

# Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Part 2: the *javanicus*-group

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## ABSTRACT

The *javanicus* species-group, belonging to the large, widespread, Southeast Asian genus *Glyphiulus* Gervais, 1847, is established for those species in which the males have legs 1 provided with medially contiguous but not entirely fused coxal processes, coupled with usually 4- or 5-segmented telopodites, along with carinotaxy patterns of the collum and metaterga that are highly characteristic and often stable. This group encompasses 19 species, all keyed here, including *Glyphiulus sinensis* (Meng & Zhang, 1993) n. comb. (before in *Podoglyphiulus* Attems, 1909), and 10 new species taken from caves: *G. oblitteratus* n. sp., *G. suboblitteratus* n. sp., *G. oblitteratoides* n. sp., *G. paroblitteratus* n. sp., *G. paracostulifer* n. sp. and *G. intermedius* n. sp. from southern China; *G. medioblitteratus* n. sp. from North Vietnam; and *G. costulifer* n. sp., *G. subcostulifer* n. sp. and *G. percostulifer* n. sp. from Laos.

## KEY WORDS

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

## RÉSUMÉ

Révision des diplopes du genre *Glyphiulus* Gervais, 1847, et description de nouvelles espèces d'Asie du Sud-Est (*Diplopoda*, *Spirostreptida*, *Cambalopsidae*). Partie 2: le groupe javanicus.

Le groupe javanicus de *Glyphiulus* Gervais, 1847, grand genre sud-est asiatique à très large répartition, est établi pour les espèces qui possèdent les caractères suivants : d'une part, la première paire de pattes du mâle est pourvue de processus coxaux médians contigus mais pas entièrement fusionnés et de télépodites habituellement à quatre ou cinq segments ; d'autre part, la structure et la disposition des carènes du collum et des métatergites sont hautement caractéristiques et souvent stables. Ce groupe comporte 19 espèces qui figurent toutes dans une clé, parmi lesquelles figurent *Glyphiulus sinensis* (Meng & Zhang, 1993) n. comb. (précédemment dans *Podoglyphiulus* Attems, 1909), et 10 espèces nouvelles et cavernicoles : *G. obliteratus* n. sp., *G. subobliteratus* n. sp., *G. obliteratoides* n. sp., *G. parobliteratus* n. sp., *G. paracostulifer* n. sp. et *G. intermedius* n. sp. de Chine du Sud, *G. mediobliteratus* n. sp. du nord du Vietnam, *G. costulifer* n. sp., *G. subcostulifer* n. sp. et *G. percostulifer* n. sp. du Laos.

## MOTS CLÉS

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

## INTRODUCTION

The large Southeast Asian genus *Glyphiulus* Gervais, 1847 has recently been reviewed by Golovatch *et al.* (2007), who showed that the *granulatus*-group corresponds to *Glyphiulus* s.s., encompassing 20 species. Members of this group are distinguished by the following characters:

1. Male legs 1 are usually very strongly reduced, represented by a sternum mainly or completely lacking any median structures, but bearing strongly separated and evidently curved prongs with a leg vestige on each side at the base (usually represented by just a few setae, less frequently also with one or two rudimentary segments). Very rarely, a nearly complete telopodite persists, but the sternum still supports a pair of widely separated and curved prongs.
2. Other male legs normal, not enlarged.
3. The 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 can always be seen, at least near the caudal margin.
4. The typical carinotaxy pattern of the metaterga is 3(2)+I+3+I+3(2). The crests are usually divided transversely into two halves, while the median crest is often doubled anteriorly, such that the formula becomes 3(2)+I+4+I+3(2) and 3(2)+i+3+i+3(2).

If the pattern is different, it can usually be 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.

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 evident transverse ventral ridge (shared with some other species groups).

The remaining nominate species of *Glyphiulus* still to be grouped (Mauriès & Nguyen Duy-Jacquemin 1997; Jeekel 2004; Golovatch *et al.* 2007) are as follows:

1. *Glyphiulus formosus* (Pocock, 1895), described as *Cambalomorpha formosa* Pocock, 1895 from a female from Hong Kong, China; known from the original description (Pocock 1895) and a partial redescription that allowed to bring this species especially close to *G. mediator* Attems, 1938 (Mauriès 1970; see below).

2. *Glyphiulus javanicus* Carl, 1911, described from Passaroean, Java, Indonesia; still only known from the original description (Carl 1911). Maybe an introduction by agricultural commerce.
3. *Glyphiulus mediator* Attems, 1938, described from Mt. Bana, Danang Province, central Vietnam (Enghoff *et al.* 2004); still only known from the original description (Attems 1938).
4. *Glyphiulus pulcher* (Loksa, 1960), described as *Octoglyphus pulcher* Loksa, 1960, from Nyu-Jie Cave near Pulung (= Fulong, near the border with Vietnam), Guangxi Prov., China; still only known from the original description (Loksa 1960).
5. *Glyphiulus reticulatus* Zhang & Li, 1982, described and still only known from Qinyuan, Zhejiang Province, China (Zhang & Li 1982).
6. *Glyphiulus siamensis* Mauriès, 1983, described and still only known from Doi Sutep, northern Thailand (Mauriès 1983). Enghoff (2005) recorded further material from the type locality.
7. *Glyphiulus vietnamicus* Mauriès, 1977, described and still only known from a cave in Ke Bang karst, Quang-Binh Province, Vietnam (Mauriès 1977; Enghoff *et al.* 2004).
8. *Glyphiulus zorzini* Mauriès & Nguyen Duy-Jacquemin, 1997, described and still only known from a few caves in Shuichang County, Guizhou Province, China (Mauriès & Nguyen Duy-Jacquemin 1997).
9. *Glyphiulus sinensis* (Meng & Zhang, 1993) n. comb., described in *Podoglyphiulus*, still only known from a cave in Gouanling Buiyau Miazu Autonomous County, Guizhou Prov., China (Meng & Zhang 1993).

This group is very close to an assemblage currently referred to as the genus *Podoglyphiulus* Attems, 1909. Its species generally match the diagnosis of the *javanicus*-group of *Glyphiulus*, but there are some important differences. Apparently, the most significant of these is a clear-cut tendency in male-based *Podoglyphiulus* species for the gonopods, especially the posterior ones, to be elongated, not so strongly condensed as in most of the species listed above. In addition, the collum is always strongly crested, the carinae being subdivided and arranged in three or four transverse rows, usually with 10 crests situated anteriorly and nine behind. The lowest, pleurosternal crest on the postcollar segments tends to be enlarged, while male legs 1, when known, have fully developed, 5-segmented telopodites and a single median process that no longer shows any traces of separation between the

coxal processes (Pocock 1893, 1895; Attems 1909; Silvestri 1923; Verhoeff 1936; Carl 1941; Mauriès 1970, 1977, 1983; Jeekel 2004).

Keeping these distinctions in mind, as well as the coherent distribution pattern shown by *Podoglyphiulus* species (Sri Lanka, India, Nepal and Myanmar, formerly Burma), there can be no doubt that *P. sinensis* Meng & Zhang, 1993, from southern China, actually belongs in the *javanicus*-group, as diagnosed here. This species is therefore transferred from *Podoglyphiulus* to *Glyphiulus* (see above).

The above checklist thus represents what is deemed to be a natural group of species which can be treated as the *javanicus*-group of *Glyphiulus*, as opposed to the *granulatus*-group which corresponds to *Glyphiulus* s.s. (Golovatch *et al.* 2007). If required in future, a generic category is already available for the *javanicus*-group, for which the oldest available name is *Cambalomorpha* Pocock, 1895 (type species: *Cambalomorpha formosa* Pocock, 1895), synonymised with *Glyphiulus* by Mauriès (1970).

In addition to the nine species listed above, the *javanicus*-group also contains 10 new species, described below. The name *javanicus* has been chosen for this group because this is the oldest male-based name in the genus that has an adequate original description (Carl 1911).

The *javanicus*-group also shows similarities with the long accepted genus *Hypocambala* Silvestri, 1897, which contains 10 species ranging from the Seychelles, Comoro Islands and Mauritius in the Indian Ocean, through Indochina and the Indo-Australian Archipelago, to New Caledonia, Loyalty Islands, Tonga and Samoa in the Pacific (Jeekel 1963, 2004). Indeed, the sole distinction between *Glyphiulus* s.l. and *Hypocambala* species lies in the lack in the latter group of tergal crests, tergal pilosity being present instead. When describing *G. vietnamicus*, Mauriès (1977) chose to place it into *Glyphiulus*, rather than *Hypocambala* Silvestri, 1897 (which is represented in Vietnam by *H. gracilis* (Attems, 1938)), only because the terga in *G. vietnamicus* were carinate.

