

# Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Part 1: the *granulatus*-group

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## ABSTRACT

The large, widespread, Southeast Asian genus *Glyphiulus* Gervais, 1847 is reviewed, with special reference to the *granulatus*-group, established for the species whose primary characteristics are that the males have sternum 1 devoid of median structures, but supplied with two widely separated prongs, at the base of which are often 1- or 2-segmented vestigial legs, along with the carinotaxy patterns of the collum and metaterga which are highly characteristic and often stable. This group currently encompasses 20 species, all keyed here, including the redescribed pantropical species *G. granulatus* (Gervais, 1847), as well as *G. subgranulatus* n. sp., *G. paragranelatus* n. sp., *G. semigranelatus* n. sp., *G. beroni* n. sp., *G. debarvengi* n. sp., *G. pergranulatus* n. sp., *G. latellai* n. sp. and *G. basalis* n. sp., all from caves in southern China, and *G. bedosae* n. sp. from a cave in Laos. The following two synonymies are established: *G. granulatus* (Gervais, 1847) = *G. vulgatus* Zhang & Li, 1982, and *G. septentrionalis* Murakami, 1975 = *G. multicarinus* Zhang & Li, 1982.

## KEY WORDS

Diplopoda,  
Cambalopsidae,  
*Glyphiulus*,  
cave,  
Southeast Asia,  
China,  
Laos,  
new species.

## RÉSUMÉ

Révision des diplopedes du genre *Glyphiulus* Gervais, 1847 et description de nouvelles espèces d'Asie du Sud-Est (*Diplopoda*, *Spirostreptida*, *Cambalopsidae*).  
Partie 1: le groupe *granulatus*.

*Glyphiulus* Gervais, 1847, genre de Cambalopsidae sud-est asiatique et à très large répartition, est révisé. Une attention particulière est portée au groupe *granulatus*, établi pour les espèces dont les caractéristiques principales sont, d'une part, le sternum 1 du mâle dépourvu de structures médianes mais présentant deux prolongements largement séparés, à la base desquels se trouvent des pattes vestigiales comportant le plus souvent un, parfois deux, articles; et, d'autre part, la structure et la disposition des carènes du collum et des métatergites hautement caractéristiques et souvent stables. Ce groupe comporte 20 espèces qui figurent toutes dans une clé. Il inclut l'espèce pantropicale *G. granulatus* (Gervais, 1847), qui est redécrite, ainsi que *G. subgranulatus* n. sp., *G. paraganulatus* n. sp., *G. semigranulatus* n. sp., *G. beroni* n. sp., *G. deharvengi* n. sp., *G. pergranulatus* n. sp., *G. latellai* n. sp. et *G. basalis* n. sp., provenant de grottes du sud de la Chine, de même que *G. bedosae* n. sp. provenant d'une grotte du Laos. Les deux synonymies suivantes sont formellement établies: *G. granulatus* (Gervais, 1847) = *G. vulgatus* Zhang & Li, 1982 et *G. septentrionalis* Murakami, 1975 = *G. multicarinatus* Zhang & Li, 1982.

## MOTS CLÉS

Diplopoda,  
Cambalopsidae,  
*Glyphiulus*,  
grotte,  
Asie du Sud-Est,  
Chine,  
Laos,  
espèces nouvelles.

## INTRODUCTION

*Glyphiulus* Gervais, 1847 was first proposed as a subgenus of the then all-embracing genus *Iulus* Linnaeus, 1758 (recte: *Iulus*) for a peculiar, strongly ornamented juliform, *J. granulatus* Gervais, 1847 (Fig. 1), taken on two of the Mascarene islands in the Indian Ocean (Gervais 1847). A similarly strongly-crested juliform was described soon afterwards as a new genus and species, *Trachyjulus ceylanicus* Peters, 1864, from Sri Lanka (Peters 1864). Karsch (1881) proposed two further species of *Glyphiulus*, but both have since been shown to belong in other genera, within the same superorder Juliformia, but only very remotely related to *Glyphiulus* (Krabbe 1982).

Pocock (1893, 1894), when describing several further strongly-crested species from Myanmar (Burma), Java and Sumatra, synonymized both *Glyphiulus* and *Trachyjulus* with *Cambala* Say, 1821, a genus created long before for the North American *C. annulata* Say, 1821. Soon afterwards, however, Pocock (1895) resurrected *Glyphiulus* for *G. granu-*

*latus*, and *Trachyjulus* for *T. ceylanicus* (misspelled as *T. ceylonicus*). He also described *Cambalomorpha formosa* Pocock, 1895, from Hong Kong, added two further species from Myanmar to *Cambalomorpha*, and proposed the genus *Cambalopsis* Pocock, 1895 for his *Cambala calva* Pocock, 1893 (incorrectly written as *Cambalopsis calvus*).

Since then, *Glyphiulus* has become one of the most speciose and characteristic genera in the millipede fauna of Southeast Asia, with about 20 species recognized to date, while the genus itself has as many as seven synonyms (Jeekel 2004). There is no general agreement concerning the scope of the genus *Glyphiulus* or of the family Cambalopsidae Cook, 1895, to which it belongs. Cambalopsidae are currently divided into three subfamilies (Mauriès 1983, 1992; Jeekel 1985, 2004). Cambalopsinae Cook, 1895 comprise the single but speciose genus *Trachyjulus* (28 species or subspecies ranging mainly from Sri Lanka, India and Nepal in the West, through Vietnam, Thailand and Malaysia up to Sulawesi, Indonesia

in the East). Besides *Glyphiulus*, the Glyphiulinae Chamberlin, 1922 include the genera *Dolichoglyphius* Verhoeff, 1938 (one species with two subspecies from the Ryukyus, Japan), *Hypocambala* Silvestri, 1897 (11 nominate species, scattered from Mauritius, Seychelles and Comoro Islands in the West, through Vietnam, Thailand and Indonesia up to the Loyalty Islands, Bismarck Archipelago and New Caledonia in the East), *Plusioglyphiulus* Silvestri, 1923 (five species in Cambodia, Malaya and Borneo) and *Podoglyphiulus* Attems, 1909 (10 species or subspecies from Sri Lanka, India, Nepal and Myanmar). Pericambalinae Silvestri, 1909 are represented by three monotypic genera, *Bilingulus* Zhang & Li, 1981, *Chonecambala* Mauriès & Enghoff, 2000 and *Pericambala* Silvestri, 1909, and by the oligotypic genus *Parabilingulus* Zhang & Li, 1981 (two species), all from China or Vietnam. These subfamilies, as well as the genera concerned, have been based primarily on differences in the conformation of the mentum of the gnathochilarium and, to a lesser degree, in anterior gonopod structure, tergal ornamentation and a few other characters (Jeekel 1963, 1985; Mauriès 1970, 1977, 1981, 1983; Hoffman 1977). Sometimes the family is even allotted the rank of a superfamily, with the constituent subfamilies thus referred to as families (Mauriès & Nguyen Duy-Jacquemin 1997).

There is no general agreement even as regards the position of the Cambalopsidae in the higher classification of the Juliformia. Hoffman (1980) and Jeekel (1985, 2004) treat the Cambalopsidae as belonging to the order Spirostreptida, whereas Mauriès (1977, 1987, 1992) considers the family to be a member of the order Julida.

In short, up to now there has been a lot of confusion concerning the status, relationships and scope of the Cambalopsidae, as well as of the subfamilies and genera included therein. For practical reasons alone, the classification adopted here follows the latest catalogue and review by Jeekel (2004), with a few minor but relevant updates at the specific level.

A large number of cambalopsids, mostly cavernicolous, originating from various parts of Southeast Asia have become available to us for study from

various sources. Because this material contains numerous new species, many of which represent *Glyphiulus* s.l., a review of the genus became warranted.

The heterogeneity of *Glyphiulus* has already been noted by Attems (1938) and Mauriès (1970, 1977), who outlined several species groups. Because of this, we have decided to focus first on the distinct group of species closely related to *G. granulatus*. Strangely enough, this widespread, pantropical species, the type of *Glyphiulus*, has hitherto been scarcely illustrated. The line drawings of Attems (1900), partly republished by Attems (1926) and reproduced here as Figure 6A-D, seem to be the only meaningful illustrations depicting the male characters of *G. granulatus*. It is therefore not surprising that this species has several junior synonyms, including one proposed as new below. Additional line drawings by Brolemann of female characters (from his unpublished "Iconographie" housed in MNHN), only some of which have been published before (Brolemann 1931), are also given here as Figure 6E-H.

The treatment of the remaining *Glyphiulus* s.l. that do not belong to the *granulatus*-group is currently in preparation (Golovatch *et al.* in press and forthcoming papers).

This paper continues the general studies of Southeast Asian cave diplopod collections carried out recently in part at the MNHN (Geoffroy & Golovatch 2004; Stoev 2004; Stoev & Geoffroy 2004; Stoev & Enghoff 2005; Mauriès 2005; Golovatch *et al.* 2006a, b).

#### ABBREVIATIONS

MCSNV	Museo Civico di Storia naturale, Verona;
MNHN	Muséum national d'Histoire naturelle, Paris;
MRAC	Musée royal de l'Afrique centrale, Tervuren;
NMNHS	National Museum of Natural History, Sofia;
SEM	scanning electron microscopy;
ZMUC	Zoological Museum, University of Copenhagen;
ZMUM	Zoological Museum, Moscow State University.

#### MATERIAL AND METHODS

The material serving as the basis for the present contribution derives from the subterranean

collections made by Anne Bedos and Louis Deharveng (MNHN) in Laos and southern China, as well as by both Josiane and Bernard Lips (Vil-leurbanne, France), Petar Beron (NMNHS) and Leonardo Latella (MCSNV) and his collaborators in southern China. The bulk of this material has been deposited in MNHN and NMNHS, with a few voucher specimens shared with the collections of MCSNV, ZMUC and ZMUM.

SEM micrographs were taken using a JEOL JSM-6480LV scanning electron microscope. Dry SEM material was coated with gold and removed as such from stubs and returned into alcohol, all samples being kept at MNHN.

The carinotaxy formulae in the descriptions below are mainly those proposed by Hoffman (1977), but with modifications. The carinotaxy formula of the collum designates the main, uninterrupted crests by Roman numerals, the interrupted ones by Arabic numerals (frontally interrupted marked “a”, caudally interrupted marked “c”), the paramedian and median crests are designated by either upper case “P” or “M” or by lower case “p” or “m”, respectively. This allows not only the number but also the location and shape of the respective crest to be indicated (*cf.* Hoffman 1977). Thus, a typical arrangement (from laterad to mesad) and form of the crests on the collum in the species group concerned is as follows: I-VI+7a+pc+ma+pc+7a+VI-I. So it differs from the simplified VI-VI and 2-m-2 formula that Hoffman (1977) provided for *G. granulatus*.

The carinotaxy pattern of metaterga first shows the number of crests below the ozoporiferous one (designated as “I”), followed by that between the “I”. A typical carinotaxy formula of metaterga in the species group concerned is as follows: 3+I+3+I+3 or 2+I+3+I+2. As the crests are usually divided transversely into two halves, while the median crest is often doubled anteriorly, the formula becomes 3(2)+I+4+I+3(2) and 3(2)+i+3+i+3(2), each part corresponding to the number of transverse rows of tubercles (Hoffman 1977).

The body segment counts follow Enghoff *et al.* (1993), with minor modifications.

## SYSTEMATICS

Order SPIROSTREPTIDA Brandt, 1833  
Suborder CAMBALIDEA Bollman, 1893

Family CAMBALOPSIDAE Cook, 1895

Cambalopsidae Cook, 1895: 6.

Trachyiulidae Silvestri, 1896 (recte: Trachyulidae): 52.

Glyphiulinae Chamberlin, 1922: 2.

Agastrophinae Verhoeff, 1924: 74.

Dolichoglyphiulinae Verhoeff, 1938: 88.

Genus *Glyphiulus* Gervais, 1847

*Glyphiulus* Gervais, 1847: 170.

*Glyphijulus* Karsch, 1881: 14. Type species: *Iulus* (recte: *Julus*) *granulatus* Gervais, 1847; a junior objective synonym, synonymized by Jeekel (1971).

*Cambalomorpha* Pocock, 1895: 363. Type species: *Cambalomorpha formosa* Pocock, 1895; synonymized by Mauriès (1970).

*Keratoglyphiulus* Attems, 1909: 63. Type species: *Iulus* (recte: *Julus*) *granulatus* Gervais, 1847; a junior objective synonym, synonymized by Verhoeff (1924).

*Formosoglyphius* Verhoeff, 1936: 56. Type species: *Formosoglyphius tuberculatus* Verhoeff, 1936; synonymized by Mauriès (1970).

*Koinoglyphius* Carl, 1941: 287. Type species: *Glyphiulus superbus* Silvestri, 1923; synonymized by Jeekel (2004).

*Octoglyphus* Loksa, 1960: 142. Type species: *Octoglyphus pulcher* Loksa, 1960; synonymized by Murakami (1975).

*Trogloglyphus* Loksa, 1960: 139. Type species: *Trogloglyphus balazsi* Loksa, 1960; synonymized by Mauriès (1970).

TYPE SPECIES. — *Iulus* (recte: *Julus*) *granulatus* Gervais, 1847.

SPECIES INCLUDED. — Below is a checklist of the species currently attributed to *Glyphiulus*, arranged in alphabetical order (after Jeekel 2004). In contrast, Mauriès & Nguyen Duy-Jacquemin (1997) referred to only 16 or 17 species as belonging to this genus, depending on synonymy.

1. *G. adeloglyphus* Zhang & Li, 1982, described from

- Xingping, Guangxi Province, China; still only known from the original description (Zhang & Li 1982).
2. *G. anophthalmus* (Loksa, 1960), described as *Trogloglyphus anophthalmus* Loksa, 1960 from Nyu-Jie Cave near Pulung (= Fulong, near the frontier with Vietnam), Guangxi Province, China; still only known from the original description (Loksa 1960).
  3. *G. balazsi* (Loksa, 1960), described as *Trogloglyphus balazsi* Loksa, 1960 from Lodjen (= Luodian, or Longping), southern Guizhou Province, China; still only known from the original description (Loksa 1960).
  4. *G. capucinus* Attems, 1938, described from Mt. Bana, Danang Province, central Vietnam (Enghoff *et al.* 2004); still only known from the original description (Attems 1938).
  5. *G. formosus* (Pocock, 1895), described as *Cambalomorpha formosa* Pocock, 1895 from Hong Kong, China; known from the original description (Pocock 1895) and a partial redescription (Mauriès 1970).
  6. *G. granulatus* (Gervais, 1847), described as *Iulus* (recte: *Julus*) (*Glyphiulus*) *granulatus* Gervais, 1847 from Mauritius and Réunion islands, Indian Ocean; currently known as a pantropical “tramp” species from Hawaii, Hong Kong, Marquesas, Society Islands, Cook Islands, Samoa, Loyalty Islands and New Caledonia in the Pacific Ocean, from the Mascarenes, Seychelles and Comoro Islands in the Indian Ocean, and from St. Helena in the Atlantic Ocean (Jeekel 2004). *Cambala nodulosa* Butler, 1876, from Rodrigues Island, Mascarene Islands, *Formosoglyphius tuberculatus* Verhoeff, 1936, from Taiwan, and *Glyphiulus vulgatus* Zhang & Li, 1982, from Longzhou, Guangxi Province, China, are junior subjective synonyms of this species (see below).
  7. *G. javanicus* Carl, 1911, described from Passaroean, Java, Indonesia; still only known from the original description (Carl 1911).
  8. *G. lipsorum* Mauriès & Nguyen Duy-Jacquemin, 1997, described and only known from a cave not in Hubei Province, China, as reported originally (Mauriès & Nguyen Duy-Jacquemin 1997), but in Guangxi Province (Fig. 30).
  9. *G. mediavor* Attems, 1938, described from Mt. Bana, Danang Province, central Vietnam (Enghoff *et al.* 2004); still only known from the original description (Attems 1938).
  10. *G. melanoporus* Mauriès & Nguyen Duy-Jacquemin, 1997, described and only known from a cave near Guilin, Guangxi Province, China (Mauriès & Nguyen Duy-Jacquemin 1997).
  11. *G. pulcher* (Loksa, 1960), described as *Octoglyphus pulcher* Loksa, 1960 from Nyu-Jie Cave near Pulung (= Fulong, near the frontier with Vietnam), Guangxi Province, China; still only known from the original description (Loksa 1960).
  12. *G. quadrohamatus* Chen & Meng, 1991, described from several caves in the Zhenning Bouyazu Miaoizu Autonomous County, Guizhou Province, China (Chen & Meng 1991).
  13. *G. rayrouchi* Mauriès & Nguyen Duy-Jacquemin, 1997, described and only known from Hei Yan Cave near Maguan, Guizhou Province, China (Mauriès & Nguyen Duy-Jacquemin 1997).
  14. *G. recticullus* Zhang & Li, 1982, described and still only known from Qinyuan, Zhejiang Province, China (Zhang & Li 1982).
  15. *G. septentrionalis* Murakami, 1975, described from Okinawa Island, Ryukyus, Japan (Murakami 1975), but apparently introduced there from continental China, given that *G. multicarinus* Zhang & Li, 1982, described from near Guilin, Guangxi Province, China (Zhang & Li 1982), is its junior synonym (see below).
  16. *G. siamensis* Mauriès, 1983, described and still only known from Doi Sutep, northern Thailand (Mauriès 1983). Enghoff (2005) records further material from the type locality.
  17. *G. superbus* Silvestri, 1923, described from Dalat, Lamdong Province, central Vietnam (Attems 1938), later recorded from Kampot, Cambodia (Attems 1953), although the latter record needs confirmation (Enghoff *et al.* 2004). The carinotaxy formula as given in the original description is somewhat ambiguous (Silvestri 1923) and difficult to interpret (see key below).
  18. *G. vietnamicus* Mauriès, 1977, described and only known from a cave in Ke Bang karst, Quang-Binh Province, Vietnam (Mauriès 1977; Enghoff *et al.* 2004).
  19. *G. zorzini* Mauriès & Nguyen Duy-Jacquemin, 1997, described and still only known from Anjia Yan Cave, Shuichang County, Guizhou Province, China (Mauriès & Nguyen Duy-Jacquemin 1997).

### The *granulatus*-group

#### REMARKS

Species of the *granulatus*-group are distinguished by the following characters:

1. Male legs 1 are usually very strongly reduced, represented solely or mainly by a sternum lacking any median structures but bearing strongly separated, evidently curved prongs with a leg vestige on each side at base (usually represented by just a few setae, more seldom also one or two rudimentary segments). Very seldom, a nearly complete telopodite persists, but the sternum still supports a pair of widely separated and

- curved prongs. [Male legs 1 with central structures on the sternum in other groups].
2. Other male legs normal or nearly so, not enlarged. [Male legs 2 sometimes incrassate in other groups].
  3. A typical carinotaxy pattern of the collum is I-VI+7a+pc+ma+pc+7a+VI-I. Quite often the pattern is different, either due to crest reduction (especially anteriorly) or hypertrophy, but a median crest is always traceable, at least near the caudal margin. [Usually typical carinotaxy formulae of the collum are different in other groups].
  4. A typical carinotaxy pattern of the metaterga is 3(2)+I+3+I+3(2). The crests usually being divided transversely into two halves, while the median crest is often doubled anteriorly, the formula becomes 3(2)+I+4+I+3(2) and 3(2)+i+3+i+3(2). If the pattern is different, it is usually readily derived from the typical one (or *vice versa*), i.e. the lateral crests are reduced to two or the crests are undivided, or some of the crests are divided into three, rather than two, transverse rows of tubercles (see also below), etc. A median crest, even when strongly reduced, is always present as well. [Usually typical carinotaxy formulae of the metaterga are different in other groups].
  5. The anterior gonopods are reduced to a plate-like coxosternum with moveable, lateral, 1-segmented telopodites. [Shared with some other species groups].
  6. The posterior gonopods are highly compressed, showing a subflagelliform (rarely subspatuliform), often plumose, distal process. [Shared with some other species groups].
  7. The pleural flaps behind the gonopod opening on male segment 7 usually do not form an apparent transverse ventral ridge. [Shared with some other species groups].

The group thus roughly corresponds to the concept of *Glyphiulus* in the sense of Verhoeff (1936) and Loksa (1960). At present it contains the following species: *G. adeloglyphus*, *G. anophthalmus*, *G. balazsi*, *G. capucinus*, *G. granulatus*, *G. lipsorum*, *G. melanoporus*, *G. quadrohamatus*, *G. rayrouchi*, *G. septentrionalis*, *G. superbus*, as well as all nine new species described below.

The remaining known cambalopsid species are considered as belonging to other groups and will be treated elsewhere.

Below a description is given of the available material, followed by a key to all of the constituent species of the *granulatus*-group, as well as a brief analysis of their variation and distribution.

*Glyphiulus granulatus* (Gervais, 1847)  
(Figs 1-6)

*Iulus granulatus* Gervais, 1847: 170, pl. 44, fig. 10.

*Glyphiulus granulatus* – Karsch 1881: 14.

*Cambala nodulosa* Butler, 1876: 444, synonymized by Jeekel (2004: 53).

*Formosoglyphius tuberculatus* Verhoeff, 1936: 57, figs 7-9, synonymized by Korsós (2004: 18, 19).

*Glyphiulus vulgatus* Zhang & Li, 1982: 85-87, figs 1-6, **n. syn.**

TYPE MATERIAL. — **Réunion** (= Île Bourbon). *La Bonite*, 1838, leg. Eydoux, lectotype ♀ (incomplete, lacking caudal body end), 5 ♀♀ paralectotypes (all fragmented), all here designated (MNHN GA 013); material in rather poor condition (most legs missing), apparently dried before being placed in alcohol.

Mauriès (1983) mentioned that only part of the type material of this species is still preserved in the MNHN, with the series from Île de France (= Mauritius) presumably being lost. The lectotype selection made here is necessary to fix the exact type locality (Réunion Island).

TYPE LOCALITY. — Réunion.

