO, the number of locations (2), and observed/inferred/projected population decline based on the threats noted (B1a,b or B2a,b). A more thorough study of this species in the field and in Brazilian herbaria would likely increase both

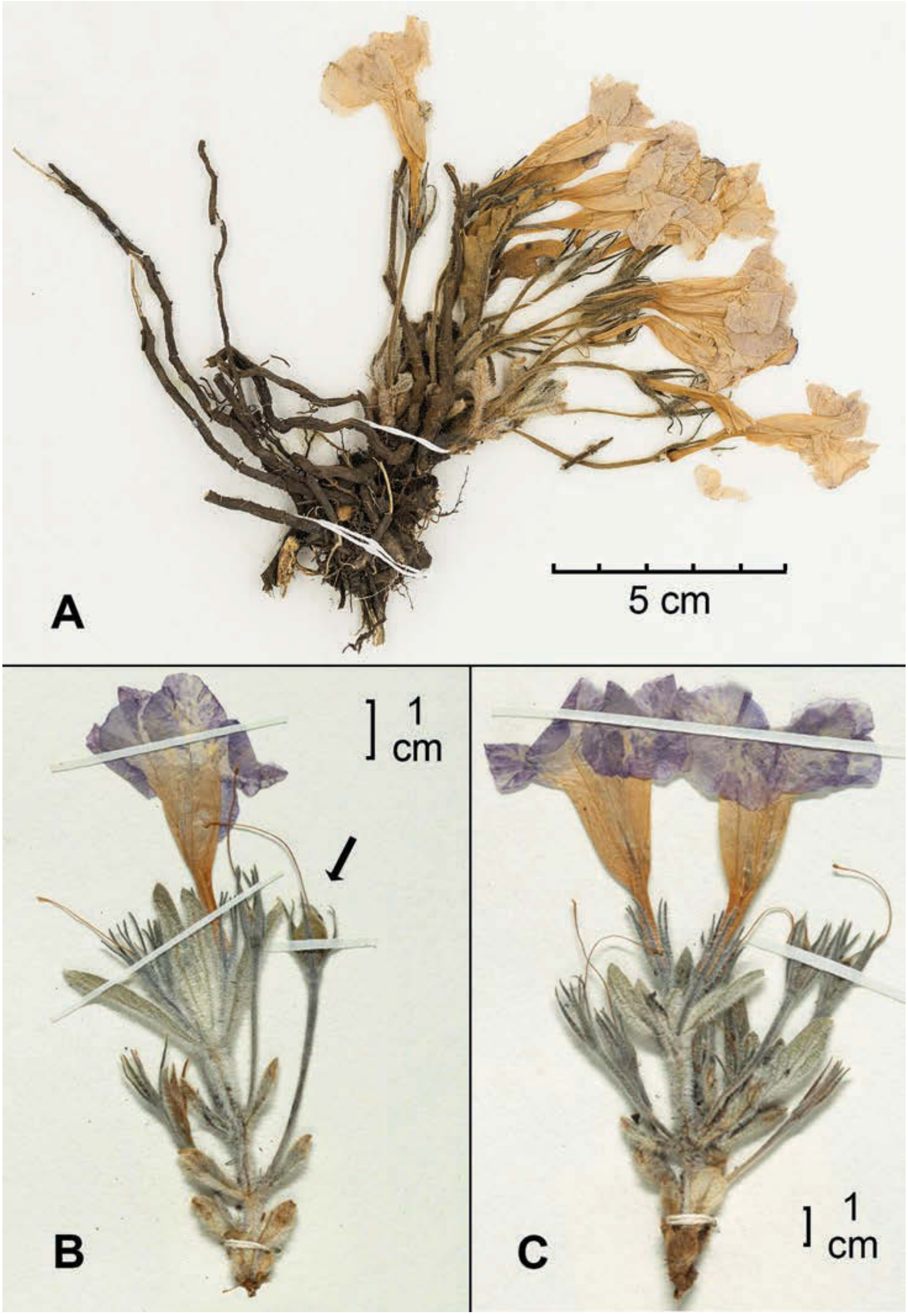

FIGURE 1. Plants of *Ruellia eriocalyx* from herbarium specimens. A. Nearly leafless flowering plant (post-fire), showing woody caudex, thick (but not tuberous) roots, and elongate pedicels, *Irwin et al. 8164* (NY), image courtesy of the C.V. Starr Virtual Herbarium (http://sweetgum.nybg.org/science/vh/), used with permission. B, C. Leafy plants (32 days following fire), showing pubescence, flowers, and capsule (at arrow), *Fonseca & Alvarenga 2054*, Catalog number 3398390, United States National Herbarium (US), Smithsonian Institution, used with permission.

the EOO and AOO, identify other threats, and provide additional data (e.g., declines/fluctuations of subpopulations) for advancing a more conclusive conservation assessment of this species.

Discussion

Leaves of plants occur at or near ground level and show considerable variation in the size and shape. Most collections cited below note that the plants appeared on burned ground following a recent fire (regrowing/flowering as soon as 10 days post-fire fide *Heringer et al. 5044*), sometimes become locally common, and usually occur in full sun. Thus, the plants appear to be pyrophytes. Whether they are passive or active pyrophytes or pyrophiles remains undetermined. Vilar (2009) noted that the species is sometimes confused with *R. brevicaulis* (Nees) Lindau. This name is illegitimate, being a later homonym of *R. brevicaulis* Baker (1885), a Malagasy species, now treated as a synonym of *Radamaea montana* Benth. in the Orobanchaceae. Plants identified as *R. brevicaulis* (Nees) Lindau are potentially conspecific with *R. dissitifolia* (Nees) Hiern. Indeed, in the protologue Nees (1847, and on his annotation of the type specimen of the basionym, *Dipteracanthus brevicaulis* Nees) indicated that *R. brevicaulis* was perhaps a variety of *R. dissitifolia*. Also, Ezcurra (1993) treated *Ruellia dissitifolia* Nees var. *humilior* Nees as synonym of *R. brevicaulis*. South American plants often identified as *R. brevicaulis* tend to be shorter in stature and more densely pubescent (hirsute) than those of *R. dissitifolia*. Variation in plant height and pubescence are somewhat variable throughout their respective geographic ranges, and at least some plants referred to *R. brevicaulis* are also pyrophytic and sympatric with *R. eriocalyx*. Additional morphological and molecular studies of plants treated as *R. brevicaulis* and *R. dissitifolia* should be helpful to determine if and how they differ, and at what taxonomic rank, if any, *R. brevicaulis* should be treated. The following key distinguishes *Ruellia eriocalyx* from its morphologically similar congener(s):

1a. Roots with fusiform-tuberous swellings; plants subcaulescent to caulescent, to 30 cm high; bracteoles present and conspicuous (more than 10 mm long); dichasia mostly 1-flowered, sessile (or borne on peduncles less than 5 mm long), flowers sessile; corollas pale blue, (35–) 50–70 mm long; capsules 12–15 mm long; central to southern Brazil, eastern Paraguay, and eastern Argentina . . . . *R. dissitifolia*/*R. brevicaulis* (Nees) Lindau

1b. Roots thickened but not with fusiform-tuberous swellings; plants subcaulescent, to 10 cm high; bracteoles absent (or inconspicuous; if present, not seen); flowers borne on pedicels (2.5–) 7–42 mm long; corollas purplish, (30–) 40–56 mm long; capsules 9-11 mm long; central Brazil (Distrito Federal, Goías) . . . . *R. eriocalyx*

Additional specimens examined

BRAZIL. Distrito Federal: Brasília, Reserva Ecológica do IBGE, 15°46'41"S, 047°53' 07"W, *M. Aparecida da Silva 6023* (IBGE-image); Brasília, Reserva Ecológica do IBGE, 15°57'03"S, 047°52'18"W, *M. Aparecida da Silva 5363-A* (IBGE-image), *5373* (IBGE-image); Brasília, Jardim Botânico de Brasília, área do Cristo Redentor, entre o córrego Tapera e Taperinha, ca. 15°22'S, 047°51'W, *M. Aparecida da Silva & D. Alvarenga 7383* (RB-image); área da UNE (FAL), *M. Azevedo & D. Alvarenga 936* (IBGE-image, US-image); Reserva Ecológica do IBGE, área de campo sujo próximo ao Córrego Taquara, 15°55'55"S, 047°53'51"W, *M. Fonseca & D. Alvarenga 2054* (IBGE-image, SPF-image, US-image); Fundação Zoobotânica, Brasília, *E. Heringer 8704* (NY-image, US-image); Bacia do Rio São Bartolomeu, *E. Heringer et al. 5044* (IBGE-image, K, MO-image); ca. 23 km SW of Brasília on road to Anápolis, [ca. 15°55'12.32"S, 048°09'54.53"W], *H. Irwin & T. Soderstrom 5984* (NY-image); immediately NW of Brasília, *H. Irwin et al. 8164* (NY, US-image); Brasília, Estação Ecológica do Jardim Botânico de Brasília, área do Cristo Redentor, 15°52'00"S, 047°51'00"W, *K. Moreira et al. 126* (HEPH-image); Reserva Ecológica do IBGE, *F. Oliveira & D. Alvarenga 130* (RB-image, US); Brasília, APA-Gama, Cabeca de Veado, Abrigo Cristo Redentor, 15°52'00"S, 047°51'00"W, *A. Ramos 902* (HEPH-image); Brasília, Jardim Botânico de Brasília (área de Cristo Redentor), 15°54'50"S, 047°52'52"W, *R. Rodrigues-da-Silva 652* (HEPH-image); Brasília, Estação Ecológica do Jardim, Botânico de Brasília, centro oeste, 15°54'58"S, 047°54'15"W, *R. Rodrigues-da-Silva 846* (HEPH-image); Estação Ecológica do Jardim, Botânico de Brasília, área do Cristo Redentor, Lago Sul, *A. Soares et al.* 292 (HEPH-image), *J. Vidal & L. Silva 169* (HEPH-image). Goiás; Município de Niquelândia, ca. 05 km da Mina de Níquel Tocantins, próximo ao povoado de Macedo, 14°23'32"S, 048°25'10"W, *J. Aparecida da Silva & C. Ferreira 3096* (RB-image, US); Municipio de Niquelândia, Macedo, próximo ao Clube dos Engenheiros, 14°21'34"S, 048°26'27"W, *M. Fonseca et al. 1118* (RB-image); Municipio de Niquelândia, Companhia de Niquel Tocantins, estrada à esquerda da mina de niquel, ca. 2 km da entrada, 14°20'37"S, 048°23' 57"W, *R. Mendonça et al. 3103* (IBGE-image).

ACKNOWLEDGMENTS

We are grateful to the following herbaria for permitting access to their collections and/or making images of their specimens available online: K, MO, NY, P, and US. We thank NY and US for permitting reproduction of some of their images, and the Herbário Virtual of Reflora Brasil for making images of collections from several Brazilian herbaria (e.g., HEPH, IBGE, SPF, IBGE) available for study. We are also most grateful for the careful reviews of C. Anderson and D. Wasshausen.

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***NOTE:** Glaziou's entire publication cited above, published between 1905 and 1913, became listed as a suppressed work under Article 34 (Turland et al. 2018), rendering all new names therein not validly published.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Medusapyga LaBonte and Maddison, a New Genus of Anillini (Coleoptera: Carabidae: Trechinae) from the Pacific Northwest of the United States

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A new genus of anilline carabid beetle, *Medusapyga* LaBonte and Maddison, is described from the Pacific Northwest. Two new species, herein described, comprise this genus. Members of the genus are distinguished from other described North American Anillini by: an extensive field of long bifurcate setae on each laterotergite IX of females, a distinct ventrobasal spine on the male profemur, and two strongly asymmetrically dilated and ventrally setose basal protarsomeres in males. Bifurcate setae on the laterotergites have not previously been described for any carabid beetle. A more restricted field of shorter bifurcate setae is also present in the Californian anilline genus *Anillaspis* Casey, which we infer to be the sister of *Medusapyga*. A molecular phylogenetic analysis based upon eight gene fragments (two nuclear ribosomal genes, five fragments of nuclear protein-coding genes, and a mitochondrial gene) demonstrates the distinctiveness of *Medusapyga*, and places it in a clade with the other genera from the United States. The sister group of *Medusapyga* + *Anillaspis* is the Californian genus *Anillodes* Jeannel. *Medusapyga alsea* LaBonte, the type species of the genus, is known only from three proximate localities in the Oregon Coast Range southwest of Corvallis in western Oregon. *Medusapyga chehalis* LaBonte is known only from four proximate localities in the Black Hills southwest of Olympia in southwestern Washington state. These are the first species of Anillini described from the Pacific Northwest. Details of habitat and natural history are provided.

KEYWORDS: endogean, anophthalmous, bifurcate setae, Trechitae, DNA phylogeny, systematics, taxonomy, subterranean trap.

This paper began as the result of two unexpected events. In May 1993 LaBonte was conducting a survey for a carabid beetle of conservation concern. Negotiating the labyrinthine backroads of the Oregon Coast Range on the slopes of Prairie Peak, he, not surprisingly, arrived at an unintended destination. Since the site included a fine stand of old conifers, a lunch break ensued. To while away the time, he desultorily turned rocks. Under one, he found about a dozen tiny brown beetles. At first, he dismissed them as Leodidae, common in these forests. Then he realized they were walking like Carabidae and were almost certainly Anillini, then unknown from Oregon or elsewhere in the Pacific Northwest. This was the discovery of *Medusapyga alsea* LaBonte (Figs 1A, 2A). Eight years later, in 2001, while identifying insects during the wee hours of an Oregon state park BioBlitz, LaBonte was chatting about his discovery of the Oregon anillines with an ant

FIGURE 1. (A) Female of *Medusapyga alsea* from the type locality. (B) Female of *M. chehalis* from USA, Washington, Thurston Co., 11 km NW of Littlerock, approximately 0.4 km SSW of the type locality, 46.9564°N 123.1366°W, 315 m elevation. Both specimens were freshly killed, and then posed and photographed on soil from their habitats. Scale bars 1 mm.

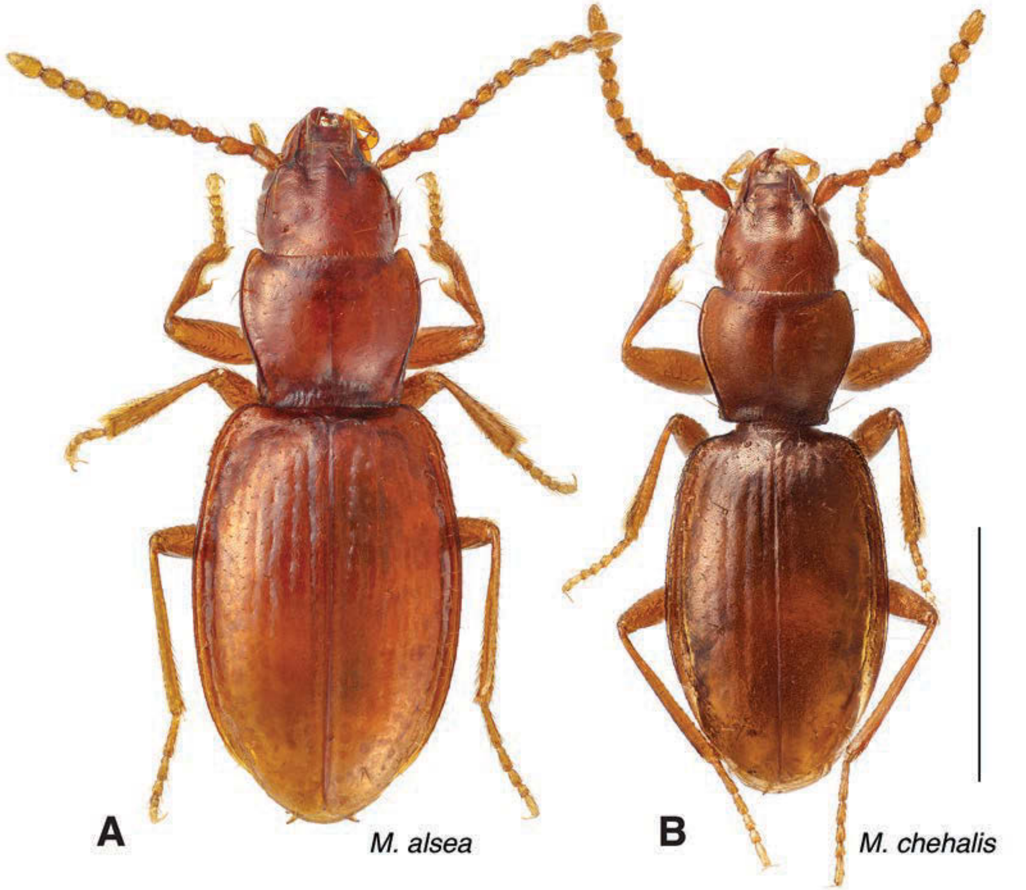


FIGURE 2. Dorsal habitus. (A) *Medusapyga alsea,* female. (B) *M. chehalis*, female. Scale bar 1 mm.

researcher, Dr. Jack Longino, then at Evergreen State University in Olympia, Washington. Jack casually mentioned that he "got a couple of those" while collecting ants near Chehalis the previous year. This chance conversation revealed the existence of *M. chehalis* LaBonte (Figs 1B, 2B). Serendipity is oft the welcome companion of the biodiversity researcher.

Members of the tribe Anillini (Coleoptera: Carabidae: Trechinae) are litter, soil, fractured-bedrock, or cave-dwelling carabids which are typically small or very small, depigmented and eyeless, with serrate margins of the humeral regions of elytra. The Anillini is a lineage of Gondwanian origins distributed throughout the world (Andújar et al. 2016). The North American fauna was previously known to extend from Maryland and Indiana south into the southeastern states and west into Texas and California (Bousquet 2012), with a diversity focus in the Appalachian mountains. The described anilline fauna of the United States includes four genera and 73 species (Bousquet 2012 and references therein, Sokolov 2012, Sokolov 2014, Sokolov 2020, Sokolov 2021, Sokolov and Carlton 2012, Sokolov et al. 2014, Sokolov et al. 2017, Sokolov and Schnepp 2021). *Anillinus* Casey (64 species) and *Serranillus* Barr (4 species) are known from the eastern states (predominantly the Southeast) west to Indiana, Oklahoma, and Texas, while *Anillaspis* Casey (2 species) and *Anillodes* Jeannel (3 species) are known only from California (Bousquet 2012). The phylogenetic relationships of these genera have not been examined in detail and no comprehensive analysis of the North American Anillini has been published.

The carabid faunas of Oregon and Washington are relatively well known, due in large part to Hatch (1953) and Lindroth (1961–1969), as well as subsequent researchers (e.g., Bousquet 1985, Kavanaugh 1984, Kavanaugh and LaBonte 2006 and 2008, LaBonte 2006, Maddison and Sproul 2020, Sproul and Maddison 2017b, Westcott et al. 2006). Consequently, it was surprising to find two undescribed species of anilline in this region. The two species documented herein are the first members of this tribe described from Oregon, Washington, and the Pacific Northwest. Furthermore, our molecular phylogenetic analysis of North American anillines, combined with morphological comparisons, indicates the two Pacific Northwest species represent a new genus, sister to the Californian genus *Anillaspis*.

MATERIALS AND METHODS

Material examined. In addition to the material of *Medusapyga* documented below, we examined the primary types of *Anillaspis caseyi* Jeannel, *A. explanata* (G.H. Horn), all species of *Anillinus* described prior to Sokolov et al. (2004) [except *A. dohrni* (Ehlers), *A. fortis* (G.H. Horn), *and A. steevesi* Barr], as well as *A. mosleyae* Sokolov and Carlton. We also examined specimens of *Anillodes debilis* (LeConte) and *A. walkeri* Jeannel, an additional specimen of *Anillaspis explanata*, two species of *Serranillus*, and other species of *Anillinus* and *Anillus*.

Specimens examined are housed in the following collections:

CAS	California Academy of Sciences, San Francisco, USA
CMNH	Carnegie Museum of Natural History, Pittsburgh, USA
CNC	Canadian National Collection of Insects, Ottawa, Canada
EMEC	Essig Museum Entomology Collection, University of California, Berkeley, USA
GLPC	Gary L. Peters Collection, Copalis Beach, USA
JRLC	James R. LaBonte Collection, Salem, USA
LACM	Los Angeles County Museum of Natural History, Los Angeles, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA
MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMUK	The Natural History Museum, London, United Kingdom
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, USA
ODAC	Oregon Department of Agriculture, Salem, USA
OSAC	Oregon State Arthropod Collection, Oregon State University, Corvallis, USA
SDSU	Severin-McDaniel Insect Collection, South Dakota State University, Brookings, USA
WSU	Maurice T. James Entomological Collection, Washington State University, Pullman, USA

Morphological methods. General habitus and appearance of each species were documented through examination under a Leica MZ16 steroscope, up to 180X. Fine details of setation and pubescence, microsculpture, and other features were acquired via images from the Oregon Department of Agriculture's (ODA) extended-depth-of-field imaging system and scanning electron microscope. The system of reference for the elytral setae follows Erwin (1974). All specimens of *Medusapyga* were determined to gender and examined for gender dimorphisms, as well as individual variation.

Female and male genitalia were prepared, after dissection from the body, by treatment in 10%

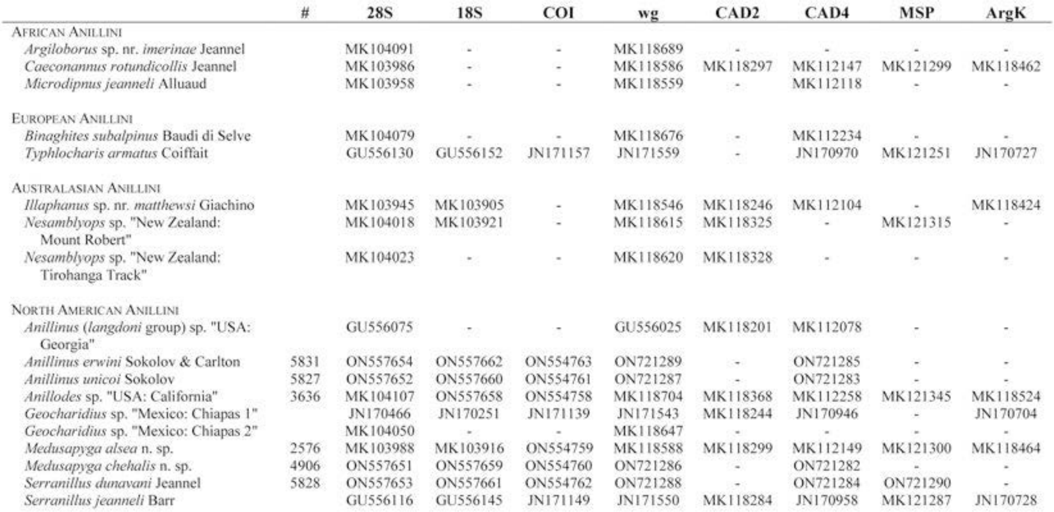
KOH at 65°C for 10 minutes followed by a series of multi-hour baths of distilled water, 5% glacial acetic acid, distilled water, and then 100% ethanol. Genitalia were then mounted in Euparal on coverslips attached to archival-quality heavyweight watercolor paper, and, once dried, pinned beneath the specimen. Membranes of the female reproductive system were stained using a weak solution of Kodak Chlorazol Black in 70% ethanol. Genitalia were examined with a Leica DM5500B compound microscope at 200–400x.

Measurements. An ocular micrometer in conjunction with various dissecting stereomicroscopes was used to acquire measurements, except for the scale bars provided in genitalic images, which were made with calibrated Leica Application Suite v4.9 associated with a Leica DM5500B compound scope. In general we followed the descriptive protocols of Sokolov (e.g., Sokolov 2016) with regard to body part measurements. These included (sometimes using slightly more intuitive acronyms): EL = elytron length, EW = elytral width, HL = head length, HW = head width, PL = pronotum length, PWa = width of pronotum across the anterior angles, PWm = maximum width of pronotum, PWp = width of pronotum across the basilateral setae, SBL = standardized body length (the total of HL + PL + EL). However, as we found that several of these measurements as defined by Sokolov (2016) were not appropriate for the taxa herein described, we deviated from them as follows: EL was measured from the apex of the scutellum to the apex of an elytron and did not include the pygidium; EW was measured at the widest point rather than at the position of the 4th marginal umbiculate setae; HW was measured at the position of the posterior supraorbital setae; PWp was measured at the narrowest point (as the posterior angles of one species are slightly anterior of the posterior pronotal margin). For *M. alsea* we measured a representative sample of 25 females and 25 males, and for *M. chehalis* 19 females and 19 males.

Images. All light-microscope specimen images other than those of genitalia, the habitus of *Anillaspis*, and posed images of Fig. 1 were created by ODA imaging technicians Joshua B. Dunlap and Thomas Shahan, using the following procedure. Images were taken using Canon EOS 5DSR cameras integrated with Dun, Inc.'s Visionary Digital LK and Passport II photo stacking systems and associated Camlift Controller software. Lighting for the Passport system was provided by 600 EX Speedlites, while Profoto D2 500 AirTTL lights were used for the Visionary Digital system. RAW photo files were stacked using Zerene Stacker software. The stacked images were edited and finalized in Adobe Photoshop CC 2018. Images of genitalia were acquired from a Leica DMC425C camera attached to a Leica DM5500B compound microscope. A stack of images from different focal positions was then merged using the PMax procedure in Zerene Systems's Zerene Stacker; the final images thus potentially have some artifacts caused by the merging algorithm. The images of *Anillaspis* and those in Fig. 1 were formed by Zerene Stacker from a stack of images taken with a Sony NEX-7 camera attached to a Leica M165C dissecting scope. Scanning electron microscope (SEM) images were acquired by ODA entomologist Joshua J. Vlach via ODA's Tescan Vega V3 SB4 variable charge, variable pressure SEM.

DNA sequence data. Eighteen species of Anillini were included in the molecular phylogenetic study, with eight from Africa, Europe, and Australasia, and ten from North America (Tables 1 and 2). We sampled all described anilline genera within the United States, except for *Anillaspis*. We did not have access to recently collected specimens of *Anillaspis*, and our attempts at sequencing a specimen of *A. explanata* in the Ulke collection (CMNH) from the type locality proved unsuccessful. We did not attempt to sequence the single known specimen of *Horologion* Valentine. It has been suggested that *Horologion* is related to Anillini (Erwin 1982). However, the evidence for that relationship is very limited and the appropriate placement of *Horologion* is uncertain (Maddison et al. 2019). A total of 81 species of outgroups were sampled (Table 3), with the majority being from other tribes of the supertribe Trechitae. The DNA data analyzed includes 34 newly

TABLE 1. Taxon sampling of Anillini with specimens and genes sequenced for the phylogenetic analysis. Four-digit numbers under "#" are D.R. Maddison DNA voucher numbers for newly sequenced specimens. Entries under each gene are the GenBank access numbers; entries that begin with ON55 or ON72 are newly acquired sequences.



	#	28S	18S	COI	wg	CAD2	CAD4	MSP	ArgK
AFRICAN ANILLINI									
Argiloborus sp. nr. *imerinae* Jeannel		MK104091	-	-	MK118689	-	-	-	-
Caeconannus rotundicollis Jeannel		MK103986	-	-	MK118586	MK118297	MK112147	MK121299	MK118462
Microdipnus jeanneli Alluaud		MK103958	-	-	MK118559	-	MK112118	-	-
EUROPEAN ANILLINI									
Binaghites subalpinus Baudi di Selve		MK104079	-	-	MK118676	-	MK112234	-	-
Typhlocharis armatus Coiffait		GU556130	GU556152	JN171157	JN171559	-	JN170970	MK121251	JN170727
AUSTRALASIAN ANILLINI									
Illaphanus sp. nr. *matthewsi* Giachino		MK103945	MK103905	-	MK118546	MK118246	MK112104	-	MK118424
Nesamblyops sp. "New Zealand: Mount Robert"		MK104018	MK103921	-	MK118615	MK118325	-	MK121315	-
Nesamblyops sp. "New Zealand: Tirohanga Track"		MK104023	-	-	MK118620	MK118328	-	-	-
NORTH AMERICAN ANILLINI									
Anillinus (*langdoni* group) sp. "USA: Georgia"		GU556075	-	-	GU556025	MK118201	MK112078	-	-
Anillinus erwini Sokolov & Carlton	5831	ON557654	ON557662	ON554763	ON721289	-	ON721285	-	-
Anillinus unicoi Sokolov	5827	ON557652	ON557660	ON554761	ON721287	-	ON721283	-	-
Anillodes sp. "USA: California"	3636	MK104107	ON557658	ON554758	MK118704	MK118368	MK112258	MK121345	MK118524
Geocharidius sp. "Mexico: Chiapas 1"		JN170466	JN170251	JN171139	JN171543	MK118244	JN170946	-	JN170704
Geocharidius sp. "Mexico: Chiapas 2"		MK104050	-	-	MK118647	-	-	-	-
Medusapyga alsea n. sp.	2576	MK103988	MK103916	ON554759	MK118588	MK118299	MK112149	MK121300	MK118464
Medusapyga chehalis n. sp.	4906	ON557651	ON557659	ON554760	ON721286	-	ON721282	-	-
Serranillus dunavani Jeannel	5828	ON557653	ON557661	ON554762	ON721288	-	ON721284	ON721290	-
Serranillus jeanneli Barr		GU556116	GU556145	JN171149	JN171550	MK118284	JN170958	MK121287	JN170728

TABLE 2. Locality information for newly sequenced Anillini. Four-digit numbers are D.R. Maddison DNA voucher numbers.

Anillinus erwini	5831	USA: North Carolina, Mitchell Co. Pisgah N.F. Grassy Ridge Bald. 6135'. 36.0985°N 82.1791°W
Anillinus unicoi	5827	USA: North Carolina, Graham Co. Nantahala NF. Stratton Gap, Cherohala Skyway. 35.3382°N 84.0249°W.
Anillodes sp. "USA: California"	3636	USA: California: San Mateo Co. Portola Redwoods State Park, 160m. 37.2550°N 122.2203°W
Medusapyga alsea	2576	USA: Oregon: Benton Co., Prairie Peak, on BLM road 14-1-6, 730m, 44.2860°N 123.5939°W
Medusapyga chehalis	4906	USA: Washington: Thurston Co., Capitol State Forest, 11.3 km NW of Littlerock, ~400 m, 46.9600°N 123.1350°W
Serranillus dunavani	5828	USA: South Carolina, Pickens Co. Sassafras Mtn. 3376'. 35.0647°N 82.7774°W

acquired sequences, as well as data from previous publications (Maddison, Baker, & Ober 1999a, 1999b; Ober 2002; Maddison 2008, 2012; Ober & Maddison 2008; Wild & Maddison 2008; Maddison & Swanson 2010; Maddison & Ober 2011; Hildebrandt & Maddison 2011; Maddison & Cooper 2014; Kanda et al. 2015; Maddison & Anderson 2016; Sproul & Maddison 2017a; Maddison & Maruyama 2018; Maddison et al. 2019; Maddison & Sproul 2020; Maddison & Porch 2021, Maddison 2023).

Genes studied, and abbreviations used in this paper, are: **28S**: 28S ribosomal DNA (D1-D3 domains); **18S**: 18S ribosomal DNA; **COI**: cytochrome c oxidase subunit I; **wg**: wingless; **CAD**: carbamoyl phosphate synthetase domain of the rudimentary gene (parts 2 and 4 of Moulton & Wiegmann 2004, here referred to as CAD2 and CAD4); **ArgK**: arginine kinase; **MSP**: Muscle Specific Protein 300.

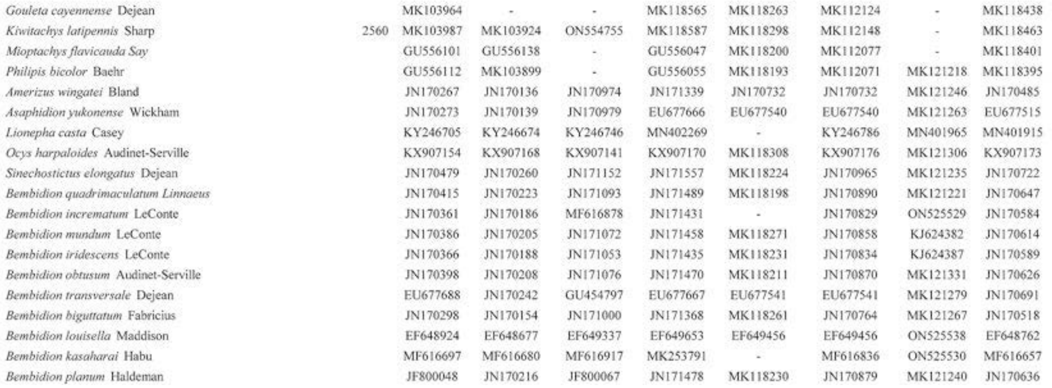
DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit. The eight gene fragments were amplified using the Polymerase Chain Reaction on an Eppendorf Mastercycler Pro Thermal Cycler, using TaKaRa Ex Taq and the basic protocols recommended by the manufacturers. Primers and details of the cycling reactions used are given in Maddison (2012), Maddison & Cooper (2014), and Maddison & Porch (2021). The amplified products were then cleaned, quantified, and sequenced at the University of Arizona's Genomic and Technology Core Facility using a 3730 XL Applied Biosystems automatic sequencer. Assembly of multiple chromatograms for each gene

TABLE 3. Taxon sampling of outgroups with specimens and genes sequenced for the phylogenetic analysis. Four-digit numbers under "#" are D.R. Maddison DNA voucher numbers for specimens for which new sequences were obtained for some genes. Entries under each gene are the GenBank access numbers; entries that begin with ON55 or ON72 are newly acquired sequences. Locality information for the specimens for which additional sequencing was performed can be found in Maddison et al. (2019).

	#	28S	18S	COI	wg	CAD2	CAD4	MSP	ArgK
Patrobus septentrionis Dejean		MK103985	-	-	MK118585	MK118296	MK112146	MK121298	MK118461
Platidiolus vandykei Kurnakov		MK103955	MK103910	-	MK118556	MK118255	MK112114	MK121262	MK118433
Andinodontis muellermotzfeldi Toledano & Erwin		MK103993	MK103918	MW291248	MK118592	MK118303	MK112154	-	MK118468
Argentinatachoides balli Sallenave, Erwin, & Roig-Juñent		MK103971	MK103912	MW291247	MK118571	MK118280	MK112132	-	MK118446
Bembidarenas reicheellum Csiki		KU233745	KU233699	KU233799	KU233874	MK118232	KU233912	-	KU233988
Tasmanitachoides sp. "Lerderderg R"		MK103950	MW291299	MW291253	MK118551	MK118250	MK112108	-	-
Tasmanitachoides baehri Maddison & Porch		MK103966	MK103911	MW291250	MK118567	MK118265	MK112126	-	MK118439
Merizodus sp. "Chile: Valdivia"		JN170471	JN170255	JN171144	JN171548	MK118275	JN170952	MK121281	JN170710
Oopterus laevicollis Bates		MK103976	-	-	MK118576	MK118289	MK112138	MK121292	MK118452
Oopterus laeviventris Sharp		GU556105	AF012488	-	GU556050	MK118182	MK112062	-	MK118385
Pseudoopterus cf. latipennis Broun		MK104036	-	-	MK118633	MK118335	MK112194	MK121321	MK118491
Sloaneana lamingtonensis Baehr		JN170481	JN170263	JN171155	JN171558	MK118285	JN170968	MK121289	JN170725
Sloaneana sp. "VIC: Acheron Gap"		MK104030	-	-	MK118627	MK118332	MK112189	-	-
Zolus wongi Sharp		GU556132	AF002787	JN171146	GU556073	MK118180	JN170955	-	JN170713
Cyphotrechodes gibbipennis Blackburn		MK103947	MK103906	-	MK118548	MK118247	MK112106	MK121256	MK118426
Paratrechodes macleayi Sloane		MK103954	MK103909	-	MK118555	MK118253	MK112112	MK121261	MK118431
Thalassophilus longicornis Sturm		GU556123	MK103900	-	GU556064	MK118209	MK112087	MK121227	MK118408
Trechobembix baldiensis baldiensis Blackburn		MK103942	MK103903	-	MK118543	MK118245	MK112101	MK121254	MK118421
Trechosiella laetula Péringuey		GU556128	GU556151	-	GU556068	MK118205	MK112082	MK121224	MK118405
Agonotrechus wuyipeng Deuve	2187	MK103969	ON557655	-	-	MK118274	MK112129	MK121280	MK118442
Aphaenops cerberus Dieck		MK104103	MK103929	-	MK118700	MK118365	MK112254	MK121342	MK118520
Blemus discus Fabricius		MK104080	MK103927	-	MK118678	MK118355	MK112236	MK121334	MK118512
Bothynotrechus castelnaui Sloane		MK103943	-	-	MK118544	-	MK112102	MK121255	MK118422
Duvalius boldorii boldorii Jeannel		MK104102	-	-	MK118699	MK118364	MK112253	-	MK118519
Homaloderodes germaini Jeannel		GU556096	-	-	MK118536	MK118214	MK112091	MK121229	MK118411
Iberotrechus bolivari Jeannel		MK104100	-	-	MK118697	MK118362	MK112251	MK121340	MK118517
Kenodactylus audouini Guérin-Méneville		GU556097	-	-	GU556043	MK118197	MK112075	MK121220	MK118399
Mimotrechus scitulus Moore		MK103952	-	-	MK118553	-	MK112110	-	MK118429
Oxytrechus sp. "Chile: Villarrica"		MK103941	MK103902	-	MK118541	MK118235	MK112096	MK121243	MK118416
Paraphaenops breuilianus Jeannel		MK104106	-	-	MK118703	MK118367	MK112257	MK121344	MK118523
Pseudocnides monolcus Putzeys		MK103983	MK103915	-	MK118583	MK118294	MK112144	MK121296	MK118459
Trechimorphus cf.brunneus Moore		MK103953	MK103908	-	MK118554	MK118252	MK112111	MK121259	MK118430
Trechinotus flavocinctus Jeannel		GU556125	GU556149	-	GU556066	MK118190	MK112069	MK121216	MK118393
Trechisibus antarcticus Dejean	2858	MK104002	-	ON554757	MK118599	MK118315	MK112163	MK121309	MK118477
Trechus humboldti Van Dyke	2948	MK104064	ON557657	-	MK118661	MK118348	MK112219	MK121328	-
Trechus hydropicus beutenmuelleri Jeannel	2412	MK103979	ON557656	-	MK118579	MK118291	MK112140	MK121294	MK118455
Trechus obtusus Erichson		MK104059	MK103925	-	MK118656	MK118346	MK112215	MK121327	MK118502
Trechus oregonensis Hatch	587	AF398673	MK103898	ON554754	MK118534	MK118192	MK112070	-	MK118394
Tropidotrechus bawbawensis Moore		MK104089	-	-	MK118687	-	MK112245	MK121337	-
Diplochaetus planatus G.H. Horn		AF438060	AF002789	JN171138	AF437938	MK118260	JN170945	MK121266	JN170703
Pogonistes gracilis Dejean		MK103962	-	-	MK118563	-	MK112122	MK121270	MK118436
Pogonus chalceus Marsham		GU556114	GU556144	JN171148	GU556057	JN170957	JN170957	MK121249	JN170715
Pogonus texanus Chaudoir		MK104109	-	-	MK118706	MK118370	MK112260	MK121347	MK118526
Sirdenus grayii Wollaston		EU677685	JN170262	JN171154	EU677665	EU677539	JN170967	MK121260	JN170724
Thalassotrechus barbarae G.H.Horn		GU556124	JN170264	JN171156	GU556065	MK118258	JN170969	MK121264	JN170726
Chaltenia patagonica Roig & Cicchino		MK103974	MK103914	-	MK118574	MK118287	MK112136	MK121290	MK118450
Phrypeus rickseckeri Hayward		GU556113	JN170258	JN171147	GU556056	MK118288	JN170956	MK121291	JN170714
Sinozolus sp. "China: Sichuan"		MK104108	MK103931	-	MK118705	MK118369	MK112259	MK121346	MK118525
Anomotachys acaroides Motschulsky		MK104037	-	-	MK118634	MK118336	MK112195	MK121322	MK118492
Elaphropus sp. "Madagascar"		MK104001	MK103920	-	MK118598	MK118314	MK112162	MK121308	MK118476
Lymnastis sp. "Malaysia: Sabah"		MK103936	GU556137	-	GU556044	MK118212	MK112089	MK121228	-
Meotachys sp. "Ecuador: Orellana"		MK104015	-	-	MK118612	MK118323	MK112176	MK121314	MK118483
Micratopus sp. "Ecuador: Orellana"		MK104027	-	-	MK118624	MK118330	MK112186	MK121319	MK118487
Nothoderis rufotestacea Hayward		GU556115	-	-	GU556058	MK118204	MK112081	MK121223	MK118404
Paratachys vorax LeConte		GU556106	MK103897	-	GU556051	MK118184	MK112064	MK121211	MK118387
Pericompsus sellatus LeConte		MK103984	-	-	MK118584	MK118295	MK112145	MK121297	MK118460
Polyderis laeva Say		MK104043	MK103923	-	MK118640	MK118340	MK112200	MK121323	MK118495
Porotachys ottomanus Schweiger		MK104101	-	-	MK118698	MK118363	MK112252	MK121341	MK118518
Tachys argentinicus Csiki	2832	MK103996	-	ON554756	MK118594	MK118309	MK112158	-	MK118471
Tachyta inornata Say		AF438141	GU556147	-	AF438002	MK118189	MK112068	MK121354	MK118392
Tachyura sp. nr. *obesulus*		GU556092	GU556136	-	GU556039	MK118185	MK112065	MK121212	MK118388
Erwiniana hilaris Bates		GU556095	AF012489	-	GU556042	MK118183	MK112063	-	MK118386

(continued next page)

TABLE 3 (continued). Taxon sampling of outgroups with specimens and genes sequenced for the phylogenetic analysis.



	#	28S	18S	COI	wg	CAD2	CAD4	MSP	ArgK
Gouleta cayennense Dejean		MK103964	-	-	MK118565	MK118263	MK112124	-	MK118438
Kiwitachys latipennis Sharp	2560	MK103987	MK103924	ON554755	MK118587	MK118298	MK112148	-	MK118463
Mioptachys flavicauda Say		GU556101	GU556138	-	GU556047	MK118200	MK112077	-	MK118401
Philipis bicolor Baehr		GU556112	MK103899	-	GU556055	MK118193	MK112071	MK121218	MK118395
Amerizus wingatei Bland		JN170267	JN170136	JN170974	JN171339	JN170732	JN170732	MK121246	JN170485
Asaphidion yukonense Wickham		JN170273	JN170139	JN170979	EU677666	EU677540	EU677540	MK121263	EU677515
Lionepha casta Casey		KY246705	KY246674	KY246746	MN402269	-	KY246786	MN401965	MN401915
Ocys harpaloides Audinet-Serville		KX907154	KX907168	KX907141	KX907170	MK118308	KX907176	MK121306	KX907173
Sinechostictus elongatus Dejean		JN170479	JN170260	JN171152	JN171557	MK118224	JN170965	MK121235	JN170722
Bembidion quadrimaculatum Linnaeus		JN170415	JN170223	JN171093	JN171489	MK118198	JN170890	MK121221	JN170647
Bembidion incrematum LeConte		JN170361	JN170186	MF616878	JN171431	-	JN170829	ON525529	JN170584
Bembidion mundum LeConte		JN170386	JN170205	JN171072	JN171458	MK118271	JN170858	KJ624382	JN170614
Bembidion iridescens LeConte		JN170366	JN170188	JN171053	JN171435	MK118231	JN170834	KJ624387	JN170589
Bembidion obtusum Audinet-Serville		JN170398	JN170208	JN171076	JN171470	MK118211	JN170870	MK121331	JN170626
Bembidion transversale Dejean		EU677688	JN170242	GU454797	EU677667	EU677541	EU677541	MK121279	JN170691
Bembidion biguttatum Fabricius		JN170298	JN170154	JN171000	JN171368	MK118261	JN170764	MK121267	JN170518
Bembidion louisella Maddison		EF648924	EF648677	EF649337	EF649653	EF649456	EF649456	ON525538	EF648762
Bembidion kasaharai Habu		MF616697	MF616680	MF616917	MK253791	-	MF616836	ON525530	MF616657
Bembidion planum Haldeman		JF800048	JN170216	JF800067	JN171478	MK118230	JN170879	MK121240	JN170636

fragment and initial base calls were made with Phred (Green & Ewing 2002) and Phrap (Green 1999) as orchestrated by Mesquite's Chromaseq package (Maddison & Maddison 2020; Maddison & Maddison 2021b) with subsequent modifications by Chromaseq and manual inspection. Multiple peaks at a single position in multiple reads were coded using IUPAC ambiguity codes.

Sequences have been deposited in GenBank with accession numbers ON554754 through ON554763, ON557651 through ON557662, and ON721282 through ON721290.

Analysis of DNA data. Alignments of 28S and 18S were conducted in MAFFT version 7.130b (Katoh & Standley 2013), using the L-INS-i search option and otherwise default parameter values. Matrices for wg, CAD2, CAD4, and MSP were aligned by first translating the sequence to amino acids in Mesquite, aligning amino acids in MAFFT, and then forcing that amino acid alignment onto the original nucleotide alignment using Mesquite. Matrices for COI and ArgK contained no evident indels, and so were aligned manually.

Sites in 28S and 18S were chosen to be excluded from consideration using the modified GBLOCKS analysis present in Mesquite with the following options: minimum fraction of identical residues for a conserved position = 0.2, minimum fraction of identical residues for a highly-conserved position = 0.4, counting fraction within only those taxa that have non-gaps at that position, maximum number of contiguous non-conserved positions = 4, minimum length of a block = 4, and allowed fraction of gaps within a position = 0.5.

Maximum likelihood analysis was conducted on a concatenated matrix containing all eight gene fragments using IQ-TREE version 2.1.3 (Minh et al. 2020), as orchestrated by Mesquite's Zephyr package (Maddison & Maddison 2021a; Maddison & Maddison 2021b). The ModelFinder feature within IQ-TREE (Kalyaanamoorthy et al. 2017) was used to find the optimal character evolution models. The TESTMERGE option sought the optimal partition of sites, beginning with each codon position for each gene fragment as a separate part (thus, the analysis began allowing for up to 20 parts: three for each of the six protein-coding gene fragments, and one for each of 28S and 18S). One hundred searches were conducted for the maximum-likelihood tree; for the bootstrap analysis, 500 bootstrap replicates were conducted.

Files containing the entire (untrimmed) sequences for each specimen as well as the inferred trees have been deposited in Dryad (data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.280gb5ms8).

RESULTS AND DISCUSSION

Taxonomy

The new genus can be distinguished from other genera of North American anillines using the following key, which is modified from Ball & Bousquet (2000), Barr (1995), Jeannel (1963a, 1963b), and Sokolov et al. (2004). *Micranillodes* Jeannel (treated in Ball & Bousquet 2000) was synonymized into *Anillinus* in Bousquet (2012). *Horologion* is not treated as there is limited evidence it is an anilline (see above).

Key to the Genera of North American (North of Mexico) Anillini

1. Mandibles extremely long and narrow, much longer than head behind the antennal insertions (Fig. 3); sides of head behind antennal insertions more-or-less parallel and straight; frontal furrows deep and long, extending to occiput (Fig. 3); lateral explanation of elytron very broad in anterior half, abruptly narrowing thereafter (Fig. 3); geographic range Sierra Nevada, California . . . . *Anillaspis* Casey
– Mandibles shorter and stouter, shorter than head behind the antennal insertions (Fig. 2); sides of head behind antennal insertions rounded; frontal furrows shallow and short, extending no more than halfway to occiput (Fig. 2); lateral explanation of elytra much narrower and broadest only near the humeri or in the anterior quarter, gradually narrowing until terminating before the apex (Fig. 2) 2

2. Mentum with a pair of setae near apex of anteromedial tooth; geographic range California, Oregon, and Washington 3
– If two setae are present on mentum tooth, then they are at base of tooth, well posterior of apex; geographic range eastern United States west to Missouri and Texas 4

3. Male profemur with a spine on ventrobasal face (Fig. 4A, C); male protarsus with tarsomeres 1 and 2 strongly asymmetrically dilated (Fig. 5); female genitalia with a field of long bifurcate setae scattered throughout the apical region of laterotergite IX (Fig. 6); geographical range Pacific Northwestern United States (Oregon and Washington) . . . . ***Medusapyga*** LaBonte and Maddison
– Male profemur without a spine on ventrobasal face; male protarsus with only tarsomere 1 dilated; each lateral tergite of female genitalia with a field of simple setae on the venter along medial or apical edges; geographical range California . . . . *Anillodes* Jeannel

4. Both sexes with apical margin of last visible abdominal ventrite evenly arcuate; right paramere present; geographic range eastern United States west to Missouri and Texas . . . . *Anillinus* Casey
– Male with apical margin of last visible abdominal ventrite toothed; right paramere apparently absent; geographic range southeastern United States . . . . *Serranillus* Barr

Medusapyga LaBonte and Maddison, new genus

Type species. *Medusapyga alsea* LaBonte, new species, here designated.

Etymology. The generic name refers to the bifurcate setae on laterotergite IX of females. The Latin *Medusa* alludes to the mythical monster (a gorgon) with snakes rather than hair on her head and the similarity of the beetles' setae to the forked tongues of snakes, while *pyga* is derived from the Greek noun *pyge* for rump, referring to the placement of the setae and that these can often be observed protruding from the posterior of the abdomen. The gender of this name is feminine.

Composition. This genus includes the two species described below.

Recognition. Diagnostic characters of species of *Medusapyga* include the field of long bifurcate setae on the ventral surface of the apical half of laterotergite IX of the female genitalia, the ventrobasal spine of the male profemur, and the two asymmetrically strongly dilated basal tarsomeres of the male protarsus, the first tarsomere with two rows and the second with one row of adhesive articulo-setae (Stork 1980) on the venter. Each species has one or more additional unique characters serving to distinguish them from members of previously described genera of North American Anillini. The mesotrochanters of both genders of *M. alsea* are quadrate, with a large, blunt, triangular tooth along the posterior margin. The profemora of female *M. chehalis* are distinctly angulate to dentate on the ventrobasal face and males of *M. chehalis* have a medial laterally compressed and posteriorly declivous keel on ventrite 2 (these species-specific characters will be addressed in more detail under the species descriptions below). Both species are relatively large for North American Anillini, especially *M. alsea*.

Description. *Habitus* (Figs 1, 2). SBL 2.03–2.65 mm. Head large and broad, HW/HL ~0.88, HW/PWm ~0.75–0.81. Pronotum large, broad, PWm/EW ~0.69, with lateral margins sinuate anterior to posterior angles. Elytra convex to distinctly flattened in lateral perspective and ovoid in dorsal perspective, EW/EL ~0.65, EW/SBL ~0.36–0.39. Translucent pale yellowish brown to reddish brown to dark brown.

Dorsal microsculpture imbricate, with the posterior margin of each sculpticell slightly raised. Sculpticell definition distinct but varies between species, among parts of the body, and among portions of those body parts. Sculpticell shape and size similarly variable, with the shape ranging from irregularly isodiametric to elongate irregularly polygonal. Body surface shiny. Dorsum with sparse vestiture of short, fine setae about 0.12–0.25 length of long pronotal and elytral interstrial setae.

Head (Fig. 7). Frontal furrows broadly impressed, parallel, ending well anterior of occiput. Frontolateral carinae distinct and sharply defined, extending from a shelf over the antennal insertions posteriorly to the level of posterior supraorbital setae. A trian-

FIGURE 3. Dorsal habitus of female *Anillaspis explanata* from USA: California: El Dorado Co., Alabaster Cave (CMNH). Scale bar 1 mm.

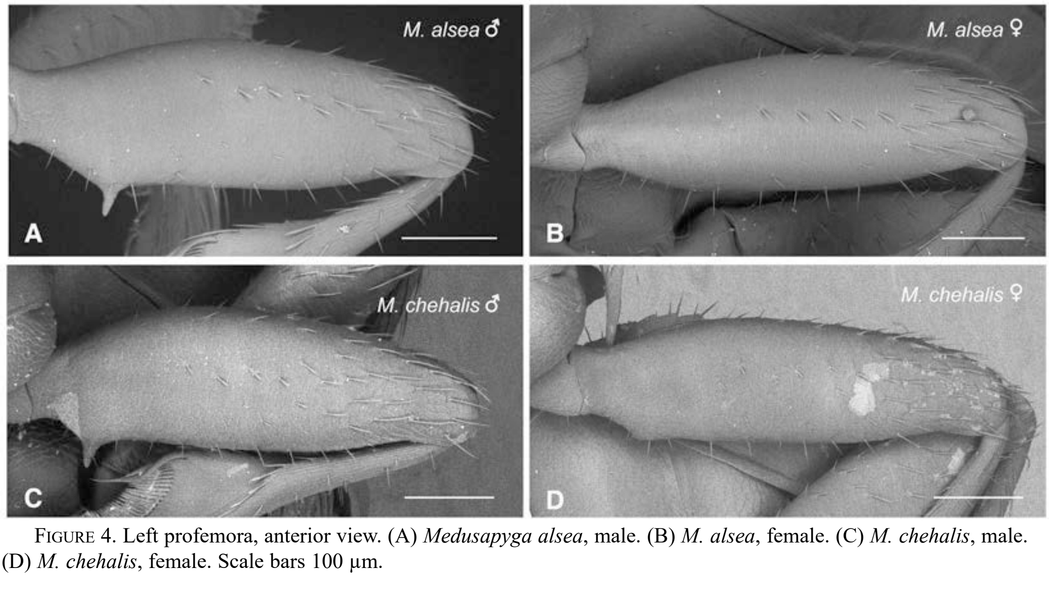


FIGURE 4. Left profemora, anterior view. (A) *Medusapyga alsea*, male. (B) *M. alsea*, female. (C) *M. chehalis*, male. (D) *M. chehalis*, female. Scale bars 100 µm.

gular protrusion extends anteriorly between the antennal carinal shelf and the clypeal seta on each side, protruding above the dorsal mandibular articulation and terminating in a small capitation. Using the terms of Sokolov (2016), there are a pair of clypeal setae, a pair of frontal setae, a pair of mediofrontal setae (sometmes represented by only a single seta), two pair of supraorbital setae (with the posterior pair set somewhat mediad of the anterior pair), and a pair of postorbital setae. Eyes absent. Genae with sparse setae of moderate length. Tempora shallowly convex and rounded to obtusely angulate. Occiput set off from the vertex by a shallow transverse depression just posterior of the posterior supraorbital setae. Mentum and submentum separated by distinct suture. Mentum with large, sharply pointed anteromedial tooth, with a pair of long setae near the apex of the medial tooth and lateral and paramedial pairs anterior of the posterior margin. Submentum trapezoidal, with a pair each of long setae anterolaterally near the anterior angles, paramedially, and medially (the shortest), and also with a row of short setae just posterior of the anterior margin. Gula broad, sides slightly convergent posteriorly, sparsely setose.

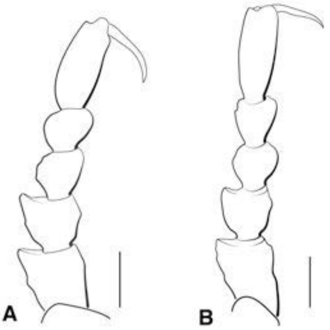


Figure 5 (above). Male right protarsi, dorsal view. (A) *Medusapyga alsea.* (B) *M. chehalis*. The view of the two specimens is not exactly equivalent, which accounts for some differences between the two images. Scale bars 50 µm.

Mandibles matching basic structure of *Bembidion* (Maddison 1993) and Anillini (Sokolov 2013). Stout, with sharp, slightly ventrally curved apices extending well beyond labrum. Each mandible of similar size and shape, except for details of mandibular teeth. Left mandible has terebral (rounded), premolar, and molar teeth. Right mandible has anterior retinacular, terebral, posterior retinacular, premolar, and molar teeth. Labrum rectangular, anterior margin distinctly arcuately emarginate, three pairs of setae (sequentially decreasing in length mediad) along anterior margin. Clypeus trapezoidal, clypeolabral suture distinct, frontoclypeal suture present; with a pair of long posterolateral fixed setae. Subterminal maxillary palpomeres sparsely setose; inner lateral margin of penultimate palpomere strongly arcuate, outer lateral margin straight; terminal palpomere subulate, about one-third as long as penultimate palpomere. Subterminal labial

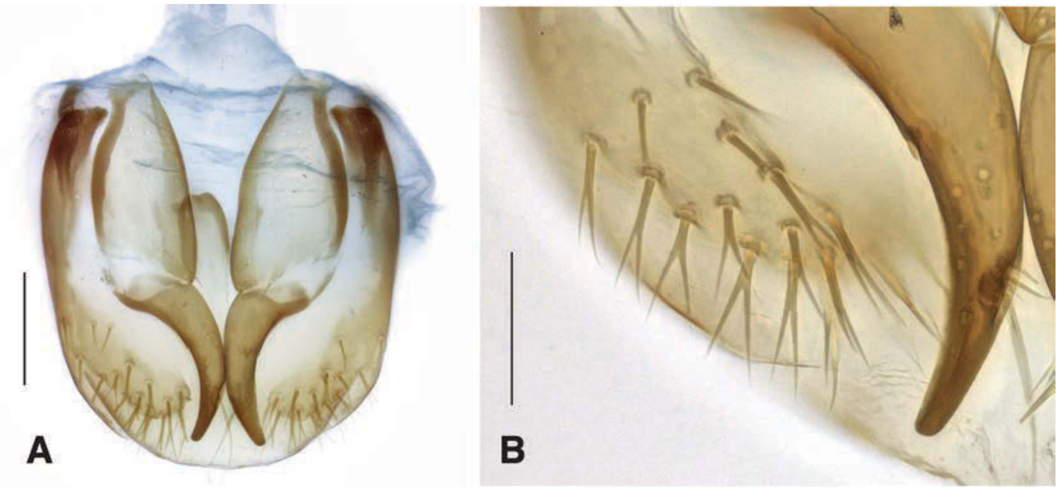


Figure 6. Female genitalia of *Medusapyga alsea* from the type locality, ventral view. (A) Overview of voucher V101505. Scale bar 100 µm. (B) Closeup of voucher V101504, showing bifurcate setae on laterotergites. Scale bar 50 µm.

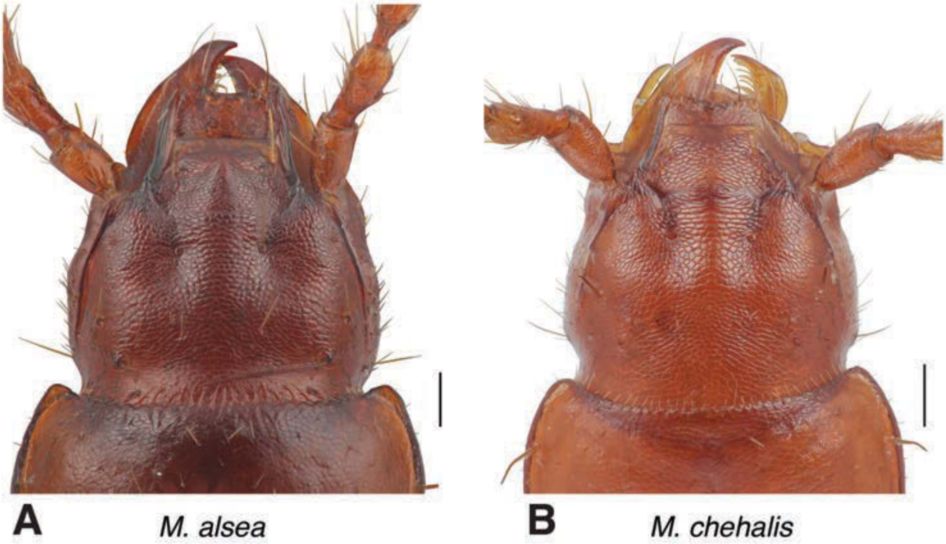


FIGURE 7. Dorsal views of heads. (A) *Medusapyga alsea*. (B) *M. chehalis*. Scale bars 100 µm.

palpomeres sparsely setose; inner lateral margin of penultimate palpomere straight, outer lateral margin strongly arcuate; terminal palpomere subulate, about half as long as penultimate palpomere. Glossa with two apical setae. Distinct, lobate paraglossae extending beyond apex of glossa, each densely setose in the apical half.

Antennae eleven-segmented, robust, antennomeres 4–10 more or less moniliform. Except for scape, all antennomeres at least partially pubescent. Scape stout, oblong, glabrous except for a few scattered setae and four long apical setae; antennomere 2 slightly pedunculate basally, otherwise ovate; antennomere 3 strongly pedunculate, very narrow basally; antennomere 11 elongate oval, narrowest anteriorly.

Pronotum (Fig. 8). Outline cordate, broadest at about one-third total pronotal length from anterior margin and posterior of lateral primary setae, width at anterior slightly greater than at posterior angles. Lateral primary setae about one-quarter of total pronotal length from anterior margin, posterior pronotal setae just anterior of or well anterior of posterior angles. Dorsum with sparse, socketed, small setae. Numerous small setae regularly distributed along lateral margins. Anterior angles rounded. Lateral margins approximately parallel from posterior angles anteriorward, then convergently arcuate to anterior angles, with several small denticles anterior of posterior angles. Posterior margin slightly convex near posterior angles. Lateral explanations distinct and reflexed, widest at posterior angles and abruptly narrowing anterior of posteromedial pronotal impression. Posterolateral depressions inside hind angles deep, short, and ovate, delimiting lateral bounds of posteromedian impression. Disc convex with well defined median longitudinal impression, deepest adjoining anteromedian and posteromedian impressions. Posteromedian impression deep, extending to posterior pronotal margin, deepest at anterior delimitation, otherwise convex throughout.

Scutellum. Small, lateral and posterior margins evenly convex, apex obtusely rounded. Almost entirely within depression anterior of elytral suture. When the pronotum is extended away from the anterior margin of the elytra, as in active, live specimens (Figs 1, 2B) or in most preserved specimens, the scutellum is visible. In live specimens at rest or in some preserved specimens, the pos-

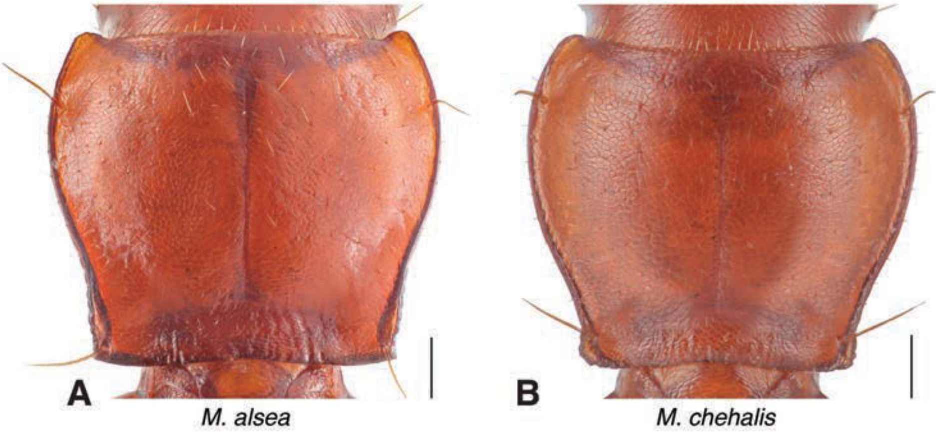


FIGURE 8. Dorsal views of pronota. (A) *Medusapyga alsea*. (B) *M. chehalis*. Scale bars 100 µm.

terior margin of the pronotum fits over and against the anterior elytral declivity (Fig. 2A), completely concealing the scutellum.