However, we refrain from formally sinking *Hypocambala* under *Glyphiulus* here, as no new material of *Hypocambala* species has become available for the present study. If it were decided in future to

synonymise these names, Jeekel's (1963, 2004) key and catalogue would still be available for incorporation into a broader concept of the *javanicus*-group.

#### ABBREVIATIONS

MCSNV	Museo Civico di Storia naturale, Verona;
MNHN	Muséum national d'Histoire naturelle, Paris;
NMNHS	National Museum of Natural History, Sofia;
OBBFUL	Biology Department, Biotechnical Faculty, University of Ljubljana;
SEM	Scanning electron microscopy;
ZMUC	Zoological Museum, University of Copenhagen;
ZMUM	Zoological Museum, State University of Moscow.

#### MATERIAL AND METHODS

The material serving as the basis for the present contribution derives from the subterranean collections made in Laos by Anne Bedos and Louis Deharveng (MNHN), in Vietnam and southern China by Boris Sket and his collaborators (OBBFUL), and in southern China by Josiane and Bernard Lips (Villeurbanne, France), Petar Beron (NMNHS), Marc Pouilly (Lyon, France) and by Leonardo Latella (MCSNV) and his collaborators. The bulk of this material has been deposited in MNHN and NMNHS, with voucher specimens shared between the collections of MCSNV, ZMUC, ZMUM and OBBFUL.

SEM micrographs were taken using a JEOL JSM-6480LV scanning electron microscope. SEM material was coated with gold and, after examination, it was removed from stubs and returned to alcohol, all such samples, except otherwise indicated, being kept at MNHN.

The carinotaxy formulae in the descriptions below follow Hoffman (1977), as modified by Golovatch *et al.* (2007). 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 *granulatus*-group is either I-VI+7a+pc+ma+pc+7a+VI-I or something similar (Golovatch *et al.* 2007).

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 2+I+3+I+2 or 1+I+3+I+1. Because the crests are usually divided transversely into two halves, the formula becomes 2(1)+I+3+I+2(1) and 2(1)+i+3+i+2(1), each part corresponding to the number of transverse rows of tubercles (Hoffman 1977). An even shorter presentation is proposed here, in which the number of slashes corresponds to that of crest divisions, i.e. 2(1)/2(1)+I/i+3/3+I/i+2(1)/2(1).

Because of complete symmetry, such formulae could be abbreviated to a half.

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

#### SYSTEMATICS

Order SPIROSTREPTIDA Brandt, 1833  
 Suborder CAMBALIDEA Bollman, 1898  
 Family CAMBALOPSIDAE Cook, 1895  
 Genus *Glyphiulus* Gervais, 1847

#### The *javanicus*-group

#### REMARKS

The *javanicus*-group can be characterised as follows:

1. Male legs 1 are normal to reduced, never hypertrophied; telopodites often complete or nearly so, even when reduced in size, usually multisegmented; coxae or coxosternum with a pair of small but evident, central, medially nearly always contiguous, sometimes partly even fused outgrowths or processes which are never coalesced completely into a strong and long sickle-shaped structure (NB: a few species known only from female material are assigned here only provisionally).
2. Male legs virtually normal, not enlarged.
3. Typical carinotaxy patterns of the collum are I-III(IV, V)+P+M+P+(V,IV)III-I or, as in the *granulatus*-group,

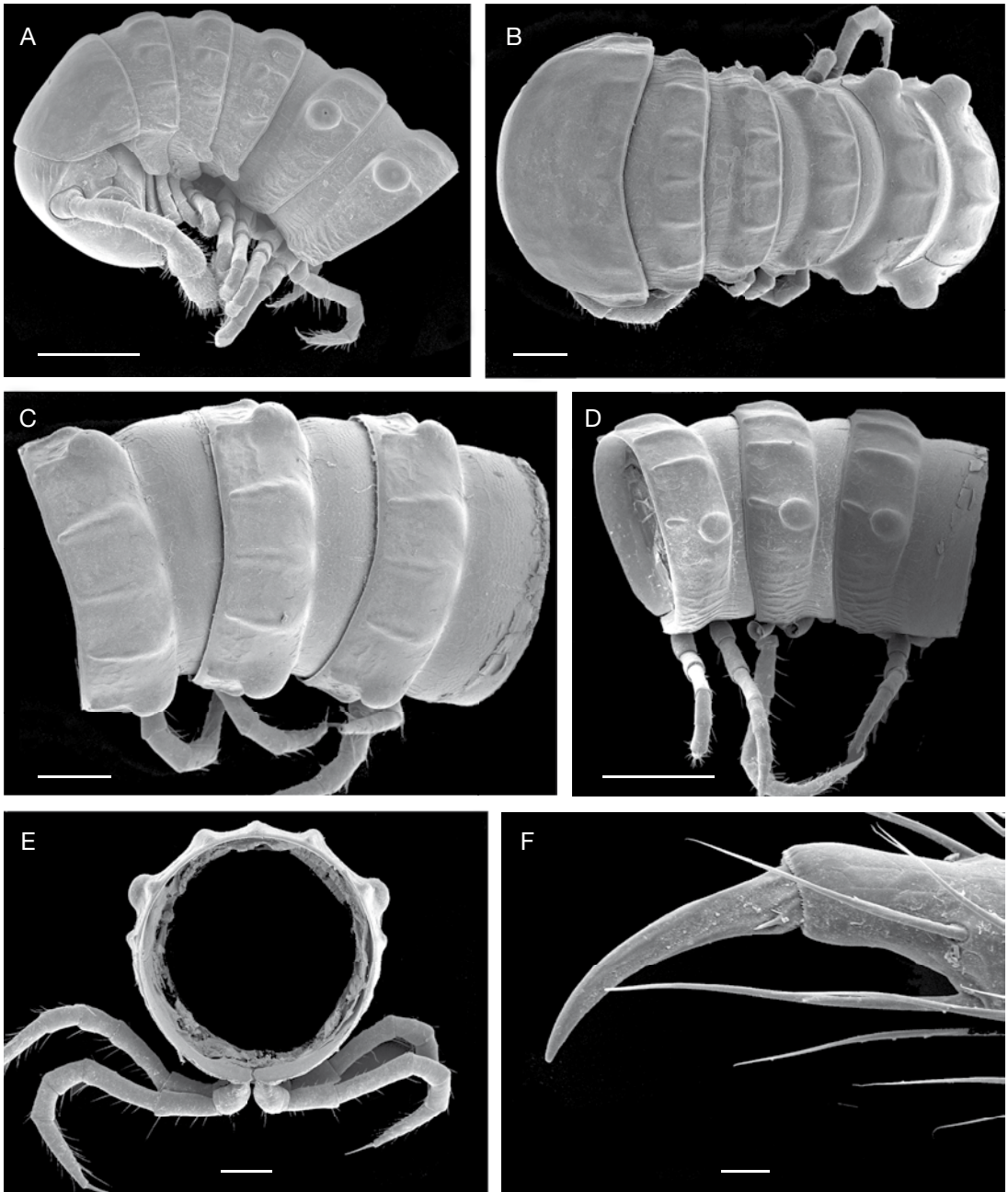


FIG. 1. — *Glyphiulus obliteratus* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, dorsal view; **D**, midbody segments, lateral view; **E**, midbody segment section; **F**, claw of midbody leg. Scale bars: A, D, 0.5 mm; B, C, E, 0.2 mm; F, 0.02 mm.

I-VI+7a+pc+ma+pc+7a+VI-I, or something close. The patterns are often different, often due to crest reduction (especially anteriorly), but a median crest is always visible at least near the caudal margin.