OTHER MATERIAL EXAMINED. — **Réunion**. 10.II.1972, leg. J. Travé, strict topotype juv. ♀ (MNHN GA 022). **Mauritius**. Near Mahébourg, sugar cane debris, 6.II.1972, leg. J. Travé, 1 ♀ (det. J.-P. Mauriès, MNHN GA 022).

**Comoros**. Mayotte Island, Mt. Combani, 12°48'S, 045°08'E, 470 m, Winkler extraction of forest litter, 22-24.II.1999, leg. Jocqué & De Smet, 3 ♂♂, 1 ♀, 1 juv. (ZMUM, ex coll. MRAC No. 017.940), several ♂♂ and ♀♀ (SEM).

**China**. Hong Kong, leg. M. Crosland, det. J.-P. Mauriès, 2 ♀♀ (MNHN GA 013).

**Fiji**. Viti Levu Island, Suva, park, in litter, 5.VI.1980, leg., det. & don. S. Golovatch, 1 ♂ (MNHN GA 013).

**Seychelles**. Mahé Island, 1892, leg. C. Alluaud, det. H. W. Brölemann, 1 complete ♀, 1 incomplete ♀ (MNHN GA 013).

**New Caledonia**. Dumbea, leg. Mme Pruvot, det. H. W. Brölemann, 4 ♂♂, 2 ♀♀ (MNHN GA 013).

**Loyalty Islands**. Lifou, leg. Mme Pruvot, det. H. Brölemann, 1 incomplete ♀ (MNHN GA 013).

DIAGNOSIS. — Differs from congeners primarily by the peculiar anterior gonopods, each showing an unusually high median outgrowth of the coxosternum, combined with the typical patterns of carinotaxy.

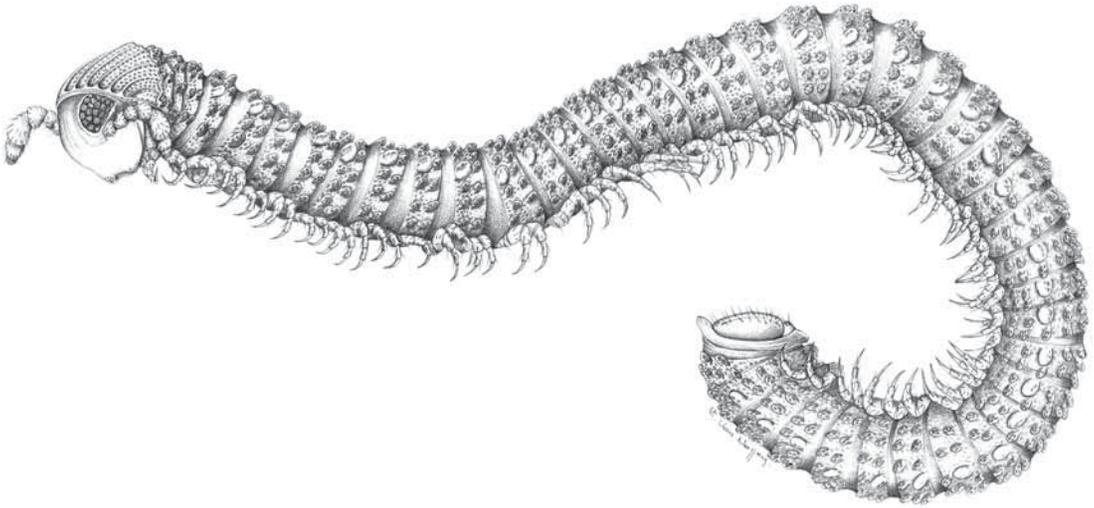


FIG. 1. — Habitus of *Glyphiulus granulatus* (Gervais, 1847), ♂ from the Comoro Islands (del. N. E. Van Noppen, MRAC).

#### DESCRIPTION

Length of adults of both sexes 10–18 mm, midbody segments round in cross-section (Fig. 3B), their width (horizontal diameter) and height (vertical diameter) similar, 0.6–0.9 mm. Coloration yellow-brown; non-faded specimens variegated, with a dark brown vertex, blackish ocellaria, mainly brown crests on collum and brownish lateral longitudinal stripes beginning from dark brown ozoporiferous tubercles. Sometimes a thin axial line traceable due to darker median crests.

Adult body with 30–53 podous segments + 4–2 apodous ones + telson (formula 30–38p+4a+T in smaller specimens, up to 44–53p+2a+T in larger ones; formulae generally following Enghoff *et al.* 1993). Clypeus with 3–6 teeth anteromedially. Eye patches transversely ribbon-shaped (smaller specimens) to ovoid (larger individuals), each composed of 11–18 rather flat ocelli in 5 or 6 irregular longitudinal rows (Fig. 4A). Antennae short and clavate (Figs 2B; 3A; 4A), antennomeres 6 and 7 with a small distodorsal field or corolla of bacilliform sensilla (Fig. 4B, C). Gnathochilarium usually, but not always ( $n = 10:1$ ), with a separate promentum (Fig. 3A).

Head width = segment 2 < collum = midbody segments (close to 18th to 20th) > segment 3 = 6 >

4 = 5 < 7 < 8 = 10; body abruptly tapering toward telson on a few posteriormost segments. Postcollar constriction very evident (Fig. 2C).

Collum with 7+7 longitudinal crests starting from fore edge, but both median crests interrupted in about caudal 1/3, being replaced there by similar 1+1+1 crests (Fig. 2A–C) (formula I–VI+7a+pc+ma+pc+7a+VI–I).

Subsequent metaterga similarly strongly crested (Fig. 2B–E), especially so from segment 5 onwards, whence enlarged pore-bearing tubercles commence, less evident on legless segments in front of telson due to loss of ozopores (Fig. 2E). Ozoporiferous tubercles round, wider than high; midbody metatergal crests divided into two about midway, each half neither especially high nor sharp (Fig. 2B–F). Carinotaxy formulae 3+1+4+1+3 and 3+i+3+i+3, the former standing for front row of crests, the latter for caudal one, both fairly independent (Figs 2D–F; 3B).

Tegument delicately alveolate-areolate, dull throughout. Fine longitudinal striations in front of stricture between pro- and metazona, remaining surface of prozona very delicately shagreened. Metatergal setae absent. Segment 2 with long pleural flaps (Fig. 2B). Limbus extremely finely and more or less regularly denticulate. Epiproct simple, devoid

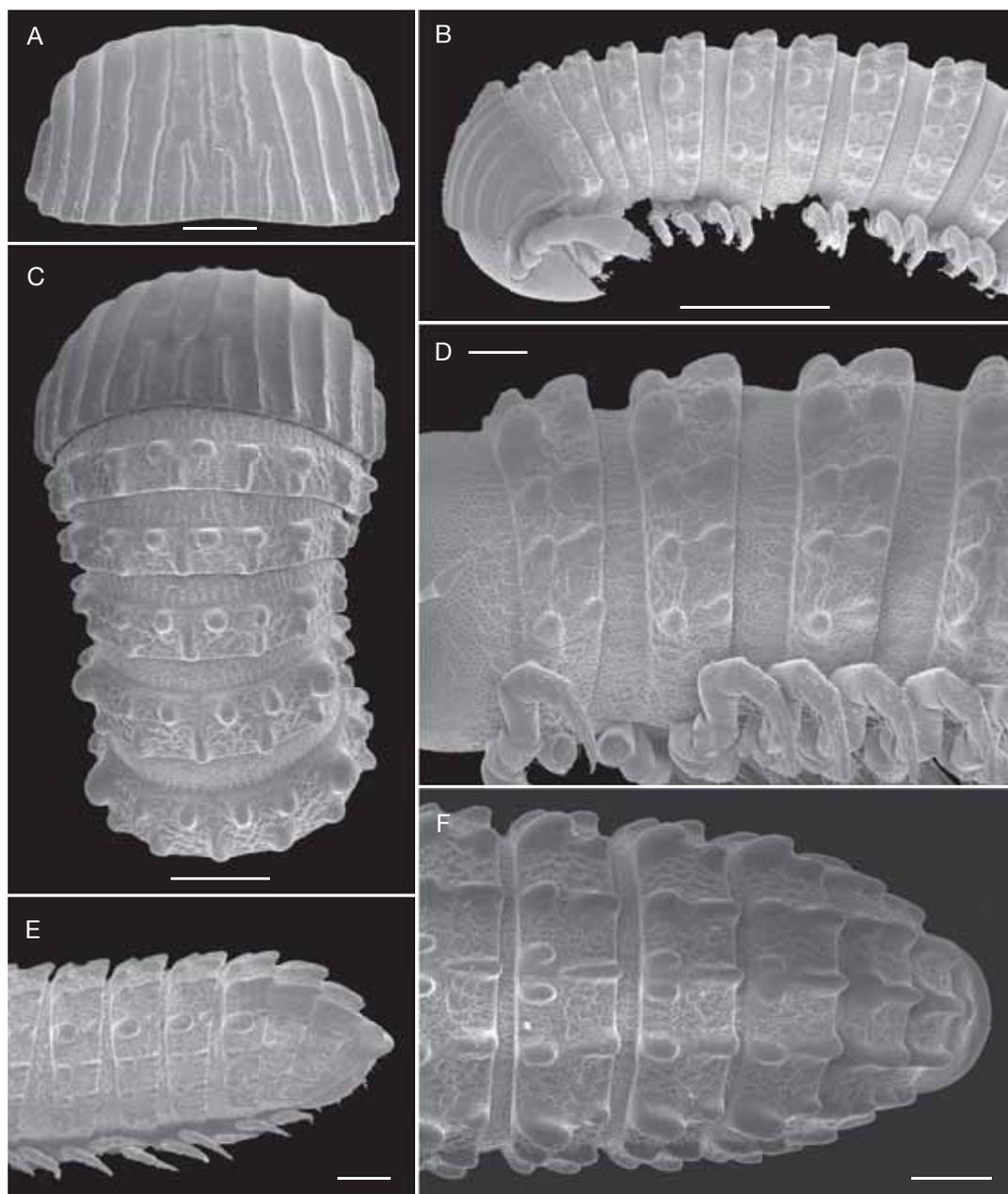


FIG. 2. — *Glyphiulus granulatus* (Gervais, 1847), specimens from the Comoro Islands: A, collum, dorsal view; B, anterior part of body, lateral view; C, same, dorsal view; D, middle part of body, lateral view; E, caudal part of body, lateral view; F, same, dorsal view. Scale bars: A, C, E, F, 0.2 mm; B, 0.5 mm; D, 0.1 mm.

of tuberculation, like a transverse rounded ridge in caudal part (Figs 2E, F; 3C, D). Paraprocts rather regularly convex, each with a row of several

setae at medial margin and 2+2 setae more laterally (Fig. 3C, D). Hypoproct rather evidently but broadly emarginate caudally to receive ventral edges

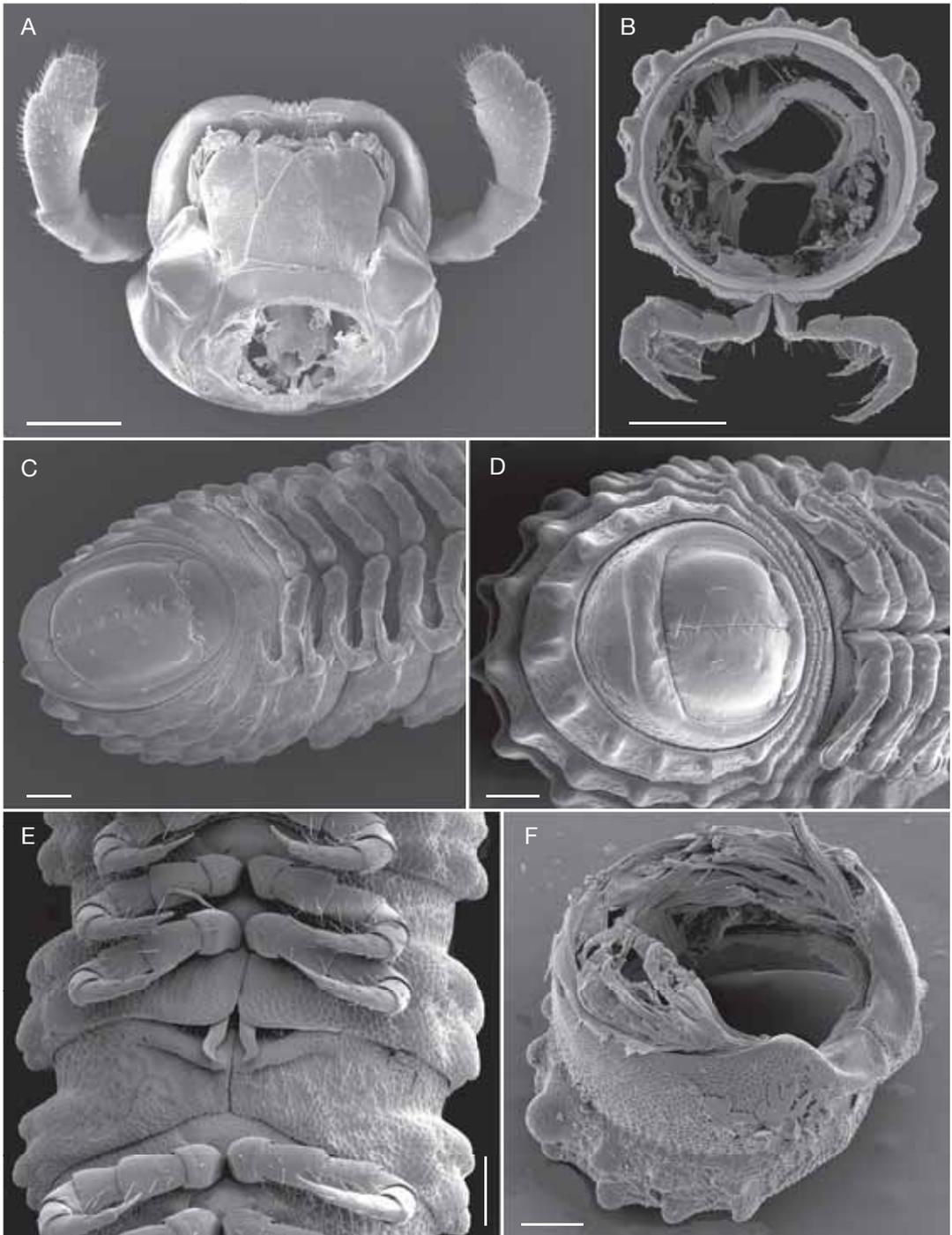


FIG. 3. — *Glyphiulus granulatus* (Gervais, 1847), specimens from the Comoro Islands: A, head, ventral view; B, midbody segment section, caudal view; C, caudal part of body, ventral view; D, same, caudal view; E, segments 6-8 of  $\sigma$ , ventral view; F, segment 7 of  $\sigma$ , frontolateral view. Scale bars: A, B, 0.2 mm; C-F, 0.1 mm.

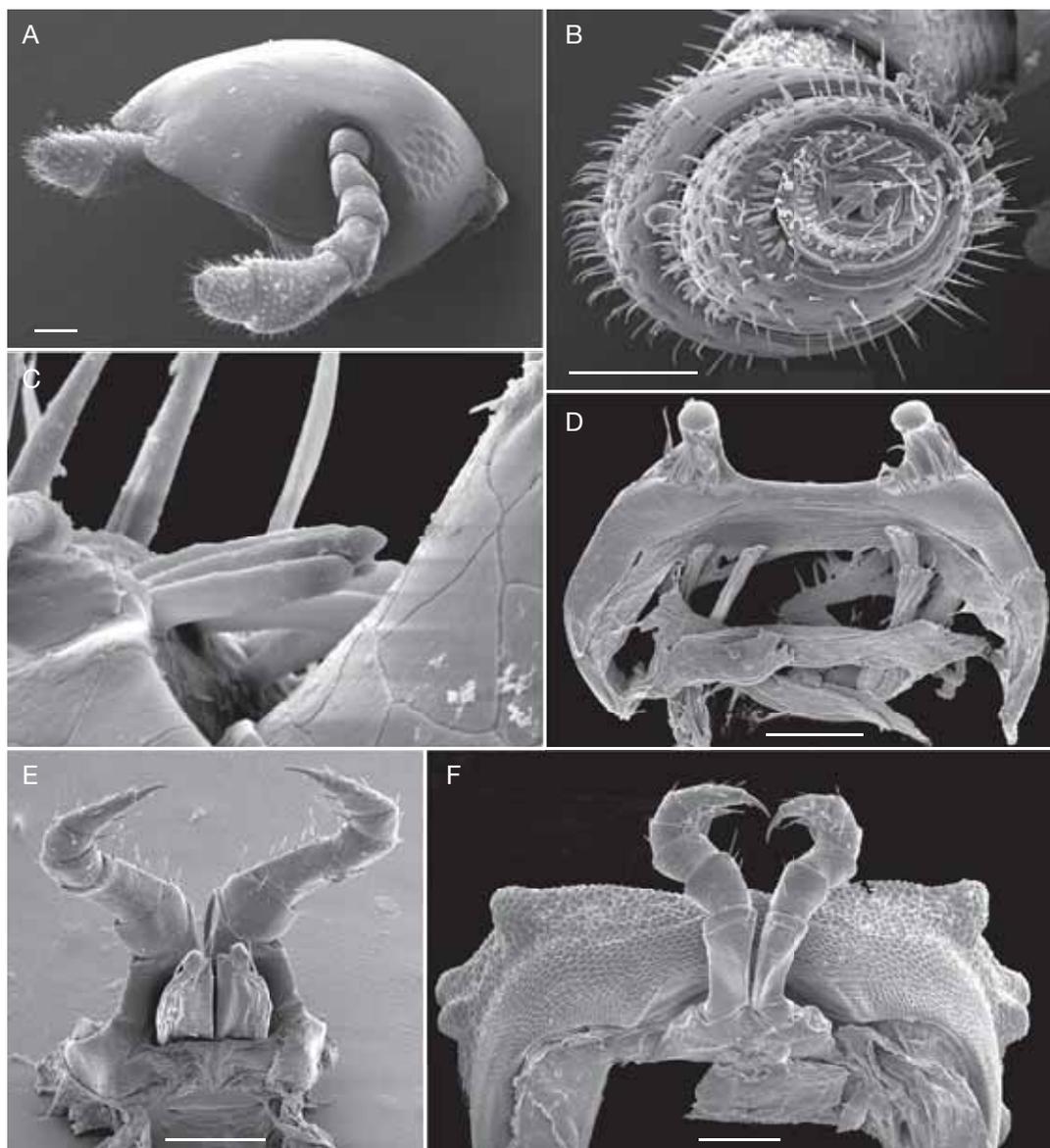


FIG. 4. — *Glyphiulus granulatus* (Gervais, 1847), specimens from the Comoro Islands: **A**, cephalic capsule, sublateral view; **B**, antenna, apical view; **C**, bacilliform sensilla on antennomere 6, lateral view; **D**, male legs 1, caudal view; **E**, male legs 2, caudal view; **F**, male legs 3, frontal view. Scale bars: A, D-F, 0.1 mm; B, 0.05 mm; C, without scale.

of paraprocts, with 1+1 strongly separated setae near caudal margin (Fig. 3C).

Ventral flaps behind gonopod opening on male segment 7 barely distinguishable as low swellings, not forming a marked transverse ridge

(Fig. 3E, F).

Legs short, on midbody segments about 3/4 length of segment height (Figs 2B, D, E; 3B). Claw at base with a strong accessory spine almost half as long as claw itself (Fig. 5D). Tarsi characteristically fringed

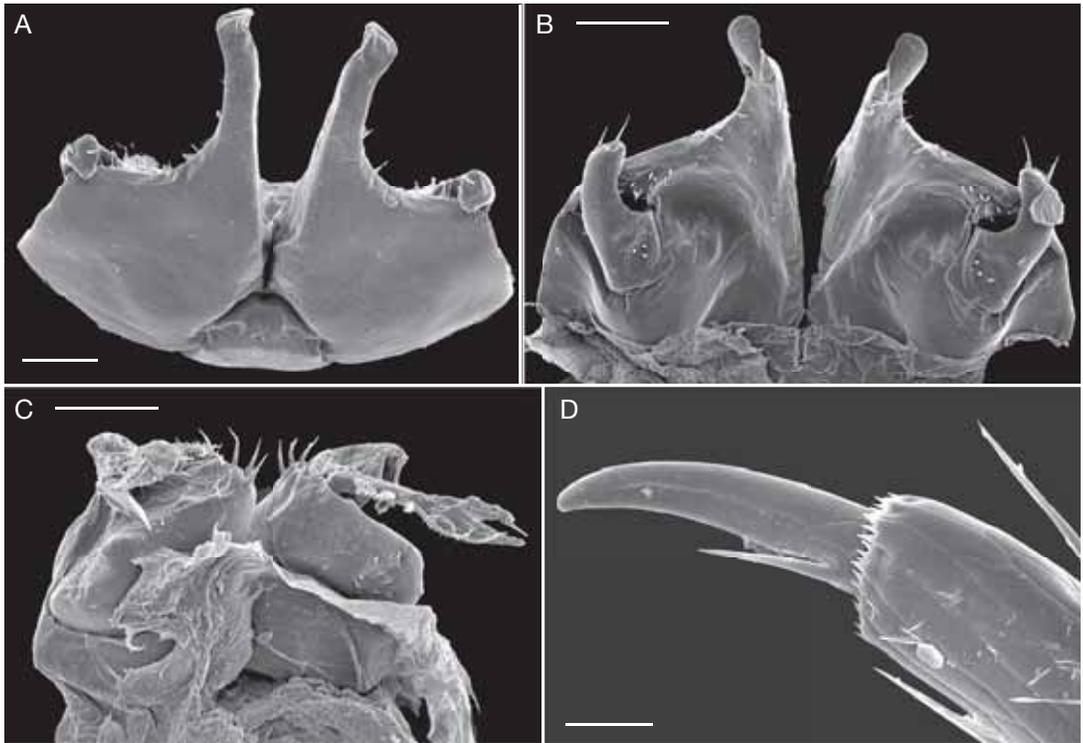


FIG. 5. — *Glyphiulus granulatus* (Gervais, 1847), specimens from the Comoro Islands: **A**, anterior gonopods, frontal view; **B**, same, caudal view; **C**, posterior gonopods, frontal view; **D**, claw of midbody leg, lateral view. Scale bars: A-C, 0.05 mm; D, 0.01 mm.

terminally, some of terminal setae with scattered denticles (Fig. 5D).

