

## Occurrence of the milliped *Sinocallipus simplipodicus* Zhang, 1993 in Laos, with reviews of the Southeast Asian and global callipodidan faunas, and remarks on the phylogenetic position of the order (Callipodida: Sinocallipodidea: Sinocallipodidae)

WILLIAM A. SHEAR<sup>1</sup>, ROWLAND M. SHELLEY<sup>2</sup> & HAROLD HEATWOLE<sup>3</sup>

<sup>1</sup> Biology Department, Hampden-Sydney College, Hampden-Sydney, Virginia 23943, U. S. A.; email <wshear@hsc.edu>

<sup>2</sup> Research Lab., North Carolina State Museum of Natural Sciences, 4301 Reedy Creek Rd., Raleigh, North Carolina 27607, U. S. A.; email <rowland.shelley@ncmail.net>

<sup>3</sup> Zoology Department, North Carolina State University, Raleigh, North Carolina 27695, U. S. A.; email <harold\_heatwole@ncsu.edu>

### Abstract

The callipodidan milliped, *Sinocallipus simplipodicus* Zhang, 1993, previously known only from a cave in Yunnan Province, China, is redescribed based on specimens from an epigeal habitat in southern Laos, some 600 mi (960 km) south of the type locality. SEM photos of the gonopods, ovipositor, gnathochilarium, midbody exoskeleton, an ozopore, and legs are presented to supplement previously published line drawings; the cannula may be the “functional” element of the gonopod that inseminates females in this species. The Callipodida occupy nine disjunct areas globally, all exclusively in the Northern Hemisphere and most in the North Temperate Zone; there are three regions each in North America, Europe (including coastal regions along the southern Black and eastern Mediterranean seas that are technically part of Asia), and Asia proper. The southeast Asian fauna comprises three families -- Sinocallipodidae, one genus and species (suborder Sinocallipodidea), and Schizopetalidae, one genus and species, and Paracortinidae, one genus, three subgenera, and seven species (both suborder Schizopetalidea). An unnamed clade may exist in the Diplopoda in which the gonopods arise solely from the 8th legs (an “8th gonopod clade”); it comprises seven orders: Callipodida, Polydesmida, Chordeumatida, Stemmiulida, Siphoniulida, Spirostreptida, and Epinannolenida. Two newly recognized characters that hold phylogenetic significance are (1) development of the gonopod from the 8th coxa alone (Chordeumatida) or from the coxa plus some telopodal articles (the other six orders), and (2) the presence (Callipodida, Polydesmida, and Stemmiulida) or absence (Chordeumatida, Spirostreptida, and Epinannolenida) of a cannula. These considerations lead to the hypothesis (Chordeumatida + (Callipodida + (Polydesmida + Stemmiulida))).

**Key words:** Callipodida, Sinocallipodidea, Sinocallipodidae, phylogeny

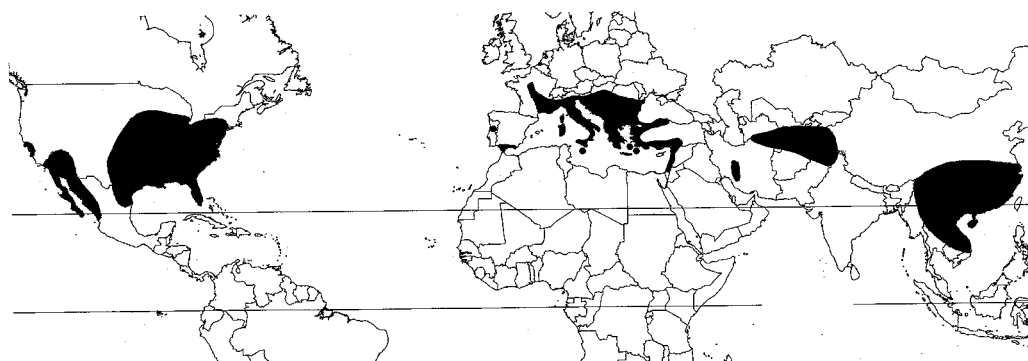
## Introduction

The milliped *Sinocallipus simplipodicus* Zhang, 1993 (misspelled as “*simplicipodus*” by Shear (2000a)), is unique in the order Callipodida, therefore Shear placed it in a separate suborder, Sinocallipodea, and postulated that its family, Sinocallipodidae, is the plesiomorphic sister-group of the other callipodidan families collectively. It has unique gonopods with a sternum like those of the walking legs, coxae with two clavate processes apiece, and telopodites with three or four slender, curvilinear, medially directed projections; additionally, the telopodites lack prostatic grooves and connections with the cannulae, which terminate freely. The original description was based on 22 adults and juveniles of both sexes from a cave in Yunnan Province, China, all of which were white or pale yellow in life; the ocelli were also depigmented with 11–16 in the ocellar patches. The third author recently collected a sizeable sample of pigmented specimens of *S. simplipodicus* from an epigeal habitat in southern Laos, some 600 mi (960 km) south of the type locality. We examined this material under light and scanning electron microscopy, and provide anatomical observations and SEM photographs of somatic and sexual features to supplement Zhang’s description, which was published in an outlet that is not widely accessible in the western world. We also summarize knowledge of the southeast Asian callipodidan fauna, present the first consolidated maps of ordinal occurrences there and globally, and provide new insight on the phylogenetic position of the Callipodida.

The Callipodida occur exclusively in the Northern Hemisphere and primarily in the North Temperate Zone, north of the Tropic of Cancer. The only parts of the documented range that are in the Tropics are the southernmost areas in Mexico, southern Sinaloa and the southern tip of Baja California Sur, and southern Yunnan, Laos, and Vietnam, in southeast Asia. To date, *Sinocallipus* and *S. simplipodicus* are known exclusively from the tropics; the only other callipodidans known to occur south of the Tropic of Cancer are *Scotopetalum* and *S. warreni*, both authored by Shear, 2000a, from Laos, and a female of *Colactis* Loomis, 1937, from southern Sinaloa, that was assigned to *C. tiburoni* (Chamberlin, 1923) by Shelley (1997). Shelley (1996) projected occurrence throughout the Baja California peninsula of Mexico based on an unidentifiable female from La Paz, which is just north of this line. The Callipodida inhabit nine disjunct regions worldwide, three each in North America, Europe, and Asia (Fig. 1), the last being the most poorly sampled and whose borders are imprecise. As the “eastern Mediterranean” area, technically part of Asia, is essentially continuous with that in the Balkans, interrupted only by the Bosphorus and Dardanelles, it is included here in the European area. The ordinal distribution covers parts of 30 countries and completely encompasses the following eight: Laos, Bulgaria, Albania, Macedonia, Yugoslavia, Bosnia/Herzegovina, Croatia, and Greece, with the possible exception of some offshore islands.

In the New World, the Callipodida comprise two families, 13 genera, and 36 species; the three regions were detailed by Shelley (1984, 1989, 1996, 1997, 2000a) and Hoffman (1999). They include a small one around San Francisco and Monterey Bays, California,

inhabited by *Tynomma* Loomis, 1937 (three species) (Schizopetalidae: Tynommatinae: Tynommatini); a broad area in the southwestern United States and northwestern Mexico occupied by *Idrionaria* Shelley, 1996 (one species) (Tynommatini) and the tynommatine tribes Colactidini (three genera, seven species), Diactidini (three genera, 10 species), and Aspidiophonini (one genus, one species); and thirdly, a large area in the eastern and central United States that extends southward into Coahuila and Nuevo León, Mexico, and which hosts *Texophon* Chamberlin, 1946 (two species) (Tynommatinae: Texophonini), and the family Abacionidae (three genera, 12 species), the latter occupying the entire area. The western taxa and *Texophon* were transferred from the family Lysiopetalidae to the Schizopetalidae by Hoffman (1980), but it has never been established that these taxa really are confamilial with true schizopetalids in the Balkan peninsula of Europe, where *Schizopetalum koelbeli* (Verhoeff, 1895), the type species of the monotypic type genus, occurs (Verhoeff, 1895). As the North American forms comprise a separate subfamily, Tynommatinae, Shelley (2003) suggested that this taxon should be elevated to full familial status but did not actually do so.