4. The typical carinotaxy pattern of the metaterga is  $2(1)/2(1)+I/i+3/3+I/i+2(1)$ , thus reflecting the fact that all or most of the crests are usually divided transversely into two halves. In contrast to species of the *granulatus*-group, the median crest is never doubled anteriorly, but sometimes it is more or less strongly reduced. If the pattern is different, it can usually be readily derived from the typical one (or *vice versa*), i.e. the lateral crests are reduced to one or the crests are undivided (see also below), etc.
5. The anterior gonopods are usually reduced to a plate-like coxosternum with moveable, lateral, 1-segmented, often curved telopodites (shared with some other species groups).
6. The posterior gonopods are usually strongly compressed, often showing a subflagelliform, sometimes plumose, distal flagellum (shared with some other species groups).
7. The pleural flaps behind the gonopod opening on male segment 7 usually form a clear, transverse, ventral ridge (shared with some other species groups).

The remaining known cambalopsids are considered to belong to other species groups, partly already treated (Golovatch *et al.* 2007) and partly to be treated elsewhere.

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

### *Glyphiulus obliteratus* n. sp.

(Figs 1; 2)

TYPE MATERIAL. — **China.** Yunnan Prov., Meele (Mile) County, Bai Long Dong Cave (White Dragon Cave), 2.I.1989, leg. P. Beron, holotype ♂ (NMNHS); paratypes 1 ♀ (SEM); 1 subadult ♂, 1 fragment (MNHN GA 044).

ETYMOLOGY. — To emphasize the nearly smooth collum and the relatively poorly developed metatergal crests.

DIAGNOSIS. — Differs from the very closely related *G. zorzini* in the considerably smaller size, the nearly smooth collum, the pigmented ocelli, the 4-segmented male telopodite 1, etc. (see also key below).

#### DESCRIPTION

Holotype with  $40p+3a+T$ , about 22 mm long and 1.4 mm wide; paratypes ♀ and fragment (caudal

body piece) 1.1 mm wide; paratype subadult male with  $32p+4a+T$ , c. 15 mm long and 1 mm wide.

Coloration completely pallid, only ocelli slightly pigmented, grey, weakly convex, arranged in a transverse ribbon of one or two rows, holotype with four on right side and five on left side of head, paratypes with five on each side. Clypeus with three indistinct teeth anteromedially. Antennae slender but not very long (Figs 1A; 2A), antennomeres 6 and 7 each with a small distodorsal group of bacilliform sensilla. Gnathochilarium with a separate promentum (Fig. 2B).

Head width = segment 2 =  $6(7) < \text{collum} = 8 = \text{midbody segments} > \text{segment } 3 > 4 > 5$ ; body first very gradually but then abruptly tapering toward telson. Postcollar constriction evident (Fig. 1B).

Collum nearly smooth, with  $3-4a+ma+3-4a$  low but evident undulations in caudal half (Fig. 1A, B). Subsequent metaterga evidently crested (Fig. 1A-E), especially so from segment 5 onwards, whence enlarged pore-bearing cones commence (Fig. 1A, B), these becoming increasingly inconspicuous towards telson and completely absent from legless segments due to loss of ozopores. Ozoporiferous tubercles round, wider than high (Fig. 1D, E); midbody metatergal crests complete (Fig. 1C, D), ozoporiferous crests distinctly divided into two about midway, their front halves being higher (Fig. 1C, D), those immediately below only indistinctly divided. Pleurosternal surface on segments behind 4th increasingly finely striate ventrad, not carinate, with about a dozen striae below single lateralmost crest. Carinotaxy formula  $1/1+I/i+3+I/i+1/1$  (Fig. 1C, D).

Tegument delicately alveolate-areolate, dull throughout. Fine longitudinal striations in front of stricture between pro- and metazona laterally and ventrolaterally, remaining surface of prozona very delicately shagreened. Metatergal setae absent. Segment 2 with long pleural flaps. Segments 2-4 each with a conspicuous, arcuate, pleurosternal crest (Fig. 1A). Limbus extremely finely and more or less regularly denticulate. Segments round in cross-section (Fig. 1E). Epiproct simple, devoid of tuberculation, with a rounded ridge in caudal part and an evident axial rib dorsally. Paraprocts rather regularly convex, each with a row of about a dozen setae at medial margin and several setae more laterally. Hypoproct lanceolate, poorly setose.

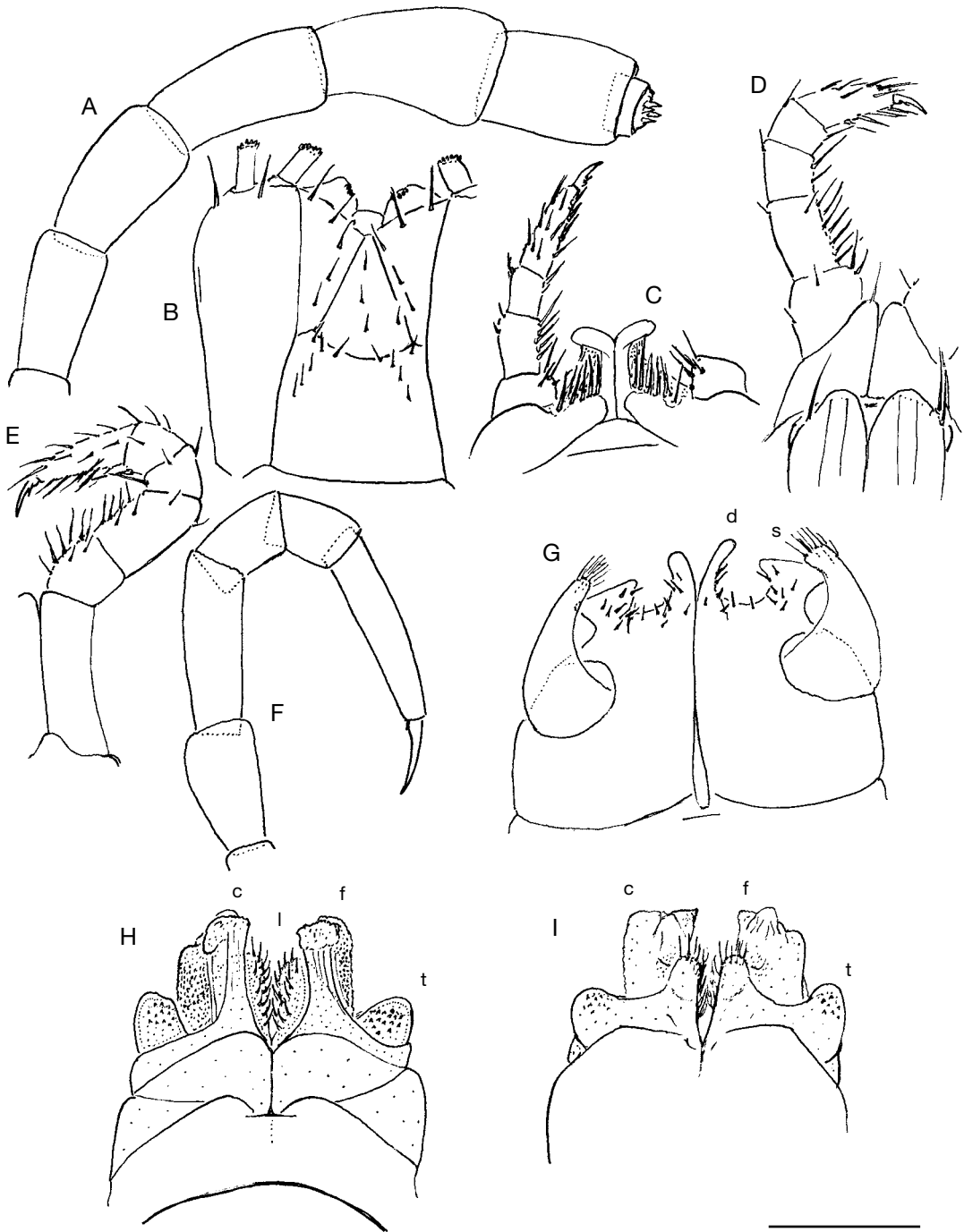


FIG. 2. — *Glyphiulus obliteratus* n. sp., paratype ♂: **A**, antenna; **B**, gnathochilarium; **C**, leg 1, frontal view; **D**, leg 2; **E**, leg 3; **F**, leg 9; **G**, anterior gonopods, caudal view; **H**, posterior gonopods, frontal view; **I**, same, caudal view. Abbreviations: c, caudal piece; d, digitiform process; f, frontal piece; l, setose lobe; s, subsecuriform process; t, (?)telopodite. Scale bar: A-F, 0.2 mm; G-I, 0.3 mm.

Ventral flaps behind gonopod opening on male segment 7 distinguishable as a low but clear transverse ridge.