Male legs 1 highly characteristic (Figs 4D; 6A) in being very strongly reduced, represented only by a sternum devoid of any median or paramedian structures but carrying 1+1 strongly separated prongs, both evidently curved posteriorly and bearing several strong setae and a minute tubercle (vestige of legs) at base on caudal face. Male legs 2 very slightly hypertrophied, only claw and, anteriorly, coxa somewhat reduced; penes broad, oblong-subtrapeziform, each with 2 or 3 strong setae distolaterally (Figs 4E; 6B). Male legs 3 modified in having coxa especially slender and elongate (Fig. 4F).

Anterior gonopods (Figs 5A, B; 6C) with a typical shield-like coxosternum which is modestly setose on caudal face and provided with a pair of con-

spicuous, high, terminally coiled, mesal processes (visible also *in situ*, Fig. 3E). Telopodite small but movable, 1-segmented, lateral in position, with 2 or 3 strong apical setae and a field of small setae at base, slightly longer than adjacent lateral corner of coxosternum. Posterior gonopods (Figs 5C; 6D) very compact, coxite medio-apically with a plumose distal process and a hyaline lobe, telopodite setose both laterally and medially, lower than both coxal process and lobe.

Vulvae very simple, bare, modestly emarginate medially (Fig. 6G, H). Female legs 1 and 2 as in Figure 6E, F, female coxa 3 as slender as in male (Fig. 6G).

Early juvenile stadia recognised by normal, large ozoporiferous tubercles on segments 5 and 6, these tubercles being considerably reduced in size on subsequent segments.

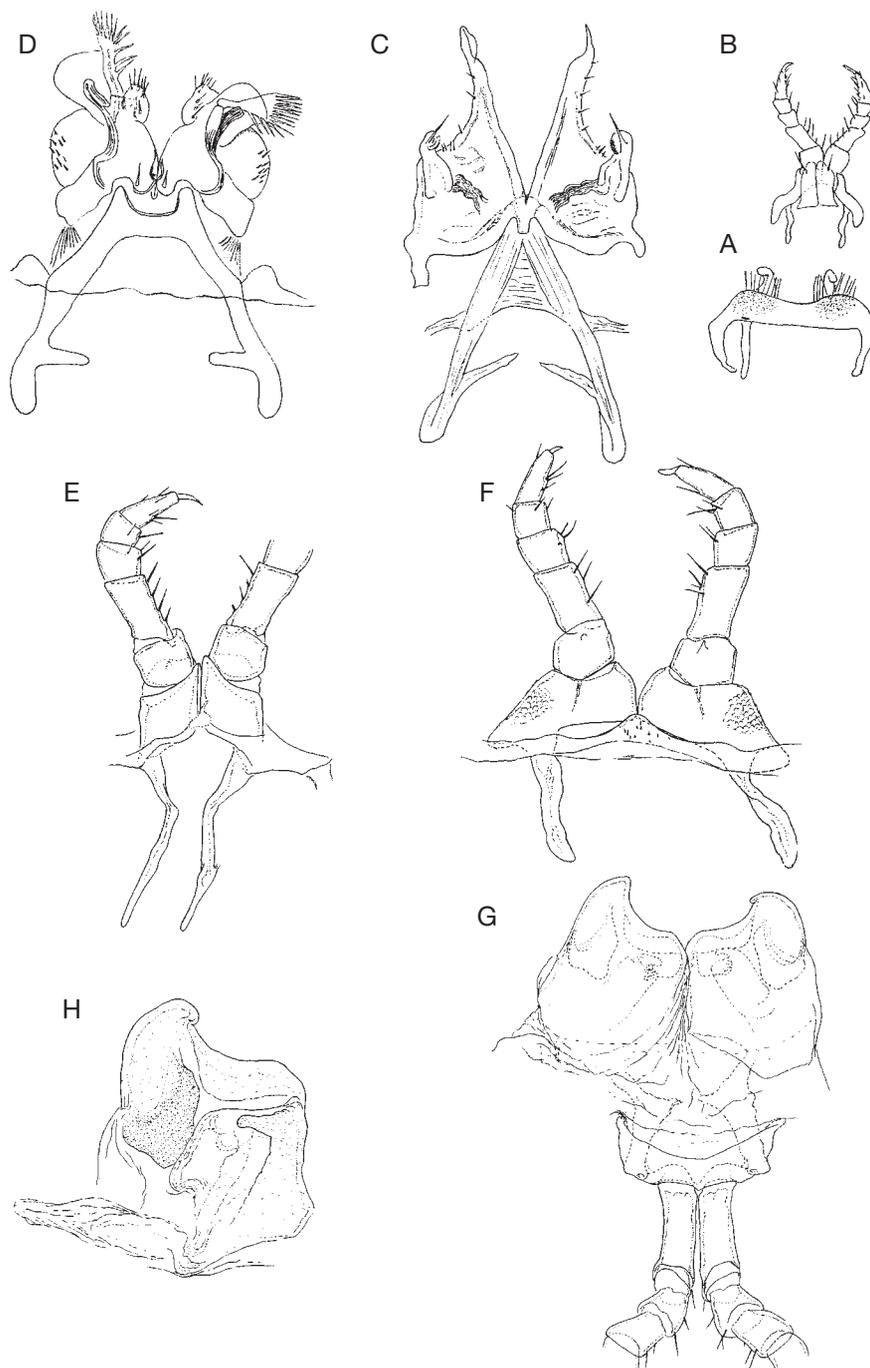


FIG. 6. — *Glyphiulus granulatus* (Gervais, 1847), ♂ (A-D), ♀ (E-H): A, legs 1; B, legs 2; C, anterior gonopods, caudal view; D, posterior gonopods, caudal view; E, legs 1; F, legs 2, caudal view; G, vulvae with base of legs 3, caudal view; H, left vulva, frontal view. Drawn not to scale. A-D, after Attems (1900); E, G, after Brolemann's "Iconographie" (kept in MNHN); F, H, after Brolemann (1931).

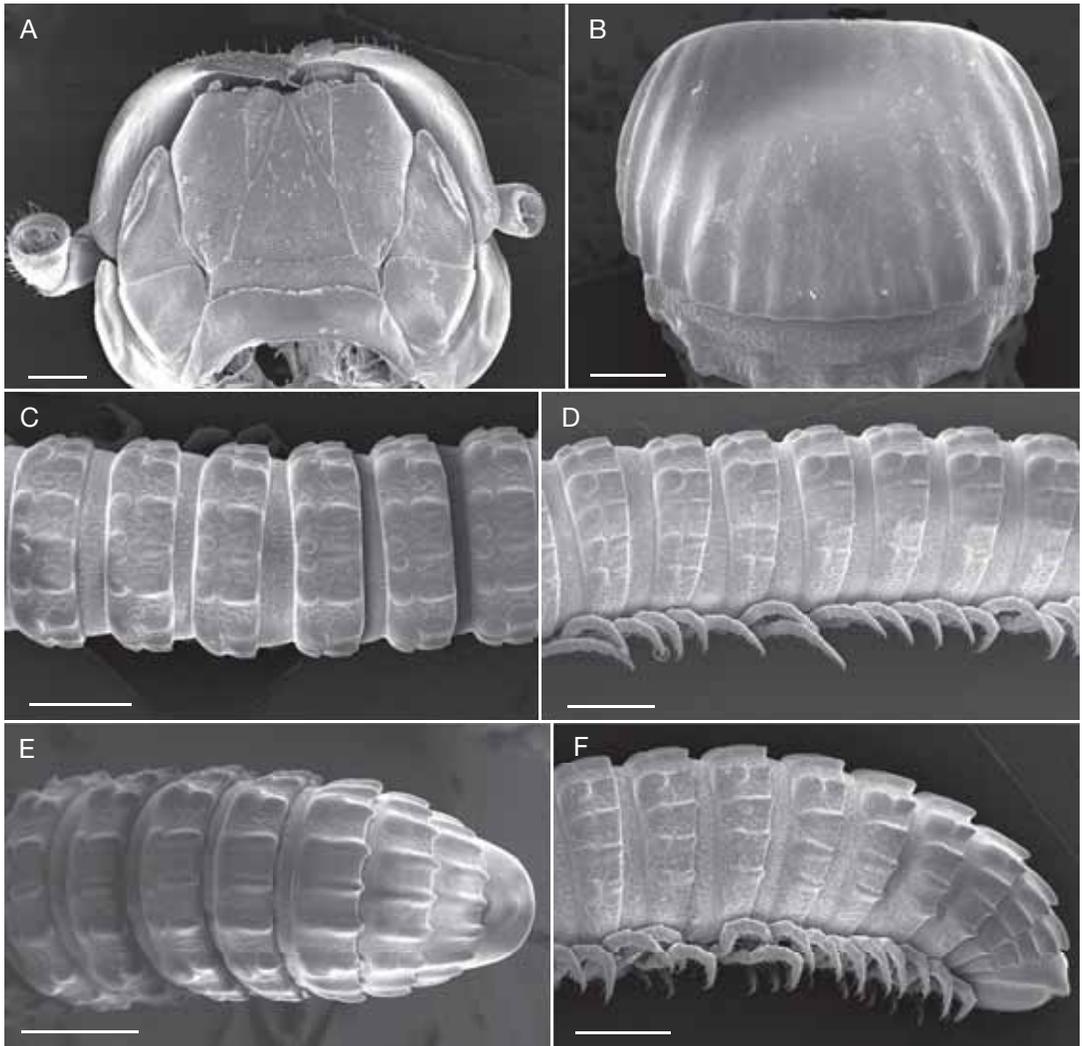


FIG. 7. — *Glyphiulus subgranulatus* n. sp., ♀ paratype: A, head, ventral view; B, collum, dorsal view; C, middle part of body, dorsal view; D, same, lateral view; E, caudal part of body, lateral view; F, same, dorsal view. Scale bars: A, 0.1 mm; B, 0.2 mm, C-F, 0.5 mm.

#### REMARKS

The above is the first formal record of *G. granulatus* in Fiji.

Based on the original description and illustrations of *G. vulgatus* alone (Zhang & Li 1982), it is clear that this taxon does not differ in any way from *G. granulatus*, thus justifying the above new synonymy. The far-inland record of *G. granulatus*

(= *G. vulgatus*) in Guangxi Province, southern China suggests a continental Chinese origin of this species, which has since become established on numerous tropical islands all over the globe. The port of Hong Kong seems to have been a plausible outlet for the recent expansion of *G. granulatus* through human agency. The fact that, of all the numerous congeners, only this species that has attained such

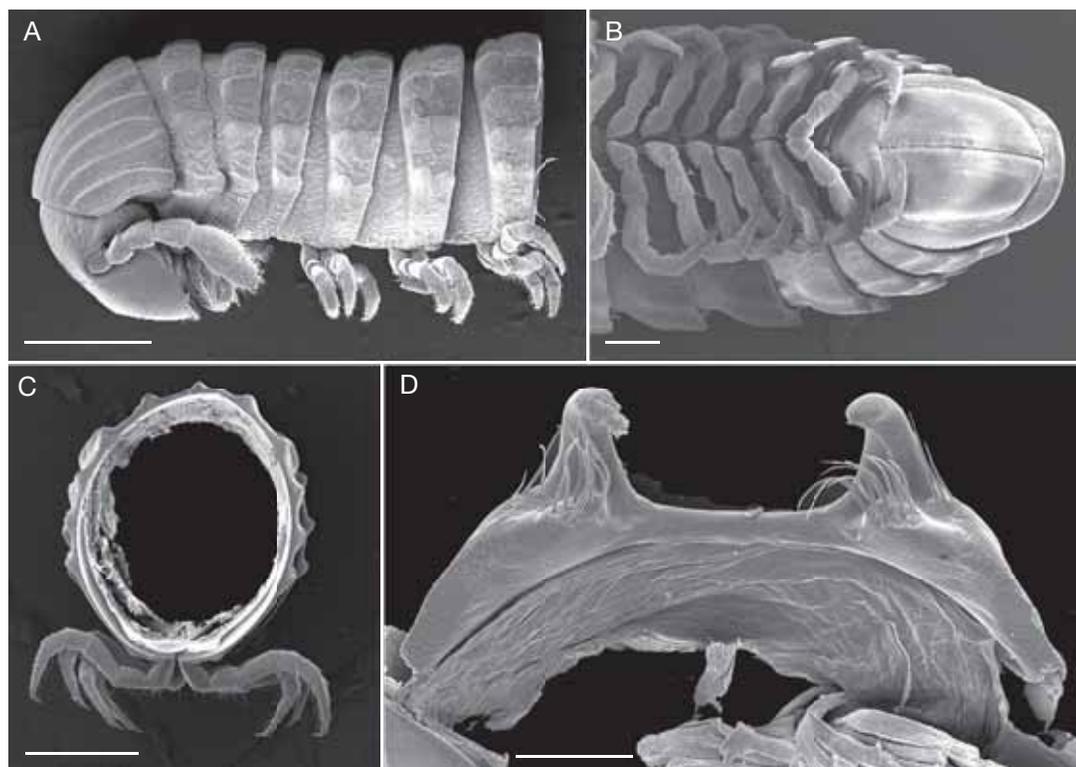


FIG. 8. — *Glyphiulus subgranulatus* n. sp., ♂ and ♀ paratypes: **A**, anterior part of body, lateral view; **B**, caudal part of body, ventral view; **C**, midbody segment section (a little damaged), caudal view; **D**, male legs 1, caudal view. Scale bars: A, C, 0.5 mm; B, 0.2 mm; D, 0.1 mm.

a vast distribution seems to be rooted in its biology and ecology, the most relevant traits being its fairly small size (on average the smallest) and, apparently, a relatively rapid development, suggested indirectly by the observations of Enghoff (1993) and Mauriès & Nguyen Duy-Jacquemin (1997). The ontogeny of certain cambalopsids is unique among Diplopoda in containing a haplopodous early juvenile stage (third?). At this stage, all body segments after the sixth are only equipped with a single pair of legs! In *G. granulatus*, the total number of such segments is only up to 13, as opposed to 18 in *G. subgranulatus* n. sp. and *G. semigranulatus* n. sp. (see below), 19 in *Trachyjulus tjampeanus* (Attems, 1903), from Java, Indonesia (NB: in the abundant material of cambalopsids taken from numerous caves from all over Java and accumu-

lated at MNHN, we have only encountered this species!), and 28 in *Glyphiulus zorzini*, a southern Chinese cavernicole. In addition, in the Hawaiiis, *G. granulatus* has been recorded as a myrmecophile (Crosland 1994).

Similarly, based solely on the original descriptions of *G. septentrionalis* and *G. multicarinus* (cf. Murakami 1975; Zhang & Li 1982), it is clear that these species cannot be separated, agreeing perfectly with each other in every character. Hence the new synonymy advanced: *G. septentrionalis* Murakami, 1975 = *G. multicarinus* Zhang & Li, 1982. The occurrence of this species on Okinawa, Ryukyus, both in caves and epigeically (Murakami 1975), seems only to represent a recent introduction through human agency, with southern China definitely having served as the source area. Much like *G. granulatus*,

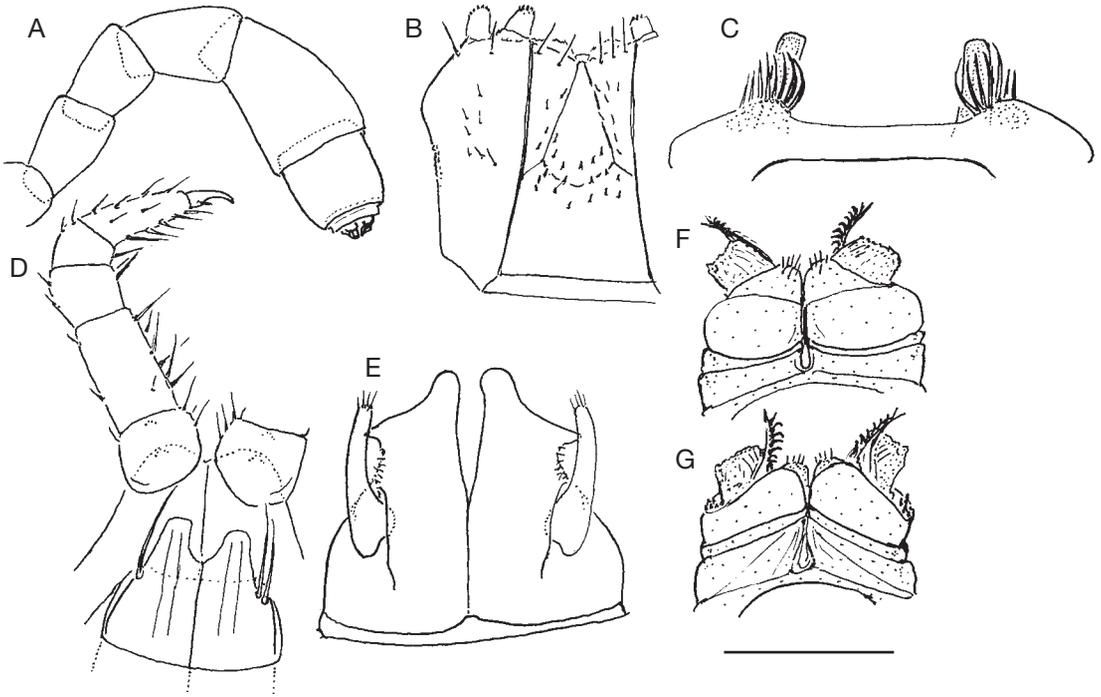


FIG. 9. — *Glyphiulus subgranulatus* n. sp., ♂ paratype: A, antenna; B, gnathochilarium, ventral view; C, legs 1, caudal view; D, legs 2, caudal view; E, anterior gonopods, caudal view; F, posterior gonopods, frontal view; G, same, caudal view. Scale bar: A, B, 0.3 mm; C-G, 0.2 mm.

*G. septentrionalis* is a relatively small species (adults 17-30 mm long), but the number of segments is usually considerably higher ( $43-66p+4-1a+T$ ), implying a longer development, which apparently reduces its vagility.

*Glyphiulus subgranulatus* n. sp.  
(Figs 7-9)

**TYPE MATERIAL.** — China. Yunnan Prov., Mengzi County, cave near footpath to plateau, 5.I.1989, leg. P. Beron, holotype ♂ (NMNHS); paratypes 7 ♂♂, 14 ♀♀, 11 juv. (NMNHS); 2 ♂♂, 2 ♀♀ (MNHN GA 035); 2 ♂♂, 2 ♀♀ (ZMUM); 1 ♂, 1 ♀ (ZMUC); 1 ♂, 1 ♀ (MCSNV); 1 ♂, 1 ♀ (SEM). — Yunnan Prov., Mengzi County, Pothole No. 2 (Ma Fa Tiao Dong), 6.I.1989, leg. P. Beron, paratype 1 ♀ (NMNHS).

**ETYMOLOGY.** — To emphasize the obvious similarity to *G. granulatus*.

**DIAGNOSIS.** — Differs from the most similar congeners by the crests on the collum being underdeveloped (especially so anteriorly), the body segments somewhat compressed laterally, the anterior gonopods with unusually slender telopodites, etc.

**DESCRIPTION**

Length of adults of both sexes 19-28 mm, width 1.0-1.3 mm; males usually a little shorter and more slender than females. Coloration much as in *G. granulatus*, variegate, yellow-brown, with a dark brown vertex, blackish ocellaria, mainly brown crests on collum and grey-brownish lateral longitudinal stripes running down from dark brown ozoporiferous tubercles; dorsum generally light, but a thin axial line mostly present due to darker median crests.

Adults with  $38-52p+5-2a+T$  in males,  $39-63p+5-1a+T$  in females; largest juvenile ♂ with  $31p+3a+T$ ; two smallest juveniles with 17 or 18 haplopodous

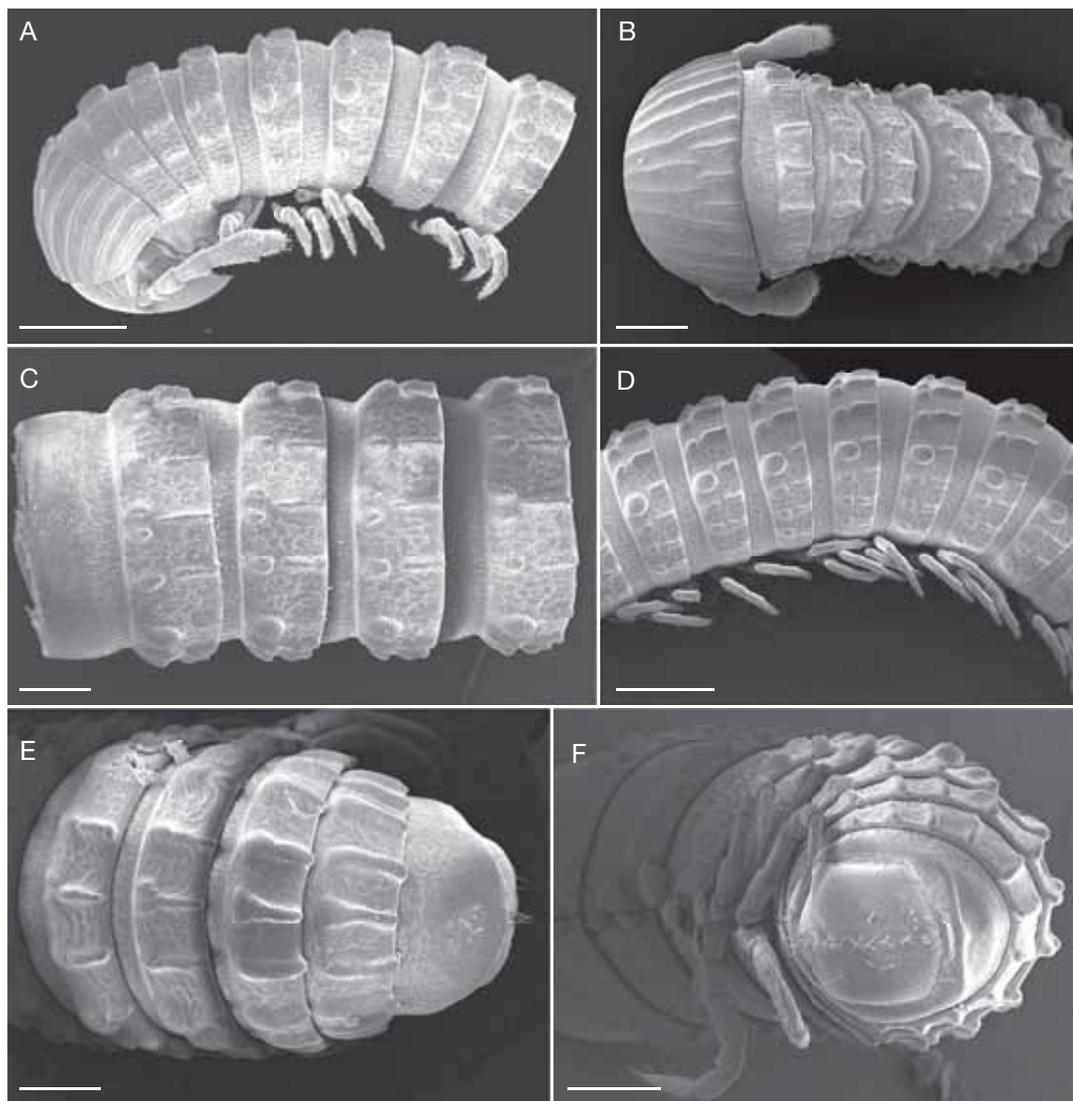


FIG. 10. — *Glyphiulus paragranelatus* n. sp., ♂ and ♀ paratypes: A, anterior part of body, lateral view; B, same, dorsal view; C, middle part of body, dorsal view; D, same, lateral view; E, caudal part of body, dorsal view; F, same, caudal view. Scale bars: A, D, 0.5 mm; B, C, E, F, 0.2 mm.

segments after 6th, plus 2a+T. Holotype about 23 mm long, 1.0 mm wide, with 47p+2a+T.

