PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Series 4, Volume 67, No. 20, pp. 451–491, 23 figs. February 15, 2023

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.

David H. Kavanaugh [1], Mollie Cueva-Dabkoski [2,3] and Hongbin Liang [4]

[1] *Department of Entomology, California Academy of Sciences, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA 94118.* [2] *Student Science Fellow, California Academy of Sciences, San Francisco, and* [3] *2355 Pearl Street, Santa Monica, CA 90405.* [4] *Key Laboratory of Zoological Systematics, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China. Corresponding author*: *David H. Kavanaugh* (*dkavanaugh@calacademy.org*)

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).

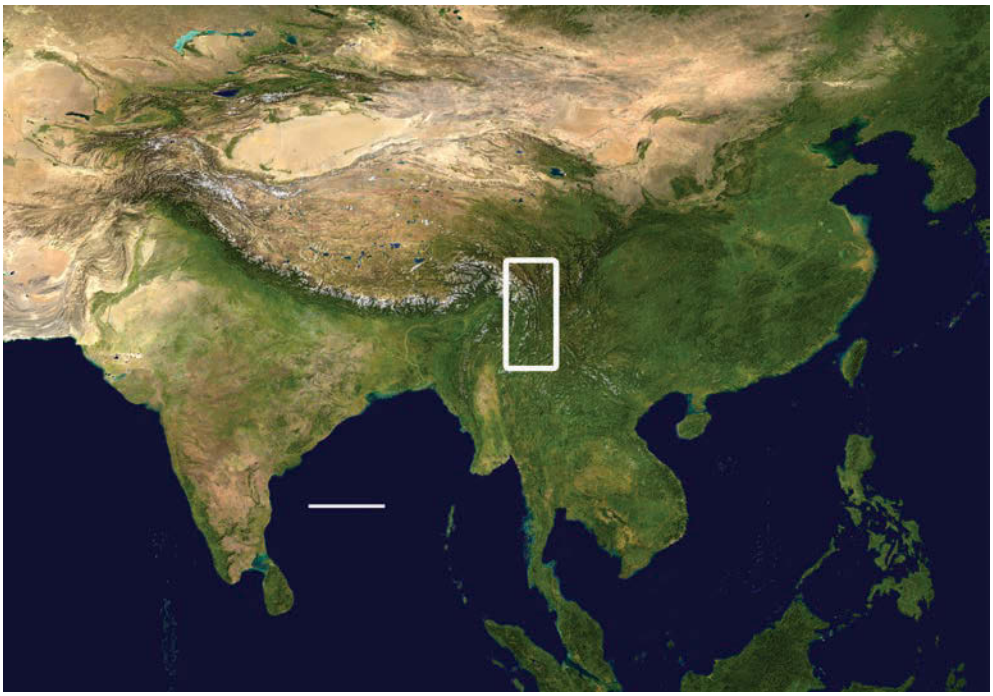


FIGURE 1. Map of Asia with study region outlined. Modified from Wikimedia Commons, World Atlas of the World, at URL: *http://upload.wikimedia.org/wikipedia/commons/8/8f/Whole_world_-_land_and_oceans_12000.jpg.* Scale line = 500 km.

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

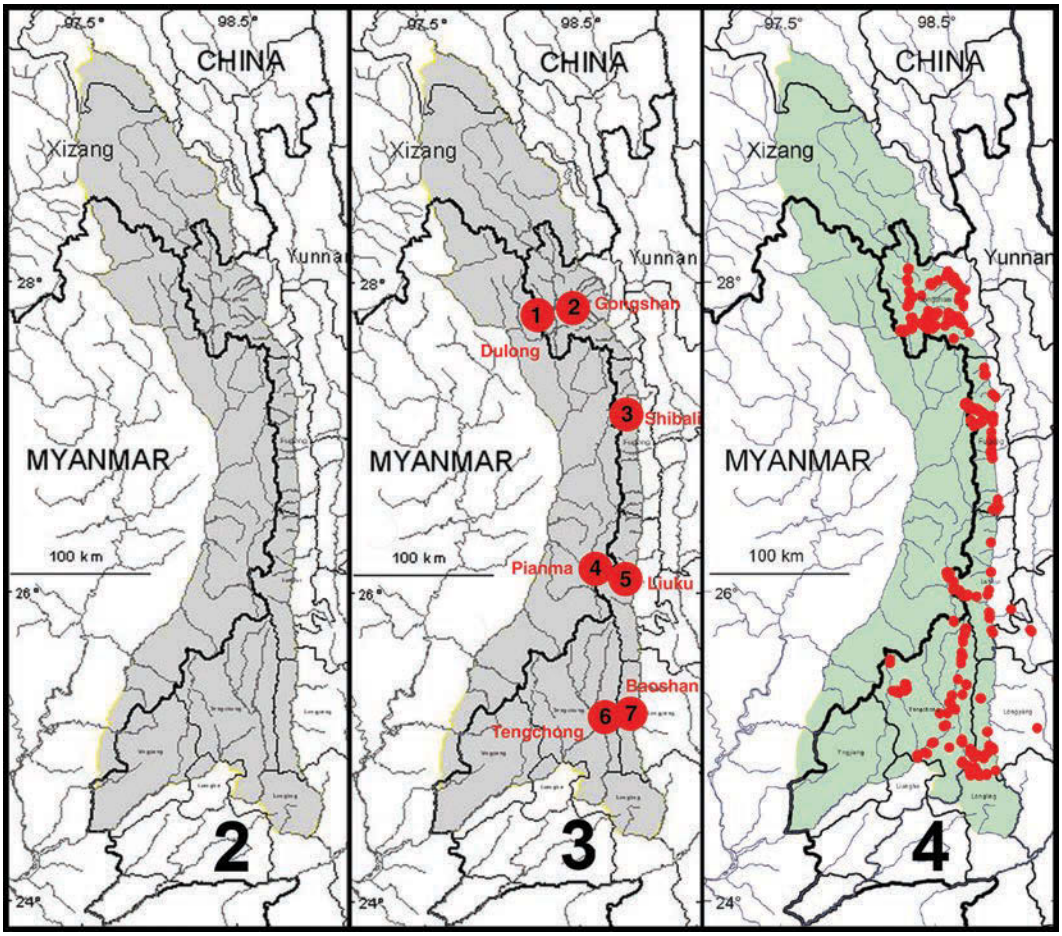
The natural physiographic limits of the study area for the project are as shown in Fig. 2 and include areas in eastern Myanmar and southern Xizang (Tibet); but we had permission to survey only those parts in Yunnan Province. Specialists for all taxonomic groups concentrated their efforts on seven core 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.

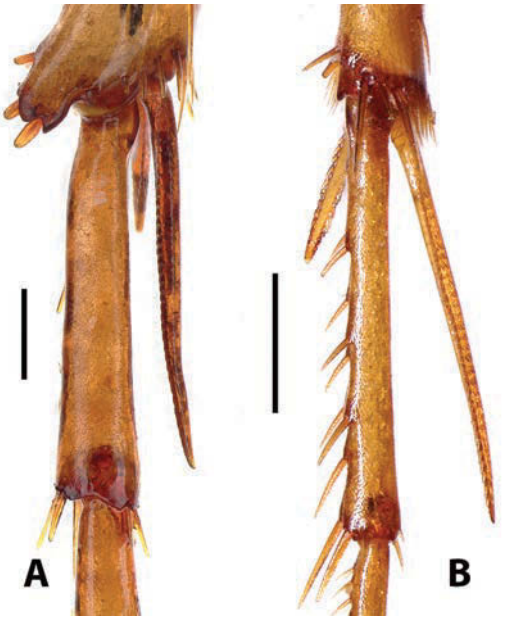


FIGURE 5. Left hind tibial medial spur and tarsomere 1, dorsal aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus elegans* Andrewes (CASENT1039499, Longchuan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

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.