Elytra (Figs 2, 9). Entire, concealing pygidium. Together elongate oval in dorsal aspect. Each elytron with lateral margin serrulate from humerus to plical crossing. Each elytron lacks basal margination, i.e., no carina from the humerus to the parascutellar seta. Lateral explanation of each elytron distinctly reflexed, narrow, narrowest just posterior of humerus and just anterior of the plical crossing. Each elytron with elytral plica distinctly crossed. Each elytron with five shallow and indistinct striae, only stria 1 complete to apex (although extremely faint in the apical quarter), all others interrupted and ending before elytral apex. Intervals each with a row of sparse, short setae. Elytral apices separately rounded. The elytral lateral umbiculate series consists of nine large setae in "Type A" arrangement (sensu Jeannel 1963a), with seta Eo9 mesad of margin and forming a geminate pair with seta Eo8 (Fig. 9). Each elytron has a large parascutellar umbiculate seta at the base of stria 2 and a large fixed seta at the apex of stria 2, while stria 3 has three large, socketed setae: one at a level posterad of lateral umbiculate seta Eo3, one at a level anterior of lateral umbiculate seta Eo5, and the last at a level posterad of the geminate pair of lateral umbiculate setae.

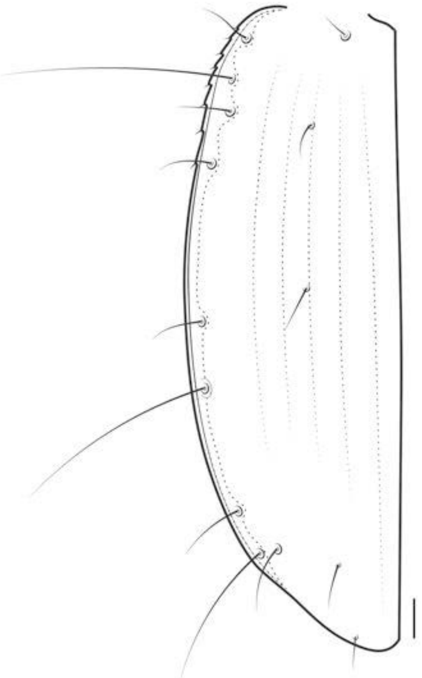


FIGURE 9. Left elytron of female *Medusapyga alsea*, showing fixed setae. Scale bar 100 µm.

Hind wings. Absent.

Legs. Male profemur with large, ventrally directed spine near the base (Fig. 4A, C); this spine projects well beyond the ventral face, with its length about two to three times its greatest diameter. Ventral face of male profemur carinate and obtusely angulate from femoral base to spine. Femora sparsely setose, more densely so near apices. Tibiae with basal half sparsely setose, apical half densely setose. Protibia with external apical angle obliquely truncate, apical one-fourth inflexed.

Protarsus with five tarsomeres; basal two tarsomeres of males strongly asymmetrically laterally expanded (both with proximal anterior angle distinctly protruding beyond the anteromedial margin) (Fig. 5); first tarsomere ventrally with two rows of between 4 and 7 adhesive articulo-setae, second tarsomere with one row of about 4 or 5 articulo-setae, both tarsomeres with some of the articulo-setae fused apically (Fig. 10); female basal tarsomeres symmetrical, not laterally expanded, and without ventral articulo-setae.

Abdominal ventrites. Intercoxal process of second visible abdominal ventrite triangular, apex obtuse to acute. Second visible abdominal ventrite longest, about as long as the following two. Apical margin of last visible abdominal ventrite entire, not serrate. Females with two pair of long paramedial fixed setae just anterior of apex of last visible ventrite, males with a single pair. A small shallow fovea, variable among species and sexes, is present on the second visible abdominal ventrite just posterior of the intercoxal process between the metacoxae.

Female genitalia (Fig. 6). Laterotergite IX with many long, bifurcate setae covering much of the ventroapical region. Gonocoxite 2 with a minute ensiform seta and a pair of nematiform setae, one long and the other minute, with the minute seta adjacent to the base of the long seta. Ventrite X slightly sclerotized, forming a single glabrous lobe (visible centrally in Fig. 6).

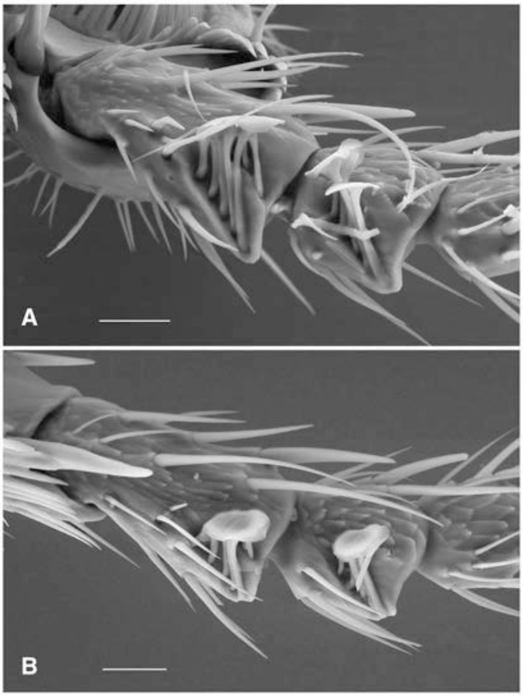


FIGURE 10. Ventral surface of basal two protarsomeres of male *Medusapyga alsea*. Protarsomere 1 is to the left of center, and protarsomere 2 to the right of center. (A) Protarsomere 1 showing two rows of adhesive setae, and protarsomere 2 showing one row of adhesive setae with partially separated apices. (B) From a second specimen, showing the fusion of apices of both rows of adhesive setae on protarsomere 1, and the fusion of apices of all setae on protarsomere 2. Scale bars 25 µm.

Male genitalia (Figs 11, 12). Aedeagus of typical form for a carabid (Fig. 11), with basal lobe open dorsally; lacking ventral setae. Parameres of typical form for a member of supertribe Trechitae, with left paramere larger (Fig. 12); both parameres with four apical setae, both without ventral setae.

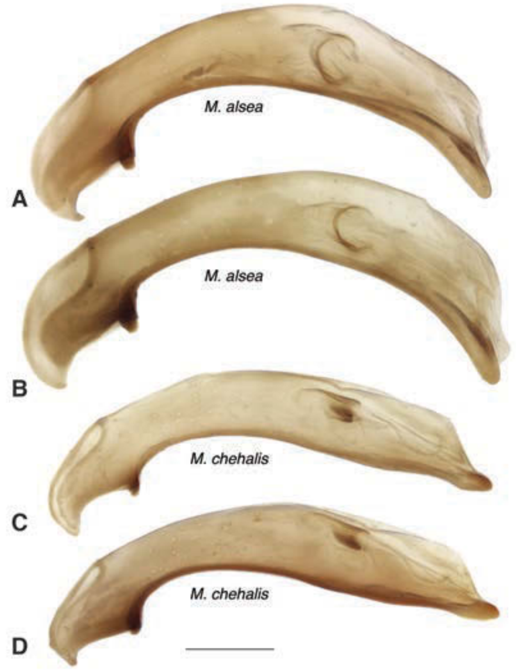


FIGURE 11. Male aedeagus, left lateral view. (A) *Medusapyga alsea*, voucher JRL002. (B) *M. alsea*, voucher JRL013. (C) *M. chehalis*, voucher JRL012. (D) *M. chehalis*, voucher JRL010. Scale bar 100 µm.

FIGURE 12. Parameres of *Medusapyga chehalis*, voucher JRL012. (A) left paramere, (B) right paramere. Scale bar 100 µm.

Key to species of *Medusapyga* LaBonte and Maddison

Head with a declivous medial frontoclypeal prominence (Figs 1A, 7A); pronotum with sharp rectangular or acute hind angles (Fig. 8A); mesotrochanter with large, blunt, triangular tooth protruding from posterior margin (Fig. 13A); male visible abdominal ventrite 2 without medial preapical keel; aedeagus as in Figs. 11A, B. . . . . **Medusapyga alsea** LaBonte

Head with the frontoclypeal region gradually and shallowly convex (Figs 1B, 7B); pronotum with rounded hind angles (Fig. 8B); posterior margin of mesotrochanter more-or-less evenly arcuate (Fig. 13B); male visible abdominal ventrite 2 with a medial preapical keel which is sharply pointed and declivous at the posterior (Fig. 14); aedeagus as in Figs. 11C, D . . . . **Medusapyga chehalis** LaBonte

Medusapyga alsea LaBonte, new species

Holotype. Male, deposited in the California Academy of Sciences, labeled: “OREGON, Benton Co., Prairie Peak, 11 km S Alsea, J.R. LaBonte, 9 V 1993, elev. 810 m, 44.2844°N 123.5858°W, under stones”, “HOLOTYPE, *Medusapyga alsea* LaBonte sp. nov., designated 2022 [red paper]”.

Paratypes. 329 (258 females, 71 males), residing in the following collections and institutions: CAS (32), CMNH (2), CNC (2), EMEC (1), GLPC (84), JRLC (155), MCZ (2), MNHN (2), NHMUK (2), NMNH (2), ODAC (17), OSAC (22), SDSU (4), WSU (2). USA, Oregon, Benton Co., Prairie Peak, 11 km south of Alsea, 44.2844°N 123.5858°W, 810 m elevation [Type locality] (296). 9 V 1993, G.L. Peters (63), J.R. LaBonte (57). 14 V 1993, J.R. LaBonte (10). 19 VI 1993, G.L. Peters (18), J.R. LaBonte (19). 26 VI 1993, G.L. Peters (1). 31 VII 1993, J.R. LaBonte, (10). 7 V 1994, G.L. Peters (2), J.R. LaBonte (7). 15 V 1995, J.R. LaBonte (6). 6 V 1998, J.R. LaBonte (6), R.L. Westcott (6). 29 IV 2002, D.H. Kavanaugh (21), J.R. LaBonte (13). 1 V 2003, J.R.

LaBonte and B. Smith (12), R.L. Westcott (9). 20 III 2010, D.R. Maddison & J.R. LaBonte (1). 29 IV 2014, D. H. Kavanaugh and J.R. LaBonte (1), J.R. LaBonte (1). 29 IV – 9 XI 2014, soil trap, J.R. LaBonte (27). 2 IV 2022, D.R. Maddison & P.R. Triplett (1). 15 V 2022, D.R. Maddison (5). USA, Oregon, Benton Co., Prairie Peak, 11 km south of Alsea, 0.6 km west of the type locality, 44.2848°N 123.5933°W, 750 m elevation (32). 6 V 1998, R.L. Westcott (2). 29 IV 2002, D.H. Kavanaugh (7), J.R. LaBonte (4). 1 VI 2004, J.R. LaBonte (9). 20 III 2010, D.R. Maddison & J.R. LaBonte (1). 30 V 2010, D.R. Maddison (4). 29 IV – 9 XI 2014, soil trap, J.R. LaBonte (2). 2 IV 2022, D.R. Maddison & P.R. Triplett (1). 15 V 2022, D.R. Maddison (1). 19 VI 2022, K.W. Will (1). USA, Oregon, Benton Co., Prairie Peak, 10 km south of Alsea, 1.1 km WNW of the type locality, 44.2881°N 123.5982°W, 715 m elevation (1). 15 V 2022, L.A. Martin (1).

Depending upon the GPS system used, and the precise spot the measurements were taken within each locality, the exact geographic coordinates and elevations may slightly differ among the labels of the different collectors and institutions.

Type Locality. USA, Oregon, Benton Co., Prairie Peak, 11 km south of Alsea, 44.2844°N 123.5858°W, 810 m elevation.

Etymology. The specific epithet refers to the Oregon Coast Range river drainage of this name and the community nearest the type locality. The name is to be treated as a noun in apposition.

Description. *Habitus* (Fig. 2A). SBL 2.20-2.65 mm. Color translucent dark testaceous to reddish brown to dark brown. Convex in lateral view.

Head (Figs 1A, 7A). The medial convexity formed by the frontolateral furrows ends in an abrupt declivous prominence near the anterior margin of the clypeus. In dorsal view, it is roughly triangular, pointed at the anterior extreme and broadening posteriorly. In lateral view, it ends at the anterior in a steep precipice. Tempora shallowly convex, rounded.

Pronotum (Fig. 8A). PWm/PL ~1.15, PWa and PWp approximately equal. Widest at about anterior third. Anterior angles strongly protuberant. Anterior margin truncate. Lateral margins distinctly sinuate, approximately parallel from posterior angles to well anterior of posteromedian impression, obliquely arcuate to PWm, then convergently arcuate to anterior angles. Lateral explanations distinct and reflexed, widest at anterior and posterior angles, narrowing from medial posterior impression anteriorly to just posterior of anterior angles, the point at which the explanations are narrowest. Lateral margins with fine, distinct denticles where margins are parallel anterior of hind angles but not extending to posterior margins of hind angles. Posterior angles right to slightly acute, sharp. Disc strongly convex. One long fixed stout seta just anterior of each posterior angle and a longer fixed seta located laterally at approximately the anterior quarter of each side.

Elytra (Figs 2A, 9). Greatest width just anterior of middle. Convex in lateral view, rather steeply ascending from anterior to just before middle, more gradually descending to apex, more or less evenly convex in cross section. Each elytron with lateral margin coarsely denticulate from humerus to about anterior one-fourth, thereafter finely denticulate to plical crossing. Humeri truncate anteriorly, distinctly and obtusely angulate. Lateral margins slightly obliquely divergent in anterior third, thereafter evenly convergently arcuate to the plical crossing, shallowly indented there, and then obliquely or obliquely-arcuate to the separately rounded apices. Intervals slightly convex.

Legs. Profemoral spine of males near basal one-quarter of ventral face, with its length about three times its greatest diameter (Fig. 4A). Females lack any evidence of the profemoral spine found in males or the carina that in males extends from the profemoral base to the male profemoral spine; the base of the ventral face of the female profemur is thus evenly rounded (Fig. 4B). Mesotrochanter with large, blunt, triangular tooth projecting from posteromedial margin (Fig. 13A).

Abdominal ventrites. Apex of intercoxal process of second visible abdomnal ventrite acute. A small fovea is present on the second visible abdominal ventrite just posterior of the intercoxal process between the metacoxae. It is the shape of an elongate oval, narrowest anteriorly and broadest near the posterior margin; it is thus tear-drop shaped. The surface of the fovea is smooth except for microsculpture.

Male genitalia (Fig. 11A,B). Aedeagus arcuate, apex angled downward; internal sac when viewed from left side with C-shaped structure.

Sexual dimorphism. In addition to the differences in protarsomeres and profemora, females are larger than males. Female SBL ranged from 2.40–2.65 mm and averaged 2.50 mm. Male SBL ranged from 2.20–2.48 mm and averaged 2.38 mm. A two-tailed Student's T-test indicated these differences in average length were highly significant (p = 0.000001). The medial anterior fovea posterior to the intercoxal process of visible ventrite 2 appears slightly larger and deeper in females.

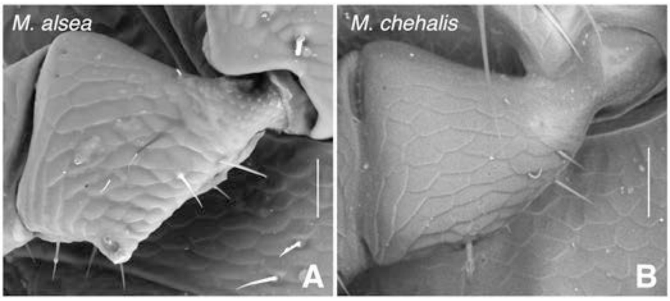


FIGURE 13. Male mesotrochanter, ventral view. (A) *Medusapyga alsea*, left trochanter. (B) *M. chehalis*, right trochanter, digitally reversed to make the image more comparable to (A). Scale bars 25 µm.

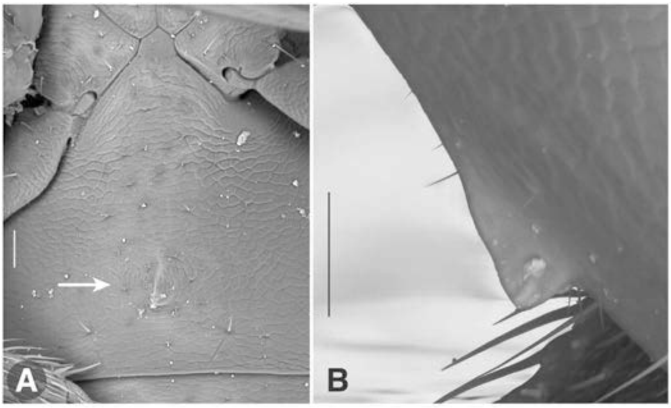


FIGURE 14. Abdominal keel of a *Medusapyga chehalis* male. (A) Ventral view second visible abdominal ventrite; arrow points toward abdominal keel. (B) Lateral view. Scale bars 50 µm.

Variation. The posterolateral pronotal margins of some specimens were slightly obliquely divergent, rather than parallel. Some individuals were distinctly paler than others, with the most extreme examples a very pale yellowish. The latter may have been teneral individuals.

Identification. Characters of *M. alsea* distinguishing it from *M. chehalis* include greater average and overall length, more robust and convex habitus, a frontoclypeal prominence, pronotum with protruding anterior angles and sharply rectangular or acute posterior angles, mesotrochanter with large triangular tooth at middle of the posterior margin, the apunctate surface of the abdominal fovea, the absence of a keel on visible abdominal ventrite 2 of males, and the more arcuate aedeagus with a C-shaped structure in the internal sac.

Geographic distribution (Fig. 15). *Medusapyga alsea* is known only from three closely approximate sites in central western Oregon: the type locality, 44.28435°N 123.58578°W, at 810 m elevation; a site 0.6 km W of the type locality, 44.28481°N 123.59331°W, at 750 m elevation; a site 1.1 km WNW of the type locality, 44.2881°N 123.5982°W, at 715 m elevation.

Note. This species was referred to as "Anillina 'USA: Oregon'" in Maddison et al. (2019).

Medusapyga chehalis LaBonte, new species

Holotype. Male, deposited in the California Academy of Sciences, labeled: "WASHINGTON, Thurston Co., 11.3 km NW Littlerock, elev. ~400 m, D.J. Cox and J.R. LaBonte, 6 May 2007, 46.9600°N 123.13450°W", "HOLOTYPE, *Medusapyga chehalis* LaBonte sp. nov., designated 2022 [red paper]".

Paratypes. 59 (32 females, 27 males), residing in the following collections and institutions: CAS (4), CMNH (2), CNC (2), JRLC (39), LACM (2), MCZ (2), NHMUK (2), OSAC (4), WSU (2). USA, Washington, Thurston Co., 9.5 km NW of Littlerock, Falls Creek Campground, 46.9333°N 123.1333°W, 200 m elevation, 30 IV 2000, J. Longino (2) (#4212, ENT 145103 LACM). USA, Washington, Thurston Co., 11.3 km NW of Littlerock, 46.96000°N 123.13495°W, between 366–412 m elevation [Type locality]. 6 V 2007, D.J. Cox and J.R. LaBonte (4). 12 V 2007, J.R. LaBonte (7). 23 V 2007, J.R. LaBonte (6). USA, Washington, Thurston Co., 11 km NW of Littlerock, 46.9564°N 123.1366°W, 315 m elevation, 2 IV 2022, J.R. LaBonte (4). USA, Washington, Thurston Co., 9.3 km NNW of Littlerock, 46.9620°N 123.1084°W, 301 m elevation, 28 IV 2014, J.R. LaBonte (27, 8 of which were extracted from soil and litter) – D.H. Kavanaugh and J.R. LaBonte (4). 22 IV 2021, J.R. LaBonte (3, all of which were extracted from soil and litter).

Depending upon the GPS system used, the exact geographic coordinates and elevations may slightly differ among the labels of the different collectors and institutions.

Type Locality. USA, Washington, Thurston Co., 11.3 km NW of Littlerock, 46.9600°N 123.1350°W, elevation ~400 m.

Etymology. The specific epithet refers to the southwestern Washington river drainage of this name and a community near the type locality. The name is to be treated as a noun in apposition.

Description. *Habitus* (Fig. 2B). SBL 2.03–2.35 mm. Color translucent testaceous to dark brown. Flattened in lateral view.

Head (Fig. 7B). The medial convexity formed by the frontolateral furrows does not end in a frontoclypeal prominence as in *M. alsea* but instead gradually and evenly decreases in elevation anteriorly. Tempora obtusely angulate.

Pronotum (Fig. 8B). PWm/PL ~1.30, PWa/PWp ~1.10. Widest at about anterior quarter, posterior of insertion of large anteriolateral setae. Anterior angles rounded and, as essentially a continuation of the slightly arcuate and emarginate anterior margin, protrude only slightly beyond the anteromedial margin. Lateral margins slightly sinuate, approximately parallel only just anterior of posterior angles, oblique to greatest pronotal width, then convergently arcuate to anterior angles. Lateral explanations distinctly narrowly reflexed, width more or less uniform throughout except broadened posterior of posteromedial impression, widest at hind angles. Hind angles right to slightly obtuse, rounded, anterior of posterior margin. Width at posterior margin less than at hind angles. Lateral margins with fine serrations at and just anterior of hind angles, extending to posterior margins of hind angles. Disc not as strongly convex as in *M. alsea*. One long, stout seta well anterior of each posterior angle (at approximately the anterior delimitation of the posteromedian impression) and a longer seta located laterally at approximately the anterior seventh of each side.

Elytra (Fig. 2B). Greatest width at mid-length. Slightly convex in lateral view, shallowly ascending from anterior margin to about anterior third, thereafter very shallowly and evenly descending to apex, more or less evenly and slightly convex in cross section. Each elytron with lateral margin finely denticulate from humerus to plical crossing. Humeri arcuate and obtusely rounded. Lateral margins slightly arcuately posteriorly divergent in anterior half, thereafter lateral margins evenly convergently arcuate to the separately rounded apices. Only very faintly indented at the plical crossing. Intervals flat.

Legs. Profemoral spine of males near basal one-sixth of ventral face, with its length about twice its greatest diameter (Fig. 4C). Females lack the elongate profemoral spine of males; however, in the same position they have a distinct obtuse angulation that can vary in expression to a short denticle (Fig. 4D). Females also have a carina extending from the profemoral base to this angulation, similar to that found in males. Mesotrochanter with posterior margin more or less evenly arcuate (Fig. 13B).

Abdominal ventrites. Apex of intercoxal process of second visible abdominal ventrite obtuse. There is a very small, shallow fovea on this ventrite just posterior of the intercoxal process between the metacoxae. It is in the shape of a broad trapezoid narrowest at the anterior and broadest at its posterior. The surface of the fovea is coarsely punctate.

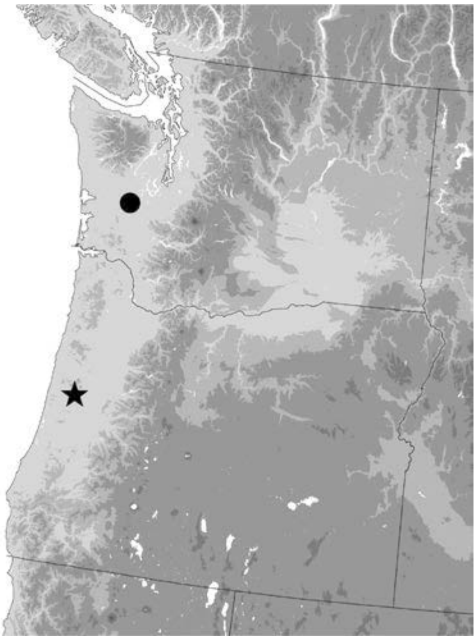


FIGURE 15. Known geographic distributions of *Medusapyga alsea* (star) in Oregon and *Medusapyga chehalis* (circle) in Washington.

In males there is a small medial laterally compressed carina (the "keel") located at about slightly more than 1/5 the total length of visible abdominal ventrite 2 from the posterior margin thereof (Fig. 14A). This keel is tallest at its posterior extent and is an elongate triangle in lateral perspective (Fig. 14B). It is most often sharply pointed (slightly rounded in a few males) at the tallest point and is perpendicularly declivous to the plane of the ventrite.

Male genitalia (Fig. 11C, D). Aedeagus with ventral margin somewhat sinuate, less arcuate than *M. alsea*, with subapical downward bulge. Internal sac with small dark structure near dorsum.

Sexual dimorphism. In addition to the differences in protarsomeres and profemora, and lack of a medial preapical keel on visible abdominal ventrite 2, females are larger than males. Female SBL ranged from 2.13–2.35 mm and averaged 2.25 mm. Male SBL ranged from 2.03–2.18 mm and averaged 2.10 mm. A two-tailed Student's T-test indicated these differences in average length were highly significant ($p = 0.0000003$). The abdominal fovea on visible abdominal ventrite 2 is much longer and broader in females, about 1/3 the length of ventrite 2 from the metacoxae to the ventrite's posterior margin. It is 2.4 times as long as the male fovea. The female fovea is also much more deeply impressed. It is almost circular, about as wide as long.

Variation. The posterolateral pronotal margins immediately anterior of the posterior margin of some specimens were slightly obliquely divergent, rather than parallel. Although most specimens were pale testaceous, a few specimens were very dark brown, almost black. A few of the paler individuals may have been teneral; this appears certain for a male with a clearly teneral aedeagus.

Identification. Characters of *M. chehalis* distinguishing it from *M. alsea* include smaller average length, depressed and less robust habitus, absence of a frontoclypeal prominence, pronotum without protruding anterior angles and with obtuse and rounded posterior angles, females with angulate to faintly denticulate profemoral bases, mesotrochanters with evenly rounded posterior margins, punctate abdominal foveae, and with a less arcuate aedeagus lacking a C-shaped structure in the internal sac.

Geographic distribution (Fig. 15). *M. chehalis* is known only from four closely proximate sites: Falls Creek Campground at 46.9333°N 123.1333°W and 200 m elevation, the type locality approximately 2.0 km to the north at 46.9600°N 123.1350°W and between 366–412 m elevation, a site approximately 0.4 km SSW of the type site at 46.9564°N 123.1366°W and 315 m elevation, and a site approximately 2.6 km east of the type locality at 46.9620°N 123.1084°W, at 301 m elevation, all in southwestern Washington. None of these sites are farther than 2.6 km apart and bound a roughly triangular area of about 270 hectares.

Phylogeny

The maximum likelihood tree (Fig. 16) for the combined DNA sequence data has most clades well supported. It shows a monophyletic Anillini, with bootstrap support of 100%. The relationships within the outgroups closely match those shown in Maddison et al. (2019); the outgroup structure is visible in the trees contained in the files available in Dryad (*https://doi.org/10.5061/dryad.280gb5ms8*). Within Anillini, the United States species form a clade (with bootstrap support of 91%), sister to all other anillines except *Nesamblyops* (Fig. 16). Within the sampled species, *Medusapyga* is monophyletic, and sister to *Anillodes* (bootstrap support 97%).

The two species of *Medusapyga* share distinctive apomorphies that also provide evidence of monophyly of the genus. Bifurcate setae on female laterotergite IX is otherwise unknown in Carabidae, and having setae scattered throughout the ventroapical surfaces of female laterotergite IX is, as far as known, unique within Anillini (Table 4). The male profemoral spine is unique among the described North American Anillini. In addition, although the expanded, asymmetric basal two protarsomeres of males are not unique within North American anillines, they appear rare and are inconsistently expressed among species in other genera (e.g., within *Serranillus*; Barr 1995, Sokolov and Carlton 2008). The only other genus described from western North America with known males, *Anillodes*, has only the basal protarsomere of males expanded and asymmetric.

The only anilline genus from the United States not included in our molecular analysis is *Anillaspis*. Only known from a few females collected over 100 years ago in the Sierra Nevada of California, it is quite distinctive in form (Fig. 3). We have examined a female of *Anillaspis explanata* (CMNH), and find that it shares two apomorphies with *Medusapyga* in the female genitalia. Like *Medusapyga*, *Anillaspis* has long setae scattered on the ventral surface of the laterotergites, including the lateral regions (Fig. 17C). In contrast, other anillines have either shorter setae or no setae in central and lateral regions of the laterotergites (Fig. 17A, B; Table 4). *Anillaspis* shares bifurcate setae with *Medusapyga*, but in *Anillaspis* they are shorter and restricted to the medial edge of the

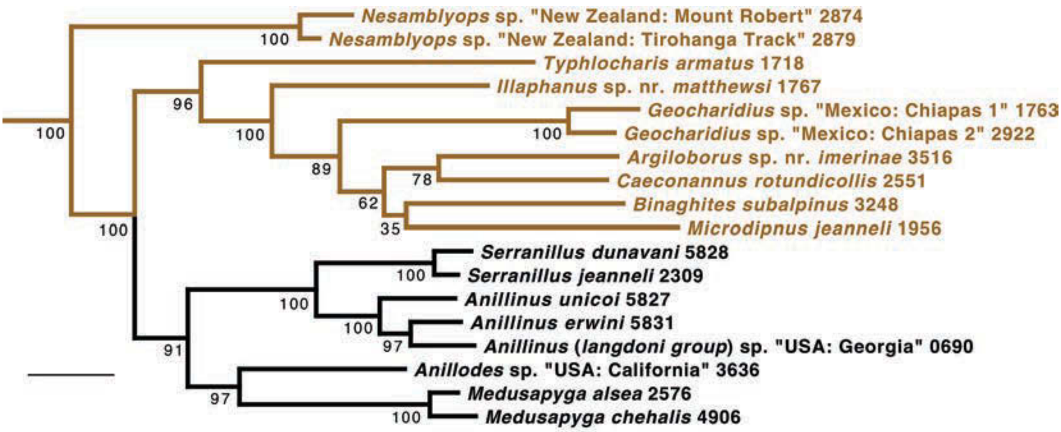


FIGURE 16. Maximum likelihood tree inferred from the concatenated, eight-gene matrix. Numbers of the branches are maximum likelihood bootstrap percentages. Outgroups omitted. Scale bar 0.1 units, as calculated by IQ-TREE.

laterotergites (Fig. 17C). There appears to be a transformation series, with most anillines having more restricted, simpler and shorter setae on the laterotergites, *Anillaspis* representing the intermediate state with long simple setae, and medium-length bifurcate setae restricted to the medial edge, and *Medusapyga* the fully derived state with long bifurcate setae scattered throughout apical regions of the laterotergites (Table 4). Based upon these results, we propose that *Anillaspis* is the sister of *Medusapyga*, with their sister being *Anillodes*. These three genera form a clade of anillines restricted to western North America.

Generic Status

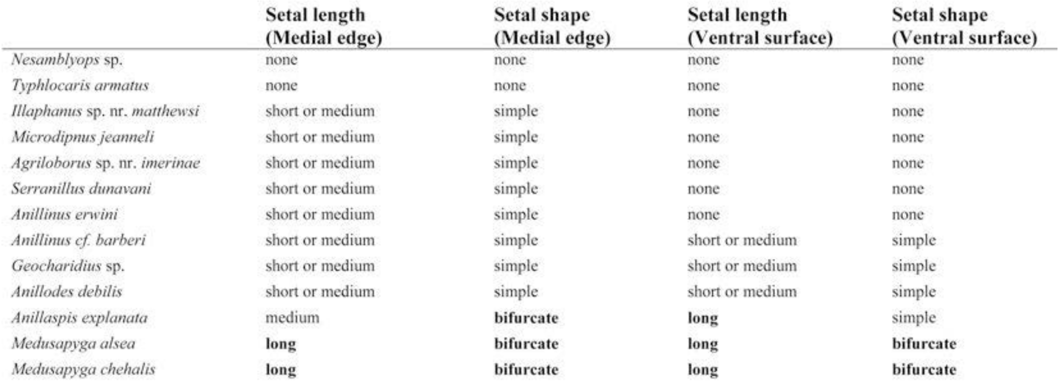
Based upon our phylogenetic results and the morphological and molecular distinctiveness of *Medusapyga*, we conclude that the two Pacific Northwest species represent a hitherto undescribed genus, the fifth described from America north of Mexico (see Bousquet 2012). As noted above, *Medusapyga* deviates in several notable morphological features from other genera of Anillini, including *Anillodes* and *Anillaspis*, the two genera close to *Medusapyga* based upon our phylogenetic analyses.

Although the distinctive morphological features of *Medusapyga* provide support for considering the group to be a separate genus, this evidence is not sufficient. These character states do not on their own argue against the group being part of a highly derived clade (along with *Anillaspis*) within a larger genus, such as *Anillodes*. As we included only one *Anillodes* species in the molecular phylogeny, we can not currently test this possibility using DNA sequence data. However, the molecular phylogeny does provide evidence of the distinctiveness of *Medusapyga* relative to *Anillodes*: the DNA divergence between *Medusapyga* and *Anillodes* is very large, at least as large as between other genera of anillines, and much more so than between *Anillinus* and *Serranillus* (Fig. 16; compare branch lengths below each of those four genera). Until *Anillaspis* DNA is available and sequenced, we will not know how molecularly divergent *Medusapyga* is from *Anillaspis*. However, the striking apomorphies of *Medusapyga* and *Anillaspis* suggest that they are reciprocally monophyletic, and both are worthy of generic status.

Habitat

Like many other anillines, *M. alsea* and *M. chehalis* appear to be true soil dwellers rather than inhabitants of the litter. Although several North American taxa are known only from caves (e.g., *Anillaspis*; Jeannel 1963a), soil or deep humus appears to be the primary habitat of members of this tribe (Barr 1964, 1995; Jeannel 1963a).

TABLE 4. Characteristics of setae on laterotergites of female genitalia of Anillini.



	Setal length (Medial edge)	Setal shape (Medial edge)	Setal length (Ventral surface)	Setal shape (Ventral surface)
Nesamblyops sp.	none	none	none	none
Typhlocaris armatus	none	none	none	none
Illaphanus sp. nr. *matthewsi*	short or medium	simple	none	none
Microdipnus jeanneli	short or medium	simple	none	none
Agriloborus sp. nr. *imerinae*	short or medium	simple	none	none
Serranillus dunavani	short or medium	simple	none	none
Anillinus erwini	short or medium	simple	none	none
Anillinus cf. barberi	short or medium	simple	short or medium	simple
Geocharidius sp.	short or medium	simple	short or medium	simple
Anillodes debilis	short or medium	simple	short or medium	simple
Anillaspis explanata	medium	**bifurcate**	**long**	simple
Medusapyga alsea	**long**	**bifurcate**	**long**	**bifurcate**
Medusapyga chehalis	**long**	**bifurcate**	**long**	**bifurcate**

Medusapyga alsea is known only from the type locality and two closely proximate sites along the eastern flank of the Oregon Coast Range; *M. chehalis* is known from the type locality and three closely proximate sites along the eastern flank of the Black Hills (Fig. 15). The Oregon Coast Range is a low (up to 1,249 m in elevation), range running north and south along the western margin of Oregon, separating the coastal plains from the western interior valleys. Similarly, the Black Hills, of which the tallest peak is 811 m in elevation, demarcate the western margin of the southern Puget Trough, along with several other sets of southwestern Washington hills. All localities are within the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973), with the dominant trees Douglas-fir (*Pseudotsuga menziesii* Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). The climate of this zone is temperate, with most of the precipitation falling as rain in the late fall through spring, resulting in dry summers (Franklin & Dyrness 1973). Average annual temperatures at both sites are similar: 9.4°C for the *M. alsea* sites and 10°C for the *M. chehalis* sites while annual average precipitation is somewhat less at the *M. alsea* sites (1,778–1,905 mm) than the *M. chehalis* sites (2,032–3,048 mm) (Corliss 1973, Pringle 1990).

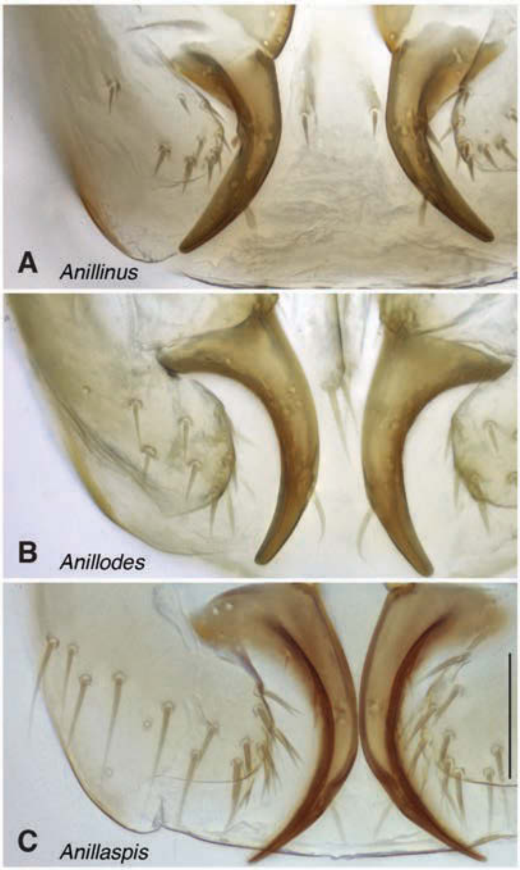


FIGURE 17. Female genitalia of three other genera of North American Anillini, ventral view. (A) *Anillinus cf. barberi* Jeannel, voucher V101515, from USA: West Virginia, Pocahontas Co. Monongahela NF. Kennison Mtn Trail, off Hwy 39 W of Cranberry Glades. 38.19114°N 80.28524°W. 10-June-2019. C.W. Harden. (B) *Anillodes debilis* voucher V101485, from the Santa Cruz Mtns, California (NMNH). (C) *Anillaspis explanata* from Alabaster Cave, El Dorado County, California (CMNH).

The type locality of *M. alsea* (Fig. 18A) was within an approximately seven hectare stand of mature hemlock that began life around 1850, with scattered old growth Douglas-fir originating from about 1790 (U.S. Bureau of Land Management, Oregon, Salem District Office). The hemlock were thus about 140 years old when the species was first discovered in 1993, and the Douglas-fir were about 200 years old. This stand was bounded by clear cuts from the early 1990's. Except for a few small gaps, the canopy was closed. Excluding scattered hemlock saplings, there were virtually no shrub or herb understories other than at the stand margins. The stand ranged in elevation from about 835 m at the southern edge to 740 m at the northern edge. Most of the stand sloped steeply to the north, although there was a more-or-less flat terrace along the southeastern margin. Most specimens (296) were found within this stand.

A few specimens (32) were collected at a site about 0.6 km west of the type site. This approximately 24-hectare site was somewhat more heterogeneous than the "type site". Young hemlock about 40 years old at the date of collection at the southern stand margin graded into older stands of Douglas-fir and hemlock (of roughly the same age as the "type stand") to the north and downslope.

FIGURE 18. Habitats of *Medusapyga*. (A) Habitat of *Medusapyga alsea*: USA, Oregon, Benton Co., Prairie Peak, 11 km south of Alsea, 44.2844°N 123.5858°W, 810 m elevation [Type locality] 20 March 2010. (B) Habitat of *M. chehalis*: USA, Washington, Thurston Co., 11 km NW of Littlerock, approximately 0.4 km SSW of the type locality, 46.9564°N 123.1366°W, 315 m elevation, 2 April 2022.

The site was virtually level at the southern margin, gradually becoming steeper, reaching slopes of about 45° approximately 500–900 m downslope. Understory characteristics were similar to those of the "type stand". Hemlock saplings were more abundant due to the somewhat more open canopy.

Of the *M. alsea* specimens, 29 were collected via soil traps designed by LaBonte and placed from 29 IV–9 XI 2014. The traps were of two styles, one with holes throughout much of its length and the other with horizontal slots (Fig. 19). The traps described in Caterino and Harden (2022) used to acquire soil-dwelling histerid beetles were based upon this slotted design. Traps were baited with raw chicken liver and propylene glycol was used in the collection jars for a preservative. The traps were then placed vertically in the soil, with the tops buried just beneath the soil surface. The bottoms of the traps were approximately 45 cm below the surface. A total of 53 specimens were trapped, although many were too decayed to mount. The slot traps performed best, capturing all but 9 specimens. One slot trap captured 42 *M. alsea*.

All sites for *M. chehalis* differ profoundly from those of *M. alsea*. Elevations are much lower, from 200 m at Fall Creek Campground, where the first two specimens were found by J. Longino in 2000, to 422 m at the highest elevation where specimens were found at the type site. The trees at all sites were much younger, smaller in diameter, and more closely spaced than those at the *M. alsea* sites. Capitol Forest, within which all the *M. chehalis* sites are found, is intensively managed for timber production. All those sites are estimated to be on at least the second rotation of regrowth following the original forest cutting.

FIGURE 19. Slot-style soil trap deployed at *Medusapyga alsea* type locality in 2014. Scale bar 10 cm.

The type site for *M. chehalis* was clear-cut in 2007. Prior to cutting, the stand was composed of Douglas-fir and western hemlock about 60 years old and thinned around the mid-1990's. The canopy was quite open, with ample light reaching the forest floor even on overcast days. There was a very scattered tall shrub understory and a dense low understory of salal, *Gaultheria shallon* Pursh, dull Oregon grape, *Mahonia nervosa* (Pursh), and sword fern, *Polystichum munitum* (Kaulf.) Presl. The remaining soil surface was largely covered by various herbaceous plants and mosses. Adjacent uncut stands had similar characteristics. The elevations where *M. chehalis* were found ranged from 366–422 m, although the slope continued up to the summit of Capitol Peak at 811 m. The site sloped steeply to the south-southeast and had several broad terraces. A total of 15 specimens were collected at this site by turning rocks.

Another *M. chehalis* site was found in 2014. This site was 2.6 km east of the type site and was somewhat different. The stand was composed solely of dense Douglas-fir approximately 25–30 cm diameter at breast height. The canopy was essentially closed, with almost no understory other than scattered ferns and shrubs, except at the stand margins. The elevation was 301 m. By turning rocks, 22 specimens were collected at this site. Another 11 were collected from soil and litter processed through Tullgren funnels.

A fourth site (Fig. 18B) for *M. chehalis* was found in 2022. This site was 0.4 km SSW of the type site and was similar. The stand was comprised of dense Douglas-fir of two sizes and ages, presumably due to past thinning, forming a closed canopy. Younger trees of perhaps 15 cm in diameter at breast height were mixed with older trees of about 30 cm diameter. Five specimens (one evaded capture) were under small but firmly imbedded rocks in a patch on the almost vertical bank of a deeply eroded trail. A few small shrubs and ferns were scattered around these rocks. The overall understory was predominantly salal, sword fern, and mosses.

Soil surface and upper horizon characteristics were similar at all *Medusapyga* sites. There was much coarse woody debris on the soil surface. Where that was absent, and at the *M. chehalis* sites where plant cover was absent, the surface was covered with twigs, cones, and conifer needles. All sites had a thin unincorporated litter layer, about 2–5 cm in depth for the *M. alsea* and the type *M. chehalis* sites. The unincorporated litter layer at the 2014 *M. chehalis* site was only about 0.5 cm in depth and about 1.0 cm deep in the immediate area where *M. chehalis* were found in 2022.

The sites differed most in deeper horizon characteristics. The litter layer at the *M. alsea* sites was underlain by a thinner incorporated organic matter (OM) layer about 0.5–1 cm thick. This layer was absent from the *M. chehalis* sites. There was a light brown, compacted, fine-grained mineral soil underlying the litter and OM layers along the southeastern terrace. As the slope descended, a dark, loose, fine-to-medium particle organic soil overlying the mineral soil became more developed and was quite deep at the bottom of the stand. In contrast, there was no mineral soil horizon at the *M. chehalis* sites. Instead, there was a single horizon to the greatest depth we exposed, about 30 cm. This horizon consisted of dark, loose, crumb-particle organic soil. Abundant rocks and small boulders were apparently more or less evenly distributed at the soil surface and within the soil profile at the *M. alsea* sites. At the *M. chehalis* sites, similar stones had a clumped distribution and were often widely scattered. Based on a 1973 soil map, the dominant soil type in the vicinity of the *M. alsea* sites is the Slickrock gravelly loam, which is typical of 25–37% slopes and can be as deep as 300 cm before reaching bedrock (Corliss 1973). The Slickrock series is part of the Bohannon-Slickrock Association of deep gravelly loams comprising about 71%, or around 81,480 hectares, of the soils in the Alsea Area (Corliss 1973). A more recent soil map of the area categorizes the dominant soil type as Murtip-Giveout-Laderly complex and Caterl-Laderly-Romanose complex (Fillmore 2009). However, the descriptions are very similar to that of the category from the 1973 map and any differences may be primarily nomenclatural. The soil type at the *M. chehalis* sites is a Boisfort silt loam or a Bunker-Boisfort complex (a gravelly loam), which can extend to more than 180 cm deep before reaching bedrock (Pringle 1990). These soils are part of the Olympic-Raught Association of very deep, well drained soils on sloping to steep uplands, which comprise about 7%, or around 13,800 hectares, of the soils in Thurston County (Pringle 1990). The soils at all sites typically support Douglas-fir and western hemlock forests (Corliss 1973, Pringle 1990).

Both species of *Medusapyga* were found well within their respective stands rather than at stand margins. They were found only under rocks, never under fallen logs or limbs, although this type of cover was assiduously searched. Productive rocks ranged from about 1 cm square to about 30 cm on a side and were always firmly imbedded, albeit often very shallowly. Individuals of *M. alsea* were strongly associated with the mineral soil and were only infrequently found in the organic soil. No *Medusapyga* were found in litter or OM layers, although some were found at litter and OM/soil interfaces along rock depression walls. These beetles were only found when all horizons of the soil profile were moist. Soil temperatures at about 5 cm, the depression depth at which many specimens were found, ranged from 9–14°C for *M. alsea*. Soil temperature at the type *M. chehalis* site, at ~4 cm depth, was 11°C, while it was 5°C at 2 cm deep at the 2022 site.

Although each species is known only from its type locality or nearby, either may be more broadly distributed. Nothing about either of the known habitats appears unique. The Douglas-fir/western hemlock plant community is widespread throughout low to moderate elevations in the

Oregon Coast Range, the southwestern Washington ranges, and the western Cascades of Oregon and Washington (Franklin and Dyrness 1973). These beetles may be restricted to deep gravelly loams. Such soils may provide sufficient depth for escaping the dry and warm conditions of summers in the western Pacific Northwest, as well as buffering the effects of the not infrequent forest fires. Relatively coarse, loose, and well drained soils are probably necessary for *Medusapyga* (and the other Pacific Northwestern forest dwelling endogeous [soil-dwelling] carabids) since these insects burrow by inserting the head and thorax into a soil interstice and then moving this unit up and down to expand the gap sufficiently to allow movement into it (LaBonte, pers. observations). Soils subject to water logging or inundation may not be suitable as these flightless species, in a medium restricting rapid movement, could be vulnerable to drowning. Soils with the presumably requisite characteristics are widespread throughout the area, as indicated by the relevant soil surveys (Corliss 1973, Pringle 1990). For instance, *M. alsea* may be distributed throughout much of the northern half of the Oregon Coast Range, as is apparently true for several other Oregon endogean carabids, i.e., *Pterostichus diana* LaBonte and *P. rothi* (Hatch) (LaBonte, unpublished data). However, if *Medusapyga* is more widely distributed, then it is surprising that specimens were not found by the outstanding coleopterists who have collected extensively in the Pacific Northwest in the past; the lack of these beetles in collections may provide some evidence that they are not widespread, or that they are generally in more cryptic habitats (e.g., deeper in the soil column).

The associated carabid and trachypachid fauna at the *M. alsea* sites were typical of a moderate elevation Coast Range conifer stand, including *Notiophilus sylvaticus* Dejean, *Promecognathus crassus* LeConte, *Pterostichus algidus* LeConte, *P. infernalis* Hatch, *P. lama* (Ménétries), *P. tuberculofemoratus* Hatch, *Scaphinotus angusticollis* (Mannerheim), *S. marginatus* (Fischer von Waldheim), *S. velutinus* (Ménétries), *Tachyta kirbyi* Casey, *Trachypachus inermis* Motschulsky, and *Zacotus matthewsii* LeConte. Carabid associates at the *M. chehalis* sites consisted of *Harpalus cordifer* Notman, *Lionepha casta* (Casey), *N. sylvaticus*, *Platynus ovipennis* (Mannerheim), *Promecognathus crassus*, *Pterostichus algidus*, *P. amethystinus* Mannerheim, *P. herculaneus* Mannerheim, *P. pumilus pumilus* Casey and *S. marginatus*. Other eyeless endogean Coleoptera were found at the *Medusapyga* sites. These included a species of Leptotyphlinae (Staphylinidae) at some of the *M. chehalis* sites and several species of *Pinodytes* (Leiodidae) at sites for both species. *Pinodytes* were particularly abundant at the *M. alsea* sites, occurring by the hundreds in the soil traps. An as yet undetermined species of *Pterostichus (Anilloferonia)* with minute eyes was also found near the *M. chehalis* sites (LaBonte, unpublished data). Other invertebrates associated with both *Medusapyga* species appeared typical for these habitats.

Medusapyga are not dependent upon the conditions found in old growth stands. Both species have been found in young stands and have obviously survived past logging. In this respect, they are similar to Oregon endogeous carabids, i.e., *Pterostichus rothi* and members of *Pterostichus* (*Anilloferonia*) Van Dyke (LaBonte 2013). Old growth may provide optimum conditions, i.e., cool and moist soils which are adequately deep and structured. Whether their endogeous habits provide such species sufficient buffering to survive current logging practices of clear cutting and subsequent burning is unknown. Hopefully, *M. chehalis* has survived the clear cutting of the type stand. LaBonte has sought *M. chehalis* there several times since the stand was logged, with no success. However, between the mechanical disturbance and the change in microclimate due to removal of the forest canopy and most of the understory, we suspect these beetles have merely retreated to greater depths than can be accessed by rolling stones.

Behavior and Phenology

Both species of *Medusapyga* appeared strongly aggregative. Several individuals were often found together even under small rocks, with groups of a half-dozen or so relatively common. In one instance, two dozen *M. alsea* were found under a single stone about 20 cm in breadth and depth and 30 cm in length.

Individuals of both species were quite active *in situ*, despite the relatively cool soil temperatures (5–14°C) at which they were found. We maintained some individuals of *M. alsea* for considerable periods in Petri dishes on a substrate of moist paper towels. Because exposure to room temperature (ca. 20°C) for even ten or fifteen minutes caused them to initially become hyperactive and subsequently hypoactive, we kept them in a refrigerator at 6°C. At this temperature, the beetles remained very active, constantly moving about in their containers. All our attempts to feed these adults were unsuccessful. A variety of small invertebrates, most found with the beetles in nature, were offered, as well as various fungi, seeds, bread, or meats. Other than occasional cannibalism of (presumably) dead conspecifics, we observed no evidence of feeding. Even under such circumstances, several individuals lived as long as eight months in captivity. A specimen of the Palearctic anilline genus *Geocharis* Ehlers was fed with live Collembola in the laboratory (Zaballos 1990). Although *M. alsea* were presented with Collembola found with them, no predation was observed. Despite maintaining groups of *M. alsea* including both sexes, we observed no copulation nor have we found any individuals *in situ in copula*.

Most individuals of *M. alsea* have been collected in May and June, with the earliest collections in late March. Specimens have also been found at the end of July (12 individuals) and in mid-December (10). The only collections of *M. chehalis* have been from early April through late May. The July collection of *M. alsea* was made during an unusually wet summer. Normally, western Oregon summer conditions dry the upper soil layers well before this time. This mid-summer record suggests that soil moisture drives the apparent seasonal vertical “migration” of this species, as seems to be true of other anillines (see Barr 1995), as well as other Oregon endogeous carabids, such as *Pterostichus rothi* (LaBonte 1994). Although no individuals were observed *in copula*, very pale (presumably teneral) specimens of *M. alsea* from early May collections suggest that species, and presumably *M. chehalis*, may overwinter as larvae, with breeding perhaps occurring in the fall, or that they overwinter as adults, with breeding occuring very early in the spring.

CONCLUDING REMARK

Medusapyga alsea and *M. chehalis* are the first anillines recorded from Oregon, Washington, and the Pacific Northwest. Just over 60 years ago, the dean of Pacific Northwestern coleopterists, Melville H. Hatch, while considering the eyeless beetles of the Pacific Northwest, remarked that “there is every reason to suspect that additional species of *Anilloferonia* exist in the region” (Hatch 1958, p. 209). While that specific prediction has not yet come to pass, the discovery of an undescribed genus and two undescribed species of eyeless, endogeous carabids near human population centers of Oregon and Washington offers hope that his remarks may prove prophetic for the discovery of additional species of Pacific Northwest anillines.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Subgenus of *Bembidion* Latreille from México and Guatemala, with Descriptions of Two New Species (Coleoptera: Carabidae)

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A new subgenus of *Bembidion, Geocosmius* subg. nov., is described from forests of México and Guatemala. *Geocosmius* includes *Bembidion nahuala* Erwin as its type species, as well as *B. franiae* Erwin, *B. elescarabajo* sp. nov., and additional forms similar to *B. nahuala*. In México this subgenus is widespread, ranging from Chiapas and Oaxaca north and west to Jalisco, Querétaro, and Hidalgo; most specimens are from cloud forests between 1700–2700m in elevation. A molecular phylogenetic analysis based upon eight genes indicates that *Geocosmius* is the sister group of subgenus *Liocosmius*, from western North America. In addition, a new species of subgenus *Liocosmius*, *B. cachagua* sp. nov., is described from three localities in California. Illumina sequencing was used to acquire DNA sequences of six pinned, dried specimens, which ranged in age from 24 to 57 years, allowing the phylogenetic placement of four of the studied species.

KEYWORDS: Ground beetle, Trechinae, Bembidiini, historical DNA, sequencing museum specimens, new species

George E. Ball would begin each of his many expeditions to México in Edmonton, Canada, by starting the engine of the truck that had been transformed into his custom-built field vehicle and camper. Beginning in August 1965 and over the course of the next several decades, three generations of campers carried George, his students, and colleagues south from Edmonton to the mountains of México in search of carabid beetles. George called the first of his campers *El Escarabajo*, and its successors *El Escarabajo Grande* and *El Escarabajo Oro*. The thousands of specimens George and his fellow explorers collected during his travels in the campers across many miles of roads throughout México are mostly now housed at the University of Alberta Strickland Museum (UASM), where they serve as a primary repository of information about the Mexican ground beetle fauna.

Within that wealth of material are about 300 specimens of small, brown *Bembidion* (Fig. 1A–C) somewhat similar in appearance to members of the North American subgenus *Hydriomicrus* Casey; in the UASM, George labelled these specimens "*Hydriomicrus*" or "*Hydriomicroides*". George and colleagues collected most of these specimens in leaf litter at a total of nearly 50 localities in the mountains of Chiapas, Oaxaca, Veracruz, Puebla, Guerrero, Michoacan, Jalisco, Querétaro, and Hidalgo. Although widespread (Fig. 2) and apparently common, this group of beetles is unreported from México.

As part of an effort to infer the relationships of the world *Bembidion* fauna using DNA

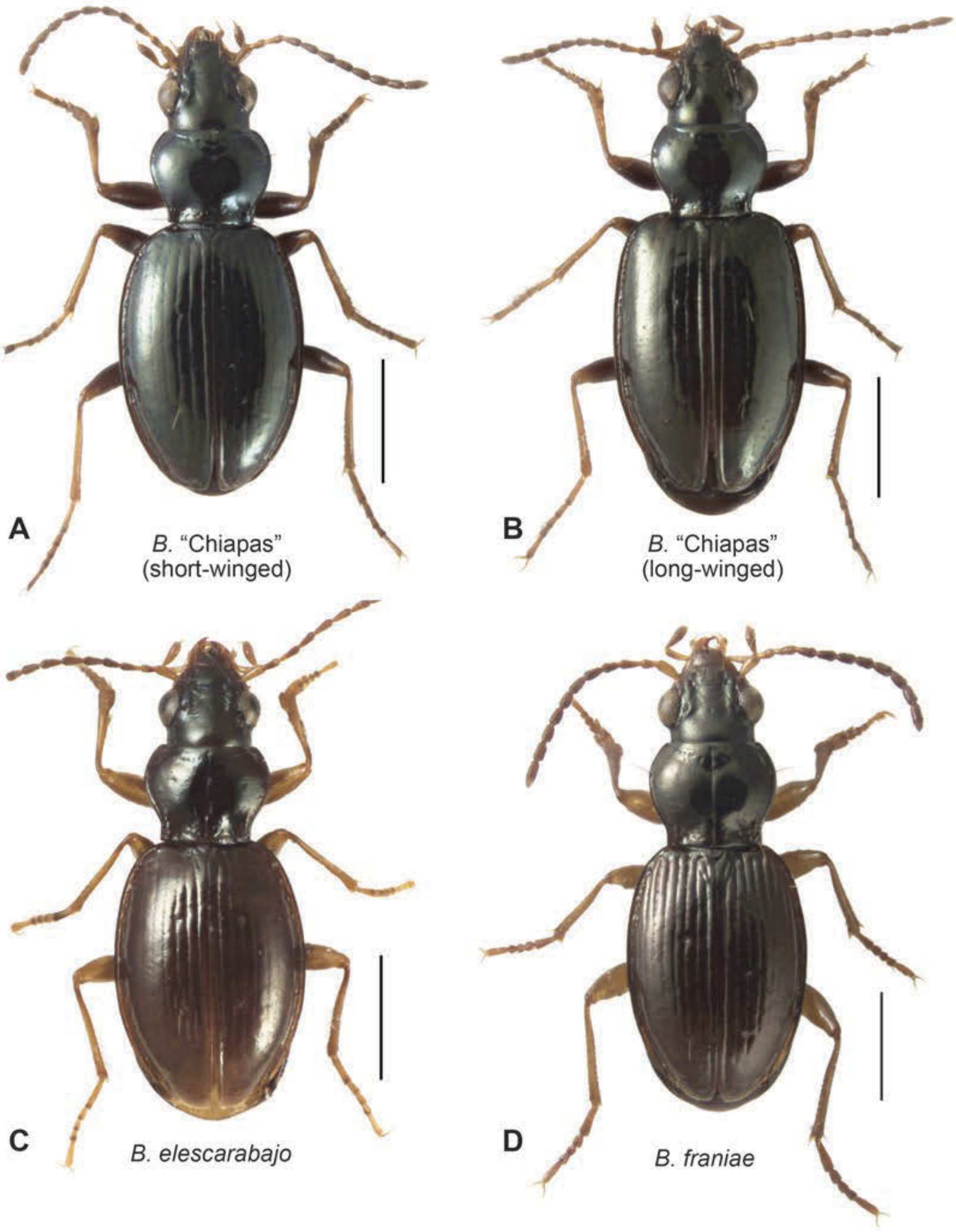


FIGURE 1. Habitus of *Geocosmius* species. (A) *Bembidion* "Chiapas", brachypterous form, voucher V101274. (B) *B.* "Chiapas", fully winged form, voucher V101273. (C) *B. elescarabajo*, paratype, voucher V101491. (D) *B. franiae*, specimen UASM371160. Note: *B. nahuala* (not shown) is extremely similar externally to *B.* "Chiapas". Scale bar 1 mm.

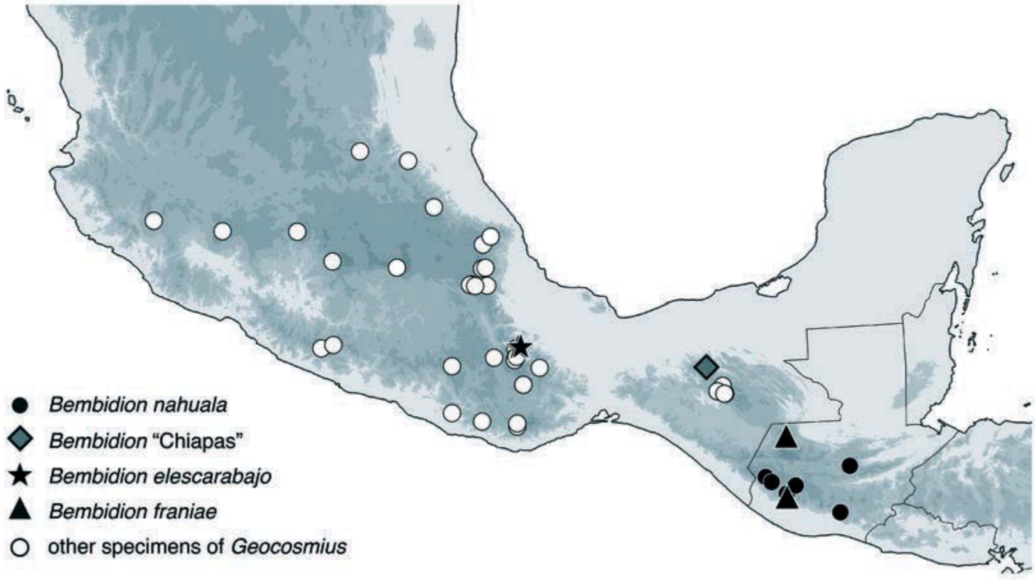


FIGURE 2. Geographic distribution of *Geocosmius* in México and Guatemala.

sequence data, I sought to sequence members of this group, as well as other enigmatic members of the Central American fauna of *Bembidion* including *Bembidion nahuala* Erwin and *Bembidion franiae* Erwin, two species from Guatemala placed in their own species groups by Erwin when he described them in 1982. Luca Toledano had noted (pers. comm. 2009) the similarity of George's Mexican "*Hydriomicroides*" to *Bembidion nahuala*, and Erwin (1982) noted the genitalic similarity of *B. nahuala* and *B. franiae*. In addition, Erwin (1982) noted that "both are similar to diverse members of the subgenus *Peryphus* [*Ocydromus* complex *sensu* Maddison (2012)] or *vernale* group".