Other characters as in *G. granulatus*, including mentum either divided ( $n = 1$ ) (Fig. 9B) or undivided ( $n = 1$ ) (Fig. 7A), 11-18 ocelli, antennae (Figs 8A; 9A), the carinotaxy formulae (Fig. 7B-F), claw, posterior gonopod structure (Fig. 9F, G), male

legs 1 and 2 (Figs 8D; 9C, D), telson (Fig. 8B), etc., but body size much larger (see above); segments compressed laterally (Fig. 8C); crests on collum (7+m+7 at caudal margin) evidently reduced in size, almost obsolete anteromedially (Figs 7B; 8A); legs somewhat longer (about 4/5 as long as body height); anterior gonopods with telopodites more

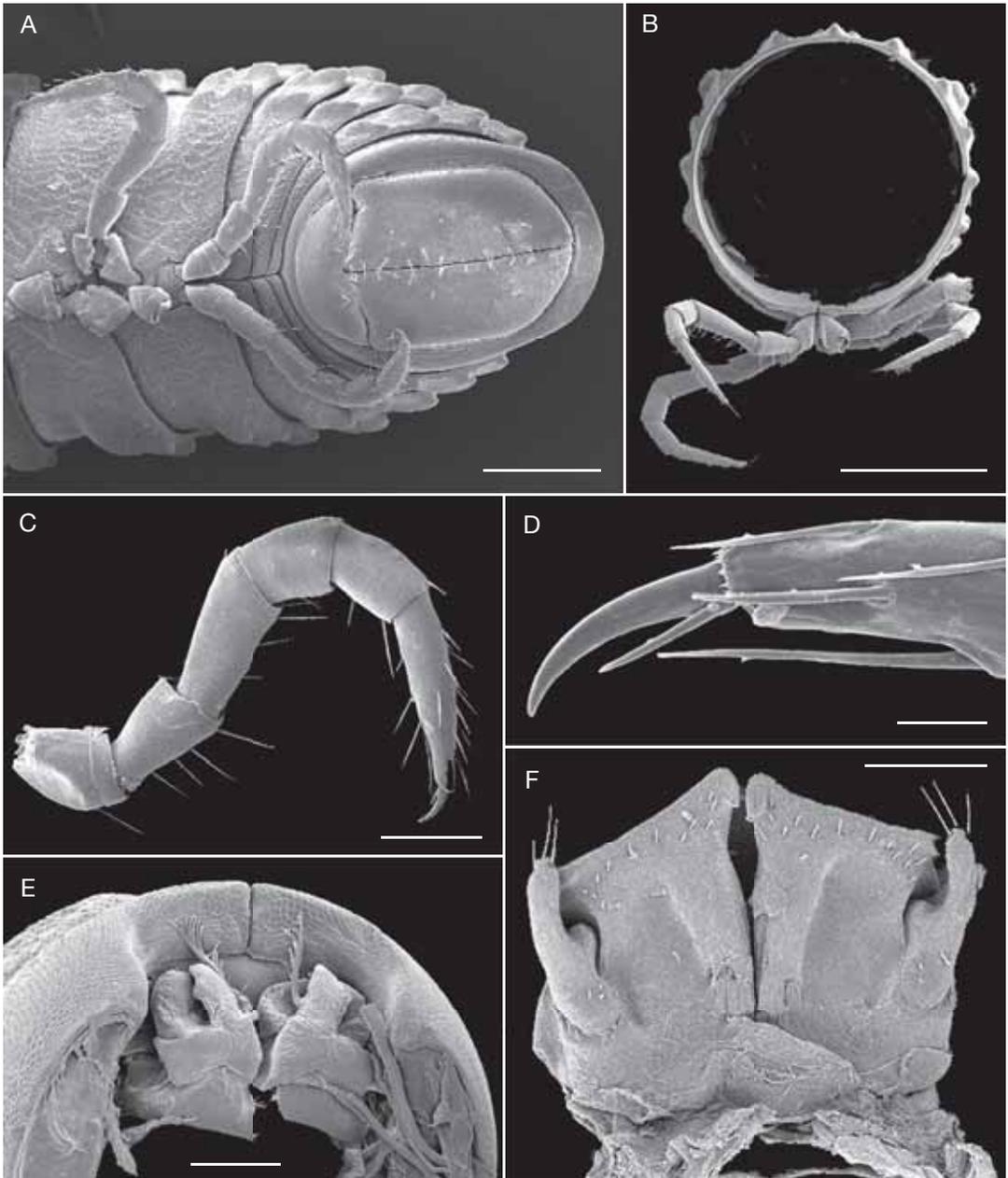


FIG. 11. — *Glyphiulus paragranelatus* n. sp., ♂ and ♀ paratypes: A, caudal part of body, ventral view; B, midbody segment section, caudal view; C, midbody leg; D, claw; E, posterior gonopods *in situ* in gonopod opening, frontal view; F, anterior gonopods, caudal view. Scale bars: A, 0.2 mm; B, 0.5 mm; C, E, F, 0.1 mm; D, 0.02 mm.

slender, while the coxosternum has much shorter distomedian outgrowths and acute distolateral corners (Fig. 9E).

#### REMARKS

In the absence of evident troglomorphic traits, this species can only be considered as troglophilic.

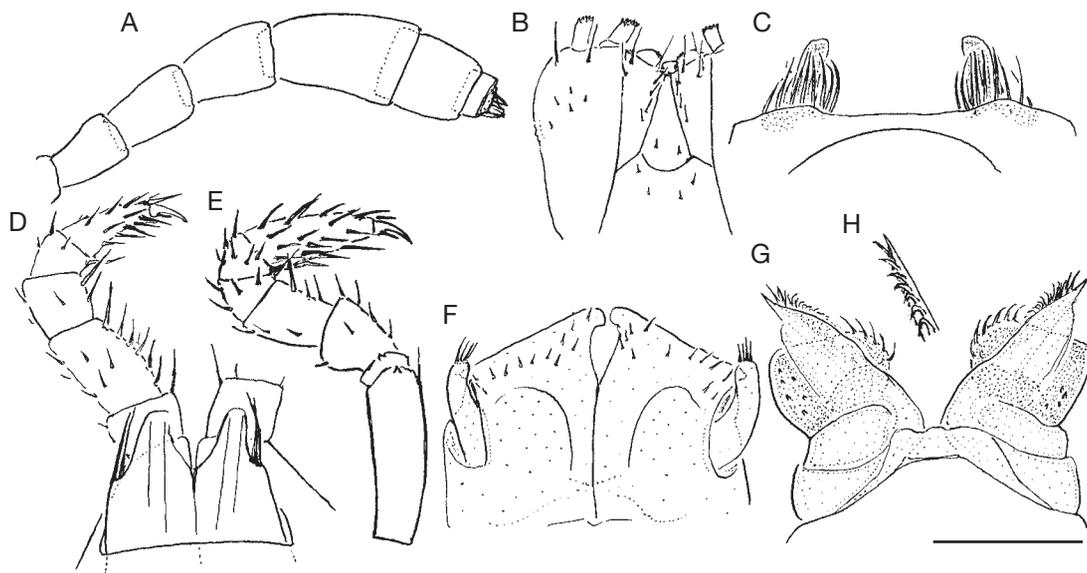


FIG. 12. — *Glyphiulus paragranelatus* n. sp., ♂ paratype: A, antenna; B, gnathochilarium, ventral view; C, legs 1, caudal view; D, legs 2, caudal view; E, leg 3; F, anterior gonopods, caudal view; G, posterior gonopods, frontal view; H, tip of distal process, caudal view. Scale bar: A, B, 0.3 mm; C-G, 0.2 mm.

*Glyphiulus paragranelatus* n. sp.  
(Figs 10-12)

**TYPE MATERIAL.** — China. Yunnan Prov., Jiashui County, Yan Dong Cave, 12.I.1989, leg. P. Beron, holotype ♂ (NMNHS); paratypes 2 ♀♀, 1 fragm. juv. (NMNHS); 1 ♂, 1 ♀ (MNHN GA 036); 1 ♂ (ZMUM); 1 ♂, 1 ♀ (SEM).

**ETYMOLOGY.** — To emphasize the obvious similarity to *G. granulatulus*.

**DIAGNOSIS.** — Differs from the most similar congeners by the antennae being more slender, the body segments somewhat compressed laterally, the ocellaria only slightly reduced, the accessory spine at the claw base especially prominent, the anterior gonopod coxosternum with small but evident distomedial outgrowths.

**DESCRIPTION**

Length of adults of both sexes 18-25 mm, width 1.0-1.2 mm. General coloration pallid, pattern much as in *G. granulatulus*, but ocellaria light brown while lateral stripes level to ozoporiferous tubercles narrow.

Adults with 39-45p+2-1a+T. Holotype about 25 mm long, 1.2 mm wide, with 44p+2a+T.

Other characters as in *G. granulatulus*, including gnathochilarium (divided into pro- and eumentum,  $n = 1$ ) (Fig. 12B), the carinotaxy formulae (Figs 10A-D; 11B), the telson (Figs 10E, F; 11A), male legs 1-3 (Fig. 12C-E), posterior gonopod structure (Figs 11E; 12G, H), etc., but body size much larger (see above); segments compressed laterally (Fig. 11B); antennae slightly elongate (Figs 10A, B; 12A); claw with a particularly prominent spine at base (Fig. 11D); only some 9-11 ocelli in adults; legs somewhat longer (about as long as body height) (Figs 10D; 11C); anterior gonopod coxosternum with small but curved distomedian outgrowths and acute distolateral corners (Figs 11F; 12F).

**REMARKS**

Even though there are some indications of troglomorphy in this species (pallid general coloration, somewhat elongated antennae and legs), its troglomorphy seems more likely than troglobiosis. The morphological evidence being inconclusive, without further

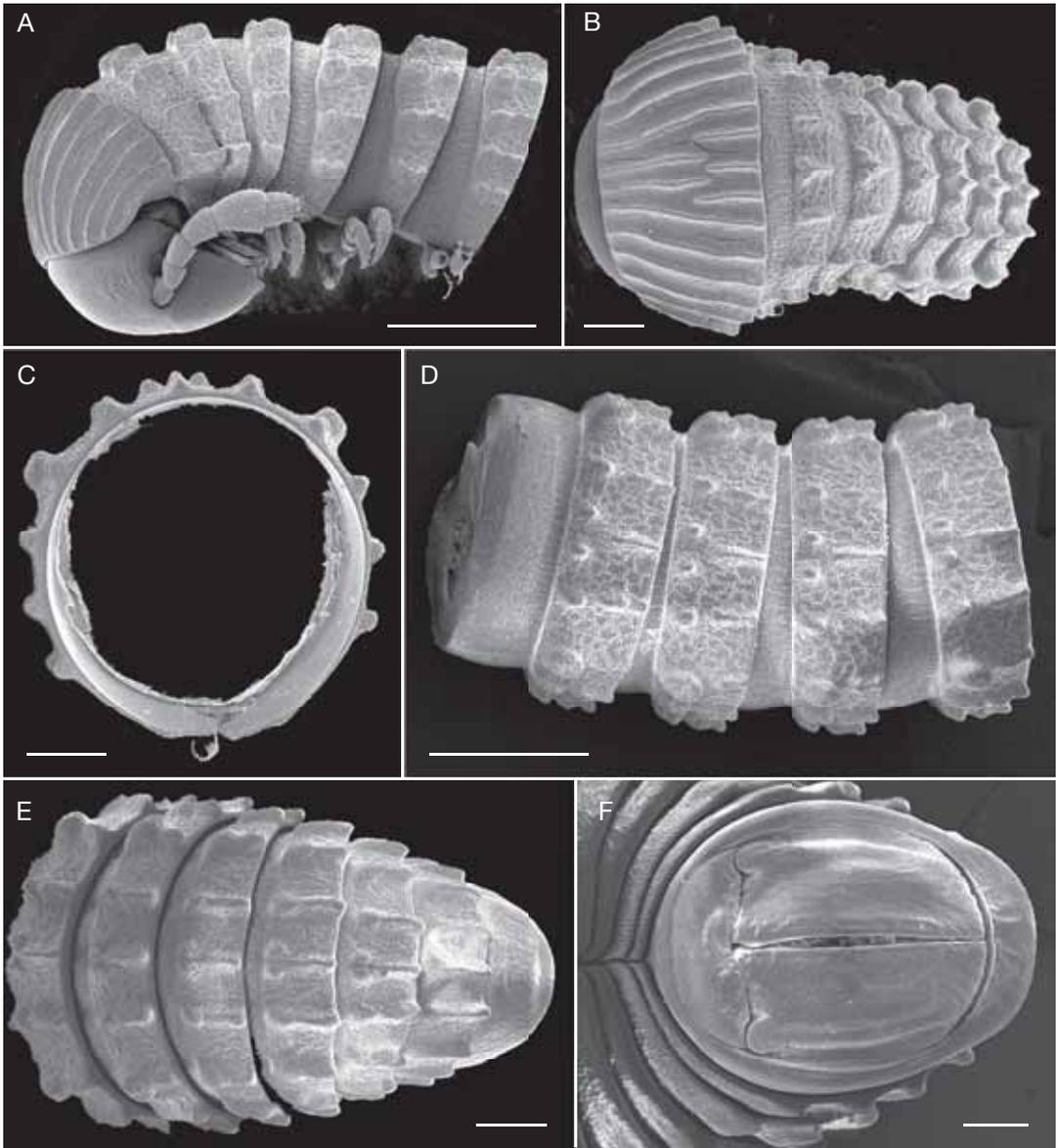


FIG. 13. — *Glyphiulus semigranulatus* n. sp., ♂ and ♀ paratypes: A, anterior part of body, lateral view; B, same, dorsal view; C, midbody segment section, caudal view; D, middle part of body, dorsal view; E, caudal part of body, dorsal view; F, telson, caudal view. Scale bars: A, D, 0.5 mm; B, C, E, 0.2 mm; F, 0.1 mm.

observations this problem can never be solved. On the other hand, *Bollmania beroni* Stoev & Enghoff, 2005 (Diplopoda, Callipodida, Caspiopetalidae Lohmander, 1931), a presumed troglobitic millipede, occurs in the same cave (Stoev & Enghoff 2005).

*Glyphiulus semigranulatus* n. sp.  
(Figs 13; 14)

TYPE MATERIAL. — China. Yunnan Prov., Meele (= Mile) County, Bai Long Dong Cave (= White Dragon Cave),

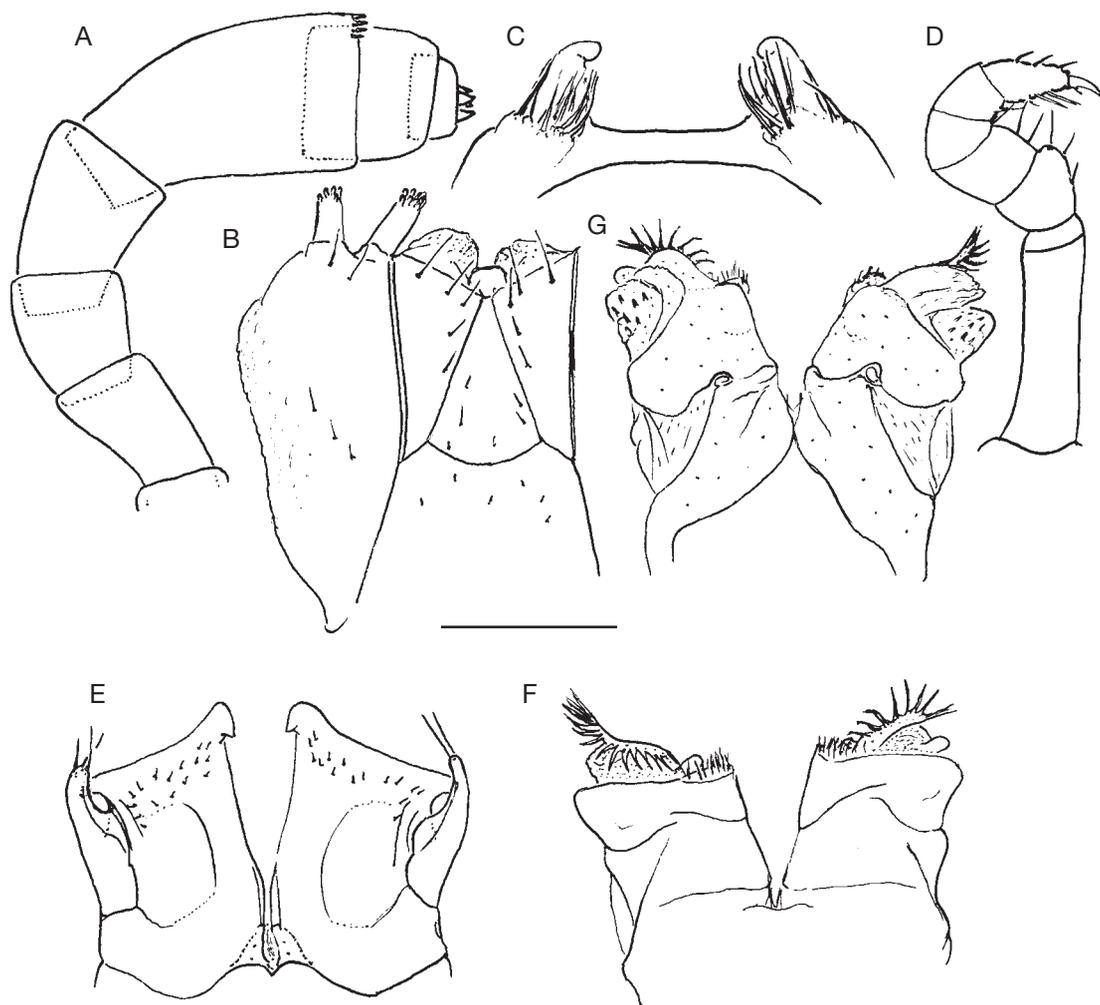


FIG. 14. — *Glyphiulus semigranulatus* n. sp., ♂ paratype: A, antenna; B, gnathochilarium, ventral view; C, legs 1, caudal view; D, leg 3; E, anterior gonopods, caudal view; F, posterior gonopods, caudal view; G, same, frontal view. Scale bar: 0.2 mm.

2.I.1989, leg. P. Beron, holotype ♂ (NMNHS); paratypes 1 ♂, 1 ♀ (NMNHS); 1 ♀ (SEM); 1 ♂ (MNHN GA 037). — Yunnan Prov., Jianshui County, Yan Zi Dong Cave, 10.I.1989, leg. P. Beron, paratypes 5 ♂♂, 3 ♀♀, 4 juv. (NMNHS); 4 ♂♂, 2 ♀♀ (MNHN GA 037); 4 ♂♂, 2 ♀♀ (ZMUM); 2 ♂♂, 2 ♀♀ (ZMUC); 1 ♂, 1 ♀ (MCSNV); 1 ♂ (SEM).

ETYMOLOGY. — To emphasize the obvious similarity to *G. granulatus*.

DIAGNOSIS. — Differs by a position somewhat intermediate between the most similar congeners *G. granulatus* and *G. paragramulatus* n. sp., i.e. coloration, carinotaxy,

antennae, claws, etc., as in *G. granulatus*, but size, segment shape, leg length and anterior gonopods more like in *G. paragramulatus* n. sp.

#### DESCRIPTION

Length of adults of both sexes 12–24 mm, width 0.8–1.2 mm.