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

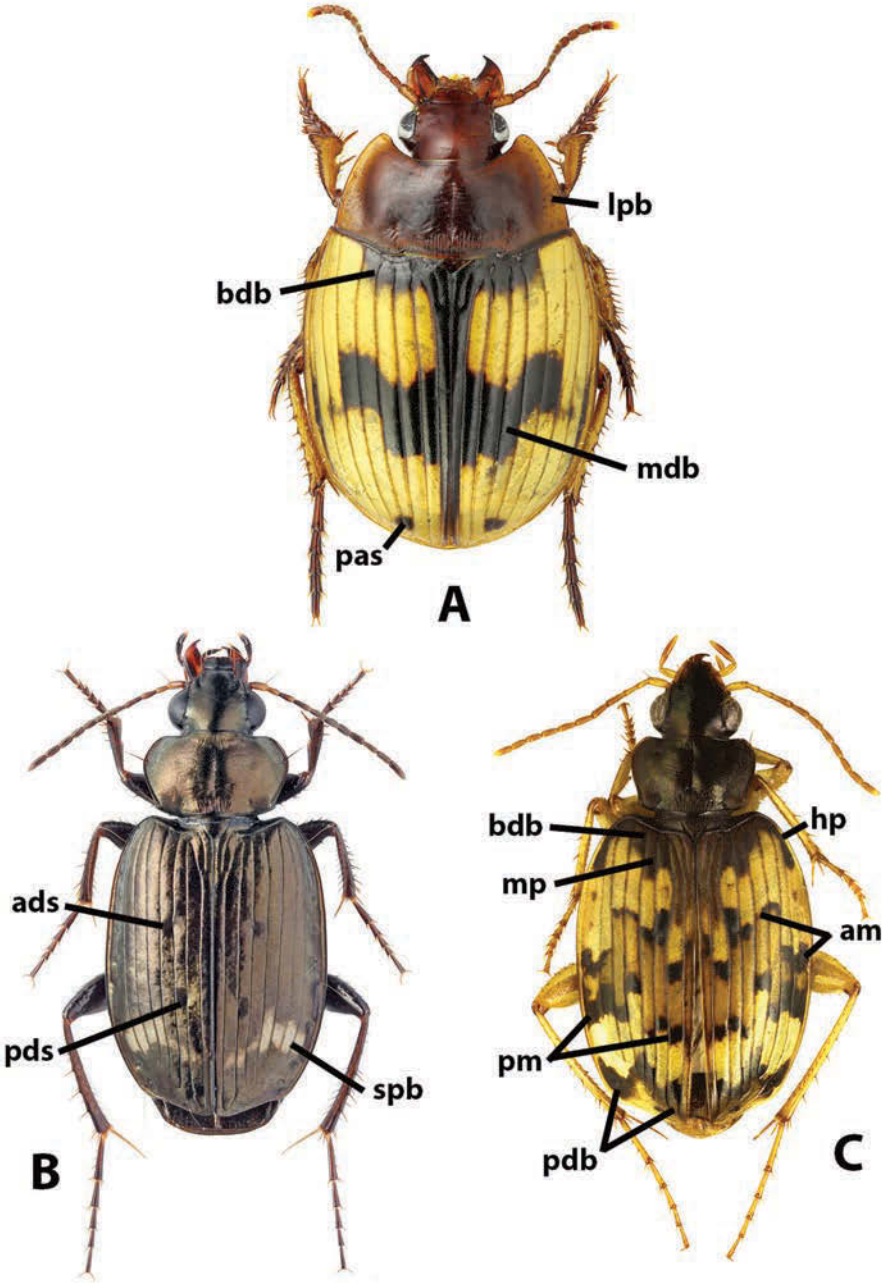


FIGURE 6. Illustration of terms used for describing color patterns in *Cyclosomus* and *Tetragonoderus* species. A. *Cyclosomus flexuosus* (Fabricius) (Kosi River valley, 5 km N Ramnagar, Uttarakhand, India; copyright © Alexander Anichtchenko); B. *Tetragonoderus intermedius* Solsky (8 km NE of the city 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.

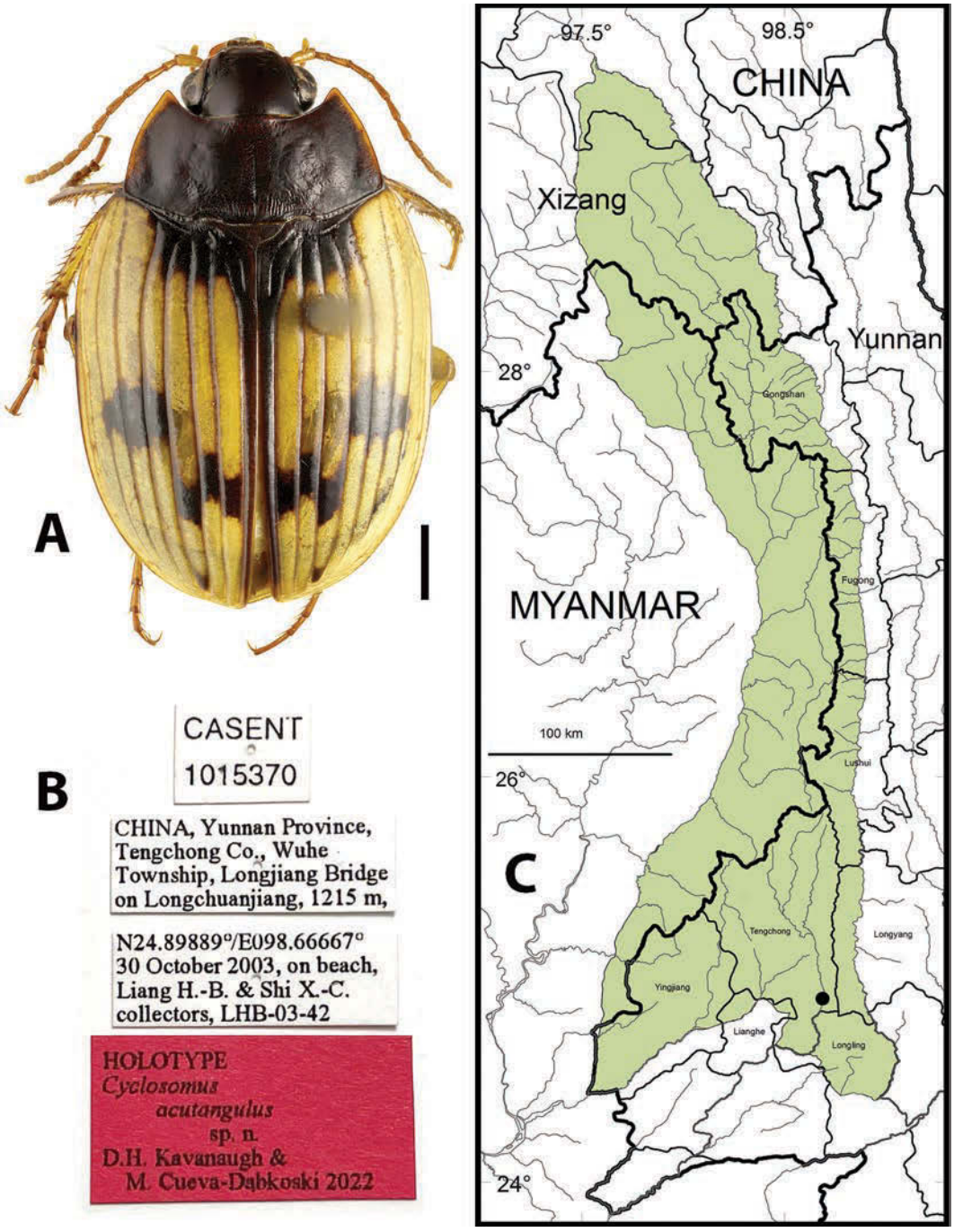


FIGURE 7. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. A. Holotype, dorsal aspect, scale line = 1.0 mm (CASENT 1015370, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. Labels associated with holotype; C. Map showing locality record (black circle)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