In this paper I report that Mexican "*Hydriomicroides*", *Bembidion nahuala*, and *Bembidion franiae* are closely related, and form a distinct lineage within *Bembidion*, well separated from others, and unrelated to subgenus *Peryphus*. The sister group of this distinct lineage is the subgenus *Liocosmius*, a group of delicate, spotted, riparian beetles found in western North America (Maddison and Cooper 2014). I describe the Mexican — Guatemalan lineage as a new subgenus, *Geocosmius*, and describe one new species within the group. In addition, a curious and rare species of *Liocosmius* was discovered after our revision of that subgenus (Maddison and Cooper, 2014) was published. I take this opportunity to describe that species, and include it in the phylogenetic analysis of the *Geocosmius* + *Liocosmius* clade.

MATERIALS AND METHODS

Members of *Bembidion* were examined from the collections listed below. Each of the collections listed begins with the code used in the text.

CAS	California Academy of Sciences, San Francisco, USA
CMNH	Carnegie Museum of Natural History, Pittsburgh, USA
CTVR	Luca Toledano Collection, Verona, Italy
CUIC	Cornell University Insect Collection, Ithaca, USA
EMEC	Essig Museum Entomology Collection, University of California, Berkeley, USA

MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA
NHMUK	The Natural History Museum, London, UK
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, USA
OSAC	Oregon State Arthropod Collection, Oregon State University, Corvallis, USA
UASM	University of Alberta Strickland Museum, Edmonton, Alberta, Canada
UIUC	University of Illinois Urbana-Champaign, Urbana and Champaign, Illinois, USA
UNAM	Universidad Nacional Autónoma de México, Mexico City, México

Morphological methods. General methods of specimen preparation for morphological work, and terms used, follow Maddison (1993; 2008). Genitalia were prepared, after dissection from the body, by treatment in 10% KOH at 65°C for 10 minutes followed by multi-hour baths of distilled water, 5% glacial acetic acid, distilled water, and finally 100% ethanol. Male genitalia were then mounted in Euparal between two small coverslips attached to archival-quality heavyweight watercolor paper, and, once dried, pinned beneath the specimen.

Photographs of entire beetles were taken with a Leica Z6Apo lens and DMC4500 camera, and of male genitalia with a Leica DM5500B compound microscope and DMC425C camera, with Leica Application Suite v4.9 software capturing each image. Microsculpture photographs were taken with a DMC425C camera attached to a DM5500B compound scope equipped with an X-Cite 110LED light source, which provides co-axial illumination, and a 20X epi-illumination objective lens. For all photographs, a stack of images from different focal positions was merged using the PMax procedure in Zerene Systems's Zerene Stacker; the final images thus potentially have some artifacts caused by the merging algorithm. Measurements were made using Leica Application Suite v4.9 from images acquired using these imaging systems.

Taxon sampling for DNA studies. We obtained DNA sequence data for seven specimens of subgenus *Geocosmius,* as well as one specimen of the new species of subgenus *Liocosmius* (Table 1). We combined these with previously published data from all described taxa of *Liocosmius* (*Bembidion cooperi* Maddison, *B. darlingtonielum* Cooper & Maddison, *B. festivum festivum* Casey, *B. festivum hilare* Casey, *B. horni* Hayward, *B. mundum* (LeConte), *B. orion* Cooper & Maddison), two species of subgenus *Trechonepha* (*B. iridescens* (LeConte) and *B. trechiforme* (LeConte)), and 191 additional *Bembidion* species as well as 20 Bembidiini in other genera. These data came from

TABLE 1. Specimens of *Bembidion* subgenera *Geocosmius* and *Liocosmius* whose DNA was sequenced for this study. Four-digit numbers in the "#" column are D.R. Maddison DNA voucher numbers. "Wing state" indicates whether the specimen sequenced is fully winged (w+) or brachypterous (w-).

	#	Wing state	Locality
Bembidion franiae	4623	w-	Guatemala: Quetzaltenango: Cerro Zuni, Fuentes Georginas, cloud forest 2400m
Bembidion nahuala	5033	w+	Guatemala: Quetzaltenango: Fuentes Georginas, 2400m, 14.7506°N 91.4804°W
Bembidion nahuala	5034	w-	Guatemala: Quetzaltenango: Fuentes Georginas, 2400m, 14.7506°N 91.4804°W
Bembidion nahuala	5946	w+	Guatemala: San Marcos, 27.0 km NW San Marcos, 15°04'N 091°52'W, 2800-2900mts [type locality; this is a paratype in NMNH]
Bembidion "Chiapas"	4882	w+	México: Chiapas, Yerba Buena Hosp. 1.5 mi N Pueblo Nuevo, 7200', cloud forest
Bembidion "Chiapas"	5317	w-	México: Chiapas, Yerba Buena Hosp. 1.5 mi N Pueblo Nuevo, 7200', cloud forest
Bembidion elescarabajo	5945	w-	México: Oaxaca: 27.5 mi.s. Valle Nacional, 5600'
Bembidion cachagua	4758	w+	USA: California: Pinnacles National Park

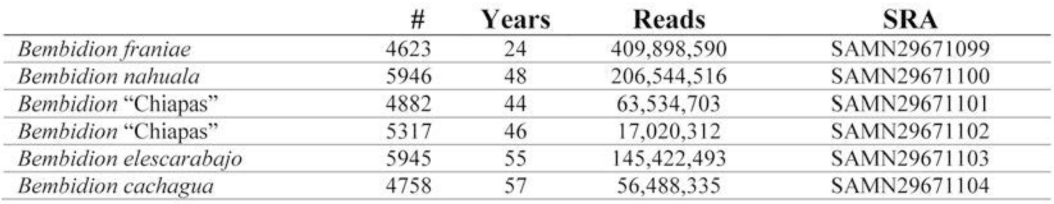
Maddison (2012), Maddison and Cooper (2014), Maddison and Maruyama (2019), Maddison and Sproul (2020), Maddison et al. (2019a), Sproul et al. (2020), and references cited therein. In addition, we sequenced a fragment of the MSP gene for 94 species outside of *Geocosmius* and *Liocosmius* that had not been previously sequenced for that gene. The full list of taxa sampled is present in the files deposited on Data Dryad (see "Data availability", below). The newly sequenced specimens are deposited in OSAC, except for *Bembidion nahuala* DNA5946 (NMNH specimen number USNM:Ent01474002) and *Bembidion cachagua* DNA4758 (EMEC specimen number 348099).

DNA sequencing. Genes studied, and abbreviations used in this paper, are: **28S:** 28S ribosomal DNA (D1-D3 domains); **18S**: 18S ribosomal DNA (near full-length); **COI**: cytochrome c oxidase subunit I; **CAD**: part 4 of carbamoyl phosphate synthetase domain of the *rudimentary* gene; **MSP**: Muscle Specific Protein 300; **Topo**: topoisomerase I; **wg**: wingless; **ArgK**: arginine kinase.

For specimens collected into 95-100% ethanol (*Bembidion nahuala* specimens 5033 and 5034), DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit. Fragments for the seven genes were amplified using the Polymerase Chain Reaction on an Eppendorf Mastercycler Pro Thermal Cycler, using TaKaRa Ex Taq and the basic protocols recommended by the manufacturers. Primers and details of the cycling reactions used are given in Maddison (2012) and Maddison and Cooper (2014). The amplified products were then cleaned, quantified, and sequenced at the University of Arizona's Genomic and Technology Core Facility using a 3730 XL Applied Biosystems automatic sequencer. Assembly of multiple chromatograms for each gene fragment and initial base calls were made with Phred (Green and Ewing, 2002) and Phrap (Green, 1999) as orchestrated by Mesquite's Chromaseq package (Maddison and Maddison, 2021a; Maddison and Maddison, 2021c), with subsequent modifications by Chromaseq and manual inspection. Multiple peaks at a single position in multiple reads were coded using IUPAC ambiguity codes.

DNA extraction and sequencing of the six dried, point-mounted specimens (Table 2) follow the protocols of Kanda et al. (2015; specimen 4623) and Sproul and Maddison (2017; remaining five specimens). In brief, DNA in specimen 4623 was extracted using the Qiagen DNeasy Blood & Tissue Kit, with a single-index library prepared using an NEBNext Ultra™ DNA Library Prep Kit for Illumina (New England BioLabs), which was then sequenced by itself on an Illumina HiSeq 2500 100-base paired-end lane at Oregon Health Sciences University. The remaining five specimens were extracted using the Qiagen QIAmp Micro Kit (using the standard protocol with carrier RNA added), with dual-index libraries prepared using the NEBNext DNA Ultra II kit (New England BioLabs), which were then sequenced on an Illumina HiSeq 3000, multiplexed on either a 100-base (specimens 4758 and 4882) or 150-base (the other specimens) paired-end run at the

TABLE 2. Dried, pinned specimens sequenced using Illumina sequencing. Four-digit numbers under "#" are D.R. Maddison DNA voucher numbers. "Years" indicates the number of years between specimen collection and DNA extraction, that is, the approximate number of years the specimens sat pinned in a drawer in a museum. The last two columns indicate the number of Illumina reads acquired for samples after trimming, and the accession number of reads in NCBI's Sequence Read Archive.



	#	Years	Reads	SRA
Bembidion franiae	4623	24	409,898,590	SAMN29671099
Bembidion nahuala	5946	48	206,544,516	SAMN29671100
Bembidion "Chiapas"	4882	44	63,534,703	SAMN29671101
Bembidion "Chiapas"	5317	46	17,020,312	SAMN29671102
Bembidion elescarabajo	5945	55	145,422,493	SAMN29671103
Bembidion cachagua	4758	57	56,488,335	SAMN29671104

Oregon State University Center for Quantitative Life Sciences. Between 17.0 million and 409.9 million reads were obtained for the samples (Table 2).

For the six specimens on which Illumina sequencing was performed, sequences of the studied genes were obtained as follows. Reads were processed in CLC Genomics Workbench (CLCGW) versions 8.5.1–20.0.4. Reads were trimmed to eliminate low-quality ends (limit=0.05 for 4623, 4882, and 5317; limit=0.000316 for 5945 and 5946), and to remove adapter sequences. The number of reads left after trimming for each sample is shown in Table 3. *De novo* assemblies were generated using Genomics Workbench from paired, trimmed reads using an automatic word and bubble size, with the minimum contig length set to 200. The *de novo* assemblies were converted to BLASTable databases using NCBI's makeblastdb tool, and BLASTed using Mesquite's (Maddison and Maddison, 2021c) local BLAST tool (1E-80 as the e-value cutoff for nuclear protein-coding genes except for specimens 4758, 5945, and 5946, for which the cutoff used was 1E-40; the cutoff for COI and ribosomal genes was 1E-100) using the sequences of *Asaphidion yukonense* as query sequences. All contigs that were returned as hits were BLASTed to NCBI's GenBank, and rejected if the top hits were not beetles. Contigs that matched beetle sequences on GenBank were accepted according to the following rules, with one exception: if there was only one contig returned from the BLASTable local database using *Asaphidion* as the query sequence, that contig was accepted as valid and included in the analysis; if two hits, and they overlapped with no differences in the overlap region, the contigs were merged and accepted; if two or more hits, but one was at least five times longer than the others, and fully contained the others, then only the long contig was accepted. One exception to this were the two contigs returned for ArgK for *Bembidion* "Chiapas" 5317, which BLASTed to carabid sequences, but which preliminary analyses suggested were not orthologous to *Bembidion* ArgK. They are presumed to be paralogs and were rejected. The other exception was for CAD for *Bembidion nahuala* 5946, which overlapped with the analyzed region by only 126 bases, and so was excluded from consideration. For the *Geocosmius* specimens, this protocol yielded accepted sequences for 28S, 18S, and COI for all three dried specimens, but nuclear protein-coding genes for only *B. franiae* (Table 3). For *B. cachagua* 4758, reference-based assembly was also conducted in CLCGW for wingless and MSP, using *Asaphidion yukonense* sequences from Maddison (2012) as references. For each of wingless and MSP, the reference-based sequence was merged with the *de novo* fragments after preliminary phylogenetic analyses showed that the referenced-based and *de novo* fragments form a clade in the phylogenetic tree.

TABLE 3. Genes studied for specimens of subgenera *Geocosmius* and *Liocosmius*. Four-digit numbers under "#" are D.R. Maddison DNA voucher numbers. Voucher numbers and other information for previously published sequences are available in their respective publications. Newly obtained sequences are those with GenBank accession numbers in the range ON525450 through ON525588.

	#	28S	18S	COI	CAD	MSP	Topo	wg	ArgK
Subgenus *Geocosmius*									
Bembidion franiae	4623	ON525474	ON525482	ON525466	ON525453	ON525583	ON525458	ON525450	ON525463
B. nahuala	5033	ON525475		ON525467	ON525454	ON525584	ON525459		
B. nahuala	5034	ON525476	ON525483	ON525468	ON525455	ON525585	ON525460	ON525451	
B. nahuala	5946	ON525477	ON525484	ON525469		ON525586			
B. "Chiapas"	4882	ON525478	ON525485	ON525470	ON525456	ON525587	ON525461		
B. "Chiapas"	5317	ON525479	ON525486	ON525471					
B. elescarabajo	5945	ON525473	ON525481	ON525465		ON525582			
Subgenus *Liocosmius*									
B. cachagua	4758	ON525480	ON525487	ON525472	ON525457	ON525588	ON525462	ON525452	ON525464
B. cooperi		KJ624158	KJ624356	KJ624318	KJ624207	KJ624364	KJ624273	KJ624243	KJ624254
B. darlingtonielum		KJ624161	KJ624357	KJ624321	KJ624210		KJ624276	KJ624245	KJ624255
B. festivum festivum		KJ624173		KJ624332	KJ624221	KJ624373	KJ624287	KJ624250	KJ624259
B. festivum hilare		JN170338		JN171034	KJ624217		KJ624283	KJ624249	JN170559
B. horni		JN170356	JN170182	KJ624338	JN170824	KJ624379	JN171228	JN171426	JN170578
B. mundum		JN170386	JN170205	JN171072	JN170858	KJ624382	JN171253	JN171458	JN170614
B. orion		KU233798	KU233698	KU233848	KU233986	KJ624385	KU234083	KU233873	KU234036

All told, sequences of between three and eight genes were obtained for each specimen of *Geocosmius* and *Liocosmius* (Table 3).

Alignment and data exclusion. Alignment was not difficult for any of the protein-coding genes. There were no insertion or deletions (indels) evident in the sampled CAD, ArgK, Topo, or COI sequences. In wingless there was a 6-base insertion in three species within subgenus *Odontium*, and a separate three-base insertion within the subgenus *Omotaphus*. Thus, the protein-coding genes could be aligned manually. Alignments of 28S and 18S was conducted in MAFFT version 7.130b (Katoh and Standley, 2013), using the L-INS-i search option and otherwise default parameter values.

Sites in 28S and 18S were chosen to be excluded from consideration using the modified GBLOCKS analysis present in Mesquite with the following options: minimum fraction of identical residues for a conserved position = 0.2, minimum fraction of identical residues for a highly-conserved position = 0.4, counting fraction within only those taxa that have non-gaps at that position, maximum number of contiguous non-conserved positions = 4, minimum length of a block = 4, and allowed fraction of gaps within a position = 0.5.

Phylogenetic analyses. Maximum likelihood analysis was conducted for each gene individually using IQ-TREE version 2.1.3 (Nguyen et al., 2015), as orchestrated by Mesquite's Zephyr package (Maddison and Maddison, 2021b; Maddison and Maddison, 2021c). The ModelFinder feature within IQ-TREE (Kalyaanamoorthy et al., 2017) was used to find the optimal character evolution models. The MFP model option was used for 28S and 18S, and the TESTMERGE option for protein-coding genes. The TESTMERGE option sought the optimal partition of sites, beginning with the codon positions in different parts. In addition, analyses with the concatenated data were conducted, with the TESTMERGE option also being used, beginning with each codon position for each gene as a separate part (thus, the analysis began allowing for up to 17 parts, three for each of the five protein-coding genes, and one for each of 28S and 18S). Fifty searches were conducted for the maximum-likelihood tree for each of the single-gene matrices, and 100 searches for the concatenated matrix; for standard, non-parametric bootstrap analyses, 500 replicates were used.

Data availability. Sequences of the studied genes have been deposited in GenBank with accession numbers ON525450 through ON525588. Illumina reads are archived on NCBI's Sequence Read Archive under the accession numbers SAMN29671099 through SAMN29671104 (Table 2). Files containing the entire (untrimmed) gene sequences for each specimen as well as the inferred trees for each gene have been deposited in Dryad (data available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.b5mkkwhgc).

PHYLOGENETIC RESULTS

Both *Geocosmius* and *Liocosmius* (with the later including *B. cachagua*, sp. nov.) are monophyletic (Fig. 3, 4A), with strong or very strong support from seven of the eight genes studied (Fig. 4B). Within *Bembidion*, *Geocosmius* is sister to subgenus *Liocosmius* (Figs 3, 4A), with moderate to very strong support from 28S, CAD, MSP, and Topo, and some support from COI (Fig. 4B). There is moderate support for the sister of *Geocosmius* + *Liocosmius* being the western North American subgenus *Trechonepha*, with two recognized species, *Bembidion iridescens* LeConte and *B. trechiforme* LeConte. Evidence for this relationship comes primarily from 28S and CAD, with some evidence provided by ArgK. Within *Geocosmius*, there is strong support for *Bembidion nahuala* being sister to *B.* "Chiapas", and weaker support for their sister being *B. elescarabajo*. Within *Liocosmius*, there is weak support for *B. cachagua* being sister to the remaining *Liocosmius*.

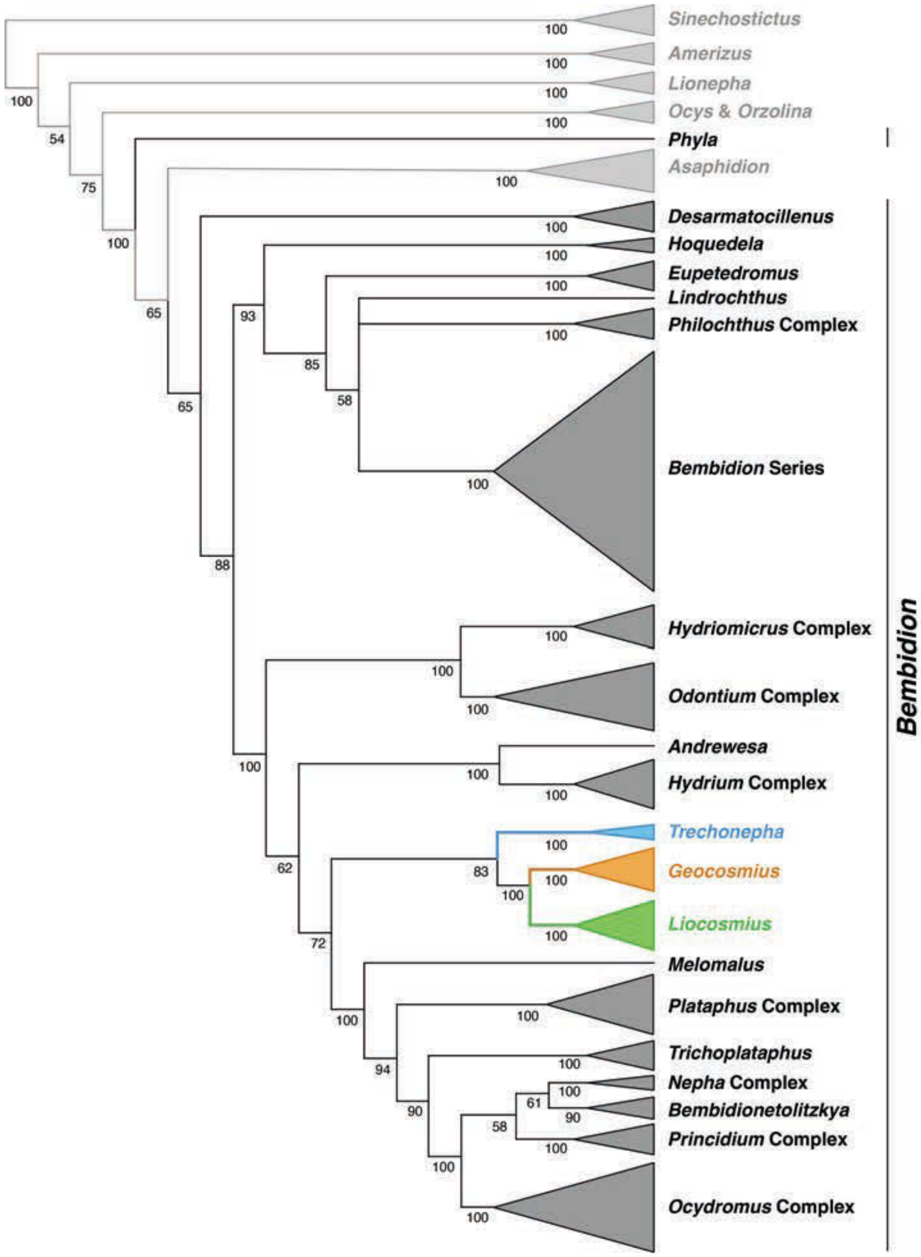
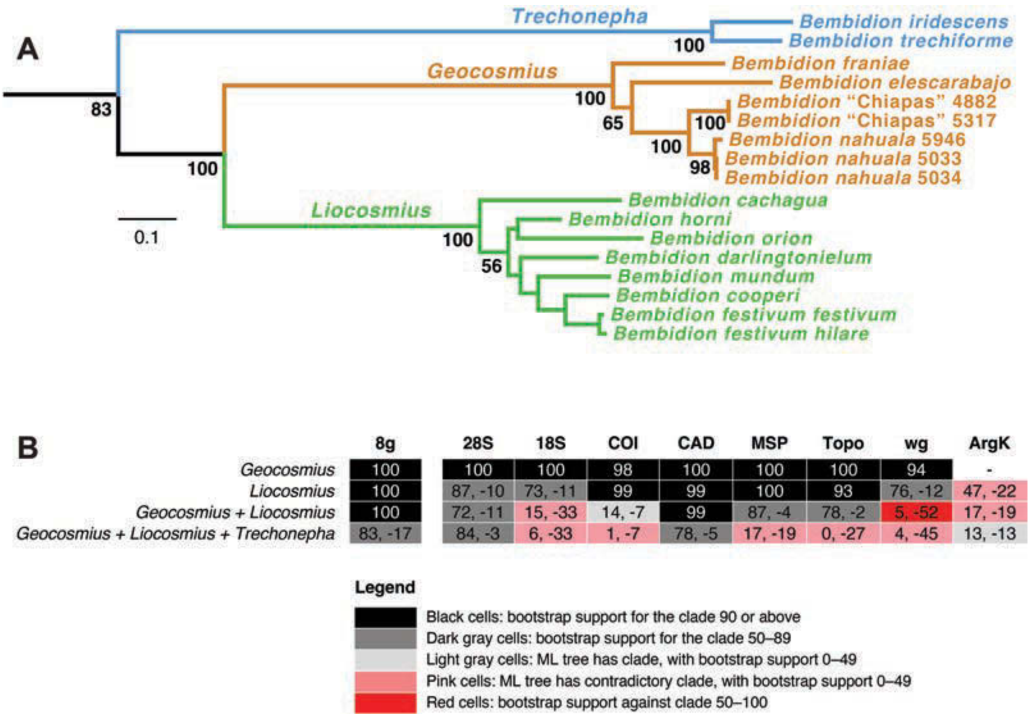


FIGURE 3. Overview of maximum likelihood bootstrap tree of Bembidiini based upon the concatenated, eight-gene matrix, showing position of the subgenera *Geocosmius*, *Liocosmius*, and *Trechonepha*. Taxon names in paler gray are genera of Bembidiini other than *Bembidion*; all other taxa are subgenera, subgeneric complexes, or subgeneric series of *Bembidion*. Triangles (clades) have their area approximately proportional to the number of species included in the analysis. Details within each clade are presented in the files submitted to Data Dryad (see Data availability section). Values below branches are the bootstrap support for that clade, expressed as a percentage.



	8g	28S	18S	COI	CAD	MSP	Topo	wg	ArgK
Geocosmius	100	100	100	98	100	100	100	94	-
Liocosmius	100	87, -10	73, -11	99	99	100	93	76, -12	47, -22
Geocosmius + *Liocosmius*	100	72, -11	15, -33	14, -7	99	87, -4	78, -2	5, -52	17, -19
Geocosmius + *Liocosmius* + *Trechonepha*	83, -17	84, -3	6, -33	1, -7	78, -5	17, -19	0, -27	4, -45	13, -13

Legend

■ Black cells: bootstrap support for the clade 90 or above
▩ Dark gray cells: bootstrap support for the clade 50–89
□ Light gray cells: ML tree has clade, with bootstrap support 0–49
🟥 Pink cells: ML tree has contradictory clade, with bootstrap support 0–49
🟥 Red cells: bootstrap support against clade 50–100

FIGURE 4. Phylogenetic results, focusing on subgenera *Geocosmius*, *Liocosmius*, and *Trechonepha*. (A) A portion of the maximum likelihood tree inferred from the concatenated, eight-gene matrix. Numbers of the branches are maximum likelihood bootstrap percentages; bootstrap values within most of *Liocosmius* not shown. Other bembidiines omitted from the image. Scale bar 0.1 units, as calculated by IQ-TREE. (B) Support for various clades, measured with bootstrap support percentages from maximum likelihood phylogenetic analyses. One or two values are given in each cell. If the bootstrap support percentage is 90 or more, only that value is listed. If bootstrap support is less than 90, two values are listed: the bootstrap support for the clade, followed by a negative value which is the bootstrap support against the clade, as measured by the bootstrap value for the contradictory clade with the highest support value. The "8g" column shows the support values for the concatenated, eight-gene matrix. "-" indicates only one species is included, and thus support for that clade cannot be measured.

TAXONOMY

Geocosmius Maddison, new subgenus

Type species *Bembidion nahuala* Erwin, 1982

Derivation of name. The first portion of the name, "Geo", consists of the first three letters of George E. Ball's given name, and is included to honor George's long-term commitment to discovering and documenting the biodiversity of México, and his role in collecting most known specimens of this subgenus. In addition, "Geo" is a Greek prefix referring to the Earth, and evokes the interesting relative geographic distributions of *Geocosmius* and its sister group, *Liocosmius*. The last portion of the name, "cosmius", was chosen to provide a linguistic connection to its sister group.

Habitus. Beetles of the subgenus *Geocosmius* have the general appearance of typical members of non-riparian cloud forest *Bembidion*; that is, they are small, dark, unspotted, and convex; most specimens lack hind wings and have rounded shoulders. A similar form has evolved multiple times within *Bembidion* in similar habitats, as in the subgenus *Ecuadion* Moret & Toledano from

Central and South America (Moret and Toledano, 2002), *Nesocidium* Sharp from Hawaii (Liebherr, 2008), subgenus *Hypsipezum* Alluaud from Africa, and some members of the *Ocydromus* complex in Central America (e.g., *B. chiriqui* Erwin) (Maddison et al., 2019b).

Morphological Diagnosis. Small to medium (2.6–3.5 mm), shiny *Bembidion,* without colored markings on the elytra. Frontal furrows single, broad, shallow, well-marked (*Bembidion franiae*), or broad, shallow, and disrupted by surface rugosity (other species), not convergent or extended onto clypeus. Eyes of normal size for *Bembidion* (*B. franiae*) or slightly reduced (other species). Mentum with anterior lateral region complete, triangular; mentum tooth triangular.

Posterior angle of pronotum with a posterolateral carina, although it is interrupted posteriorly in *B. franiae* and some specimens of other species. Posterior margin of pronotum not strongly sinuate laterally; basal transverse furrow weak, disrupted by shallow punctures, and in many specimens interrupted by the medial furrow extending posteriorly to the hind margin of the pronotum; hind angles right or slightly acute.

Elytron with lateral bead ending at humerus, not prolonged onto base, although in *B. franiae* a short carina extends from the end of the bead toward the center of the elytral disc at an angle, giving the impression of an angulate shoulder bead. Striae vary in depth, from anteriorly deep in *B. franiae* to much shallower in most other species, with lateral striae increasingly evanescent; all striae absent or nearly so in the posterior quarter of the elytra, except for the first stria; two discal setae in third stria. Elytra slightly iridescent in *B. franiae*, because of the transverse microsculpture, and slightly dull in *B. elescarabajo*, because of the nearly isodiametric sculpticells; elytral microsculpture absent from specimens of the *nahuala* group. Mesoventral process without subapical setae. Metaventral process unmargined.

Apex of last visible abdominal sternite with two setae in males, four setae in females. Apices of each paramere normally with three setae, but some individuals have two or four setae on the left paramere, and one has four setae on the right paramere.

Within the geographic range of *Geocosmius* live several other species of *Bembidion* with small, convex adults without spots: *B. purulha* Erwin (a member of the *Ocydromus* complex), as well as *B.* (*Cyclolopha*) *cyclodes* Bates and *B.* (*Cyclolopha*) *championi* Bates. *Bembidion purulha* can be distinguished by the elytral striae, which abruptly transition at about the halfway point from large, distinct punctures anteriorly to fully effaced striae posteriorly, as well as a fully margined metaventral process. The two *Cyclolopha* species can be distinguished by the much broader pronotum with very rounded hind angles, with the posterior lateral seta notably anterior to the posterior margin of the pronotum at the midline.

All known specimens of *B. franiae* and *B. elescarabajo* lack hind wings. *Bembidion nahuala* and *B.* “Chiapas” are wing dimorphic, with most specimens lacking hind wings, and with more rounded elytra and notably rounded shoulders (Fig. 1A). A minority of specimens of both species are fully winged, with more parallel-sided elytra and less rounded shoulders, giving these specimens a rather different appearance (Fig. 1B).

Habitat. Based upon the available label data, species in this group live in cloud forests (Guatemala, Chiapas, Oaxaca, Guerrero, and Puebla), oak-pine forests (Guatemala, México, Oaxaca), pine forests (Veracruz), pine-alder forests (Veracruz), wet oak forests (Puebla), and oak-alder forests (Guerrero).

Geographic distribution. This subgenus is known from southern México and Guatemala (Fig. 2).

Composition. The known species of subgenus *Geocosmius* are *Bembidion franiae* Erwin, *Bembidion elescarabajo* Maddison, sp. nov., and then a group of similar forms (the *nahuala* group) including *Bembidion nahuala* Erwin and *B.* “Chiapas”. I have examined 5 specimens of *B. frani-*

ae, 13 of *B. elescarabajo*, and 311 specimens of the *nahuala* group (UASM, CUIC, CMNH, NMNH, UNAM, CTVR, and OSAC).

Members of the *nahuala* group are very similar to one another. With the exception of a form with deeper elytral stria from Volcán de Colima in Jalisco, and the differences associated with wing dimorphism and gender, this widespread complex shows no obvious patterns of external morphological variation. *Bembidion nahuala* Erwin and *B.* "Chiapas" appear to be different species based upon DNA sequences (Fig. 4) and male genitalia (Fig. 5). The two forms differ by 4 bases in 28S, and by 27 bases or 4.1% in COI; these nucleotide differences in COI imply two amino acid differences between the species.

Key to adults of species of *Bembidion* subgenus *Geocosmius*

1. Elytra with evident microsculpture 2
— Elytra without evident microsculpture . . . . *nahuala* group

2. Entire dorsal surface with evident microsculpture, including on the top of the head and disc of pronotum; throughout the disc of the pronotum there are clearly and completely edged sculpticells. Elytral microsculpture more transverse (Fig. 6A). All striae deep in anterior quarter of the elytra, with intervals notably convex in this region. Eyes of normal size for *Bembidion* (Fig. 1D) . . . . *Bembidion franiae* Erwin
— Dorsal surface of head shiny, without microsculpture, at least at center; pronotal disc shiny, without clear microsculpture. Elytral microsculpture more or less isodiametric (Fig. 6B). Lateral striae absent or nearly so, even in anterior region of elytra. Eyes slightly less protruding than typical for *Bembidion* (Fig. 1C) . . . . ***Bembidion elescarabajo*** sp. nov.

Bembidion elescarabajo, sp. nov.

(Figures 1C, 5C, 5D, 6B)

Holotype male, in UASM, labeled "MEX. Oaxaca Rte. 175. 28 mi. s. Valle Nacional. 2040 m. Aug. 25, 1974" [handwritten], "MIDDLE AMER. EXP. 1974, H. Frania & G.E. Ball collectors", "David R. Maddison V101490 Voucher Specimen", "HOLOTYPE Bembidion elescarabajo David R. Maddison [partly handwritten, on red paper]", "UASM# 410000" [printed on white paper]. Genitalia mounted in Euparal in between coverslips pinned with specimen.

Paratypes (6 males, 6 females). "Mexico: Oaxaca. 27.5 mi s. Valle Nacional. 5600' VIII.15-16.65", "George E. Ball and D.R. Whitehead collectors" (2: UASM, CTVR). "MEXICO: Oaxaca. 27.5 mi s. Valle Nacional. 5600' V.4-5.1966", "George E. Ball and D.R. Whitehead collectors" (5: UASM, UNAM, OSAC, NHMUK, NMNH). "MEXICO Oaxaca 36.2 km s. Valle Nacional, Rte. 175 cloud forest ca. 2010 m., April 27, 1977", "MEXICAN EXP. 1977 J.S. Ashe, H.E. Frania, D. Shpeley coll." (1: UASM). "MEX. Oaxaca Rte. 175. 28 mi. s. Valle Nacional. 2040 m. Aug. 28, 1974", "MIDDLE AMER. EXP. 1974, H. Frania & G.E. Ball collectors" (1: UASM). "MEX. Oaxaca 35.1 mi.n. Istlan de Juarez, Rte. 175. 2050m, 22.07.1975", "MEX. EXP. 1975, H. Frania & G.E. Ball collectors" (3: UASM, UNAM, OSAC).

Type locality. México: Oaxaca: 28 miles (45 km) south of Valle Nacional (San Juan Bautista Valle Nacional) along route 175; this is approximately 17.594°N 96.427°W.

Derivation of specific epithet. This species is named in honor of George Ball's three *El Escarabajo* campers. George and his colleagues used those trusty vehicles to explore the regions of México inhabited by *Geocosmius*, and on these journeys most known specimens of the subgenus were collected, including the type series of this species. The name is to be treated as a noun in apposition.

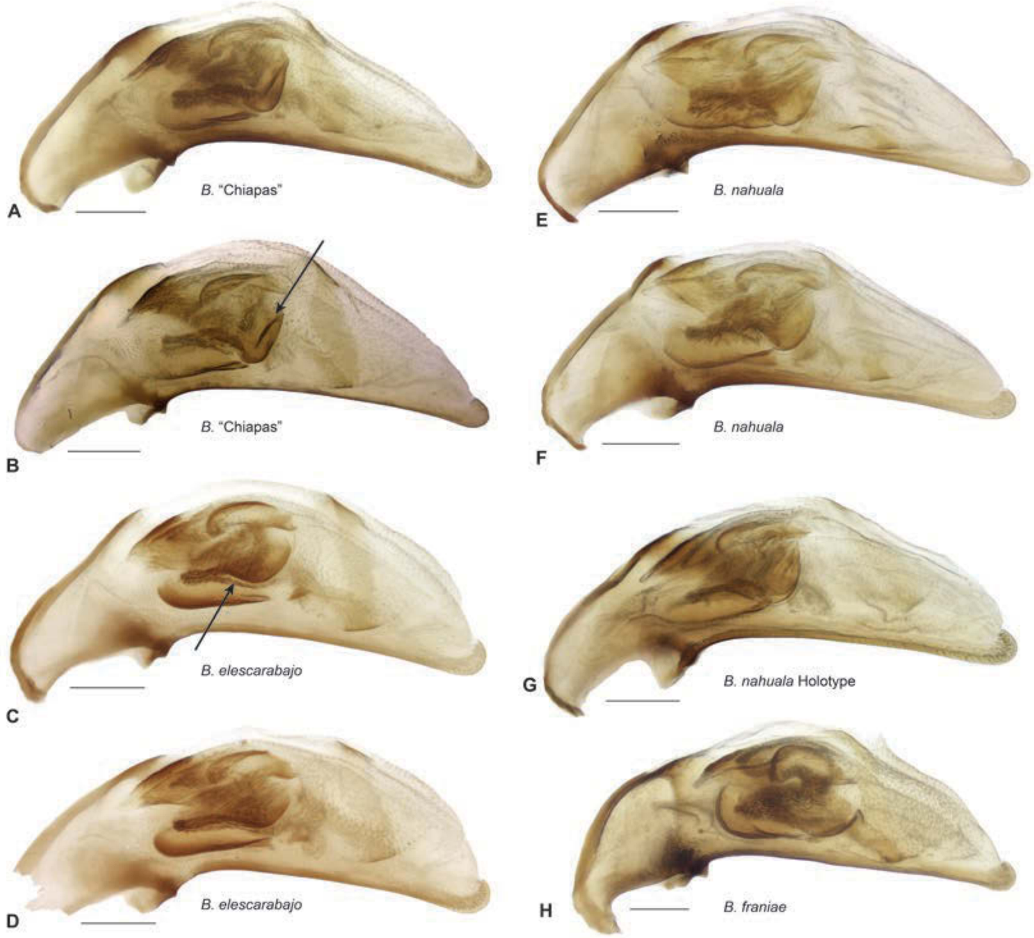


FIGURE 5. Aedeagi of *Geocosmius*. (A) *Bembidion* "Chiapas", voucher DNA5317. (B) *B*. "Chiapas", voucher DNA4882. Arrow indicates the prominent ridge characteristic of this species. (C) *B. elescarabajo*, voucher V101490. Arrow indicates the less curved sclerite margin characteristic of this species. (D) *B. elescarabajo*, voucher V101489. (E) *B. nahuala* voucher DNA5033. (F) *B. nahuala* voucher DNA5034. (G) *B. nahuala*, holotype. (H) *B. franiae*, voucher DNA4623. Scale bar 100 µm.

Description. Body length 3.25–3.90 mm. Body brown, with head and pronotum slightly darker than elytra. Legs uniform in color, testaceous or slightly infuscated; antennomere 1 testaceous, antennomeres 2 and 3 with distal half slightly infuscated, remaining antennomeres slightly infuscated; penultimate maxillary palpomere infuscated, antepenultimate testaceous. Mentum with anterior lateral regions large, triangular; medial tooth triangular with rounded tip; frontal furrows weakly defined, somewhat rugose; eyes not prominent; prothorax with greatest width in front of middle; sides sinuate, with sides in front of hind angle straight; hind angle approximately right; posterolateral carina evident, moderately long, and straight; posterior region of pronotum slightly rugose with poorly defined punctures. Elytra with lateral bead not prolonged medially at shoulder; inner three striae well-defined around ed3; striae 4 and 5 faint, even anteriorly, with striae 6 and 7 extremely faint; only first stria evident to apex, with other striae more or less absent from apical fourth. Microsculpture absent from dorsal surface of head at center and from pronotal disc; evident in both sexes over entire surface of elytra, nearly isodiametric (Fig. 6B). Pronotum with two lateral setae on each side; elytron with two setae in third stria. Aedeagus (Fig. 5C, D) similar to members of the *nahuala* group (Fig. 5A, B, E, F, G), but with ventral margin of the large central sclerite less abruptly bent.

Additional characteristics. All thirteen specimens examined lack hind wings.

Geographic distribution. Known only from four closely proximate localities in Oaxaca along route 175 between San Juan Bautista Valle Nacional and Ixtlán de Juárez, between about 17.604°N 96.381°W and 17.594°N 96.460°W (Fig. 2, star). These localities are at most 9 km apart.

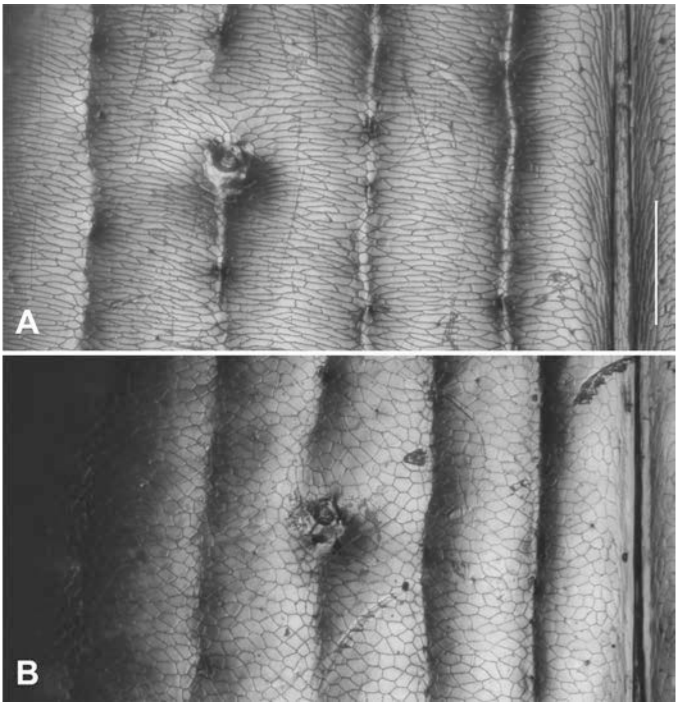


FIGURE 6. Microsculpture of *Geocosmius*. (A) *Bembidion franiae,* voucher DNA4623, (B) *B. elescarabajo*, voucher V101491. Scale bar 100 µm.

Geographic relationships with other species. One specimen of a *nahuala*-group species (perhaps *Bembidion* "Chiapas") was collected at the same place and time as five of the paratypes of *B. elescarabajo*: "Mexico: Oaxaca. 27.5 mi s. Valle Nacional. 5600' VIII.15-16.65".

Habitat. Based upon imagery in Google Earth, and the annotation "cloud forest" on the label of the 1977 specimen, the known localities are all in cloud forest.

Subgenus *Liocosmius* Casey

Type species *Ochthedromus mundus* LeConte (1852), designated by Lindroth (1963).

A revision of *Liocosmius* is provided in Maddison and Cooper (2014). The species described here as *Bembidion cachagua* became known shortly before the publication of that work, but it was not recognized as a *Liocosmius* until after a genitalic dissection and DNA sequencing revealed that it belonged to the subgenus. Within *Liocosmius*, *B. cachagua* is unusual for its microsculptured pronotum and head, rugose pronotum (at least in the posterior portion), low-contrast color pattern on the elytra, and slight metallic sheen on elytra. The species can be identified in the key provided by Maddison and Cooper (2014) if an additional couplet is added at the beginning:

0. Evident microsculpture throughout dorsal surface of head (except, in some specimens, between eyes near midline), and over most of the pronotum; microsculpture near apex of elytra evident as distinct sculpticells that are only slightly transverse. Ground color of elytra brown, slightly depigmented, contrasting only weakly with pale spots (Fig. 7A). Entire dorsal surface with slight yellow-green or brown-green metallic sheen, including on the elytra.

Appendages infuscated. Posterior region of pronotum evidently wrinkled, at least medially, and with many punctures (Fig. 7B) .... ***B. cachagua*** sp. nov.

— Most of the dorsal surface of head without microsculpture; pronotum with at most weak, very transverse microsculpture restricted to lateral margins; microsculpture absent from apex of elytra or consisting of very transverse sculpticells. If ground color of elytra brown and contrasting only weakly with pale spots, then appendages testaceous, not infuscated (Maddison and Cooper 2014, Fig. 2). Elytra without metallic sheen. Posterior region of pronotum smoother (e.g., Maddison and Cooper 2014, Fig. 7) 1

Bembidion cachagua, sp. nov.
(Figures 7, 8)

Holotype male, in CAS, labeled: "U.S.A.: CALIFORNIA: Monterey Co., Hastings Nat. History Reserve. J.M. Linsdale Colln.", "C.A.S. Accession 29-V-48 Cachagua Creek", "David R. Maddison DNA3842 DNA Voucher" [pale green paper], "HOLOTYPE Bembidion cachagua David R. Maddison" [partly handwritten, on red paper]. Genitalia mounted in Euparal in between coverslips pinned with specimen; extracted DNA stored separately.

Paratypes (2 males, 4 females). Same data as holotype (3: CAS, OSAC). "Pinnacles Nat'l Mon. 4.19.58 Toschi" (1: EMEC; this is D.R. Maddison DNA voucher number 4758, and EMEC specimen number 348099). "Santa Barbara Cal. May '91 L.E.R." (1: MCZ, Hayward Collection). "S. Cal." (1: UIUC).

Type locality. Cachagua Creek does not flow through Hastings Natural History Reserve, although a tributary, Finch Creek, does. At its nearest Cachagua Creek is approximately 2.7 km from the boundary of the Reserve. It is reasonable to presume that the upper label on the holotype, "U.S.A.: CALIFORNIA: Monterey Co., Hastings Nat. History Reserve. J.M. Linsdale Colln.", was a generic label used for all specimens from the Linsdale collection, as J.M. Linsdale was the Director of the Hastings Natural History Reserve at the time (Alagona, 2012). The lower label presumably allowed customization for each specimen, and the locality information on the second label is thus likely more accurate. Thus, the type locality would more accurately be stated to be "Cachagua Creek near Hastings Natural History Reserve".

Derivation of specific epithet. Named after Cachagua Creek, the locality at which four of the seven known specimens were found. Treated as a noun in apposition.

Description. Body length 3.45–3.90 mm. Forebody dark brown or piceous, with metallic greenish-yellow or brassy sheen; elytra pale chestnut brown, with the four testaceous elytral spots contrasting only slightly against the ground color (Fig. 7). In four specimens, the antennae are infuscated throughout; in the other three specimens, two of which appear to be teneral, the basal 2.5 antennomeres are testaceous; legs pale reddish brown, slightly infuscated. Frontal furrows shallow, not prolonged onto clypeus. Mentum with anterior lateral regions triangular, large; central tooth of mentum triangular, slightly rounded. Prothorax narrow, only slightly wider than head; hind angles slightly obtuse; posterolateral carina of pronotum long and more or less straight; posterior region of pronotum rugose, wrinkled and with evident punctures (Fig. 7). Elytra with lateral bead not prolonged medially at shoulder; striae shallow, poorly defined, with extremely small punctures. Microsculpture evident throughout the dorsal surface of the forebody in most specimens, more or less isodiametric or slightly transversely stretched, in some specimens effaced in the center of the head between the eyes, and in the center of the pronotal disc; microsculpture effaced from most of elytra, but evident behind the second dorsal discal seta (ed5) as defined, slightly transverse sculpticells. Pronotum with two lateral setae on each side; elytron with two setae in third stria. Aedea-

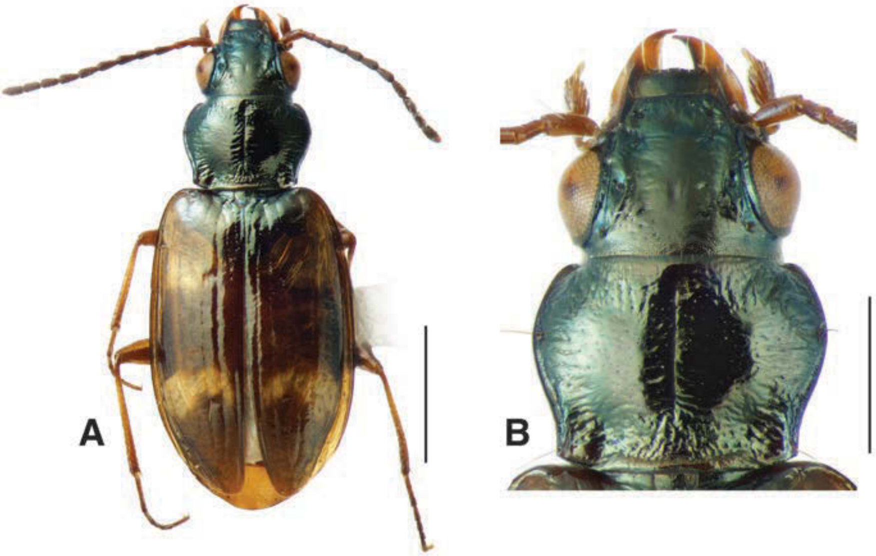


FIGURE 7. Holotype of *Bembidion cachagua*. (A) Habitus, scale bar 1 mm. (B) Forebody, scale bar 0.5 mm.

gus (Fig. 8) with a small brush sclerite similar to that of *B. horni*, but with a long, slightly curved flagellum, most similar to that of *B. festivum*.

Most easily distinguished from other *Liocosmius* by the stronger and more widespread microsculpture, the greenish-yellow metallic sheen on the dorsal surface, and the relatively low-contrast pattern on the elytra. In comparison to *Bembidion horni* in particular, the pronotum in *B. cachagua* is much narrower, with straighter sides.

Variation. Some specimens have numerous punctures on the dorsal surface of the head and in anterior regions of the pronotum.

Geographic Distribution. Known only from California from Monterey and San Benito Counties south to Santa Barbara County (Fig. 9).

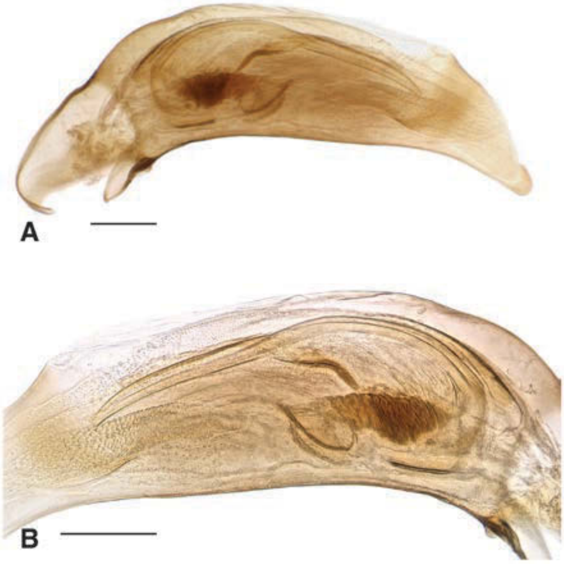


FIGURE 8. Aedeagus of holotype of *Bembidion cachagua*. (A) Left lateral view. (B) Right lateral view. Scale bar 100 µm.

Geographic relationships with other species. Found sympatrically with four other species of subgenus *Liocosmius*: *Bembidion horni*, *B. mundum*, *B. darlingtonielum*, and *B. festivum*.

Habitat. Unknown. It may occur in similar habitats as other *Liocosmius*, that is, on sandy shores of creeks, most often in shaded or partly shaded areas, and in general where the sand banks are relatively steep.

Notes. I have seen no specimens of this species collected since 1958. In late April and early

May 2014, John Sproul and I searched at multiple known localities for this species, including at Hastings Natural History Reserve, Pinnacles National Park, around Santa Barbara, and at many other localities in between. We searched in typical *Liocosmius* microhabitats (including steep sand banks in partial shade), with no success. Along Finch Creek in Hastings Natural History Reserve, the only *Bembidion* in those microhabitats was *B. iridescens* LeConte; in nearby microhabitats along the creek shore were three species of *Bembidion*: *B. californicum* Hayward, *B. perspicuum* LeConte, and *B. lugubre* LeConte.

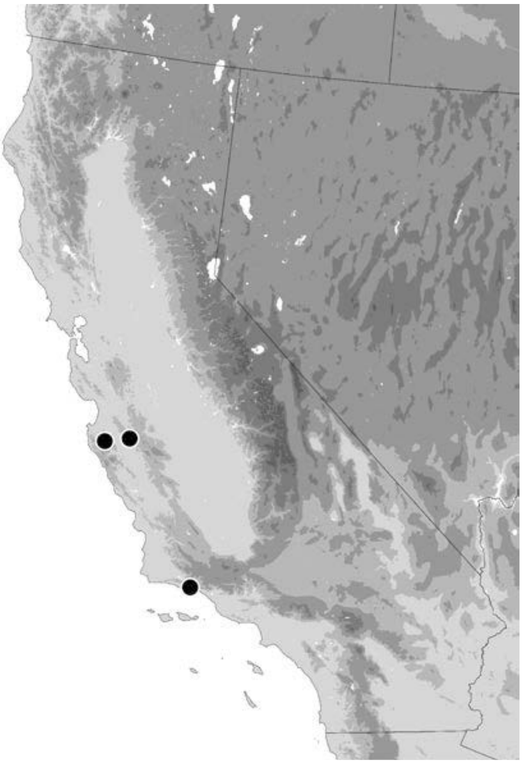


FIGURE 9. Map of California showing the geographic distribution of *Bembidion cachagua*.

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I am grateful to the curators who have looked after *Bembidion* specimens in the world's museums, and who have lent us specimens for study: David H. Kavanaugh (CAS), Robert Davidson (CMNH), Jim Liebherr (CUIC), Kipling Will (EMEC), Philip Perkins and Crystal Maier (MCZ), Terry Erwin (NMNH), George E. Ball, Danny Shpeley, and Felix Sperling (UASM), and Tommy McElrath (UIUC). Thanks as well to Luca Toledano for passing along the *Geocosmius* he had in his care. I am especially grateful to Felix Sperling for granting permission to distribute paratypes to several collections.

Numerous other people helped this project in important ways, and I am very thankful to all of them. John S. Sproul, Olivia F. Boyd, and R. Antonio Gomez prepared the libraries for Illumina sequencing. Kojun Kanda collected the first available specimens in ethanol of *Geocosmius*. John Sproul and Paul G. Johnson helped look for *Bembidion cachagua*. Vincent Voegeli of the Hastings Natural History Reserve gave permission to search for *B. cachagua* there, and gave advice about habitats. Both David H. Kavanaugh and Wayne Maddison helped in numerous ways over the years, including providing valuable advice.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Inventory of the Carabid Beetle Fauna of the Gaoligong Mountains, western Yunnan Province, China: Species of the Tribe Cyclosomini Laporte, 1934 (Coleoptera: Carabidae), with Descriptions of Two New Species.

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Our study of 184 specimens of cyclosomine carabid beetles collected during a ten-year biodiversity inventory project in the Gaoligong Shan region of western Yunnan Province, China, recognized five different species, representing two genera, as occurring in the study area. Two species are described as new: *Cyclosomus acutangulus* sp. nov. (type locality: China, Yunnan, Tengchong County, Wuhe Township, Longchuan River at Longjiang Bridge) and *Tetragonoderus parviculus* sp. nov. (type locality: China, Yunnan, Tengchong County, Wuhe Township, Longchuan River just below bridge at Menglian village). Lectotypes are designated for *Tetragonoderus arcuatus* Dejean, 1829, and *Bembidium punctatus* Wiedemann, 1823. We present a key for identification of adults of species in the study area as well as nomenclatural data, diagnoses, illustrations of dorsal habitus, male genitalia and other diagnostic features. We also provide information about geographical, altitudinal, and habitat distributions within the study area and overall geographical distribution for each species.

KEYWORDS: Coleoptera, Carabidae, Cyclosomini, *Cyclosomus*, *Tetragonoderus*, new species, Asia, China, Yunnan, Gaoligong Shan, distribution, biogeography, biodiversity hotspot

The Gaoligong Shan (Gaoligong Mountains) of extreme western Yunnan Province, China (Fig. 1) represents the southeasternmost extension of the Transhimalaya (Akciz et al. 2008). The range extends for more than 600 km north to south and, in the central part of the range, its crest forms the border between China and Myanmar. It also separates and forms parts of the watersheds of two of Southeast Asia's major rivers, the Irrawaddy and the Salween (known in China as the Nujiang). Elevations within the region range from a low of about 650 m in the south to more than 5000 m in the north. Chaplin (2006) reviewed the physical geography of the region. Because of its geographic isolation and rugged topography, much of this area has remained less disturbed than most other parts of China. Previous biological exploration of the area over the past 150 years has revealed exceptionally high species richness, based mainly on records for vertebrates (e.g., Stattersfield et al. 1998) and vascular plants (Li et al. 2000). Because of these traits, two large nature reserves have been established in the area, and the region has been included in the Three Parallel Rivers of Yunnan World Heritage Site (UNESCO 2003).

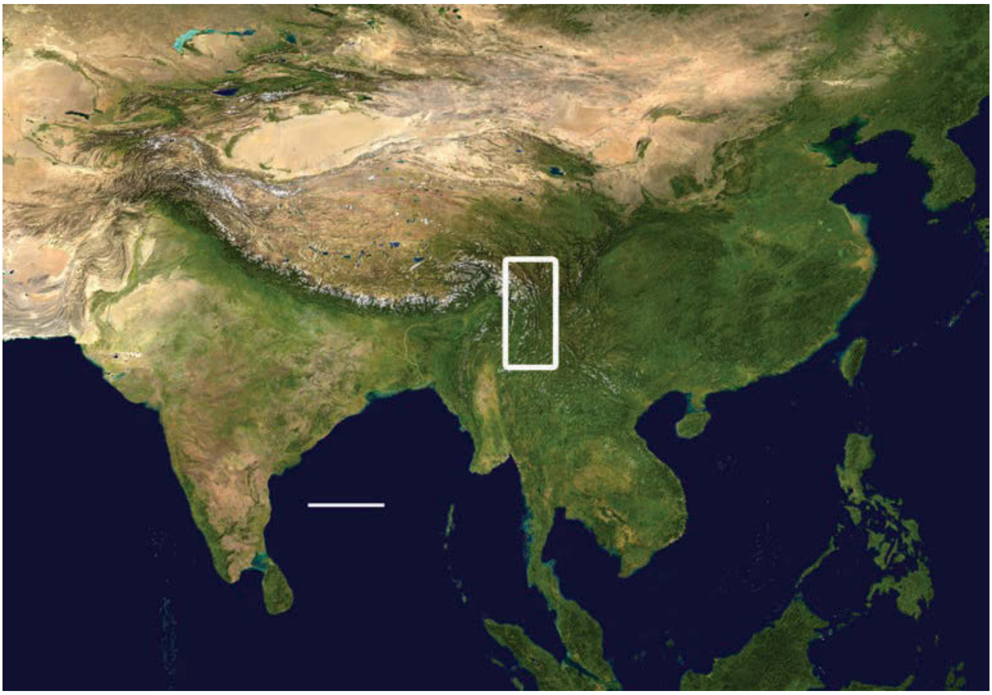


FIGURE 1. Map of Asia with study region outlined. Modified from Wikimedia Commons, World Atlas of the World, at URL: *http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_-_land_and_oceans_12000.jpg.* Scale line = 500 km.

During the period 1998 to 2007, the California Academy of Sciences participated in a joint project with the Kunming Institutes of Botany and Zoology of the Chinese Academy of Sciences to conduct a biodiversity inventory of the Gaoligong Mountains. Scientists from several additional institutions, including the Institute of Zoology (Beijing) and Royal Botanical Garden (Edinburgh) joined in the collaboration. Principal target groups for the inventory included bryophytes and vascular plants, all vertebrate groups, arachnids, myriapods and insects, especially the Neuropteroidea, Mecoptera, and Coleoptera (the Carabidae in particular). Multidisciplinary and multi-institutional teams carried out biotic sampling through more than 25 separate expeditions during that period. Numerous reports on the project have been published to date, including partial results for bryophytes, higher plants, birds, amphibians, fishes, spiders, and carabid beetles (see Deuve et al. 2016 for pertinent references).

The beetle family Carabidae includes approximately 40,000 described species of fast-running, mainly predatory, mainly nocturnal beetles, most of which are somber black or brown in color. The Gaoligong Shan (GLGS) biodiversity inventory project has increased the number of carabid beetle species known from this region from about 50 (Yu 2002) to more than 550 species, an eleven-fold increase. The task that remains is to identify all of those 500 additional species and describe any that are new to science. To date, four reports have been published, dealing with the Zabrini (Kavanaugh et al. 2014), Trechini (Deuve et al. 2016), Omophronini (Kavanaugh et al. 2021), and Broscini (Kavanaugh and Liang 2021), respectively, of the region. Subsequent reports will appear as taxonomic work on each group can be completed and not in any particular taxonomic or phylogenetic order. In this report, we present the results of our study of those species representing the tribe Cyclosomini Laporte, 1834.

Cyclosomines are beetles found mainly on the sandy shores of rivers, lakes, or oceans in some areas. Typically, they are nocturnally active beetles that spend daylight hours burrowed in the sand or hidden under other cover in their habitat. They are characterized by having a pair of setae above each eye, mandibles without scrobal setae, more or less truncate elytral apices, and extremely long hind tibial spurs (Fig. 5). Adults of many cyclosomine species have distinctive light and dark elytral color patterns (Figs. 6).

Chaudoir (1876) provided the first worldwide revision of the group. At present, the Cyclosomini, as restricted by Ball and Bousquet (2000), comprise a group of about 125 species with a combined geographical range that is essentially worldwide, but best represented in tropical and subtropical regions. Ball and Bousquet recognized four genera in the tribe: *Tetragonoderus* Dejean (1829), *Cyclicus* Jeannel (1949), *Cyclosomus* Latreille (1829), and *Mnuphorus* Chaudoir (1873). The most diverse of these taxa is *Tetragonoderus*, with about 100 described species and a distribution including all faunal regions, although the single species in the Australian Region is adventive (Lawrence et al. 1987). Although Ball and Bousquet treated *Cyclicus* as a distinct genus, we follow Bousquet (2017) and include the 23 described species and one additional subspecies previously assigned to this taxon in subgenus *Tetragonoderus* s. str. Justification for this assignment will be provided in a subsequent treatment of the Asian *Tetragonoderus* currently in preparation. Genus *Cyclosomus*, which currently includes 11 described species, is restricted to the Oriental and Afrotropical Regions. The fourth genus, *Mnuphorus*, treated by Lorenz (2005) as a genus of subtribe Masoreina, includes nine described species and one additional subspecies and is restricted to the southcentral part of the Palaearctic Region. Two of these genera, *Cyclosomus* and *Tetragonoderus*, are represented in the study area.

There has been little comprehensive taxonomic research done on the genera *Tetragonoderus* and *Cyclosomus* in China or elsewhere in Asia. Dejean (1829) included the five Asian species of *Tetragonoderus* known at that time in his review of the genus and described one of them as a new species. Andrewes (1930) reviewed current knowledge of cyclosomines at that time in his catalog of the Indian fauna. The most recent study of *Tetragonoderus* in China (Jian & Tian 2009) recorded only four species, including one described as new. *Tetragonoderus microthorax* Jian & Tian, 2009 was recorded from Hainan and Yunnan Provinces, *Tetragonoderus fimbriatus* (Bates, 1886) from Hainan, Cambodia, India and Sri Lanka, *Tetragonoderus rhombophorus* Schmidt-Göbel, 1846 from Hainan Province, Cambodia and Laos, and *Tetragonoderus quadrisignatus* (Quensel, 1806) from Hainan and Guangdong Provinces, as well as Hong Kong, Cambodia, Thailand, and India. Park et al. (2013) recorded an additional new species, *Tetragonoderus sinanensis* Park, from Korea. To date, there has been no recent revision of the Asian *Cyclosomus* species, and only *Cyclosomus inustus* Andrewes, 1924 has been recorded from anywhere in China (Hong Kong and Nanoa Island in Guangdong Province (Wang et al. 2017)).