Legs long, those on midbody segments slightly longer than segment diameter (Fig. 1E). Claw with a rudimentary accessory spine at base (Figs 1F; 2F), this spine being slightly longer on legs 1 and 2.

Male legs 1 highly characteristic (Fig. 2C) in showing nearly fully developed, 4-segmented telopodites and a pair of large, subdigitiform, medially contiguous but apically diverging coxal processes with groups of long, strong setae at base. Male legs 2 nearly normal, only claw and, anteriorly, coxa somewhat reduced, and femur abbreviated on frontal face; penes broad, rounded, each with one or two strong setae distolaterally (Fig. 2D). Male legs 3 modified in having coxa especially slender and elongate (Fig. 2E).

Anterior gonopods (Fig. 2G) with a typical shield-like coxosternum, this being modestly setose on caudal face and, on each side, provided with a conspicuous notch separating a high digitiform process (d) and a slightly lower subsecuriform process (s). Telopodite typical, rather large, stout, movable, 1-segmented, lateral in position, with several strong apical setae and a field of small setae at base, about as long as paramedian processes of coxosternum. Posterior gonopods (Fig. 2H, I) highly compact, both contiguous basally until about midheight; two densely setose lobes (l) paramedially; each half with two higher central pieces with a seminal groove in-between, frontal piece (f), elongate, apparently homologous with the apical flagelliform process observed in numerous congeners, caudal piece (c) subquadrate, membranous, micropapillate frontolaterally; a characteristic, rounded tubercle (?telopodite, t) with an apical field of coniform microsetae laterally.

#### REMARKS

In spite of the presence of slightly pigmented ocelli, this species could possibly be considered as troglitic, as several other traits are evidently troglomorphic (unpigmented tegument, elongated legs and antennae, perhaps also the nearly smooth collum). The cave it has been found in also supports a presumed trogliphilic congener, *G. semigranulatus*

Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2007 (see Golovatch *et al.* 2007).

### *Glyphiulus subobliteratus* n. sp.

(Figs 3-5)

TYPE MATERIAL. — **China**. Yunnan Prov., Shilin County, 85 km SE of Kunming, Shilin (Stone Forest), Zi Yung Dong Cave, 1.X.1988, leg. P. Beron, holotype ♂ (NMNHS), paratypes 5 ♂♂, 10 ♀♀, 9 juvs (NMNHS); 1 ♀ (SEM); 2 ♂♂, 2 ♀♀ (MNHN GA 045); 1 ♂, 1 ♀ (ZMUM); 1 ♂, 1 ♀ (ZMUC); 1 ♂, 1 ♀ (MCSNV).

ETYMOLOGY. — To emphasize the apparent resemblance to *G. obliteratus* n. sp.

DIAGNOSIS. — Differs from the most closely related species *G. obliteratus* n. sp. and *Glyphiulus zorzini* by the pigmented body, the collum undulate caudally (more strongly so than in *G. obliteratus* n. sp. but less so than in *G. zorzini*), the mostly higher and subdivided metatergal crests, some details of gonopod structure, etc. (see also key below).

#### DESCRIPTION

Holotype with 53p+2a+T, about 36 mm long and 2.0 mm wide; adult paratypes (♂, ♀) with 42-56p+4-1a+T, length 27-40 mm, width 1.6-2.0 mm.

Coloration marbled pale to dark grey-brown, especially infuscate due to metatergal crests; venter, antennae and legs yellowish. Ocelli black-brown, arranged in two transverse rows, seven or eight in each patch.

Antennae (Figs 3A; 4C; 5A), gnathochilarium (mentum divided,  $n = 7$ ) (Fig. 5B), segment shape (Fig. 4A), epiproct (Fig. 3E, F), male legs 2 and 3 (Fig. 5E, F), pleurosternal crests on segments 2-4 (Fig. 3A), accessory spine at base of claw (Fig. 4D) and posterior gonopods (Fig. 5H-K) generally as in *G. obliteratus* n. sp., but crests/undulations on collum low and incomplete, formula 1a+2p+3a-4a+ma+4a-3a+2p+1a (Fig. 3A, B); crests on subsequent segments higher (even adding another lateral crest below ozoporiferous one), mostly indistinctly subdivided (except for several anterior- and posteriormost segments); carinotaxy pattern 2/2+1/i+3/3+1/i+2/2, with anterior parts smaller than posterior ones (Fig. 3); legs shorter than body diameter (Fig. 4A); hypoproct with several scattered setae (Fig. 4B); male leg 1



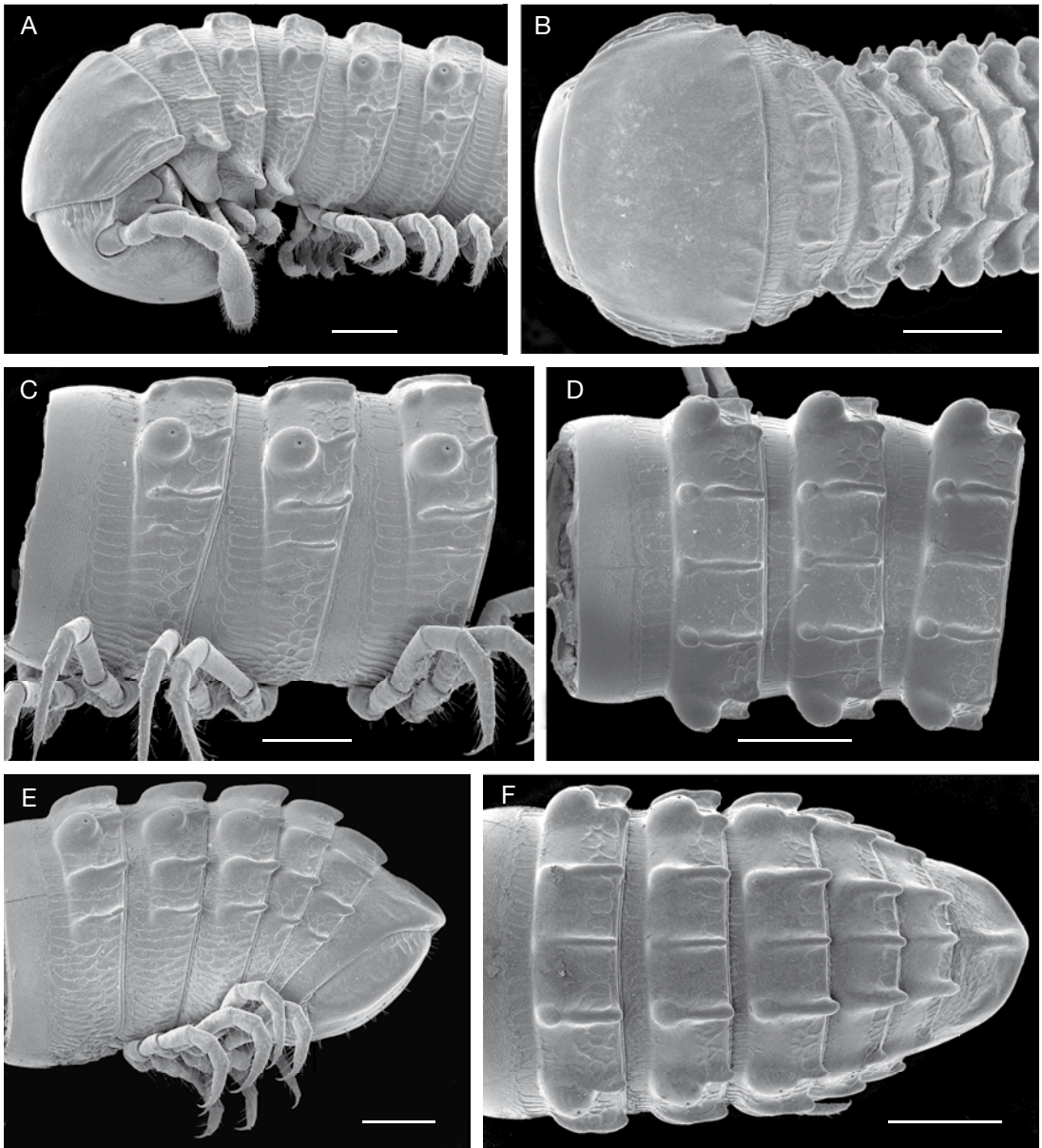


FIG. 3. — *Glyphiulus subobliteratus* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal body end, lateral view; **F**, same, dorsal view. Scale bars: 0.5 mm.

with particularly strongly developed paramedian coxal outgrowths and 5-segmented, though slightly reduced, telopodites (Fig. 5C, D); notch on each half-anterior gonopod less deep (Fig. 5G), etc.