**FIGURE 1.** Approximate global distribution of the order Callipodida.

The ordinal occurrence in Europe was depicted by Kime (2000, fig. 7), but two localities of *Lusitanipus alternans* (Verhoeff, 1893), from Guarda and Coimbra, Portugal (Verhoeff, 1893; Ladeira, 1943), were overlooked. This fauna is considerably more diverse than that in western North America, with two suborders (Callipodidea and Schizopetalidea sensu Hoffman, 1980, and Shelley, 2003), three families, 18 genera/subgenera, and ca. 80 species/subspecies. The Iberian peninsula, which encompasses the entire distribution of the subfamily Cyphocallipodinae (Dorypetalidae: Schizopetalidea), contains two of the three aforementioned areas. All three cyphocallipodine genera are monotypic; *Lusitanipus* Mauriès, 1978, occurs in central Portugal, and *Cyphocallipus* and *Dorycallipus*, both authored by Verhoeff, 1909, occur along the southern periphery of Spain. The primary callipodidan region in Europe is a large, continuous, irregularly shaped area that extends from France through Italy to the Balkan peninsula, spreads across the Bosphorus and Dardanelles into coastal Turkey, and continues southward along the eastern Mediterranean

coast through Lebanon and western Syria to northern Israel; it includes the following islands — Corsica, Sardinia, Sicily, Malta, Crete, and a number of Greek islands in the Cyclades and Dodecanese archipelagos in the Aegean Sea — but the Callipodida have not been recorded from Cyprus. The fauna in this large area consists of 16 genera/subgenera and ca. 75 species/subspecies (Strasser, 1966, 1969, 1973, 1975; Hoffman, 1980; Minelli, 1985; Enghoff & Schembri, 1989; Ceuca, 1992; Glaubrecht & Spelda, 1993; Foddai *et al.*, 1995; Mauriès *et al.*, 1997; Stoev & Enghoff, 2003). The northernmost records are from Paris, France, based on an undoubtedly introduced population of *Callipus foetidissimus gallicus* Brolemann, 1930, in the catacombs of the Muséum National d'Histoire Naturelle that Demange (1946) named “*denticulatus*” nov. var., and *Dorypetalum degenerans* (Latzel, 1884) from the Buda side of Budapest, Hungary, that Korsós (1994) suspected to be of anthropogenic origin.

In Asia proper, the Callipodida occupy three areas: southwestern Iran; the primarily mountainous region in southern Turkmenistan, Uzbekistan, Tadjikistan, and northern Pakistan and Afghanistan; and southeast Asia, whose area and fauna are detailed in the ensuing section. As these regions are so poorly sampled, broad areas are shaded in fig. 1 where the order plausibly occurs, based on the few available records. The faunas of the first two areas comprise only six described species in the genus *Bollmania* Silvestri, 1896 (family Caspiopetalidae); they conceivably could connect through the mountains of northern Iran and along the southern border of the Caspian Sea. There are only two records from Iran that we are aware of, *Bollmania nematogonum* (Attems, 1951), from the vicinity of Esfahan, Esfahan Province, and *B. gracilis* Golovatch, 1983, from 31.3 mi (50 km) west of Shiraz, Fars Province (Attems, 1951; Golovatch, 1983). These two sites are ca. 200 mi (320 km) apart and may represent a faunal region centered in the Zagros Mountains (shaded in fig. 1). The second area includes four species plus several records of *Bollmania* sp. based on unidentifiable juveniles from sites that are more widely dispersed and may not interconnect; with so few records, we treat the sites as one faunal area. From east to west, the total distance is about 950 mi (1,520 km) and extends from near Aydere and Aschabad in the Kopetdagh Mountains in southern Turkmenistan, which doubtlessly spreads across the border into northeastern Iran, to Punjab Province, Pakistan; north-south, it ranges from Buchara, Uzbekistan, to Kohala, Pakistan, a distance of around 450 mi (720 km), that encompasses Tadjikistan and northern Afghanistan, where unidentified species of *Bollmania* have been reported from caves (Golovatch, 1979, 1983, 1991; Lindberg, 1961, 1962; Lohmander, 1932). Discovery in Kirghizstan, the mountains on the western fringe of China (Xinjiang Prov.), and northern India (Kashmir) is expected, and these areas are shaded in fig. 1.

### The Order Callipodida in Southeast Asia

Prior to 1981, the easternmost record of the Callipodida in Eurasia was that of *Bollmania*

*kohalana* (Attems, 1936), from Kohala, Punjab Province, Pakistan (Attems, 1936). In that year, Golovatch (1981) discovered two unidentifiable females from Jiangsu (=Kiangsu) Province, China, in the collection at the Institute of Zoology, Polish Academy of Sciences, Warsaw. He assigned them to *Bollmania*, then the most geographically proximate genus, although the Pakistan locality is on the other (south) side of the Himalayas and some 2,550 mi (4,080 km) west of the Chinese site; he (Golovatch, 1983, 1991) also referenced this record. We think it unlikely that this genus and family occurs in eastern China not far from Shanghai, so we assign this record to the most common Chinese family, Paracortinidae, as an unidentifiable genus and species.

Zhang (1993) was the first to propose a new taxon for Chinese callipodidans when he erected the family Sinocallipodidae for *Sinocallipus simplipodicus*, n. gen., n. sp., from Xian Cave, Yunnan Province. Later that year, Wang and Zhang (1993) established the family Paracortinidae for three new genera and seven new species — *Paracortina* (two species), *Relictus* (two species), and *Altum* (three species) — and all the new generic and familial taxa were subsequently cited by Shelley *et al.* (2000). Wang and Mauriès (1996) likewise listed all these taxa, reducing *Relictus* and *Altum* to subgenera under *Paracortina* and transferring their species into this genus, but Wang (1996), in a subsequent paper in this volume, recognized three full genera, which technically is the latest word on their statuses. Our analysis of the gonopod drawings of Wang and Zhang (1993) and our experience with distantly related callipodidans in North America indicate that there is probably only one valid genus, so we favor the arrangement of Wang and Mauriès (1996). However, the status of *Relictus* and *Altum* as subgenera of *Paracortina*, rather than outright synonyms, remains open to question.

Shear (2000a) proposed *Scotopetalum* for a new species collected in a cave near Hanoi, Vietnam, and assigned it to the family Schizopetalidae, otherwise known from Europe, the mid-East, and, at least for now, western North America. In addition to erecting the suborder Sinocallipodidea, Shear also suggested that the Paracortinidae probably should be considered only a subfamily of the Schizopetalidae but did not formalize this status without examining authentic specimens. Thus, the composition of the Callipodida in southeast Asia is as follows; taxa are listed in chronological order by genera and species along with type localities and other occurrences, all of which are mapped in fig. 2.

## Order Callipodida

Suborder Sinocallipodidea Shear, 2000a

Family Sinocallipodidae Zhang, 1993

Genus *Sinocallipus* Zhang, 1993

*S. simplipodicus* Zhang, 1993. China, Yunnan Prov., Hekou Yaozu Autonomous County, Xiao Cave (Zhang, 1993). Also occurring in Laos, Champasak/Attapu Provs., Bolavens Plateau (this paper).

## Suborder Schizopetalidea Verhoeff, 1909

## Family Paracortinidae Wang and Zhang, 1993

Genus *Paracortina* Wang and Zhang, 1993Subgenus *Paracortina* Wang and Zhang, 1993

*P. (P.) leptoclada* Wang and Zhang, 1993. China, Yunnan Province, Zhong Dian County (Wang and Zhang, 1993).

*P. (P.) voluta* Wang and Zhang, 1993. China, Sichuan Province, Ya Jang County (Wang and Zhang, 1993).

Subgenus *Relictus* Wang and Zhang, 1993

*P. (R.) stimula* Wang and Zhang, 1993. China, Yunnan Province, Zhong Dian County (Wang and Zhang, 1993).

*P. (R.) thallina* Wang and Zhang, 1993. China, Sichuan Province, Ba Tang County. Also recorded from Yunnan Province, Zhong Dian County (Wang and Zhang, 1993).

Subgenus *Altum* Wang and Zhang, 1993

*P. (A.) viriosa* Wang and Zhang, 1993. China, Yunnan Province, Zhong Dian County. Also recorded from Tibet, Mang Kang County (Wang and Zhang, 1993).

*P. (A.) serrata* Wang and Zhang, 1993. China, Tibet, De Qin Autonomous Region (Wang and Zhang, 1993). This site is in the south-east periphery of Tibet, just across the border from Yunnan Province.