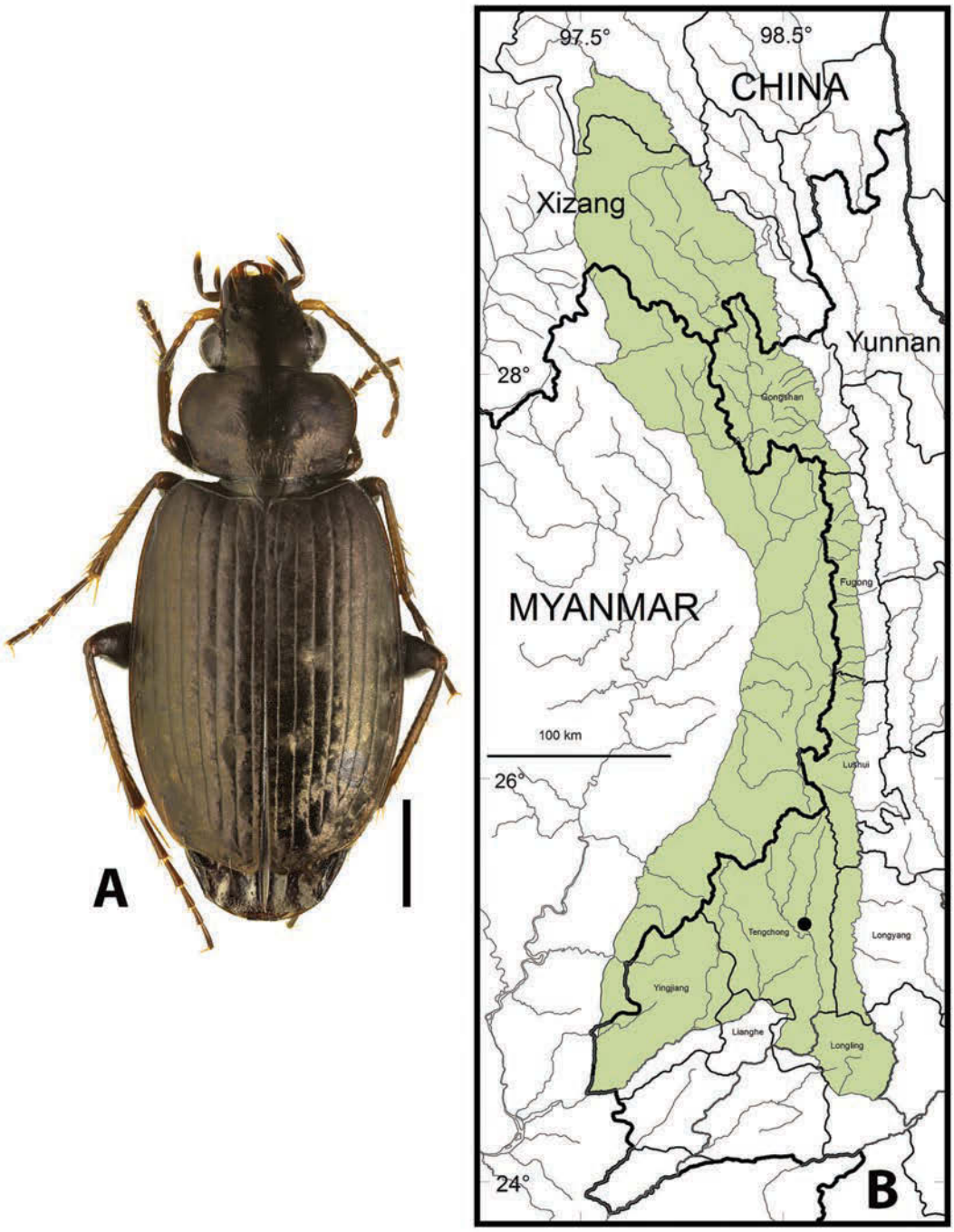


FIGURE 9. *Tetragonoderus arcuatus* (Dejean). A. Dorsal aspect, scale line = 1.0 mm (CASENT1013512, Xiaojiangqiao, Qushi Township, Tengchong County, Yunnan, China); B. Map showing locality record (black circle) for this species in the Gaoligong Shan region, scale line = 100 km.

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.

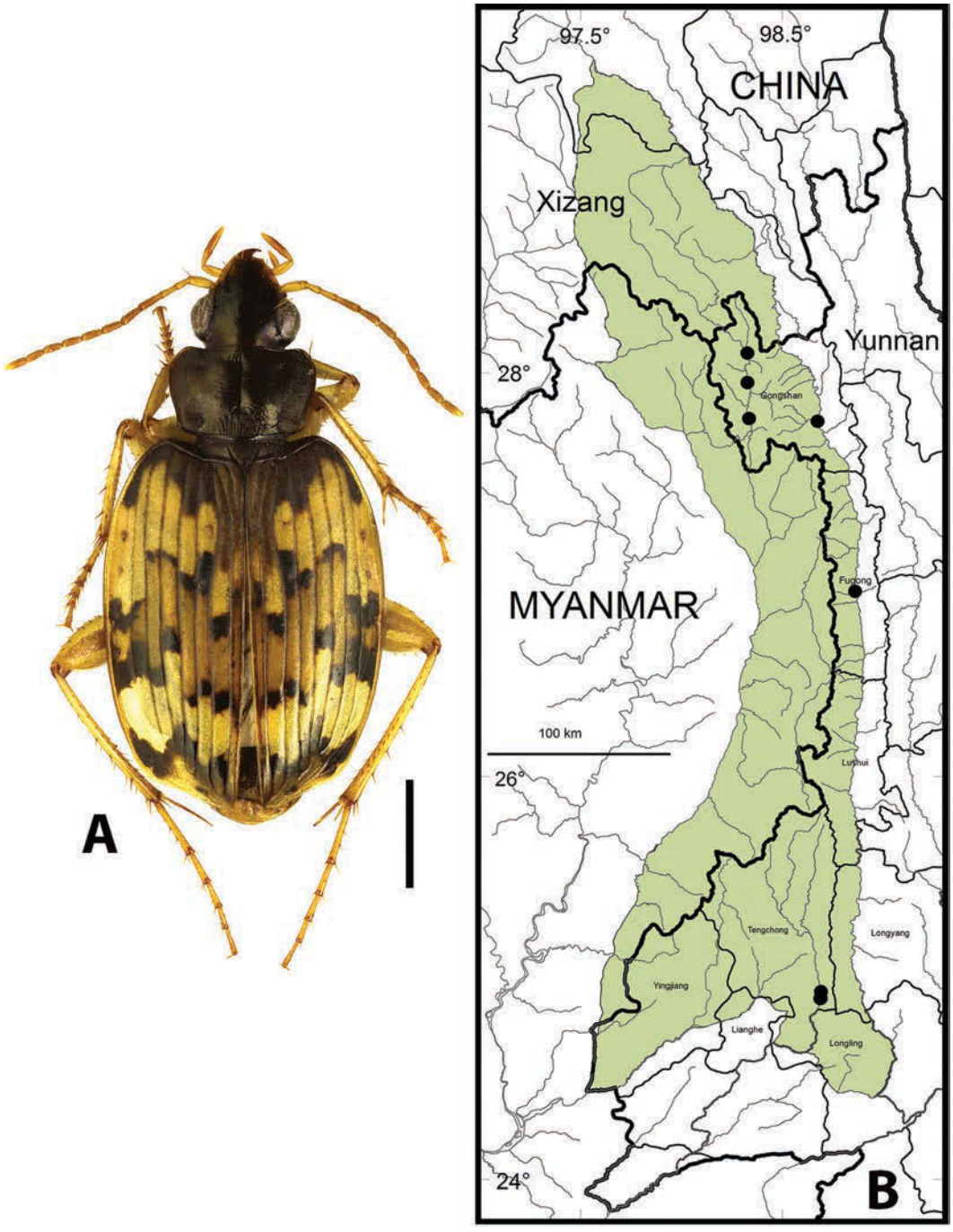


FIGURE 10. *Tetragonoderus elegans* Andrewes. A. Dorsal aspect, scale line = 1.0 mm (CASENT1039409, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); B. Map showing locality records (black circles) for this species in the Gaoligong Shan region, scale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

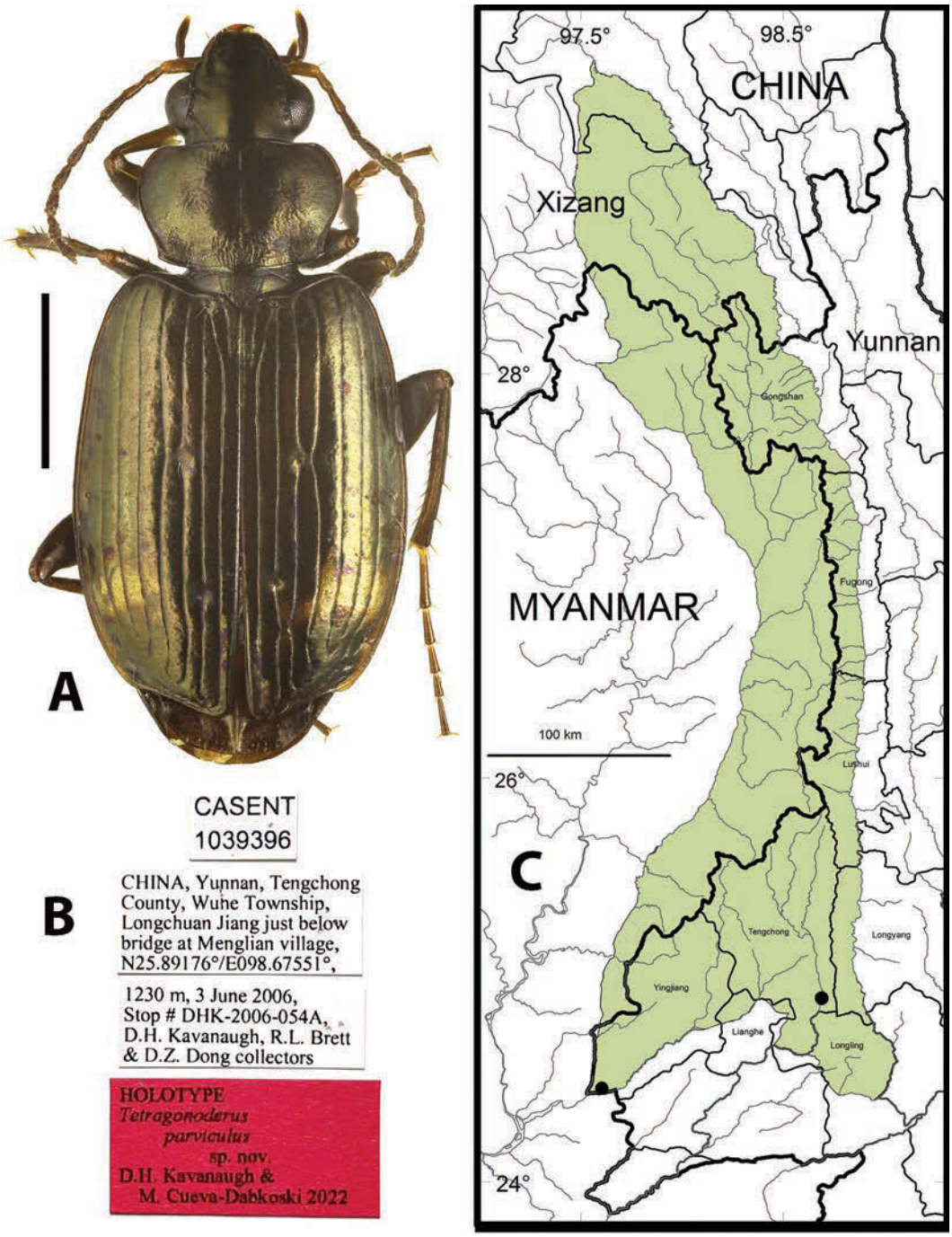


FIGURE 11. *Tetragonoderus parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov. A. Holotype, dorsal aspect, scale line = 1.0 mm (CASENT1039396, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); B. Labels associated with holotype; C. Map showing locality 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,