Based on our study of the material collected for the project and additional specimens from the region deposited in other collections, we recognize a total of five cyclosomine species as occurring in the study area. We present here a key for identification of adults of these species, as well as nomenclatural data, diagnoses, illustrations of dorsal habitus, male genitalia, and other features, and information about geographical and habitat distributions within the study area and overall geographical distribution for each species. We also discuss geographical distributions of the species with respect to different parts of the study area (see below about "core areas") and to each other, as well as the broader geographical range patterns and the altitudinal ranges of these species.

Because so little comprehensive work has been done on the cyclosomines of China and southeast Asia generally, the study of type specimens was essential to confirm identifications of the Gaoligong Shan species. We reviewed material representing the known Eurasian genera and most of the species and their types wherever possible. Among the species represented in the fauna, we recognize two as new to science, one in each of the genera represented.

MATERIALS AND METHODS

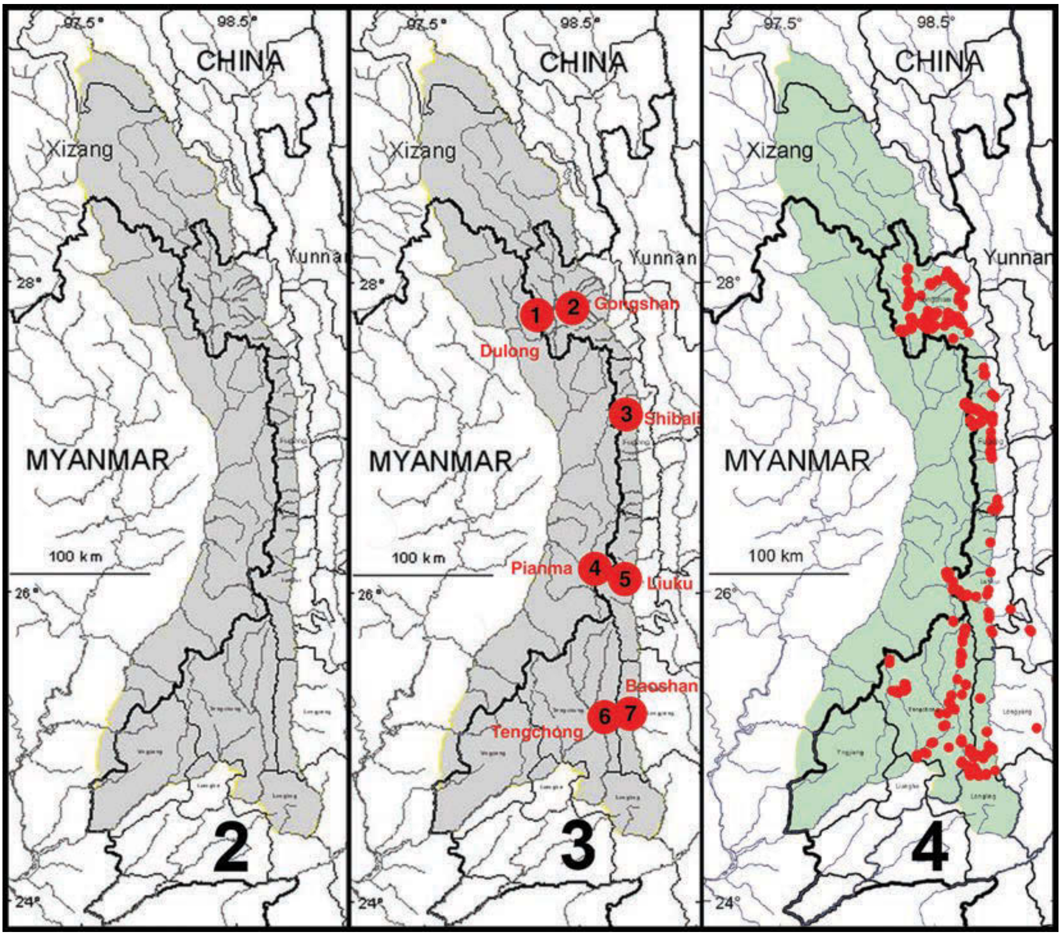
The natural physiographic limits of the study area for the project are as shown in Fig. 2 and include areas in eastern Myanmar and southern Xizang (Tibet); but we had permission to survey only those parts in Yunnan Province. Specialists for all taxonomic groups concentrated their efforts on seven core areas within the project region (Fig. 3), selected to facilitate comparisons of possible north to south and east to west spatial differences within the regional biota, as well as recognition of areas of local endemism. Other areas were sampled as time and opportunity permitted. The entomological team made a total of 13 expeditions to the Gaoligong region. Our sampling sites within the region are shown in Fig. 4.

A total of 184 cyclosomine specimens were collected during the study. More than 500 additional specimens from localities in Asia, including type specimens and other identified and undetermined specimens, were also studied. Codes used throughout this report for collections from which specimens were borrowed and/or in which specimens, including primary types, are deposited are as follows:

CAS	California Academy of Sciences, San Francisco, California, U.S.A.
IOZ	National Zoological Museum of China, Institute of Zoology, Beijing, China
KUEC	Kyushu University Entomological Collection, Fukuoka, Japan
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMUK	British Museum (Natural History), London, United Kingdom
NMPC	National Museum (Natural History), Prague, Czech Republic
RMNH	Naturalis Biodiversity Center, Leiden, Netherlands.
SCAU	South China Agricultural University, Guangzhou, China
SMTD	Senckenberg Museum für Naturkunde, Dresden, Germany
ZIN	Zoological Institute Academy of Sciences, St. Petersburg, Russia
ZMHB	Museum für Naturkunde, Institut für Systematische Zoologie, Berlin, Germany
ZMMU	Zoological Museum, Moscow University, Moscow, Russia
ZMUC	Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Denmark
ZSM	Zoologische Staatssammlung, Munich, Germany

Measurements. Body length (BL) was measured from the anterior margin of the clypeus to the apex of the longer elytron with the head, pronotum, and elytra aligned in the same vertical plane. Measures of body length provided by previous authors typically included the mandibles and labrum, so our body length values are slightly shorter in most cases but less subject to varied positioning of the moveable mouthparts. Additional measurements included: pronotal length (PL), measured along the midline from the anterior margin to posterior margin of the pronotum; pronotal apical width (PWA), measured between the apices of the anterior angles; pronotal basal width (PWB), measured between the posterior angles; pronotal maximum width (PWM), measured across the pronotum at its widest point; elytral length (EL), measured from transverse groove on scutellum (where the posterior edge of pronotum rests in aligned specimens) to the apex of the longer elytron; and elytral width (EW), measured across both elytra at their widest point (less any gap between the elytra on a specimen).

Color and color patterns. The predominant features used to describe and distinguish cyclosomine species throughout the taxonomic history of the group have been those dealing with color and/or color pattern. As noted by Kavanaugh (2015) for the African species of *Cyclosomus*, the



FIGURES 2–4. Fig. 2. Map showing natural extent of study area, colored in gray (however, sampling was permitted only in those portions in Yunnan Province). Fig. 3. Map showing location of core sampling areas. Fig. 4. Map showing locations of all entomological sampling sites. Scale lines = 100 km.

problem with reliance on these features is that, in most if not all species, these features may be varied, both within and between populations, and undoubtedly are subject to intense selection for concealment from predators in the open beach environment in which these beetles live. These color patterns and variations among them are very similar to those seen among *Omophron* species (Carabidae, tribe Omophronini) (Kavanaugh et al. 2021), which share the same habitats.

Although a few cyclosomine species have members fully dark or pale in color (i.e., without a pattern of contrasting pale and dark areas on the elytra or the pronotum), members of most species exhibit at least some contrasting color pattern, particularly on the elytra, but also on the pronotum in *Cyclosomus* species and in a few *Tetragonoderus* species occurring outside the study area. Kavanaugh (2015) described the basic elytral pattern in *Cyclosomus* species, adults of which are basically pale (testaceous to a pale reddish brown) in ground color with a variously developed contrasting dark pattern (Fig. 6A). This pattern includes some elements (e.g., a basal dark band) shared with the pattern seen in some but not all *Tetragonoderus* species. Among *Tetragonoderus* species occurring in the study area, two main patterns are seen. The first is found in beetles that have completely dark elytra except for a subapical band of pale spots (separated by darkened striae) that extends from intervals 2, 3, or 4 to interval 8 or 9 (Fig. 6B). This band can be extremely faint, at least in part, in some individuals from some areas. In the second pattern (Fig. 6C), the elytral ground color is pale, with basal, middle, and apical or preapical dark bands or series of dark spots. The middle band is complex in that it is comprised of continuous or disrupted dark anterior and posterior edges with an intervening paler zone that is either as pale as the elytral ground color (Fig. 12) or a slightly or distinctly darker orange-brown (Fig. 6C). The extent, shape, and continuity of these dark areas and dark connections between them vary within the group, and both among and within species.

Of course all of these dark areas may be indistinct or even invisible in newly-emerged adults that are still teneral and have not yet developed their full pigmentation pattern. Such individuals are difficult if not impossible to properly identify with color characters alone. Another feature that is useful in distinguishing members of some species, metallic reflection, requires the presence of a dark background for the reflection to be seen distinctly. Consequently, teneral specimens may not exhibit metallic reflection that would be visible if they were fully pigmented. All the above comments are provided as caution against exclusive reliance on these obvious features of the beetles in attempts to identify them.

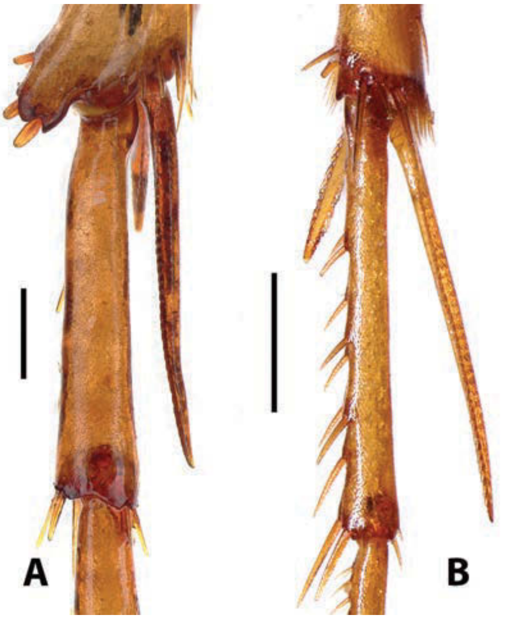


FIGURE 5. Left hind tibial medial spur and tarsomere 1, dorsal aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus elegans* Andrewes (CASENT1039499, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China). Scale lines = 0.2 mm.

Dissections. Dissections of male genitalia were prepared from specimens relaxed in hot (near boiling) soapy water by severing the membranes between the genital capsule and tergite VII and sternite VII and extracting the capsule intact. The dissections were then cleared in warm 10% KOH and further dissected to separate the sclerotized parts enough to visualize structures to be compared.

Illustrations. Digital images of dorsal habitus, pronotum, and elytra were taken using a Canon EOS 6D Mark II DSLR camera with a 65mm 2.8-5X macro lens. Multiple images at different focal planes were taken using a StackShot Macro Rail Package and merged using Helicon Focus software. Digital images of portions of legs and of male genitalia were taken using a Keyence VHX-7000 digital microscope. A “CASENT” number associated with an image, as noted in figure captions, is a unique identifier that refers to the particular specimen photographed and its CAS database record. The distributional map for Fig. 4 was created from geographical coordinate data using the ArcMap program in ArcGIS for Desktop version 10.2 software from Esri. The map illustrating summary distributions was created using Inkscape 1.2 software and a base map modified from Wikimedia Commons, World Atlas of the World, at URL: *http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_-_land_and_oceans_12000.jpg.*

Distributional data. Because locality names and geopolitical units throughout Asia have

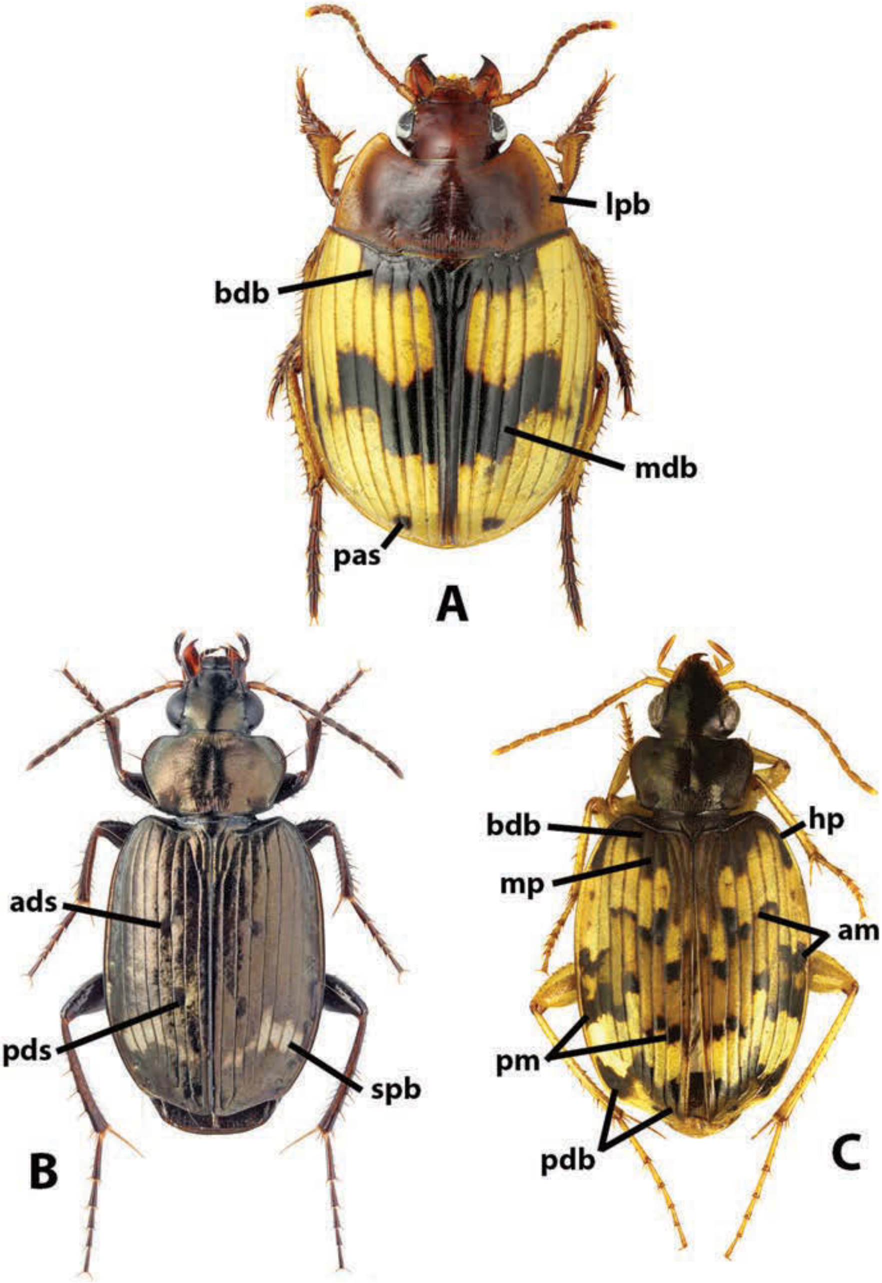


FIGURE 6. Illustration of terms used for describing color patterns in *Cyclosomus* and *Tetragonoderus* species. A. *Cyclosomus flexuosus* (Fabricius) (Kosi River valley, 5 km N Ramnagar, Uttarakhand, India; copyright © Alexander Anichtchenko); B. *Tetragonoderus intermedius* Solsky (8 km NE of the city of Parkhar, Tajikistan; copyright ©Kirill Makarov); C. *Tetragonoderus elegans* Andrewes (Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); ads = anterior discal seta; am = anterior dark margin of niddle band; bdb = basal dark band; hp = humeral portion of basal dark band; lpb = lateral pale band of pronotum; mdb = middle dark band; mp = medial portion of basal dark band; pas = preapical dark spot; pdb = preapical dark band; pds = posterior discal seta; pm = posterior dark margin of middle band; spb = subapical pale band.

changed so dramatically and repeatedly throughout the last few centuries, type localities are cited using the current country, regional, and locality names for them, not necessarily as in the original citations. Locality records for other specimens have also been converted to their current names where this could be done unambiguously.

In describing the geographical and ecological relationships among cyclosomine species in the region, we use the term *sympatric* to indicate that two species overlap in their geographical ranges and the term *syntopic* to indicate that they also occur together in the same habitat at the same locality.

TAXONOMY

We recognize five cyclosomine species found to occur in the study area, including two that are new to science. Adult specimens of these different species can be distinguished using the following key. A sixth species, *Tetragonoderus microthorax* Jian & Tian, 2009, which has not yet been recorded from the study area but may occur there, is also included in the key.

Key for identification of adult cyclosomine species of the Gaoligong Shan region of China

1 Size larger, BL = 6.8 mm or more; pronotum (Fig. 13A) very broad, trapezoidal, almost as wide as elytra at humeral angles, distinctly widest at base; elytra broadly rounded apically, elytral color pattern as in Fig. 7A; front tarsomeres 1 to 3 markedly expanded laterally (Figs. 14A, 15A) in both males and females . . . . ***Cyclosomus acutangulus*** **Kavanaugh and Cueva-Dabkoski, sp. nov.**

1’ Size smaller, BL = less than 6.0 mm; pronotum (Figs. 13 B-D) narrower, widest at or anterior to middle; elytra slightly to distinctly and obliquely truncate apically, elytral color pattern varied; front tarsomeres 1 to 3 without distinct lateral expansions (Figs. 14B-F), broader in males than in females . . . . *Tetragonoderus* spp. 2

2 (1’) Femora dark black or piceous; elytra dark without pale markings in basal half, with or without pale markings in apical half (Figs. 9A, 11A) 3

2’ Femora pale tan; elytra with pale areas in both basal and apical halves (Figs. 10A, 12A, 20). 4

3 (2’) Size smaller, BL = 4.5 mm or less; elytra with distinct transverse subapical band of pale spots extended from interval 4 to interval 8 (Fig. 11A), faintly present also on interval 3 in some individuals, posterior discal setiferous puncture on interval 3 inserted more posteriad, at level of pale transverse subapical band; dorsal surfaces shiny, with distinct aeneous-greenish metallic reflection, of similar sheen throughout, elytral microsculpture comprised of more or less regularly transverse meshes, except their orientation slightly distorted in or near discal setal pore punctures . . . . ***Tetragonoderus parviculus*** **Kavanaugh and Cueva-Dabkoski, sp. nov.**

3’ Size larger, BL = 4.9 mm or more; elytra (Fig. 9A) with only faint pale markings in region of subapical band, most evident on intervals 7 and 8, posterior discal setiferous puncture on interval 3 inserted distinctly anterior to level of pale subapical markings (i.e., closer to anterior discal setiferous pore); dorsal surfaces duller, with distinct bronze/copper metallic reflection, sericeous (silky) and mottled in posterior half, with elytral microsculpture comprised of a complex pattern of transverse, longitudinal, and oblique patches of elongate meshes, most distorted near discal and umbilicate setal pore punctures . . . . *Tetragonoderus arcuatus* Dejean

4 (3’) Elytral color pattern as in Fig. 10A, with dark areas more expansive; connection between medial portion of the basal dark band and humeral portion broader, at least one-quarter length of the humeral portion; middle band with portion between anterior and posterior dark edges distinctly darker (orange-brown) than remainder of pale elytral areas; pronotum dark, black or piceous, with distinct greenish or bronze metallic reflection, slightly narrowed basally (ratio PWM/PWB =1.13 to 1.20); male with middle tarsomeres 1 to 4 (Fig. 16C) distinctly wider than in female and with pads of adhesive setae ventrally

(Fig. 17C); median lobe of male genitalia (Figs. 19A,B) with conspicuous large spines on the internal sac . . . . *Tetragonoderus elegans* Andrewes

4’ Elytral color pattern as in Figs. 12A, 20, with dark areas less expansive; connection between medial portion of the basal macula and humeral macula absent or very narrow, less than one-fifth the length of humeral macula; middle discal band with portion between anterior and posterior dark edges not or only very slightly darker than remainder of pale elytral areas; pronotum piceous or rufopiceous, with or without faint greenish metallic reflection, narrowed basally or not; male with middle mesotarsomeres (Figs. 16E,F) only slightly wider than in female and with only tarsomeres 1 to 3 with pads of adhesive setae ventrally (i.e., tarsomere 4 without adhesive setae ventrally) (Figs. 17E,F); median lobe of male genitalia (Figs. 19C-F) without spines on the internal sac 5

5 (4’) Pronotum (Fig. 13E) slightly shorter and wider (ratio PWM/PL = 1.52 to 1.70), widest near mid-length and posterior to insertion of midlateral seta, not or only very slightly narrowed basally (ratio PWB/PWA = 1.15 to 1.25), lateral margins slightly and evenly convex or straight or very slightly sinuate anterior to basal angles; elytra intervals flat and striae moderately impressed; median lobe of male genitalia (Figs. 19C,D) with apical lamella slightly shorter and broader. . . . . . *Tetragonoderus punctatus* (Wiedemann)

5’ Pronotum (Fig. 13F) slightly longer and narrower (ratio PWM/PL = 1.48 to 1.57), widest anterior to mid-length at or near insertion of midlateral seta, slightly to moderately narrowed basally (ratio PWB/PWA = 1.04 to 1.14), lateral margins slightly to moderately sinuate anterior to basal angles; elytra intervals slightly convex and striae deeply impressed; median lobe of male genitalia (Figs. 19E,F) with apical lamella slightly longer and narrower . . . . [*Tetragonoderus microthorax* Jian & Tian]

Genus *Cyclosomus* Latreille, 1829

Scolytus Fabricius, 1790:221, in part [junior homonym of *Scolytus* Geoffroy, 1762] (type species *Carabus limbatus* Fabricius, 1801, designated by Latreille (1810:426)). Fabricius (1792:180); Bousquet (2012:89).

Cyclosomus Latreille, 1829:394 (type species *Carabus flexuosus* Fabricius, 1775, by monotypy).

Diagnosis. Adults of *Cyclosomus* can be distinguished from those of *Tetragonoderus* species in the study area by the following combination of character states: Body size larger, BL = 7.0 mm or more; pronotum (Fig. 13A) very broad, trapezoidal, almost as wide as elytra at humeral angles, distinctly widest at base; elytra broadly rounded apically, elytral color pattern as in Fig. 7A; front tarsomeres 1 to 3 markedly expanded laterally (Figs. 14A, 15A) in both males and females.

Diversity: At present, only five species are recognized in the Asian fauna, and here we record one, a new species, from the study area.

Cyclosomus acutangulus Kavanaugh and Cueva-Dabkoski, sp. nov.

Figures 5A, 7, 8, 13A, 14A, 15A, 16A, 17A, 21, and 23.

Type material. HOLOTYPE, a male, deposited in IOZ, labeled: “CASENT 1015370”/ “CHINA, Yunnan Province, Tengchong Co., Wuhe Township, Longjiang Bridge on Longchuanjiang, 1215 m,”/ “N24.89889°/E098.66667° 30 October 2003, on beach, Liang H.-B. & Shi X.-C. collectors, LHB03-42”/ “HOLOTYPE *Cyclosomus acutangulus* sp. n. D.H. Kavanaugh & M. Cueva-Dabkoski 2022” [red label]. A total of 28 paratypes: five males and six females, in CAS, same label data as holotype, except first label [unique identifier label] different (“CASENT 1012641” to “CASENT 1012646” and “CASENT 1015371” to “CASENT 1015375”, respectively); six males and seven females, in IOZ. labeled: “China, Yunnan, Tengchong, Wuhe, on beach of Longchuan river, N24.8941, E98.6750,” / “1215 m, 2015.3.22 N, Liu Y., Shi H.L. collectors”; one male and one female, in CAS and IOZ, labeled: “China, Yunnan Prov., Tengchong, Wuhe, Longjiangqiao, beach, 24.89176°N/98.67551°E / 1230 m, 2006.6.3, Kavanaugh D., Brett R.”; one male and one female, both in NHMUK, labeled: “NE India, ASSAM, Bhalukpong, 26.v.-3.vi.2006. 27° 02’N 92° 35’E, 150m, P. Pacholátko leg.”/ “L. Dembicky & P. Pacholátko BMNH {E} 2006-

48” Each paratype also bears the following label: “PARATYPE *Cyclosomus acutangulus* sp. n. D.H. Kavanaugh & M. Cueva-Dabkoski 2022” [yellow label].

Type locality. China, Yunnan, Tengchong County, Wuhe Township, Longchuan River at Longjiang Bridge.

Etymology. The species epithet, *acutangulus*, is a combination of the Latin adjective, *acutus*, meaning sharp or pointed, and the Latin noun, *angulus*, meaning corner or angle, here used as a noun in apposition. It refers to the apical angles of the pronotum, which are exceptionally narrow and pointed in members of this species.

Diagnosis. Adults of *C. acutangulus* can be distinguished from those of all other *Cyclosomus* species in Asia by the following combination of character states: Dorsal habitus as in Fig. 7A; pronotum (Fig. 13A) with anterior angles acute, narrow, lateral margins slightly to distinctly sinuate near anterior angles, lateral pale bands very narrow. Members of this species can be distinguished from those of other cyclosomines in the study area by the following combination of character states: Size larger, BL = more than 6.8 mm; pronotum (Fig. 13A) very broad, trapezoidal, almost as wide as elytra at humeral angles, distinctly widest at base; elytra broadly rounded apically, elytral color pattern as in Fig. 7A; front tarsomeres 1 to 3 markedly expanded laterally (Figs. 14A, 15A) in both males and females.

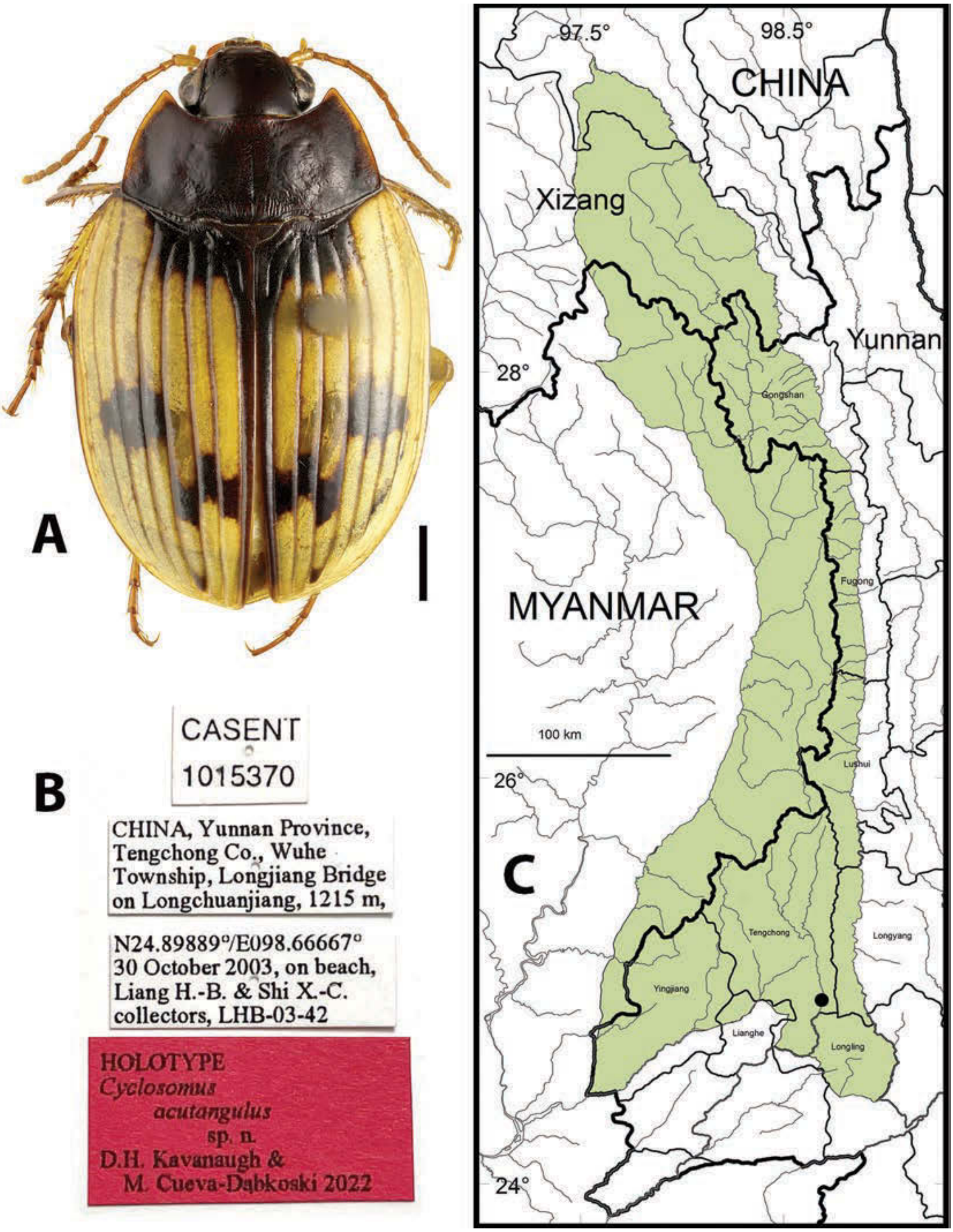
Description. (Fig. 7A). Size. Medium for genus, BL males = 7.1 to 8.2 mm, females = 6.8 to 8.2 mm.

Color. Head piceous except clypeus, labrum, and venter rufous or rufopiceous; antennae, mandibles, maxillae, and maxillary and labial palpi pale yellow-tan. Pronotum piceous with very narrow pale (yellow-tan or rufous) lateral band). Elytra mainly yellow-tan, with black to piceous markings; basal dark band extended laterally to humerus on base anterior to basal margination but only to interval 5 posterior to basal margination; interval 1 piceous to apex or nearly so, middle transverse dark band moderately thick, irregular, extended from intervals 2 to 6, 7, or slightly onto interval 8 in some specimens, portion on intervals 2 to 4 located at about three-fourths of elytral length and with spot on interval 3 offset anteriorly relative to those on intervals 2 and 4, portion on interval 5 to 7 or 8 near midlength of elytra and formed more or less in a transverse row; preapical dark spot present or absent, if present then small. Venter piceous laterally, rufo-piceous medially, elytral epipleurae and apical portion of last abdominal sternite pale yellow-tan. Legs pale yellow-tan.

Reflection, luster, and microsculpture. Dorsum and venter without metallic reflection. Head and pronotum dull, with microsculpture moderately impressed and comprised of isodiametric meshes; elytra slightly shiny with isodiametric meshes slightly less deeply impressed; venter with isodiametric to slightly transverse meshes shallowly impressed.

Head. Eyes large, hemispheric; antennae slightly short, extended only to basal one-fifth of elytra; clypeus bisetose; labrum with three pairs of setae in most individuals, four pairs in a few; mentum asetose, with a broad, apically emarginate medial tooth; submentum anteriorly with a single pair of setae.

Prothorax. Pronotum (Fig. 13A) broad but slightly narrow for genus (ratio PWM/PL = 2.12 to 2.43), trapezoidal, almost as wide as elytra at humeral angles, with anterior angles acute, narrow; apical margin markedly concave between anterior angles; lateral margins slightly to distinctly sinuate near anterior angles, otherwise smoothly curved or nearly straight; basal margin markedly bisinuate, lobate medially; anterior and lateral margination absent or extremely faintly impressed, basal margination distinct laterally, obsolete medially; midlateral setae inserted slightly anterior to mid-length, basolateral setae inserted on lateral edge of pronotum and just anterior to posterior angles. Prosternal intercoxal process moderately long, lanceolate, with complete margination.



CASENT
1015370

CHINA, Yunnan Province,
Tengchong Co., Wuhe
Township, Longjiang Bridge
on Longchuanjiang, 1215 m,

N24.89889°/E098.66667°
30 October 2003, on beach,
Liang H.-B. & Shi X.-C.
collectors, LHB-03-42

HOLOTYPE
Cyclosomus
acutangulus
sp. n.
D.H. Kavanaugh &
M. Cueva-Dabkoski 2022

FIGURE 7. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. A. Holotype, dorsal aspect, scale line = 1.0 mm (CASENT 1015370, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. Labels associated with holotype; C. Map showing locality record (black circle) for this species in the Gaoligong Shan region, scale line = 100 km.

Elytra. Broadly ovate, not or only slightly longer than wide (ratio EL/EW = 1.00 to 1.02), broadly rounded apically, humeri obtusely angulate; elytral striae deeply impressed throughout, elytral intervals slightly convex, smooth; parascutellar setiferous pore present at base of interval 1 near junction of striae 1 and 2; two discal setiferous pores present on interval three adjacent to stria 2, one near elytral mid-length and the other near apical one-third; apical seta present, inserted near apex of interval 3; umbilicate series comprised of 11 to 13 setae.

Legs. Tarsal claws, smooth, edentate. Males (Fig. 14A) and females with front tarsi similar in shape and width, but males with tarsomeres 1 to 3 with two rows of adhesive squamosetae (Stork 1980) ventrally (Fig. 15A), females without such setae; middle tarsi with tarsomeres 1 to 3 distinctly broader in males (Fig. 16A) than in females and with two rows of adhesive squamosetae ventrally (Fig. 17A), absent from females.

Male genitalia. Median lobe (Fig. 8) stout, smoothly arcuate, and with apical lamella tapered to a rounded point apically in lateral view, slightly sinusoidal and with apical lamella broadly rounded in dorsal view. Internal sac without evident spines.

Geographical variation. The two specimens from India lack a preapical dark spot found in specimens from the study area, but otherwise are similar.

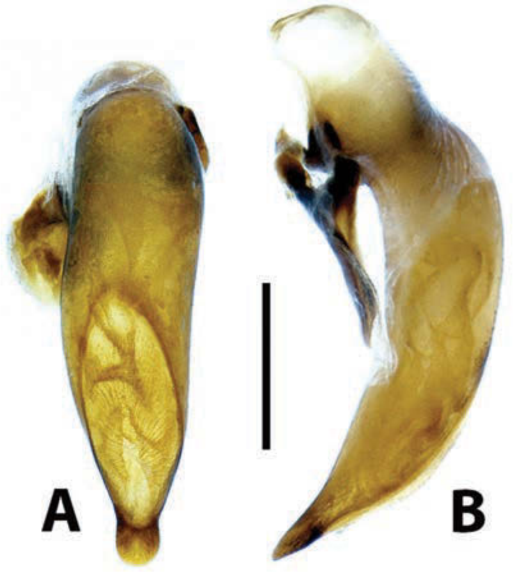


FIGURE 8. Male genitalia, *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012642, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China). A. Dorsal aspect; B. Left lateral aspect; scale line = 0.5 mm.

Habitat distribution. Specimens of this species were collected mainly at night, with the aid of headlamps, on the upper edges of open sandy beaches along the Longchuan River (Fig. 21) at an elevation of 1215 m, where they were found active on the surface of dry or only slightly damp sandy substrate with no or only widely scattered and low vegetation. Members of this genus are known to burrow quickly into dry sand to hide when disturbed during the daytime (Nietner 1857).

Geographical distribution within the Gaoligong Shan. Fig. 7B. We examined a total of 29 specimens (13 males and 16 females) from the study area (see list of type specimens above).

Members of this species were collected only in the southwestern part of the study area (Core Area 6).

Overall geographical distribution. Fig. 23**.** At present, this species is known only from single areas in western Yunnan Province, China and northcentral Assam, India. These two areas are about 650 km apart, and it is likely that this species occurs also in suitable habitats in the intervening region, including northern Myanmar (Kachin State), and northeasternmost India, at low elevations (below 1500 m) along rivers draining the western and southern slopes of the Himalayan ranges in these areas, respectively.

Geographical relationships with other *Cyclosomus* species. No other species of *Cyclosomus* has been recorded from the Gaoligong Shan region, but members of *C. acutangulus* were found syntopic with *C. flexuosus* members at the locality in Assam [NHMUK], which is the easternmost known locality for the latter species and the westernmost for *C. acutangulus*. Other cyclosomine species found syntopic with *C. acutangulus* at the type locality along the Longchuan River include *Tetragonoderus elegans* and *T. punctatus*.

Genus *Tetragonoderus* Dejean, 1829

Bembidium Gyllenhal, 1810:12, in part [unjustified emendation for *Bembidion* Latreille, 1802; invalid name (Bousquet 2012:535)].

Tetragonoderus Dejean, 1829:485 (type species *Carabus quadrum* Fabricius, 1792, designated by Hope 1838:89); Bousquet 2012:1272.

Cyclicus Jeannel, 1949:870 (type species *Tetragonoderus perrieri* Fairmaire, 1900, by original designation).

Metacyclicus Jeannel, 1949:871 (type species *Tetragonoderus bastardi* Alluaud, 1897, by original designation).

Diagnosis. Adults of *Tetragonoderus* can be distinguished from those of *Cyclosomus* species in the study area by the following combination of character states: Body size smaller, BL = less than 6.0 mm; pronotum (Figs. 13B-F) narrower, widest at or anterior to middle; elytra slightly to distinctly and obliquely truncate apically, elytral color pattern varied; front tarsomeres 1 to 3 without distinct lateral expansions (Figs. 14B-F, 15B-F), broader in males than in females.

Diversity: At present, 16 species are recognized in the Asian fauna, and here we record four from the study area, including one new species.

Tetragonoderus arcuatus Dejean

Figures 9, 13B, 14B, 15B, 16B, 17B, 18A-B, 22, and 23.

Tetragonoderus arcuatus Dejean, 1829:495. LECTOTYPE, here designated, a female, deposited in MNHN and labeled: “Egypte” [handwritten]/ “TYPE arcuatus” [red label]/ “arcuatus Dejean Egypte Coll. Dejean” [handwritten, white label with black border]/ “LECTOTYPE *Tetragonoderus arcuatus* Dejean 1829 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2022” [red label]. Type locality: Egypt [but Dejean viewed this record as uncertain]. Chaudoir, 1876:38; Felix, 2009:116; Assmann et al., 2015:57; Bousquet (2017:498).

Tetragonoderus cardoni Bates, 1891:338. HOLOTYPE, a female, deposited in MNHN. Type locality: India, Jharkhand, Konbir. Bates 1892:416. Synonymy by Andrewes, 1921:150.

Notes on nomenclature and types. In his original description, Dejean (1829) was unclear with regard to how many specimens he had examined (Thierry Deuve, personal communication). He noted that he had received material from Klug and that he had not seen a male specimen. In addition to a single female specimen in MNHN, there are four specimens from Egypt in ZMHB, which were probably part of Klug’s original series and include one male (Bernd Jaeger, personal communication). It seems most likely that Dejean saw only the single female specimen now deposited in MNHN, but we cannot be sure. Consequently, we designate that female as lectotype (International Code of Zoological Nomenclature, Recommendation 73F).

When he proposed the synonymy of *T. cardoni* Bates with *T. arcuatus*, Andrewes (1921:150) also noted the pronounced variation in the degree of development of the sericeous sheen seen among specimens of this species. Specimens from the study area and adjacent regions appear to have the most markedly sericeous elytra while those from areas to the west, including the type locality (Egypt), have the least sericeous elytra. There is also conspicuous variation in the distinctness and extent of the subapical pale band of spots. In the single specimen from the study area, and also in those from adjacent parts of the eastern end of the range of the species (e.g., Assam, Myanmar and northern Thailand), the subapical pale band of spots is faint to very faint, almost invisible in some specimens, and apparent only on intervals 7 and 8 or extremely faintly visible also on more mediad intervals in some specimens. In contrast, specimens from the western part of the range of

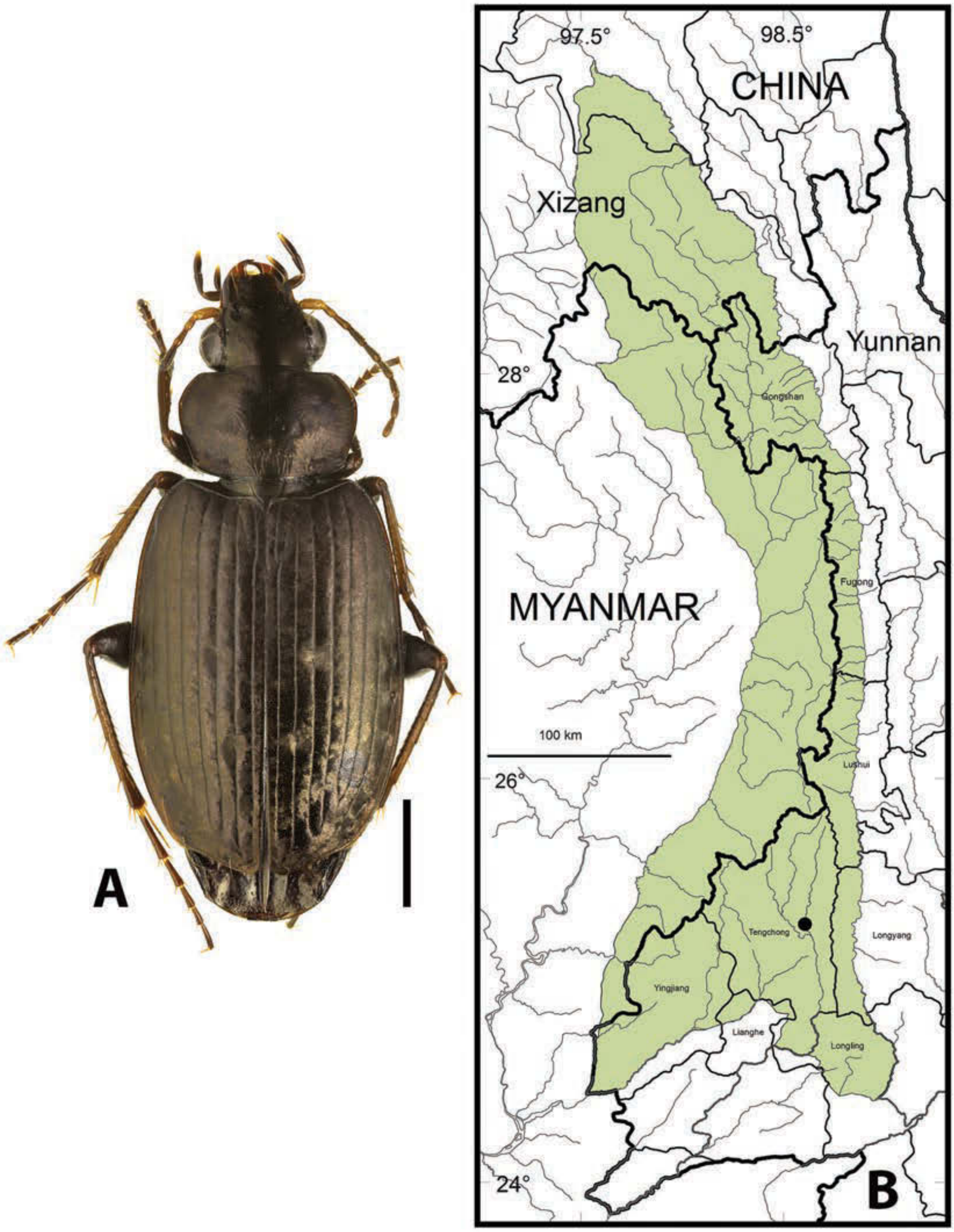


FIGURE 9. *Tetragonoderus arcuatus* (Dejean). A. Dorsal aspect, scale line = 1.0 mm (CASENT1013512, Xiaojiangqiao, Qushi Township, Tengchong County, Yunnan, China); B. Map showing locality record (black circle) for this species in the Gaoligong Shan region, scale line = 100 km.

the species (i.e., North Africa, the Middle East and Central Asia) have the subapical band much more distinct and extended from interval 2 to interval 8. The female type of *T. cardoni* is intermediate between specimens from the western part of the species range and those from the study area and adjacent regions in both of these features. Because of this pronounced variation, features noted in the key above and in the diagnosis presented below are applicable specifically for specimens from the study area and adjacent regions.

Adults of several additional Asian taxa presently treated as distinct species are very similar to those of *T. arcuatus*. These include *Tetragonoderus assamensis* Jedlička, 1964, *Tetragonoderus cinchona* Jedlička, 1964, *Tetragonoderus intermedius* Solsky, 1874, and *Tetragonoderus nakaoi* Jedlička, 1966. The taxonomic status of these names is currently under review, but none of them have been recorded from the study area and all are more recently described than *T. arcuatus*. Consequently, none of them would challenge *T. arcuatus* as the valid name of this species if one or more are synonymized with the latter name in the future.

Diagnosis. Adults of *T. arcuatus* can be distinguished from those of other cyclosomine species in the study area by the following combination of character states: Body size medium for genus, BL males = 4.9 to 5.1 mm, females = 5.0 to 5.7 mm; forebody uniformly dark, elytra dark without pale markings in basal half, in the study area with faint pale band of spots in apical half (Fig. 9A, mainly visible on intervals 7 and 8, femora dark black or piceous, tibiae paler; dorsal surfaces dull, with slight to distinct bronze/copper metallic reflection, elytra sericeous (silky) and mottled, especially in posterior half, with elytral microsculpture comprised of a complex pattern of transverse, longitudinal, and oblique patches of elongate meshes, most distorted near discal and umbilicate setal pore punctures; pronotum widest at or anterior to middle; elytra slightly to distinctly and obliquely truncate apically, posterior discal setiferous puncture on interval 3 inserted distinctly anterior to level of pale subapical markings; front tarsomeres 1 to 3 without lateral expansions (Figs. 14B, 15B), middle tarsi of males (Fig. 16B) with tarsomeres 1 to 4 broader than in females and with pads of adhesive setae ventrally (Fig. 17B); median lobe of male genitalia (Figs. 18A,B) long and slender, with apical lamella also elongate, slender and rounded apically.

In the study area, specimens of *T. arcuatus* (Fig. 9A) are similar only to those of *T. parviculus* (Fig. 11A) but differ from them in having larger body size, elytra with less distinct and more restricted subapical band and distinctly sericeous sheen, and male genitalia with the median lobe more slender and with a longer and narrower apical lamella (refer to key for additional differences).

Habitat distribution. The lone specimen collected in the study area was found in daytime under a stone on an open beach of the Longchuan River on a mix of sandy and rocky substrate and at an elevation of 1445 m. Assmann et al. (2015) found members of this species "on heavy soils close to water in semi-desert areas" in Israel.

Geographical distribution within the Gaoligong Shan. Fig. 9B. We examined a single female specimen from the following locality: ***Tengchong County:*** Qushi Township (Xiaojiangqiao, N25.23944°/E098.61667°, 1445 m, 21 October 2003, Liang H.-B. & Shi X.-C. collectors).

At present, this species has been recorded only from the southwestern part of the study area (Core Area 6).

Overall geographical distribution. Fig. 23. The known range of this species as presently conceived extends from North Africa (Niger, Chad, Sudan, Egypt, and Ethiopia) eastward across the Middle East (Israel, Iraq, United Arab Emirates, Oman, and Yemen), Central Asia (Iran and Pakistan), Nepal, India (Bihar, Jharkand, Sikkim, and Assam) Bhutan, Bangladesh, Myanmar, and western China (western Yunnan Province) and south to northwestern Thailand. A large series of specimens (a total of 95 males and females, in IOZ) from Mafang, Lancang County, Yunnan

(N22.57925°/ E099.99849°, 1723m, W.B. Gu collector, December 2003-January 2005) represents the eastern most record for this species.

Geographical relationships with other *Tetragonoderus* species. The geographical range of *T. arcuatus* overlaps with several other species in different parts of its range, and these relationships will be addressed in a forthcoming review of the Asian *Tetragonoderus* fauna (in preparation). In the study area, its range overlaps with those of *T. elegans*, *T. parviculus*, and *T. punctatus*, although it has not yet been found syntopic with any of these species. As noted below, *T. microthorax* (see treatment for *T. punctatus*) has not yet been recorded from the study area, but its range overlaps with that of *T. arcuatus* elsewhere and may also do so in the study area.

***Tetragonoderus elegans* Andrewes**

Figures 5, 6, 10, 13C, 14C, 15C, 16C, 17C, 19A-B, 21, and 23.

Tetragonoderus elegans Andrewes, 1931:524. HOLOTYPE, a female, in NHMUK. Type locality: India, Uttarakhand, Dehradun, Bindal River. Csiki (1932:1296).
Cyclicus elegans (Andrewes), Lorenz 2005:453.

Diagnosis. Adults of *T. elegans* can be distinguished from those of other *cyclosomine* species in the study area by the following combination of character states: Body size medium for genus, BL males = 4.4 to 5.2 mm, females 4.6 to 5.6 mm; pronotum dark, black or piceous, with distinct greenish or bronze metallic reflection, slightly narrowed basally (ratio PWM/PWB =1.13 to 1.20); elytral color pattern as in Fig. 10A, with dark areas more expansive; connection between medial portion of the basal dark band and humeral portion broader, at least one-quarter length of the humeral portion; middle band with portion between anterior and posterior dark edges distinctly darker (orange-brown) than remainder of pale elytral areas; femora pale tan; pronotum widest at or anterior to middle, slightly narrowed basally (ratio PWM/PWB =1.13 to 1.20); elytra slightly to distinctly and obliquely truncate apically; front tarsomeres 1 to 3 without lateral expansions (Figs. 14CA, 15C); male with middle tarsomeres 1 to 4 (Fig. 16C) distinctly wider than in female and with pads of adhesive setae ventrally (Fig. 17C); median lobe of male genitalia (Fig. 19A,B) with apical lamella long and bent ventrally, internal sac with several large and conspicuous spines.

In the study area, specimens of *T. elegans* (Fig. 10A) might be confused with those of *T. punctatus* (Fig. 12A) and also those of *T. microthorax* (Fig. 20), although the latter has not yet been recorded from the study area. Refer to the key for features distinguishing members of these three species and the Diagnosis section for *T. punctatus* below for further discussion of these differences.

Habitat distribution. Within the study area, members of this species have been found only on open sandy shores of medium- to large-sized rivers, where they remain buried in the sand or under cover during daylight hours and are active on the sand surface in moist areas at night. A few specimens have been collected during the day from under small stones and drift debris in the same habitat. At night, these beetles are active in upper beach areas, where zones of slightly moist and dry sand meet (Fig. 21). Members of this species were found at night together with *T. punctatus* adults at two localities along the Longchuan River and in daytime under stones in the same habitat with *T. parviculus* adults. Within the Gaoligong Shan region, this species occurs at relatively low elevations, below 2000 m, with our records documenting its occurrence in the 1185 to 1890 m range.

Geographical distribution within the Gaoligong Shan. Fig. 10B. We examined a total of 107 specimens (42 males and 65 females) from the following localities: ***Fugong County:*** Shangpa Township (west bank of Nu Jiang, 26.90668°/98.86339°, 1185 m, 13 October 2002, D.H. Kavanaugh, P.E. Marek, H.B. Liang & D.Z. Dong collectors [1 female; CAS]). ***Gongshan County:*** Cikai Township (Nu Jiang at Dashada, 27.73845°/98.67092°, 1430 m, 8-9 October 2002, D.H.

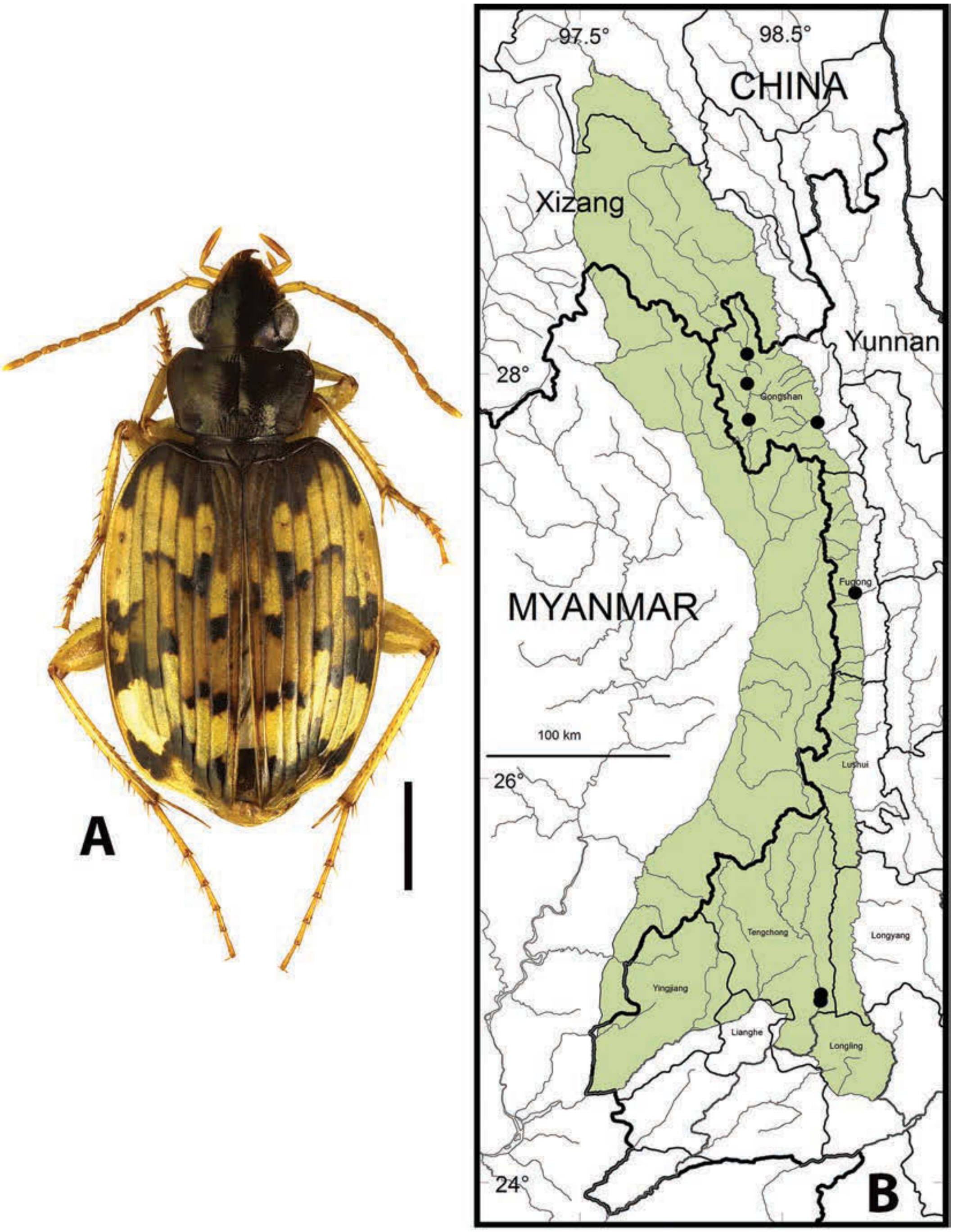


FIGURE 10. *Tetragonoderus elegans* Andrewes. A. Dorsal aspect, scale line = 1.0 mm (CASENT1039409, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); B. Map showing locality records (black circles) for this species in the Gaoligong Shan region, scale line = 100 km.

Kavanaugh, P.E. Marek & H.B. Liang collectors [6 males and 13 females; CAS, IOZ]); Dulongjiang Township (Bapo, Mulangdang, 27.75256°/98.34745°, 1355 m, 4 November 2004, H.B. Liang collector [3 males and 11 females; CAS, IOZ]), (south edge of Dizhengdang village along Silalong He, 28.07654°/98.32603°, 1890 m, 30 October 2004, D.H. Kavanaugh, G. Tang & D.Z. Dong collectors [2 males and 3 females; CAS, IOZ]), (Kongdang, 27.89791°/98.33843°, 1581 m, 30 May 2021, H.B Liang & Y. Xu Y. collectors [8 males, 5 females, IOZ]), (Pukawang, on road / 27.84016°/98.32233, 1458 m, 2021.5.29 N, H.B Liang & Y. Xu collectors [1 female, IOZ]). ***Tengchong County:*** Wuhe Township (Longchuan Jiang just below bridge at Menglian village, 24.89176°/98.67551°, 1230 m, 3 June 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [30 males and 35 females; CAS, IOZ]), (Longchuan Jiang at Longjiang Bridge, 24.89889°/98.66667°, 1215 m, 28 October 2003, H.B. Liang & X.C. Shi collectors [1 male and 2 females; CAS, IOZ].

Members of this species were collected from the northern to the southern parts of the study area (Core Areas 1, 2, 3 and 6), on both sides of mountain range in the north, only on the eastern side in the central part (Core Area 3) and only on the western side in the southern part (Core Area 6). This distribution pattern is most likely an artifact of inadequate sampling on the western slope of the mountain range, much of which is in Myanmar, and in the small southeastern part of the study area.

Overall geographical distribution. (Fig. 23). This species has been known previously only from a few localities on the southern slope of the Himalaya in northcentral India (Uttarakhand). Records of its occurrence in the study area represent the first for China and the easternmost limit of its known distribution. Other new records from China are within Tibet (***Medog County*****:** Ximohe bridge, 29.3519/95.3417°, 707 m, 25 August 2015, H.B. Liang collector [5 males, 5 females, IOZ]; Zha-Mo road Km 62, light trap, 29.7086°/95.5775°, 2787 m, 30 August 2015, H.B. Liang collector [1 male, IOZ]. ***Zayu County:*** Xia Zayu, 28.50760°/97.00965°, 1651 m, 4 July 2011, Y. Liu collector [9 males, 4 females, IOZ]). It is likely that *T. elegans* occurs also in suitable habitats in the intervening region, including northern Myanmar (Kachin State), northeasternmost India, Bhutan, and Nepal, at elevations between 400 and 2000 m along rivers draining the southern slopes of the Himalayan ranges in these areas.

Geographical relationships with other *Tetragonoderus* species. In the study area, members of this species have been found synotopic with those of *T. parviculus* and *T. punctatus*. The distributional range also overlaps that of *T. arcuatus* in the study area, but the two species have not yet been found syntopic. As noted above for *T. arcuatus*, the range of *T. elegans* broadly overlaps that of *T. microthorax*, but the latter species has not yet been recorded from the study area. *Tetragonoderus elegans* is also likely sympatric with *T. arcuatus*, *T. microthorax*, *T. punctatus*, and *Tetragonoderus taeniatus* (Wiedemann, 1823), in suitable habitats in at least some localities along the southern slope of the Himalaya between Uttarakhan and western Yunnan.

Tetragonoderus parviculus **Kavanaugh and Cueva-Dabkoski, sp. nov.**

Figures 11, 13D, 14D, 15D, 16D, 17D, 18C-D, 21, and 23.

Type material. HOLOTYPE, a male, deposited in IOZ, labeled: "CASENT1039396"/ "CHINA, Yunnan, Tengchong County, Wuhe Township, Longchuan Jiang just below bridge at Menglian village, 24.89176°/98.67551°,"/ "1230 m, 3 June 2006, Stop # DHK-2006-054A, D.H. Kavanaugh, R.L. Brett & D.Z. Dong collectors"/ "HOLOTYPE *Tetragonoderus parviculus* sp. nov. D.H. Kavanaugh & M. Cueva-Dabkoski 2022" [red label]. A total of four paratypes: three males, in CAS and IOZ, same label data as holotype, except first label [unique identifier label] different, "CASENT1039394", "CASENT1039395" and "CASENT1039397", respectively; one female, in NMPC, labeled: “CHINA: YUNNAN Prov. 5.9 km W Tongbiguan, 24°36.78’N, 97°45.38’E, J. Hájek, J. Růžička, & C.-B. Wang leg.”/ “(CH12) 25.-27.vi.2016; 1290 m, baited pitfall trap #06 (fish meat, ripening cheese), secondary broadleaved forest, valley near stream”. Each paratype also bears the following label: “PARATYPE *Tetragonoderus parviculus* sp. nov. D.H. Kavanaugh & M. Cueva-Dabkoski 2022” [yellow label].

Type locality. China, Yunnan, Tengchong County, Wuhe Township, Longchuan River just below bridge at Menglian village.

Etymology. The species epithet, *parviculus*, is a combination of the Latin adjective, *parvus*, meaning small, and the Latin qualifier, -ic*ulus*, meaning somewhat, here used as an adjective in the masculine form. It refers to the relatively small size of members of this species.

Diagnosis. Adults of *T. parviculus* can be distinguished from those of other *cyclosomine* species in the study area by the following combination of character states: Body size slightly small for genus, BL males = 3.7 to 4.2 mm, female = 4.4 mm; elytra dark without pale markings in basal half, with distinct transverse subapical band of pale spots extended from interval 4 to 8 (Fig. 11A), faintly present also on interval 2 and/or 3 in some individuals, femora dark black or piceous; dorsal surfaces shiny, with distinct aeneous-greenish metallic reflection, of similar sheen throughout; elytral microsculpture comprised of more or less regularly transverse meshes, except their orientation slightly distorted in or near discal setal pore punctures; pronotum widest anterior to middle; elytra slightly to distinctly and obliquely truncate apically; posterior discal setiferous puncture on interval 3 inserted more posteriad, at level of pale transverse subapical band; front tarsomeres 1 to 3 without lateral expansions (Figs. 14D, 15D).

In the study area, specimens of *T. parviculus* (Fig. 12A) might be confused only with those of *T. arcuatus* (Figs. 9A). Refer to the key and Diagnosis section for *T. arcuatus* for features distinguishing these taxa.