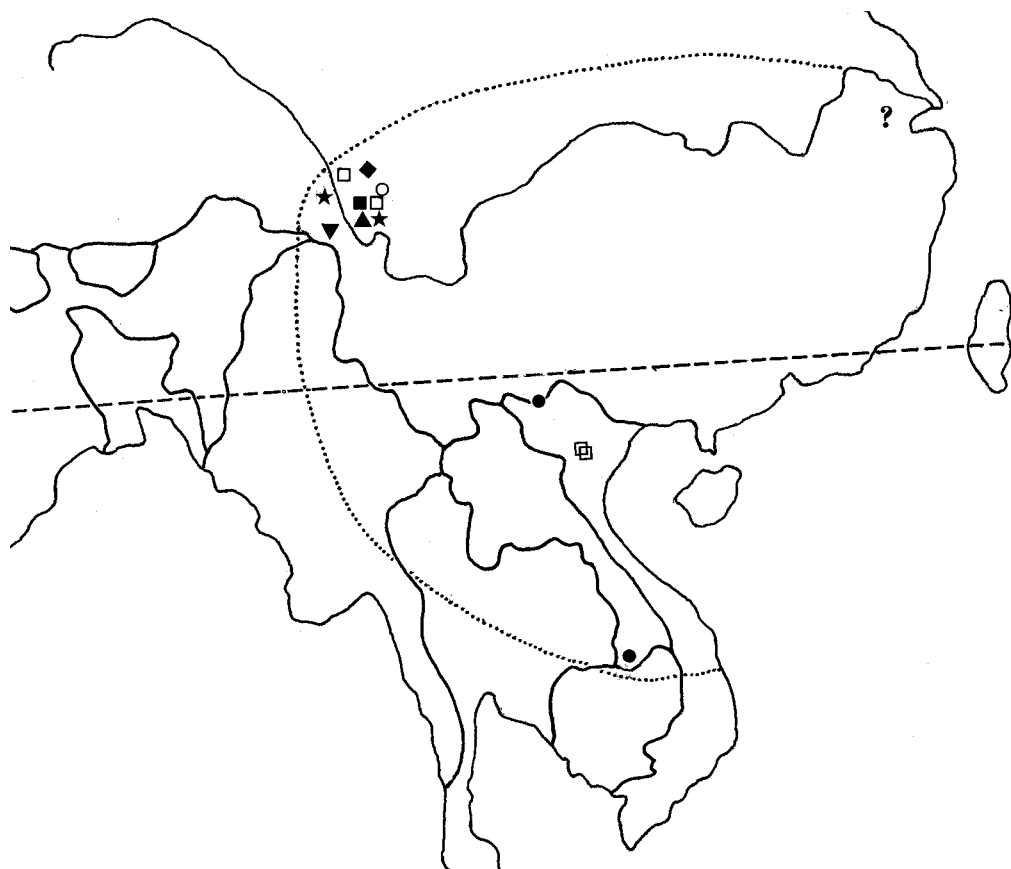
*P. (A.) carinata* Wang and Zhang, 1993. China, Yunnan Province, Zhong Dian County (Wang and Zhang, 1993).

Unidentifiable genus and species. China, Jiangsu Province, Cisian-shan, ca. 15.6 mi (25 km) S Nanjing (Golovatch, 1981).

## Family Schizopetalidae Verhoeff, 1909

Genus *Scotopetalum* Shear, 2000a

*S. warreni* Shear, 2000a. Vietnam, northwest of Hanoi, anunnamed cave at Hong Mat; also tentatively recorded from Huang Tua Cave northwest of Hanoi (Shear, 2000a). The exact locations of these sites, which are south of the Tropic of Cancer, are unknown, and Hong (Huong, Hoang, Hung) Mat is not on any map available to us, nor can we find any town with the word, "Mat," as part of its name. The coordinates given for the type locality are in fact southwest, not northwest, of Hanoi, and we have placed them on the map accordingly (fig. 2).



**FIGURE 2.** Distribution of the Callipodida in southeastern Asia. The Yangtze River is indicated in China; the dotted line, a smooth curve drawn around range extremes, shows the border of the projected ordinal distribution shaded in fig. 1; and the dashed line represents the Tropic of Cancer. Dots, *Sinocallipus simplipodicus*; upright triangle, *Paracortina (P.) leptoclada*; solid diamond, *P. (P.) voluta*; solid square, *P. (Relictus) stimula*; open squares in China, *P.(R.) thallina*; stars, *P. (Altum) viriosa*; inverted triangle, *P. (A.) serrata*; circle, *P. (A.) carinata*; open squares in Vietnam, *Scotopetalum warreni*; ?, unknown paracortinid genus and species.

The occurrence of identifiable callipodidans in Tibet, Sichuan, and Yunnan Provinces, China, northern Vietnam, and southern Laos, and the discovery of unidentifiable females in eastern Jiangsu Province, ca. 180 mi (288 km) west of metropolitan Shanghai and not far from the mouth of the Yangtze River, is evidence of a widespread callipodidan fauna in southeastern Asia (Figs. 1–2). Most of the material comes from montane areas around the contiguous corners of Tibet, Sichuan, and Yunnan Provinces; drawing a smooth curve around range extremes produces a general area of roughly 1,500 mi (2,400 km), east-west, and 1,200 mi (1,920 km), north-south, which equals some 1,800,000 sq. mi. (4,608,000 sq. km). In China, localities exist both north and south of the Yangtze River, and the northern- and westernmost records indicate that callipodidans may potentially be discovered in parts or all of the following 15 provinces: Tibet, Qinghai, Sichuan, Yunnan, Guizhou, Guangxi,

Guangdong, Hunan, Jiangxi, Fujian, Zhejiang, Hubei, Anhui, Jiangsu, and Shanghai Shi. This includes essentially the entire area south of the Yangtze except for distant reaches near the headwaters and likely extends northward for an unknown distance. Judging from known records, the region probably extends well into Myanmar, Thailand, Cambodia, and southern Vietnam, and possibly covers the entire Indochinese Peninsula; occurrences in the easternmost part of India (Assam), the Malay Peninsula, and Hainan Island, China, are also plausible. This vast, poorly investigated area is roughly equivalent in size to that in eastern North America and surely harbors many undiscovered species and genera. Based upon its size, Shear (2000a) was surely correct in suggesting that southeast Asia constitutes a third center of ordinal diversity in addition to southwestern North America and the eastern Mediterranean (Fig. 1). Indeed, this may be an understatement; its diversity may be greater, such that southeast Asia may be the primary center worldwide. Wang and Mauriès (1996) stated that probably no more than 5% of the total Chinese myriapod species had been discovered, and to some degree this statement also applies to southeast Asia in general, the Callipodida being a case in point. Field work in the area in which the order is projected to occur is greatly desired.

## Taxonomy

### Genus *Sinocallipus* Zhang, 1993

*Sinocallipus* Zhang, 1993:129. Shelley *et al.*, 2000:59.

*Type species.* *Sinocallipus simplipodicus* Zhang, 1993, by original designation.

*Diagnosis.* A genus of moderate-size Callipodida with low, narrow, primary crests, secondary and tertiary crests absent, without crest transition or setal migration. Gonopodal coxa with two medial, clavate processes anteriad and long, slender cannula, either curved or coiled, directed anteriolaterad, terminating freely, not interconnecting apically with telopodite; latter without prostatic groove, with three or four slender, narrowly separated, terminal projections directed anteriomedial and overlapping or terminating close to coxal processes. 9th legs in males with distomedial, deeply excavated trochanteral lobe, possessing central pore and spur-like to subspiniform projections.

*Distribution.* Known from one locality each in Yunnan Province, China, and Champasak/Attapu Provinces, in southern Laos, both of which are south of the Tropic of Cancer. These sites are approximately 600 mi (960 km) apart, which constitutes the known generic range.

*Species.* One is known, but others may exist in the projected ordinal area in southeastern Asia. Callipodidan telopodites usually exhibit distinct prostatic grooves and are the presumably “functional” elements that inseminate females. They are also typically elaborate structures possessing most of the taxonomic characters at the specific levels, so with-



out such a telopodite and with so few specimens available, it is unknown how specific differences manifest themselves in *Sinocallipus*. Whether features like a markedly longer cannula that curves rather than coils reflect reproductive isolation remains for future workers to determine. Cannula length could also vary geographically or clinally, being longer in southern populations and indicative of geographic races that may warrant taxonomic recognition at the subspecific level. The Laotian specimens differ from Zhang's account of those from China in both somatic and gonopodal features; not knowing how much taxonomic value to place on them, we adopt the conservative treatment and assign the specimens to *S. simplipodicus*. Additional material from other localities is needed before species and subspecific distinctions in *Sinocallipus* can be properly evaluated.

***Sinocallipus simplipodicus* Zhang, 1993**

Figs. 3–14

*Sinocallipus simplipodicus* Zhang, 1993:129, figs. 1–16.