Head width = segment 2 = 6 < collum = 7(8) = midbody segments > segment 3 > 4 > 5; body first gently but then abruptly tapering toward telson. Postcollar constriction evident (Fig. 3B).

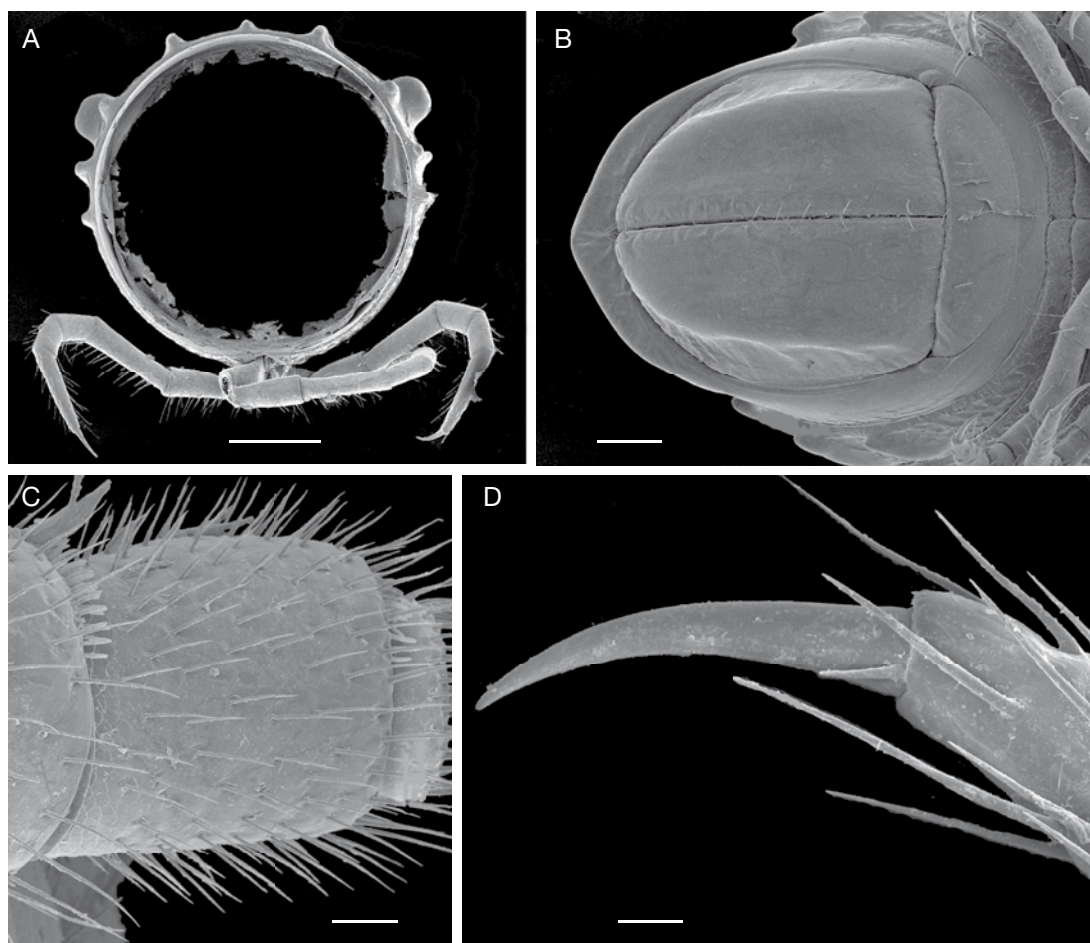


FIG. 4. — *Glyphiulus subobliteratus* n. sp., paratype ♀: **A**, midbody segment section; **B**, telson, ventral view; **C**, antennal sensilla; **D**, claw. Scale bars: A, 0.5 mm; B, 0.2 mm; C, 0.05 mm; D, 0.02 mm.

Ozoporiferous cones round, wider than high (Fig. 4A).

Penes broad, rounded, each with two to four strong setae distolaterally (Fig. 5E).

Anterior gonopods (Fig. 5G) with both digitiform (d) and subsecuriform (s) processes lower than in *G. obliteratus* n. sp.

#### REMARKS

The sample contains three haplopodous juveniles with 28p+2a+T, each with the ozoporiferous tubercles fully developed only on segments 5 and 6.

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

#### *Glyphiulus mediobliteratus* n. sp. (Figs 6-8)

TYPE MATERIAL. — **Vietnam**. Ninh Binh Prov., Cuc Phuong National Park, Cave 4: Song Cung Cave, 21.VI.2003, leg. P. Trontelj & B. Sket, holotype ♂ (MNHN GA 046); paratypes 3 ♂♂, 2 ♀♀, 1 fragm., 1 juv. (MNHN GA 046); 1 ♂ (SEM); 1 ♀ (ZMUC); 1 ♀ (ZMUM); 1 ♀ (MCSNV); 1 ♀ (NMNHS); 1 ♀

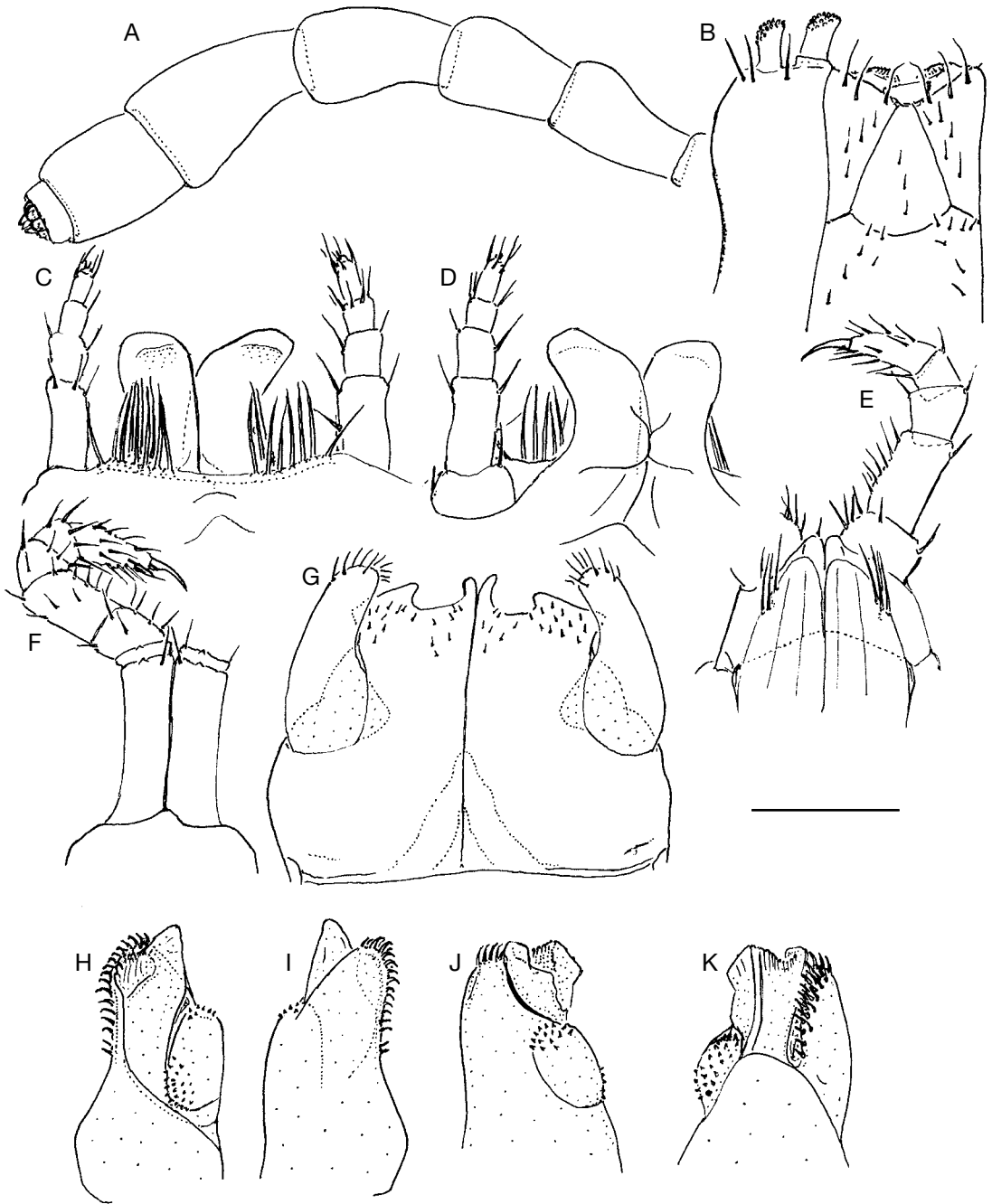


FIG. 5. — *Glyphiulus subobliteratus* n. sp., paratype ♂: **A**, antenna; **B**, gnathochilarium; **C**, leg 1, frontal view; **D**, same, caudal view; **E**, leg 2; **F**, leg 3; **G**, anterior gonopods, caudal view; **H-K**, posterior gonopods, frontal, caudal, lateral, and mesal views, respectively. Scale bar: A, B, E, F, 0.3 mm; C, D, G-K, 0.2 mm.