Adults of both sexes with 31–64p+5–1a+T; largest juvenile ♂ with 28p+5a+T, largest juvenile ♀ with 27p+5a+T; two smallest juveniles with 15 or 18 haplopodous segments after 6th, plus 2a+T or

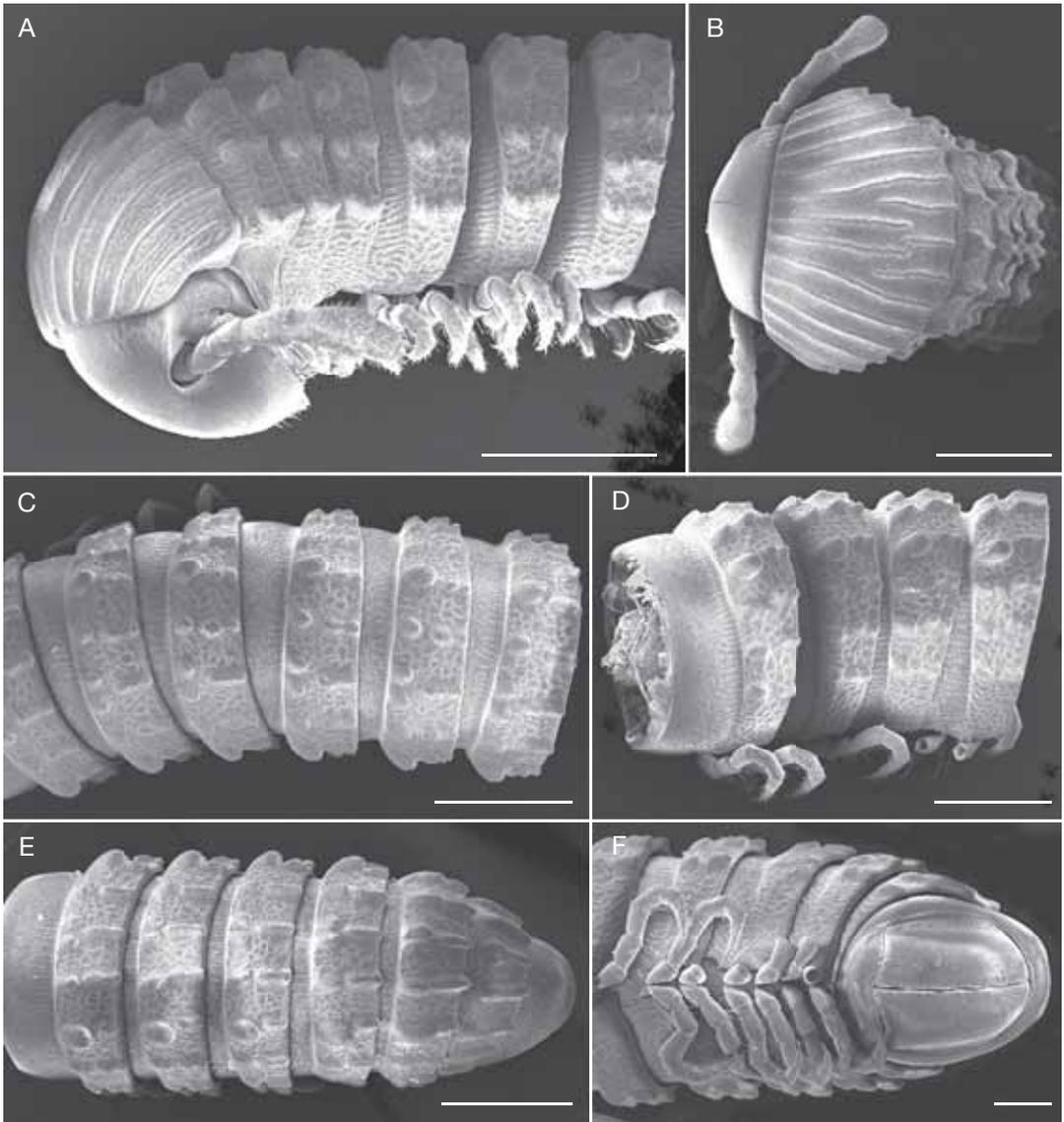


FIG. 15. — *Glyphiulus beroni* n. sp., ♀ paratype: A, anterior part of body, lateral view; B, same, dorsofrontal view; C, middle part of body, dorsal view; D, same, lateral view; E, caudal part of body, dorsal view; F, same, ventral view. Scale bars: A-E, 0.5 mm; F, 0.2 mm.

1a+T, respectively. Length of holotype about 22 mm, width 1.0 mm, with 45p+3a+T.

Coloration, carinotaxy (Fig. 13A-E), antennae (Figs 13A; 14A), gnathochilarium, claws, etc. (Fig. 14B-D, F, G) basically as in *G. granulatus*, but body size (usually much larger), segment

shape (slightly compressed laterally) (Fig. 13C), telson (Fig. 13E, F) with peculiar flaps on paraprocts near hypoproct (Fig. 13F), legs (somewhat longer) and anterior gonopods (Fig. 14E) more like those of *G. paragr anulatus* n. sp. Adults with 11-15 ocelli.

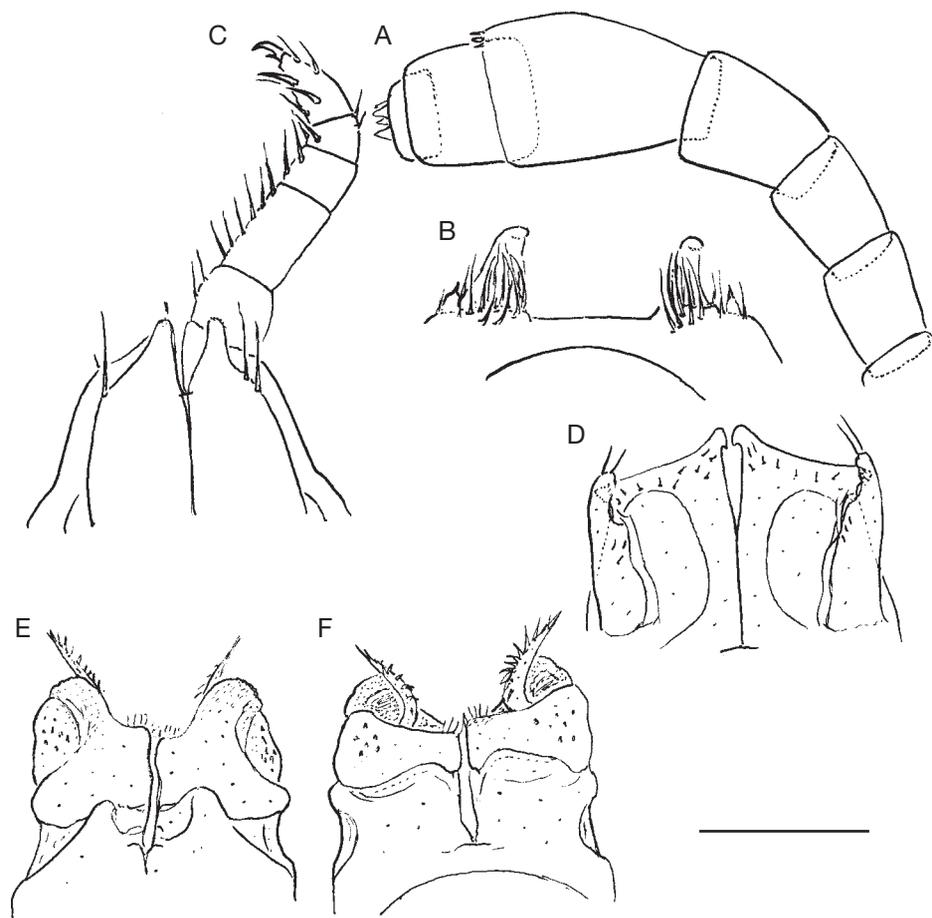


FIG. 16. — *Glyphiulus beroni* n. sp., ♂ paratype: A, antenna; B, legs 1, caudal view; C, legs 2, caudal view; D, anterior gonopods, caudal view; E, posterior gonopods, caudal view; F, same, frontal view. Scale bar: 0.2 mm.

**REMARKS**

In the absence of any evident troglomorphic traits, this species can only be considered as troglophilic at most. This is supported by *G. semigranulatus* n. sp. being present in several relatively strongly isolated caves, sometimes in significant numbers.

*Glyphiulus beroni* n. sp.  
(Figs 15; 16)

**TYPE MATERIAL.** — China, Yunnan Prov., Jianshui County, Cave Ba Guo Dong, 11.I.1989, leg. P. Beron, holotype ♂ (NMNHS); paratypes 2 ♂♂, 6 ♀♀, 3 juv. (NMNHS);

2 ♂♂, 2 ♀♀ (MNHN GA 038); 1 ♂, 1 ♀ (ZMUM); 1 ♂, 1 ♀ (ZMUC); 1 ♀ (SEM).

**ETYMOLOGY.** — Honours Petar Beron, the collector.

**DIAGNOSIS.** — Differs by the crests just below and above the ozopore-bearing crests being divided into three, not two, transverse rows of tubercles, coupled with an evident mediadorsal tubercle present in front of the caudal edge of the epiproct.

**DESCRIPTION**

Length of adults 11-17 (♂) or 12-24 mm (♀), width 0.8-1.0 (♂) or 0.8-1.3 mm (♀). Coloration nearly entirely light yellowish, only ocellaria brown,

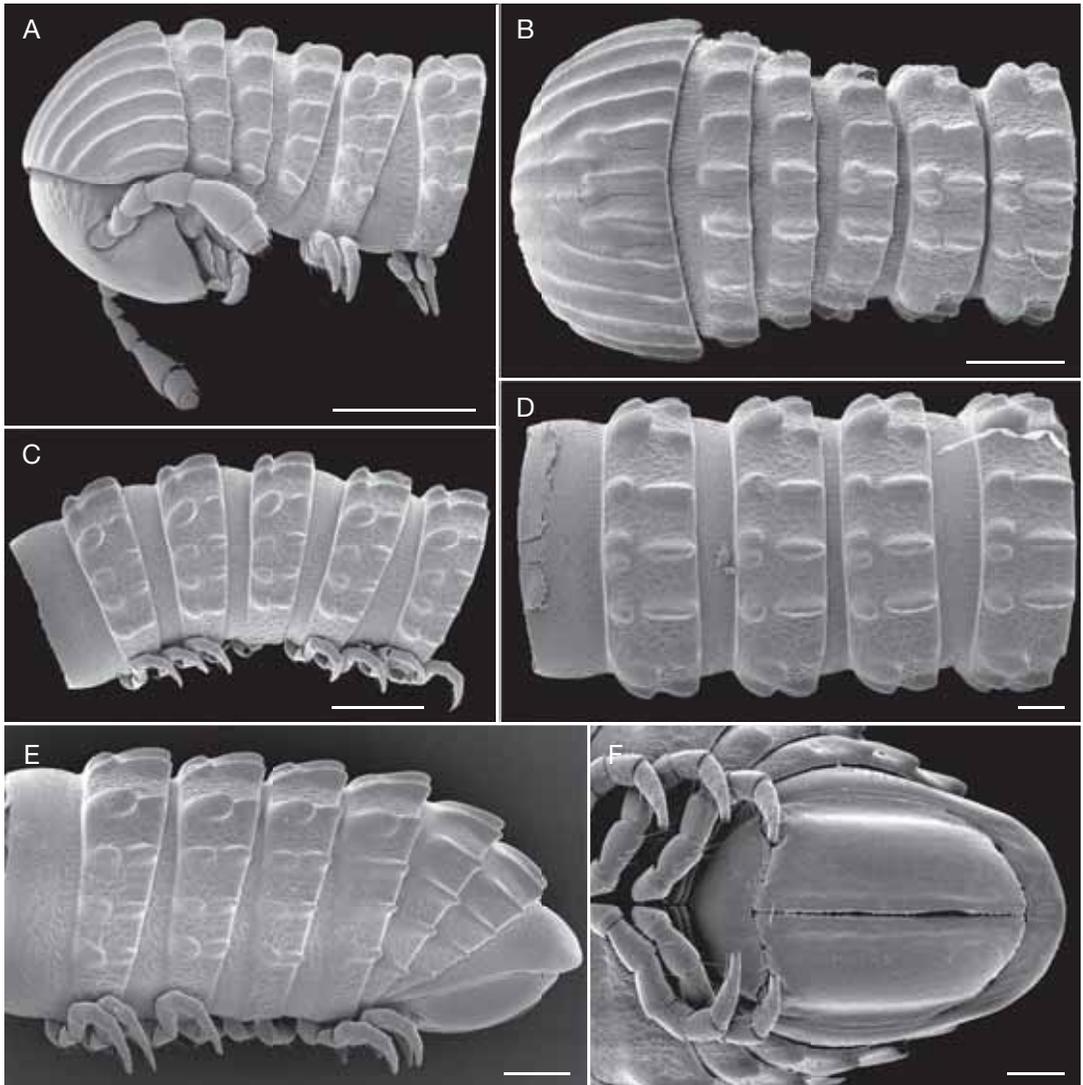


FIG. 17. — *Glyphiulus bedosae* n. sp., ♀ paratype: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, middle part of body, lateral view; **D**, same, dorsal view; **E**, caudal part of body, lateral view; **F**, telson, ventral view. Scale bars: **A**, **C**, 0.5 mm; **B**, **D**, **E**, 0.2 mm; **F**, 0.1 mm.

as well as sometimes a vague lateral line level to ozoporiferous crests.

Adults with 28-40p+5-2a+T (♂) or 28-53p+5-1a+T (♀); largest juvenile ♂ with 27p+5a+T, largest juvenile ♀ with 27p+4a+T. Length of holotype about 17 mm, width 1.0 mm, with 40p+2a+T.

Carinotaxy of collum typical (Fig. 15A, B), that of trunk segments generally typical but, starting from segment 7 until 6 or 7 penultimate segments, crests just below as well as between ozopores divided into three, not two, transverse rows of tubercles (Fig. 15C, D). An evident middorsal tubercle just above caudal edge of epiproct (Fig. 15E).

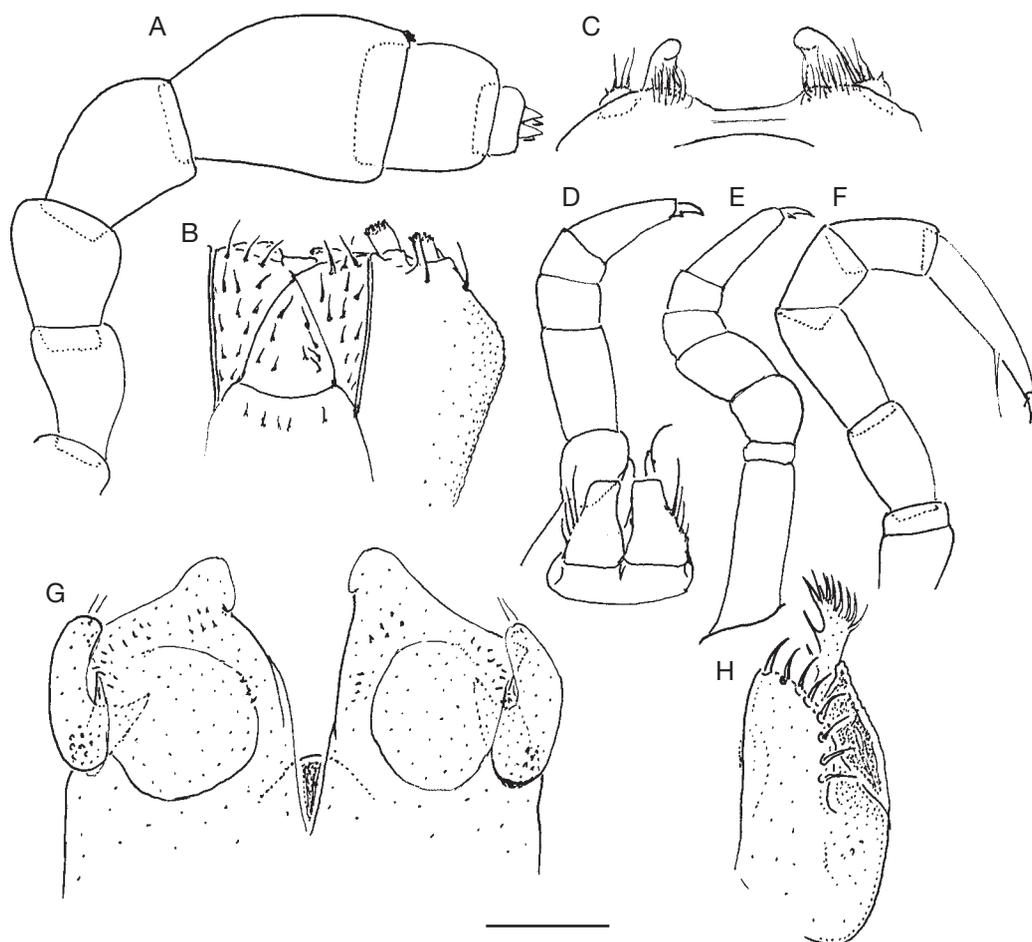


FIG. 18. — *Glyphiulus bedosae* n. sp., ♂ paratype: A, antenna; B, gnathochilarium, caudal view; C, legs 1, caudal view; D, legs 2, caudal view; E, leg 3; F, midbody leg; G, anterior gonopods, caudal view; H, posterior gonopod, subcaudal view. Scale bar: A-F, 0.2 mm; G, H, 0.1 mm.

Antennae (Figs 15A, B; 16A), legs (Fig. 16B, C), claws, posterior gonopods (Fig. 16E, F), etc., as in *G. granulatus*, but body size (often much larger), segment shape (slightly compressed laterally) and anterior gonopods (Fig. 16D) more like those of *G. semigranulatus* n. sp. Adults with 5-13 ocelli. Male legs 1 with tubercular leg vestiges near base of prongs (Fig. 16B).

REMARKS

In the absence of any clearly troglomorphic traits, except perhaps for its nearly completely unpigmented body and the somewhat reduced ocellaria, this

species can hardly be considered as more than troglomorphic.

*Glyphiulus bedosae* n. sp.  
(Figs 17; 18)

TYPE MATERIAL. — Laos. Luang Prabang Prov., Nong Kiaw (= Muang Ngoy), Tham Pha Kouang Cave, 29.XII.2000, leg. A. Bedos & L. Deharveng (LAO-099), holotype ♂ (MNHN GA 039); paratypes 1 ♂ (MNHN GA 039), 1 ♀ (SEM).

ETYMOLOGY. — Honours Anne Bedos, one of the collectors.

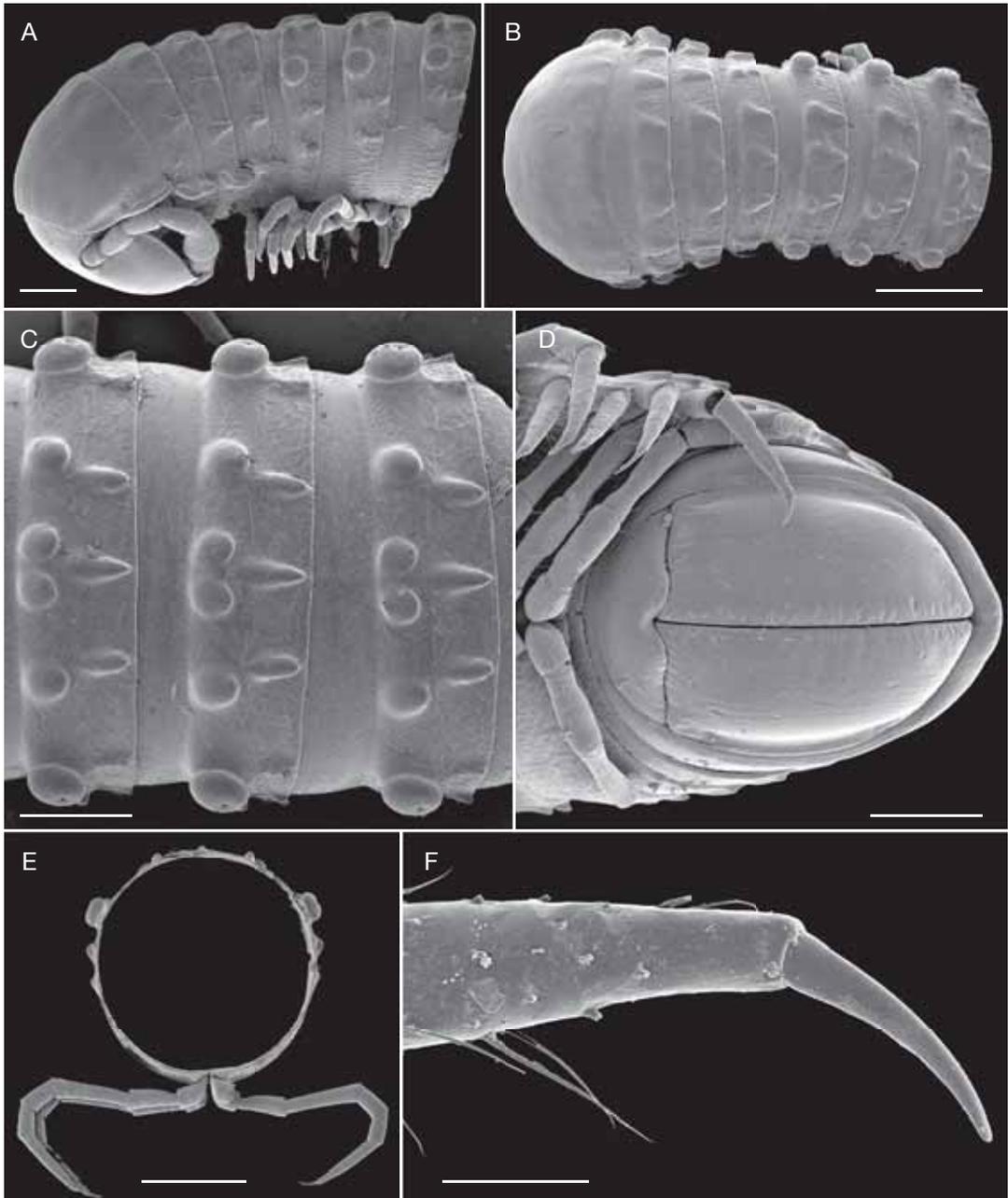


FIG. 19. — *Glyphiulus deharvengi* n. sp., ♀ paratype: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, middle part of body, dorsal view; **D**, telson, ventral view; **E**, midbody segment section, caudal view; **F**, claw of a midbody leg. Scale bars: **A**, **C**, **D**, 0.5 mm; **B**, **E**, 1.0 mm; **F**, 0.1 mm.