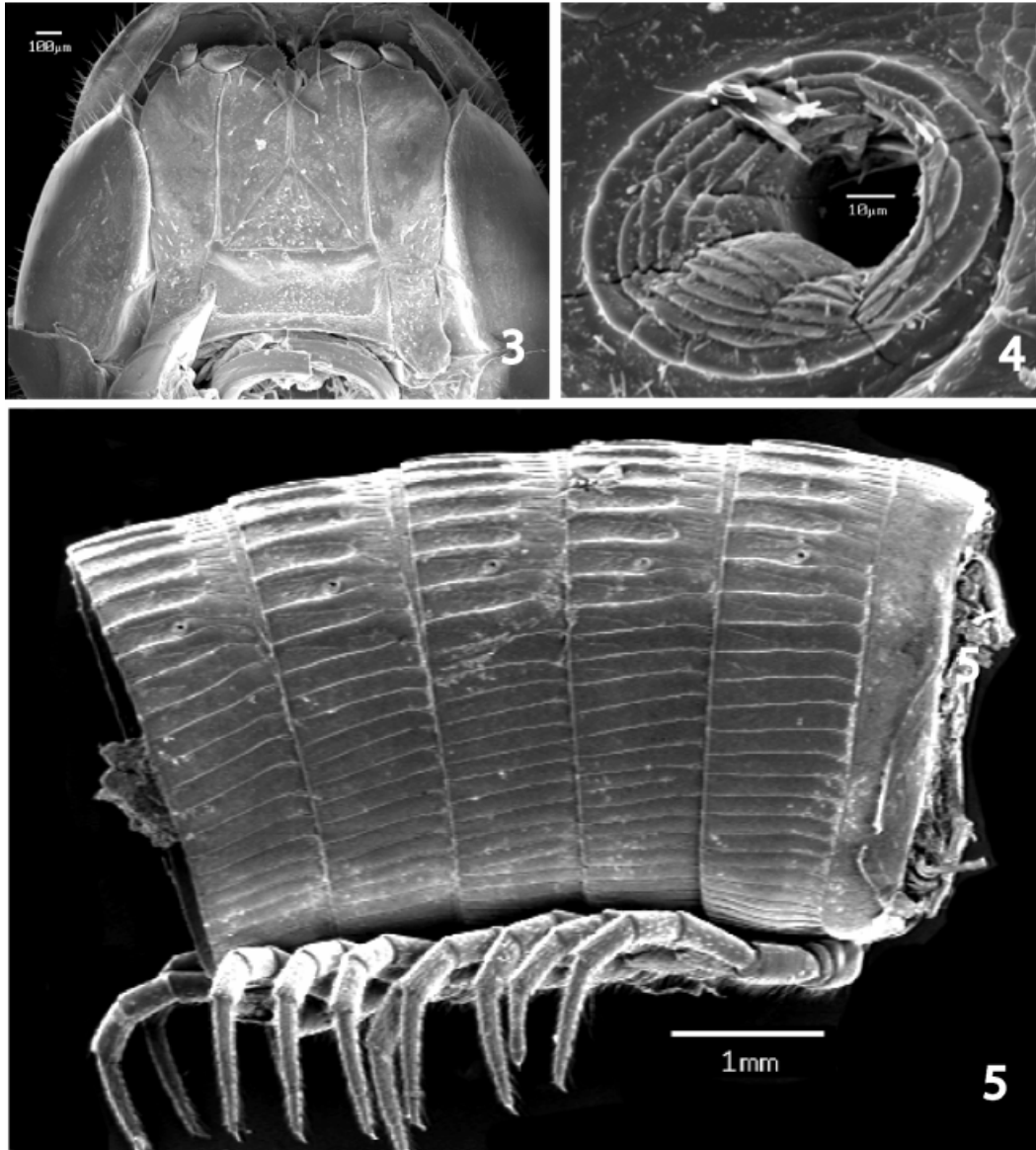
*Type specimens.* Male holotype, female allotype, and 15 male (one juvenile) and 5 female (one juvenile) paratypes collected by F. Zhang, D. Wang, X. Chen, and H. Lu, 8 and 13 April 1992, in Xiao Cave, Hekou Yaozu Autonomous County, Yunnan Province, China (not examined). The repository is not stated specifically in the original description (Zhang, 1993) but presumably is the Institute of Zoology, Chinese Academy of Sciences, Beijing.

*Diagnosis.* With the characters of the genus.

*Description of Laotian specimens.* Color (after two years in preservative, but presumably close to this in life): Ocellar patches black; interantennal and epicranial regions of head brownish. Collum, segment 2, prozonum and anterior half of metazonum of 3rd pleurotergite, and epiproct white, completely unpigmented; remaining pleurotergites mottled brownish-gray with a light, narrow middorsal stripe.

Segment counts as follows (because of the difficulty in distinguishing segments at the caudal end, where they are smaller and closely packed together, an error of  $\pm 2$  segments is assumed): adult males (with gonopods) with 54–68 segments, females with 61–69. Measurements (on two relatively straight individuals of both sexes): males 44.0 & 46.0 mm long, 2.3 & 2.4 mm wide; females 48.0 & 51.7 mm long, 2.8 & 3.0 mm wide.

Head densely setose, especially frontal and subantennal regions, setae diminishing in number and becoming longer on epicranium. 41 ocelli in right ocellarium in one adult male. Gnathochilarium (Fig. 3): laminae linguales broad, touching distal to midlength in midline, with distal setae but without palps, narrowing proximad and separated by broad, triangular mentum; stipes long and broad, extending for entire length of gnathochilarium along lateral margins of lamina linguales, separated basally by broad, subrectangular prebasilare, with two apical palps apiece, each with a row of apical papillae.



**FIGURES 3–5.** *Sinocallipus simplipodicus*, exoskeletal features. 3, gnathochilarium. 4, pleurotergites, lateral view of right side of five midbody segments. 5, ozopore. Scale bars indicate magnifications on each figure.

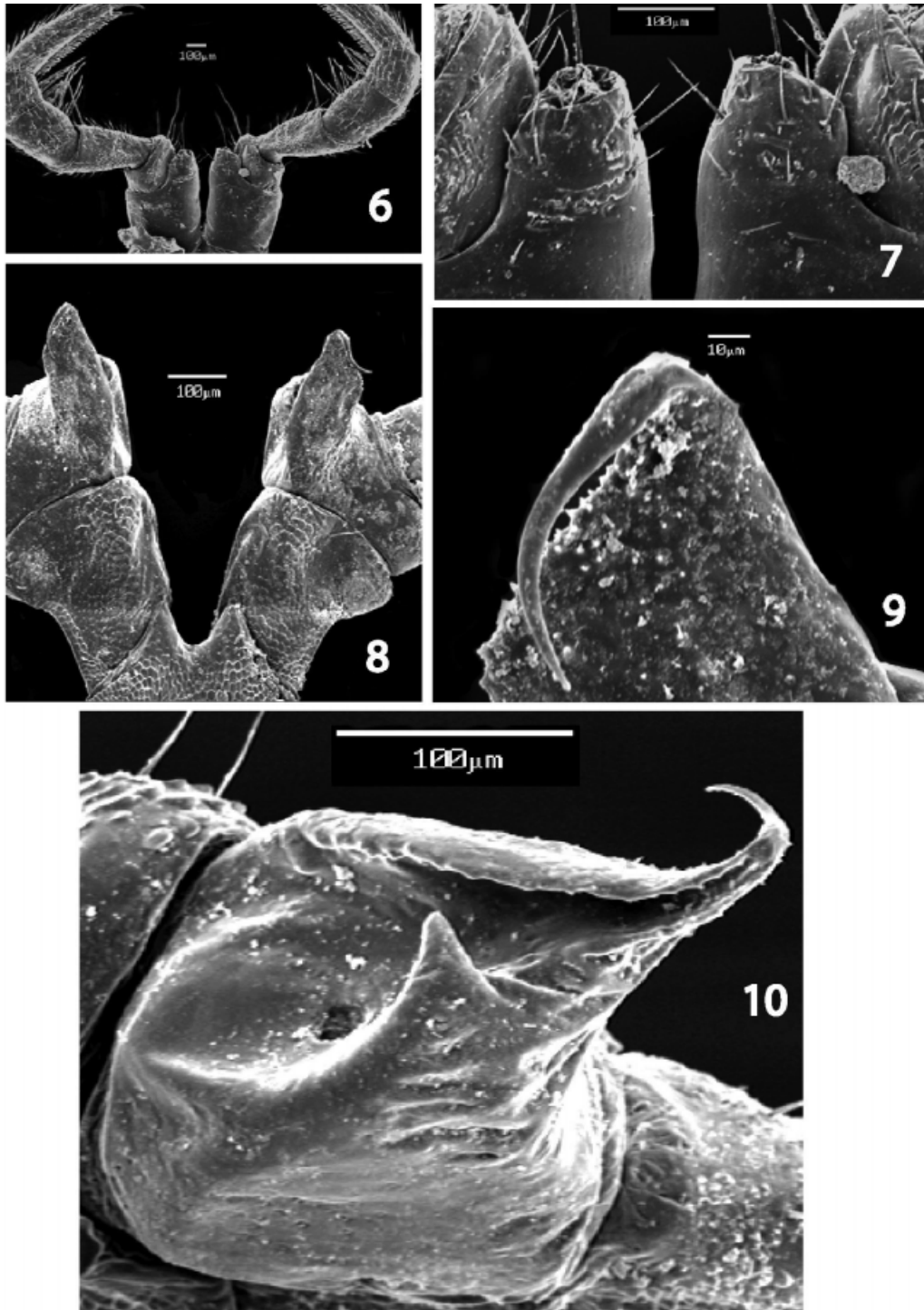
Collum and second segment smooth; crests arising on 3rd pleurotergite, low, broad, and poorly defined, only slightly more distinct on 4th pleurotergite; carinae on remaining pleurotergites low and narrow, not prominent, becoming progressively lower laterad and grading into striae ventrolaterad (Fig. 4), first crest on each side of midline inconspicuous; only primary crests present, secondary and tertiary ones absent, without crest transition. Ozopores (Fig. 5) relatively broad, arising on segment 6, located between 3rd and 4th