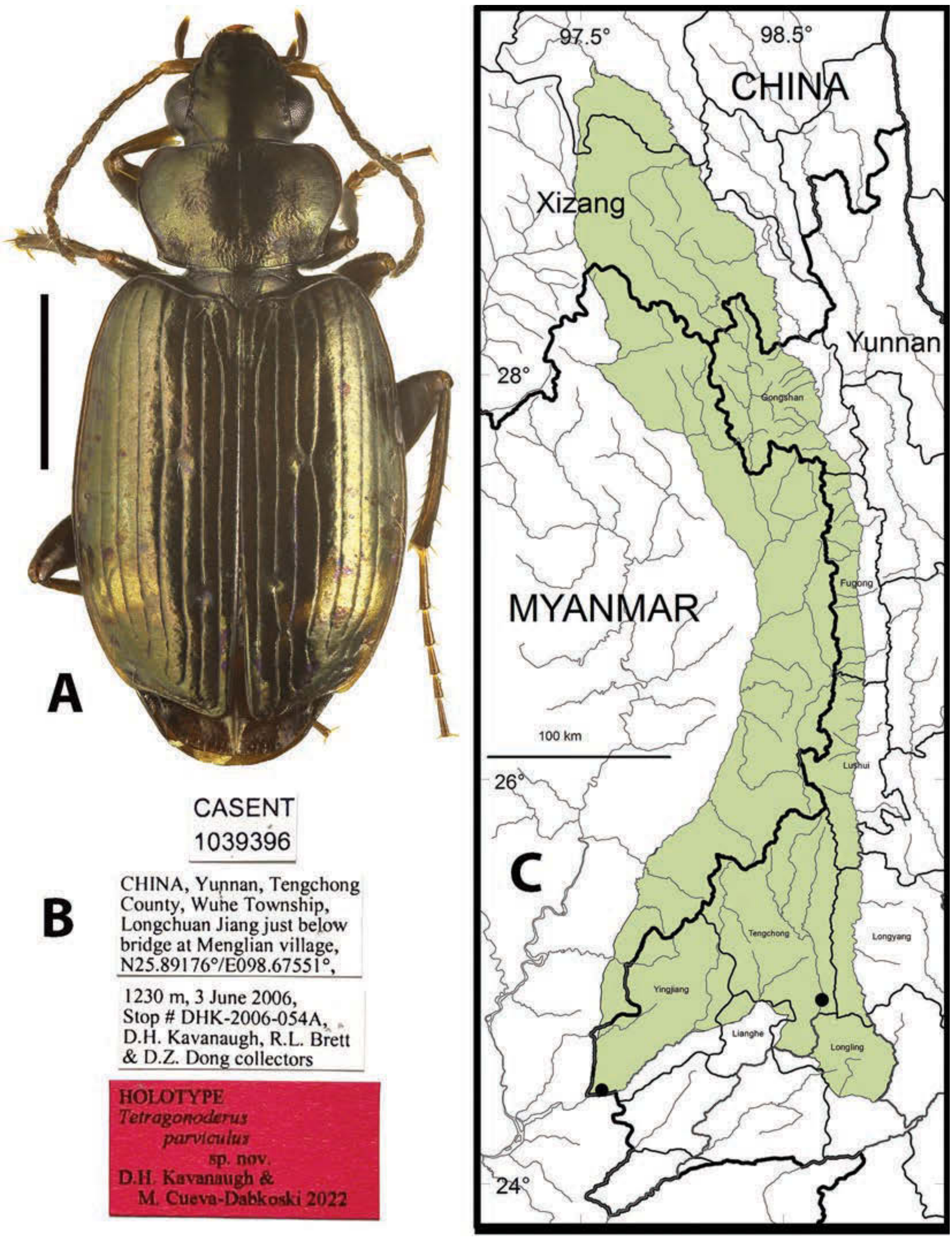
Description. Size. Small for genus, BL males = 3.7 to 4.2 mm, female = 4.4 mm.

Color. (Fig 11A). Head, including venter, piceous to black except mandibles paler subapically and antennae with antennomeres 1, 1 to 2, or 1 to 3 paler. Pronotum piceous to black. Elytra piceous to black but with transverse subapical band of pale spots at about five-sixths elytral length, extended from interval 2, 3, or 4 to interval 8, with spots on intervals 2 and 3 less distinct in most specimens, those on intervals 2 to 4 shorter, and spots on intervals 5 to 8 longer, extended more anteriad, and more distinct. Venter piceous laterally, rufo-piceous medially, elytral epipleurae paler rufopiceous. Legs, piceous to rufopiceous, with femora darker than tibiae or tarsi or tibiae paler than femora and tarsi.

Reflection, luster, and microsculpture. Dorsum of head, pronotum and elytra with distinct aeneous-greenish metallic reflection. Head and pronotum slightly duller than elytra, with microsculpture moderately impressed and comprised of isodiametric meshes; elytra shiny, with microscuplture slightly less deeply impressed and comprised of moderately to markedly transverse meshes, meshes slightly distorted only in immediate vicinity of discal setae; abdominal venter dull laterally and shiny and slightly iridescent medially, with microsculpture moderately impressed and comprised of isodiametric to slightly transverse meshes laterally, more shallowly impressed and formed of transverse microlines and markedly transverse meshes medially.

Head. Eyes large, hemispheric; antennae slightly short, extended only to basal one-fifth of elytra; clypeus bisetose; labrum with three pairs of setae; mentum asetose, with a broadly rounded medial tooth; submentum anteriorly with a single pair of setae.

Prothorax. Pronotum (Fig. 13D) slightly narrow (ratio PWM/EW = 0.61 to 0.65), distinctly narrowed basally (ratio PWB/PWA = 1.04 to 1.09), widest distinctly anterior to mid-length, with anterior angles very short and broadly rounded; posterior angles slightly obtuse and slightly pro-



CASENT
1039396

CHINA, Yunnan, Tengchong
County, Wuhe Township,
Longchuan Jiang just below
bridge at Menglian village,
N25.89176°/E098.67551°,

1230 m, 3 June 2006,
Stop # DHK-2006-054A,
D.H. Kavanaugh, R.L. Brett
& D.Z. Dong collectors

HOLOTYPE
Tetragonoderus
parviculus
sp. nov.
D.H. Kavanaugh &
M. Cueva-Dabkoski 2022

FIGURE 11. *Tetragonoderus parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov. A. Holotype, dorsal aspect, scale line = 1.0 mm (CASENT1039396, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); B. Labels associated with holotype; C. Map showing locality records (black circle) for this species in the Gaoligong Shan region, scale line = 100 km.

jected laterally; apical margin straight or very slightly concave between anterior angles; lateral margins arcuate and with a short and shallow sinuation just anterior to posterior angles; basal margin faintly bisinuate, not or only slightly lobate medially; anterior margination distinct laterally, more or less effaced medially; lateral margination distinct and complete, joined with apical and basal margination at anterior and posterior angles, respectively; basal margination distinct laterally, less distinct medially; midlateral setae inserted on lateral margination ("lateral bead") at about one-fourth pronotal length; basolateral setae inserted on margination at posterior angles. Prosternal intercoxal process short, rounded, with complete but faint margination apically.

Elytra. Broadly ovate, longer than wide (ratio EL/EW = 1.27 to 1.37), widest slightly posterior to mid-length, obliquely truncate apically, humeri obtusely rounded; elytral striae deeply impressed throughout, elytral intervals flat or slightly convex, smooth; parascutellar setiferous pore present at base of interval 1 at junction of striae 1 and 2; two discal setiferous pores present on interval three, the anterior seta inserted adjacent to stria 3 near elytral midlength, the other inserted adjacent to stria 2 near apical one-fourth at level of subapical pale band; apical seta present, inserted near apex of interval 3; umbilicate series comprised of 11 or 12 setae.

Legs. Tarsal claws finely denticulate medially. Males (Figs. 14D, 16D) with front and middle tarsi with tarsomeres 1 to 4 distinctly broader than in females; male front tarsomeres 1 to 3 with two rows of adhesive squamosetae ventrally (Fig. 15D), females without such setae; middle tarsi with tarsomeres 1 to 4 (Fig. 17D) with pads of adhesive setae ventrally, absent from females.

Male genitalia. Median lobe (Fig. 18C,D) long and slender, shaft smoothly arcuate dorsally and ventrally, gradually tapered toward apex, with apical lamella slightly sinuate and tapered to a rounded point apically in lateral view, shaft symmetrically tapered and with apical lamella slightly expanded and apically rounded in dorsal view. Internal sac without evident spines.

Geographical variation. The female specimen from Tongbiquan Township differs from the male specimens from Wuhe Township in having antennae with only antennomere 1 pale (antennomeres 1 to 2 or 3 pale in the other specimens), the tarsi darker than the tibiae (both tibiae and tarsi paler than the femur in the other specimens), and the elytral subapical pale band evident from interval 2 to interval 8 (pale band visible mainly from interval 4 to interval 8 and only very faintly evident on interval 3 in the other specimens). All of these specimens otherwise are similar.

Habitat distribution. Members of this species were found under small stones on the open sandy shore of the Longchuan River, a medium-sized stream, at an elevation of 1230 m and together with adults of *T. elegans and T. punctatus*. The specimen from the Tombiguan area was collected in a baited pitfall trap near a stream through secondary (disturbed) broadleaf forest at an elevation of 1290 m.

Geographical distribution within the Gaoligong Shan. Fig. 11B. We examined a total of five specimens (four males and one female) from the following localities: ***Tengchong County:*** Tongbiguan Township (5.9 km W of Tongbiguan, 24.61276°/97.59121°, 1290 m, 25-27 June 2016, J. Hájek, J. Růžička, & C.B. Wang collectors [1 female; NMPC]; Wuhe Township (Longchuan Jiang just below bridge at Menglian village, 24.89176°/98.67551°, 1230 m, 3 June 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [4 males; CAS, IOZ]).

At present, this species is known only from the southwestern part of the study area (Core Area 6).

Overall geographical distribution. (Fig. 23). Known only from Tengchong County, western Yunnan Province, China.

Geographical relationships with other *Tetragonoderus* species. Members of this species have been found synotopic with those of *T. elegans* and *T. punctatus* in the study area. The range of this species also overlaps that of *T. arcuatus* in the study area, but these two species have not yet been found syntopic. Also, the range of *T. microthorax* overlaps that of *T. parviculus*, but the former species has not yet been recorded from the study area.

Tetragonoderus punctatus (Wiedemann)

Figures 12, 13E, 14E, 15E, 16E, 17E, 19C-D, 21, and 23.

Bembidium punctatum Wiedemann, 1823:61. LECTOTYPE, here designated, a male, in ZMUC, labeled: "TYPE" [red label]/ "Bengala Westermann Punctatus Wied." [handwritten]/ "ZMUC 00027869"/ "LECTOTYPE *Bembidium punctatum* Wiedemann, 1823 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2022" [red label]. Paralectotypes examined: 1 female, in ZMUC, labeled: "Mus. Westerm."/ "TYPE" [red label]/ "Bengal Maj. 1808. Punctatus Wied." [handwritten]/ "ZMUC 00027868" [label upside down]/ "PARALECTOTYPE *Bembidium punctatum* Wiedemann, 1823 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2022" [yellow label]. Type locality: "Bengalia" [area which now includes West Bengal (eastern India) and Bangladesh].

Tetragonoderus punctatus (Wiedemann), Dejean (1829:505); Schmidt-Göbel (1846:92); Chaudoir (1876:48); Andrewes (1921:174); Csiki (1932:1298); Lorenz (2005:453).

Diagnosis. Adults of *T. punctatus* can be distinguished from those of other *cyclosomine* species in the study area by the following combination of character states: Body size medium for genus, BL males = 4.5 to 4.8 mm, females = 4.6 to 5.4 mm; pronotum piceous or rufopiceous, with or without faint greenish metallic reflection; elytral color pattern as in Fig. 12A, with dark areas less expansive, connection between medial portion of the basal dark band and humeral portion absent or very narrow, less than one-fifth the length of humeral portion, middle discal band with portion between anterior and posterior dark edges not or only slightly darker than remainder of pale elytral areas; femora pale tan; pronotum (Fig. 13E) widest near mid-length and posterior to insertion of midlateral seta, not or only very slightly narrowed basally (ratio PWB/PWA = 1.15 to 1.25), lateral margins slightly and evenly convex or straight or very slightly sinuate anterior to basal angles; elytra slightly to distinctly truncate apically; front tarsomeres 1 to 3 without lateral expansions (Figs. 14E, 15E); male with middle mesotarsomeres (Fig. 16E) only slightly wider than in female and with only tarsomeres 1 to 3 with pads of adhesive setae ventrally (i.e., tarsomere 4 without adhesive setae ventrally) (Fig. 17E); median lobe of male genitalia (Figs. 19C,D) with apical lamella short and broad, internal sac without spines.

In the study area, specimens of *T. punctatus* (Fig. 12A) might be confused with those of *T. elegans* (Fig. 10A) and also with those of *T. microthorax* (Figs. 13F, 14F, 15F, 16F, 17F, 19E-F, and 20), although the latter has not yet been recorded from the Gaoligong Shan region. *Tetragonoderus punctatus* members differ from those of *T. elegans* in having the forebody slightly lighter in color (i.e., less heavily pigmented) and the elytral pattern of dark areas less extensive, with connection between medial portion of the basal dark band and humeral portion absent or very narrow, less than one-fifth the length of the humeral portion (at least one-fourth the length of the humeral portion in *T. elegans*), the middle discal band with the area between anterior and posterior dark edges not or only very slightly darker than remainder of pale elytral areas (distinctly darker tan-orange in *T. elegans*), and with a less distinct and discontinuous preapical dark band. Also the pronotum is proportionally slightly wider (ratio PWM/EW = 0.55 to 0.57; in *T. elegans* = 0.51 to 0.55), widest at or near midlength, posterior to the insertion of the midlateral seta (widest more anteriad and at or near the insertion of the midlateral seta in *T. elegans*), less distinctly narrowed basally (ratio PWM/PWB = 1.06 to 1.13; in *T. elegans* = 1.13 to 1.20), and the lateral margins are not at all or only very slightly sinuate anterior to the basal angles (distinctly sinuate in *T. elegans*). Males differ in several additional features. In *T. punctatus* males, the middle tarsi are only slightly wider than those in females and middle tarsomere 4 lacks a pad of adhesive setae ventrally (Figs. 16E,

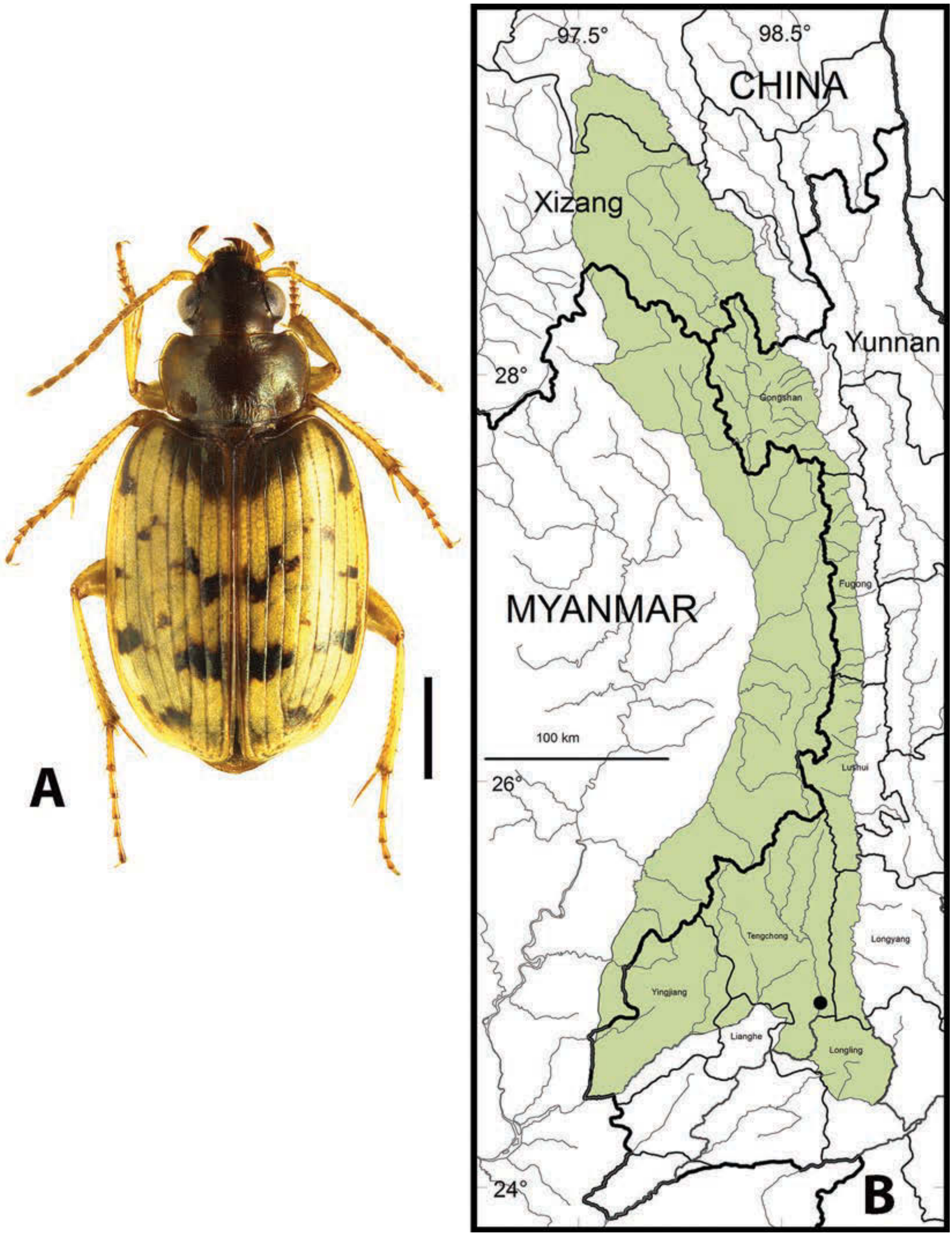


FIGURE 12. *Tetragonoderus punctatus* (Wiedemann). A. Dorsal aspect, scale line = 1.0 mm (CASENT1039412, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); B. Map showing locality record (black circle) for this species in the Gaoligong Shan region, scale line = 100 km.

17E), whereas middle tarsomeres 1 to 4 are distinctly wider than in females and bear adhesive setae ventrally in *T. elegans* males (Figs. 16C, 17C). Males also differ in the form of their genitalia, with the median lobe (Figs. 19C,D) slightly shorter and distinctly thicker, the apical lamella shorter and broader, and the internal sac without distinct spines in *T. punctatus*. In contrast, the median lobe of *T. elegans* males (Figs. 19A,B) is longer and more slender, the apical lamella is much longer, narrower, and distinctly curved ventrad, and the internal sac is armed with five or more large and distinct spines.

Members of *T. punctatus* are extremely similar to those of *T. microthorax* and these two species are no doubt confused in collections. Most specimens of *T. punctatus* are slightly larger (BL males = 4.5 to 4.8 mm, females = 4.6 to 5.4 mm) than those of *T. microthorax* (BL males = 3.9 to 4.6 mm, females = 4.2 to 4.7 mm). They have the pronotum (Fig. 13E) slightly shorter and wider (ratio PWM/PL = 1.52 to 1.70), widest at or near midlength and posterior to insertion of midlateral seta and not or only very slightly narrowed basally (ratio PWB/PWA = 1.15 to 1.25), and with the lateral margins slightly and evenly convex or straight or very slightly sinuate anterior to the basal angles. In *T. microthorax*, the pronotum (Fig. 13F) is slightly longer and narrower (ratio PWM/PL = 1.48 to 1.57), widest anterior to mid-length at or near insertion of midlateral seta, slightly to moderately narrowed basally (ratio PWB/PWA = 1.04 to 1.14), and with the lateral margins slightly to moderately sinuate anterior to the basal angles. Unfortunately, the ranges in size and pronotal proportions (except for ratio PWB/PWA) seen among specimens of these two species overlap slightly, so measurements alone cannot distinguish all specimens of the two. The male genitalia are also very similar, except that the apical lamella of the median lobe is slightly shorter and broader in *T. punctatus* males (Figs. 19C,D) than in *T. microthorax* (Figs. E,F) males. There are also subtle differences in the convexity of the elytral intervals (flat in *T. punctatus* and slightly convex in *T. microthorax*) and depth of impression of the striae (moderately deep in *T. punctatus*, even deeper in *T. microthorax*).

Habitat distribution. Members of this species were found at night, running on the surface of the open sandy shores of the Longchuan River (Fig. 21), a medium-sized stream, at two sites (at elevations of 1215 and 1230 m, respectively). They were running on the same beaches with adults of *T. elegans*, which were much more abundant. They appear to prefer upper beach areas, where zones of slightly moist and dry sand meet.

Geographical distribution within the Gaoligong Shan. Fig. 12B. We examined a total of five specimens (one male and four females) from the following localities: ***Tengchong County:*** Wuhe Township (Longchuan Jiang just below bridge at Menglian village, 24.89176°/98.67551°, 1230 m, 3 June 2006, D.H. Kavanaugh, R.L. Brett, H.B. Liang & D.Z. Dong collectors [one male and three females; CAS, IOZ]), (Longchuan Jiang at Longjiang Bridge, 24.89889°/98.66667°, 1215 m, 28 October 2003, H.B. Liang & X.C. Shi collectors [1 female; CAS].

At present, this species has been recorded only from the southwestern part of the study area (Core Area 6).

Overall geographical distribution. Fig. 23. We have examined specimens of this species only from "Bengala" (i.e., West Bengal (India) and/or Bangladesh) and the localities in the Gaoligong Shan as listed above. Its occurrence in the study area represents the eastern limit of its known geographical range and also a first record for China. It is likely that this species occurs also in northern Myanmar and northeastern India along rivers draining the western slope of the Gaoligong Shan and the southern slope of the eastern part of the Himalaya Mountains, respectively, at low elevations (1000 to 1300 m).

Geographical relationships with other *Tetragonoderus* species. Members of this species have been found synotopic with those of *T. elegans* and *T. parviculus* in the study area. The range of this species also overlaps that of *T. arcuatus* in the study area, but these two species have not yet been found syntopic. Also, the range of *T. microthorax* broadly overlaps that of *T. punctatus*, but the former species has not yet been recorded from the study area. We note that all current records of *T. microthorax* are from localities well below 1000 m in elevation and such elevations are absent from all but the extreme southwesternmost part of the study area, which we were unable to sample.

Discussion

The Gaoligong Shan region is part of one of the world's biodiversity hotspots (Myers et al. 2000), as well as near the center of the Asian distribution of cyclosomines. With the two new species described here, it has one of the most diverse local cyclosomine faunas in the world.

Broad geographical distribution patterns. The known overall geographical ranges of the five cyclosomine species represented in the study area are graphically approximated in Fig. 23. One of these species, *Tetragonoderus parviculus*, is known only from the southwestern part of the study area. Another of the species, *T. punctatus*, has been recorded west of the study area but only as far as eastern India. *Tetragonoderus arcuatus*, is widespread toward the west (as far as North Africa), southwest (to southern India and Sri Lanka), and south (as far as northern Thailand). The two remaining species, *Cyclosomus acutangulus* and *T. elegans*, range westward from the study area along the southern edge of the Himalaya to varied extents, with the former as far as Assam and the latter as far as Uttarakhan. This distribution is similar to that seen for *Omophron chelys* Andrewes (Kavanaugh et al. 2021), *Broscosoma holomarginatum* Kavanaugh and Liang (Kavanaugh & Liang 2021), *Perileptus imaicus* Jeannel (Deuve et al. 2016) and *Amara* (*Bradytus*) *elegantulus* Tschitschérine (Kavanaugh et al. 2014), all represented in the study area.

For four of the five cyclosomine species found in the study area, their presence represents their easternmost occurrence. The geographical range of the fifth species, *T. arcuatus*, extends slightly farther east to southcentral Yunnan and northern Thailand, but no other species of this tribe that occurs east of the study area has been recorded in the Gaoligong Shan regional fauna.

Regional geographical and altitudinal distribution patterns. Within the study area, four of the five cyclosomine species represented are narrowly restricted, both geographically and altitudinally. This is not surprising given the fact that members of all these species prefer the open sandy banks of medium- to large-sized rivers. Such habitats are found only at lower elevations in the study area.

All five species represented in the study area were recorded from Core Area 6, the southernmost area sampled on the western slope of the Gaoligong Shan. All the streams in that Core Area are part of the Irrawaddy River drainage system. Only *Tetragonoderus elegans* was found elsewhere, in Core Areas 1, 2, and 3 as well 6. Core Areas 2 and 3 are on the eastern slope of the Gaoligong Shan and streams in these areas are part of the Nujiang (Salween) River drainage system, whereas those in Core Area 1 are Irrawaddy tributaries. It is likely that *T. elegans* eventually will be found to occur in suitable habitats in all of the Core Areas. That species also occupies the broadest altitudinal range in the study area, recorded from 1185 to 1890 m, whereas the other four species all have been found only in the 1200 to 1450 m range.

Syntopy of species in the regional fauna. Several of the cyclosomine species were found together in the study area. *Cyclosomus acutangulus* was found syntopic with *Tetragonoderus elegans* and *T. punctatus*, and specimens of *T. parviculus* were collected with those of *T. elegans* and *T. punctatus* at a different locality. Although the geographical range of *Tetragonoderus arcuatus* overlaps those of the other species in the fauna, *T. arcuatus* has not yet been collected together with any of them.

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Illustrations

Figures 13–23

FIGURE 13. Pronota of cyclosomines, dorsal aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (CASENT 1013512, Xiaojiangqiao, Qushi Township, Tengchong County, Yunnan, China); C. *T. elegans* Andrewes (CASENT1039499, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); D. *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov., (CASENT1039394, holotype, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); E. *T. punctatus* Wiedemann (CASENT 1039412, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); F. *T. microthorax* Jian & Tian (8 km S of Jamiri, northeastern India). Scale lines = 0.5 mm.

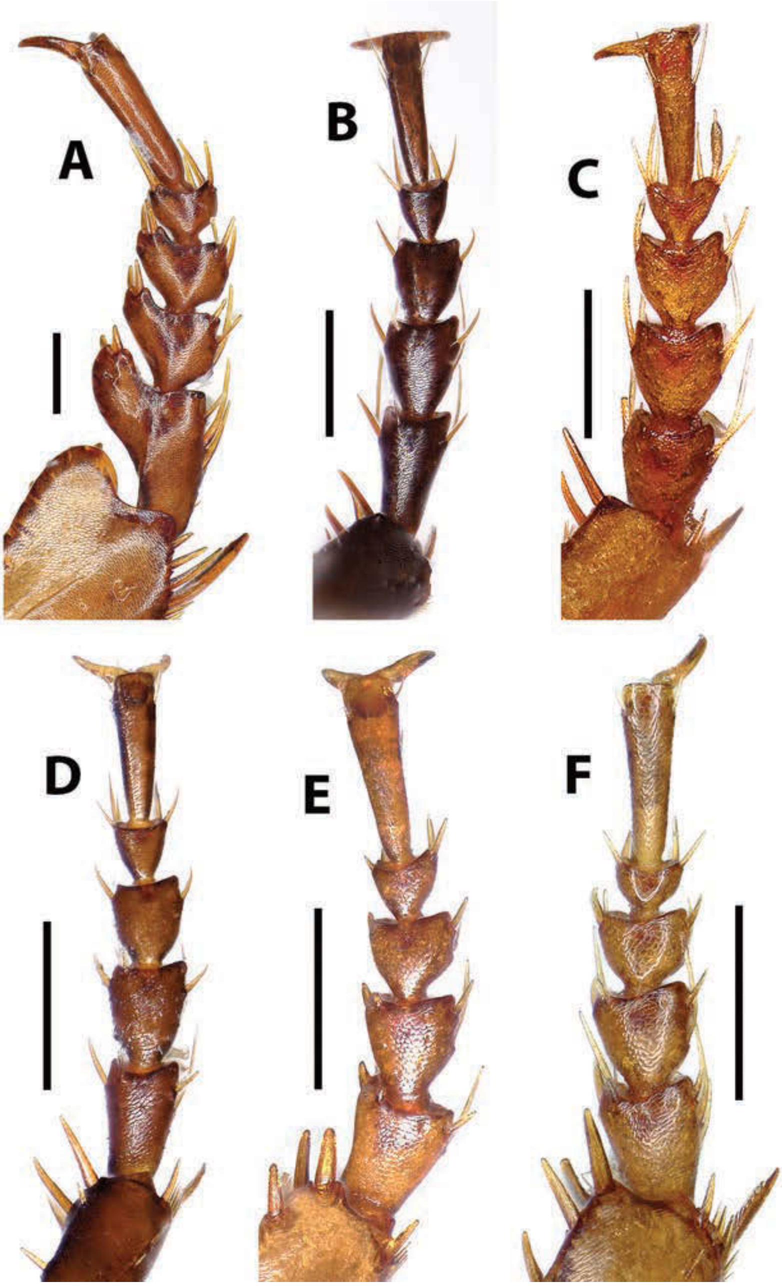

FIGURE 14. Male front tarsus, dorsal aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); C. *T. elegans* Andrewes (CASENT1039499, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); D. *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT1039397, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); E. *T. punctatus* Wiedemann (CASENT1039548, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); F. *T. microthorax* Jian & Tian (8 km S of Jamiri, northeastern India). Scale lines = 0.2 mm.

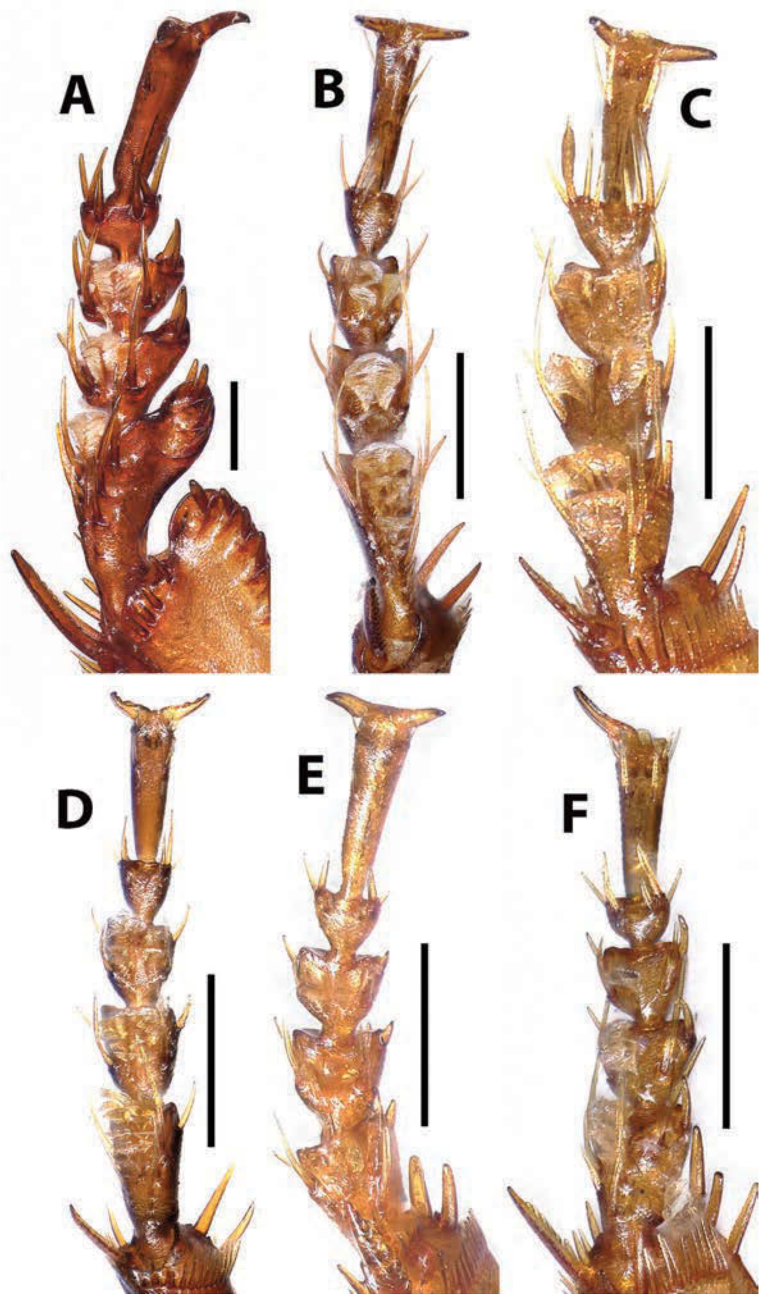

FIGURE 15. Male front tarsus, ventral aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); C. *T. elegans* Andrewes (CASENT1039499, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); D. *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT1039397, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); E. *T. punctatus* Wiedemann (CASENT1039548, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); F. *T. microthorax* Jian & Tian (8 km S of Jamiri, northeastern India). Scale lines = 0.2 mm.

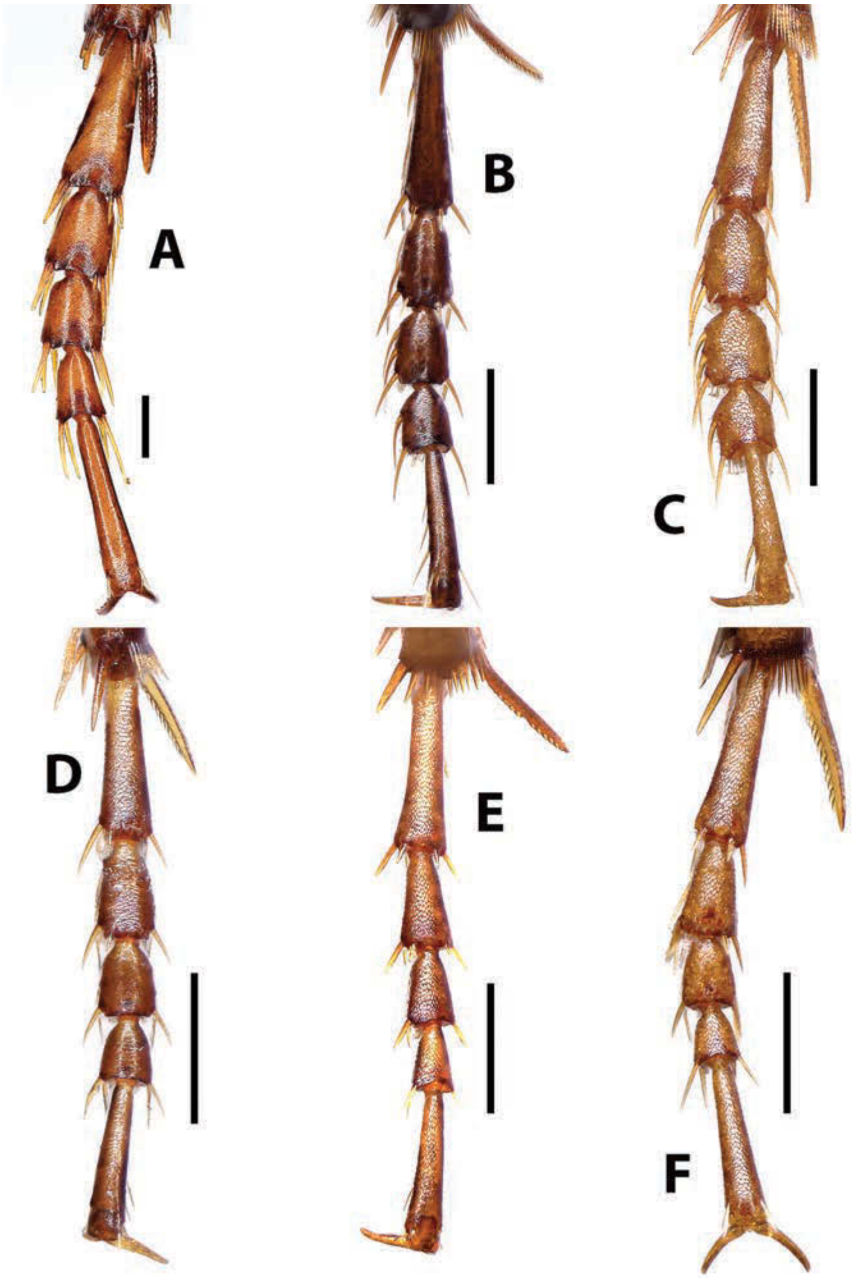

FIGURE 16. Male middle tarsus, dorsal aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); C. *T. elegans* Andrewes (CASENT103499, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); D. *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT1039397, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); E. *T. punctatus* Wiedemann (CASENT1039548, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); F. *T. microthorax* Jian & Tian (8 km S of Jamiri, northeastern India). Scale lines = 0.2 mm.

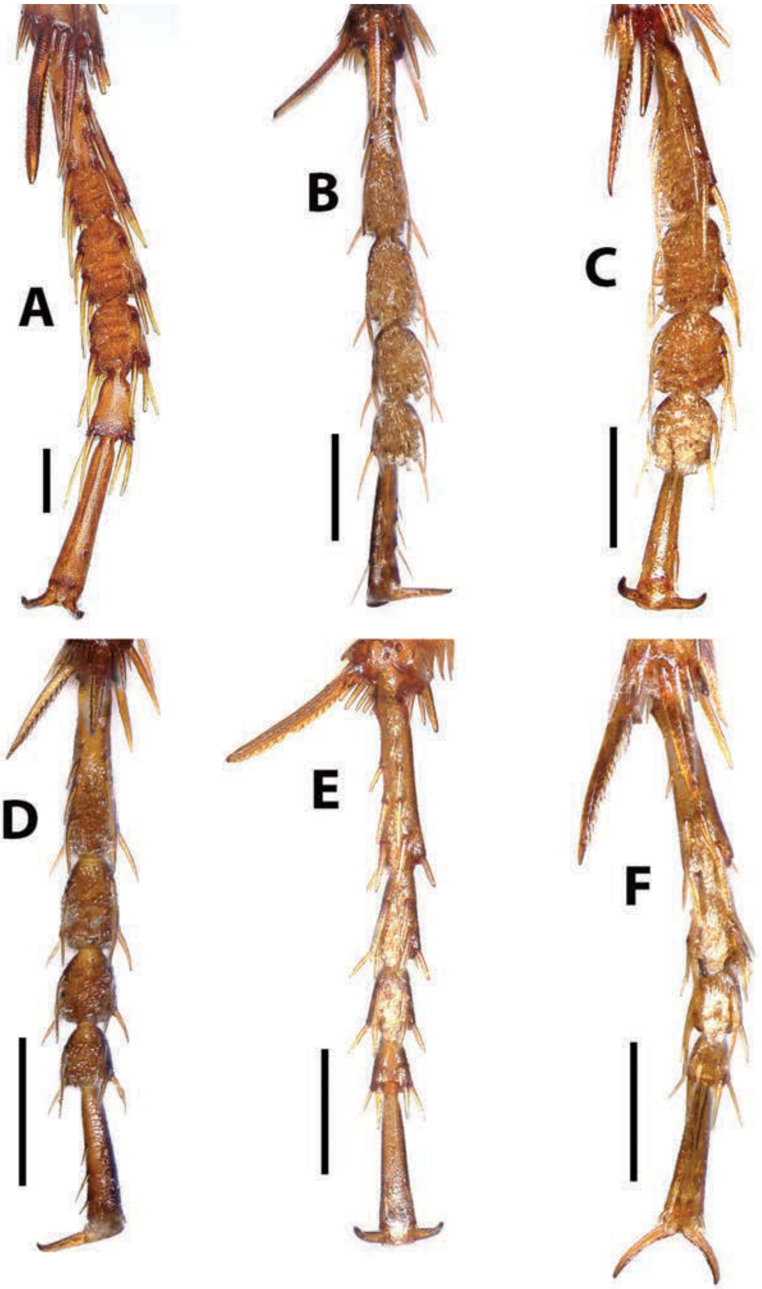

FIGURE 17. Male middle tarsus, ventral aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); C. *T. elegans* Andrewes (CASENT103499, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); D. *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT1039397, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); E. *T. punctatus* Wiedemann (CASENT1039548, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); F. *T. microthorax* Jian & Tian (8 km S of Jamiri, northeastern India). Scale lines = 0.2 mm.

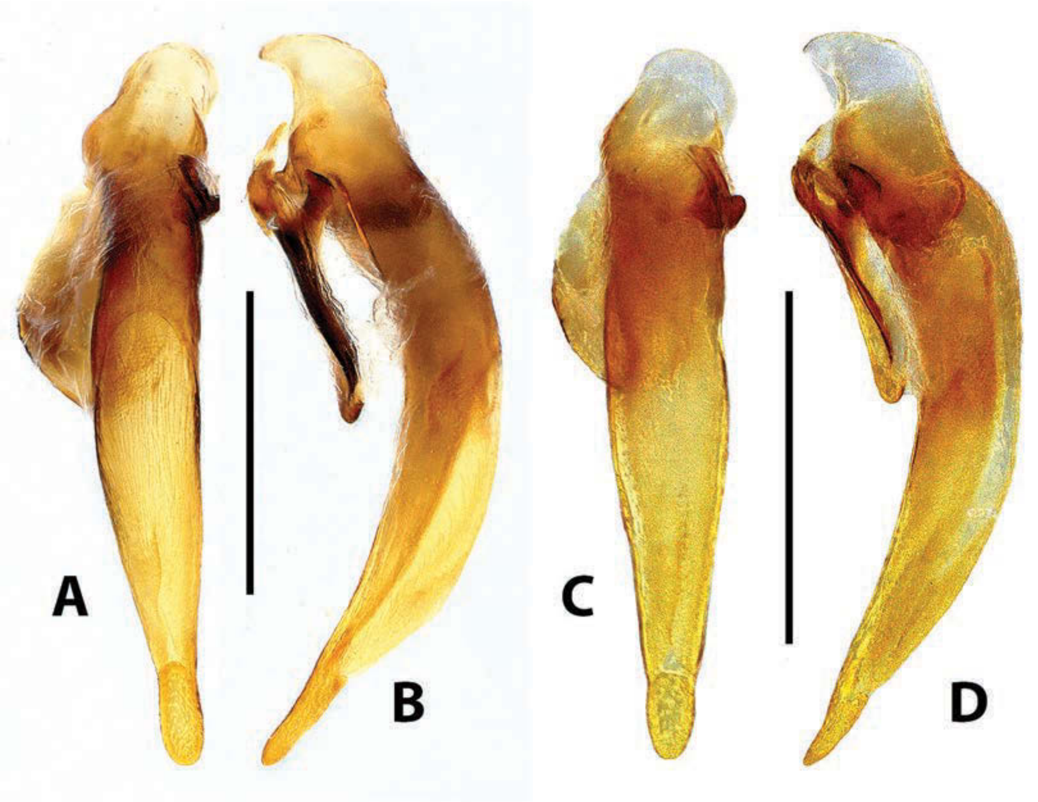

FIGURE 18. Male genitalia, *Tetragonoderus* spp. A, B. *T. arcuatus* Dejean (Nepalgunj, Banke District, Nepal); C, D. *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov., (CASENT1039396, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China). A, C. Dorsal aspect; B, D. Left lateral aspect; scale lines = 0.5 mm.

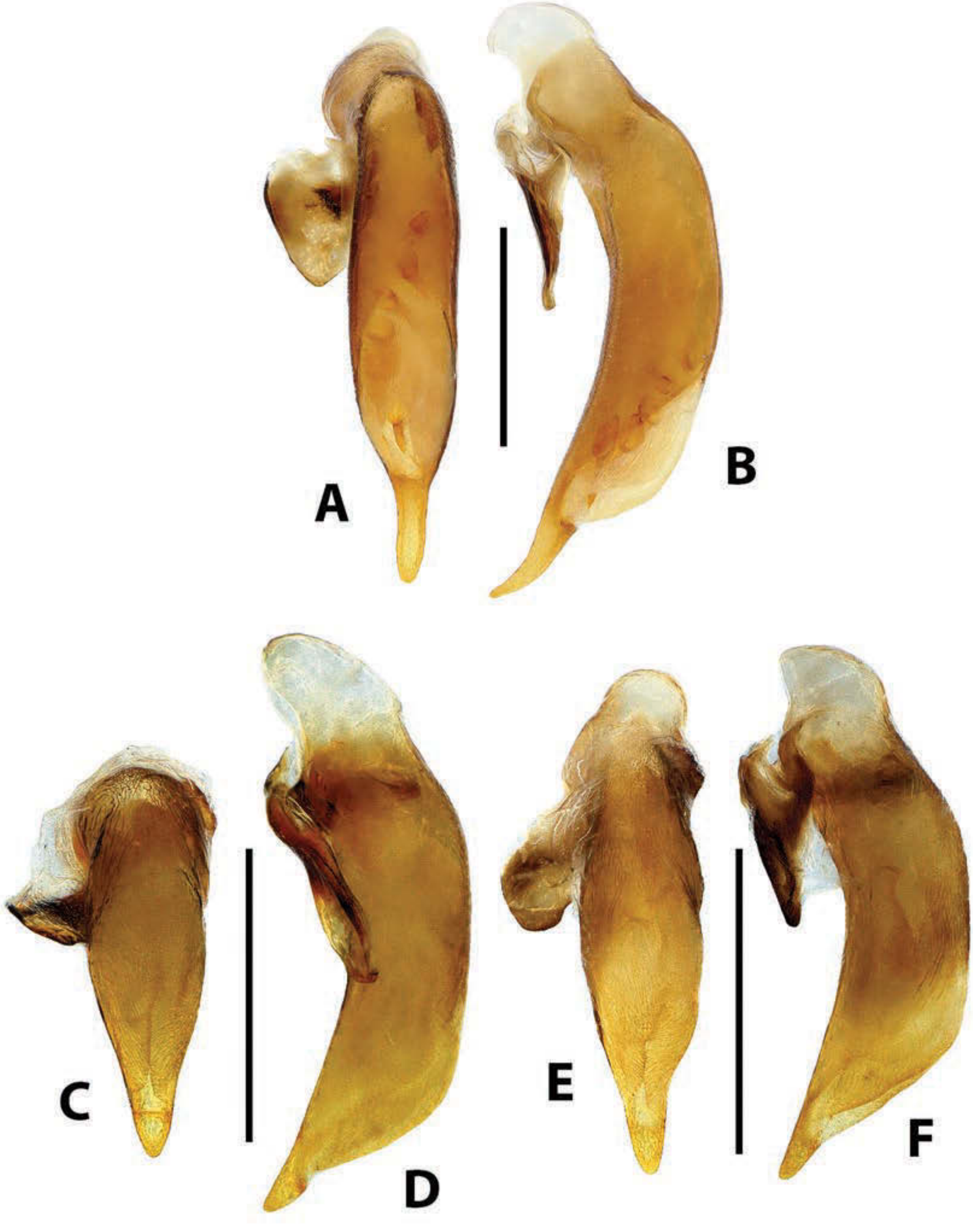

FIGURE 19. Male genitalia, *Tetragonoderus* spp. A, B. *T. elegans* Andrewes (CASENT1039498, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); C, D. *T. punctatus* (Wiedemann) (CASENT1039548, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); E, F. *T. microthorax* Jian and Tian (Jamiri-Sessa, Arunachal, India). A, C, E. Dorsal aspect; B, D, F. Left lateral aspect; scale lines = 0.5 mm.

FIGURE 20. *Tetragonoderus microthorax* Jian and Tian, dorsal habitus of holotype (Jinghong, Yunnan, China); scale line = 1.0 mm.

FIGURE 21. Photographs of habitat for cyclosomine species, *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov., *Tetragonoderus elegans* Andrewes, *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov., and *T. punctatus* Wiedemann at Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China. A. lower river bank; B. sandy upper bank with sparse vegetation. Photos by David H. Kavanaugh.

FIGURE 22. Photographs of habitat for *Tetragonoderus arcuatus* Dejean at Longchuan Jiang at Xiaojiangqiao, Qushi Township, Tengchong County, Yunnan, China. A. overview of river bank; photograph by David H. Kavanaugh. B. upper sandy bank with sparse vegetation; photograph by Roberta L. Brett.

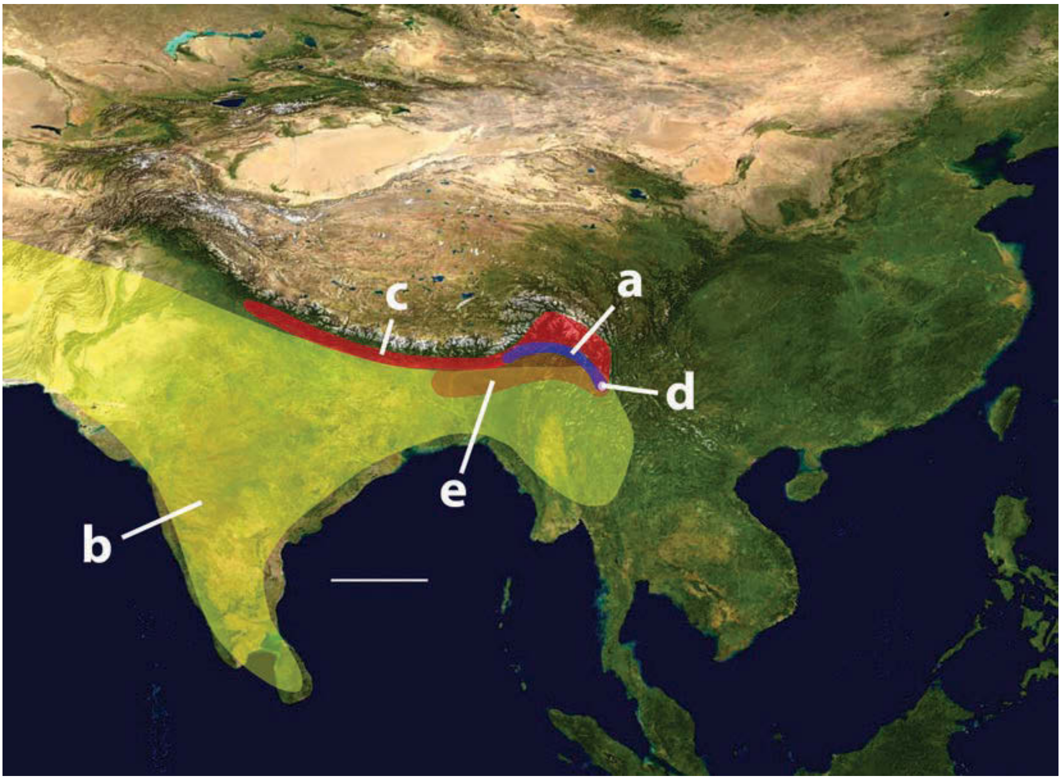

FIGURE 23. Map showing approximate known overall geographical distributions of cyclosomine species occurring in the Gaoligong Shan. a (blue) = *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov.; b (yellow) = *Tetragonoderus arcuatus* Dejean; c (red) = *T. elegans* Andrewes; d (white dot) = *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov.; e (orange) = *T. punctatus* Wiedemann. Modified from Wikimedia Commons, World Atlas of the World, at URL: *http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_-_land_and_oceans_12000.jpg*. Scale line = 500 km.

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A Review of Genus *Cyclosomus* Latreille (Coleoptera: Carabidae: Lebiinae: Cyclosomini) in Asia.

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A comparative morphological study of 317 specimens of genus *Cyclosomus* Latreille accumulated through personal collecting and loans has permitted recognition of nine species in Oriental and southern Palearctic regions of Asia. Two species are described as new: *Cyclosomus pallidus* Kavanaugh and Cueva-Dabkoski sp. nov. (type locality: Karachi, Sindh Province, Pakistan) and *C. vespertilio* Cueva-Dabkoski and Kavanaugh sp. nov. (type locality: Royal Chitwan National Park, Nepal). Lectotypes are designated for four species-group names: *Carabus flexuousus* Fabricius, *Cyclosomus dytiscoides* Nietner, *Cyclosomus marginatu*s Motschulsky, and *Scolytus suturalis* Wiedemann. A key is provided for the identification of adults to species and the known habitat and geographical distributions of each species are summarized. Also included are discussions of geographical and habitat distribution patterns, sympatry and syntopy in the fauna, and potentially fruitful next steps for research on this fauna.

KEYWORDS: Coleoptera, Carabidae, Cyclosomini, *Cyclosomus*, new species, Asia, distribution, key to species

Cyclosomus Latreille (1829) is a modestly diverse genus in the carabid beetle tribe Cyclosomini of subfamily Lebiinae, with only 13 described species prior to this study (Lorenz 2005, Kavanaugh et al. 2023). The geographical range of the genus includes the warm-temperate southern edge of the Palearctic Region and the Oriental and Afrotropical Regions. Members of all species in the genus share a common overall body form (as in Fig. 1) and all are basically pale in dorsal body color with or without a variously developed pattern of dark areas on the pronotum and elytra. These beetles live on the exposed sandy banks of mid- to large-size rivers, lakes, or sea beaches and associated dune systems (Figs. 18, 19). They are active on the surface mainly at night and hidden in the sand or under surface debris during the day. They can be driven to the surface by splashing water on the sand or by compressing the sand with one's feet (Jeannel 1949). Once so disturbed, they can dig themselves back into the sand with surprising speed (Nietner 1857), aided by uniquely modified front tarsi and tibiae (Figs. 2B, C). Examination of gut contents and field observations have shown that they are general predators on other arthropods in their habitat. Several records of their collection at lights, and the presence of moth scales on some museum specimens confirming capture in light traps, indicate that they can and do fly, at least at night. They are very similar to members of the carabid genus *Omophron* species (tribe Omophronini) in their basic body form and coloration, in their habitat preferences, and in their behavior, although the two

FIGURE 1. *Cyclosomus inustus* Andrewes, adult male feeding on a small fly (photograph reproduced from Wang et al. 2017 with permission of Liang-Jong Wang).

groups are not closely related. This suggests that species in both groups are under similar selective pressures in their habitat and have evolved in parallel in both body form and color pattern.

As part of a study on the cyclosomines of the Gaoligong Shan region in western Yunnan Province, China, we reviewed material on loan from museums in North America and Eurasia representing *Cyclosomus* species from all of Asia. We examined type specimens themselves, or high resolution images of them, for all but one of the described species and their synonyms, as well as both identified and unidentified specimens from the region. Individuals in charge of several collections (see below) generously made specimens available on loan or, where that was not possible, arranged for photographs of critical specimens.

The history of taxonomic work on *Cyclosomus* in Asia mainly has been one of a few isolated descriptions of new species (Fabricius 1775; Wiedemann 1819; Nietner 1857; Motschulsky 1864; Bouchard 1903; Heller 1923; and Andrewes 1924) with minimal associated comparative information in most cases. Chaudoir (1876) reviewed the species known at that time and Andrewes (1921) discussed synonymies among and the validity of nominal species. Later, Andrewes (1924) provided a key to species. While Kavanaugh (2015) reviewed the African *Cyclosomus* fauna, there has been no recent treatment of the Asian species. The most recent reports on the genus involved the discovery and distribution of *Cyclosomus inustus* Andrewes, 1924 in Taiwan and Guangdong Province, China (Wang et al. 2017, 2022) and description of one new species (Kavanaugh et al. 2023).

A study of the material available has led us to recognize nine species in the Asian fauna, including two new species. We discuss features of form and structure that we use to distinguish them, provide a key for identification of their respective adults, and summarize their known habi-

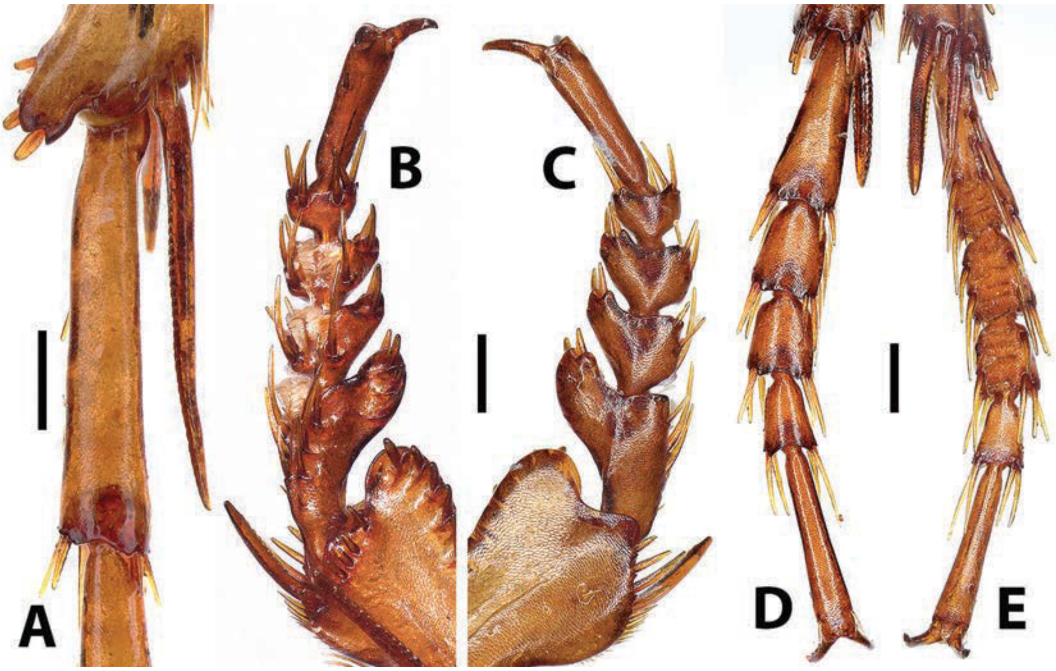


FIGURE 2. Parts of legs, *Cyclosomus acutangulus* Kavanaugh and Cueva-Dabkoski (Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China). A. Left hind tibial medial spur and tarsomere 1, dorsal aspect; B,C. Male front tarsus, B. ventral aspect, C. dorsal aspect; D,E. Male middle tarsus, D. dorsal aspect, E. ventral aspect. Scale lines = 0.2 mm.

tat and geographical distributions and geographical relationships among these species. We also designate lectotypes for four species-group names.

MATERIALS AND METHODS

A total of 317 cyclosomine specimens from Asia were examined during this study, including primary type specimens for all species names and their synonyms except for that of *Cyclosomus sumatrensis* Bouchard. More than 300 additional specimens, including type specimens and other identified specimens from the Afrotropical Region, were also examined. Codes used throughout this report for collections from which specimens were borrowed and/or in which specimens, including primary types, are deposited are as follows:

CAS	California Academy of Sciences, San Francisco, California, U.S.A.
EMEC	Essig Museum of Entomology, University of California, Berkeley, California, U.S.A.
IOZ	National Zoological Museum of China, Institute of Zoology, Beijing, China
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MFNB	Museum für Naturkunde, Berlin, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris, France
NHMUK	British Museum (Natural History), London, United Kingdom
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden
NMNH	U. S. National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.
SMTD	Senckenberg Museum für Naturkunde, Dresden, Germany

ZMMU	Zoological Museum, Moscow University, Moscow, Russia
ZMUC	Zoological useum, Natural History Museum of Denmark, University of Copenhagen, Denmark
ZMUK	Zoological Museum, University of Kiel, Kiel, Germany

Examination of specimens. Specimens were examined using a Leica MZ9.5 stereoscopic microscope with a Proline 80 LED Ring Illuminator.

Measurements. Several measurements (Fig. 3A) were recorded for specimens examined: head length (HL), measured from the apex of the labrum to the occipital ridge of the head; pronotal length (PL), measured along midline from anterior margin to posterior margin (i.e., length of anterior angles not included in PL); pronotal width at widest point (PWM); pronotal width between apices of the anterior angles (PWA); elytral length (EL), measured from the basal groove of the scutellum (i.e., the point at which base of the pronotum contacts the scutellum, which is exposed in specimens where the forebody is bent downward relative to the elytra) to the apex of longer elytron; and elytral width (EW), measured across both elytra at their widest point (less any gap between the elytra on a specimen). Body length (BL) was calculated as the sum of HL + PL + EL. Ratios BL/EW, PWM/PL, PWM/PWA, PWM/EW, and EL/EW were calculated based on those measurements. All measurements were taken with the aid of the Leica MZ9.5 stereoscopic microscope fitted with ocular grid and calibrated scale reticules.

Color and color patterns. The predominant features used to describe and distinguish *Cyclosomus* species throughout the taxonomic history of this taxon have been those dealing with color and/or color pattern. To illustrate this point, we cite Dupuis' key to the African *Cyclosomus* (Dupuis 1912), which was the most comprehensive key for that fauna at the time. With it, he distinguished four species and an additional subspecies based on color (including presence or absence of metallic reflection) and color pattern only. The problem with reliance on these features is that, in several if not all species, they are highly varied, both within and between populations, and undoubtedly subject to intense selection for concealment from predators in the open beach environment in which these beetles live. These color patterns and variations among them are reminiscent of those seen among *Omophron* species, which share some of the same habitats.

Members of all Asian *Cyclosomus* species have the same basic pattern of pale and dark elements, but with those elements varied in their development, form, and presence or absence. All of the following comments are provided as a caution against excessive reliance on these most obvious features in attempts to identify these beetles. The basic pattern is illustrated in Fig. 3B. The pronotum has a more or less dark discal region and paler lateral regions, which we call the lateral pale bands (= lpb in Fig. 3B). Color of the discal region is varied from a light brown to black. The pale bands range from pale yellow-tan to rufous and are varied in their width and shape and how sharply they are defined medially from the discal color. We observe that the width, shape, and definition of the lateral pale bands of the pronotum appear to be more consistent within species than are most of the elytral features discussed below, so they are more reliable characters for identification and we use them in our key.

In contrast, the elytra in all Asian species are basically pale in color with a pattern of dark elements more or less developed on that background. The pale background is varied from yellow-tan to pale rufous and the dark elements from rufopiceous to black among specimens examined. For descriptive purposes, we recognize four separate elements. The first element, the basal dark band (=bdb in Fig. 3B), occupies the basal one-fifth or one-sixth of the elytra and extends laterally to interval 5 or 6 but is varied in thickness and degree of definition. The second element is the longitudinal dark band (=ldb in Fig. 3B), restricted to interval 1 in most specimens but extended slightly onto interval 2 in a few specimens of some species. This element was found in all *Cyclosomus*

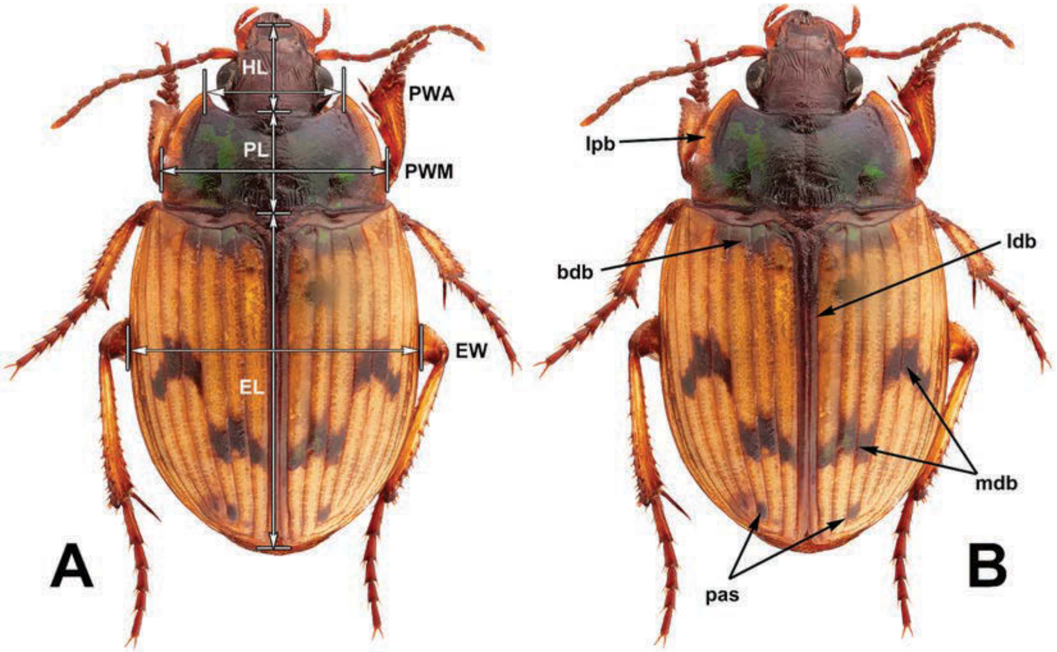


FIGURE 3. A. Illustration of measurements recorded. EL = elytral length; EW = elytral width; HL = head length; PL.= pronotal width; PWA = width between apices of apical angles of pronotum; PWM = width across widest part of pronotum. B. Illustration of terms used for describing the dark color pattern in *Cyclosomus* species (example image is of a widespread African species, *Cyclosomus buqueti* Kolbe). bdb = basal dark band; ldb = longitudinal dark band; lpb = lateral pale band of pronotum; mdb = middle transverse dark band; pas = preapical dark spot.

specimens examined but varied in color from light brown to black. The third element is the middle transverse dark band, or simply middle dark band (=mdb in Fig. 3B), which is the most distinctive and has been the most frequently used element in past species descriptions. Unfortunately, it is also the element subject to the most variation both within and between species and populations. It is varied in color from pale reddish brown to black and is absent from members of one species. Where present, this band is fused with the longitudinal dark band medially and its form ranges from a thin compound-W shape (as in Fig. 7A), extended across both elytra to interval 6, to a broad band extended laterally onto interval 9 and extended anteriorly and posteriorly on that interval as well as on intervals 2 to 4 in some specimens (e.g., Fig. 6A). A variety of forms intermediate between these extremes is also seen. The fourth element is the preapical dark spot (= pas in Fig. 3B), centered on the preapical area of interval 3 and confined to that interval in several species or extended medially onto interval 2 and/or laterally onto one or more of intervals 4, 5, or 6. The presence or absence of this element is relatively consistent within and between species, with all specimens examined of three species exhibiting the preapical spot, all those of four species lacking the spot, and those of the remaining two species dimorphic for this feature as potential geographic variation. The presence or absence of this feature is used in our key.