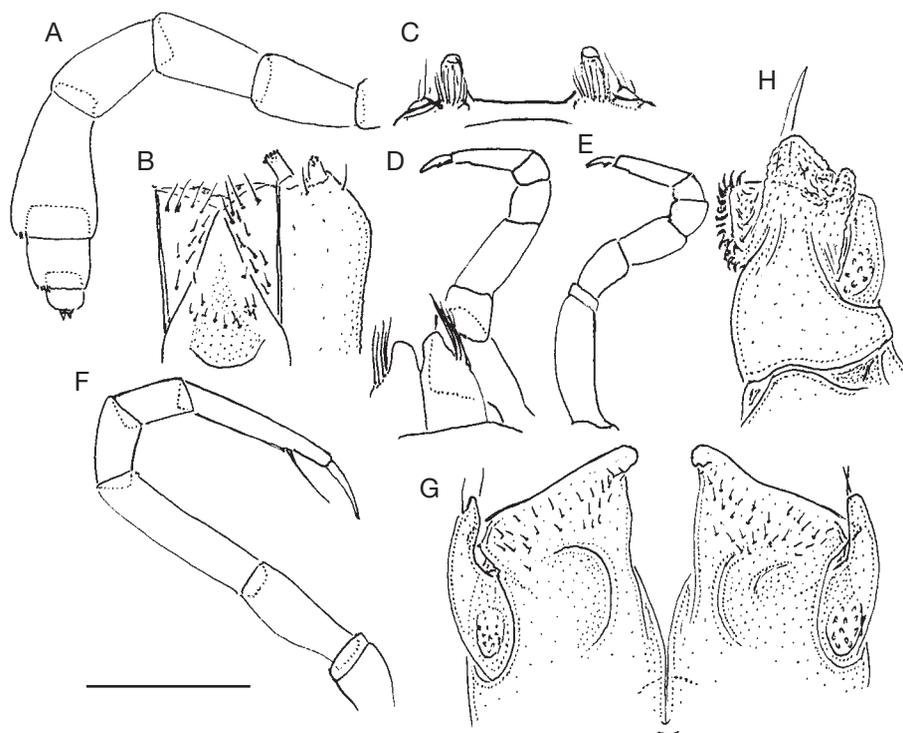


FIG. 20. — *Glyphiulus deharvengi* n. sp., ♂ paratype: A, antenna; B, gnathochilarium, caudal view; C, legs 1, caudal view; D, legs 2, caudal view; E, leg 3; F, midbody leg; G, anterior gonopods, caudal view; H, posterior gonopod, subfrontal view. Scale bar: A-F, 0.6 mm; G, H, 0.3 mm.

**DIAGNOSIS.** — Differs from other species by the paraprocts showing a clear median marginal ridge, combined with a plumose spatuliform distal process of the posterior gonopods and a subunciform distomedian corner of the anterior gonopods.

**DESCRIPTION**

Length of adults of both sexes 16-20 mm, width 1.0-1.1 mm.

Holotype 16 mm long, 1.0 mm wide, with 40p+3a+T and 11 ocelli; paratype ♂ about 20 mm long, 1.1 mm wide, with 54p+2a+T and 14 ocelli.

Coloration, antennae (Figs 17A; 18A), gnathochilarium (mentum divided,  $n = 1$ ) (Fig. 18B), carinotaxy (Fig. 17A-E), segment shape, legs (Fig. 18C-F), etc., generally as in *G. granulatus*, but paraprocts with a low, but evident, median marginal ridge (Fig. 17F).

Anterior gonopods like those of *G. semigranulatus* n. sp. (Fig. 18G), but posterior gonopods with a

plumose spatuliform distal process (Fig. 18H), i.e. much as in *G. quadrohamatus* or *G. lipsorum*.

**REMARKS**

In the absence of any troglomorphic traits, this species can only be considered troglophilic at most.

*Glyphiulus deharvengi* n. sp.  
(Figs 19; 20)

**TYPE MATERIAL.** — **China.** Hunan Prov., Longshan: Huoyan, Feihu Dong Cave (Flying Tiger Cave), 11.VIII.1995, leg. A. Bedos & L. Deharveng (CHI-022), holotype ♂ (MNHN GA 040); paratype 1 ♂ (MNHN GA 040). — Hunan Prov., Longshan, Huoyan, Baiyan Dong Cave (White Rocks Cave), 15.VIII.1995, leg. A. Bedos & L. Deharveng (CHI-032), paratypes 1 ♂, 1 ♀, 1 ♀ juv. (MNHN GA 040); 1 ♂ (ZMUM). — Hunan Prov., Longshan: Huoyan,

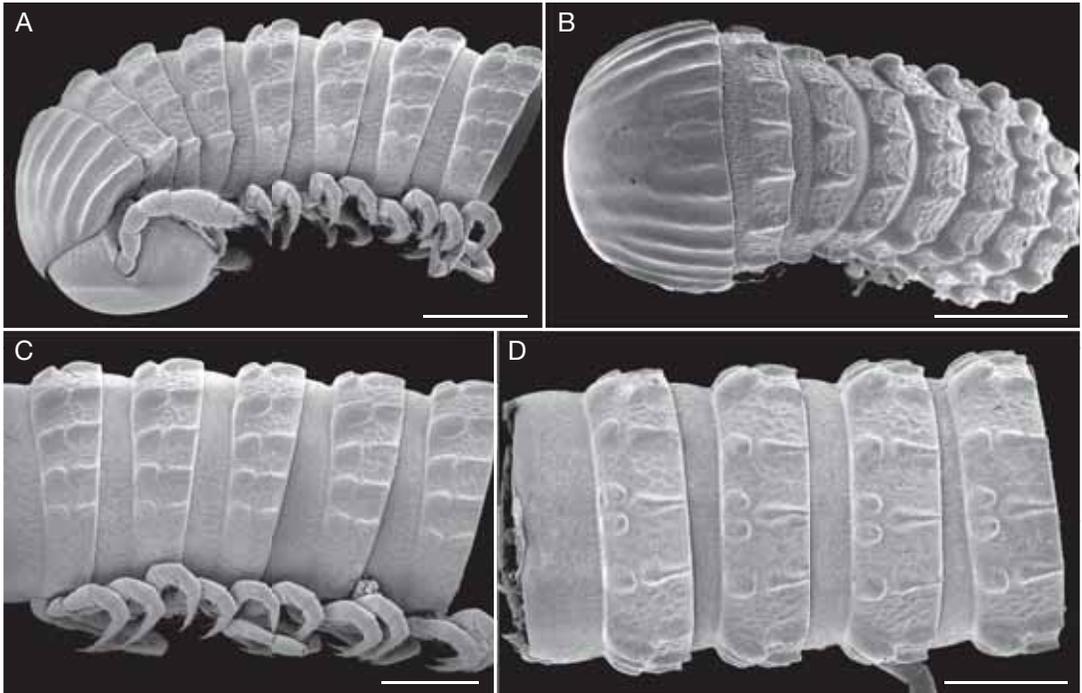


FIG. 21. — *Glyphiulus pergranulatus* n. sp., ♀ paratype: A, anterior part of body, lateral view; B, same, dorsal view; C, middle part of body, lateral view; D, same, dorsal view. Scale bars: 0.5 mm.

Renmi Dong Cave, 19.VIII.1995, leg. A. Bedos & L. Deharveng (CHI-043); paratypes 1 ♂ (MNH GA 040); 1 ♀ (SEM).

ETYMOLOGY. — Honours Louis Deharveng, one of the collectors.

DIAGNOSIS. — Differs by the relatively large size, the nearly completely smooth collum, the complete depigmentation (even of ocellaria), the elongated legs (with claws devoid of a spine at base from leg 4 onwards), the low, but evident, transverse pleural ridge behind the gonopod opening on male segment 7, the bare but flagelliform distal process of the posterior gonopods, etc.

#### DESCRIPTION

Length of adults of both sexes 40–55 mm, width 2.0–2.3 mm. Coloration usually uniformly dark brown due to heavy sclerotization, tegument being coloured only due to chitin; sometimes ozoporiferous tubercles reddish.

Adults with 55–68p+4–1a+T; juvenile ♀ with 40p+5a+T, recognised by considerably reduced ozoporiferous tubercles on segments 7–33, plus 5a+T. Length of holotype about 55 mm, width 2.3 mm, with 67p+1a+T.

Antennae slightly more elongate than usual (Figs 19A; 20A). Ocellaria unpigmented, barely traceable, with about 10 or 11 ocelli in largest specimens. Gnathochilarium (Fig. 20B) with an undivided mentum ( $n = 1$ ).

Carinotaxy of collum unusual in that all crests are nearly obliterated (Fig. 19A, B), though a typical pattern is traceable. Carinotaxy of subsequent metaterga typical (Fig. 19A–C, E), but crests low, especially dorsal ones on segments 2–6; only two lateral crests below ozoporiferous ones, divided from segment 7 onwards, followed by a dozen striae. A low, but evident, transverse pleural ridge behind gonopod opening on male segment 7. Epiproct slightly elongate apically, more narrowly rounded

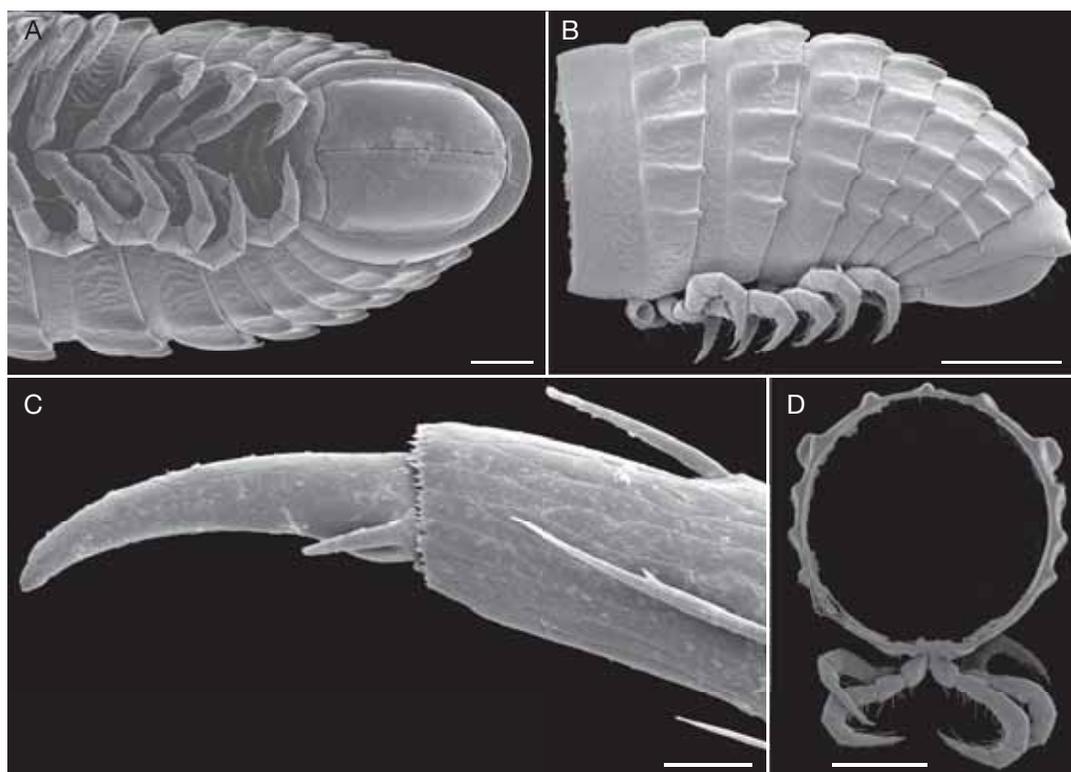


FIG. 22. — *Glyphiulus pergranulatus* n. sp., ♀ paratype: **A**, caudal part of body, ventral view; **B**, same, lateral view; **C**, claw of a midbody leg; **D**, midbody segment section, caudal view. Scale bars: A, 0.2 mm; B, D, 0.5 mm; C, 0.01 mm.

than usual; hypoproct more narrowly emarginate at caudal margin (Fig. 19D).

Legs elongate (Fig. 20F), claws strongly elongate, without a spine near base starting from leg 4 (Fig. 19F).

Male legs 1 with vestigial tubercular coxites (Fig. 20C). Penes with 4 or 5 long setae distolaterally (Fig. 20D), male legs 3 elongate, much as in *G. granulatus* (Fig. 20E). Anterior gonopods with small subunciform protuberances at median corners of coxosternum (Fig. 20G). Posterior gonopods with a flagelliform but bare distal process (Fig. 20H).

#### REMARKS

Based on its evident troglomorphic traits, this species seems to be a troglobite.

#### *Glyphiulus pergranulatus* n. sp. (Figs 21-23)

**TYPE MATERIAL.** — **China.** Guizhou Prov., Guanling County, Huajiang, Da Dong Cave, 4.IV.2004, leg. L. Latella & Ghen Hu, holotype ♂ (MNHN GA 041); paratypes 1 ♂ (MNHN GA 041); 1 ♀ (SEM). — Guizhou Prov., Guanling County, Huajiang, An Jia Da Dong Cave, 4.IV.2004, leg. L. Latella & R. Zorzin, paratype 1 ♀ (MNHN GA 041).

**ETYMOLOGY.** — To emphasize the close affinities to *G. granulatus*.

**DIAGNOSIS.** — Characterized by the somewhat larger ocellaria, the underdeveloped tergal crests (becoming almost obliterated in the median part of the collum), coupled with the medium body size, slightly elongated legs, simple anterior gonopods, etc.

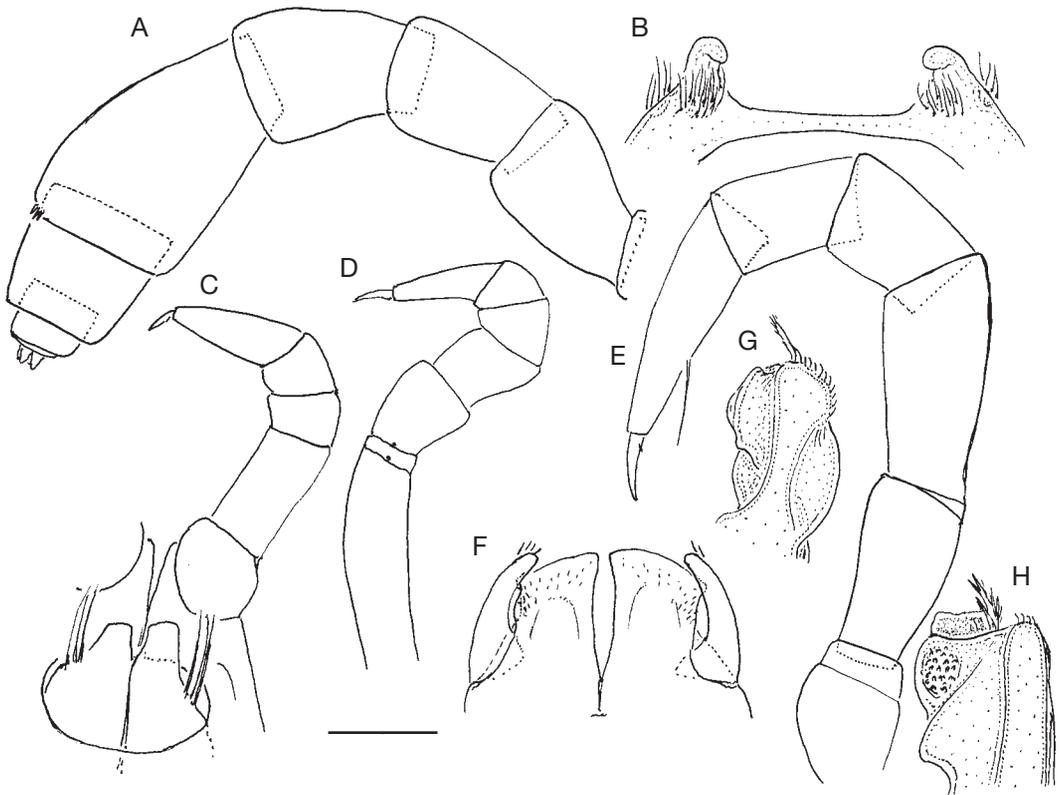


FIG. 23. — *Glyphiulus pergranulatus* n. sp., ♂ paratype: A, antenna; B, legs 1, caudal view; C, legs 2, caudal view; D, leg 3; E, midbody leg; F, anterior gonopods, caudal view; G, posterior gonopod, subfrontal view; H, same, frontal view. Scale bar: 0.2 mm.

#### DESCRIPTION

Length of holotype and of paratype ♀ from An Jia Da Dong about 30 mm, of paratype ♂ about 33 mm, width 1.5, 1.5 and 1.7 mm, with  $56p+2a+T$ ,  $67p+1a+T$  and  $57p+2a+T$ , respectively.

Coloration, antennae (Figs 21A; 23A), segment shape (Fig. 22D), carinotaxy patterns (Fig. 21), male legs 1-3 (Fig. 23B-D), etc., as in *G. granulatus*, but tergal crests somewhat underdeveloped (Figs 21; 22B, D), almost obliterated in median part of collum (Fig. 21A, B). Ocellaria rounded-triangular, black, each with 23-25 poorly convex ocelli. Claws slightly longer, spine at base slightly shorter (Fig. 22C); legs about 4/5 as long as midbody height (Fig. 23E). Epiproct with a faint but evident middorsal tubercle (Fig. 22B); hypoproct more narrowly emarginate at caudal margin (Fig. 22A).

Anterior gonopod coxosternum particularly simple (Fig. 23F). Posterior gonopods with a typical flagelliform and plumose distal process (Fig. 23G, H).

#### REMARKS

Even though taken from caves, this species seems to represent only a troglophile at most. However, this cave harbours another, apparently troglobitic congener from a different species group, to be described elsewhere.

#### *Glyphiulus latellai* n. sp. (Figs 24-26)

TYPE MATERIAL. — China. Guizhou Prov., Gianxi County, Hong Lin Village, Chang Tu Dong Cave, 13.XI.2003, leg. L. Latella, holotype ♂ (MNHN GA

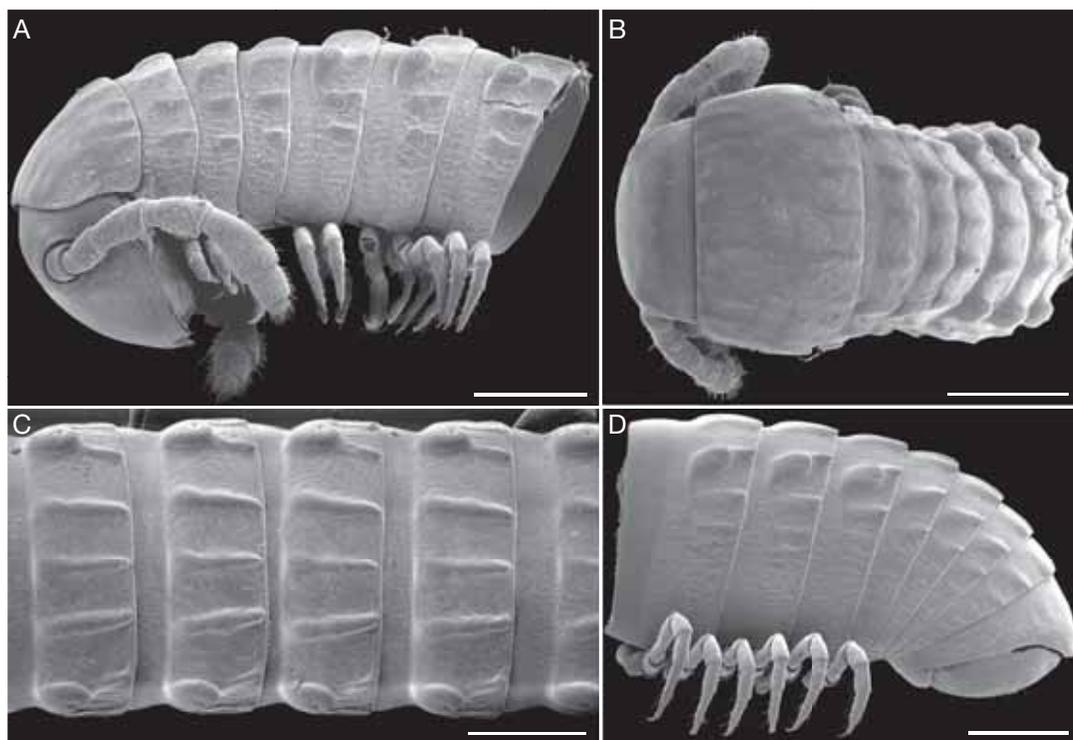


FIG. 24. — *Glyphiulus latellai* n. sp., ♀ paratype: A, anterior part of body, lateral view; B, same, dorsal view; C, middle part of body, dorsal view; D, caudal part of body, lateral view. Scale bars: 0.5 mm.

042); paratypes 2 ♂♂, 1 ♀ (MNHN GA 042), 1 ♀ (SEM). — Same locality, 3.IV.2004, leg. L. Latella, paratype 1 ♀ (MCSNV). — Guizhou Prov., Gianxi County, Hong Lin Village, Xiao Dong Cave, 16.XI.2003, leg. Latella & Cioperelli-Repetto, paratype 1 ♂ (ZMUM). — Guizhou Prov., Gianxi County, Hong Lin Village, Xi Xiang Dong Cave, 14.XI.2001, leg. L. Latella, paratype 1 ♀ (MNHN GA 042). — Guizhou Prov., Gianxi County, Hong Lin Village, Dayan Dong Cave, 22.XI.2003, leg. L. Latella, paratype 1 ♀ (ZMUC). — Guizhou Prov., Gianxi County, Hong Lin Village, Tiao Shuz Dong Cave, 18.XI.2001, leg. L. Latella, D. Avesani & G. Rossi, paratypes 1 ♀, 3 juv. (MNHN GA 042); 1 ♀ (SEM). — Guizhou Prov., Gianxi County, Hong Lin Village, Lu Diao Ai Dong Cave (= Cow Fell Down Cave), XI.2003, leg. L. Latella, paratype 1 ♂ (NMNHS). — Guizhou Prov., Gianxi County, Hong Lin Village, Shu Jia Yan Dong Cave, 17.XI.2001, leg. Latella & Berzacola, paratypes 2 ♂♂, 1 ♀, 1 juv. (MNHN GA 042). — Guizhou Prov., Gianxi County, Ishui Luo Dong Cave, 20.XI.2001, leg. L. Latella, paratype 1 ♂ (MNHN GA 042).