crests on each side of midline. Segments with strong, distinct strictures between pro- and metazona (Fig. 4). Dorsal setae sparse and scattered, short and inconspicuous, seemingly broken and apparently obliterated by abrasion with substrate, present only on anteriormost segments, extending to segments 4–5 in most individuals but to segments 6 and 9 in two females; all setae on anterior positions on carinae, no evidence of setal migration. Epiproct short and apically broad, margin nearly linear, with two long, prominent spinerets projecting caudad from ventral surface.

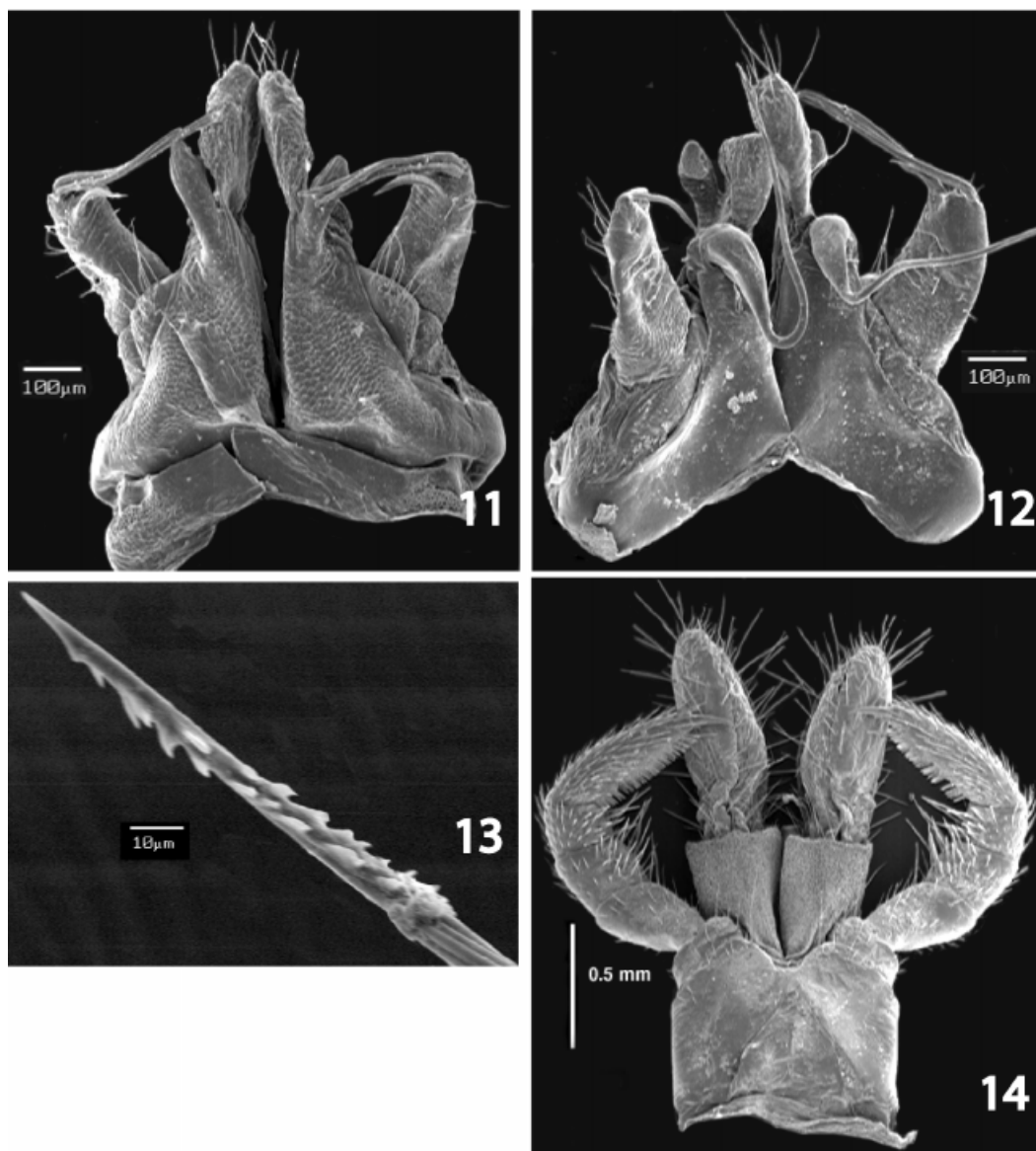
Males with first two legs slightly incrassate, first comprising only six articles, second with seven podomeres and gonapophyses arising mediad from coxae (Figs. 6–7). Remaining legs composed of 7 articles; trochanters of 9th legs with short, broad, deeply excavated, caudomedial lobes (Figs. 8–10), possessing central pore, a short spur on anteriomedial corner, and curved, spiniform projection on caudomedial corner, lying across distal margin of lobe on some legs to form a “chelicera-like” appearance (Figs. 10). Prefemora on legs in anterior 2/3 of males with ventral pads; all tarsi with ventral comb rows (Fig. 6).

Gonopods *in situ* with telopodal projections directed anteromedial, constituting anteriormost part of structure; apices of cannulae directed anteriolaterad, overhanging midlength of telopodal projections. Gonopod structure as follows (Figs. 11–12): Coxae connected basally by broad sternum extending for entire breadth of gonopods, each with two clavate processes extending directly ventrad on anterior side, a short, glabrous, anterior process arising basally from anterior side of longer, caudal process, latter apically setose, with several long setae on lateral margin at articulation with telopodite. Telopodite short and broad, positioned lateral to coxa and extending directly ventrad, without prostatic groove, with three slender, acicular, narrowly separated terminal projections directed strongly mediad; caudalmost projection longest, in some males divided near midlength into two subequal, closely appressed subbranches, curvilinear, overlapping longer coxal process and in one male (not photographed) extending slightly beyond medial margin of latter and nearly meeting corresponding projection from opposite gonopod; medial projection slightly shorter, also curvilinear, overhanging longer or shorter coxal processes; anteriormost projection shortest, broad and subfalcate, extending slightly beyond telopodal margin and terminating well short of coxal processes. Cannula long and slender, not coiled, arising near midlength of caudal side of coxa at level of origin of shorter anterior process, angling dorsomedial basally and converging with opposite member, then curling and diverging, angling anteriolaterad (anteriad in dissected specimens), apices either overhanging coxal processes or midlength of telopodal projections, or dislodged (as in right cannula in Fig. 12) and remaining on caudal side of telopodite, terminating freely, not inserting into groove or pit in telopodite, with minute barbs distally and grooves curving around structure for an unknown distance proximad (Fig. 13).

Female ovipositor as in fig. 14. Second legs with tarsal combs.



**FIGURES 6–10.** *S. simplipodicus*, male legs. 6, 2nd legs and gonapophyses, caudal view. 7, gonapophyses. 8, 9th legs, caudal view of sternum, coxae, and trochanters. 9, distal extremity of right trochanteral lobe, caudal view. 10, trochanteral lobe of a different male, ventral view. Scale bars indicate magnifications on each figure.