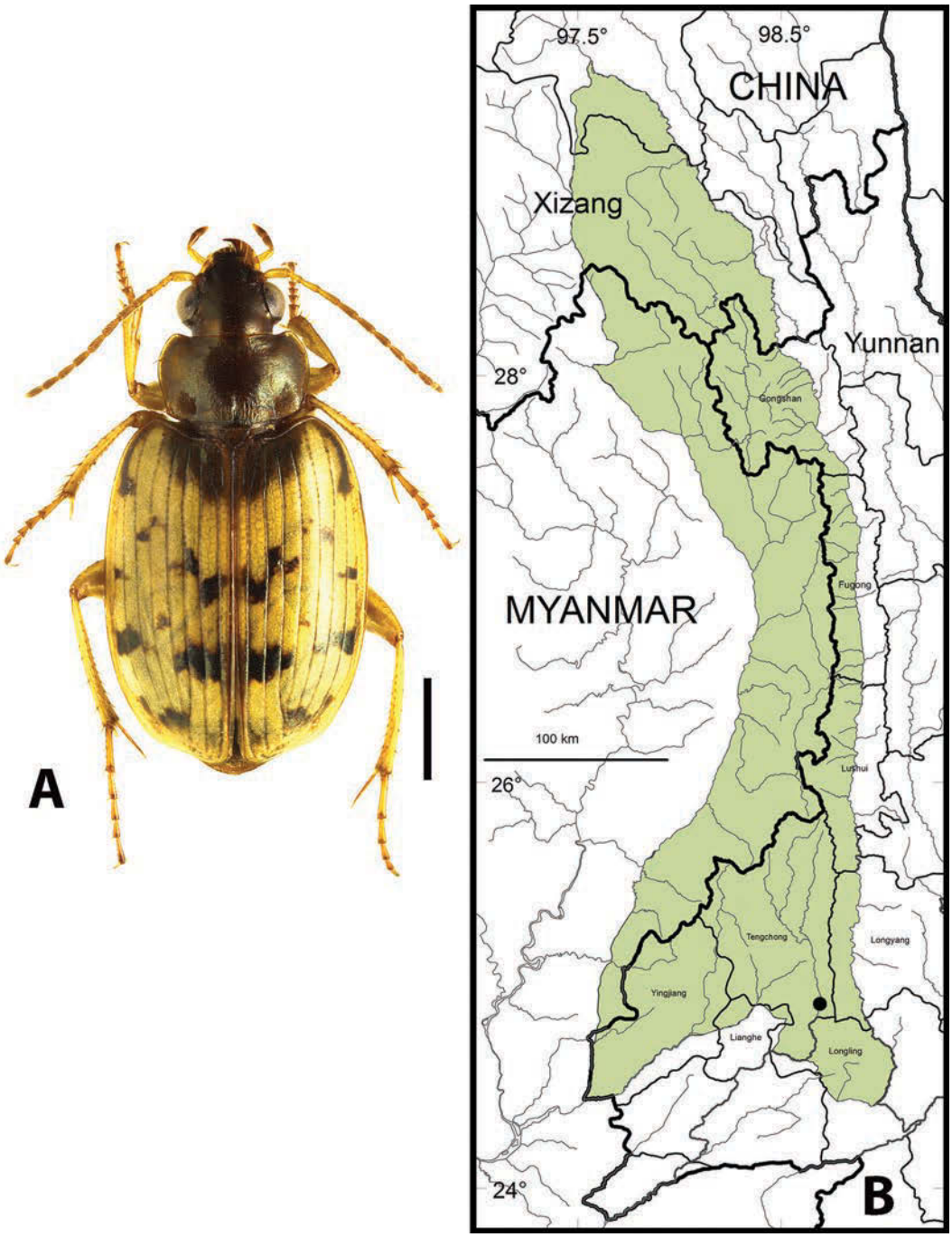


FIGURE 12. *Tetragonoderus punctatus* (Wiedemann). A. Dorsal aspect, scale line = 1.0 mm (CASENT1039412, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); B. Map showing locality record (black circle) for this species in the Gaoligong Shan region,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

Acknowledgements

We thank our home institutions, the California Academy of Sciences (CAS) and the Institute of Zoology (IOZ), for ongoing support of our research programs, and, especially, donors to the Student Science Fellows Program at CAS. The Kunming Institutes of Botany and Zoology provided organization and logistical support for all our expeditions. The Yunnan Provincial Division of Forestry and Baoshan-Gaoligong and Nujiang Prefecture Forest Reserves granted access and collecting permits for our work in the reserves, and staffs of these institutions assisted with collecting and other efforts in these areas. Support for our fieldwork was provided through Grant No. DEB-0103795 from the National Science Foundation (Biotic Surveys and Inventories Program), Grant No. 31970400 to LHB from the National Natural Science Foundation of China (NSFC), grants from the National Geographic Society and the John D. and Catherine T. MacArthur Foundation, and private donations to the China Natural History Project at CAS. We also thank Rachel Diaz-Bastin, Lisa Bhattacharyya, Roberta Brett, Seth Cotterell, Rebecca Morin, and Diane Sands of CAS for logistical, library, or technical assistance with this project. Crucial support for this project was provided by curators of institutional collections who facilitated loans of type and other specimens for this study or provided images of specimens in their care, namely Alexander Anichtchenko (Daugavpils, Latvia), Michael Balke (ZMS), George Ball (University of Alberta, Edmonton, Canada), Terry Erwin (NMNH), Beulah Garner and Max Barclay (NHMUK), Jiri Hájek (NMPC), Matthias Hartmann (Naturkundemuseum Erfurt, Germany), Bernd Jaeger (ZMBH), Olaf Jäger (SMTD), Kiril Makarov and Alexey Gusakov (ZMMU), Toshihara Mita and Sadahisa Yagi (KUEC), Nikolay Nikitsky (ZMMU), Joachim Schmidt (University of Rostock, Germany), Alexey Solodovnikov and Sree Gayathree Selvantharan (ZMUC), Azadeh Taghavian and Thierry Deuve (MNHN), Ming-yi Tian (SCAU), Manfred Uhlig (ZMHB), and Oscar Vorst (RMNH). Special thanks are due to D. Logunov (Manchester Museum, Great Britain), who was able to forward type material from ZMMU to us for study, and Seiji Morita for his help in locating type specimens in collections in Japan.

Copies of important publications were provided by Alexander Anichtchenko, Thierry Deuve (MNHN), Boris Kataev (ZIN), David Maddison (Oregon State University, Corvallis), Wendy Moore (University of Arizona, Tucson), and Kipling Will (University of California, Berkeley); and translations of critical sections of certain descriptions from the literature were provided by Thierry Deuve and Henri Goulet (Ottawa, Ontario, Canada) from French and Francisco Hita Garcia (CAS) and Joachim Schmidt from German. Finally, the second author sends special thanks to other participants in the Student Science Fellow Program at CAS, Rachel Liu and Logan Kahle, for their comradeship and enthusiasm.

References

Akciz, S., B.C. Burchfiel, J.L. Crowley, J.Y. Yin, and L.Z. Chen. 2008. Geometry, kinematics, and regional significance of the Chong Shan shear zone, Eastern Himalayan Syntaxis, Yunnan, China. *Geosphere* 4:292–314.

Alluaud, C. 1897. Coléoptères recueillis à Majunga (Madagascar) par M. Bastard. *Bulletin du Muséum d'Histoire Naturelle* 1896:371–376.

Andrewes, H.E. 1921. Notes on synonymy and some types of Oriental Carabidae in various foreign collections. *Transactions of the Entomological Society of London* 1921:145–195.

Andrewes, H.E. 1924. XXII. On the Oriental Carabidae of the "Reise Novara." *Transactions of the Entomological Society of London* 1923:459–68.

Andrewes, H.E. 1926. A catalogue of Philippine Carabidae. *Philippine Journal of Science* 31:345–361.

ANDREWES, H.E. 1927. Papers on the Oriental Carabidae. XIX. *Annals and Magazine of Natural History* (Ser. 9) 19:97–111.