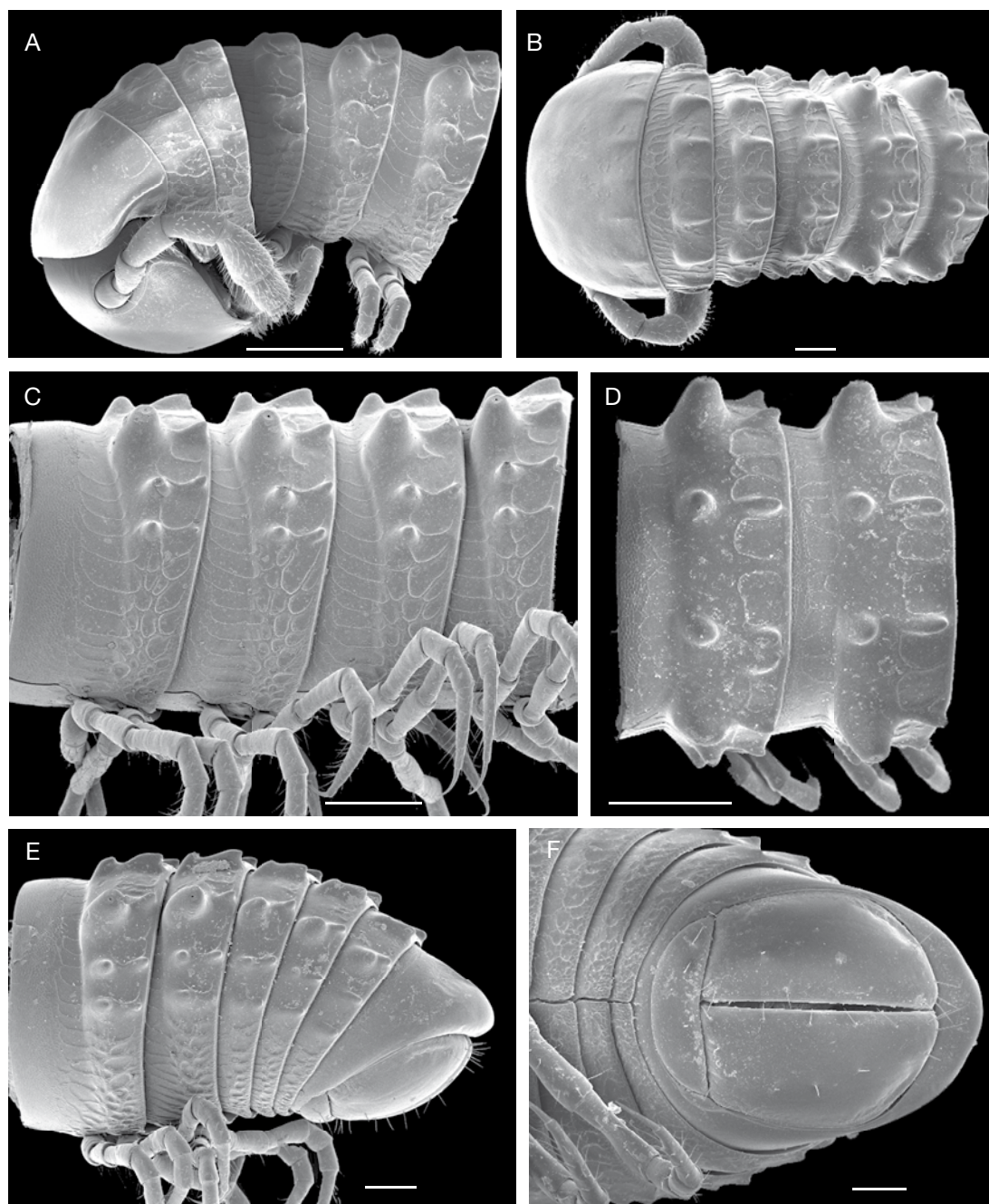


FIG. 6. — *Glyphiulus mediobliteratus* n. sp., paratype  $\sigma$ : **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal body end, lateral view; **F**, telson, ventral view. Scale bars: A, C, D, 0.5 mm; B, E, F, 0.2 mm.

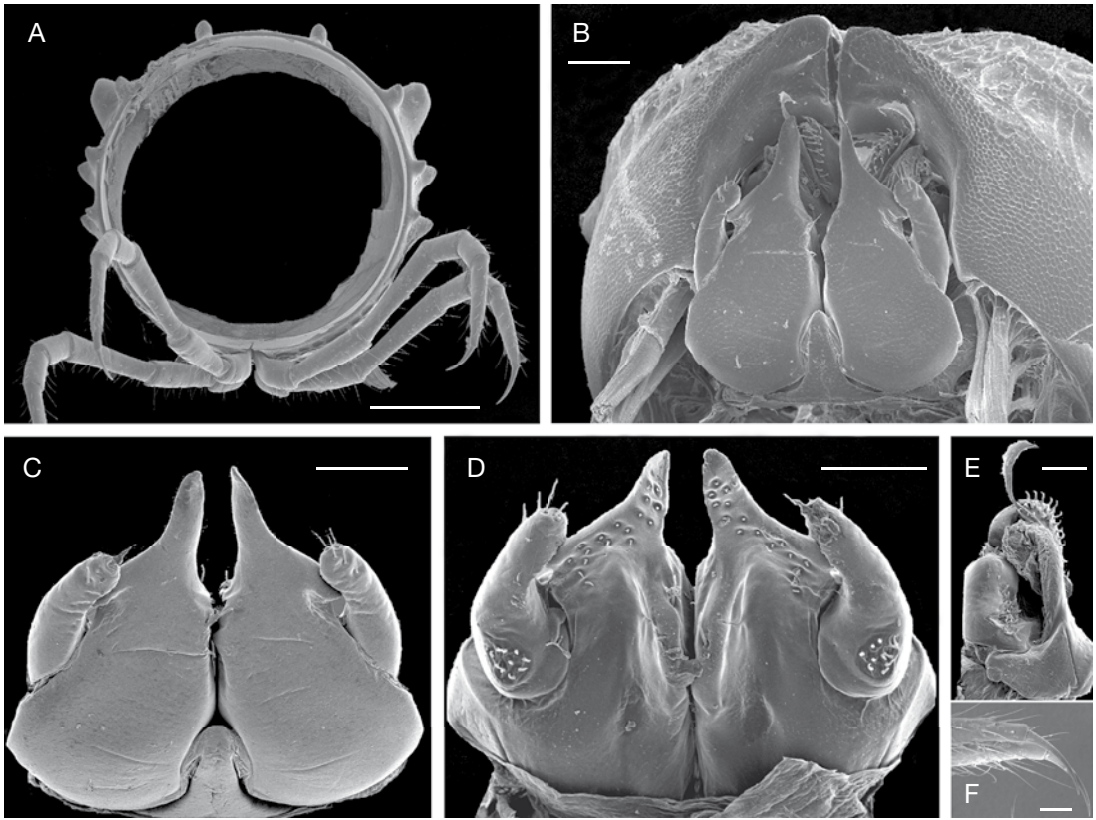


FIG. 7. — *Glyphiulus mediobliteratus* n. sp., paratype ♂: **A**, midbody segment section; **B**, both gonopods *in situ*, frontal view; **C**, anterior gonopod, frontal view; **D**, anterior gonopod, caudal view; **E**, posterior gonopod, subfrontal view; **F**, claw. Scale bars: A, 0.5 mm; B-D, 0.1 mm; E, F, 0.05 mm.