**FIGURES 11–14.** *S. simplipodicus*, sexual features. 11, gonopods, anterior view. 12, the same, caudal view. 13, distal extremity of cannula showing apical barbs and more proximal grooves. 14, 2nd legs and ovipositor of a female, anterior view. Scale bars indicate magnifications on each figure.

*Variation.* The Laotian specimens show a few differences from Zhang's characterization (1993) of the Chinese specimens beyond the obvious one of pigmentation. The spinnerets arise from beneath the epiproct, instead of on its caudal margin, and extend well beyond the latter. Zhang characterized the family Sinocallipodidae as one in which the diplosegments lack interzonal strictures, but as shown in fig. 4, they are distinct in the Laotian material. The gonopods agree closely with Zhang's illustrations of Chinese males (the

anterior view is of a paratype, the caudal view, the holotype [Zhang, 1993, figs. 12 & 13, respectively]), the main difference being the length and configuration of the cannula. In the Yunnan specimens, the structure is short and coiled, and lies wholly on the caudal side of the coxal processes, perhaps to some degree an artifact of the illustrations reflecting foreshortening; however, the cannula in Laotian males curves but does not coil and is much longer, extending *in situ* ventrolaterad and over (ventral to) the telopodal projections. The number of the latter can also vary; it usually is three but occasionally there are four caused by division, near midlength, of the caudalmost branch into two equivalent sub-branches that are closely appressed to each other. In one Laotian male, the left telopodite has four branches and the right, three.

In the few individuals that could be measured and whose segments could be counted, females are longer and broader than males. Segment counts are comparable; the available males have lower counts, but females show less variation.

The pigmentation and number of ocelli (41) in the Laotian specimens, compared to the lack of pigmentation and reduced number of ocelli (11–16) in those from Yunnan, imply a degree of cave adaptation in the latter.

*Natural history observations.* The Laotian specimens were encountered at around 984 ft. (300 m) elevation, 4–5 cm deep in leaf litter and humus in a wet evergreen forest. No information is available on the microhabitat of the Yunnan specimens other than the fact that they were taken in a cave.

*Distribution.* Same as that of the genus. Xiao Cave is in the southern fringe of Yunnan Province, near the town of Hekou on the Hong River near Lao Cai, Vietnam. This part of Yunnan projects southward into Laos, and Xiao Cave is at the tip of this point, just on the Chinese side of the border. The Laotian site (details below) is some 600 mi (960 km) to the south-southeast in the southernmost provinces of Laos, ca. 50 mi (80 km) from both the Thailand and Cambodian borders at their closest points.

LAOS: *Champasak/Attapu Provs.*, Dong Hua Sao National Biodiversity Conservation Area, along the Houry Phak River near the SW edge of Bolavens Plateau (lat. 15°04'37"N, long. 106°10'45"E), 5M, 9F, September 1999, H. Heatwole (North Carolina State Museum of Natural Sciences and Virginia Museum of Natural History collections).

*Remarks.* Definitive studies on the roles of the parts of the gonopod in reproduction have not been conducted, but even though the telopodal branches are, *in situ*, the anterior-most part of the gonopod of *S. simplipodicus*, we believe the cannula may be the “functional” element that directly inseminates females particularly because it terminates freely and the telopodite lacks a prostatic groove. The telopodite is also firmly attached and stationary, whereas the cannula is movable at the articulation with the coxa as evidenced by how easily it is dislodged during dissection. In the introduction to his work, Zhang (1993) stated “seminal furrow (= prostatic groove) obscurely visible,” but it is not shown on his figures nor mentioned in the gonopodal characterization in the species’ description. Care-

ful examination of the Laotian gonopods reveals no evidence of a prostatic groove, and we believe it is indeed absent. Without the groove and a connection between the cannula and telopodite, the most plausible method of spermatophore/ seminal fluid transfer seems to be by the cannula directly, which in the Laotian males is the longest gonopodal structure, could most easily contact the openings of the vasa deferentia to be “charged,” and subsequently penetrate the female cyphopods during copulation. Observing the gonopods *in situ*, it is evident that the body could be flexed and the cannulae “pushed” forward to contact the gonapophyses and cyphopods of females. If the cannulae are the “functional” element instead of the telopodite as in other callipodidans, this could be interpreted as a plesiomorphy, an early stage in gonopod development in which a “functional” telopodite is obviated by a more direct method of spermatophore transmittal that requires a less intricate structure. The presence on the 9th legs of the trochanteral lobe with short projections and an internal duct of some sort as evidenced by the central pore (Figs. 8–10) is an unknown here. This is another unique feature in *Sinocallipus*, as it is unknown from any other callipodidan.

### The Phylogenetic Position of the Callipodida

Regier and Shultz (2001) based their analysis of milliped phylogeny on the sequence of a protein-coding gene (elongation factor 1-alpha) and amino acid sequences (Pol II). Their maximum parsimony analysis placed the Callipodida as sister taxon to the Chordeumatida, the two orders together being sister-group to the Spirobolida [(Callipodida + Chordeumatida) + Spirobolida]; in turn, this clade was sister to one containing Polydesmida, Julida, Polyzoniida, and Platydesmida. This novel hypothesis contrasts with earlier ones and would not be supported by the present array of morphological evidence; the genera used may not have been appropriate for the analysis, as the authors themselves admitted. Using maximum likelihood, *Abacion* Rafinesque, 1820, the representative callipodidan, was sister to *Orthoporus* Silvestri, 1897, a spirostreptidan, while the Chordeumatida was basal to other Chilognatha. Likewise, this tree would not be supported by morphological data and would likely be unacceptable to most diplopod systematists.

The most recent attempt to hypothesize the phylogenetic position of the Callipodida was that of Sierwald *et al.* (2003), who employed standard methods of parsimony analysis and summarized previous opinions. These authors used the anatomical characters of Eng-hoff (1984) with a few additional ones and some recoding, criteria that were criticized by Regier and Shultz (2001) as leading to “Hennigian” rather than matrix-based trees. The preferred cladogram of Sierwald *et al.* (2003) showed Callipodida as sister taxon to the Chordeumatida; further structure was (Callipodida + Chordeumatida) + Stemmiulida) + Polydesmida))). Because of a dearth of characters, Siphoniulida was excluded from the preferred cladogram, but a consensus tree of the seven shortest trees that included this order did not show clear relationships between these five taxa. The loss of resolution was attributed to the large number of characters that could not be scored for the Siphoniulida.

A rigorous analysis of diplopod phylogeny based on combined anatomical and molecular data is desirable but is beyond the scope of this contribution. However, we believe new insight into ordinal relationships is possible through a reinterpretation of gonopodal characters, and as diplopod phylogeny is presently unsettled, we present the following ideas that derive primarily from broadly based research on gonopod structure by the first author. These studies suggest that the three suborders of the Spirostreptida — Cambalidea, Epinannolenidea, and Spirostreptidea (*sensu* Hoffman, 1980 and Shelley, 2003) — warrant consideration as full orders, at least the first more closely related to the Julida than to the Spirostreptidea. We are not prepared to formally elevate these taxa herein but for present purposes treat them as full orders.

In the Callipodida, Polydesmida, Chordeumatida, Stemmiulida, Siphoniulida, Spirostreptida, and Epinannolenida, the gonopods develop solely from the 8th legpair, the anterior legs on segment 7. Sierwald *et al.* (2003) believed that this group, with the possible exclusion of Spirostreptida and Epinannolenida, forms a clade (an “8th gonopod clade”) that has not been formally named. The 9th legpair in this clade may be unmodified (a normal walking leg), reduced in size or vestigial, or function as an accessory gonopod. This condition contrasts with those in the other two principal helminthomorph clades: the subclass Colobognatha, in which the “functional” gonopods seemingly develop from the 10th legs, and the eugnathan superorder Juliformia (which would include Julida, Cambalida, and Spirobolida), in which they derive from the 9th legpair; the anterior (9th and 8th) gonopods are accessory appendages in the Colobognatha and Juliformia, respectively. Definitive studies on the functions of the anterior and posterior gonopods in the latter two clades have never been conducted, and anatomical considerations are subject to varying interpretations by different researchers; the two gonopod pairs may also function differently in different families in each order. However, we note that, *in situ*, the posterior gonopods in most colobognathans and some representatives of the Julida project anteriorly and lie between the anterior gonopods, which are accordingly widely separated; consequently, the most anterior part of the gonopod complex is the distal extremity of the posterior gonopods, which exhibit distinct prostatic grooves in the tribe Aniulini of the julidan family Parajulidae (Shelley 2000*b, c*, 2001, 2002). This arrangement suggests that the posterior gonopods are the truly “functional” ones that inseminate females and that the anterior gonopods serve as “guides” to properly orient the posterior ones to contact the openings of the vasa deferentia, become “charged” with seminal fluid/a spermatophore, and subsequently transfer this to the female cyphopods.