ANDREWES, H.E. 1930. *Catalogue of Indian Insects. Part 18—Carabidae.* Government of India Publication Branch, Calcutta, xxii + 389 pp.

ANDREWES, H.E. 1931. Papers on Oriental Carabidae. XXV. *Annals and Magazine of Natural History* (Ser. 10) 7:513–528.

ASSMANN, T., E. BOUTAUD, J. BUSE, V. CHIKATUNOV, C. DREES, A.-L.-L. FRIEDMAN, W. HÄRDTLE, K. HOMBURG, T. MARCUS, I. RENAN, AND D.W. WRASE. 2015. The ground beetle tribe Cyclosomini s. l. in Israel (Coleoptera, Carabidae). *Spixiana* 38:49–69.

BALL, G.E., AND Y. BOUSQUET. 2000. Carabidae Latreille, 1810. Pages 32-132 *in* Arnett, R.H., Jr., and M.C. Thomas (editors) *American beetles. Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press, Boca Raton (Florida), xv + 443 pp.

BATES, H.W. 1886. On the geadephagous Coleoptera collected by Mr. George Lewis in Ceylon. *Annals and Magazine of Natural History (Ser. 5)* 17:68-212, 214–221.

BATES, H.W. 1891. List of the Carabidae (ord. Coleoptera) obtained by Père Cardon in Chota-Nagpore. *Annales de la Société entomologique de Belgique* 35:324–340.

BATES, H.W. 1892. Viaggio di Leonardo Fea in Birmania e regioni vicine. *Annali del Museuo Civico di Storia Naturale di Genova* (Serie 2ª) 12:267–428.

BOUSQUET, Y. 2012. Catalogue of Geadephaga (Coleoptera, Adephaga) of America, North of Mexico. *ZooKeys* 245:1–1722.

BOUSQUET, Y. 2017. Tribe Cyclosomini. Pages 498-499 *in* Löbl, I., and D. Löbl (editors) *Catalogue of Palaearctic Coleoptera. Volume 1. Revised and Updated Edition. Archostemata-Myxophaga-Adephaga*. Brill, Leiden, xxxiv + 1143 pp.

CHAPLIN, G. 2006. Physical geography of the Gaoligong Shan area of Southwest China in relation to biodiversity. *Proceedings of the California Academy of Sciences* (Series 4) 56:527–556.

CHAUDOIR, M. 1873. Essai monographique sur le genre *Cymindis* proprement dit. *Berliner Entomologische Zeitschrift* 17:53–120.

CHAUDOIR, M. 1876. Etude monographique des Masoréides, des Tetragonodérides et du genre *Nemotarsus*. *Bulletin de la Société Impériale des Naturalistes de Moscou* 51:1–84.

CSIKI, E. 1932. *Coleopterorum catalogus. Pars 124. Carabidae: Harpalinae VII.* W. Junk, Berlin, pp. 1279–1598.

DEJEAN, P.F.M.A. 1829. *Species général des coléoptères, de la collection de M. le Comte Dejean. Tome quatrième.* Méquignon-Marvis, Paris, vii + 520 pp.

DEUVE, T., D.H. KAVANAUGH AND H.B. LIANG. 2016. Inventory of the Carabid Beetle Fauna of the Gaoligong Mountains, Western Yunnan Province, China: species of the tribe Trechini (Coleoptera: Caraboidea), with descriptions of four new genera, one new subgenus and 19 new species. *Proceedings of the California Academy of Sciences* (Series 4) 63:341–455.

FABRICIUS, J.C. 1775. *Systema entomologica, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus.* Libraria Kortii, Flensburgi et Lipsiae, xxxii + 832 pp.

FABRICIUS, J.C. 1790. Nova insectorum genera. *Skrivter af Naturhistorie-Selskabet* 1:213–228.

FABRICIUS, J.C. 1792. *Entomologia systematica emendate et aucta, secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. Tome I. Pars I.* Proft, Hafniae, xx + 330 pp.

FABRICIUS, J.C. 1801. *Systema eleutheratorum secundum ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus. Tomus I.* Bibliopolii Academici Novi, Kiliae. xxiv + 506 pp.

FAIRMAIRE, L. 1900. Descriptions de coléoptères recueillis par M. H.Perrier de la Bathie à Madagascar. *Bulletin de la Société Entomologique de France* 1900:85–90.

FELIX, R.F.F.L. 2009. Order Coleoptera, family Carabidae. *Arthropod Fauna of the UAE* 2:66–141.

GEOFFROY, E.L. 1762. *Histoire abrégée des insectes qui se trouvent aux environs de Paris; dans laquelle ces animaux sont rangés suivant un ordre méthodique. Tome premier.* Durand, Paris. xxviii + 523 pp. + 10 pls.

GYLLENHAL, L. 1810. *Insecta Suecica. Classis I. Coleoptera sive Eleuterata. Tom. I. Pars II.* Leverentz, Scaris. xx + 660 pp.

HOPE, F.W. 1838. *The coleopterist's manual, part the second, containing the predaceous land and water bee-*

tles of Linnaeus and Fabricius. Henry G. Bohn, London. xvi + 168 pp. + 3 pls.

Jeannel, R. 1949. *Faune de l'empire Français XI. Coléoptères Carabiques de la région Malagache (Troisième partie).* Librairie Larose, Paris, pp.767–1146.

Jedlička, A. 1964. Neue Carabiden aus Indien (Coleoptera-Carabidae). *Entomologische Arbeiten aus dem Museum G. Frey* 15:305–318.

Jedlička, A. 1966. 2. Family Carabidae. Neue Carabiden aus Vietnam und Thailand (Coleoptera-Carabidae). *Memoirs of the Faculty of Education. Kagawa University* (Part II) 140:11–16

Jian, M.L., and M.Y. Tian. 2009. A review of the genus *Tetragonoderus* Dejean (Coleoptera: Carabidae: Cyclosomini) in China. *Journal of the Entomological Research Society* 11:31–38.

Kavanaugh, D.H. 2015. A Review of the genus *Cyclosomus* Latreille (Coleoptera: Carabidae: Cyclosomini) in the Afrotropical Region. *Proceedings of the California Academy of Sciences* (Series 4), 62:267–298.

Kavanaugh, D.H., R.L. Brett and H.B. Liang. 2021. Inventory of the carabid beetle fauna of the Gaoligong Mountains, western Yunnan Province, China: species of the tribe Omophronini (Coleoptera: Carabidae), with a key and review for all species recorded from China. *Proceedings of the California Academy of Sciences* (Series 4) 67:21–54.

Kavanaugh, D.H., F. Hieke, H.B. Liang, and D.Z. Dong. 2014. Inventory of the carabid beetle fauna of the Gaoligong Mountains, western Yunnan Province, China: species of the tribe Zabrini (Coleoptera: Carabidae). *ZooKeys* 407: 55–119.

Kavanaugh, D.H., and H.B. Liang. 2021. Inventory of the carabid beetle fauna of the Gaoligong Mountains, western Yunnan Province, China: species of the tribe Broscini (Coleoptera: Carabidae). *Proceedings of the California Academy of Sciences* (Series 4) 67:85–182.

Laporte, F.L.N. de 1834. *Etudes entomologiques, ou descriptions d'insectes nouveaux: et observations sur leur synonymie.* Méquignon-Marvis Père et Fils, Paris, 94 pp. + 2 pls.

Latreille, P.A. 1802. *Histoire naturelle, générale et particuliere des crustacés et des insectes. Ouvrage faisant suite a l'histoire naturelle générale et particuliere, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Tome troisieme.* F. Dufart, Paris, xii + pp. 13–467.

Latreille, P.A. 1810. *Considérations générales sur l'ordre naturel des animaux composant les classes des crustacés, des arachnides, et des insectes; avec un tableau méthodique de leurs genres, disposes.en familles.* F. Schoell, Paris, 444 pp.

Latreille, P.A. 1829. *Les crustacés, les arachnides et les insectes, distribués en familles naturelles, ouvrage format les tomes 4 et 5 de celui de M. le Baron Cuvier sur le règne animal (deuxième édition). Tome premier.* Déterville, Paris, xxvii + 584 pp.

Lawrence, J.F., T.A. Weir and J.E. Pyke. 1987. *Zoological Catalogue of Australia. Volume 4. Coleoptera: Archostemata, Myxophaga and Adephaga.* Australian Government Publishing Press, Canberra, viii + 444 pp.

Li, H., H.J. Guo, and Z.L. Dao. 2000. *Flora of Gaoligong Mountains.* Science Press, Beijing, xxiii + 1344 pp.

Lorenz, W. 2005. *Systematic List of Extant Ground Beetles of the World (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae).* Second edition. W. Lorenz, Tutzing, 530 pp.

Myers, N., R.A Mittermeier, G.A. Mittermeier, G.A.B. de Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.

Nietner, J. 1857. Entomological papers, being chiefly descriptions of new Ceylon Coleoptera with such observations on their habits etc., as appear in any way interesting. *Journal of the Asiatic Society of Bengal* 26:132–153.