(OBBFUL). — Same locality, Cave 2: Thanh Yen Water Cave, 20.VI.2003, leg. P. Trontelj & B. Sket, paratypes 1 ♂ (ZMUM); 1 ♀ (MNHN GA 046).

ETYMOLOGY. — To emphasize the strongly obliterated collum and axial crests.

DIAGNOSIS. — Differs from congeners by the unpigmented ocelli and, in part, body, coupled with the nearly smooth collum, the rudimentary axial crests, the lack of a notch on each anterior gonopod half, the highly conspicuous, slightly plumose flagellum of the posterior gonopod, etc. (see also key below).

#### DESCRIPTION

Holotype with 61p+1a+T, about 43 mm long and 2.0 mm wide; adult paratypes (♂, ♀) with 51-62p+2-1a+T, length 32-42 mm, width 1.8-2.0 mm.

Coloration entirely pallid to pale brown, only tips of tubercles of tergal crests often brownish to dark brown. Ocelli not visible.

Antennae (Figs 6A; 8A), gnathochilarium (mentum divided,  $n = 5$ ) (Fig. 8B), segment shape (Fig. 7A), epiproct (Fig. 6E), paraprocts, hypoproct, male legs 2 and 3 (Fig. 8D, E), texture (Fig. 6A-E) generally as in *G. obliteratus* n. sp., but sparse striation present in front of stricture both laterally and dorsally; conspicuous pleurosternal crests on segments 2-4 wanting (Fig. 6A); collum (Fig. 6A, B) with 1a-4a+ma+4a-1a very weak undulations in caudal 1/3, undulation ma being shortest; tergal crests higher, even adding another lateral crest below ozoporiferous one; ozoporiferous cones especially high, about as high as wide (Fig. 7A), each crest

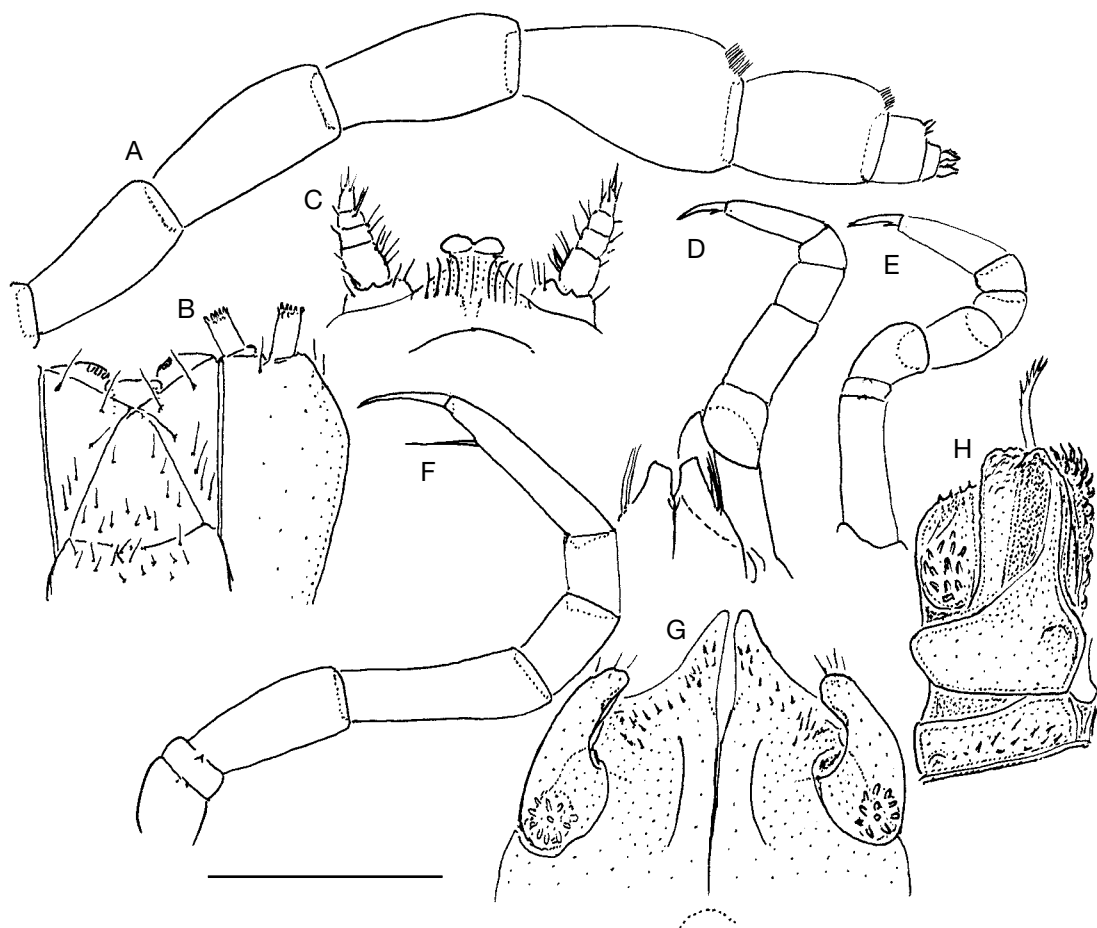


FIG. 8. — *Glyphiulus mediobliteratus* n. sp., paratype ♂: A, antenna; B, gnathochilarium; C, leg 1, frontal view; D, leg 2; E, leg 3; F, leg 9; G, anterior gonopods, caudal view; H, right posterior gonopod, frontal view. Scale bar: A-F, 0.3 mm; G, H, 0.4 mm.

distinctly subdivided into two usually subtriangular halves, except for nearly absent axial crests (m); carinotaxy pattern thus  $2/2+1/i+1/1+m+1/1+1/i+2/2$  (Figs 6A-E; 7A); a small accessory spine present at base of claw on legs 2 and 3 only (Fig. 8D, E), thereafter virtually missing (Fig. 7E, 8F); legs slightly shorter than body diameter (Fig. 7A); male legs 1 with strongly developed paramedian coxal outgrowths and 5-segmented, slightly reduced, telopodites (Fig. 8C).

Head width = segment 2 = 6 < collum = 7(8) > segment 3 = 5 < 7 < 8 < 9 < 10 < 11 = midbody segments; body gradually but then abruptly taper-

ing toward telson. Postcollar constriction modest (Fig. 6B).

Penes broad, rounded, each with three or four strong setae distolaterally (Fig. 8D).

Anterior gonopods (Figs 7B-D; 8G) without notches, processes (d) especially high. Posterior gonopods (Figs 7E; 8H) with characteristic, long, distally plumose flagella.

#### REMARKS

The presence of completely unpigmented ocelli suggests that this species may be troglobitic, but further observations are needed to confirm this.