Two previously unrecognized characters appear to hold phylogenetic significance and necessitate a different interpretation of callipodidan relationships from the traditional placement in the superorder Nematophora along with Chordeumatida and Stemmiulida (Hoffman, 1980; Shelley, 2003). Information on gonopod homologies in the Siphoniulida is absent, but in the remaining components of the “8th gonopod clade,” aside from Chordeumatida, it is evident that the gonopods develop from the entire 8th appendage including



some telopodal articles. Supporting evidence is found in anatomical studies associated with relevant systematic revisions, for example that of Krabbe (1982) for the family Spirostreptidae (Spirostreptida), and for callipodidans beginning with the description of *Rhopalopetalum blanci* Brolemann, 1932 (see also Hoffman and Lohmander, 1964; Shelley, 1996; and Stoev and Enghoff, 2003). In the Chordeumatida, however, the telopodite of legpair 8 is lost and the gonopod develops solely from the coxa, a distinguishing feature of this order (Shear 2000*b*). The second trait is the presence in the Callipodida, Polydesmida, and Stemmiulida of a cannula, an articulated, movable process that arises from the gonopodal coxa and is a presumed homologue of the julidan and cambalidan flagella. The function of the cannula is not understood, but it inserts into a basal groove or pit in the telopodite and is absent from the Chordeumatida, Spirostreptida, and Epinannolenida.

We interpret the coxal origin of chordeumatidan gonopods as an autapomorphy, because outgroup analysis to the subterclass level argues that telopodal gonopods are ancestral. This character, while suggestive, does not explicitly disrupt the postulated sister-group relationship between Callipodida and Chordeumatida, but the presence of a cannula is clearly apomorphic by outgroup comparison and supports the arrangement (Chordeumatida + (Callipodida + Polydesmida + Stemmiulida)). A character that may potentially resolve the trichotomy is the presence in Polydesmida and Stemmiulida of dimorphic sterna that are fused to the pleurotergites, whereas in Callipodida, the sterna are essentially homogeneous, the plesiomorphic state. This reasoning leads to (Chordeumatida + (Callipodida + (Polydesmida + Stemmiulida))). While this argumentation holds intellectual merit, the addition of these and other characters to the matrix of Sierwald *et al.* (2003) did not yield significantly different trees. Callipodida still emerged as sister-group to the Chordeumatida, and a strict consensus tree did not resolve the relationships between Stemmiulida, Callipodida, and Polydesmida.

Selecting characters for phylogenetic analyses is difficult, and many of those used at present are probably homoplasious. For example, “ring formation” (fusion of the pleurotergites and sterna of the individual diplosegments) may have evolved independently in the three clades represented by gonopodal traits (the “8th gonopod clade,” Colobognatha, and Juliformia), and the character “dimorphic sterna” is potentially homoplasious because the elongation of the anterior sternum correlates with the presence of a “ball and socket joint” between diplosegments in “ring formation.” Similarly, paranota have evolved independently four times in the subclass Chilognatha — in the orders Platydesmida (essentially the entire order), Siphonophorida (the genus *Pterozonium* Attems, 1951, only), Chordeumatida (several families, for example Rhiscosomididae and Tingupidae), and Polydesmida (most families) — and appear to have been repeatedly lost and even regained in the last. Sexual characters may also vary widely in a single order. In the Chordeumatida, the 9th legs may be slightly modified walking legs, moderately to strongly reduced in size and segmentation, vestigial, or, in the superfamily Heterochordeumatoidea (suborder Heterochordeumatidea), may assume the role of spermatophore transfer while the original/ante-

rior gonopods (8th legs) nearly disappear. Similarly, beginning studies on the Parajulidae by the second author show that marked differences also exist in this julidan family because the *in situ* gonopodal arrangements in other tribes differ strikingly from the previously described condition in the Aniulini. In some, the anterior gonopods are close together while the posterior gonopods are small, insignificant structures that lack a prostatic groove and adhere closely to the bases of the former, such that they cannot possibly be the “functional” element because a physically impossible distortion of the body would be required to bring the posterior gonopods into contact with the vasa deferentia and female cyphopods.

Monophyly of some milliped orders is not firmly established. Shelley (2003) formally elevated the suborder Siphonocryptidea (order Polyzoniida) to full ordinal status<sup>1</sup>, and the position of the Cambalida is controversial, being treated as an independent order and a subordinate taxon of both the Spirostreptida and Julida. Regier and Shultz (2001) based monophyly of the Julida, Polydesmida, Chordeumatida, Spirobolida, and Sphaerotheriida on molecular evidence, but only 2–5 species in these orders were examined, hardly a broad spectrum. There has never been a serious attempt to utilize intensive molecular sampling, as well as morphological characters, in a modern phylogenetic analysis of the internal composition of any diplopod order (but see Enghoff [1991]), and interordinal relationships are certainly subject to considerable debate. Despite advances, milliped phylogenetics is still at an early stage of development and needs new character systems, broader taxon sampling, and further analysis. However, we think future workers should factor the presence of an “8th gonopod clade” (including Polydesmida, Callipodida, Chordeumatida, Stemmiulida, Siphoniulida, and possibly Spirostreptida and Epinannolenida) into their considerations along with the characters, presence/absence of a cannula and development of the “functional” gonopod from coxal or telopodal and coxal articles. The possibility of the relationship, (Chordeumatida + (Callipodida + (Polydesmida + Stemmiulida))), should also be assessed.

### Acknowledgements

We thank Daqing Wang, Celia Pratt, librarian at the University of North Carolina Map Library, and Robert Murowchick, Boston University, for finding and advising on Asian localities; our colleague, S. I. Golovatch, kindly checked a literature reference that we do not have. The specimens were collected by HH on a field trip to Laos supported by National Geographic Society Grant No. 6247-98. Travel by the first author to Chicago and publication of this study were supported by National Science Foundation Partnerships-for-Enhancing-Expertise-in-Taxonomy (PEET) grant number DEB 9712438 to P. Sierwald and W. A. Shear.

---

1. Following the unpublished analysis of Shear, which found siphonocryptids to be more closely related to the order Platydesmida than to the Polyzoniida.