Park, J.K., H.K. Min, and J. Park. 2013. A new species of the genus *Tetragonoderus* (Coleoptera: Carabidae) from Korea. *Journal of Asia-Pacific Entomology* 16:373–374.

Quensel, C. 1806. Footnote "h) *Car. Quadrisignatus*", Page 212 *in* Schönherr, C.J. *Synonymia insecterorum, oder: Versuch Synonymie Aller bisher bekannten Insecten; nach Fabrici Systema Eleutheratorum geordnet. Mit Berichtigungen und Anmerkungen, wie auch Beschreibungen neuer Arten. Erster Band. Eleutherata oder Käfer. Erster Theil. Lethrus—-Scolytes.* A. Nordström, Stockholm, xxii + 293 pp. + 3 plates.

SCHMIDT-GÖBEL, M. 1846. *Faunula coleopterorum Birmaniae, adjectis nonnulis Bengaliae indigenis. Med. Dr. Johann Wilhelm Helfer's hinterlassene Sammlungen aus Vorder- und Hinter-Indien. Nach seinem Tode im Auftrage des böhm.* National-Museums unter Mitwirkung Mehrerer bearbeitet und herausgegeben. G.Haase Söhne, Prague, viii + 94 pp. + plates 1–3.

SOLSKY, S.M. 1874. Zhestkokrylye (Coleoptera). In: Fedchenko, A.P. *Puteshestvie v Turkestan. Izvestiya Imperatorskogo Obshchestva Lyubitelei Estestvoznaniya, Anthropologii I Etnografii* (5) 11: iv + 222 pp. + 1 pl.

STATTERSFIELD, A.J., M.J. CROSBY, A.J. LONG, AND D.C.WEGE. 1998. *Endemic bird areas of the world: priorities for biodiversity and conservation. Bird Life Conservation Series, No. 7.* BirdLife International, Cambridge, United Kingdom, 846 pp.

STORK, N.E. 1980. A scanning electron microscope study of tarsal adhesive setae in Coleoptera). *Zoological Journal of the Linnaean Society* 68:173–306.

UNESCO. 2003. *Three Parallel Rivers of Yunnan Protected Area (Paragraph 27, Communique 8C.4)* World Heritage. United Nations Educational, Scientific and Cultural Organization, Paris.

WANG, L.J., J.J. CHENG, AND D.H. KAVANAUGH. 2017. First records for *Cyclosomus inustus* Andrewes (Coleoptera: Carabidae: Cyclosomini) for Taiwan, with notes on habitat and behavior. *Proceedings of the California Academy of Sciences* (Series 4) 64:107–116.

WIEDEMANN, C.R.W. 1823. Zweihundert neue Käfer von Java, Bengalen und dem Vorgebirge der guten Hoffnung. *Zoologisches Magazin* 2:1–135, 162–164.

YU, P.Y. 1992. *Coleoptera: Carabidae. Insects of the Hengduan Mountains Region. Volume 1.* Science Press, Beijing, pp. 470–478.

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.

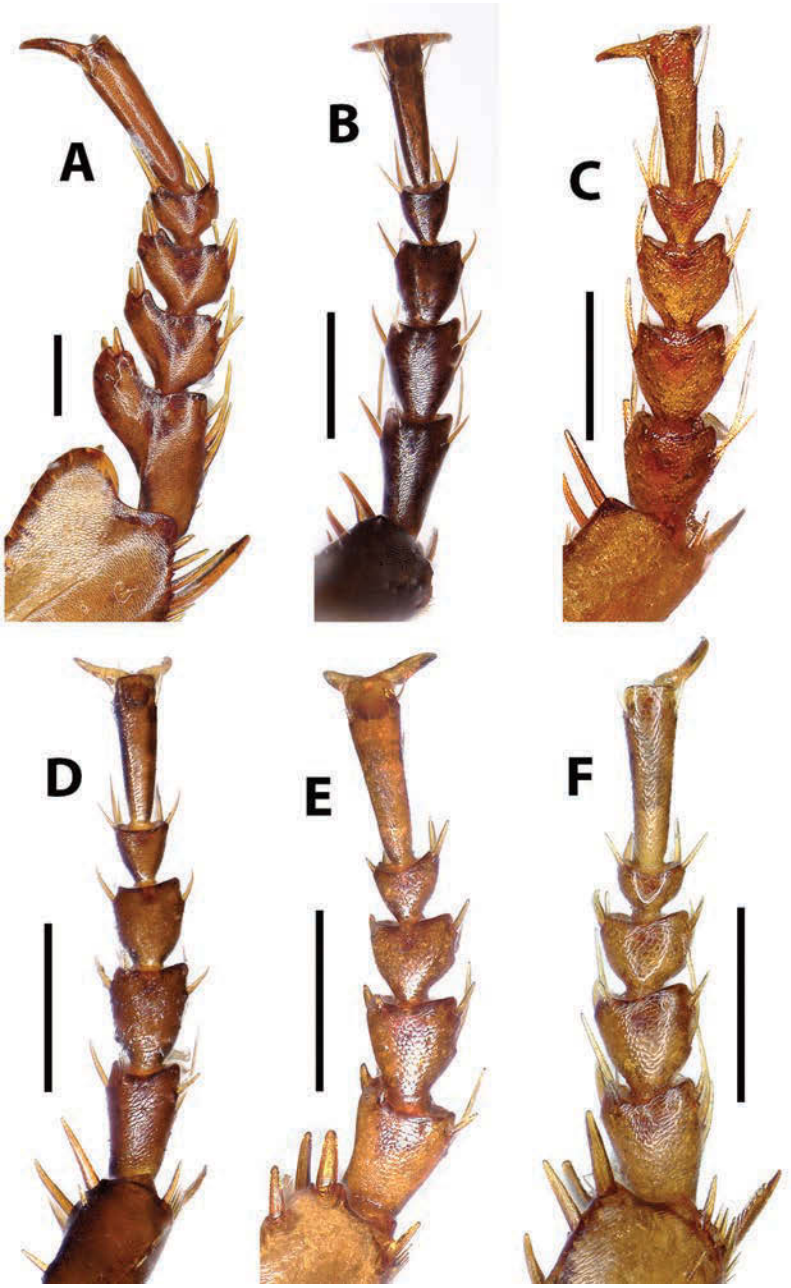


FIGURE 14. Male front tarsus, dorsal aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); 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.

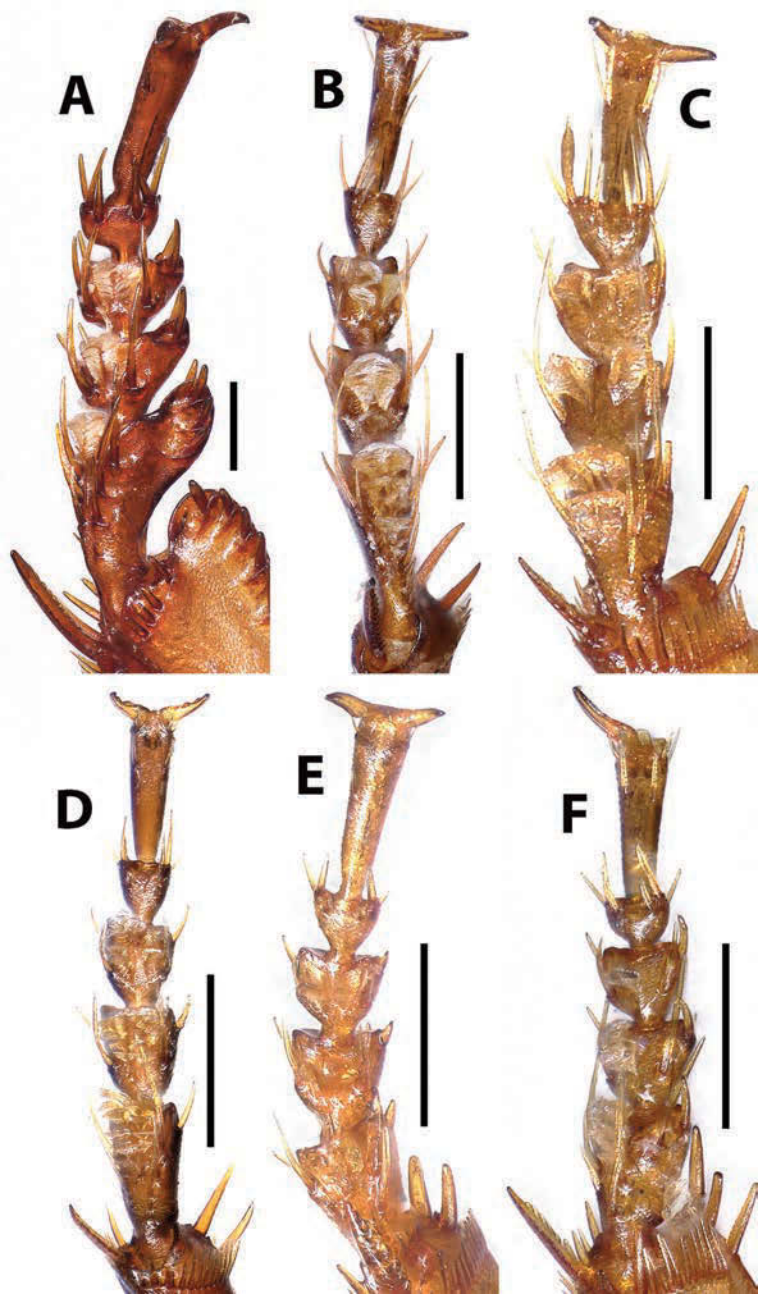


FIGURE 15. Male front tarsus, ventral aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); 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.