ETYMOLOGY. — Honours Leonardo Latella, the collector.

DIAGNOSIS. — Differs from congeners by the strongly reduced crests on the collum and metaterga, the completely undivided dorsal crests (the mediodorsal ones also undivided anteriorly), the complete depigmentation (even of ocellaria), the evidently elongated antennae and legs, the low, but evident, transverse pleural ridge behind the gonopod opening on male segment 7, etc.

#### DESCRIPTION

Length of adults of both sexes 18–45 mm, width 1.3–2.0 mm. Coloration usually uniformly dark brown due to heavy sclerotization, sometimes ozoporiferous tubercles reddish; more rarely, coloration uniform yellowish.

Adults of both sexes with 42-63p+6-1a+T; largest juveniles (♀) with 35p+4a+T or 36p+5a+T.

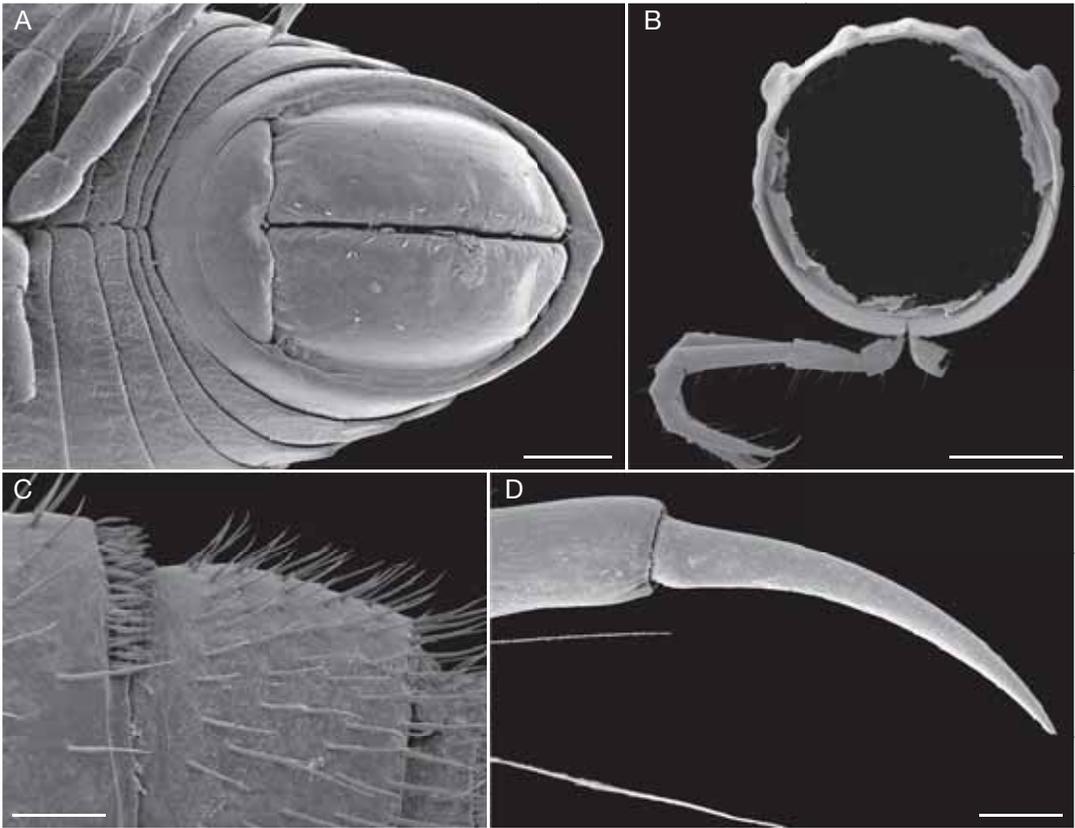


FIG. 25. — *Glyphiulus latella* n. sp., ♀ paratype: A, telson, ventral view; B, midbody segment section, frontal view; C, bacilliform sensilla on antennomere 6; D, claw of a midbody leg. Scale bars: A, 0.2 mm; B, 0.5 mm; C, 0.05 mm; D, 0.02 mm.

Length of holotype about 30 mm, width 1.3 mm, with  $50p+3a+T$ .

Antennae much more elongate than usual (Figs 24A; 26A), with especially numerous and dense distodorsal sensilla on antennomeres 5 and 6 (Fig. 25C). Ocellaria, if any, unpigmented, ocelli, when present, 1-11, irregularly spaced, barely traceable. Gnathochilarium usual, mentum divided ( $n = 2$ ) (Fig. 26B).

Carinotaxy of collum rather typical, though hardly traceable because of crests being nearly obliterated, especially anteromedially (Fig. 24A, B). Carinotaxy of subsequent metaterga deviating slightly from typical formula (Figs 24; 25B) in that none of the dorsal crests is divided transversely or longitudinally; all crests somewhat reduced (Fig. 25B),

with only 2 or 3 very low lateral ones (formula  $2(3)+I+3+I+2(3)$ ). From segment 7 on, crest below "I" (i.e. below ozoporiferous tubercle) poorly divided at about midway; further ventrad, segments with 1 or 2 barely distinguishable crests followed by about a dozen fine striae (Fig. 24A, D). A low, but evident, transverse pleural ridge present behind gonopod opening on male segment 7. Epiproct slightly elongate apically, more narrowly rounded than usual; hypoproct more narrowly emarginate at caudal margin (Fig. 25A).

Legs elongate (Fig. 25B), about as long as midbody height; claws strongly elongate, with a small spine near base on legs of anterior  $1/5-1/4$  body (Fig. 26F), thereafter devoid of any basal spines (Fig. 25D). Male legs 1 with rudimentary tubercular

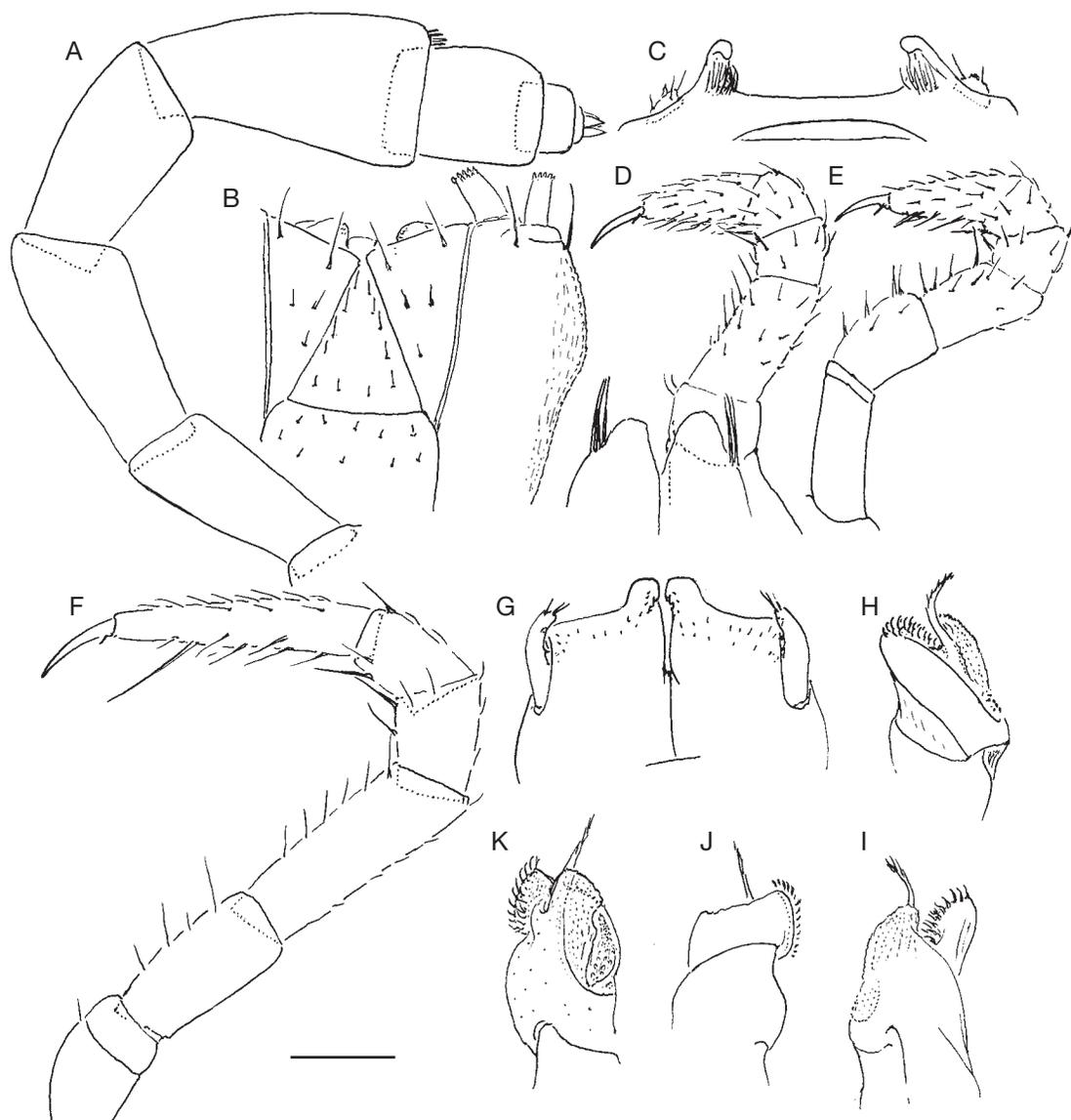


FIG. 26. — *Glyphiulus latellai* n. sp., ♂ paratype: A, antenna; B, gnathochilarium, caudal view; C, legs 1, caudal view; D, legs 2, caudal view; E, leg 3; F, leg 11; G, anterior gonopods, caudal view; H, left posterior gonopod, caudal view; I, same, frontal view; J, right posterior gonopod, submedial view; K, same, sublateral view. Scale bar: 0.2 mm.

coxites (Fig. 26C); male legs 2 and 3 typical (Fig. 26D, E).

Anterior gonopods with small, subunciform protuberances at median corners of coxosternum (Fig. 26G). Posterior gonopods with a flagelliform and

plumose distal process (Fig. 26H-K).

**REMARKS**

Based on its troglomorphic traits, this species seems to be a troglobite. It coexists in four of the caves

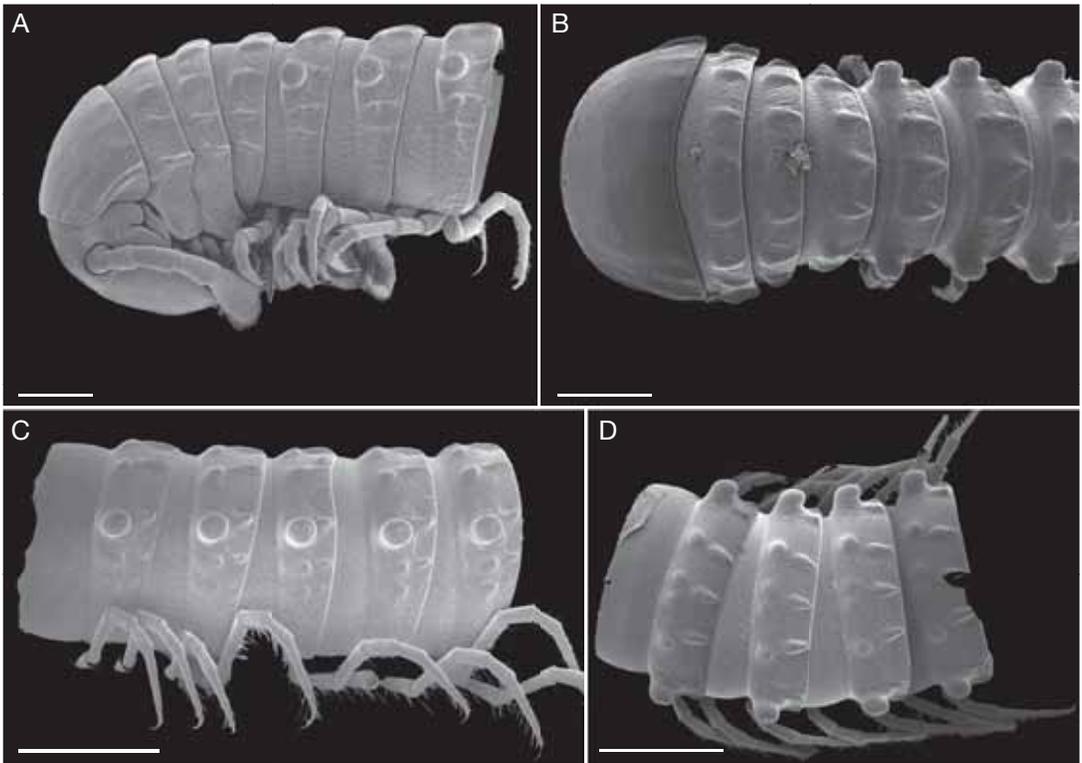


FIG. 27. — *Glyphiulus basalis* n. sp., ♀ paratype: A, anterior part of body, lateral view; B, same, dorsal view; C, middle part of body, lateral view; D, same, dorsal view. Scale bars: A, B, 0.5 mm; C, D, 1 mm.

with still another millipede troglobite, *Guizhousoma latellai* Mauriès, 2005 (Chordeumatida, Guizhousomatidae) (Mauriès 2005).

*Glyphiulus basalis* n. sp.  
(Figs 27-29)

**TYPE MATERIAL.** — China. Sichuan Prov., Xin Long County, Gan Chuan Cave, Nos 414, 417 and 421, 6.VIII.1999, leg. J. & B. Lips, holotype ♂ (MNHN GA 043); paratypes 1 ♂, 3 ♀♀ (MNHN GA 043); 1 ♀ (ZMUM); 1 ♀ (ZMUC); 1 ♀ (SEM).

**ETYMOLOGY.** — To emphasize the presumed basal position of this species within the group.

**DIAGNOSIS.** — Differs primarily by the retained telopodites of male legs 1, coupled with the large size, the crests on the collum and the spines at claw base both

strongly reduced, the crests on metaterga reduced but the ozoporiferous tubercles high, the troglomorphic traits (complete depigmentation, the lack of ocelli, the evidently elongated antennae and legs), the low, but evident, transverse pleural ridge behind the gonopod opening on male segment 7.

**DESCRIPTION**

Length of ♂, 30-32 mm, width 1.8 mm; of ♀, 23-42 and 1.5-2.2 mm, respectively. Length of holotype about 30 mm, width 1.3 mm. Coloration usually uniformly yellowish, sometimes dark red-brown due to heavy sclerotization.

Holotype with 48p+3a+T; ♂ paratype with 45p+4+T; ♀ paratypes with 40-59p+4-1a+T.

Antennae much more elongate than usual (Figs 27A; 29A). Ocelli absent. Gnathochilarium with (n = 1) or without (n = 2) division of mentum (Fig. 29B).

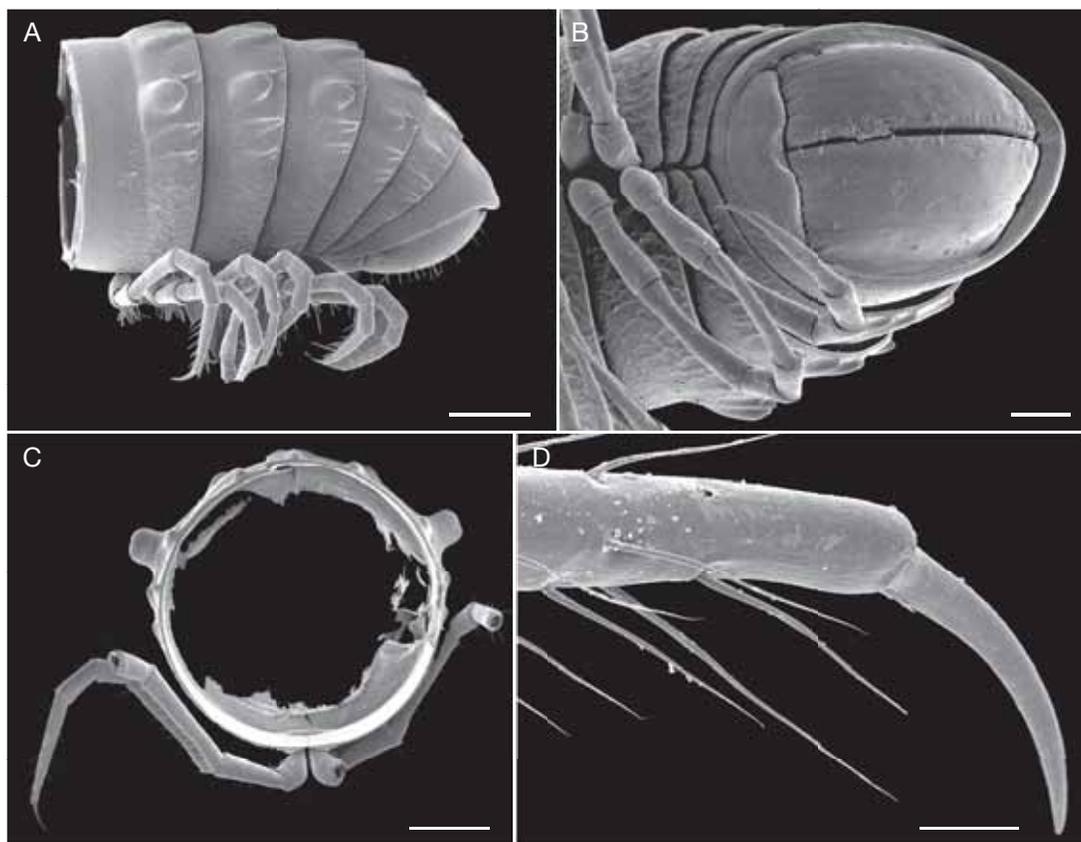


FIG. 28. — *Glyphiulus basalis* n. sp., ♀ paratype: A, caudal part of body, lateral view; B, same, ventral view; C, midbody segment section, frontal view; D, claw of a midbody leg. Scale bars: A, C, 0.5 mm; B, 0.2 mm; D, 0.05 mm.

Crests on collum, dorsad of a well-developed lateral carina, nearly completely obliterated, pattern visible only as (4)5+m+5(4) extremely faint undulations at caudal margin (Fig. 27A, B). Carinotaxy of subsequent metaterga typical (Fig. 27D; 28D), but only two crests present below rather strikingly elongated ozoporiferous tubercles; all other crests distinctly underdeveloped (Figs 27A, D; 28A, C). From segment 7 or 8 on, median crest clearly doubled anteriorly (Fig. 27D). Midbody segments round in cross-section (Fig. 28C). A low, but evident, transverse pleural ridge present behind gonopod opening on male segment 7. Epiproct narrower caudally, hypoproct more narrowly emarginate at caudal margin (Fig. 28B).

Legs elongate (Figs 27C; 28C; 29F), longer than midbody height; claws strongly elongate, with a very small spine at base (Fig. 28D). Male legs 1 unusual in being fully leg-like, only very modestly reduced: a coxa, a 3-segmented telopodite and a claw supplied with a spine at base are all very clearly expressed (Fig. 29C); male legs 2 and 3 typical (Fig. 29D, E), but penes devoid of strong setae distolaterally.

Anterior gonopods with evident, subunciform protuberances at median corners of coxosternum (Fig. 29G). Posterior gonopods with a flagelliform and micropilose distal process (Fig. 29H).

#### REMARKS

Based on morphological evidence alone, this species seems to be a troglobite.

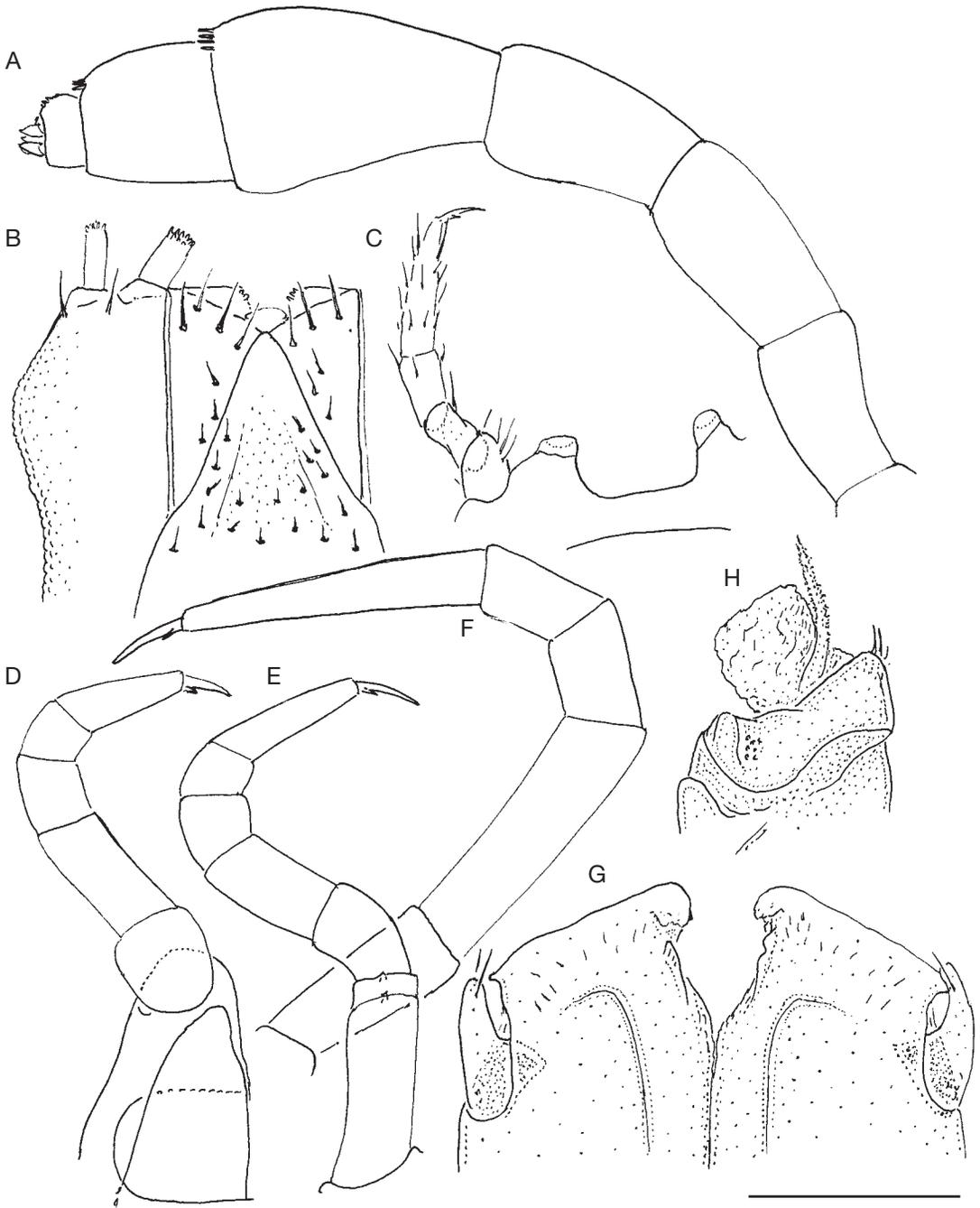


FIG. 29. — *Glyphiulus basalis* n. sp., ♂ paratype: A, antenna; B, gnathochilarium, caudal view; C, legs 1, caudal view; D, leg 2, caudal view; E, leg 3; F, leg 11; G, anterior gonopods, caudal view; H, right posterior gonopod, caudal view. Scale bar: A-F, 0.4 mm; G, H, 0.3 mm.