- Attems, C. (1936) Diplopoda of India. *Memoirs of the Indian Museum*, 11, 133–323.
- Attems, C. (1951) Myriopoden vom Iran gesammelt von der Expedition Heinz Löffler und Genossen 1949/50. *Sitzungsberichte der österreichischen Akademie der Wissenschaften, Abteilung. I*, 160, 387–426.
- Brolemann, H.W. (1932) Lysiopétalide (Myriapode-Diplopode) cavernicole nouveau recueilli en Grèce par M. Le Dr. Georges Blanc, directeur de l'Institut Pasteur du Maroc. *Bulletin de la Société zoologique de France*, 55, 45–53.
- Demange, J.-M. (1946) *Callipus foetidissimus gallicus denticulatus* nov. var. des catacombes du Muséum d'Histoire Naturelle de Paris (Myriapodes Diplopodes). *Bulletin du Muséum National d'Histoire naturelle, Paris, 2nd Série.*, 18(5), 394–396.
- Enghoff, H. (1984) Phylogeny of millipedes — a cladistic analysis. *Zoologische Systematik und Evolutionsforschung*, 22, 8–26.
- Enghoff, H. (1991) A revised cladistic analysis of the millipede order Julida. With establishment of four new families and description of a new nemasomatid genus from Japan. *Zoologische Systematik und Evolutionsforschung*, 29, 241–263.
- Enghoff, H., & Schembri, P.J. (1989) The millipedes of the Maltese Islands (central Mediterranean). *Bolletino della Società entomologica Italiana, Genova*, 120(3), 164–173.
- Foddai, D., Minelli, A., Scheller, U., & Zapparoli, M. (1995) Chilopoda, Diplopoda, Pauropoda, Symphyla. Fasc. 32, pp. 1–35 In: Minelli, A., Ruffo, S., & LaPosta, S., eds., Checklist delle Species della Fauna Italiana. Comitato Scientifico per la Fauna d'Italia, Ministero dell'Ambiente Servizio Conservazione della Natura, Commission of the European Communities, Edizioni Calderini, Bologna.
- Glaubrecht, M., & Spelda, J. (1993) On the genus *Eurygyrus* Kock, 1847 (Diplopoda: Callipodida: Schizopetalidae) in the Dodecanese; zoogeography and female choice theory. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 90, 285–311.
- Golovatch, S.I. (1979) The composition and zoogeographic relationships of the diplopod fauna of middle Asia. Part I. *Zoologicheskii Zhurnal*, 58(7), 987–1001 (In Russian).
- Golovatch, S.I. (1981) Some east-Asiatic millipedes (Diplopoda) in the collection of the Institute of Zoology of the Polish Academy of Sciences. *Annales Zoologic Warszawa*, 36, 161–168.
- Golovatch, S.I. (1983) A contribution to the millipede fauna of Iran (Diplopoda). *Annalen des Naturhistorischen Museums in Wien*, 85, 157–169.
- Golovatch, S.I. (1991) On a small collection of millipedes (Diplopoda) from northern Pakistan and its zoogeographic significance. *Revue suisse de Zoologie*, 98(4), 865–878.
- Hoffman, R.L. (1980 [1979]) *Classification of the Diplopoda*. Muséum d'Histoire Naturelle, Genève, 237 pp.
- Hoffman, R.L., & Lohmander, H. (1964) The Diplopoda of Turkey. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 62, 101–151.
- Kime, R.D. (2000) Present knowledge of the distribution of European millipedes (Diplopoda). *Fragmenta Faunistica Warszawa Supplement*, 43, 281–294.
- Korsós, Z. (1994) Checklist, preliminary distribution maps, and bibliography of millipedes in Hungary (Diplopoda). *Miscellanea Zoologica Hungarica*, 9, 29–82.
- Krabbe, E. (1982) Systematik der Spirostreptidae (Diplopoda, Spirostreptomorpha). *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, 24, 1–476.
- Ladeiro, J.M. (1943) Catálogo dos Miriópodes de Portugal existentes no Museu Zoológico de Coimbra. *Memórias e estudos do Museu Zoológico da Universidade de Coimbra No. 146*, 1–16.
- Lindberg, K. (1961) Recherches biospéléologiques en Afghanistan. *Lunds Univerites Årsskrift.*, N. F. 2, 57(1), 1–39.
- Lindberg, K. (1962) Recherches biospéléologiques en Afghanistan II. *Lunds Univerites Årsskrift.*, N. F. 2, 58(2), 1–15. (Not seen, referenced based on citation by Golovatch (1983)).
- Lohmander, H. (1932) Über Diplopoden aus Zentralasien. *Arkiv för Zoologi*, 25A(6), 1–71.
- Mauriès, J.-P. (1978) Myriapodes — Diplopodes du sud de l'Espagne. *Annalen des Naturhistorischen Museums in Wien*, 81, 575–588.
- Mauriès, J.-P., Golovatch, S.I., & Stoev, P. (1997) The millipedes of Albania: recent data, new taxa; systematical, nomenclatural and faunistical review (Myriapoda, Diplopoda). *Zoosystema*, 19(2–3), 255–292.
- Minelli, A. (1985) Catalogo dei Diplopodi e dei Chilopodi cavernicoli italiani. In: Cianficconi, F., Moretti, G.P., Minelli, A., Brignoli, P.M., & Poggi, R., Contributi alla Conoscenza Della Fauna Cavernicola Ital-

- iana. *Memorie del Museo Civico di Storia Naturale di Verona (II Serie) Sez. Biologica*, 4, 1–50.
- Regier, J.C., & Shultz, J.W. (2001) A phylogenetic analysis of Myriapoda (Arthropoda) using two nuclear protein-coding genes. *Zoological Journal of the Linnean Society*, 132, 469–486.
- Shear, W.A. (2000a) A new genus and species of callipodidan milliped from Vietnam (Callipodida: Schizopetalidae). *Myriapodologica*, 6(11), 95–100.
- Shear, W.A. (2000b) On the milliped family Heterochordeumatidae, with comments on the higher classification of the order Chordeumatida (Diplopoda). *Invertebrate Taxonomy*, 14, 363–376.
- Shelley, R.M. (1984) A synopsis of the milliped genus *Abacion* Rafinesque (Callipodida: Caspiopetalidae). *Canadian Journal of Zoology*, 62, 980–988.
- Shelley, R.M. (1989) The milliped genus *Texophon* Chamberlin and the new tribe Texophonini (Callipodida: Schizopetalidae). *Southwestern Naturalist*, 34(3), 381–391.
- Shelley, R.M. (1996) The milliped order Callipodida in western North America (Schizopetalidae: Tynommatinae). *Entomologica Scandinavica*, 27, 25–64.
- Shelley, R.M. (1997) *Colactoides grandis*, n. gen., n. sp., a new callipodoid milliped from Chihuahua (Schizopetalidae: Tynommatinae: Colactidini). *Myriapodologica*, 5(3), 33–39.
- Shelley, R.M. (2000a) A new callipodoid milliped genus and species from Sinaloa, with the proposal of a new tribe in the subfamily Tynommatinae (Schizopetalidae). *Myriapodologica*, 6(9), 83–86.
- Shelley, R.M. (2000b) Parajulid studies II. The subgenus *Hakiulus* Chamberlin (Julida: Parajulidae: Parajulinae: Aniulini). *Myriapodologica*, 6(14), 121–145.
- Shelley, R.M. (2000c) Parajulid studies III. The genus *Gyniulus* Loomis (Parajulinae: Aniulini). *Myriapodologica*, 7(3), 19–28.
- Shelley, R.M. (2001) A synopsis of the milliped genus *Aniulus* Chamberlin (Julida: Parajulidae: Parajulinae: Aniulini). *Texas Memorial Museum Speleological Monographs*, 5, 73–94.
- Shelley, R.M. (2002) The milliped genus *Oriulus* Chamberlin (Julida: Parajulidae). *Canadian Journal of Zoology*, 80, 100–109.
- Shelley, R.M. (2003) A revised, annotated, family-level classification of the Diplopoda. *Arthropoda Selecta*, 11, 187–207.
- Shelley, R.M., Sierwald, P., Kiser, S.B., & Golovatch, S.I. (2000) *Nomenclator Generum et Familiarum Diplopodorum II, A List of the Genus and Family-Group Names in the Class Diplopoda from 1958 through 1999*. Pensoft Publishers, 167 pp.
- Stoev, P., & Enghoff, H. (2003) Systematics, phylogeny and biogeography of the genus *Balkanopetalum* Verhoeff, 1926 (Diplopoda: Callipodida: Schizopetalidae). *Zootaxa*, 272, 1–26.
- Strasser, K. (1966) Über Diplopoden Bulgariens. *Annales Zoologici, Warszawa*, 23, 325–385.
- Strasser, K. (1969) Über Diplopoden Bulgariens, II. *Annales Zoologici, Warszawa*, 27, 133–168.
- Strasser, K. (1973) Über Diplopoden Bulgariens, III. *Annales Zoologici, Warszawa*, 30, 411–470.
- Strasser, K. (1975) Weiterer Beitrag zur Kenntnis der bulgarischen Diplopoden. *Acta zoologica bulgarica*, 3, 70–77.
- Verhoeff, K.W. (1893) Neue Diplopoda der Portugiesischen Fauna. *Zoologischer Anzeiger*, 16, 156–159, 169.
- Verhoeff, K.W. (1895) Aphorismen zur Biologie, Morphologie, Gattungs- und Art-Systematik der Diplopoden. *Zoologischer Anzeiger*, 18, 203–211, 213–226, 237–244.
- Verhoeff, K.W. (1900) Zur vergleichenden Morphologie, Phylogenie, Gruppen- und Art-systematik der Lysio-petaliden. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Thiere*, 13, 36–70.
- Verhoeff, K.W. (1909) Neues System der Diplopoda-Lysio-petaloida und über italienische *Callipus*-Arten. *Sitzungsberichte der Gesellschaft Naturforschender Freunde [Berlin] No. 4*, vol. for 1909, 209–219.
- Wang, D. (1996) A preliminary study on phylogeny and biogeography of the family Paracortinidae (Myriapoda: Callipodida): a cladistic analysis. *Mémoires de Musée national d'Histoire naturelle*, 169, 307–311.
- Wang, D. & Mauriès, J.P. (1996) Review and perspective of study on Myriapodology of China. *Mémoires de Muséum national d'Histoire naturelle*, 169, 81–99.
- Wang, D. & Zhang, C. (1993) A new family of millipeds (Diplopoda: Callipodida) from southwestern China. *Memoirs of the Peking Natural History Museum*, 53, 375–390.
- Zhang, C. (1993) Diplopoda from Yunnan caves II. Contribution to the study of a new cavernous taxon of the nematophoran millipeds (Diplopoda: Coelocheta: Callipodida). *Proceedings of the XI International Congress of Speleology*, vol. for 1993, 128–130.