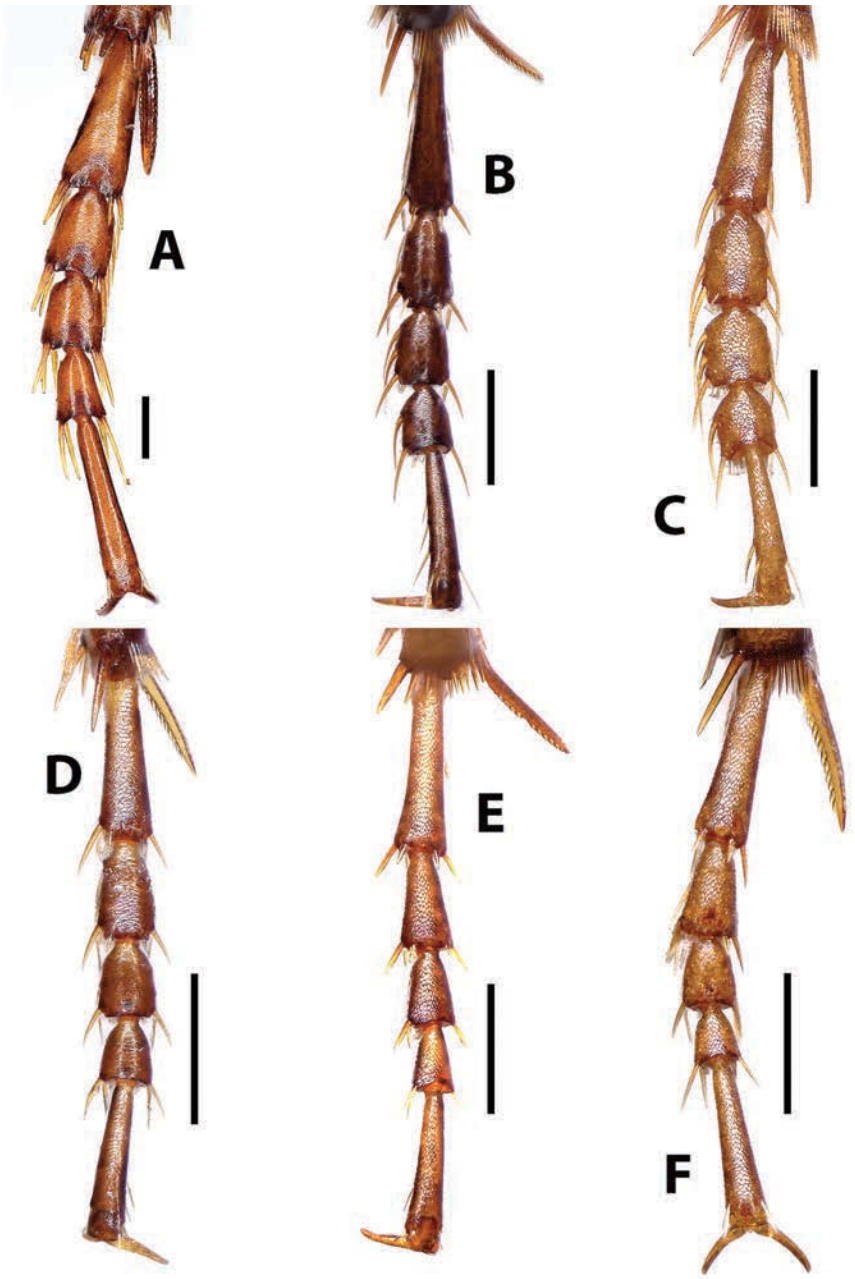


FIGURE 16. Male middle tarsus, dorsal aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); 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.

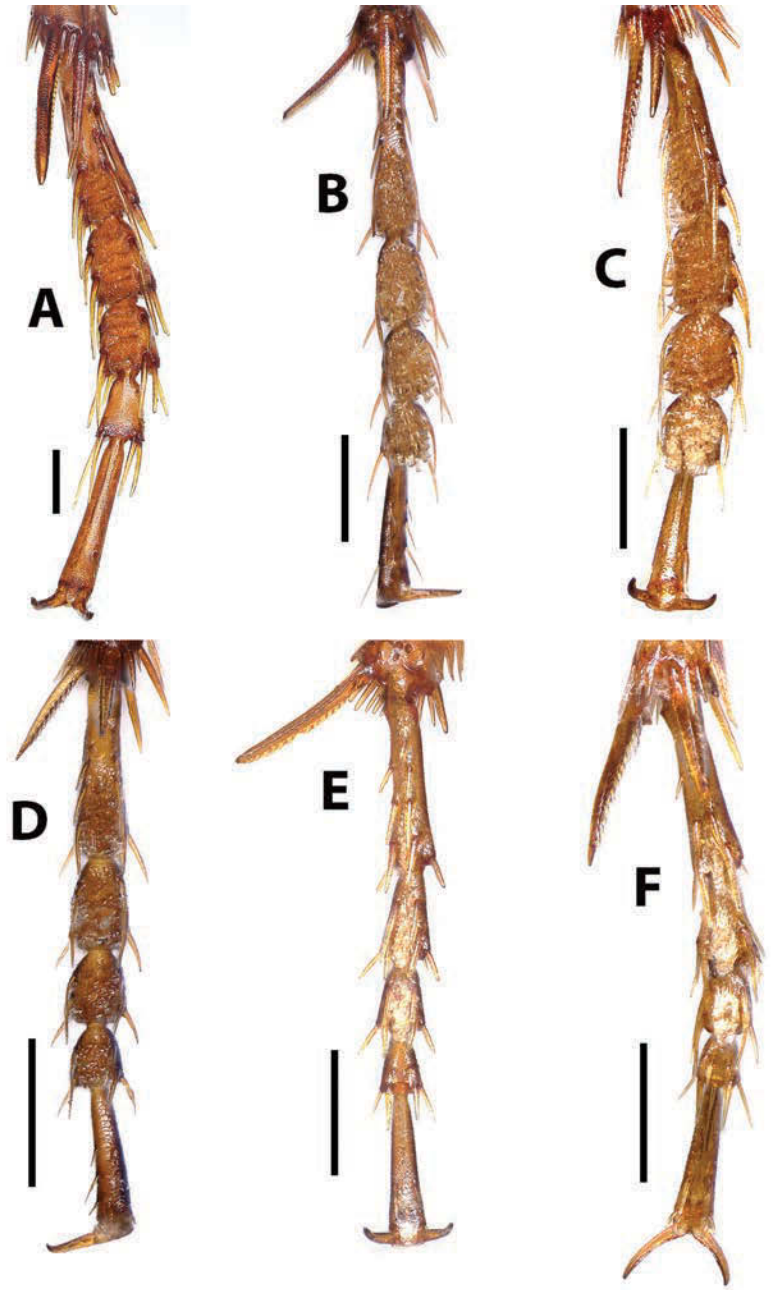


FIGURE 17. Male middle tarsus, ventral aspect. A. *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov. (CASENT 1012643, Longchuan Jiang at Longjiang Bridge, Wuhe Township, Tengchong County, Yunnan, China); B. *Tetragonoderus arcuatus* Dejean (Nepalgunj, Banke District, Lumbini Province, Nepal); 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.