KEY TO SPECIES OF *GLYPHIULUS* GERVAIS, 1847 OF THE *GRANULATUS*-GROUP

1. Carinotaxy patterns of collum and body segments typical, all crests well-developed: carinotaxy formula of collum: I-VI+7a+pc+ma+pc+7a+VI-I, i.e. middle part of collum with two abbreviated paramedian crests over front 2/3 collum, as well as three abbreviated crests medially in caudal 1/3 collum (Figs 2A; 10B; 13B; 15B; 17B); carinotaxy of midbody segments 3(2)+I+4+I+3(2) and 3(2)+i+3+i+3(2) (Figs 2B-F; 3B; 7C-F; 10C, D; 13C, D; 17C, D; 19A-C, E; 21; 22D; 27D), rarely even with a third row of 3(2)+i+3+i+3(2) (Fig. 15C, D), but median crest always doubled anteriorly. Relatively small species: length of adults  $\leq 25$  mm, width  $\leq 1.3$  mm ..... 2
  - Carinotaxy patterns of collum and body segments deviating from the typical ones, i.e. crests on collum either at least partly obliterated (Figs 7B; 19A, B; 21B; 24A, B; 27A, B) or, more seldom, showing a different formula, or some crests hypertrophied and differentiated, whereas midbody segments with either a typical (2+I+4+I+2 and 2+i+3+i+2) or an atypical formula, e.g., 3(2)+I+3+I+3(2) (Fig. 24). Often larger species ..... 7
2. Midbody segments in cross-section slightly compressed laterally (Fig. 13C). Legs slightly elongate, about as long as midbody height. Yunnan Prov., China ..... 3
  - Midbody segments round in cross-section (Figs 3B; 19E; 22D; 25B), not compressed laterally. Legs usually slightly shorter, rarely evidently longer, than midbody height .... 4
3. Antennae elongate (Fig. 12A). Spine at base of claw more than half as long as claw (Figs 11D; 12D, E) ..... *G. paragranelatus* n. sp.
  - Antennae stout (Fig. 14A). Spine at base of claw less than half as long as claw (Fig. 14D) ..... *G. semigranelatus* n. sp.
4. Crests on midbody segments divided into three tubercles (Fig. 15D, E). Epiproct with a small but evident middorsal tubercle (Fig. 15E). Posterior gonopods with a plumose and subflagelliform distal process (Fig. 16E, F) ..... *G. beroni* n. sp.
  - Crests on midbody segments divided into two tubercles (Figs 2D; 7C, D; 17C, D; 21C, D). Epiproct without a middorsal tubercle (Figs 2E; 17E). Posterior gonopods with a plumose but subspatuliform distal process (Fig. 18H) ..... 5
5. Paraprocts evidently elevated, ridge-like along midline (Fig. 17F). Anterior gonopods with thicker telopodites, distomedial corners subunciform (Fig. 18G). Northern Laos .....
  - ..... *G. bedosae* n. sp.
  - Paraprocts virtually flat and smooth at midline (Figs 3C, D; 8B; 25D). Anterior gonopods with telopodites more slender, distomedial corners different ..... 6
6. Legs evidently shorter than midbody height (Fig. 3B). Antennae short and stout (Figs 3A; 4A). Anterior gonopods with characteristic, very high, distomedial processes (Figs 3E; 5A, B; 6C). Pantropical ..... *G. granulatus*
  - Legs only slightly shorter than midbody height. Antennae slightly longer and more slender (more like in Figure 26A). Anterior gonopods much like in Figure 18G, distomedial processes low and broadly rounded. Hubei Prov., China ..... *G. lipsorum*
7. Collum conspicuously hypertrophied due to crests I-IV, but paramedian crests complete and contrastingly low in anterior 1/3 collum. Vestigial 2-segmented leg remains on male sternum I. Anterior gonopods much as in *G. granulatus* (Fig. 5A, B), distomedial processes similarly high but much wider. Posterior gonopods strongly constricted in distal 1/3. Mountains of central Vietnam ..... *G. capucinus*
  - Collum not hypertrophied, often some of its crests more or less obliterated. Male legs 1 either completely reduced to 1-segmented tubercular (usually) or leg-like. Anterior

- gonopods usually with much lower distomedial processes, if any. Posterior gonopods not so constricted in distal part (Fig. 7F, G) ..... 8
8. Midbody segments with median crest doubled anteriorly (Figs 7C; 19C; 21D; 27D). At least some crests on collum partly obliterated (Figs 7B; 21A, B; 24A, B), only seldom reduced very strongly (Fig. 27A, B) ..... 9
- Midbody segments with median crest not doubled anteriorly (Fig. 24C). Carinotaxy pattern of collum either atypical or difficult to trace due to crest reduction (Figs 19A, B; 24B) ..... 14
9. Midbody segments slightly compressed laterally in cross-section ..... 10
- Midbody segments round in cross-section (Figs 19E; 28C) ..... 11
10. Length of adults 19-28 mm, width 1.0-1.3 mm. Collum with 7+m+7 small rounded crests well visible at least near caudal edge (Figs 7B; 8A). Midbody segments with three lateral crests below ozoporiferous one (Fig. 7D, F). Claws as well as entire legs shorter (Figs 7D, F; 8C). Anterior gonopod telopodites especially slender, distomedial corners of coxosternum broadly rounded, lateral corners clearly dentiform (Fig. 9E). Distal process of posterior gonopod flagelliform and plumose (Fig. 9F, G). Troglobite from Yunnan Prov., China ..... *G. subgranulatus* n. sp.
- Length of adults 40-55 mm, width 2.0-2.3 mm. Collum with only a few undulations barely traceable near caudal edge (Fig. 19A, B). Body segments showing only two lateral crests below ozoporiferous one (Fig. 19A). Claws as well as entire legs longer (Fig. 19E, F). Anterior gonopod telopodites not particularly slender, distomedial corners of coxosternum subunciform (Fig. 20G). Distal process of posterior gonopod flagelliform but bare (Fig. 20H). Troglobite from Hunan Prov., China ..... *G. deharvengi* n. sp.
11. Carinotaxy pattern of midbody segments typical, with three lateral crests below ozoporiferous one (Fig. 21). Crests on collum visible at both posterior and anterior margins (Fig. 21A, B). Obvious troglomorphic traits absent. Guizhou Prov., China ..... 12
- Carinotaxy pattern of midbody segments also typical, but with two lateral crests below ozoporiferous one (Figs 24C; 25B; 27C; 28C). Crests on collum (4)5+m+5(4), hardly visible only at posterior margin. Troglomorphic traits very obvious ..... 13
12. Collum with 7+7 flat crests at anterior and 5+m+5 similarly flat crests at posterior margin, central part nearly smooth. Anterior gonopod coxosternum with a small subunciform projection at distomedial corner. Distal process of posterior gonopod blade-shaped, bare ..... *G. quadrohamatus*
- Collum with 7+m+7 flat crests at posterior margin, anteromedial part nearly smooth, but carinotaxy pattern discernible as typical (Fig. 21A, B). Anterior gonopod coxosternum particularly simple, subtruncate (Fig. 23F). Distal process of posterior gonopod flagelliform and plumose (Fig. 23G, H) ..... *G. pergranulatus* n. sp.
13. Male legs 1 leg-like (Fig. 29C). Ozoporiferous tubercles unusually prominent compared with the other, strongly reduced crests. Troglobite from Sichuan Prov., China ... *G. basalis* n. sp.
- Male legs 1 strongly reduced (as in Figure 4D). Ozoporiferous tubercles low, much wider than high ..... 14
14. Collum with rather evident crests at caudal margin, but entirely smooth over anterior 1/3. Ocelli completely reduced. Troglobite from Guangxi Prov., China ..... *G. anophthalmus*
- Collum with crests barely visible in posterior 1/3, being totally obliterated over anterior 2/3. Ocelli present but unpigmented, reduced in number to about 6. Troglobite from Guizhou Prov., China ..... *G. balazsi*

15. Carinotaxy pattern of midbody segments strongly atypical, formula being 2+I+2+I+2 and 2+i+3+i+2. Collum with 5+ma+5 flat crests/undulations barely visible at posterior margin. Guangxi Prov., China ..... *G. adeloglyphus*  
 — Carinotaxy pattern of midbody segments easily derivable from typical one. Collum varying from strongly carinate to virtually smooth, usually easily derived from typical carinotaxy pattern ..... 16
16. Collum strongly carinate, no crests being obliterated. Legs and claws relatively short, legs shorter than midbody height ..... 17  
 — Collum evidently carinate only at posterior margin at most, crests always being obliterated over central and/or anterior parts (Fig. 24A, B), or collum entirely smooth. Presumed troglobites, legs at least as long as midbody height (Fig. 25B); claw slender and long (Fig. 25D), at least as long as tarsus ..... 18
17. Length of adults 17-30 mm, width up to 1.2 mm. Carinotaxy pattern of collum deviating from typical mainly in having both paramedian crests complete, holoseriate, with formula I-VI+7a+P+ma+P+7a+VI-I. Epiproct with three weak crests dorsally. Anterior gonopod coxosternum with a short distomedian outgrowth. Guangxi Prov., China (also introduced to Okinawa Island, Japan) ..... *G. septentrionalis*  
 — Length of adults up to 85 mm, width up to 5.0 mm. Carinotaxy pattern of collum deviating in having at least both paramedian and median crests incomplete (formula I+2c+III-IV+(5c?)+VI+7p+8a+pc+ma+pc+8a+7p+VI+(5c?)+IV-III+2c+I). Epiproct with a weak crest dorsally. Anterior gonopod coxosternum much as in *G. granulatus*, with a very long and slender distomedian process. Mountains of central Vietnam .... *G. superbus*
18. Dorsal crests on midbody segments high, clearly divided into two halves. Ozoporiferous tubercles higher than wide. Guangxi Prov., China ..... *G. melanoporus*  
 — Dorsal crests on midbody segments invariably very low and undivided (Fig. 24A, D). Ozoporiferous tubercles wider than high (Fig. 24C). Guizhou Prov., China ..... 19
19. Collum completely smooth. Hypoproct very poorly emarginate medially .... *G. rayrouchi*  
 — Collum with poor but evident crests/undulations, a rather typical carinotaxy pattern visible at least medially (Fig. 24A, B). Hypoproct emargination nearly notch-like caudomedially (Fig. 25A) ..... *G. latellai* n. sp.

## CONCLUDING REMARKS

Now that the *granulatus*-group contains 20 species, and numerous presumed congeners from other groups that will be described elsewhere, it seems appropriate to provide brief analyses of variation in *Glyphiulus* and of the distribution of its constituent species. For the sake of convenience, and in agreement with Verhoeff (1936) and Loksa (1960), it seems best for the moment to accept the *granulatus*-group as being the same as *Glyphiulus* s.s. However, with further accumulation of material and its analysis, it may become necessary to adopt a broader concept of *Glyphiulus*.

Although the value of the classical division of the gnathochilarial mentum into a promentum and a eumentum has long been disputed and suspected as being overestimated in the systematics of cambaloid Juliformia (Verhoeff 1936; Attems 1938), the present discovery of infraspecific variation in this character in three species of the *granulatus*-group, *G. granulatus*, *G. subgranulatus* n. sp. and *G. basalis* n. sp., was quite surprising. This means that, within the Cambalopsidae at least, the mentum only tends to be divided in *Glyphiulus*. Similarly, the different degrees of setation of the gnathochilarium, from oligo- to polytrichous, also seem to reflect nothing but individual variation. In other words, the

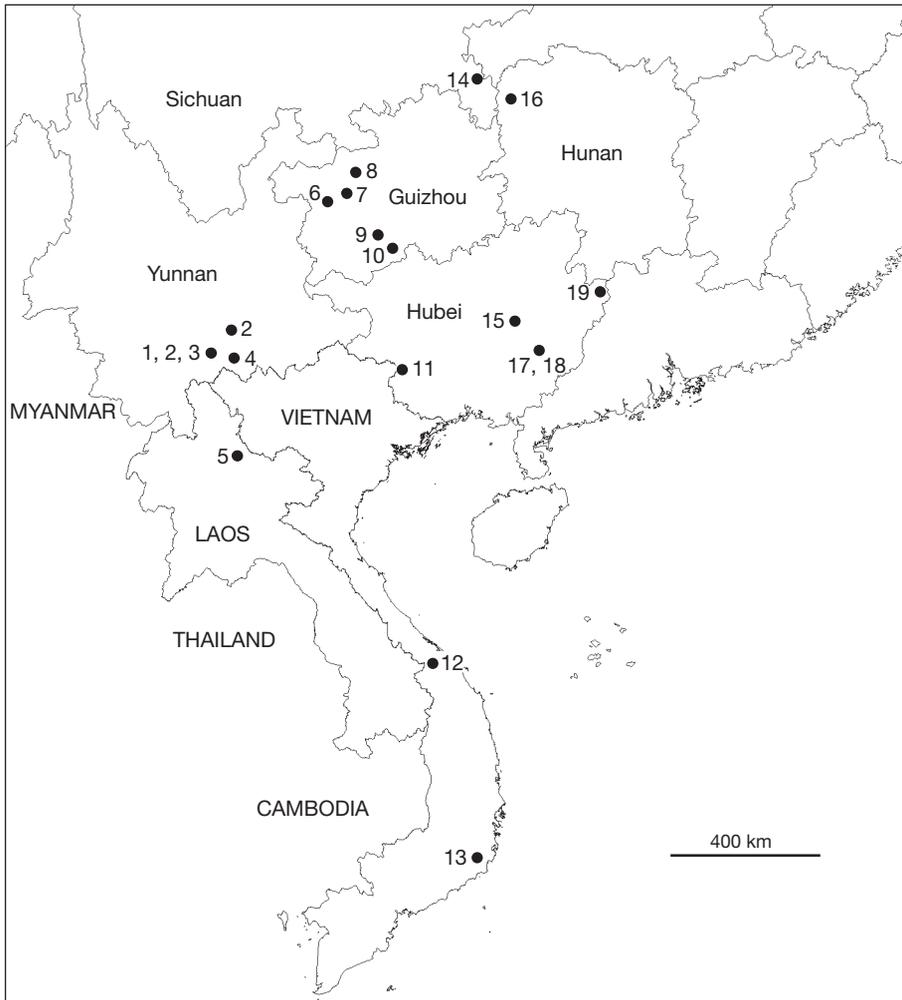


FIG. 30. — Distribution of species *Glyphiulus* Gervais, 1847 of the *granulatus*-group (that of *G. granulatus* (Gervais, 1847) being pan-tropical, it is omitted here), shown more or less from west to east: 1, *G. paragranelatus* n. sp.; 2, *G. semigranelatus* n. sp.; 3, *G. beroni* n. sp.; 4, *G. subgranelatus* n. sp.; 5, *G. bedosae* n. sp.; 6, *G. pergranelatus* n. sp.; 7, *G. rayrouchi* Mauriès & Nguyen Duy-Jacquemin, 1997; 8, *G. latellai* n. sp.; 9, *G. quadroharmatus* Chen & Meng, 1991; 10, *G. balazsi* (Loksa, 1960); 11, *G. anophthalmus* (Loksa, 1960); 12, *G. capucinus* Attems, 1938; 13, *G. superbus* Silvestri, 1923; 14, *G. basalis* n. sp.; 15, *G. lipsorum* Mauriès & Nguyen Duy-Jacquemin, 1997; 16, *G. deharvengi* n. sp.; 17, *G. melanoporus* Mauriès & Nguyen Duy-Jacquemin, 1997; 18, *G. septentrionalis* Murakami, 1975; 19, *G. adelogyphus* Zhang & Li, 1982.

structure of the gnathochilarium seems more or less useless at the specific level. The division versus non-division of the mentum should only be applied to the genus level and even higher classification of cambaloids with extreme care, representing more of an evolutionary trend to be checked using sufficiently representative material.

As regards the carinotaxy in *Glyphiulus*, the patterns, but not the degrees of expression, of crests on the collum and body segments seem to be quite stable. Hence the patterns prove to be highly useful in the classification, often allowing the grouping of species. The degrees of expression of the crests prove to be very stable both between sexes and at

various developmental stages, making it a very useful character for species discrimination.

The carinotaxy pattern of the collum is often, but not always, correlated to that of the metaterga. In several cases at least, this correlation is difficult to elucidate because the crests on the collum are nearly or entirely obliterated. Crest reduction always concerns the anterior and/or central parts of the collum. Complete loss of crests/undulations is rare (i.e. *G. rayrouchi*). In general, crest arrangements and forms tend to be more variable on the collum than on the metaterga. Crest size reduction or hypertrophy concerns all of the metatergal crests simultaneously or nearly so, except perhaps the ozoporiferous tubercles, which always remain the largest and sometimes (in *G. basalis* n. sp.) even become enlarged against a background of the other strongly reduced crests. Reduction is especially evident due to loss of the ventrolateral crest, which turns into a stria similar to several other striae located further ventrad.

Changes in the carinotaxy formulae of the collum from the typical I-VI+7a+pc+ma+pc+7a+VI-I down to I-IV(V)+5(6)a+pc+ma+pc+5(6)a+(V)IV-I, due to fusion/loss of one or two lateralmost crests, are rather common. The pattern shown by the paramedian and median crests, when these are traceable, seems to be much more stable and important. Usually it is pc+ma+pc, only seldom P+ma+P (*G. septentrionalis*). Only one species, *G. capucinus*, has the crests strongly differentiated (some are hypertrophied, some others reduced), but the formula is only slightly different from that of *G. superbus*.

Variation in the carinotaxy formulae of the metaterga is more modest. Usually the crests are clearly divided near the middle into two half-crests, thus forming two transverse rows of tubercles. Usually the tubercles in the anterior row are smaller than those in the posterior row. In one case only (*G. beroni* n. sp.), most of the crests are divided transversely into three rows, whereas the crests are undivided only in *G. rayrouchi* and *G. latellai* n. sp. A typical pattern is 3(2)+1+4+1+3(2) and 3(2)+i+3+i+3(2), meaning that the median crest is doubled anteriorly. This formula is highly characteristic of the *granulatus*-group, with only relatively few, rather minor deviations that show no anterior duplication of the

middorsal crest. The strongest deviation observed is 2+I+2+I+2 and 2+i+3+i+2 (*G. adeloglyphus*).

Several species of the group are presumed troglobites. Besides showing the typical traits of troglomorphism (general depigmentation, eye reduction, elongation of legs, claws and antennae, "gigantism", although all relatively modestly expressed in comparison with some examples in Polydesmida or even Julida), such species tend to have more or less strongly obliterated crests on the collum, as well as reduced crests on the metaterga. In addition, they tend to show a more narrowly rounded epiproct and a more narrowly emarginate hypoproct. Although there is a pattern of elongated claws in the troglobitic species of *Glyphiulus* s.s., there seems to be no correlation between this and the size of the accessory spine at the claw base.

Legs 1 of the male are normally strongly reduced, but in *G. superbus*, besides a small coxa, a rudimentary telopodite segment is still discernible. Furthermore, *G. basalis* n. sp. seems to be even more primitive in this respect, showing a nearly fully developed, 3-segmented telopodite crowned with a typical claw and a spine at its base. What remains invariable is that the sternum is devoid of any median or paramedian structures, being supplied instead with two widely separated prongs curved caudally. This character is of primary importance in delimiting *Glyphiulus* s.s. from the other cambalopsids.

Because the vulvae in *Glyphiulus* are surprisingly monotonous in structure, they are hardly of use systematically. In addition, the peripheral characters of the female (and even of the juveniles) are so abundant and evident that they are quite sufficient for species recognition, as well as safe sex and stadium matches. Unsurprisingly, there are many species of Cambalopsidae described solely from female material.

The general distribution of the *granulatus*-group shows quite a coherent pattern (Fig. 30), occupying a region between Sichuan, Hubei and Shanghai in the North and central Vietnam in the South. There is no doubt that these generally subtropical to tropical, highly montane and often karstic areas contain many new species of *Glyphiulus* waiting to be found and described.

The fact that the species of the *granulatus*-group are mostly highly local in distribution deserves attention. This can often be accounted for by their being troglobites naturally restricted to their cave or a group of caves. However, the impression that most of the species are scarcely more than troglaphiles suggests that a wealthy, barely sampled fauna exists epigeically as well. This is because most of the expeditions to these often remote and poorly accessible places have been speleological, concentrating on the “mystique” of the underground world, thus giving the biased impression that cambalopsids in general, and *Glyphiulus* species in particular, are especially common in caves. Above-ground explorations will certainly reveal a far richer fauna of forest-dwelling species in that region. Summarising the poor state of current knowledge, we seem to have only touched the top of an iceberg.

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