All of the dark areas on the pronotum or elytra may be indistinct or even invisible in newly-emerged adults that are still teneral and have not yet developed their full pigmentation pattern. Such individuals are difficult if not impossible to properly identify based solely on color characters. Another feature that is useful in distinguishing members of some African species, the presence (see images in Fig. 3) or absence of metallic reflection on the pronotum, could not be used for distinguishing the Asian species because none of them have members with any metallic reflection. Further complicating identification is the fact that at least some members of several species have elytral color patterns more similar to some or all members of other species than to other members of their own species. Consequently creating a reliable key to species was difficult; but we trust that the one provided, along with species diagnoses, descriptions, and distributional data, will facilitate identification.

Dissections. Dissections of male genitalia were prepared from specimens relaxed in hot (near boiling) soapy water by severing the membranes between the genital capsule and tergite VII and sternite VII and extracting the capsule intact. The dissections were then cleared in warm 10% KOH and further dissected to separate the sclerotized parts enough to visualize structures to be compared.

Illustrations. Digital images of dorsal habitus, pronotum, and elytra were taken using a Canon EOS 6D Mark II DSLR camera with a 65mm 2.8-5X macro lens. Multiple images at different focal planes were taken using a StackShot Macro Rail Package and merged using Helicon Focus software. Digital images of portions of legs and of male genitalia were taken using a Keyence VHX-7000 digital microscope. All stacked imaged were edited and arranged into plates using Adobe Photoshop CS5.

Distributional data. Because locality names and geopolitical units throughout Asia have changed so dramatically and repeatedly over the last few centuries, type localities are cited using the current country, regional, and locality names for them, not necessarily as in the original citations. Locality records for other specimens have also been converted to their current names where this could be done unambiguously. Maps illustrating the locations of localities for specimens examined were modified from the "Whole world – land and oceans 12000.jpg" map available from Wikipedia Commons online at *https://commons.wikimedia.org/wiki/File:Blue_Marble_2002.png#/media/File:Whole_world_-_land_and_oceans_12000.jpg.*

TAXONOMY

Tribe Cyclosomini LaPorte de Castelnau, 1834

Genus *Cyclosomus* Latreille, 1829

Scolytus Fabricius, 1790:221, in part [junior homonym of *Scolytus* Geoffroy, 1762] (type species *Carabus limbatus* Fabricius, 1801, designated by Latreille (1810:426). Fabricius (1792:180); Bousquet (2012:89).

Cyclosomus Latreille, 1829:394 (type species *Carabus flexuosus* Fabricius, 1775, by monotypy).

Diagnosis. Adults of *Cyclosomus* species can be distinguished from those of other Asian carabid species by the following combination of character states: Body medium-sized, BL = 6.5 mm to 9.5 mm; body form broadly ovoid (e.g., Fig. 3), *Omophron*-like; head with two pairs of supraoribital setae; labrum with anterior margin deeply emarginate; mentum with medial tooth present, apically emarginate; pronotum (Fig. 14) very broad, trapezoidal, almost as wide as elytra at humeral angles, distinctly widest at or near base; elytra broadly rounded apically, elytral basic color pattern as in Fig. 3B; middle and hind tibiae with medial spurs long and serrulate (Fig. 2A); front tarsomeres 1 to 3 markedly expanded laterally (Figs. 2B, C) in both males and females; middle tarsomeres 1 to 3 broad and with pads of adhesive squamosetae (Stork 1980) ventrally in males (Figs. 2D, E), narrower and without ventral setal pads in females.

Diversity: At present, six species are recognized in the Afrotropical Region and seven species in the Asian fauna. We here recognize nine *Cyclosomus* species as occurring in Asia, with two of these new to science.

Key for Identification of Adults of *Cyclosomus* species of Asia

Both male and female adults of *Cyclosomus* species from the region can be identified using the key below. We have avoided gender-specific features as much as possible in creating the key, and where features unique to males are used, they are presented only as secondary in importance. However, these features can be very helpful in confirming the identification of males. Male specimens of all species included in the key have small pads of adhesive setae on the ventral surfaces of front tarsomeres 1 to 3. Females have no such pads. Although in most carabid beetle species these front tarsomeres are also distinctly broader in males than in females, in the Asian *Cyclosomus* species these differences are very slight and therefore difficult to assess. Contributing to this difficulty is the fact that both males and females have the basal three tarsomeres asymmetrically expanded laterally as flat plates that undoubtedly aid in digging into the sandy substrate they inhabit. More reliable features for distinguishing the sexes are middle tarsomeres 1 to 3, which are distinctly broader in males than in female and have ventral adhesive setae, which are absent from females. We recommend that users of the key review the cautions given in the section entitled "Color and color patterns" under Materials and Methods above because the elytral color pattern is highly varied within some species and similar among at least some members of different species.

1 Pronotum (Fig. 14A) with anterior angles narrow, distinctly acute, lateral margins slightly to distinctly sinuate near anterior angles, disk dark piceous to black, with lateral pale bands well-defined and very narrow; median lobe of male genitalia with shaft evenly arcuate and tapered to a thick apical lamella, slightly ventrally deflected in lateral aspect (Fig. 16A), shaft slightly broadened for most of its length, then tapered to base of short, narrow, smoothly rounded apical lamella in dorsal aspect (Fig. 17A) .... *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski

1' Pronotum (Figs. 14B-I) with anterior angles broader, lateral margins not sinuate or (in very few specimens) faintly sinuate near anterior angles, lateral pale bands wider, well-defined or not, male genitalia as in Figs. 16B-H, 17B-H 2

2 (1')Elytra without (Figs. 7A, 7C, 8-10,13) a preapical spot or with only a small and faint (Fig. 7D) spot (seen in some specimens from inland parts of Indochina) 3

2' Elytra (Figs. 5, 6, 11, 12,) with distinct preapical dark spot 7

3 (2)Elytral epipleuron with long setae over entire length, visible from dorsal aspect in most specimens (Fig. 10A) [but best viewed from below because setae may be bent posteriorly in some specimens]; pronotum (Fig. 14F) relatively narrow (ratio PWM/PL = 2.06 to 2.33) and less broadened basally (ratio PWM/PWA = 1.45 to 1.59), with disc piceous to black and lateral pale band wide and well-defined; free apex of prosternal intercoxal process long (as in Fig. 15C); elytral dark pattern varied (Figs. 10A, C), with basal and middle bands of average to greater than average thickness; median lobe of male genitalia with shaft arcuate basally and nearly straight subapically, tapered to a long and pointed apical lamella in lateral aspect (Fig. 16E), shaft moderately broad basally, gradually tapered to moderately broad and apically blunted, sublaceolate apical lamella in dorsal aspect (Fig. 17); specimen from Philippine Islands (Fig. 21) .... *Cyclosomus philippinus* Heller

3' Elytral epipleuron with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; pronotum (Figs. 14 C, D, E, I) relatively broader in most specimens (ratio PWM/PL = 2.33 to 2.93) and more broadened basally (ratio PWM/PWA = 1.63 to 1.75), with disc varied in color (pale tan-orange to black) and lateral pale band well-defined or not; free apex of prosternal intercoxal process varied in length, from long to short (Fig. 15); elytral dark pattern varied, with basal and middle bands of average to less than average thickness or middle band absent; median lobe of male genitalia not sublanceolate, rounded in dorsal aspect (Figs. 17C, D, H); specimen not from Philippine Islands 4

4 (3')Pronotum (Fig. 14C) relatively longer and narrower (ratio PWM/PL less than 2.50), with disc varied in color (rufous to piceous) and lateral pale bands medium-width and well-defined; free apex of prosternal intercoxal process long (as in Fig. 15C); body form (Figs. 7A, C, D) more elongate-ovoid (ratio BL/EW = 1.47 to 1.53), with elytra widest at or slightly anterior to midlength; elytral dark pattern varied in both form and color (Figs. 7A, C, D), with dark maculae rufous to piceous and with basal and middle bands of average to less than average thickness and continuity or middle band absent; elytral striae very deeply impressed, elytral intervals (especially intervals 3 to 5) slightly but distinctly convex; median lobe of male genitalia long and more slender, shaft of approximately equal thickness throughout, ventral curvature gradually and only slightly arcuate in apical two-thirds in lateral aspect (Fig. 16C), apical lamella longer, rounded apically, and not or only slightly narrowed basally in dorsal aspect (Fig. 17C); specimen from southern Asia, from northeastern coastal India, through Indochina, to coastal southeastern and eastern China and Taiwan (Fig. 20) . . . . *Cyclosomus inustus* Andrewes

4' Pronotum (Figs. 14D, E, I) shorter and very broad (ratio PWM/PL equal to or greater than 2.65); body form (Figs. 8A, 9A, 13A, 13C, 13D) shorter in most specimens (ratio BL/EW = 1.36 to 1.49), more roundly ovoid, broader apically; elytral dark pattern varied in both form and color; elytral striae less deeply impressed in most specimens, elytral intervals flat or nearly so; median lobe of male genitalia varied in form (Figs. 16D, H) 5

5 (4')Dorsal surface (Fig. 9A) mainly pale tan-orange, with only pronotal disc, elytral basal dark band and longitudinal dark band on elytral interval 1 slightly darker brown, middle dark band absent; pronotum (Fig. 14E) very broadly flattened laterally (especially anteriorly), lateral pale bands very broad and only slightly contrasting with color on disc; free apex of prosternal intercoxal process short (as in Fig. 15D); specimen from southeastern Pakistan (Fig. 21); males unknown . . . . ***Cyclosomus pallidus* Kavanaugh & Cueva-Dabkoski sp. nov.**

5' Dorsal surface (Figs. 8A, 13A, C, D) with distinctly contrasting pale and dark areas; pronotal disc darker, rufopiceous to black, with lateral pale bands broad but narrower than above (Figs. 14D, 14I); elytra pale yellowish-brown with basal, middle and longitudinal dark bands present and dark reddish brown to black; free apex of prosternal intercoxal process short (as in Fig. 15D) or medium in length (as in Fig. 15B) 6

6 (5')Body form (Fig. 8A) roundly ovoid (ratio BL/EW = 1.46 to 1.49; ratio EL/EW = 0.94 to 0.96); free apex of prosternal intercoxal process medium in length (as in Fig. 15B); elytra with middle transverse dark band narrow, extended laterally onto interval 6, portion on intervals 2 to 4 connected to portion on intervals 5 and 6 by in narrow, oblique dark line; median lobe of male genitalia with shaft of approximately equal thickness throughout, ventral curvature straightened subapically in lateral aspect (Fig. 16D), apical lamella slightly shorter in dorsal aspect (Fig. 17D) . . . . *Cyclosomus marginatus* Motschulsky

6' Body form (Fig. 13A, C, D) even more roundly ovoid (ratio BL/EW = 1.36 to 1.41; ratio EL/EW = 0.88 to 0.93); free apex of prosternal intercoxal process short (Fig. 15D); elytra with middle transverse dark band varied, moderately thick in most specimens (Fig. 13A), markedly thickened (Fig. 13C) or narrowed (Fig. 13D) (much as in C. marginatus), in a few specimens; median lobe of male genitalia with shaft distinctly thicker and more arcuate, ventral curvature distinctly curved throughout in lateral aspect (Fig. 16H), apical lamella longer in dorsal aspect (Fig. 17H) . . . . ***Cyclosomus vespertilio* Cueva-Dabkoski & Kavanaugh sp. nov.**

7 (2')Elytral epipleuron with long setae over entire length, visible from dorsal aspect in most specimens [but best viewed from below because setae may be bent posteriorly in some specimens]; pronotum (Fig. 14B) light reddish brown to rufopiceous, with lateral pale bands moderately broad but not sharply defined, apical angles broad and broadly rounded apically; elytral dark pattern more thickly developed than average in most specimens (Figs. 5C, 6A) but less than average (Figs. 5A, 6B) in a few specimens; male median lobe with apical lamella slightly recurved dorsally in relation to ventral curvature of shaft in lateral aspect (Fig. 16B), apical lamella broadly triangular with a distinct, more narrowly-rounded projection apicomedially in dorsal aspect (Fig. 17B) .... *Cyclosomus flexuosus* (Fabricius)

7' Elytral epipleuron with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; pronotum rufopiceous to black, with lateral pale bands narrower at least in apical half and better defined, apical angles narrower and less broadly rounded; elytral dark pattern less varied, with middle band of average (Fig. 12A) to distinctly greater than average (Figs. 11A, B, C) thickness; male median lobe with apical lamella extended in line with ventral curvature of shaft in lateral aspect (Figs. 16F, G), apical lamella in dorsal view (Figs. 17F, G) not as above 8

8 (7')Size slightly smaller, BL males = 7.7 to 8.1 mm, females =7.1 to 7.4; elytra (Figs. 11A, B) with middle transverse dark band extended from midline at least across interval 8, also onto interval 9 in some specimens; pronotum (Fig. 14G) relatively narrow (ratio PWM/PL = 2.25 to 2.43), piceous to black with lateral pale bands slightly narrower, distinctly defined, and slightly narrowed basally; median lobe of male genitalia with apical lamella rounded and of medium length in dorsal aspect (Fig. 17F); specimen from West Malaysia or northern Indonesia (Fig. 22) .... *Cyclosomus sumatrensis* Bouchard

8' Size slightly larger, BL males = 8.2 to 8.6 mm, female = 9.2 mm; elytra (Figs. 12A, C) with middle transverse dark band extended from midline to interval 6 in most specimens, onto interval 7 and part of interval 8 in some specimens; pronotum (Fig. 14H) relatively broader (ratio PWM/PL = 2.44 to 2.50), rufopiceous piceous to black with lateral pale bands slightly broader, less well-defined, and distinctly broadened basally; median lobe of male genitalia with apical lamella short and bluntly triangular in dorsal aspect (Fig. 17G); specimen from eastern India to westernmost Yunnan (Fig. 22) .... *Cyclosomus suturalis* (Wiedemann)

Cyclosomus acutangulus Kavanaugh & Cueva-Dabkoski

Figures 2, 4, 14A, 15A, 16A, 17A, 18A, 20

Cyclosomus acutangulus Kavanaugh & Cueva-Dabkoski, 2023: 459. HOLOTYPE, a male, deposited in IOZ. Type locality: China, Yunnan, Tengchong County, Wuhe Township, Longchuan River at Longjiang Bridge.

Diagnosis. Adults of *C. acutangulus* can be distinguished from those of all other *Cyclosomus* species in Asia by the following combination of character states: Body size medium for genus, males = 7.1 to 8.2 mm, females = 6.8 to 8.2 mm; pronotum (Fig. 14A) with anterior angles narrow, distinctly acute, lateral margins slightly to distinctly sinuate near anterior angles, disk dark piceous to black, with lateral pale bands well-defined and very narrow; free apex of prosternal intercoxal process long (as in Fig. 15C); elytra with preapical dark spot present or absent; elytral epipleura with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; median lobe of male genitalia with shaft evenly arcuate and tapered subapically, with apical lamella thick, slightly deflected ventrally in lateral aspect (Fig. 16A), shaft slightly broadened for most of its length, then tapered to base of short, narrow, smoothly rounded apical lamella in dorsal aspect

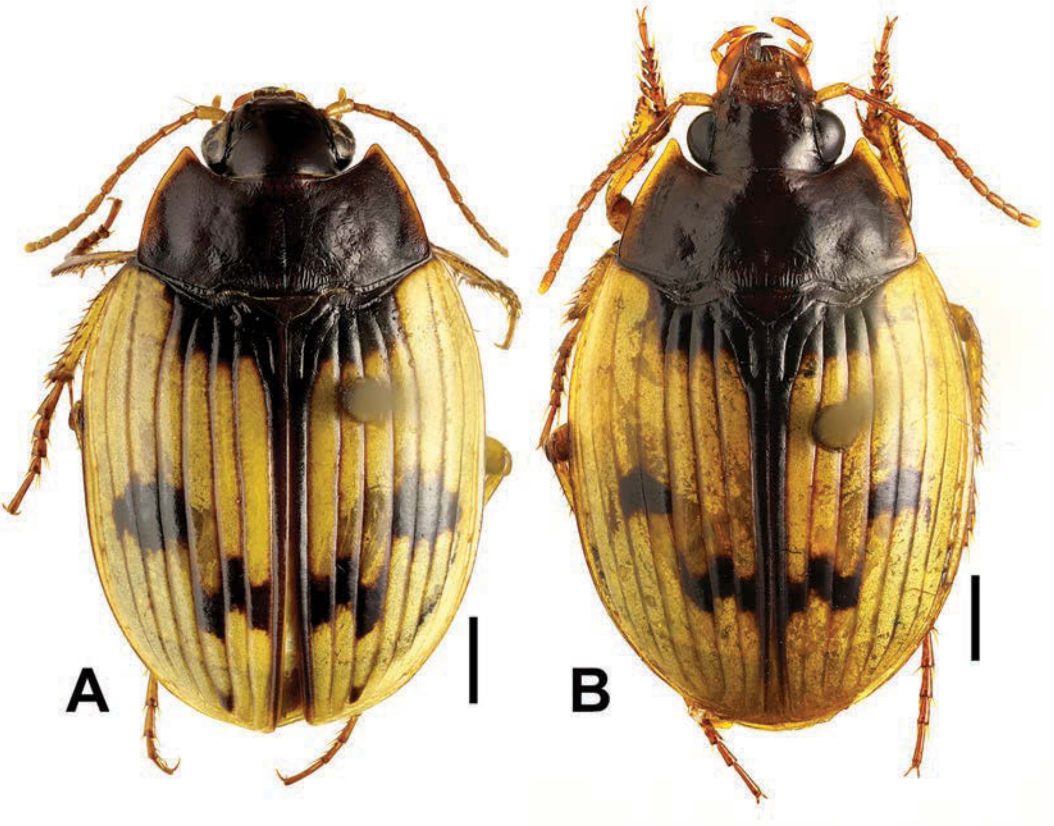


FIGURE 4. *Cyclosomus acutangulus* Kavanaugh and Cueva-Dabkoski, dorsal habitus. A. Holotype male (Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. Female (Bhalukpong, Arunachal Pradesh, India). Scale lines = 1.0 mm.

(Fig. 17A).

Members of *C. acutangulus* are most similar to those of *C. suturalis* but differ from the latter in having the pronotum with anterior angles narrow and markedly acute, lateral margins slightly to distinctly sinuate near the anterior angles, and the lateral pale bands well-defined and very narrow. Males of the two species also differ in the curvature of the median lobe in lateral aspect (compare Fig. 16A with Fig. 16G) and in shape of the apical lamella in dorsal aspect (compare Fig. 17A with Fig. 17G).

Habitat distribution. In Yunnan, specimens of this species were collected only at night, with the aid of headlamps. They were found active on the surface of dry or only slightly damp sandy substrate, with no or only widely scattered and low vegetation, on the upper edges of open sandy beaches along the Longchuan River (Fig. 18A) and Nanwanhe at elevations of 1215 and 931 m, respectively.

Geographical distribution. We examined a total of 30 specimens (14 males and 16 females) from the following localities: **CHINA**: Yunnan: Longchuan County, Zhangfeng (Nanwanhe, 24.1959°/97.7844°, 931 m, 25 March 2015, Y. Liu and H.L. Shi collectors [one female; IOZ]); Tengchong County, Wuhe Township (Longjiang Bridge on Longchuanjiang, 24.89889°/98.66667°, 1215 m, 30 October 2003, H.B. Liang and X.C. Shi X collectors [six males and six females]), (beach of Longchuan River, 24.8941/98.6750°, 1215 m, 22 March 2015, Y. Liu and H.L. Shi collectors [six males and seven females; CAS and IOZ]), (Longjiangqiao, 24.89176°/98.67551°, 1230 m, 3 June 2006, D.H. Kavanaugh and R.L. Brett collectors [one male and one female]). **INDIA**: Arunachal Pradesh: Bhalukpong (27.0333°/92.5833°, 150 m, 26 May-3 June 2006, P. Pacholátko collector [one male and one female; NHMUK]).

At present, this species is known only from one locality in northeastern India and two localities in western Yunnan Province, China (Fig. 20). The localities in India and Yunnan are about 650 km apart, and it is likely that this species occurs also in suitable habitats in the intervening region, including northern Myanmar (Kachin State), and northeastern India (Arunachal Pradesh and Nagaland states), at low elevations (below 1500 m) along rivers draining the western and southern slopes of the Himalayan ranges in these areas, respectively.

Geographical variation. The specimens from the locality in northeastern India lack the preapical dark spot found in specimens from the localities in Yunnan, but otherwise are similar.

Geographical relationships with other *Cyclosomus* species. Members of *C. acutangulus* have been found syntopic with those of *C. flexuosus* at Bhalukpong, Arunachal Pradesh, India [NHMUK] but nowhere with any other species. The geographical ranges of *C. acutangulus* and *C. suturalis* may overlap slightly in westernmost Yunnan. In fact, both species have been found on sandy beaches along the Longchuan River (Longchuanjiang) but at different localities more than 150 km apart along the river course and at different elevations (the former above 1200 m and the latter at 734 m). Otherwise, the range of *C. acutangulus* is not known to overlap with that of any other *Cyclosomus* species.

Cyclosomus flexuosus (Fabricius)

Figures 5, 6, 14B, 15B, 16B, 17B, 20

Carabus flexuosus Fabricius, 1775:246. LECTOTYPE, here designated, a male, deposited in ZMUK, labeled: “Scolytus flexuosus“ [handwritten]/ “LECTOTYPE *Carabus flexuosus* Fabricius 1775 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2022” [red label]. Type locality: eastern India.

Scolytus flexuosus (Fabricius), Fabricius (1790:221; 1792:180).

Cyclosomus flexuosus (Fabricius), Andrewes (1921:153 and 166, 1924a:464, 1927:105, 1930:365); Heller (1923:302); Csiki (1932:1295); Lorenz (2005:452); Kavanaugh (2015).

Cyclosomus dytiscoides Nietner, 1857:312. LECTOTYPE, here designated, a female, deposited in MFNB, labeled: “Ceylon, Nietner” [handwritten]/ “Type” [red label]/ “SYNTYPUS Cyclosomus dytiscoides Nietner 1857” [red label]/ “LECTOTYPE *Cyclosomus dytiscoides* Nietner 1857 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2023” [red label]. Paralectotypes examined: one female, also in MFNB, labeled: “Cyclosomus dytiscoides Nietner” [handwritten]/ “Type” [red label]/ “SYNTYPUS Cyclosomus dytiscoides Nietner 1857 labeled by MNHUB 2013” [red label]/ “PARALECTOTYPE *Cyclosomus dytiscoides* Nietner 1857 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2023” [yellow label]. Type locality: Sri Lanka, Western Province, Negombo. Chaudoir (1876:31); Bouchard (1903:174); Andrewes (1921:154, 1927:105); Csiki (1932:1295); Kavanaugh (2015:281). Synonymy proposed by Andrewes (1921:154)

Notes on types and nomenclature. We follow Andrewes (1921:31) in recognizing the Fabrician specimen at ZMUK as the type of *C. flexuosus* and provide lectotype designations for both *C. flexuosus* and *C. dytiscoides* to promote nomenclatural stability.

Diagnosis. Adults of *C. flexuosus* can be distinguished from those of other *Cyclosomus* species in Asia by the following combination of character states: Body size larger for genus, BL males = 8.2 to 9.4 mm, females = 8.3 to 9.8 mm; body form (Figs. 5A, 5C, 6A, 6B) slightly elongate ovoid; pronotum (Fig. 14B) relatively broader (ratio PWM/PL = 2.45 to 2.69), disc light reddish brown to rufopiceous, with lateral pale bands moderately broad but not sharply defined, anterior angles

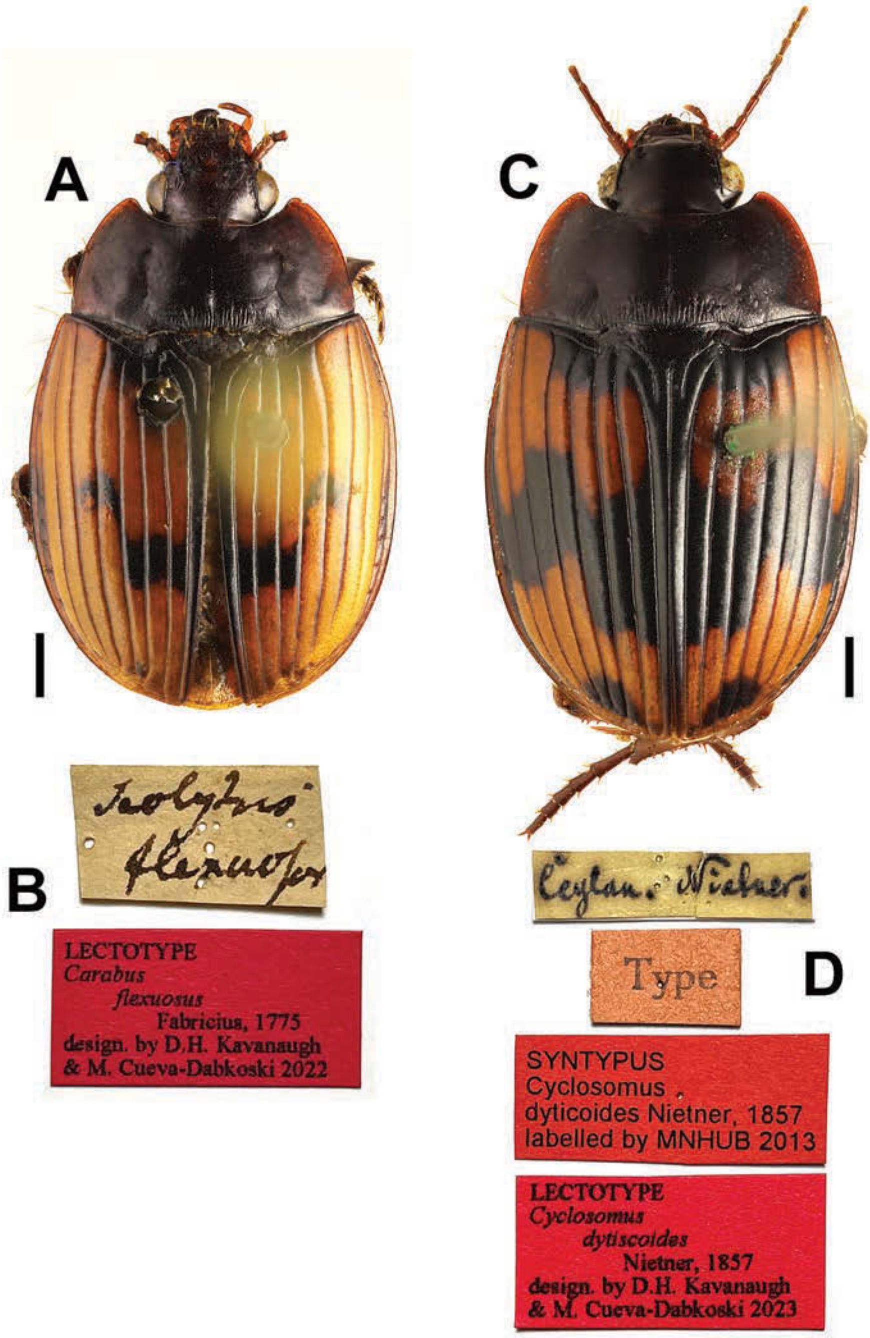


FIGURE 5. *Cyclosomus flexuosus* Fabricius. A. Holotype male, dorsal habitus; B. Labels associated with *C. flexuosus* holotype; C. *Cyclosomus dytiscoides* Nietner, lectotype female, dorsal habitus; D. Labels associated with *C. dytiscoides* lectotype. Scale lines = 1.0 mm.

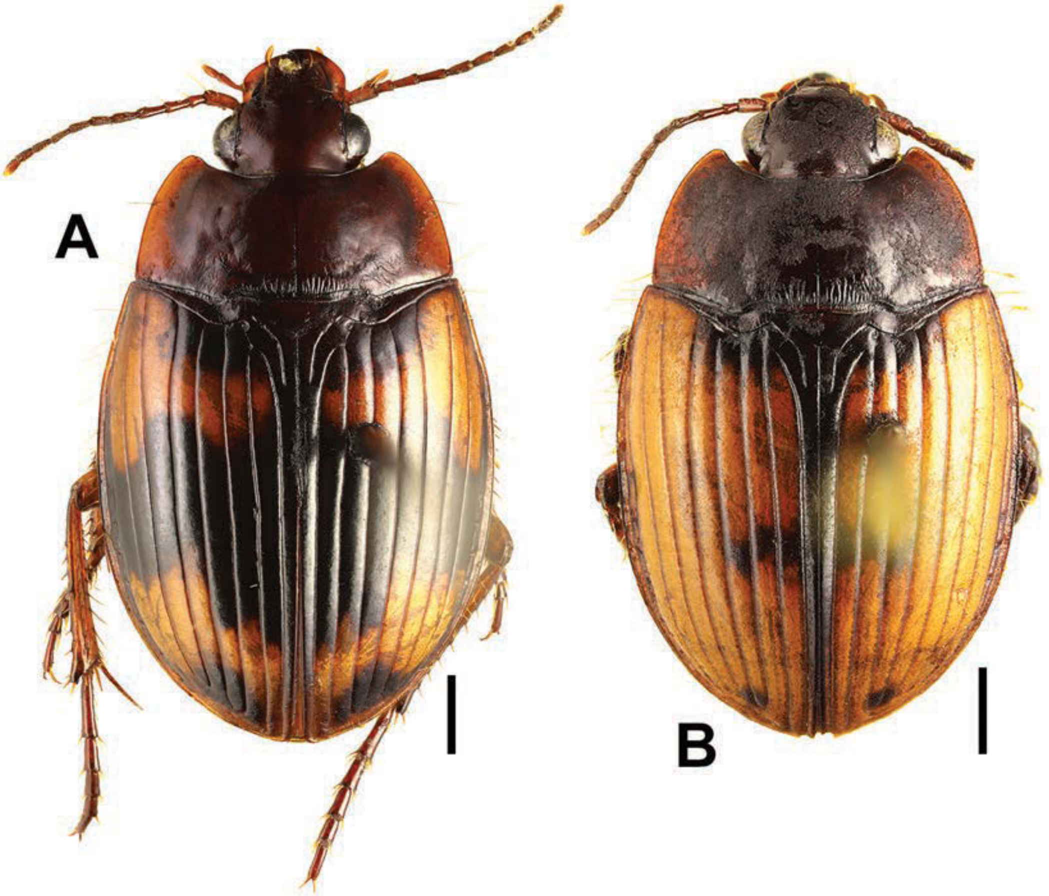


FIGURE 6. *Cyclosomus flexuosus* Fabricius, dorsal habitus. A. Dark male (Cinkona, Anaimalai Hills, Tamil Nadu, India); B. Pale female (Tiruchirappalli, Tamil Nadu, India). Scale lines = 1.0 mm.

broad and broadly rounded apically, lateral margins smoothly arcuate, not sinuate near anterior angles; elytra with pattern of dark maculae more extensively developed than average in most specimens (Figs. 5C, 6A) but highly varied and less than average (Figs. 5A, 6B) in a few specimens, preapical dark spot present; elytral epipleuron with long setae over entire length (although many of these are broken off in many specimens); male median lobe with apical lamella slightly recurved dorsally in relation to ventral curvature of shaft in lateral aspect (Fig. 16B), apical lamella broadly triangular with a distinct, more narrowly-rounded projection apicomedially in dorsal aspect (Fig. 17B).

In describing *C. flexuosus*, Kavanaugh (2015) incorrectly stated “Male with middle tarsomeres 1 to 3 not laterally expanded and without ventral pads of adhesive setae.” In fact, *C. flexuosus* males, like those of all the other *Cyclosomus* species represented in Asia for which males are known, have middle tarsomeres 1 to 3 distinctly expanded in comparison with those in females and have two longitudinal rows of squamatous adhesive setae ventrally on tarsomeres 1 to 3. In contrast, most (four of six) species in the Afrotropical Region have the male middle tarsi similar to those of females in form (i.e., more slender) and in the absence of ventral adhesive setae.

This species demonstrates the greatest range of variation in elytral dark color pattern seen among all species in the Asian fauna. The extremes are represented in Fig. 6, with the most broadly developed dark pattern (Fig. 6A) covering more than 50% of the elytral surface, and the least developed pattern (Fig. 6B) restricted to the basal dark band, a typical longitudinal dark band, a relatively narrow middle dark band extended only to interval 4, and a small preapical spot. The patterns seen in the type specimens of *C. flexuosus* (Fig. 5A) and its junior synonym, *C. dytiscoides* (Fig. 5B), are close to the opposite extremes for the species, so it is certainly understandable that they would have been described as distinct species on the basis of different color patterns.

Members of this species share epipleura having relatively long setae throughout their length only with those of *C. philippinus*; but they differ from the latter in having a prepical pale spot present and pronota with the pale lateral bands less well-defined medially. Males of the two species differ markedly in the curvature of the male median lobe in lateral aspect (compare Fig. 16B with Fig. 16E) and shape of the apical lamella in dorsal aspect (compare Fig. 17B with Fig. 17E). The elytra color pattern of darker specimens of *C. flexuosus* is most similar to that seen in *C. sumatrensis* (Fig. 11) and some *C. suturalis* (Fig. 12C) specimens; but members of both of these species have long epipleural setae only on the humeral and subhumeral regions and progressively and distinctly shorter setae to toward the apex. Also, males of these species have the male median lobe less curved in lateral aspect (Figs. 16F, G) and the apical lamella of distinctly different shape (compare Fig. 17B with Figs. 17F and 17G).

Habitat distribution. Not yet reported, but presumed to be restricted to sandy substrates in the vicinity of streams or other water bodies and any associated dune systems, and likely also to occur in such sandy areas along ocean shores. Several localities from coastal areas both on the Indian Subcontinent and in Sri Lanka likely represent occurrences in coastal sand beach or dune habitats. The apparent elevational range of this species extends from at or near sea level (3 m on Mannar Island, Sri Lanka) to at least 500 m (near Kurseong in West Bengal, northern India).

Geographical distribution. We have examined a total of 176 specimens (90 males and 86 females) from the following localities: **BANGLADESH/ INDIA**: “Bengala” ([one female; MFNB]). **INDIA** ([two males and one female; IRSNB]): Arunachal Pradesh: Bhalukpong (27.0333°/92.5833°, 150 m, 26 May-3 June 2006, P. Pacholátko collector [two females; NHMUK]); Gujarat: Kinara ([one female; NHMUK]); Karnataka: Belagavi ([one female; NHMUK]); Shivamogga ([one male; NHMUK]); Kerala: Malabar ([16 males and 17 females; IRSNB], [two females; NHMUK]); Madhya Pradesh: Barwai ([one males and three females; IRSNB]); Odisha: Brahmapur ([one female; NHMUK]); Puducherry: Karaikal (Karaikal, July 1962, P.S. Nathan collector [eight male and four females; EMEC], August 1955 [one male; NMNH]), July 1956 [16 males and seven females; CAS], [one male and two females; MFNB]), (Nedungadu, June 1931 [one female; NHMUK], 10 May 1932 [one male and one female; NHMUK]), Mahé (Malabar Coast, July 1951, M. Maindron collector [12 males and three females; IRSNB]); Tamil Nadu: Anaimalai Hills (Cinkona, 1070 m, May 1966, P.S. Nathan collector [five males and ten females; MFNB]), Chennai ([one male and one female; NHMUK]), Coimbatore (October 1958 [three males and two females]; NHMUK]), Ramanathapuram ([one male; IRSNB]), Tiruchirappalli (1905, P. du Breuil collector [one male and four females; IRSNB], R.P. Castets collector [one male and two females; IRSNB],([two males and two females; IRSNB], [one female; MFNB]); Uttarakhand: Kumaon Division (West Almora, November 1918, H.G. Champion collector [two females; NHMUK]); West Bengal: Kurseong (1904 [three males and one female; IRSNB]); “Ind. Or.” ([one female; MFNB]); “Inde Meridionale” ([one female; IRSNB]); “South India” ([one female; NHMUK]). **NEPAL** ([one female; NHMUK]): Bagmati Province: Chisapani Garhi District (Hetauda, 540 m, 26 September 1960, H. Brydon collector [one male and one female; CAS]); Lumbini Province: Bardiya National Park (Babi River, 200 m, 28 June 2000, T.W. Harman collector [one female; NHMUK]). **SRI LANKA** ([one female; MFNB]), ([two males and one female; NHMUK]): Sabaragamuva Province: Kitulgala (Kitulgala Rest House, 150 m, 24-26 October 1977, K.V. Krombein, T. Wijesinhe, M. Jayaweera, and P.A. Panawatta collectors [one male; NMNH]), Uggalkaltota (150 m, 10-14 October 1970, O.S. Flint, Jr. collector [two males; NMNH]); North Central Province: Polonnaruwa (4 May 19080, W.N. Mathis, T. Wijesinhe, and L. Jayawickrema collectors [one female; NMNH]); Northern Province: Kondachchi (Ma Villu, 11-12 April 1981, K.V. Krombein, L. Weeratunga, and P. Leanage collectors [one female; NMNH], Mannar Island (3.2 km W of Pesalai, 3 m, 24 March 1970, Davis and Rowe collectors [six males and one female; NMNH]); Western Province: Colombo ([one female; NHMUK]), Negombo ([two females; MFNB]). Specimens without or with illegible locality data: (5 July 1909 [one male; NHMUK]) ([one male; NHMUK]).

The known geographical range of *C. flexuosus* (Fig. 20) covers most of the Indian Subcontinent, from the southern base of the Himalayan Mountains in the north to Sri Lanka in the south. We have examined specimens from Arunachal Pradesh, Gujarat, Karnataka, Kerala, Madhya Pradesh, Odisha, Puducherry, Tamil Nadu, Uttarakhand, and West Bengal states in India, as well as Nepal, and Sri Lanka. Kavanaugh (2015) reported on a disjunct record of this species from "Nubia" (historical name for the area including southern Egypt and northern Sudan centered on the Nile River valley) and commented on that occurrence.

Geographical variation. Although there is evident individual variation (Figs. 5A, 5C, 6) in development of the dark color pattern of the elytra throughout the range of this species, we could not discern any particular geographic component to that variation.

Geographical relationships with other *Cyclosomus* species. This species has been found synotopic only with *C. acutangulus* (in Arunachal Pradesh, India) at the northwesternmost known locality for the latter species. The range of *C. flexuosus* overlaps that of *C. vespertilio* sp. nov. in northern India and Nepal, but these two species have not yet been found together. Known localities for *C. flexuosus* in northern West Bengal and *C. suturalis* in southernmost Sikkim are less than 30 km apart, so at least some overlap in their ranges is likely. Because of uncertainty with respect to the respective geographical ranges of *C. inustis*, *C, marginatus*, and *C. suturalis* (see discussions below), it is possible but not yet confirmed that one or more of these overlap with *C. flexuosus* at least in the eastern part of its range.

***Cyclosomus inustus* Andrewes**

Figures 1, 7, 14C, 16C, 17C, 19, 20

Cyclosomus inustus Andrewes, 1924:464. HOLOTYPE, a male, deposited in NHMUK. Type locality: China, Hong Kong. Csiki (1932:1295); Lorenz (2005:452); Bousquet (2017:498); Wang et al. (2017, 2022).

Notes on types and nomenclature. In his original description of this species, Andrewes (1924:464) indicated that he had compared "sixteen specimens labeled "Hong Kong: and "China": these latter include examples in the British Museum, Cambridge University Museum, the "Reise Novara" example, and specimens from my own collection" with specimens of *C. flexuosus* and *C. suturalis*. He added that "As a result of this I think that the Hong Kong examples form a distinct species." We examined three specimens from "Hong Kong", one labeled "Type" (i.e., the specimen we list above as holotype) and the other two labeled "Cotype", two specimens from "China" labeled "Cotype," as well as single specimens from Chandipore, (India) and Dom Toum (Laos) labeled "Cotype". All of these cotypes were mentioned in Andrewes' description as conspecific, so each of these, as well as any other specimens labeled "Cotype" by Andrewes, should be considered as paratypes of *C. inustus*.

Diagnosis. Adults of *C. inustus* can be distinguished from those of all other *Cyclosomus* species in Asia by the following combination of character states: Body size medium for genus, BL males = 7.3 to 8.0 mm, females = 6.6 to 7.8 mm; body form (Figs. 7A, C, D) more elongate-ovoid (ratio BL/EW = 1.47 to 1.53), with elytra widest at or slightly anterior to mid-length; pronotum (Fig. 14C) relatively longer and narrower (ratio PWM/PL = 2.33 to 2.93) and more broadened basally (ratio PWM/PWA = 1.63 to 1.75), with disc varied in color (rufous to piceous) and lateral pale bands of medium width and well-defined, anterior angles broad, lateral margins not sinuate near anterior angles; free apex of prosternal intercoxal process long (as in Fig.15C); elytral dark pattern varied in both form and color, with dark maculae rufous to piceous in color and with basal and middle bands of average (Fig. 7D) to less than average (Fig. 7A) thickness and continuity or middle band absent (Fig. 7C), preapical dark spot absent or only faintly present (Fig. 7D) in a few specimens (from inland areas in Indochina); elytral striae very deeply impressed, elytral intervals (especially intervals 3 to 5) slightly but distinctly convex; elytral epipleura with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; median lobe of male genitalia long and more slender, with shaft of approximately equal thickness throughout, ventral curvature gradually and only slightly arcuate in apical two-thirds in lateral aspect (Fig. 16C), apical lamella longer, smoothly rounded apically, and not or only slightly narrowed basally in dorsal aspect (Fig. 17C); specimen from southern Asia, from northeastern coastal India, through Indochina, to coastal southeastern and eastern China and Taiwan (Fig. 20).

In his original description of this species, Andrewes (1924) included specimens demonstrating variation among populations in different parts of the range of the species. He noted that a specimen from Pak Lay (Laos) was exceptionally dark and convex and that specimens from Nanoa Island (Guangdong Province, China) were exceptionally small and pale. Our examination of genitalia of males from these areas and the others listed below found that they all have similar overall form but that the shape and length of the apical lamella is slightly varied both within and among populations. Nonetheless, Andrewes concluded that these diverse populations were all conspecific and we tentatively follow him here.

Specimens of *C. inustus* with the elytral preapical pale spot absent are similar to those of *C. marginatus*, *C. pallidus*, and *C. vespertilio*. They are distinguished from *C. pallidus* members by their more elongate body form and somewhat narrower pronotum (compare Fig. 14C with Fig. 14E) with lateral pale bands much narrower and lateral areas less broadly flattened. Most (but not all) of these *C. inustus* specimens have the middle dark band, or at least a vestige of it, evident on the elytra, whereas *C. pallidus* specimens lack this band altogether (Fig. 9A). Members of *C. inustus* can be distinguished from those of *C. vespertilio* by their more elongate body form, slightly broader basal dark band on the elytra, and narrower reflexed lateral elytral margins. Males of these two species also differ distinctly in the shape of the median lobe of the genitalia, with the shaft much shorter and thicker in *C. vespertilio* males (Fig. 16H) than in *C. inustus* (Fig. 16C) males in lateral aspect.

Distinguishing specimens of *C. inustus* from those of *C. marginatus* is more difficult, at least partly because there are so few specimens of the latter known (just three) that it remains difficult to fully characterize its members. As presently conceived, members of the two species differ slightly in body shape (slightly more elongate-ovoid in *C. inustus*), pronotal shape (relatively longer and narrower and with narrower lateral pale bands in *C. inustus*; compare Fig. 14C with Fig. 14D), and length of the free apex of the prosternal intercoxal process (longer in *C. inustu*s, as in Fig. 15C; medium length in *C. marginatus*, as in Fig. 15B). Because the lectotype of *C. marginatus* is a female, we cannot be certain that the male specimen we tentatively identify as that species is conspecific with the type. Genitalia of that male (Fig. 16D and 17FD) and those of *C. inustus* (Figs.

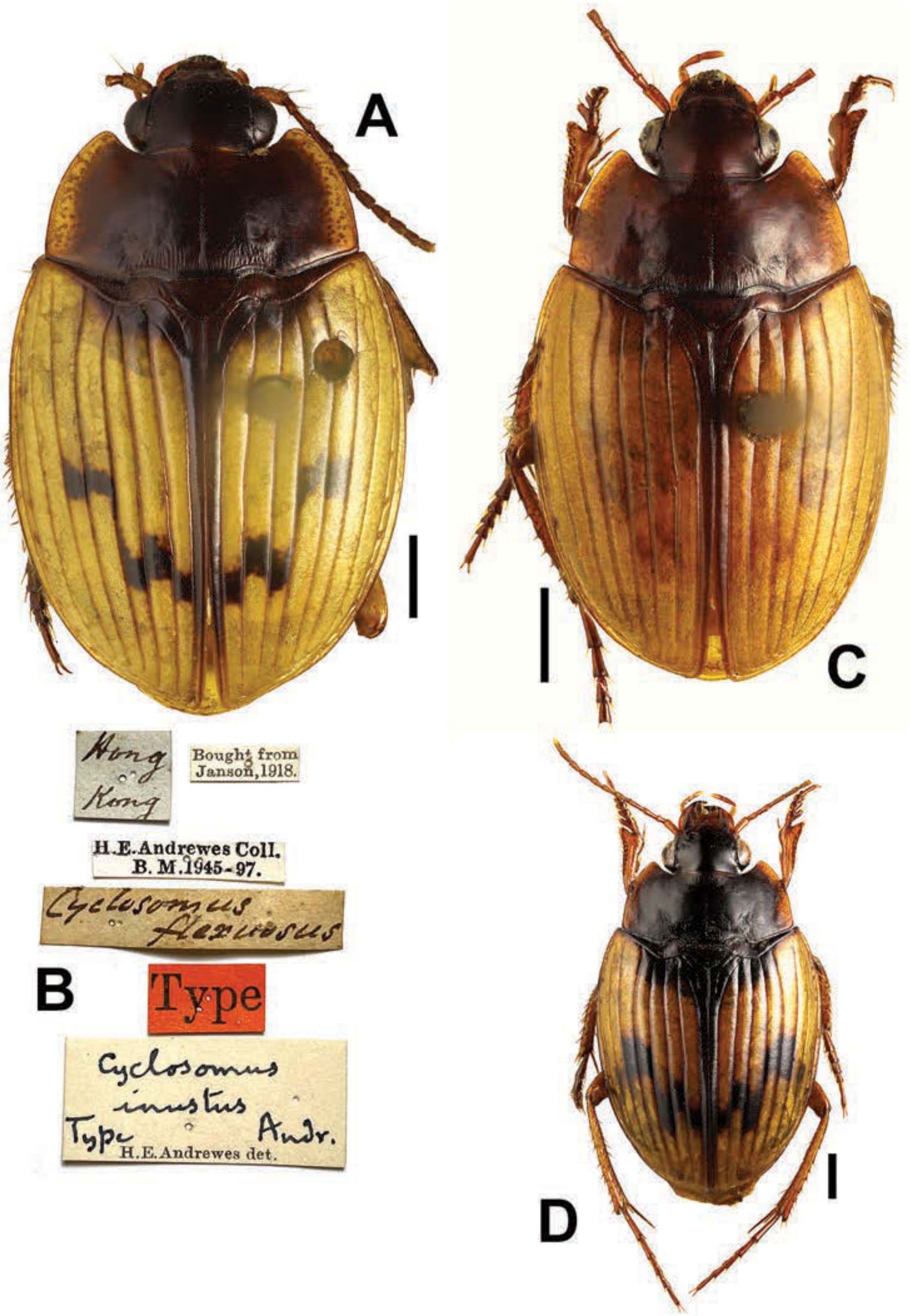


FIGURE 7. *Cyclosomus inustus* Andrewes. A. Holotype male, dorsal habitus; B. Labels associated with holotype; C. Pale female (Nanoa Island, Guangdong, China); D. Dark male ("Hat Baoho", Steong Treng, Cambodia). Scale lines = 1.0 mm.

16C and 17C) are similar in form but differ slightly in the shape of the apical lamella in dorsal aspect (compare Figs. 17C and 17D). However, the shape of the apical lamella in one of two male specimens of *C. inustus* from Cambodia is similar to that of the male we identify as *C. marginatus*, although the two differ in all the external features noted above to distinguish these two species. We certainly need to consider that *C. inustus* and *C. marginatus* may, in fact, be conspecific. However, the paucity of material referable to the latter and the uncertainty (see below) about its actual geographical and habitat distributions renders a taxonomic decision in this regard premature at this time.

Those few atypical specimens of *C. inustus* that we have seen with a faint preapical dark spot on the elytra (Fig. 7D) (see section on Geographical Variation below) are externally very similar to members of *C. suturalis* and reliably distinguished from the latter only by reference to the male genitalia. The apical lamella of such *C. inustus* males is rounded and slightly (as in Fig. 17D) to moderately elongate (Fig. 17C), whereas that of *C. suturalis* males is shorter and bluntly triangular (Fig. 17G). It is certainly possible that these specimens with preapical pale spots from inland localities in Indochina, which we identify here as *C. inustus*, actually represent a separate, perhaps undescribed species (see below).

Habitat distribution. Waterhouse (1850-51:104) quoted text from a letter written by J.C. Bowring and dated June 9, 1851 describing his encounter with this species in Hong Kong, the type locality, as follows: “I inclose [sic] a pair of Cyclosomus insularis, *White* [a nomen nudum], a species I met yesterday morning for the first time. This beetle burrows to some depth in the sand by the seashore; it is very active in its movements, and when exposed on the surface disappears beneath the sand with truly wonderful rapidity, diving down head foremost. I captured about twenty specimens by turning up the sand for some distance to a depth of five or six inches”. Wang et al (2017) reported on the discovery of *C. inustus* in coastal sun dune areas (Fig. 19) in northern and northeastern Taiwan, and Wang et al. (2022) found addition coastal dune localities in Taiwan and on Kinmen Island just off the Chinese mainland. They also searched extensively for these beetles in similarly exposed sandy habitats along river and lake shores in both areas but without success. Additional records (see below) from Fuzhou and Ningbo (China), and probably also from Ban Hua Hin (Thailand), and Chandipur (India) likely also represent coastal sandy beach or dune occurrence. At least in Taiwan and on Kinmen Island, this species appears to be restricted to coastal sandy areas.

The habitats for specimens collected at inland localities in Indochina (i.e., in Cambodia, Laos, and central Thailand) are unknown but likely were along streams with exposed sandy banks. This may reflect either a broader habitat range for *C. inustus* in this region or a species difference between these inland populations and the coastal *C. inustus* populations.

Geographical distribution. We have examined a total of 41 specimens (23 males and 18 females) from the following localities: **CAMBODIA**: Steong Treng, “Hat Baoho” (7-10 May 2012, J.K. Li collector [two males; NHMUK]). **CHINA** ([one male and two females; NHMUK]), ([two males; NHRS]), ([one female; IRSNB]): Fujian: Fuzhou (31 May 1935-36, M.S. Yang collector [three females; NHMUK]); Guangdong: Nanoa Island (J.J. Walker collector [two males and one female; NHMUK]); Hong Kong: ([two males and one female; NHMUK]); Zhejiang, Ningobo ([one female; MFNB]); “W China” ([one male; NHMUK]. **INDIA** (one male; MFNB]), ([one male and one female; NHMUK]): Odisha: Chandipur (near Balasore, 3-7 June 1915, F.H. Gravely collector [one female; NHMUK]). **LAOS**: Champasak Province, Khone area (Dom Toum, 24 October 1916, R.V. de Salvaza collector [one male; NHMUK]); Sainyabuli Province: Pak Lay (January 1916, R.V. de Salvaza collector [one female; MFNB]). **TAIWAN**: New Taipei City: Shihmen (Lingshanbi, 3 October 2013, L.J. Wang collector [six males and five females; CAS]). **THAI-**

LAND: Prachuap Khiri Khan Province: Ban Hua Hin (15 January 1990, J. Nielsen collector [one male; CAS]); Uthai Thani Province: Lan-Sak (25 km NW, 110 m, December 1990 [two males; MFNB]). Specimens with illegible locality data: ([one male; MFNB]).

As presently conceived, the known geographical range of *C. inustus* (Fig. 20) extends across Southeast Asia from the coast of India (Odisha State) on the Bay of Bengal eastward to coastal Fujian, Guangdong, and Zhejiang provinces (China) and Taiwan, and south into Cambodia and Thailand. This species has not yet been recorded from Myanmar, Vietnam, or Hainan Island (China), but it is likely to occur also in these areas.

Geographical variation. Most specimens of *C. inustus* from localities in Taiwan and on Kinmen and Nanao Islands (Guangdong) are smaller than those from mainland areas and have the elytral dark pattern paler (rufous or rufopiceous rather than piceous) and reduced in extent (see Wang et al. 2017 for images showing this variation), with the middle dark band absent from some specimens (Fig. 7C). At least some specimens from inland parts of Indochina (Cambodia and Thailand) have a small and faint preapical dark spot present (Fig. 7D). Specimens from these areas (and Laos) are more darkly pigmented (pronotum piceous rather than rufopiceous or rufous, middle dark band of the elytra black rather than rufopiceous). However, all of these specimens have male genitalia similar to those of other *C. inustus* males.

Geographical relationships with other *Cyclosomus* species. To date, this species has not been found syntopic with any other congeneric species; however, it may be sympatric with *C. flexuosus*, *C, marginatus*, and/or *C. suturalis* in the western part of its range, but none of these relationships have been demonstrated to date.

Cyclosomus marginatus Motschulsky

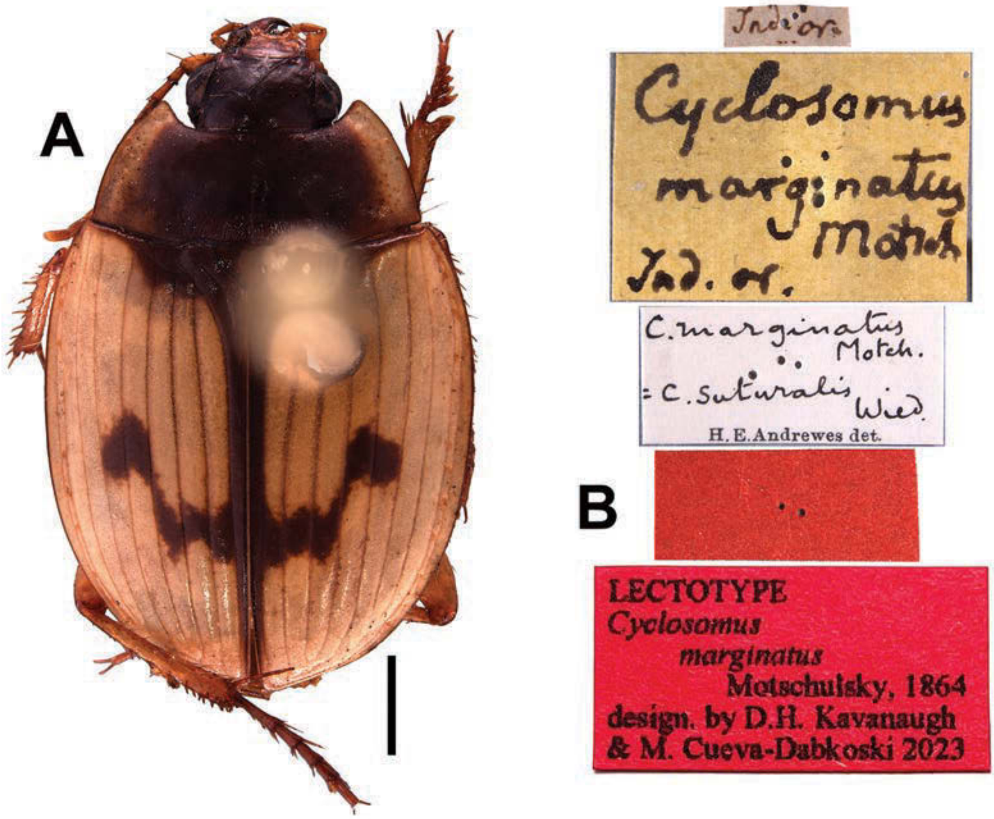
Figures 8, 14D, 16D, 17D, 21

Cyclosomus marginatus Motschulsky, 1864:200. LECTOTYPE, here designated, a female, deposited in ZMMU, labeled: "Ind. Or." [handwritten]/ "Cyclosomus marginatus Motsch. Ind. Or."/ "C. marginatus Motch = C. suturalis Wied. H.E. Andrewes det."/ "LECTOTYPE *Cyclosomus marginatus* Motschulsky 1864 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2023" [red label]. Type locality: eastern India. Chaudoir 1876: 32.

Cyclosomus suturalis, Andrewes (1921:166, 1924a:464); Csiki (1932:1295); Lorenz (2005:452).

Notes on types and nomenclature. See below under *C. suturalis* (Wiedemann) for further discussion about types. We must note here that if, as discussed above, *C. marginatus* and *C. inustus* were to be considered conspecific, then the name *C. marginatus* has priority. We choose not to propose that synonymy at this time.

Diagnosis. Adults of *C. marginatus* can be distinguished from those of other *Cyclosomus* species in Asia by the following combination of character states: Body size medium for genus, BL male = 7.3 mm, female = 7.0 mm; body form (Fig. 8A) roundly ovoid (ratio BL/EW = 1.46 to 1.49; ratio EL/EW = 0.94 to 0.96), with elytra widest at or near mid-length; dorsal surface (Figs. 8A) with distinctly contrasting pale and dark areas; pronotum (Fig. 14D) relatively broad (ratio PWM/PL = 2.67 to 2.92) and more broadened basally (ratio PWM/PWA = 1.65 to 1.67), with disc rufopiceous to black, lateral pale bands broad and well-defined, anterior angles broader, lateral margins not sinuate or very faintly sinuate near anterior angles; free apex of prosternal intercoxal process medium in length (as in Fig. 15B); elytra (Fig. 8A) pale yellowish-brown with basal, middle and longitudinal dark bands present and dark reddish brown to black, preapical dark spot absent, basal and middle bands of average thickness, middle transverse dark band narrow, extended laterally onto interval 6, portion on intervals 2 to 4 connected to portion on intervals 5 and 6 by a narrow, oblique dark line; elytral striae moderately impressed, elytral intervals flat or nearly so;



Ind. or.

Cyclosomus
marginatus
Motsch
Ind. or.

C. marginatus
Motch.
= C. suturalis
Wied.
H. E. Andrewes det.

LECTOTYPE
Cyclosomus
marginatus
Motschulsky, 1864
design. by D.H. Kavanaugh
& M. Cueva-Dabkoski 2023

FIGURE 8. *Cyclosomus marginatus* Motschulsky. A. Lectotype female, dorsal habitus (photograph by Rachel Diaz-Bastian); B. Labels associated with lectotype. Scale line = 1.0 mm.

elytral epipleura with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; median lobe of male genitalia with shaft of approximately equal thickness throughout, ventral curvature straightened subapically in lateral aspect (Fig. 16D), apical lamella short and smoothly rounded in dorsal aspect (Fig. 17D); specimen not from Philippine Islands.

Specimens of *C. marginatus* are most similar to those of *C. inustus*, *C. pallidus*, and *C. vespertilio*. Features distinguishing specimens of *C. marginatus* from those of *C. inustus* are discussed above in the Diagnosis section for the latter species. The elytra of all known specimens of *C. marginatus* have the middle dark band present and in the form of a compound-W, whereas *C. pallidus* members have the middle band absent. Members of *C. marginatus* differ from those of *C. vespertilio* in having the free apex of the prosternal intercoxal process moderate in length, as in Fig. 15B, rather than short, as in Fig. 15D. Most members of these two species also differ in the development of the middle dark band. In the all three known specimens of *C. marginatus*, the band is relatively thin and in the compound-W form (Fig. 8A). In contrast, the middle dark band in *C. vespertilio* is similarly shaped but distinctly thicker (Figs. 13A, 13B) in most specimens, as thin as in *C. marginatus* in only two specimens that we have seen (Fig. 13D).

Habitat distribution. Unknown, but presumed to be restricted to the sandy shores of medium to large rivers at low elevation, like members of most other species of the genus.

Geographical distribution. We have examined a total of three specimens (one male and two females) from the following localities: **BANGLADESH/ INDIA/ MYANMAR**: "Bengal" (May 1809 [one male; ZMUC]). Eastern India ("India Or.") [one female; ZMMU]. Northern India ("N India" ([one female; NHMUK]).

The lectotype specimen from 'eastern India' could have been collected anywhere in present-day India, Bangladesh, or Myanmar, the specimen from "Bengal" from anywhere in West Bengal (India) or Bangladesh, and the specimen from 'northern India' from anywhere from Pakistan to Myanmar along the southern base of the Himalaya. Consequently, the range of this species remains undefined (Fig. 21) and problematic. The record of its occurrence in "Indo-China" (Andrewes 1921) probably is based on a misidentification of specimens of *C. inustus*, which species Andrewes subsequently described (Andrewes 1924) as distinct (see above). Some other records from India may have been based on misidentified specimens of *C. vespertilio*, which is described below. If *C. inustus* is actually restricted to sandy sea coast areas everywhere it occurs as it is in Taiwan and apparently in southeast coastal China, then records from inland parts of Indochina (i.e., in Cambodia, Laos, and Thailand) may, in fact, represent either *C. marginatus* or another, undescribed species.

Geographical variation. There is insufficient material available at present to recognize any possible geographical variation in this species, unless the specimens from inland part of Indochina are considered as conspecific with *C. marginatus* rather than *C. inustus* (see comments about geographical variation in that species above).