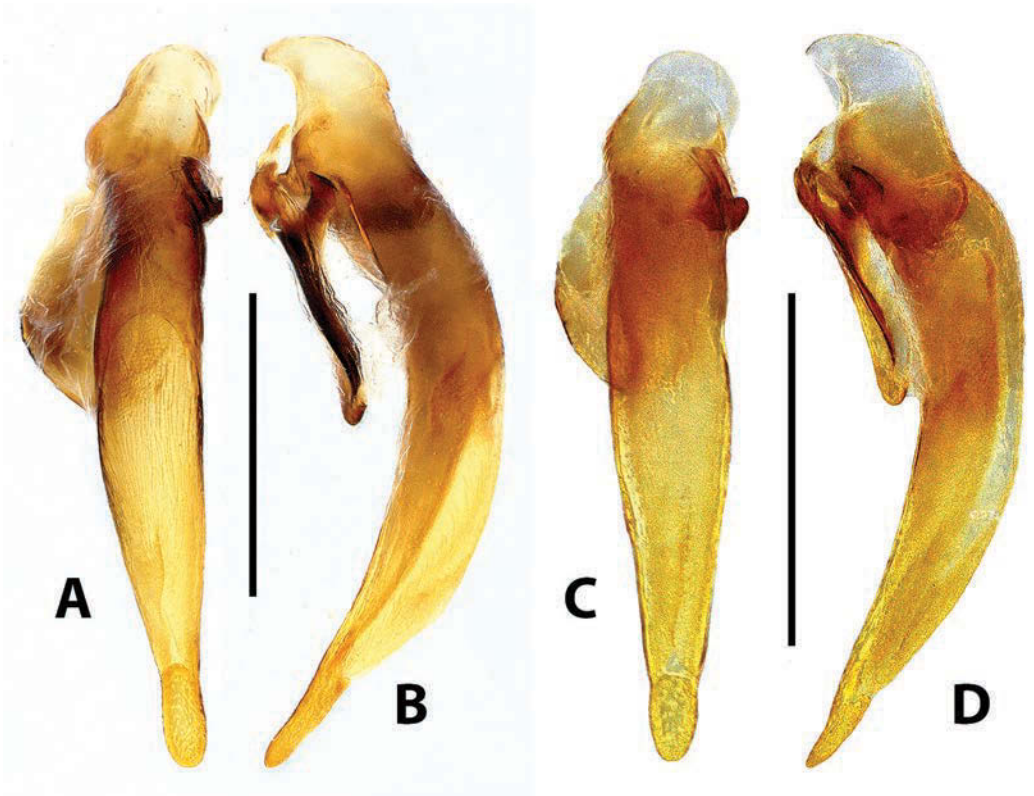


FIGURE 18. Male genitalia, *Tetragonoderus* spp. A, B. *T. arcuatus* Dejean (Nepalgunj, Banke District, Nepal); C, D. *T. parviculus* Kavanaugh & Cueva-Dabkoski, sp. nov., (CASENT1039396, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China). A, C. Dorsal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

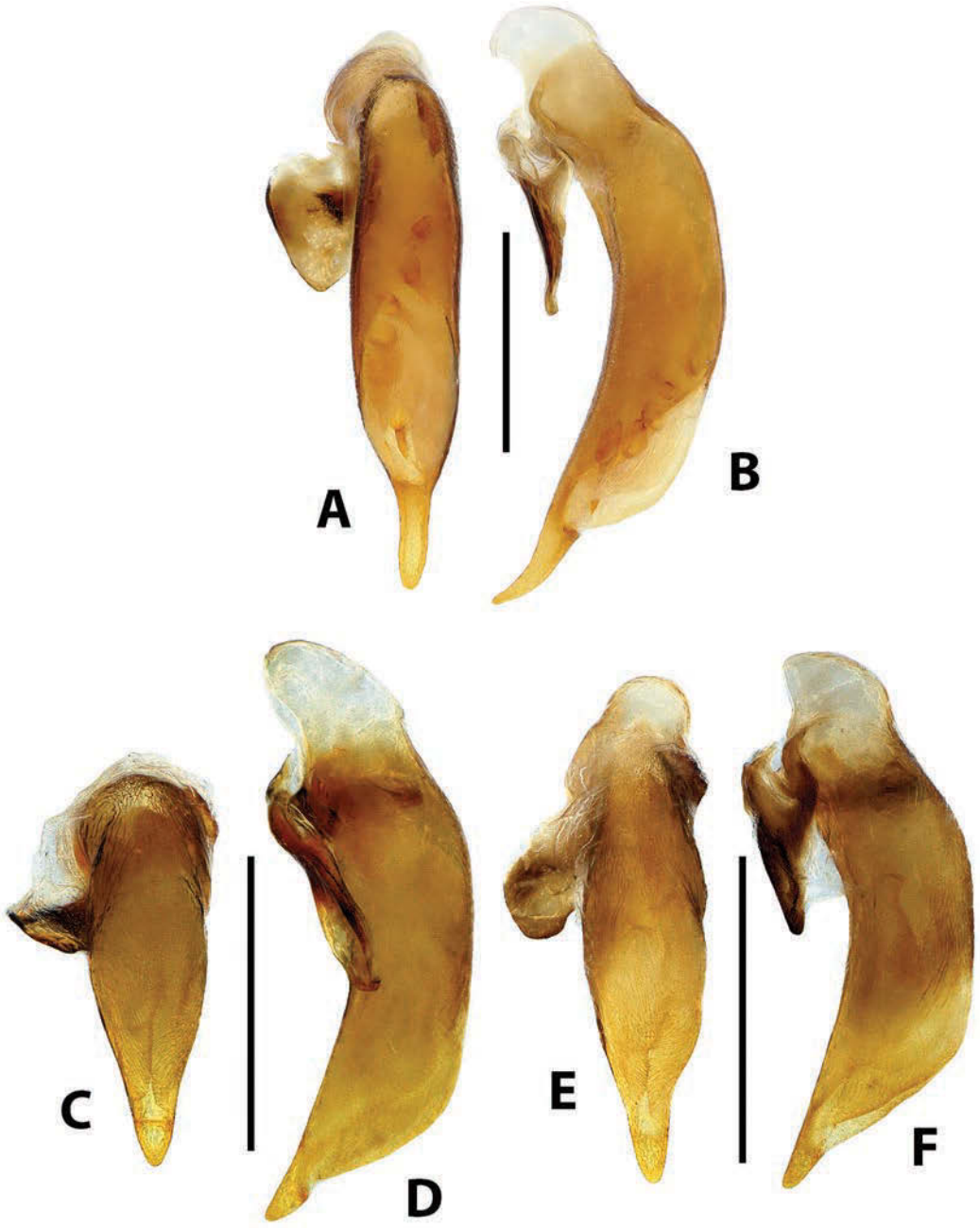


FIGURE 19. Male genitalia, *Tetragonoderus* spp. A, B. *T. elegans* Andrewes (CASENT1039498, Longchuan Jiang just below bridge at Menglian village, Wuhe Township, Tengchong County, Yunnan, China); C, D. *T. punctatus* (Wiedemann) (CASENT1039548, Longchuan Jiang just below bridge at Menglian village, 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.

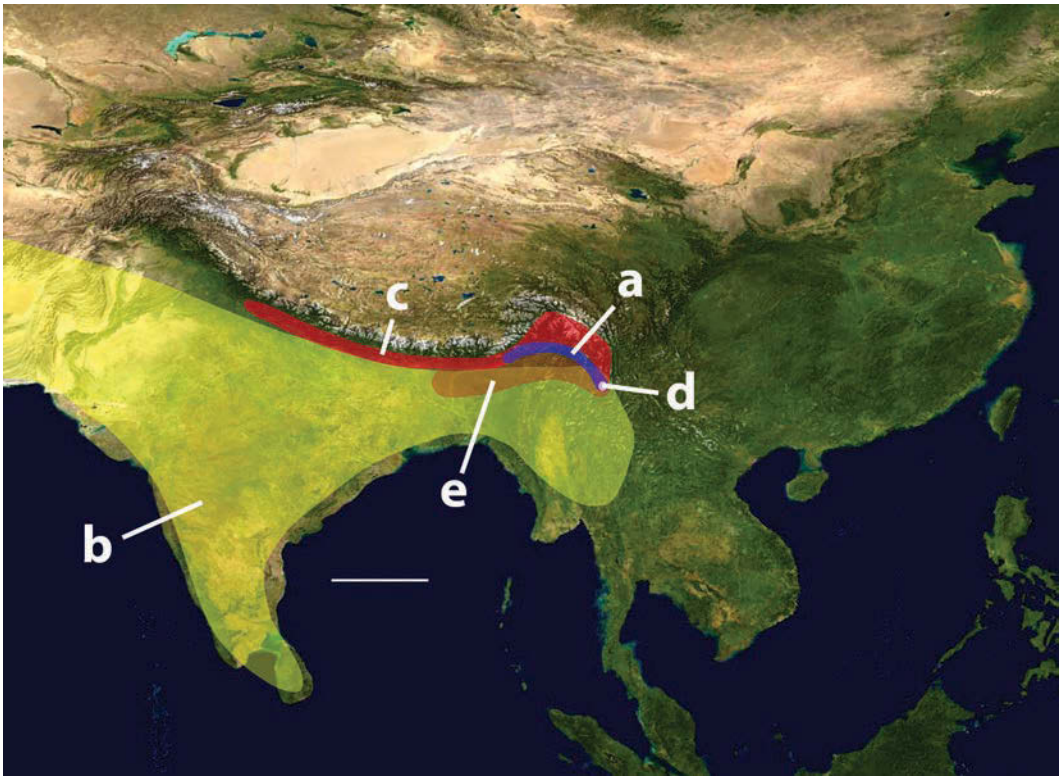


FIGURE 23. Map showing approximate known overall geographical distributions of cyclosomine species occurring in the Gaoligong Shan. a (blue) = *Cyclosomus acutangulus* Kavanaugh & Cueva-Dabkoski, sp. nov.; b (yellow) = *Tetragonoderus arcuatus* Dejean; c (red) = *T. elegans* Andrewes; d (white dot) = *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.