Geographical relationships with other *Cyclosomus* species. In the absence of any specific locality records for this species, its syntopy or even sympatry with any other congeners cannot be confirmed. *Cyclosomus suturalis* is also known from "Bengala", again without specific locality, so it is possible that these species co-occur. Also, eastern India is within the broad geographical range of *C. flexuosus* (recorded from northernmost West Bengal) and at the western limit of the range of *C. inustus*, so there is at least potential for co-occurrence with either or both of these species.

Cyclosomus pallidus Kavanaugh & Cueva-Dabkoski, sp. nov.

Figures 9, 14E, 21

Type material. HOLOTYPE, a female, deposited in NHMUK, labeled: "T. R. Bell, Karachi."/ "H. E. Andrewes Coll. B. M. 1945-97."/ "Cyclosomus suturalis Wied. ? var. H.E. Andrewes det."/ "HOLOTYPE *Cyclosomus pallidus* sp. n. D.H. Kavanaugh & M. Cueva-Dabkoski 2023" [red label]. Paratypes: 1 female, also in NHMUK, labeled: "T. R. Bell, Karachi."/ "In loose sand where it hid itself by burrowing …[illegible]…28 6 04" [handwritten label]/ "T.R. Bell collection B. M. 1934-394"/ "Cyclosomus suturalis Wied. new var. ? H.E. Andrewes det."/ "PARATYPE *Cyclosomus pallidus* sp. n. D.H. Kavanaugh & M. Cueva-Dabkoski 2023" [yellow label].

Type locality. Pakistan, Sindh Province, Karachi.

Etymology. The specific epithet is a Latin adjective, *pallidus*, in the masculine form, meaning pale, in reference to the pale color of the entire body.

Diagnosis. Adults of *C. pallidus* can be distinguished from those of other *Cyclosomus* species in Asia by the following combination of character states: Body size slightly small for genus, BL females = 6.8 to 6.9 mm (male unknown); body form (Fig. 9A) shorter (ratio BL/EW = 1.38 to 1.39), roundly ovoid, with elytra widest at mid-length; dorsal surface (Fig. 9A) mainly pale tan-orange, with only pronotal disc, elytral basal dark band and longitudinal dark band on elytral interval 1 slightly darker brown, middle dark band and preapical dark spot absent; pronotum (Fig. 14E) short and very broad (ratio PWM/PL = 2.71 to 2.79), more broadened basally (ratio PWM/PWA = 1.70 to 1.73), very broadly flattened laterally (especially anteriorly), lateral pale bands very broad

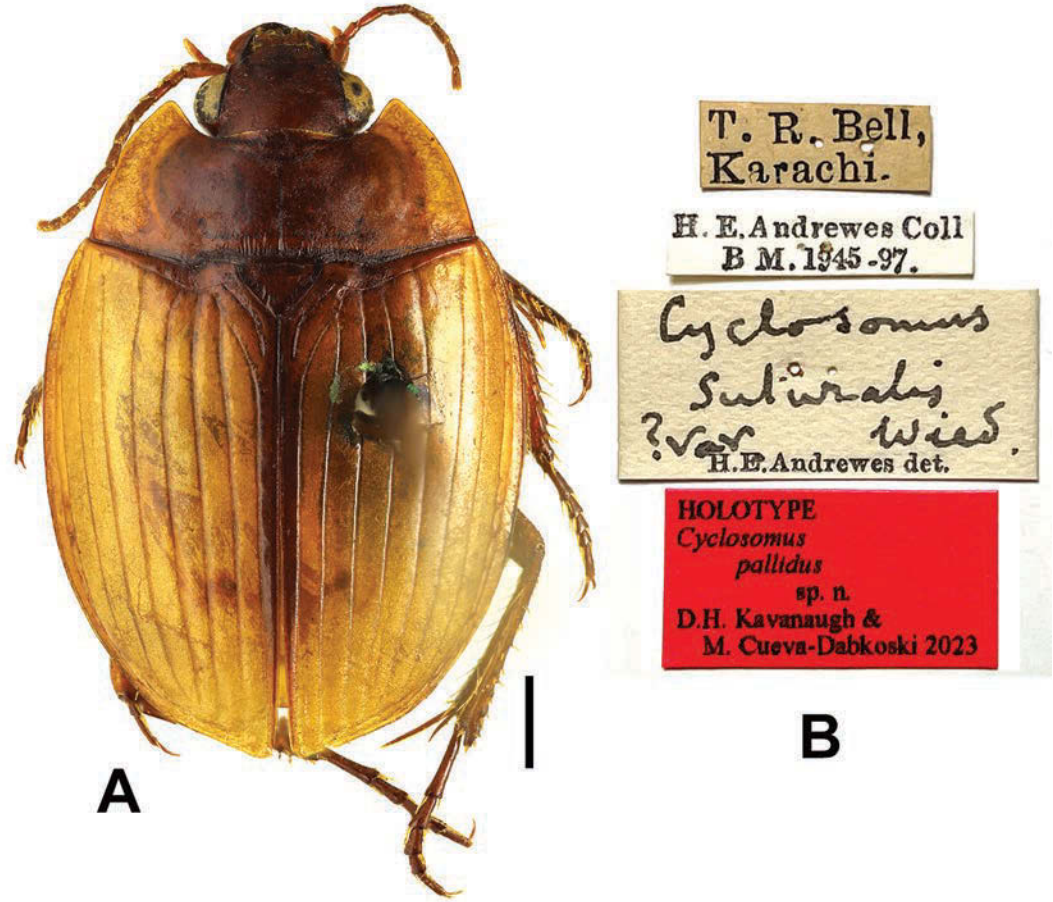


FIGURE 9. *Cyclosomus pallidus* Kavanaugh and Cueva-Dabkoski sp. nov. A. Holotype female, dorsal habitus; B. Labels associated with holotype. Scale line = 1.0 mm.

and only slightly contrasting with color on disc, anterior angles broader, lateral margin not sinuate near anterior angles; free apex of prosternal intercoxal process short (as in Fig. 15D); elytra with striae moderately impressed and intervals flat or nearly so; elytral epipleura with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; males unknown; specimen from southeastern Pakistan (Fig. 21).

Members of *C. pallidus* are most similar to those of *C. inustus*, *C. marginatus*, and *C. vespertilio*. Refer to the key and Diagnosis sections for each of those species for distinguishing features.

Description. Size slightly small for genus, BL of females = 6.8 to 6.9 mm; body form (Fig. 9A) shorter (ratio BL/EW = 1.38 to 1.39), roundly ovoid, with elytra widest at mid-length.

Color. Head with dorsum, venter, and all mouthparts and other appendages light brown. Pronotum with disc light brown and lateral pale bands very wide and pale tan-orange. Elytra mainly yellow-tan, with elytral base, scutellum, and longitudinal dark band on elytral interval 1 darker brown, basal dark band diffusely and very slightly darker than pale disc, middle dark band and preapical dark spot absent. Venter light brown, proepipleura tan-orange, elytral epipleura yellow-tan, and apical portion of last abdominal sternite pale yellow-tan. Legs pale, light brown.

Reflection, luster, and microsculpture. Dorsum and venter without metallic reflection. Head and pronotum dull, with microsculpture moderately impressed and comprised of isodiametric meshes; elytra slightly shiny with isodiametric meshes slightly less deeply impressed; venter with isodiametric to slightly transverse meshes shallowly impressed.

Head. Eyes large, hemispheric; antennae slightly short, extended only to basal one-fifth of elytra; clypeus bisetose; labrum with apical margin deeply emarginate, three pairs of setae present; mentum asetose, with a broad, apically emarginate medial tooth; submentum anteriorly with a single pair of setae.

Prothorax. Pronotum (Fig. 14E) trapezoidal, almost as wide as elytra at humeral angles, short and very broad (ratio PWM/PL = 2.71 to 2.79), more broadened basally (ratio PWM/PWA = 1.70 to 1.73), very broadly flattened laterally (especially anteriorly); anterior angles broad, narrowly rounded apically; anterior margin between anterior angles nearly straight at middle; lateral margins gently arcuate, not sinuate near anterior angles; basal margin moderately bisinuate, faintly lobate medially; anterior and basal margination distinct laterally, obsolete medially; lateral margination very slender and finely impressed; midlateral setae present, inserted just medial to lateral margination and at about one-third the distance between the anterior and basal angles along the lateral margin; basolateral setae present, inserted on lateral edge of pronotum and just anterior to posterior angles. Prosternal intercoxal process moderately long and slender, lanceolate, with complete margination, free apex of process short (as in Fig. 15D).

Elytra. Broadly ovate (Fig. 9A), slightly shorter than wide (ratio EL/EW = 0.90), broadly rounded apically, humeri slightly obtuse, angulate; elytral striae moderately impressed throughout; elytral intervals flat or nearly so, smooth; parascutellar setiferous pore present at base of interval 1 near junction of striae 1 and 2; two discal setiferous pores present on interval 3 adjacent to stria 2, one inserted just posterior to elytral mid-length and the other inserted near apical one-third; apical seta present, inserted near apex of interval 3; umbilicate series comprised of 12 to 13 setae.

Legs. Middle and hind tibiae with medial tibial spurs long and serrulate (as in Fig. 2A). Females with front tarsomeres 1 to 3 markedly expanded laterally (as in Figs. 2C), but without adhesive setae ventrally, and middle tarsomeres slender and without adhesive setae ventrally; tarsal claws smooth.

Habitat distribution. A partially-legible, handwritten label associated with the paratype of *C. pallidus* states that it was collected from "loose sand" and that it "hid by burrowing…," presumably into that sand. There are several large rivers with sandy shores in the Karachi region, as well as extensive sandy sea beaches and associated dune systems, so the species may occur in either or both of these habitat types.

Geographical distribution. Fig. 21**.** Known only from the type locality.

Geographical relationships with other *Cyclosomus* species. No other congeneric species is known to occur in Pakistan; and the nearest *Cyclosomus* record we have found to the type locality of *C. pallidus* is one for *C. flexuosus*, from Kinara, Gujarat State, India (in NHMUK), just over 500 km distant toward the southeast.

Cyclosomus philippinus Heller

Figures 10, 14F, 16E, 17E, 21

Cyclosomus philippinus Heller, 1923:302. HOLOTYPE, a female, deposited in SMTD. Type locality: Philippines, Luzon Island, Laguna Province, Los Baños. Andrewes (1926:349); Csiki (1932:1295).

Diagnosis. Adults of *C. philippinus* can be distinguished from those of other *Cyclosomus* species in Asia by the following combination of character states: Body size medium for genus, BL males = 7.2 to 7.6 mm, females = 7.0 to 7.5 mm; pronotum (Fig. 14F) relatively narrow (ratio

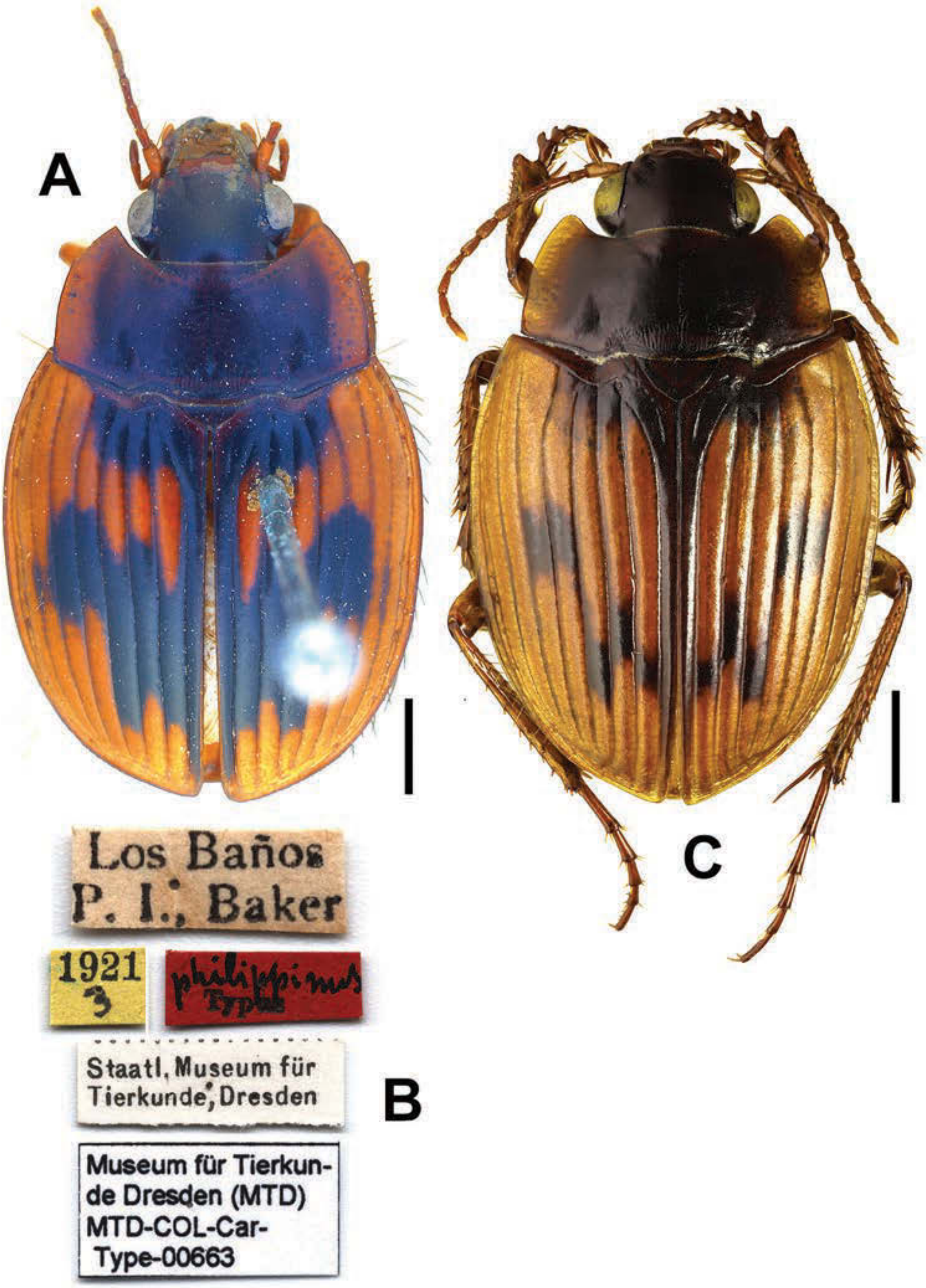


FIGURE 10. *Cyclosomus philippinus* Heller. A. Holotype female, dorsal habitus (photograph by Olaf Jäger); B. Labels associated with holotype; C. Pale male (Zambales Mountains, Luzon Island, Philippines). Scale lines = 1.0 mm.

PWM/PL = 2.06 to 2.33) and less broadened basally (ratio PWM/PWA = 1.45 to 1.59), with disc piceous to black and lateral pale bands wide and well-defined, anterior angles broadly rounded, lateral margins not sinuate near anterior angles; free apex of prosternal intercoxal process long (as in Fig. 15C); elytral dark pattern varied (Figs. 10A, C) [slight blue cast to the dark elements seen in Fig. 10A is an imaging artifact], with basal and middle bands of average to greater than average thickness for the genus, preapical dark spot absent; elytral epipleura with long setae over entire length; median lobe of male genitalia with shaft arcuate basally and nearly straight subapically, tapered to a long and pointed apical lamella in lateral aspect (Fig. 16E), shaft moderately broad basally, gradually tapered to moderately broad, apically blunted, and sublanceolate apical lamella in dorsal aspect (Fig. 17E); specimen from Philippine Islands (Fig. 21).

Only *C. philippinus* and *C. flexuosus* members share elytral epipleura with long setae over their entire length. Specimens of these two species can be distinguished by the presence (in *C. flexuosus*) or absence (in *C. philippinus*) of a preapical dark spot. Males of the two species also differ distinctly in the shape and curvature of the median lobe in lateral aspect (compare Fig. 16B with Fig. 16E) and shape of the apical lamella in dorsal aspect (compare Fig. 17B with Fig. 17E).

Habitat distribution. Unknown, but presumed to be restricted to the sandy shores of medium to large rivers at low elevation, like members of most other species of the genus.

Geographical distribution. We examined a total of six specimens (four males and two females) from the following localities: PHILIPPINES: Luzon Island: Los Baños (C.F. Baker collector [one female; SMTD]), Zambales Mountains (Pili, 150 m, 5-7 November 1998, Mey and Spiedel collectors [two males and one female; MFNB]). Specimens without locality: ("Acc. No. 4696" and "Acc. No. 5451", C.S. Banks collector [two males; MFNB]).

This species is known only from Luzon Island, Philippines (Fig. 21).

Geographical variation. The range of variation in the thickness of the middle dark band of the elytra seen among specimens examined is shown in Figs. 10A and 10C, with the holotype specimen presenting the thickest band seen. We were unable to identify any geographical component to this variation in our sample of specimens.

Geographical relationships with other *Cyclosomus* species. No other congeneric species is known to occur in the Philippines; and the nearest *Cyclosomus* records are for *C. inustus*, on Taiwan (about 1000 km to the north) and Hong Kong and Guangdong Province (across the South China Sea and more than 1100 km distant to the northwest).

***Cyclosomus sumatrensis* Bouchard**

Figures 11, 14G, 15C, 16F, 17F, 22

Cyclosomus sumatrensis Bouchard, 1903a:174. HOLOTYPE, sex and present location unknown (see notes below). Type locality: Indonesia, Sumatra, Palembang. Andrewes (1930:364); Csiki (1932:1295); Lorenz 2005:452).

Notes on types and nomenclature. Andrewes (1930:364) reported on his study of the unique type of *C. sumatrensis* in the Förster collection, which was housed at that time in the Museum of the Lycée at Mulhouse, Strasbourg (France). Our efforts to borrow and study the Bouchard holotype were facilitated by Thierry Deuve, who contacted colleagues in several institutions in Strasbourg on our behalf. According to Mary Meister (Zoological Museum of Strasbourg (ZMSC)), the insects from the Lycée at Mulhouse collection were at one time offered to the ZMSC but a transfer was never completed. Efforts to learn whether or not the Mulhouse collection still exists have failed thus far. It seems likely that the collection, including the holotype of *C. sumatrensis*, has been lost or destroyed. However, this species is geographically and morphologically distinct enough from other *Cyclosomus* species that we see no need to designate a neotype until the loss of the holo-

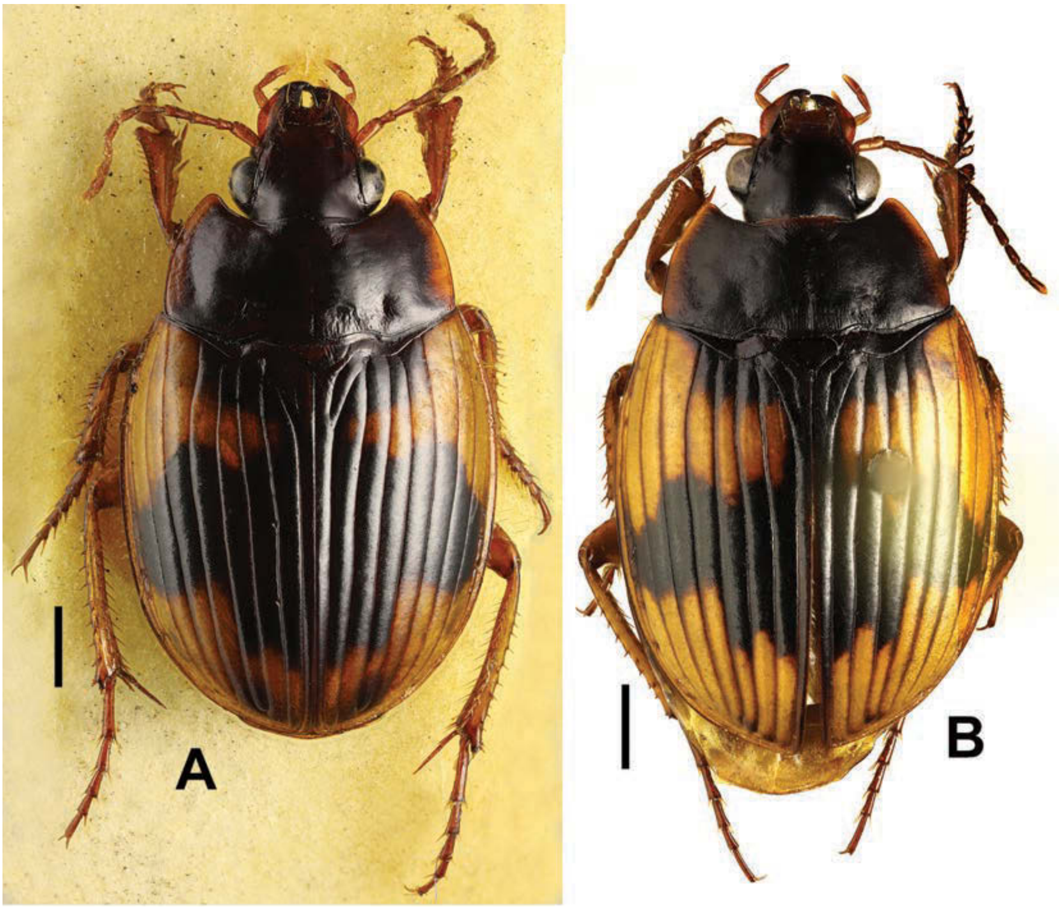


FIGURE 11. *Cyclosomus sumatrensis* Bouchard, dorsal habitus. A. Dark male (Kras, Kediri, East Java, Java, Indonesia); B. Pale male (Taman Negara, Pahang, Malaysia). Scale lines = 1.0 mm.

type can be confirmed.

Diagnosis. Adults of *C. sumatrensis* can be distinguished from those of other *Cyclosomus* species in Asia by the following combination of character states: Body size medium for genus, BL males = 7.7 to 8.1 mm, females = 7.1 to 7.4 mm; body form (Fig. 11) slightly elongate ovoid; pronotum (Fig. 14G) relatively narrow (ratio PWM/PL = 2.25 to 2.43), disc piceous to black with lateral pale bands slightly narrower than average for genus, distinctly defined, and slightly narrowed basally, apical angles narrower and less broadly rounded, lateral margins smoothly arcuate, not sinuate near anterior angles; elytra (Fig. 11) with pattern of dark maculae more extensively developed and less varied than average for genus, with middle transverse dark band thick and extended from midline at least across interval 8, also onto interval 9 in some specimens, preapical dark spot present; elytral striae deeply impressed and intervals slightly to moderately convex; elytral epipleura with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; male median lobe with apical lamella extended in line with ventral curvature of shaft in lateral aspect (Fig. 16F), apical lamella rounded and of medium length in dorsal aspect (Fig. 17F); specimen from West Malaysia or northern Indonesia (Fig. 22).

Andrewes (1930) distinguished members of *C. sumatrensis* from those of *C. flexuosus* on the basis of their smaller size, narrower form, and deeper elytral striae, as well as minor differences in elytral color pattern. He concluded that *C. sumatrensis* was probably a distinct species closely related to *C. flexuosus*, but suggested that additional material might show it to be only a "variety" of the latter. Specimens of *C. sumatrensis* can be confused only with those of *C. flexuosus*, but members of these species are easily distinguished by the setae of the epipleura, which are long only in the humeral and subhumeral regions and progressively and distinctly shorter toward the apex in *C. sumatrensis* specimens but longer throughout the epipleural length in *C. flexusosus* members. Specimens of *C. sumatrensis* are also slightly smaller (7.1 to 8.1 mm compared with 8.2 to 9.8 mm for *C. flexuosus* specimens), and males have the apical lamella of the median lobe longer and narrower in dorsal aspect (compare Fig. 17F with Fig. 17B).

Habitat distribution. Unknown, but presumed to be restricted to the sandy shores of medium to large rivers at low elevation, like members of most other species of the genus.

Geographical distribution. We have examined a total of 14 specimens (six males and eight females) from the following localities: **INDONESIA**: Java: East Java (Kediri, Kras [one female; IRSNB], [one female; MFNB], [five males and three females; NHMUK], [one female; NHRS]); Sumatra: Bengkulu (Mana ["Manna"] 1902, M. Knappert collector [one female; NHMUK]); North Sumatra (Deli Serdang ["Deli"], 1894, W. Reisch collector [one female; MFNB]). **MALAYSIA**: Pahang: Taman Negara (5 January 1992, J. Nielsen collector [one male; CAS]).

The known geographical range of *C. sumatrensis* (Fig. 22) extends from the Malaysian portion of the Malay Peninsula south to Sumatra and Java. It was previously known only from Sumatra, Indonesia and specimens reported here from the Malay Peninsula and Java represent new records for these areas.

Geographical variation. We found slight individual variation (Figs. 11A, B) in development of the dark color pattern of the elytra within the largest sample of this species (from Kras, East Java). Specimens from all other localities were similar to at least some specimens from that sample, so we recognized no particular geographical variation.

Geographical relationships with other *Cyclosomus* species. No other congeneric species is known to occur in Malaysia or Indonesia; and the nearest *Cyclosomus* records are for *C. inustus*, in Cambodia, across the Gulf of Thailand and more than 800 km distant to the northeast, and *C. flexuosus* in Sri Lanka, across the Bay of Bengal and more than 1600 km distant to the west.

***Cyclosomus suturalis* (Wiedemann)**

Figures 12, 14H, 16G, 17G, 18B, 22

Scolytus suturalis Wiedemann, 1819:169. LECTOTYPE, here designated, a male, in ZMUC, labeled: "Type" [red label]/ "Bengala Westermann flexuosus F. suturalis Wied." [handwritten]/ "ZMUC 00022690"/ "LECTOTYPE *Scolytus suturalis* Wiedemann 1819 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2023" [red label]. Paralectotypes examined: 1 male, also in ZMUC, labeled: "Mus. Westerm."/ "TYPE" [red label]/ "S. flexuosus var. S. suturalis Wied. Bengal May 1809" [handwritten]/ PARALECTOTYPE *Scolytus suturalis* Wiedemann 1819 design. by D.H. Kavanaugh & M. Cueva-Dabkoski 2023" [yellow label]/ "*Cyclosomus marginatus* Motschulsky det. D.H. Kavanaugh 2023". Type locality: "Bengal" [area which now includes West Bengal (eastern India) and Bangladesh].

Cyclosomus flexuosus, Chaudoir 1876:32.

Cyclosomus suturalis (Wiedemann), Chaudoir (1876:32); Andrewes (1921:166, 1924:464); Csiki (1932:1295); Lorenz (2005:452).

Notes on types and nomenclature. Chaudoir (1876:32) considered *C. suturalis* as a junior synonym of *C. flexuosus*, but Andrewes (1921:166) confirmed its status as a distinct species. In that same paper, Andrewes recognized *C. marginatus* as a junior synonym of *C. suturalis*. This difference of opinion between these two superb taxonomists can possibly be explained by the fact that the type series of *C. suturalis* includes two specimens, which are not, in our view, conspecific. Thus, they may have examined different specimens in making their assessments. The male specimen that we have selected as lectotype actually resembles some small male specimens of *C. flexuosus* in size and elytral color pattern. The female specimen we designate as paralectotype appears to be a specimen of *C. marginatus*, with the size and elytral color pattern matching the lectotype of that species. If Chaudoir had studied the male specimen and Andrewes the female specimen, their respective opinions are quite understandable. Because of variation in elytral color pattern seen in each of these species, Wiedemann's original description is insufficient to distinguish between specimens of *C. flexuosus*, *C. marginatus*, and *C. suturalis*. By selecting the male specimen as lectotype of *C. suturalis*, we are able to recognize Motschulsky's *C. marginatus* as the valid name for a distinct species (see above). If we had chosen the female specimen as lectotype, then *C. marginatus* would have remained a junior synonym of *C. suturalis* and the male specimen would represented a new species currently without a name.

Diagnosis. Adults of *C. suturalis* can be distinguished from those of other *Cyclosomus* species in Asia by the following combination of character states: Body size medium to large for genus, BL males = 8.2 to 9.1 mm, female = 9.2 mm; body form (Fig. 12A, C) slightly elongate ovoid; pronotum (Fig. 14H) relatively broader (ratio PWM/PL = 2.44 to 2.50), disc rufopiceous to black, lateral pale bands well-defined, slightly narrowed at least in apical half and broadened basally, apical angles slightly narrowed and less broadly rounded, lateral margins smoothly arcuate, not sinuate near anterior angles; elytra with pattern of dark maculae less varied, with middle band of average (Fig. 12A) to distinctly greater than average (Fig. 12C) thickness for the genus and extended from midline to interval 6 in most specimens, onto interval 7 and part of interval 8 in some specimens, preapical dark spot present, striae deeply impressed and intervals flat or slightly convex; elytral epipleura with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; male median lobe with apical lamella extended in line with ventral curvature of shaft in lateral aspect (Fig. 16G), apical lamella short and bluntly triangular in dorsal aspect (Fig. 17G); specimen from eastern India to westernmost Yunnan (Fig. 22).

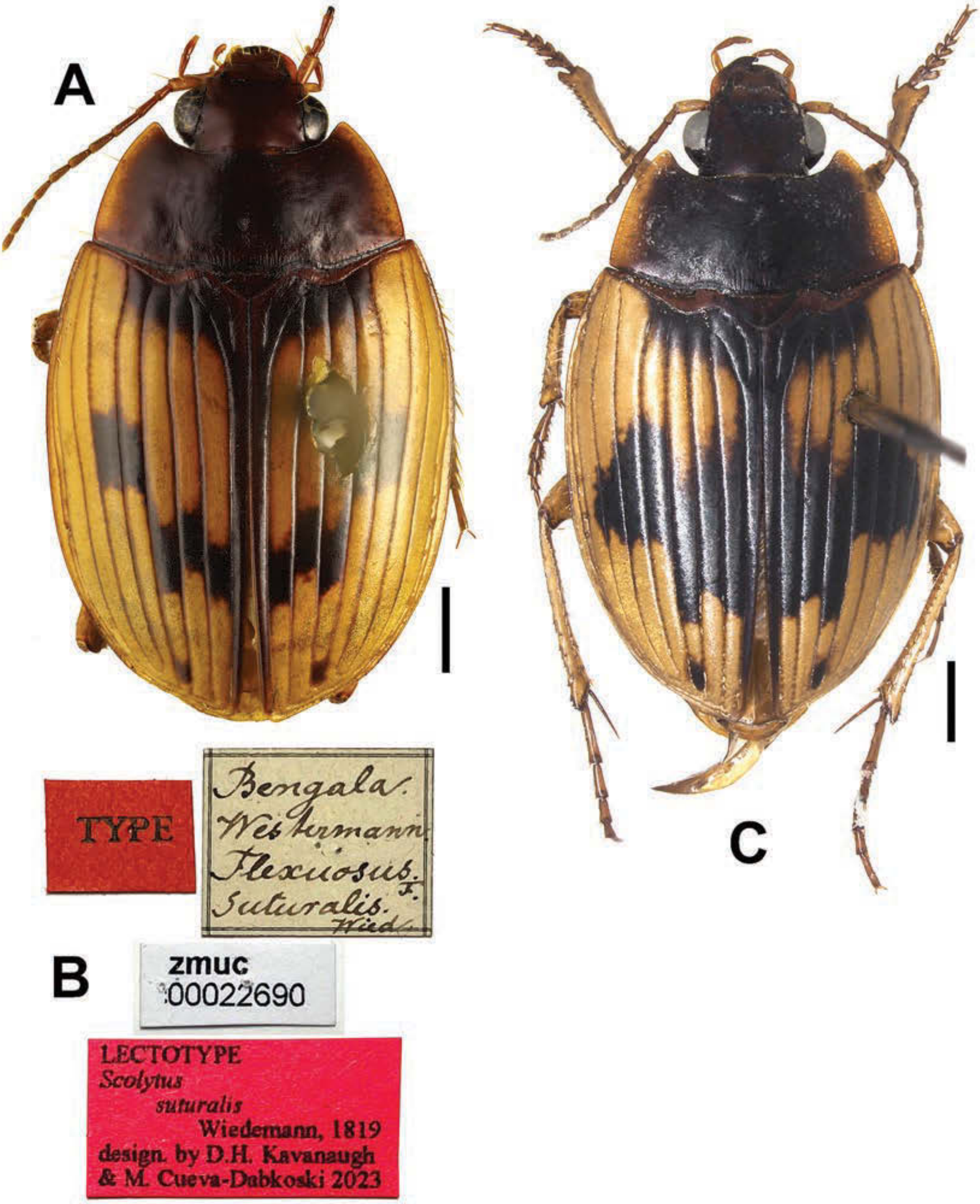
Specimens of *C. suturalis* are most similar to those of *C. acutangulus* and atypical specimens of *C. inustus* that have the elytral preapical dark spot present. Refer to the key and Diagnosis sections for each of those species for distinguishing features.

Habitat distribution. Specimens from Yunnan were collected at night on the upper sandy banks of the Longchuan River (Fig. 18B) at an elevation of 734 m (H.B Liang, personal communication).

Geographical distribution. Fig. 22. We examined a total of seven specimens (four males and three females) from the following localities: **CHINA**: Yunnan: Mangshi, Zhefang Township (Longchuan Jiang at Nongkan village, 24.16534°/98.10266°, 734 m, 22 May 2020, H.B. Liang and Y. Xu collectors [two males and two females; IOZ]). **BANGLADESH/ INDIA**: "Bengala" ([one male; ZMUC]). **BANGLADESH/ INDIA/ MYANMAR**: "India Or." ([one female; MNFB]). **INDIA**: Sikkim: Melli (Teesta River valley, 240 m, 14 October 1918, H. Stevens collector [one male; NHMUK]).

This species ranges from the type area, "Bengala" or "Bengal" (no specific locality), which includes present-day eastern India and/or Bangladesh, at least to westernmost Yunnan Province, China. The westernmost confirmed limit of the species is in Sikkim and the easternmost limit in western Yunnan. Andrewes' records from northern India (Andrewes 1921) may have been based on misidentified specimens of *C. vespertilio*, which is described below.

Geographical variation. We found some individual variation (Figs.12A, C) in development



TYPE

Bengala.
Westermann.
Flexuosus. F.
Suturalis.
Wied.

zmuc
00022690

LECTOTYPE
Scolytus
suturalis
Wiedemann, 1819
design. by D.H. Kavanaugh
& M. Cueva-Dabkoski 2023

FIGURE 12. *Cyclosomus suturalis* (Wiedemann). A. *Scolytus suturalis* Wiedemann, lectotype male, dorsal habitus; B. Labels associated with lectotype; C. Dark male ((Longchuan Jiang at Nongkan village, Zhefang Township, Mangshi, Yunnan, China). Scale lines = 1.0 mm.

of the dark color pattern of the elytra within the sample of this species from Mangshi, Yunnan, China. Specimens from all other localities were similar to one or more of the specimens from that sample, so we recognized no particular geographic variation.

Geographical relationships with other *Cyclosomus* species. Because of the uncertainty with regard to where the exactly the type specimen was collected in "Bengala", the northwestern limits to the range of this species remain unclear. *Cyclosomus marginatus* is also known only from the similarly vague "India Or.," again without specific locality, so it is possible that these species co-occur or at least overlap in their geographical ranges. Whether or not the range of *C. suturalis* overlaps those of *C. flexuosus* and/or *C. vespertilio* cannot yet been confirmed. The range of *C. inustis* approaches that of *C. suturalis* at least in northern Indochina so there is at least potential for co-occurrence of these species, although the two have not yet been found near each other.

Cyclosomus vespertilio Cueva-Dabkoski & Kavanaugh, sp. nov.

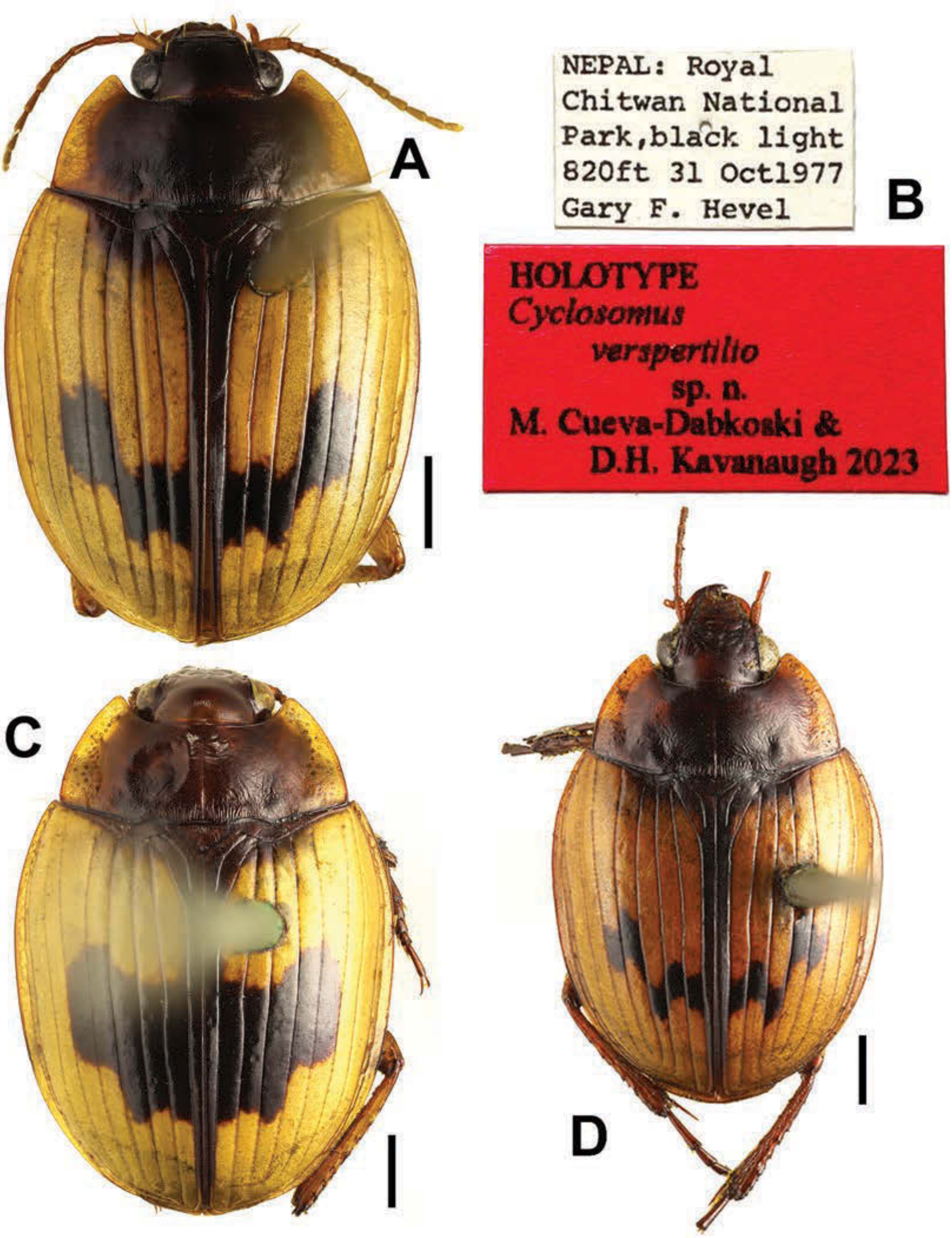
Figures 13, 14I, 15D, 16H, 17H, 22

Type material. HOLOTYPE, a male, in NMNH, labeled: "NEPAL: Royal Chitwan National Park, black light 820ft 31 Oct1977 Gary F. Hevel"/ "HOLOTYPE *Cyclosomus vespertilio* sp. n. M. Cueva-Dabkoski and D.H. Kavanaugh 2023" [red label]. A total of 44 paratypes: one male and one female, in CAS and NMNH, same label data as holotype; one male, in NHMUK, labeled: "India"/ "Bowring, 63.47*"/ "NHMUK 010795925"; one female, in NHMUK, labeled: "India"/ "Bowring, 63.47*"/ "H.E.Andrewes Coll. B.M.1945-97."/ "Ex coll. Brit. Mus."/ "Cyclosomus marginatus Motch. Compared with type H.E.A."; one male, in NHMUK, labeled: "Indian Orient"/ "Fry Coll. 1905.100."/ "NHMUK 010796097"; one male, in NMNH, labeled: "INDIA New Delhi"/ "14-VII-1967 KEGibson light trap"; one female, in NHMUK, labeled: "India 77.15 K." [handwritten]; 12 males and 22 females, in NHMUK and CAS, labeled: "India. Nevinson Coll. 1918-14"; one female, in NHMUK, labeled: "India. Nevinson Coll. 1918-14"/ "Cyclosomus marginatus Motch."/ "NNHMUK 010796368"; one male, in NHMUK, labelled: "India. Nevinson Coll. 1918-14"/ "Ex coll. Brit. Mus."/ "H.E.Andrewes Coll. B.M.1945-97."/ "Cyclosomus suturalis Wied. (see back) Compared with type H.E.A." [back labeled: "The median band in type is very narrow"]/ "NNHMUK 010796362"; one female, in NHMUK labeled: "India Dilhi [sic]"/ "39155" [= Moradabad, based on NHMUK accession records (M. Barclay, personal communication)]/ Fry Coll. 1906.100."/ Cyclosomus marginatus Mots. India Or. v. major" [handwritten]/ "NMHUK 0100795973". Each paratype also bears the following label: "PARATYPE *Cyclosomus vespertilio* sp. n. M. Cueva-Dabkoski and D.H. Kavanaugh 2023" [yellow label].

Type locality. Nepal, Royal Chitwan National Park

Etymology. The species epithet, *vespertilio*, is a Latin word for bat, here used as a noun in apposition. It refers to the shape of the middle transverse dark band of the joined elytra, which resembles a black bat with its wings spread in most specimens.

Diagnosis. Adults of *C. vespertilio* can be distinguished from those of other *Cyclosomus* species in Asia by the following combination of character states: Body size medium for genus, BL males = 6.6 to 7.4 mm, females = 6.5 to 7.6 mm; body form (Fig. 13A, C, D) roundly ovoid (ratio BL/EW = 1.36 to 1.41; ratio EL/EW = 0.88 to 0.93), with elytra widest at or near mid-length; dorsal surface with distinctly contrasting pale and dark areas; pronotum (Fig. 14I) relatively broad (ratio PWM/PL = 2.79 to 2.93) and more broadened basally (ratio PWM/PWA = 1.63 to 1.75), with disc rufous to piceous, lateral pale bands broad and more or less well-defined, anterior angles broad, lateral margins evenly arcuate, not or faintly sinuate near anterior angles; free apex of prosternal intercoxal process short (Fig. 15D); elytra pale yellowish-brown with basal, middle, and longitudinal dark bands present and dark reddish brown to black, preapical dark spot absent, mid-



NEPAL: Royal
Chitwan National
Park,black light
820ft 31 Oct1977
Gary F. Hevel

HOLOTYPE
Cyclosomus
verspertilio
sp. n.
M. Cueva-Dabkoski &
D.H. Kavanaugh 2023

FIGURE 13. *Cyclosomus vespertilio* Cueva-Dabkoski and Kavanaugh sp. nov. A. Holotype male, dorsal habitus; B. Labels associated with holotype; C. Dark male (India); D. Pale male (India). Scale lines = 1.0 mm.

dle transverse dark band varied, moderately thick in most specimens (Fig. 13A), markedly thickened (Fig. 13C) or narrowed (Fig. 13D) (much as in *C. marginatus*), in a few specimens; elytral striae moderately impressed, elytral intervals flat or nearly so; elytral epipleura with long setae only in humeral and subhumeral areas, setae in apical two-thirds distinctly shorter; median lobe of male genitalia with shaft distinctly thicker and more arcuate, ventral curvature distinctly curved throughout in lateral aspect (Fig. 16H), apical lamella smoothly rounded and slightly elongate in dorsal aspect (Fig. 17H); specimen from northern India or Nepal.

Specimens of *C. vespertilio* are most similar to those of *C. inustus* and *C. marginatus*. Most specimens of *C. vespertilio* have the middle dark band of the elytral color pattern darker and thicker than those of the other two species, with its form in most specimens as in Fig. 13A or intermediate between that form and the extreme as shown in Fig. 13C. The extreme minimally developed form shown in Fig. 13D was found in only two specimens, and these specimens resemble those of *C. marginatus*. Refer to the key and Diagnosis sections for *C. inustus* and *C. marginatus* for distinguishing features.

Description. Size medium for genus, BL males = 6.6 to 7.4 mm, females = 6.5 to 7.6 mm; body form (Fig. 13A, C, D) roundly ovoid (ratio BL/EW = 1.36 to 1.41; ratio EL/EW = 0.88 to 0.93), with elytra widest at or near mid-length.

Color. Head rufous to black, clypeus and labrum slightly lighter in dark specimens, venter rufous; antennae, mandibles, maxillae, and maxillary and labial palpi pale yellow-tan to rufous. Pronotum with disc rufous to piceous, lateral pale bands yellow-tan, broad and more or less well-defined. Elytra mainly yellow-brown, with piceous to black markings; elytral base, scutellum, and longitudinal dark band on elytral interval 1 dark reddish brown to black, dark basal band slender, piceous to black, extended laterally to interval 5; middle transverse dark band piceous or black, varied in form, moderately thick in most specimens (Fig. 13A), markedly thickened (Fig. 13C) or narrowed (Fig. 13D) (much as in *C. marginatus*), in a few specimens; preapical dark spot absent. Venter rufous, proepipleura and elytral epipleura pale yellow-tan. Legs pale, yellow-tan to rufous.

Reflection, luster, and microsculpture. Dorsum and venter without metallic reflection. Head and pronotum dull, with microsculpture moderately impressed and comprised of isodiametric meshes; elytra slightly shiny with isodiametric meshes slightly less deeply impressed; venter with isodiametric to slightly transverse meshes shallowly impressed,

Head. Eyes large, hemispheric; antennae slightly short, extended only to basal one-fifth of elytra; clypeus bisetose; labrum with apical margin deeply emarginate, three pairs of setae present; mentum asetose, with a broad, apically emarginate medial tooth; submentum anteriorly with a single pair of setae.

Prothorax. Pronotum (Fig. 14I) trapezoidal, almost as wide as elytra at humeral angles, relatively broad (ratio PWM/PL = 2.79 to 2.93) and more broadened basally (ratio PWM/PWA = 1.63 to 1.75), anterior angles broad, rectangular or slightly acute, narrowly rounded apically; anterior margin smoothly concave between anterior angles; lateral margins gently arcuate, not or faintly sinuate near anterior angles; basal margin slightly bisinuate, faintly lobate medially; anterior and basal margination thin but distinct laterally, obsolete medially; lateral margination very slender and finely impressed; midlateral setae present, inserted just medial to lateral margination and at about one-third the distance between the anterior and basal angles along the lateral margin; basolateral setae present, inserted on lateral edge of pronotum and just anterior to posterior angles. Prosternal intercoxal process moderately long, lanceolate, with complete margination, free apex of process short (as in Fig. 15D).

Elytra. Broadly ovate, slightly shorter than wide (ratio EL/EW = 0.88 to 0.93), broadly rounded apically, humeri slightly obtuse, angulate; elytral striae moderately impressed throughout; elytral intervals flat or nearly so, smooth; parascutellar setiferous pore present at base of interval 1 near junction of striae 1 and 2; two discal setiferous pores present on interval 3 adjacent to stria 2, one inserted just posterior to elytral mid-length and the other inserted near apical one-third; apical seta present, inserted near apex of interval 3; umbilicate series comprised of 11 to 13 setae.

Legs. Males and females with front tarsi similar in shape and width (as in Fig. 2C), but males with tarsomeres 1 to 3 with two rows of adhesive squamosetae ventrally (as in Fig. 2B), females without such setae; middle tarsi with tarsomeres 1 to 3 distinctly broader in males (as in Fig. 2D) than in females and with two rows of adhesive squamosetae ventrally (as in Fig. 2E), absent from females. Tarsal claws smooth, edentate.

Male genitalia. Median lobe with shaft distinctly thickened and markedly arcuate, ventral curvature distinctly curved throughout, shaft tapered gently to apex in lateral aspect (Fig. 16H), apical lamella smoothly rounded and slightly elongate, slightly narrowed basally in dorsal aspect (Fig. 17H).

Habitat distribution. Unknown, but presumed to be restricted to the sandy shores of medium to large rivers at low elevation, like members of most other species of the genus. The elevation of New Delhi is about 200m, of Morababad about 190 m, and that of suitable habitat in Chitwan National Park about 550 m, so members of this species occupy at least that altitudinal range at the southern base of the Himalayan Mountains.

Geographical distribution. Fig. 22. This species is apparently restricted to northern India and Nepal, along tributaries of the Ganges River draining the southern slope of the Himalayan Mountains. We have found only three specific records, two of which represent the known extremes of the range of the species. The western locality is New Delhi (Delhi State, India [in NMNH]) and the eastern site is in Chitwan National Park (Narayani Zone, Nepal [in CAS, NMNH]). However, most of the specimens we examined were labeled simply "India" and were from the "Nevinson Collection" in NHMUK. According to Max Barclay (NHMUK, personal communication), most of the Nevinson material labeled "India," and for which no further supporting specificity has been found, has been from northern India, including Punjab, Sikkim and West Bengal ("Darjeeling"). It is likely, therefore, that the range of this species extends somewhat further east and west along the southern edge of the Himalaya than has yet been confirmed.

Geographical variation. Although there is some individual variation (Figs. 13A, C, D) in development of the dark color pattern of the elytra in this species, we could not discern any particular geographic component to that variation.

Geographical relationships with other *Cyclosomus* species. The known range of *C. vespertilio* is within the broad range of *C. flexuosus* at its northern limit, so these two species may be sympatric or even syntopic in at least some areas. However, they have not yet been recorded together from any locality. It is also possible that *C. vespertilio* is sympatric with *C. marginatus* and/or *C. suturalis* in the eastern or southeastern part of its range, depending on just where in "Bengal" (i.e, the area now including West Bengal, India and Bangladesh [see above]) the last two actually occur.

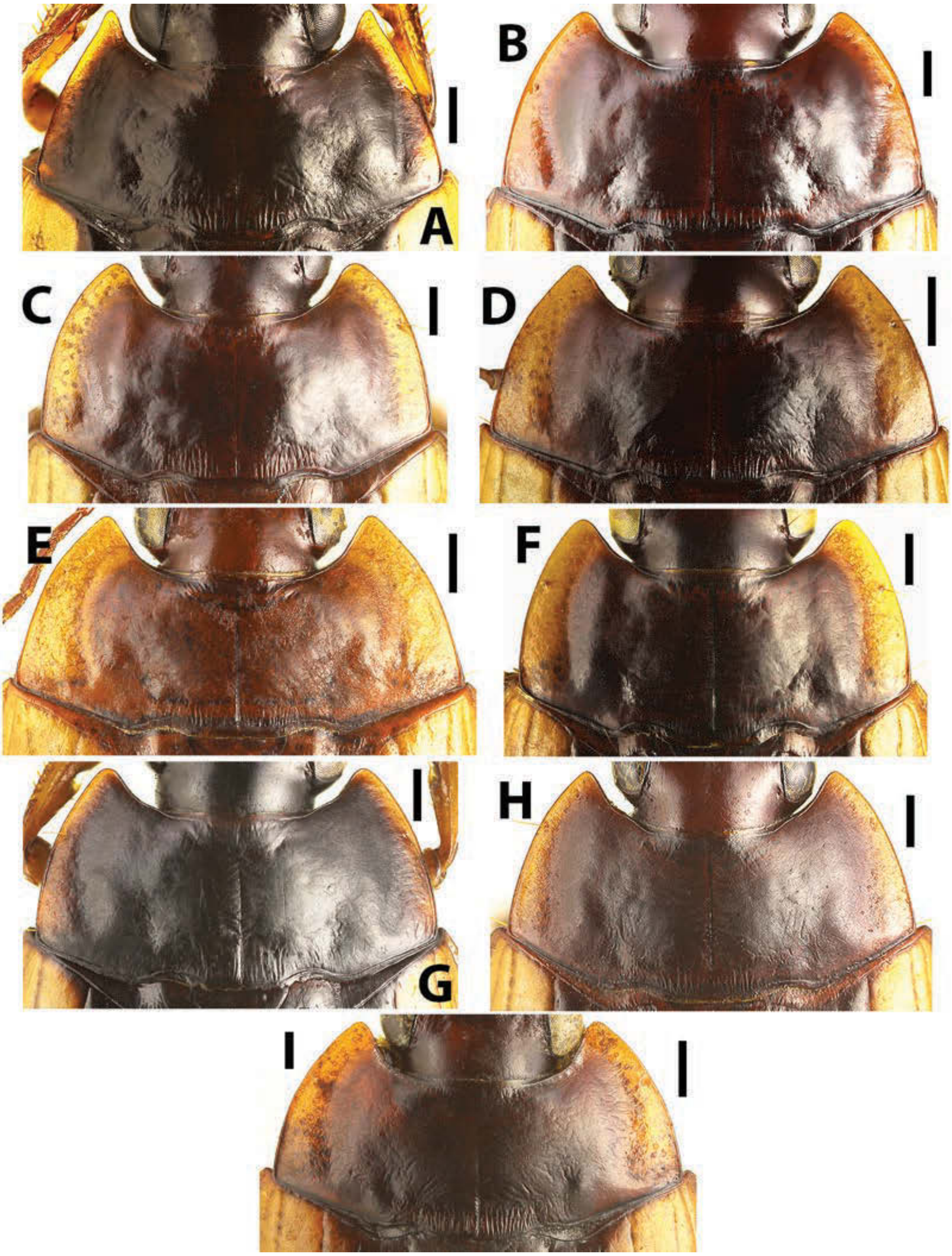


FIGURE 14. Pronota, *Cyclosomus* spp., dorsal aspect. A. *C. acutangulus* Kavanaugh and Cueva-Dabkoski (Bhalukpong, Arunachal Pradesh, India); B. *C. flexuosus* (Fabricius) (Hetauda, Bagmati Province, Nepal); C. *C. inustus* Andrewes, holotype (Hong Kong, China); D. *C. marginatus* Motschulsky (India); E. *C. pallidus* Kavanaugh and Cueva-Dabkoski sp. nov. (Karachi, Sindh Province, Pakistan); F. *C. philippinus* Heller (Pili, Zambales Mountains, Luzon, Philippines); G. *C. sumatrensis* Bouchard (Taman Negra National Park, Pahang, Malaysia); H. *C. suturalis* (Wiedemann) , lectotype ("Bengala", India); I. *C. vespertilio* Cueva-Dabkoski and Kavanaugh sp. nov. Scale lines = 0.5 mm.

FIGURE 15. Prosternal intercoxal process, *Cyclosomus* spp., left lateral aspect. A. *C. acutangulus* Kavanaugh and Cueva-Dabkoski (Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *C. flexuosus* Dejean (Cinkona, Anamalia Hills, Tamil Nadu, India); C. *C. sumatrensis* Bouchard (Taman Negara, Pahang, Malaysia); D. *C. verspertilio* Cueva-Dabkoski and Kavanaugh sp. nov. (New Delhi, Delhi, India). Scale lines = 0.5 mm.

FIGURE 16. Male genitalia, Cyclosomus spp., left lateral aspect. A. *C. acutangulus* Kavanaugh and Cueva-Dabkoski (Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *C. flexuosus* Dejean (Karaikal, Puducherry, India); C. *C. inustus* Andrewes ("China"); D. *C. marginatus* Motschulsky ("Bengal", India); E. *C. philippinus* Heller (Pili, Zambales Mountains, Luzon, Philippines); F. *C. sumatrensis* Bouchard (Taman Negara, Pahang, Malaysia); G. *C. suturalis* (Wiedemann), lectotype ("Bengala", India); H. *C. verspertilio* Cueva-Dabkoski and Kavanaugh sp. nov. (New Delhi, Delhi, India). Scale lines = 0.5 mm.

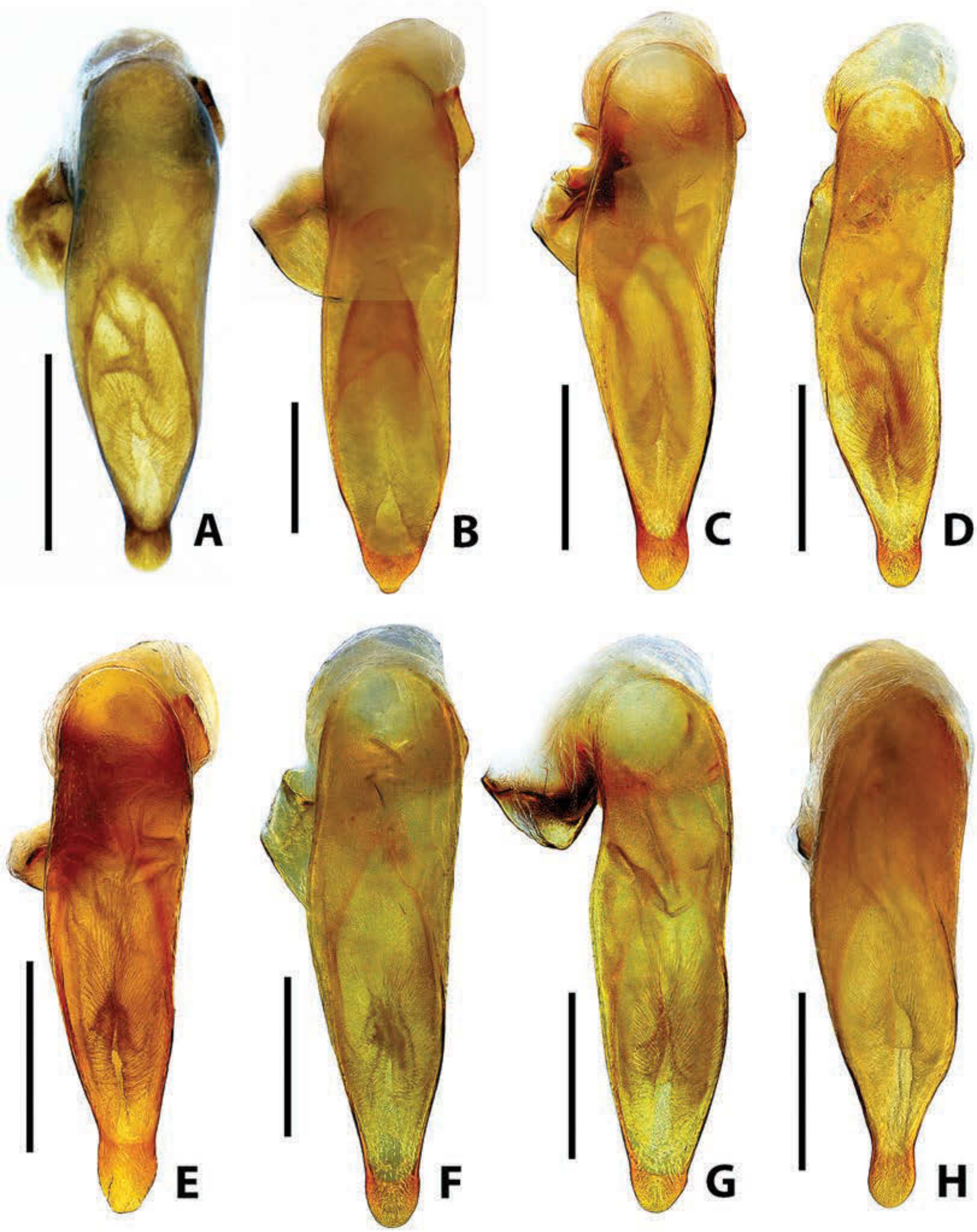


FIGURE 17. Male genitalia, Cyclosomus spp., dorsal aspect. A. *C. acutangulus* Kavanaugh and Cueva-Dabkoski (Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *C. flexuosus* Dejean (Karaikal, Puducherry, India); C. *C. inustus* Andrewes ("China"); D. *C. marginatus* Motschulsky ("Bengal", India); E. *C. philippinus* Heller (Pili, Zambales Mountains, Luzon, Philippines); F. *C. sumatrensis* Bouchard (Taman Negara, Pahang, Malaysia); G. *C. suturalis* (Wiedemann), lectotype ("Bengala", India); H. *C. verspertilio* Cueva-Dabkoski and Kavanaugh sp. nov. (New Delhi, Delhi, India). Scale lines = 0.5 mm.

FIGURE 18. Photographs of habitats for *Cyclosomus* species. A. *C. acutangulus* Kavanaugh & Cueva-Dabkoski (Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China; photograph by David H. Kavanaugh); B. *C. suturalis* (Wiedemann) (Longchuan Jiang at Nongkan village, Zhefang Township, Mangshi, Yunnan, China; photograph by Hong-Bin Liang).

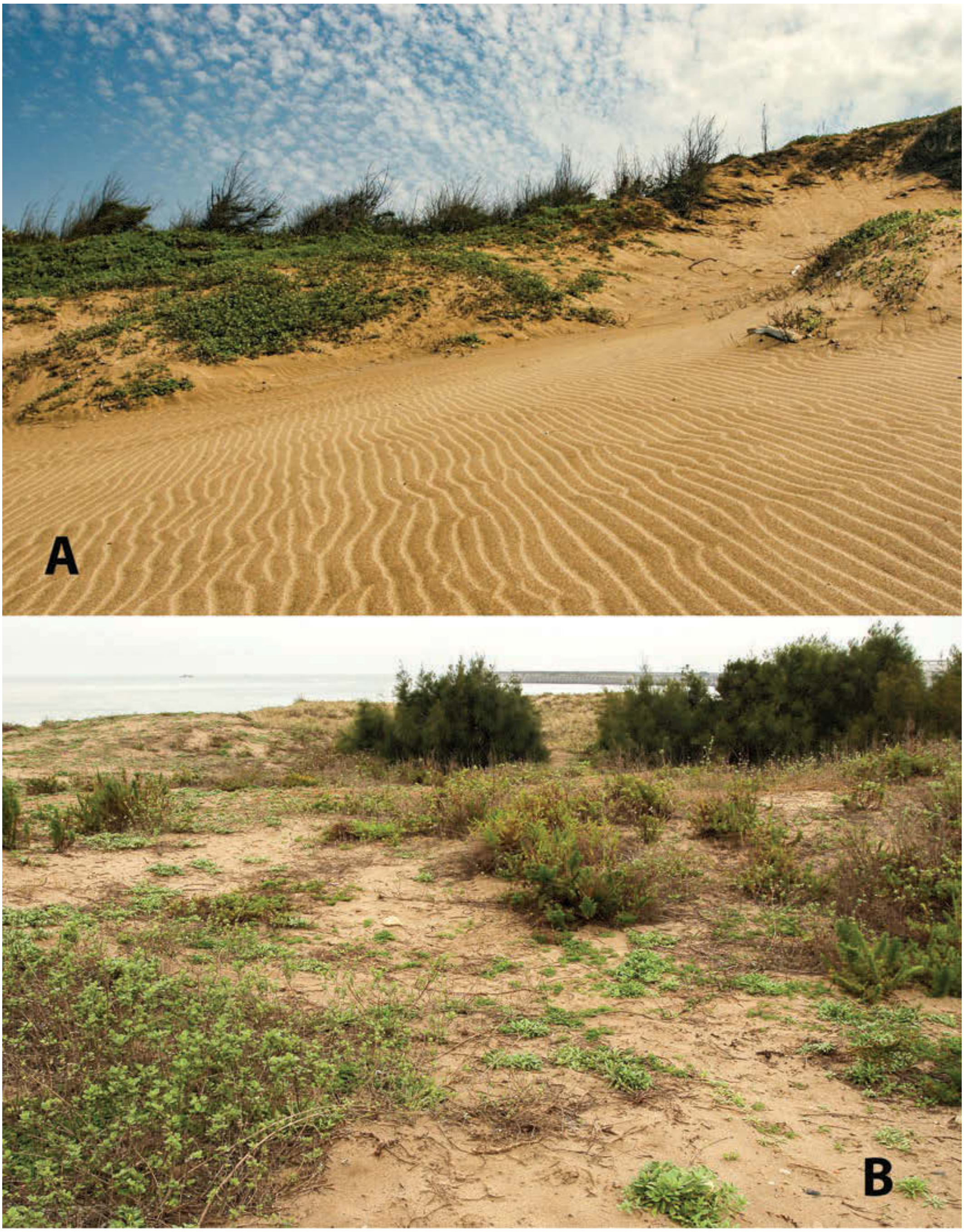


FIGURE 19. Photographs of habitats for *Cyclosomus inustus* Andrewes. A. Lingshanbi, Shihmen District, New Taipei City, Taiwan; B. Shalun, Danshui District, New Taipei City, Taiwan. Photographs reproduced from Wang et al. 2017 with permission of Liang-Jong Wang.

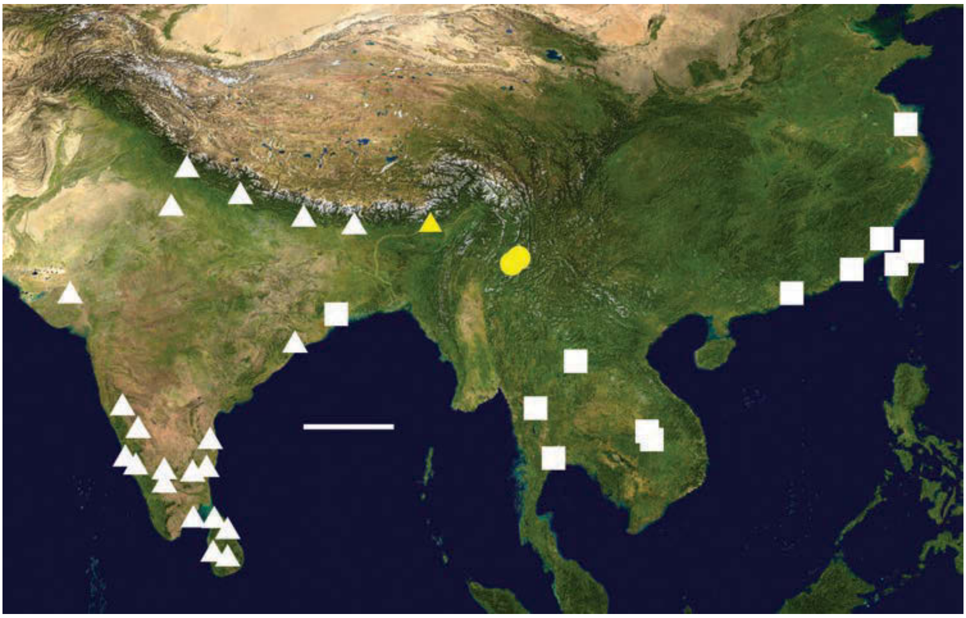


FIGURE 20. Map showing distribution of locality records for *Cyclosomus* specimens examined. Yellow circles = *C. acutangulus* Kavanaugh and Cueva-Dabkoski; white triangles = *C. flexuosus* Dejean; yellow triangle = locality where *C. acutangulus* and *C. flexuosus* have been found together; white squares = *C. inustus* Andrewes. Modified from Wikimedia Commons, World Atlas of the World, at URL: <*http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_land_and_oceans_12000.jpg*>. Scale line = 500 km.

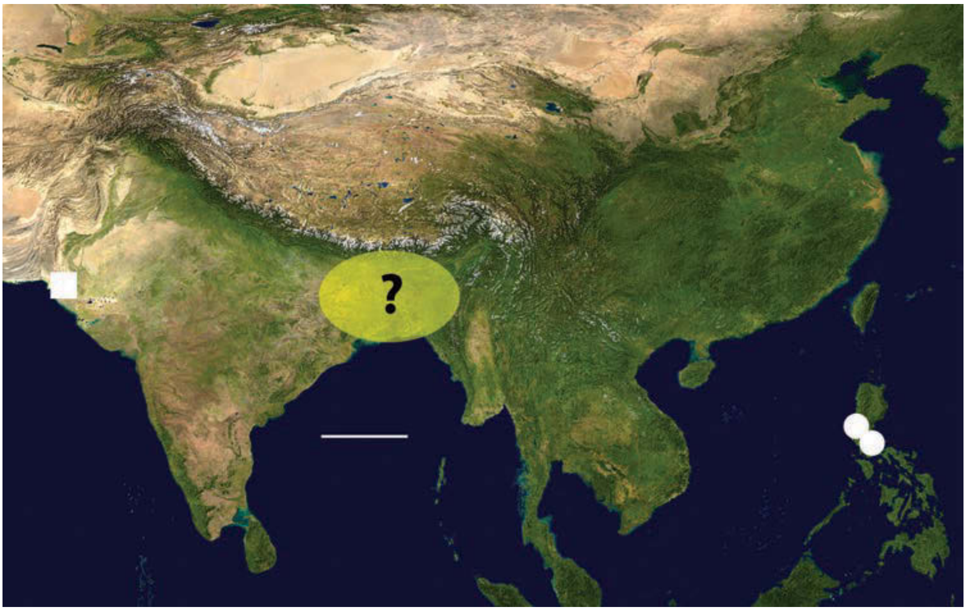


FIGURE 21. Map showing distribution of locality records for *Cyclosomus* specimens examined. Yellow highlighted area with black question mark = type area for *C. marginatus* Motschulsky; white square = *C. pallidus* Kavanaugh and Cueva-Dabkoski sp. nov.; white circles = *C. philippinus* Heller. Modified from Wikimedia Commons, World Atlas of the World, at URL: <*http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_-_land_and_oceans_12000.jpg*>. Scale line = 500 km.

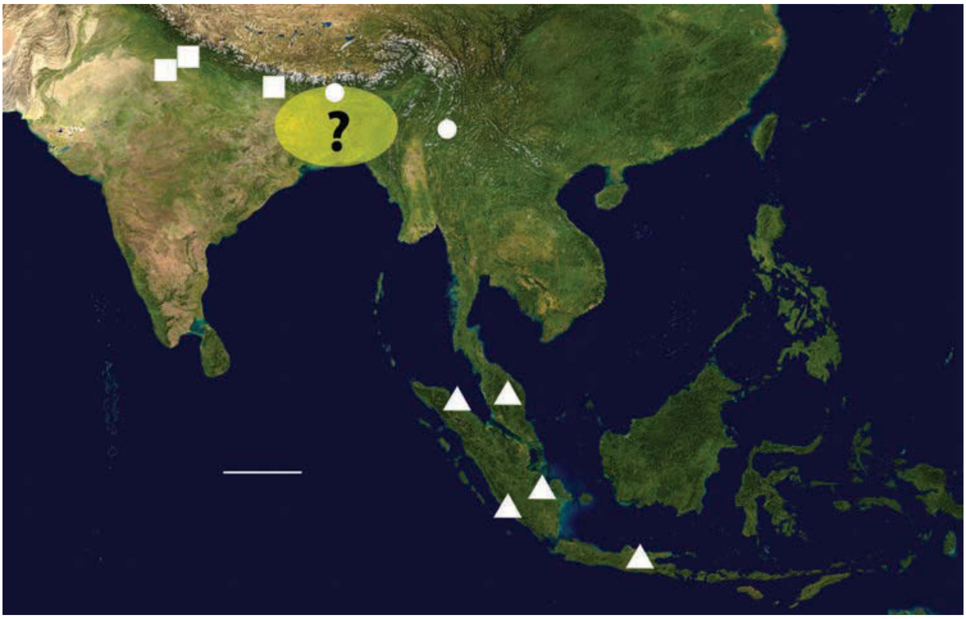


FIGURE 22. Map showing distribution of locality records for *Cyclosomus* specimens examined. White triangles = *C. sumatrensis* Bouchard; yellow highlighted area with black question mark = type area for *C. suturalis* (Wiedemann); white circles = other localities for *C. suturalis*; white squares = *C. vespertilio* Cueva-Dabkoski and Kavanaugh sp. nov. Modified from Wikimedia Commons, World Atlas of the World, at URL: <*http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_-_land_and_oceans_12000.jpg*>. Scale line = 500 km.

DISCUSSION

Geographical distribution pattern. The geographical range of *Cyclosomus* in Asia is essentially confined to those parts traditionally assigned to the Oriental Region, although several species (i.e., *C. acutangulus*, *C. flexuosus*, *C. suturalis* and *C. vespertilio*) occur along streams draining the warm-temperate southern and southeastern bases of the Himalayan mountain system, which are sometimes considered as part of the Palearctic Region. The known latitudinal range of the genus extends from about 30°N (with *C. flexuosus* in the Kumaon region, Uttarakhand, India and *C. inustus* at Ningbo, Zhejiang, China) to 8°S (with *C. sumatrensis* at Kras, East Java, Indonesia); and its longitudinal range extends from 67°E (with *C. pallidus* at Karachi, Pakistan) to about 121°E (with *C. inustus* on Taiwan and *C. philippinus* at Los Baños, Luzon Island, Philippines). Highest recorded species diversity is in India, with five species (*C. acutangulus*, *C. flexuosus*, *C. inustus*, *C. suturalis*, and *C. vespertilio*) already recorded from there and *C. marginatus* likely also to occur there. Two species are recorded as occurring in Nepal (*C. flexuosus* and *C. vespertilio*) and Yunnan (*C. acutangulu*s and *C. suturalis*), but all other countries in the region have at most single recorded species. No species has been confirmed to occur in in Bangladesh or Myanmar, but it is likely that two or more species occur in these areas as yet undetected. Only three species (i.e., *C. flexuosus*, *C. inustus*, and *C. sumatrensis*) are confirmed to have extensive geographical ranges. The known ranges of the other six species are more limited or, as for *C. marginatus*, still undefined.

A review of the maps illustrating the distributions of species (Figs. 20-22) shows just how little is known about the distributions of species in the vast expanse of the Oriental Region. Although suitable habitats along the many major river systems or sea beach areas occur throughout most of region, records for *Cyclosomus* species are relatively few and far between. Most records to date have resulted from incidental collecting, especially collecting at lights or in light traps. Because these beetles are nocturnally active and are able to hide during daytime directly in their loose sandy substrate, they largely avoid discovery and capture by collectors using routine collecting procedures. Carabid beetle collectors typically search under stones, logs, or other surface debris for specimens during daylight hours, but *Cyclosomus* specimens are found in such places only rarely.

Habitat range pattern. Members of all *Cyclosomus* species share special morphological adaptations described above for life on and in loose sand. Most species live in sandy habitats along rivers and streams large enough to develop large sandy banks and/or associated dune systems. *Cyclosomus inustus* has been found to occur in similar habitats along sea beaches in Taiwan and at least in Hong Kong and may actually be restricted to seacoast sandy habitats. Although *C. flexuosus* is widespread across most of India, several records, particularly some from southern India and Sri Lanka, suggest that it may also occur in sandy seacoast habitats. As noted above, Wang et al. (2022) tried in vain to find *C. inustus* species in riverside or lakeshore sandy habitats in Taiwan and concluded that the species indeed was restricted to the seacoast habitats. This leads us to question whether specimens that we identify as *C. inustus* from inland localities in several countries in Indochina are really conspecific with that species or represent some other known or undescribed species.

On a broader scale, it is apparent that *Cyclosomus* species occupy suitable sandy habitats along streams and rivers in a broad range of biomes, including warm-temperate, grassland, savanna, subtropical, tropical (*C. philippinus* and *C. sumatrensis*), and even desert (*C. pallidus*) areas. However, additional field research is needed to better document these habitat ranges for individual species.

Sympatry and syntopy among species. The general pattern for species of *Cyclosomus* is one of allopatry and, in some instances, with large range disjunctions. This is most apparent for species isolated at the periphery of the range of the genus, such as *C. pallidus* (in southern Pakistan), *C. philippinus* (in the Philippines), and *C. sumatrensis* in (Malaysia and Indonesian). The known range of *C. flexuosus* overlaps those of *C. acutangulus*, *C. suturalis*, and *C. vespertilio*, and possibly also *C. inustus* and *C. marginatus*. The known ranges of *C. acutangulus* and *C. suturalis* in westernmost Yunnan are separated by just a few kilometers and may in fact overlap, or at least interdigitate at different elevations along the same or different rivers in western Yunnan and/or northern Myanmar. The only record of syntopy (specimens of two different species found together in the same habitat at the same locality) that we have found is for *C. acutangulus* and *C. flexusosus* at Bhalukpong, Arunachal Pradesh, India. Focused collecting in the future is needed to better define the geographical relationships among all these species.

SUGGESTED DIRECTIONS FOR FUTURE RESEARCH

We suggest that the most useful way to advance our knowledge of these specialized and intriguing beetles, their habitats, and their geographical distributions would be through extensive and focused collecting. This will require collecting at night, using headlamps or other illumination, in their loose sandy habitats. We have found this method to be highly productive. Bowring (see Waterhouse 1850-51) had surprising success collecting in daytime by stirring through loose sand in coastal areas in Hong Kong (habitats that may not still exist there today) to a depth of "five or six inches." This method should also work in similar habitats along rivers away from the seacoast. Special efforts should be directed toward discovery of new and precise localities for *C. marginatus* in "eastern India" (i.e., West Bengal, Bangladesh, and Myanmar) so that the geographical range of that species can be better defined. Such collecting is necessary to better understand the geographical ranges of these species and to improve our baseline against which potential changes in those distributions because of climate and other changes can be tracked.

We remain dissatisfied with our ability to resolve certain species boundaries within the genus *Cyclosomus*, particularly those between *C. inustus* and *C. marginatus* and between seacoast and inland populations of what we have considered as *C. inustus*. Additional specimens of *C. marginatus* would be particularly useful for improved morphological comparisons. Fresh material (specifically material collected into 95% ethanol) from throughout the range we have outlined for *C. inustus*, as well as for any of the other species, may help to resolve remaining taxonomic uncertainties by supporting phylogeographical analyses using DNA data.

We hope that the information provided in this report, and particularly the key for identification of species and tips for collecting these beetles, will both stimulate and facilitate future work with *Cyclosomus* species in Asia.

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Heterobranch Sea Slugs from Hazard Canyon Reef, San Luis Obispo County, California

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From 1999 to 2021 we sampled the rocky intertidal at Hazard Canyon Reef, California 50 times for benthic heterobranch sea slugs, recording a total of 5919 individuals from 63 species, 57 of which were nudibranchs. We consistently observed the highest number of both species and individuals in the spring. The dorid nudibranch *Diaulula sandiegensis* was the most frequently encountered species, followed by the dorids *Okenia rosacea*, *Rostanga pulchra*, *Triopha catalinae*, *T. maculata*, and *Peltodoris nobilis*, each observed on >80% of our sampling trips. *Okenia rosacea* was the most abundant species, accounting for nearly 20% of total individuals recorded, followed by *Dendronotus subramosus*, *T. maculata*, and the aeolids *Hermissenda opalescens* and *Diaphoreolis lagunae*. The prevalence of southern species (largely from the California Biogeographic Province) relative to northern species from the Oregon Province generally tracked the El Niño Southern Oscillation as measured by the Multivariate ENSO Index. During the strong 2015–16 El Niño the northern species *Doris montereyensis*, *Peltodoris nobilis*, and *Dendronotus albus* declined sharply in abundance, while the southern species *Doriopsilla albopunctata*, *D. fulva*, *Triopha maculata*, and especially *Okenia rosacea* peaked in abundance. At about the same time, *Cadlina luteomarginata*, which we had observed frequently during the first 14 years of our study, was replaced by its more southerly congener *Cadlina* cf. *sparsa* and not found again. Fifty-nine total species of nudibranchs have now been recorded in the literature from Hazard Canyon Reef, making it one of the richest sites for these specialized predators in the Oregon Biogeographic Province.

With its extensive tide pools and long, deeply undercut rocky ledges, Hazard Canyon Reef, in Montaña de Oro State Park near Morro Bay, San Luis Obispo County (Figs. 1 and 2), is a popular tide-pooling location and supports a rich intertidal biota, including diverse nudibranch sea slugs and their invertebrate prey. Indeed, of the 71 species of heterobranch sea slugs documented from San Luis Obispo County by Roller and Long (1969) and Roller (1970) during their two-year study, 42 were recorded from Hazard Canyon[1].

Hazard Canyon Reef marks the southernmost known limit of distribution for the nudibranchs *Antiopella fusca* O'Donoghue, 1924 (McDonald 1983, 2021; Goddard et al. 2018, p. 125) and

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[1] Roller and Long (1969) lumped nearby collecting sites under one place name, and the dorid nudibranch *Acanthodoris hudsoni* MacFarland, 1905 that they listed from Hazard Canyon was actually from nearby Spooner's Cove, also in Montaña de Oro State Park (see McDonald 1970).

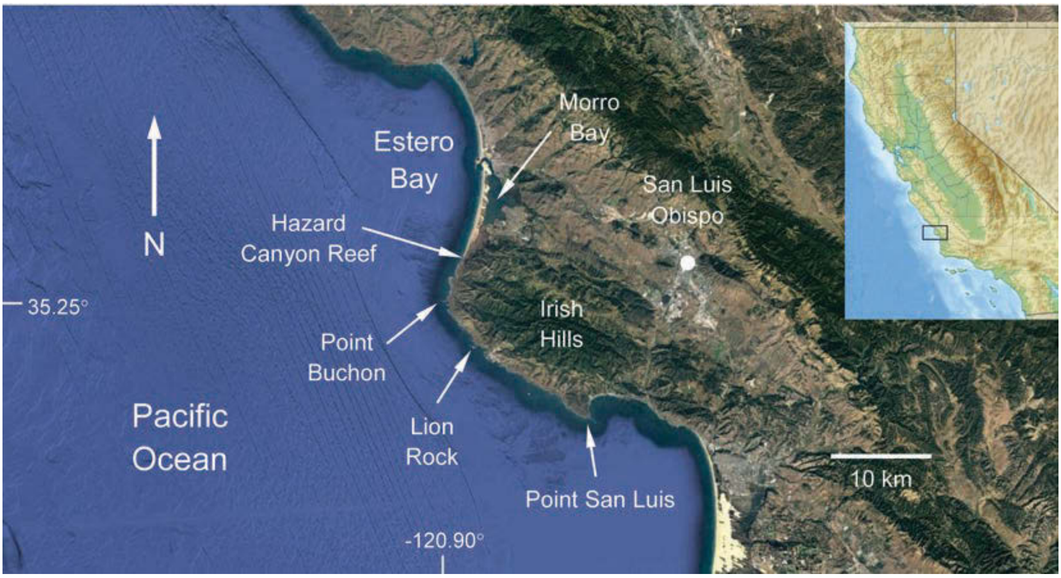


FIGURE 1. Map showing location of Hazard Canyon Reef between Morro Bay and Point Buchon, San Luis Obispo County, California.

Cuthonella cocoachroma (Williams and Gosliner, 1979) (Ukeda 2014), and the northernmost for *Janolus anulatus* Camacho-Garcia and Gosliner, 2006 (Goddard 2019). In addition, *Atalodoris jannae* (Millen, 1987) is known south to Hazard Canyon Reef and from the nearby vicinity of Lion Rock (see Fig. 1) (Roller 1970; McDonald 1983, 2014; Millen 1987). Additional heterobranch sea slugs from Hazard Canyon Reef documented in the literature include the nudibranchs *Hallaxa chani* Gosliner and Williams, 1975 (Gosliner and Williams 1975; McDonald (1983, p. 271) and *Diaphoreolis flavovulta* (MacFarland, 1966) (McDonald 1983, p. 267).

The senior author first sampled Hazard Canyon Reef for heterobranch sea slugs (hereafter heterobranchs) during field trips in 1999 and 2000 with Invertebrate Zoology classes from the University of California, Santa Barbara (UCSB). He returned to the site in November 2003 and again in May 2005. Thereafter, JG returned once or a few times every year through 2021, often accompanied by the junior authors starting in 2010. Through May 2021, we recorded nearly 6000 individuals of heterobranchs in 63 species, including marine heatwave-related population booms documented by Goddard et al. (2016) of *Aplysia californica* (Cooper, 1863) in December 2013 and *Okenia rosacea* (MacFarland, 1905) in winter 2014-15, as well as the aforementioned records of (1) *Antiopella fusca* (found by ZG in May 2011) and (2) *Janolus anulatus*, the first record of this Californian and Panamic species north of Point Conception, California.

Here, we document the full heterobranch fauna we observed at Hazard Canyon Reef and, following our contemporaneous studies on the south coast of Santa Barbara County (Goddard et al. 2020, 2021), present data on (1) their abundance and frequency of occurrence, (2) seasonal patterns of occurrence and egg-laying of the most abundant species, and (3) interannual changes in the abundance of southern versus northern species with the El Niño Southern Oscillation (ENSO). Some of the latter fluctuations at Hazard Canyon Reef were shown for the period 2009–15 by Goddard et al. (2016, Fig. 8), which included a sharp increase in southern species during the marine heatwaves observed in the NE Pacific starting in late 2013 (Bond et al. 2015; Sanford et al. 2019). We also tabulate records made by other observers of additional species of heterobranchs found (1) intertidally at Hazard Canyon Reef, or (2) subtidally in the vicinity of Montaña de Oro State Park.

STUDY SITE

Hazard Canyon Reef (35.2897°, -120.8840°) is located in Montaña de Oro State Park on the south side of Estero Bay in San Luis Obispo County, California (Fig. 1). The reef is composed of Monterey shale, whose layers dip seaward at a shallow angle and are pocketed by numerous tide pools and cut by long channels with low ledges overhanging some tide pools by up to 1 m (Fig. 2). Cobbles and boulders are scarce on the reef and lie in some of the more wave-protected pools.

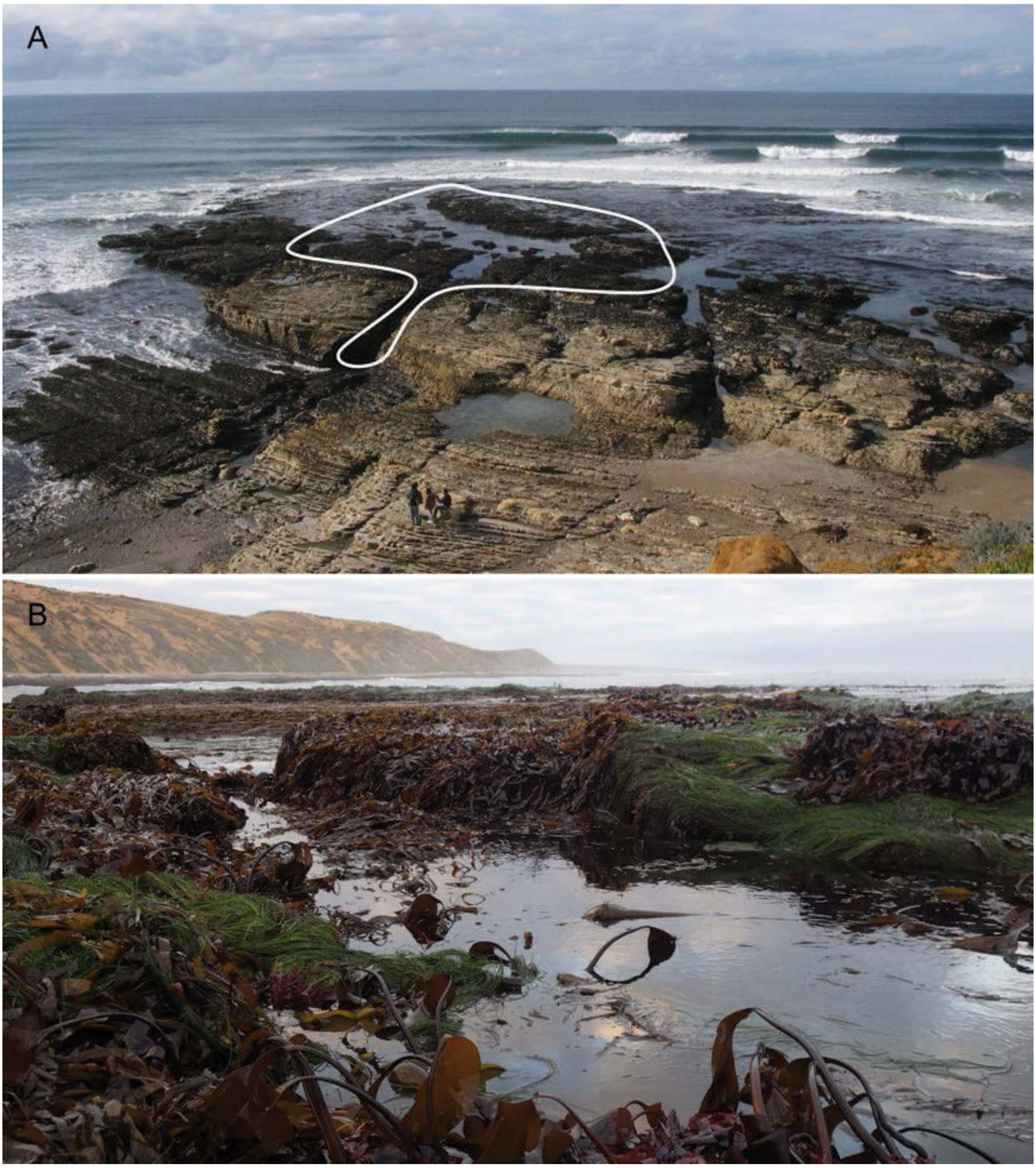


FIGURE 2. Hazard Canyon Reef. (A) Study site (outlined in white), looking northwest, 23 November 2011, -0.33 m tide, with a building ocean swell. The crevice forming the slender extension of the study area visible here is about 25 m long. (B) At northwestern-most part of study area, 26 May 2017, tide level at -0.46 m.

Landward, the reef is backed by an uplifted marine terrace about 12 m high and covered with sand dunes largely stabilized by maritime chaparral, coastal scrub, and, just inland, non-native *Eucalyptus* trees originally planted in the area in 1908 by Alexander S. Hazard, the rancher after whom Hazard Canyon proper and nearby Hazard Peak were named. The canyon opens immediately south of the reef and carries a seasonal stream.

Facing northwest, Hazard Canyon Reef is exposed to powerful winter swells generated in the North Pacific Ocean. However, the gentle slope of the reef breaks the force of large waves, and its biota is typical of protected outer-coast rocky shores in central California as described by Ricketts et al. (1985). Since 1995, the Multi-Agency Rocky Intertidal Network (MARINe) has monitored common biota on emergent, lighted (as opposed to shaded) substrata on the reef. Lists compiled by MARINe of common species at Hazard Canyon Reef and graphs of their abundance over time can be accessed here: *https://marine.ucsc.edu/sitepages/hazards.html*. To their species lists we would add *Macrocystis pyrifera* (Linnaeus) C.Agardh, 1820 and *Nereocystis luetkeana* (K. Mertens) Postels & Ruprecht, 1840, both of which are abundant during the spring and summer on the lowest tide levels of the reef, often mixed with *Eregia menziesii* (Turner) Areschoug, 1876. Additionally, large pholad bivalves, especially *Chaceia ovoidea* (Gould, 1851), are common on the reef (JG, personal observations), and generations of their boring activity has significantly pocketed and eroded the substratum, greatly increasing the surface area available under ledges for benthic fauna, including the encrusting prey of nudibranchs.

Hazard Canyon Reef (hereafter Hazard Canyon) lies in the California Transition Zone of the Oregon biogeographic Province (Briggs and Bowen 2012; Toonen et al. 2016). Average sea surface temperatures measured 1996–2022 from a buoy 1.9 km SE of Lion Rock (see Figure 1) varied from about 12° C during the upwelling season in April to 15° C in September and October, and daily extremes during our study period reached a low of 8.3° C in April 1999 during the strong 1998–99 La Niña, and highs of about 23° C in October 2014 during “the Blob” (Bond et al. 2015), and again in August and September 2015 during the 2015–16 El Niño (Data from the Coastal Data Information Program, Scripps Institution of Oceanography available here: *http://cdip.ucsd.edu/m/products/climatology/?stn=076p1&param=sstSeaSurfaceTemperature*).

METHODS

On low tides falling below -0.2 m and occurring between dawn and dusk, we searched low intertidal pools, walls, and under ledges for heterobranchs. We used waterproof lights while searching before sunrise, and while searching under ledges. On each trip we recorded the number of individuals of each species found and the presence of their egg masses. The latter were recorded only when identification was unequivocal, and egg masses recorded in the absence of adults were used in counts of number of species present, but not in counts of total number of individuals. We counted all individuals when populations were sparse, but when dense, we subjectively estimated abundance by order of magnitude. While there were bounds to our study area (Figure 2), and on different trips we sampled many of the same ledges and pools, we were not always able to examine the full area and therefore quantified our counts by time spent searching and number of observers, rather than by area. A spreadsheet containing the abundance data we collected during this study is available online from ResearchGate (*https://doi.org/10.13140/RG.2.2.12372.07040*). Our nomenclature follows Behrens et al. (2022), and to a lesser degree the World Register of Marine Species (WoRMS, *https://www.marinespecies.org/index.php*) as of September 2022.

During the early years of this study we photographed only rare or unusual species, or species whose mode of development the senior author was examining. However, beginning in 2014 and using a Pentax WG III waterproof camera, we started photographing *in situ* more of the species encountered, and later, using an Olympus TG-6, most if not all species found on each sampling trip. Since 2017 we have posted these images on the online database iNaturalist (*https://www.inaturalist.org/*). They can be found by searching the senior author's observations (https://www.inaturalist.org/observations/jeffgoddard) using the place name "Hazard Reef, CA, US" in combination with the taxon name "Opisthobranchs." Specific observations on iNaturalist mentioned below are referenced by their unique observation numbers (e.g., iNaturalist 27174191).

We sampled Hazard Canyon in 47 months from April 1999 to May 2021, averaging 2.3 monthly visits per year (SD = 1.8, range 1 – 4 months per year). We did not sample in 2001, 2002, or 2004. Across all years sampled, we did not sample in August or September, and we sampled the remaining 10 calendar months an average of 3.9 ± 3.9 times, ranging from once in March to 12 times in May. By season, we sampled most frequently in spring (April through June, n = 21), followed by fall (October through December, n = 15,), winter (January through March, n = 8), and summer (n = 3). We sampled May 2014, May 2016, and May 2021 two times each; in the above summary of our sampling effort, as well as for data summaries and analyses, the counts of species and individuals in each of these three months were combined and treated as one, as were the total number of hours searched per observer.

During the course of our study, the nominal taxa *Doriopsilla albopunctata* (J. G. Cooper, 1863), *Hermissenda crassicornis* (Eschscholtz, 1831), and *Limacia cockerelli* (MacFarland, 1905) were determined to be species complexes, each with two newly delineated species overlapping in geographic distribution in central California, including Hazard Canyon (Hoover et al. 2015; Lindsay and Valdes 2016; Uribe et al. 2017; and for the overlapping geographic distributions of the two species of *Hermissenda* in California see Goddard et al. 2018). Consequently, what we had been recording as three species became six. Therefore, in order to calculate the total number of individuals of each of the six species found during our entire study we used the total number of each found following its delineation to estimate its number found prior to delineation. For example, after hearing of the results of Lindsay and Valdes on *Hermissenda* (A. Valdes, personal communication to JG, 8 Dec 2015), we recorded over the remainder of our study at Hazard Canyon totals of 6 *H. crassicornis* and 149 *Hermissenda opalescens* (J. G. Cooper, 1863). We then multiplied 6/155 by the 175 total *Hermissenda* we found prior to delineation to estimate that 7 of those 175 were *H. crassicornis*, resulting in an estimated total of 13 *H. crassicornis* for the entire study. We used analogous calculations to estimate frequency of occurrence over the entire study of each of the other five species. We note these estimates where presented below.

Owing to the relatively low frequency of our sampling, we utilize two types of time series in presenting results: (1) by season, averaging the monthly data in each season across all years sampled, and (2) by year, averaged across all months sampled each year. Changes in abundance are standardized as number of individuals found per hour per observer. Counts of individuals recorded and used in these analyses were by JG, supplemented by counts of species observed by other observers, but not by JG. Counts of the number of species present were by all observers combined.

For records of species at Hazard Canyon that we did not observe during our own sampling we searched (1) published literature, (2) the Invertebrate Zoology Collection at the California Academy of Sciences (*https://researcharchive.calacademy.org/research/izg/iz_coll_db/index.asp*), and (3) iNaturalist (*https://www.inaturalist.org/*).

RANGES AND OCEANOGRAPHIC INDICES

We assigned each species to a geographic range group as follows: (1) northern species as those ranging south as far as northern Baja California and northward to at least central Oregon, (2) southern species as those ranging south to at least Baja California Sur and northward usually only into California, and (3) widespread species as those ranging from at least as far south as Baja California Sur and frequently at least as far north as Washington. By this classification, northern species are primarily from the Oregon Biogeographic Province, and southern species are mainly from the California Province or the California Transition Zone of the Oregon Province. Owing to the above mentioned systematic revisions in the middle of our study of *Doriopsilla albopunctata*, *Hermissenda crassicornis*, and *Limacia cockerelli*, we treated their species complexes as single taxa in this analysis and assigned them as southern, widespread, and widespread, respectively. We tallied the number of species in each range group found each year and then converted those counts to proportions by dividing them by the total number of species found in each range group over the entire study. For each year, we subtracted the proportion of northern species from the proportion of southern species and then compared yearly changes in the difference with fluctuations in the Multivariate ENSO Index Version 2 (NOAA Physical Sciences Laboratory, available from: *https://psl.noaa.gov/enso/mei/)*, the bimonthly values of which we also averaged by year.

RESULTS

Species composition and abundance

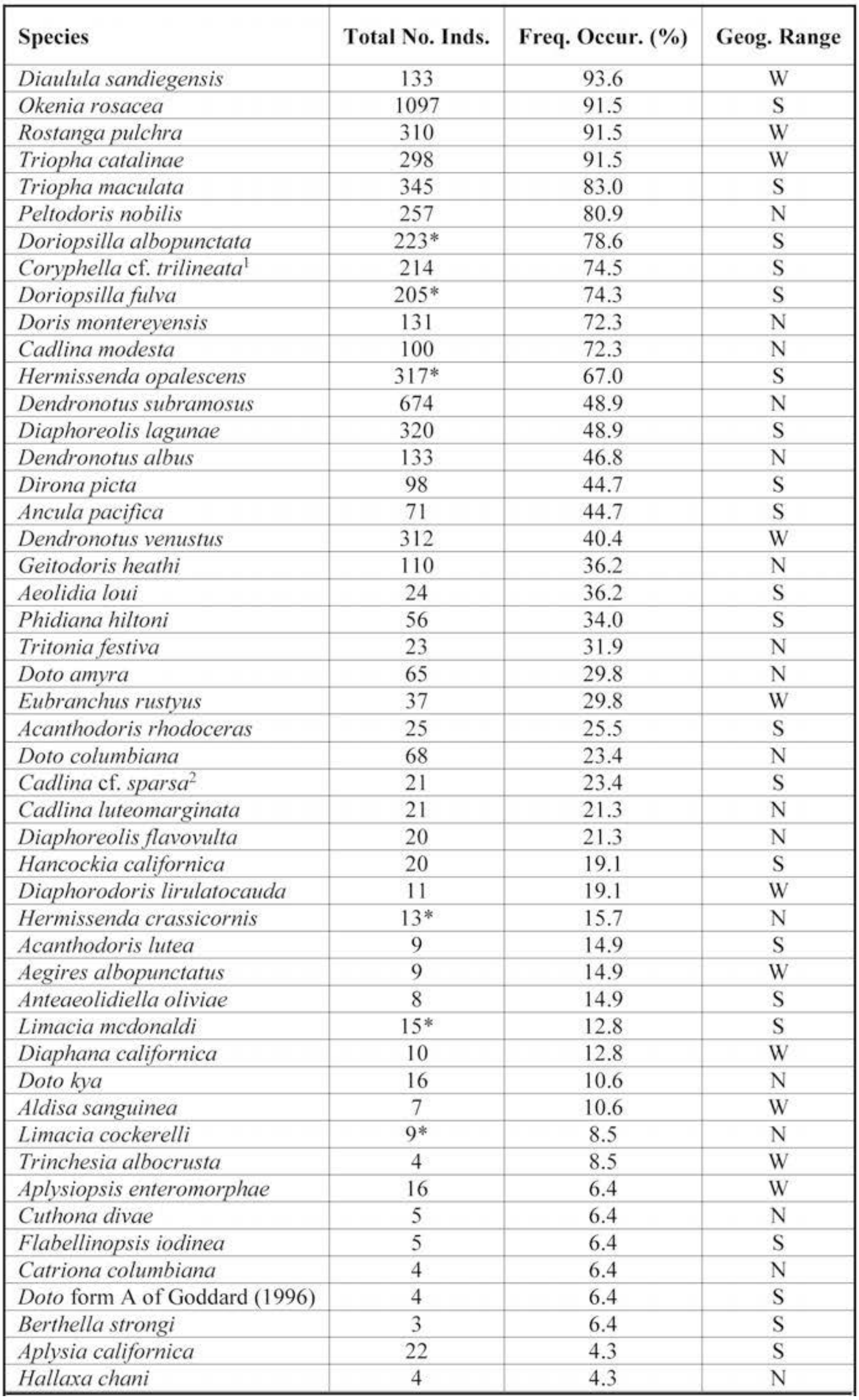
In 50 total trips to Hazard Canyon, we recorded 5919 individuals and 63 species of heterobranchs (Table 1). These included 57 species of nudibranchs, the pleurobranchid *Berthella strongi* (MacFarland, 1966), the sacoglossans *Aplysiopsis enteromorphae* (Eliot, 1905) and *Hermaea oliviae* (MacFarland, 1966), the aplysiids *Aplysia californica* J. G. Cooper, 1863 and *A. vaccaria* Winkler, 1955, and the cephalaspidean *Diaphana californica* Dall, 1919.

At Hazard Canyon we obtained images of 55 of the 63 total species of heterobranchs (see https://www.inaturalist.org/observations/jeffgoddard). Images of five of the remaining species (*Acanthodoris hudsoni* MacFarland, 1905; *Aldisa sanguinea* (Cooper, 1863); *Antiopella fusca*; *Aplysiopsis enteromorphae* (Eliot, 1905); and *Hallaxa chani* Gosliner and Williams, 1975) have been obtained by other observers at Hazard Canyon and can be found on iNaturalist. *Aplysia vaccaria* Winckler, 1955 and *Eubranchus olivaceus* (O'Donoghue, 1922) from San Luis Obispo County, but not Hazard Canyon, have been pictured on iNaturalist, leaving (as of September 2022) only *Zelentia fulgens* (MacFarland, 1966) without an observation from the County on iNaturalist (observations of this species exist from neighboring Monterey and Santa Barbara Counties [e.g., iNaturalist 5162389, 40531968]).

The dorid nudibranchs *Diaulula sandiegensis* (J. G. Cooper, 1863), *Okenia rosacea*, *Rostanga pulchra* MacFarland, 1966, and *Triopha catalinae* (J. G. Cooper, 1863) occurred at greater than 90% frequency at Hazard Canyon, and *O. rosacea*, was also the most abundant heterobranch we observed (Table 1). *Okenia rosacea* and the nudibranchs *Dendronotus subramosus* MacFarland, 1966, *Triopha maculata* MacFarland, 1905, *Diaphoreolis lagunae* (O'Donoghue, 1926), *Hermissenda opalescens*, and *Dendronotus venustus* MacFarland, 1966 accounted for 3065, or 52%, of the total number of individuals we recorded. At the opposite extreme, 12 species were represented by only single specimens (Table 1). Only 50 total individuals of non-nudipleurans were found in this study, accounting for less than 1% of the 5919 individuals of heterobranchs recorded.

In addition to the 63 species we found during the present study, other observers have recorded

TABLE 1. Heterobranch sea slugs from Hazard Canyon Reef, 1999–2021. Species listed by frequency of occurrence, which was calculated from number of months found out of 47 total months sampled.



Species	**Total No. Inds.**	**Freq. Occur. (%)**	**Geog. Range**
Diaulula sandiegensis	133	93.6	W
Okenia rosacea	1097	91.5	S
Rostanga pulchra	310	91.5	W
Triopha catalinae	298	91.5	W
Triopha maculata	345	83.0	S
Peltodoris nobilis	257	80.9	N
Doriopsilla albopunctata	223*	78.6	S
Coryphella cf. *trilineata*[1]	214	74.5	S
Doriopsilla fulva	205*	74.3	S
Doris montereyensis	131	72.3	N
Cadlina modesta	100	72.3	N
Hermissenda opalescens	317*	67.0	S
Dendronotus subramosus	674	48.9	N
Diaphoreolis lagunae	320	48.9	S
Dendronotus albus	133	46.8	N
Dirona picta	98	44.7	S
Ancula pacifica	71	44.7	S
Dendronotus venustus	312	40.4	W
Geitodoris heathi	110	36.2	N
Aeolidia loui	24	36.2	S
Phidiana hiltoni	56	34.0	S
Tritonia festiva	23	31.9	N
Doto amyra	65	29.8	N
Eubranchus rustyus	37	29.8	W
Acanthodoris rhodoceras	25	25.5	S
Doto columbiana	68	23.4	N
Cadlina cf. *sparsa*[2]	21	23.4	S
Cadlina luteomarginata	21	21.3	N
Diaphoreolis flavovulta	20	21.3	N
Hancockia californica	20	19.1	S
Diaphorodoris lirulatocauda	11	19.1	W
Hermissenda crassicornis	13*	15.7	N
Acanthodoris lutea	9	14.9	S
Aegires albopunctatus	9	14.9	W
Anteaeolidiella oliviae	8	14.9	S
Limacia mcdonaldi	15*	12.8	S
Diaphana californica	10	12.8	W
Doto kya	16	10.6	N
Aldisa sanguinea	7	10.6	W
Limacia cockerelli	9*	8.5	N
Trinchesia albocrusta	4	8.5	W
Aplysiopsis enteromorphae	16	6.4	W
Cuthona divae	5	6.4	N
Flabellinopsis iodinea	5	6.4	S
Catriona columbiana	4	6.4	N
Doto form A of Goddard (1996)	4	6.4	S
Berthella strongi	3	6.4	S
Aplysia californica	22	4.3	S
Hallaxa chani	4	4.3	N

(Continued on next page)

TABLE 1 (continued). Heterobranch sea slugs from Hazard Canyon Reef, 1999–2021. Species listed by frequency of occurrence, which was calculated from number of months found out of 47 total months sampled.

Polycera atra	3	4.3	S
Zelentia fulgens	2	2.1	N
Acanthodoris hudsoni	1	2.1	N
Acanthodoris nanaimoensis	1	2.1	N
Antiopella fusca	1	2.1	N
Aplysia vaccaria	1	2.1	S
Cadlina flavomaculata	1	2.1	S
Corambe steinbergae	1	2.1	W
Doriopsilla gemela	1	2.1	S
Eubranchus cf. *rupium*[3]	1	2.1	N
Hermaea oliviae	1	2.1	N
Janolus anulatus	1	2.1	S
Atalodoris jannae	1	2.1	N
Coryphella cooperi	1	2.1	S
Total No. Inds.	5919		

1 Has orange-tipped rhinophores and oral tentacles (see Behrens et al. 2022, p. 124).
2 See Behrens et al. (2022, p. 89).
3 See Behrens et al. (2022, p. 131).
* Estimates based on data collected after published delineations of species (see Methods).

Table 2. Species of heterobranch sea slugs not observed in the present study, but found by other observers intertidally at Hazard Canyon Reef (or within 400 m of the reef), or subtidally from the area between Spooner's Cove, Montana de Oro State Park and the vicinity of Point Buchon.

Species	Habitat	Date	Source
Baptodoris mimetica	Intertidal	11 Aug 2014	iNaturalist 839987
Corambe pacifica	Intertidal	12 Aug 2014	iNaturalist 829614
Corambe pacifica	Intertidal	12 Aug 2014	iNaturalist 1113720
Corambe pacifica	Intertidal	31 Oct 2020	iNaturalist 63938683
Okenia angelensis	Intertidal	1 Nov 1971	Roller (1971)
Trapania velox	Intertidal	28 Jan 1968	Roller (1968), Roller and Long (1969)
Antiopella barbarensis	Intertidal	11 Aug 2014	iNaturalist 1104438
Melibe leonina	Intertidal	11 Aug 2014	iNaturalist 1104466
Cuthonella cocoachroma	Intertidal	17 May 2014	iNaturalist 684973
Rictaxis punctocaelatus	Subtidal	21 Aug 2019	iNaturalist 90096895, 84371738
Berthella chacei	Subtidal	11 Aug 2011	iNaturalist 66581258
Crimora coneja	Subtidal	3 Jun 2011	Goddard and Hoover 2011; iNaturalist 66586125
Felimare porterae	Subtidal	3 Sept 2020	iNaturalist 90079641
Babakina festiva	Subtidal	12 Aug 2020	iNaturalist 90054706

seven more species, all nudibranchs, intertidally at Hazard Canyon (Table 2). An additional five species of heterobranchs have been observed subtidally in the vicinity of Montaña de Oro State Park and Point Buchon (Table 2).

Seasonality and egg-laying

We found the highest number of species per month in spring and summer (22.1 and 21.3 species, respectively) and lowest in fall and winter (12.3 and 14.9, respectively; Fig. 3A). The highest number of species we recorded in single months from each season was 26 species in January 2018, 35 in May 2016 (total from two trips that month), 27 in July 2016, and 24 in December 2008. The most species we recorded on single trips to Hazard Canyon was 30 in May 2009 and 30 again in May 2014. On average, we found the most species of heterobranchs in May (mean = 25.2, n = 12), followed by July (mean = 21.3, n = 3), June (mean = 21.0, n = 2), and April (Mean = 17.1, n = 7).

The number of individuals of heterobranchs at Hazard Canyon we found each season ranged from 40.1 inds. hr^{-1} observer^{-1} in summer to 52.9 inds. hr^{-1} observer^{-1} in spring (Fig. 3B), with a grand mean of 48.0 inds. hr^{-1} observer^{-1} (n = 4 seasons).

Ten of the 15 most abundant species in this study exhibited seasonal changes in abundance and fell into two groups: those tending to peak in spring or summer (Fig. 4A–E), and those tending to peak in winter or fall and winter (Fig. 4F–J). Of the other 15 most abundant species not included in Fig. 4, *Dendronotus albus* MacFarland, 1966 exhibited seasonal variation in abundance very similar to that of its congeners shown in Fig. 4A and 4D;

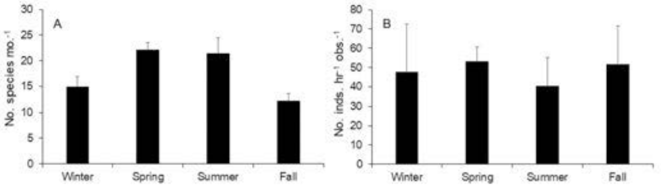


FIGURE 3. Seasonal variation at Hazard Canyon Reef in (A) number of species of Heterobranchia found per month, and (B) total number of individuals of Heterobranchia found per observer per hour. Values shown are means ± 1 SE of monthly data averaged by season across all years sampled (n = 8, 21, 3, 15 for winter, spring, summer, fall, respectively)..

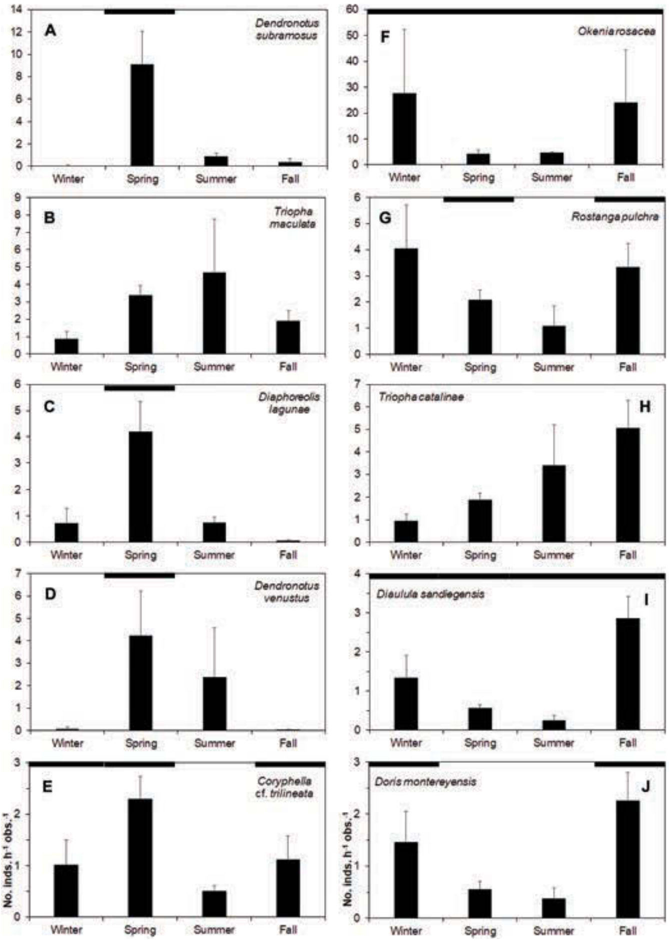


FIGURE 4. Seasonal variation in abundance and egg-laying activity of 10 of the 15 most abundant heterobranchs at Hazard Canyon Reef, 1999–2021. Values shown are means ± 1 SE of monthly number of individuals per hour per observer (n = 8, 21, 3, 15 for winter, spring, summer, fall, respectively). Black bars at top of graphs indicate egg masses were observed at least once in a given season.

Peltodoris nobilis (MacFarland, 1905) showed little seasonal variation, fluctuating between 1.4 and 2.5 inds. h^{-1} observer^{-1}; and three species (*Doriopsilla albopunctata*, *Doriopsilla fulva* (MacFarland, 1905), and *Hermissenda opalescens*) were not included because until about 2014 we had recorded each under previously accepted names, which recent systematic revisions showed to be complexes of species overlapping in distribution at Hazard Canyon (see Methods).

We observed egg masses of *Okenia rosacea* and *Diaulula sandiegensis* every season (Fig. 4F and I), and did not find any eggs laid by *Triopha maculata* and *T. catalinae* (Fig. 4B, and H). Egg masses of *Dendronotus subramosus*, *Dendronotus venustus*, and *Diaphoreolis lagunae* were only found in the spring (Fig. 4A, C, and D), as were those of *Dendronotus albus* (not shown). Of the remaining 15 most abundant species in this study, we found egg masses laid by *Coryphella trilineata* O'Donoghue, 1921, *Rostanga pulchra*, *Doris montereyensis* (J. G. Cooper, 1863) (Fig. 4 E, G, and J), and (not shown) *Hermissenda opalescens* in spring and summer, *Peltodoris nobilis* in spring and fall, and *Doriopsilla albopunctata* s.l. in November 2000 and November 2003, prior to the delineation of the *Doriopsilla albopunctata* by Hoover et al. (2015).

Interannual variability

The proportion of northern species exceeded that of southern species at Hazard Canyon in 2006–08 and 2011–12 (and slightly in 2000 and 2014), while the reverse was true in 2003–05, 2009–10, and 2015-21, roughly coincident with fluctuations in the El Niño Southern Oscillation as measured by the yearly mean MEI (Fig. 5).

During the marine heat waves of 2014–16 in the NE Pacific, three of the most abundant and conspicuous northern species of nudibranchs at Hazard Canyon declined in abundance and then remained at low numbers through 2021 (Figure 6A). At the same time, the three most abundant taxa of southern nudibranchs increased in abundance (*Okenia rosacea* markedly so), but then following the heat waves returned to roughly pre-2013 abundances (Figure 6B). The northern species *Cadlina luteomarginata* MacFarland, 1966 and the southern species *Cadlina* cf. *sparsa* (Odhner, 1922) were not

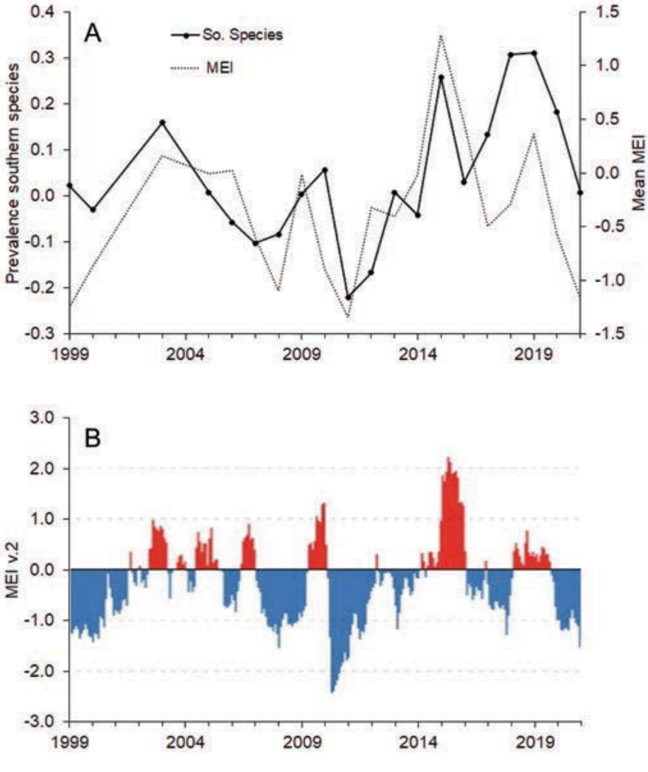


FIGURE 5. (A) Change in relative prevalence of southern species of heterobranchs at Hazard Canyon Reef, with yearly mean of the Multivariate ENSO Index, v.2 (MEI), 1999–2021. Relative prevalence of southern species calculated as the proportion of southern species found each year out of the total number of southern species (n = 23) found throughout the entire study, minus the same proportion calculated each year for northern species (also n = 23). (B) Bimonthly values of the MEI. Positive values are shown in red, clusters of which indicate El Niño events of differing strength, and negatives values in blue, indicating La Niña events of varying strength. Values between 0.5 and –0.5 are considered ENSO neutral.

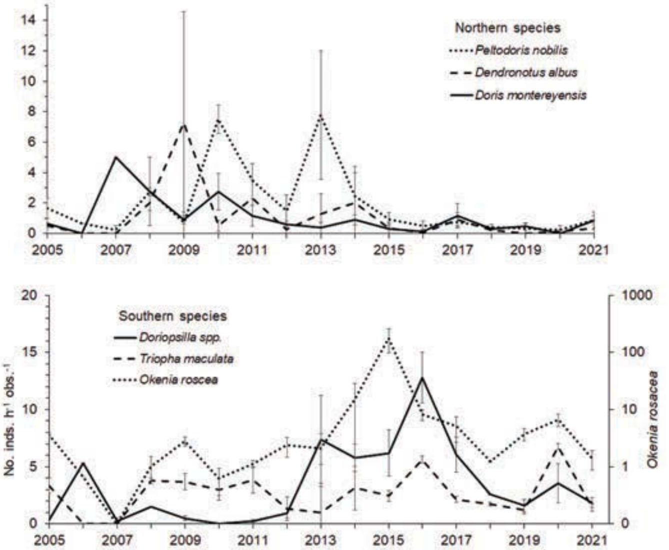


FIGURE 6. Yearly change in abundance of the most abundant nudibranchs at Hazard Canyon, 2005–2021. (A) three northern species, and (B) three southern taxa. Values shown are yearly means +- 1 SE of monthly number of individuals per hour per observer; note separate, logarithmic axis in (B) for *Okenia rosacea*. In (B) *Doriopsilla* spp. = *D. albopunctata* and *D. fulva*, which combined were considered *D. albopunctata* until delineated by Hoover et al. (2015).

included in Figure 6, owing to their lesser total abundances at Hazard Canyon, but were noteworthy for their temporal shifts in occurrence. In 37% of 27 months sampled from 1999 through 2013, we found 21 total *C. luteomarginata*. During the next 20 months of our study, we found none. We found *C.* cf. *sparsa* at Hazard Canyon for the first time in 2011, none in 2012, and then 19 total in 41% of 22 months sampled from 2013 through 2021.

DISCUSSION

We observed 63 species of heterobranch sea slugs at Hazard Canyon, 57 of which were nudibranchs (Table 1). Including *Trapania velox* (Cockerell, 1901) and *Okenia angelensis* Lance, 1966, reported from Hazard Canyon by Roller and Long (1969) and Roller (1971), respectively, 59 species of nudibranchs have now been documented in the literature from Hazard Canyon Reef. We tallied the total number of nudibranch species reported in the literature from other sites known for their nudibranch species richness in the Oregon Biogeographic Province (Appendix). Only Pillar Point, 283 km to the northwest in San Mateo County, with 56 species, comes close to the total known from Hazard Canyon. The high species richness of nudibranchs at Hazard Canyon likely stems from its topographical complexity, as well as its closer proximity to the Southern California Bight (SCB) and northern boundary of the California Biogeographic Province in the vicinity of the Palos Verdes Peninsula (Briggs and Bowen 2012).

Roller and Long's (1969) record of *Trapania velox* from Hazard Canyon is noteworthy, as it remains the only intertidal record of this species north of Point Conception and the SCB. They observed it in January 1968, nearly two years removed from the 1965–66 El Niño, suggesting that if it did not originate from the SCB, it may have recruited from nearby subtidal populations, two of which were actually discovered later inside Morro Bay and Port San Luis (see McDonald 1983; Behrens 2004). Roller (1968) noted finding the nudibranch "on gray sponge," which we think was likely *Spheciospongia confoederata* Laubenfels, 1930, a massive sponge we observed at Hazard Canyon and periodically checked for the presence of *T. velox*.

Marine heatwaves, including El Niño events, had profound effects on the species composition and abundance of nudibranchs and allies at Hazard Canyon (Figures 5 and 6). The two most abundant species observed in our study, the southern *Okenia rosacea* and the northern *Dendronotus subramosus*, illustrate this further. More than 75% of the total *O. rosacea* we recorded in this study were observed during the marine heatwaves of 2014–16. In contrast, only 2.1% of the *D. subramosus* were observed during this same period. Additionally, December 2013–16 was the only period during our entire study that we found the aeolid nudibranch *Flabellinopsis iodinea* and the sea hare *Aplysia californica*. Both are southern species that only occur episodically in the intertidal north of Point Conception, usually during warm-water periods (Goddard et al. 2016).

We found *Janolus anulatus* at Hazard Canyon in June 2019, near the end of the weak 2018–19 El Niño (see Figure 5B). This surprised us, as we had not found it during the warm-water anomaly of 2014 nor the very strong 2015–16 El Niño, both of which drove northward shifts in the distribution and abundance of many heterobranchs and other marine taxa in California (Cavole et al. 2016; Goddard et al. 2016, 2018, present study; Sanford et al., 2019; Lonhart et al. 2019). However, other notable nudibranch range extensions were recorded in the region in 2018–19, indicating advection of larvae or juveniles from the south. These included *Cuthona hamanni* Behrens, 1987 from San Diego to Anacapa Island in December 2018 (iNaturalist 21516059), *Doriopsilla rowena* Er. Marcus and Ev. Marcus, 1967 from San Diego to Anacapa Island in August 2019 (iNaturalist 30371388), *Cerberilla pungoarena* Collier and Farmer, 1964 from San Diego to southern Ventura County in April 2018 (iNaturalist 38638344) and then to Morro Bay in November 2019 (iNaturalist 36088852), and in July 2019 *Crimora coneja* Er. Marcus, 1961 at Anacapa Island (iNaturalist 29593119), the first observation of this species in California since numerous observations associated with the 2014–16 marine heatwaves (Goddard et al. 2016; and see *https://www.inaturalist.org/observations?taxon_id=50057*). 2019 was also the only year we have noticed a population boom of the Gould Beanclam *Donax gouldii* Dall, 1921 at Tar Pits Reef, Carpinteria (iNaturalist 30073485), one of our other long-term nudibranch study sites (Goddard et al. 2021). The arrival of these species, and their persistence in the region since - despite La Niña conditions the past few years (see Figure 5B) - is similar to what we observed with *Cadlina* cf. *sparsa* starting a few years earlier at Hazard Canyon (see Results on Interannual Variability) and suggests underlying changes in coastal oceanographic processes are in progress in the SCB.

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APPENDIX

Number of nudibranch species from intertidal sites in the Oregon Biogeographic Province. Numbers based on published studies, to which we have added, where geographically appropriate, members of species complexes in the region delineated since 2015 (see Methods). To standardize comparison between sites, we have not included species documented solely on the web platform iNaturalist (e.g., Table 2).

Site	Geographic Coordinates	No. Species	Sources
Kayostla Beach, WA	48.0321°, -124.6855°	38	Goddard et al. (1997)
Cape Arago, OR	43.3026°, -124.4007°	51	Goddard (1984, 1990, 1997), Goddard et al. (2018)
Abalone Beach, CA	41.1225°, -124.1558°	40	Jaeckle (1984)
Duxbury Reef, CA	37.8894°, -122.6995°	51	Gosliner and Williams (1970, 1973), Gosliner (1990), Goddard et al. (2011), Goddard et al. 2018)
Pillar Point, CA	37.4938°, -122.4994°	56	Bertsch et al. (1972), Schultz et al. (2011)[1]
Scott Creek, CA	37.0455°, -122.2380°	51	Schultz et al. (2011)
Asilomar, CA	36.6282°, -121.9421°	53	Nybakken (1974, 1978), Schultz et al. (2011)
Hazard Canyon, CA	35.2897°, -120.8840°	59	Roller and Long (1969), Roller (1970), Present study
Naples Point, CA	34.4320°, -119.9493°	48	Goddard et al. (2020)
Tar Pits Reef, CA	34.3869°, -119.5165°	45	Goddard et al. (2021)

[1] Schultz et al. (2011) analyzed data on 45 species of nudibranchs found by William Pence and Douglas Mason during 78 timed counts of nudibranchs at Pillar Point from 1988 to 1995. Pence and Mason's original data included an additional 25 untimed sampling trips during which an additional 7 species of nudibranchs were found, which we have added here.

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