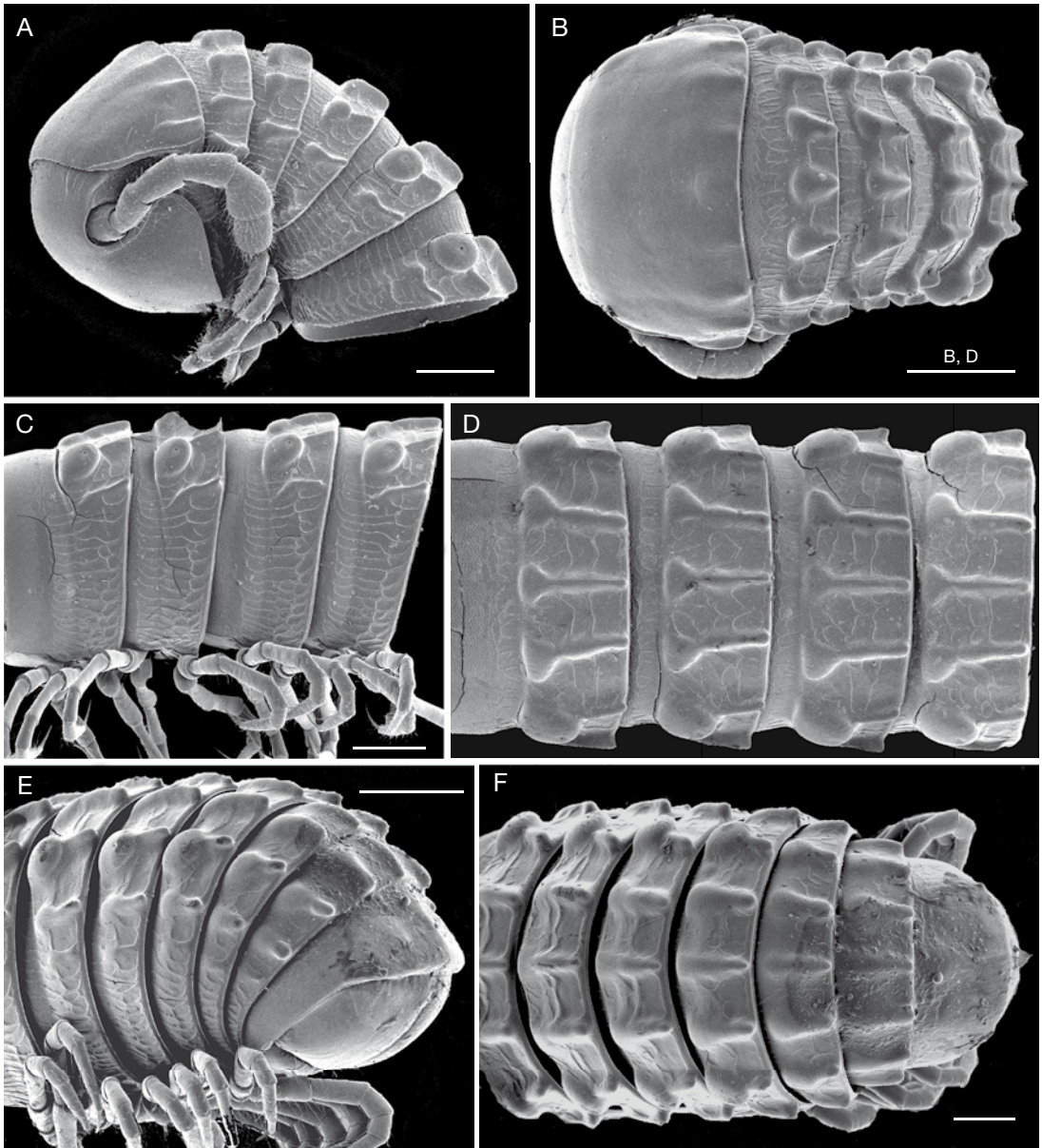


FIG. 9. — *Glyphiulus obliteratoides* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal body end, lateral view; **F**, same, dorsal view. Scale bars: A-E, 0.5 mm; F, 0.2 mm.

*Glyphiulus obliteratoides* n. sp.  
(Figs 9-11)

TYPE MATERIAL. — China. Ghizhou Prov., Anshun County, Luangshuijing, Tian Xian Dong Cave (aquatic),

22.II.2004, leg. S. Prevorčnik & B. Sket, holotype ♂ (MNHN GA 047); paratypes 1 ♂, 1 ♀, 4 juvs (MNHN GA 047); 1 ♂, 1 ♀, 2 juvs (ZMUM); 1 ♀ (OBBFUL); 1 ♀ (SEM); 1 subad. ♀ (ZMUC). — Same cave, 23.II.2004, leg. B. Sket & S. Prevorčnik, 1 juv. (OBBFUL).

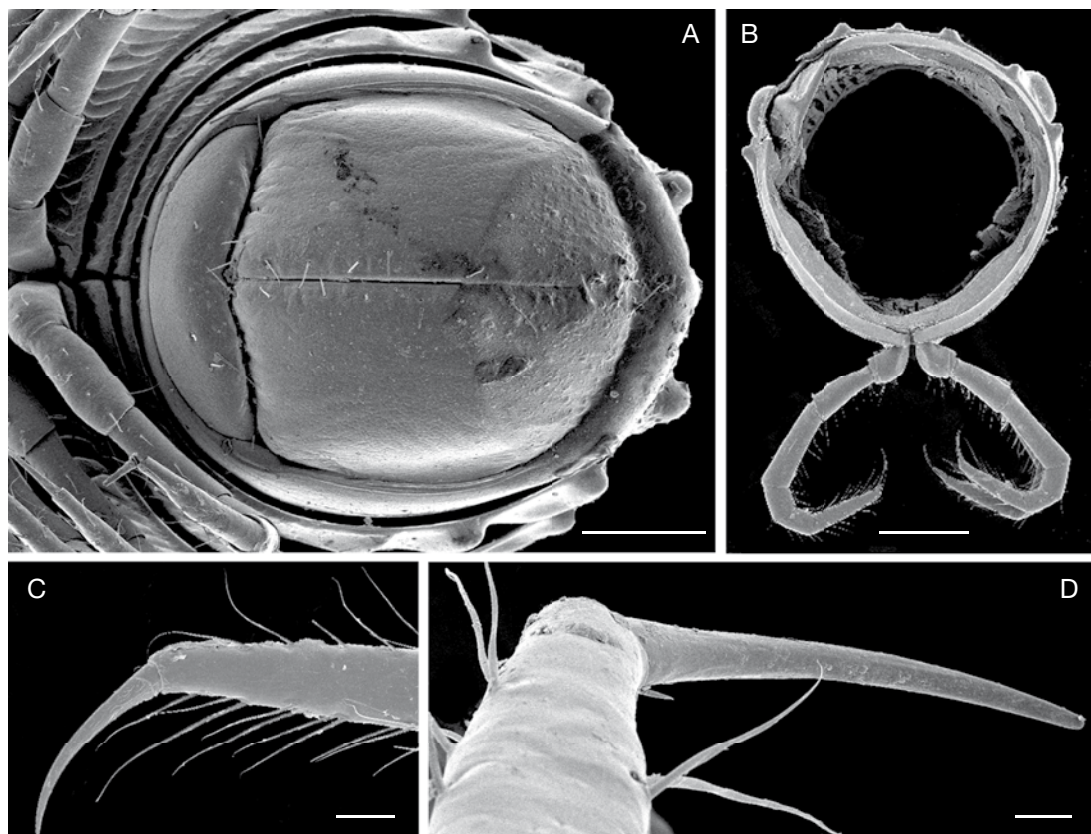


FIG. 10. — *Glyphiulus obliteratoides* n. sp., paratype ♀: **A**, telson, ventral view; **B**, midbody segment section; **C**, claw of midbody leg; **D**, claw. Scale bars: A, 0.2 mm; B, 0.5 mm; C, 0.05 mm; D, 0.02 mm.

**ETYMOLOGY.** — To emphasize the very close resemblance to *G. obliteratus* n. sp.

**DIAGNOSIS.** — Differs from congeners by the pigmented ocelli and body, coupled with the more distinctly undulate collum, the undivided crests, etc. (see also key below).

#### DESCRIPTION

Holotype with 59p+1a+T, about 32 mm long and 1.9 mm wide; adult paratypes (♂, ♀) with 45-60p+2-1a+T, length 22-35 mm, width 1.3-1.9 mm.

Coloration entirely pallid in young juvenile stadia, becoming marbled red-brown in adults, tergal crests dark castaneous brown; antennae, legs and venter light red-brown in adults. Adults with 7-9 blackish ocelli in a subtriangular eye patch.

Antennal sensilla, segment shape (Fig. 10B), tergal crests (including ozoporiferous ones) (Figs 9;

10B), epiproct (Fig. 9E, F), paraprocts (Fig. 9E), male legs 2 and 3 (Fig. 11D, E), penes (Fig. 11D), gonopods (Fig. 11G, H) generally as in *G. obliteratus* n. sp., but antennae (Figs 9A; 11A) slightly shorter, gnathochilarium (mentum divided,  $n = 3$ ) (Fig. 11B) more polytrichous; collum (Fig. 9A, B) with 1a-4a+ma+4a-1a undulations at caudal margin, undulation ma being shortest; hypoproct (Fig. 10A) very faintly emarginate caudomedially, conspicuous pleurosternal crests on segments 2-4 wanting (Fig. 9A); tergal crests similarly low and undivided, even adding another lateral crest below ozoporiferous one, which is barely traceable as a low anterior tubercle, but anterior end of all dorsal crests broadened (Fig. 9); carinotaxy pattern thus 1/0+1+I/i+3+I/i+1+1/0 (Figs 9C, D; 10B); a small accessory spine present at base of claw on



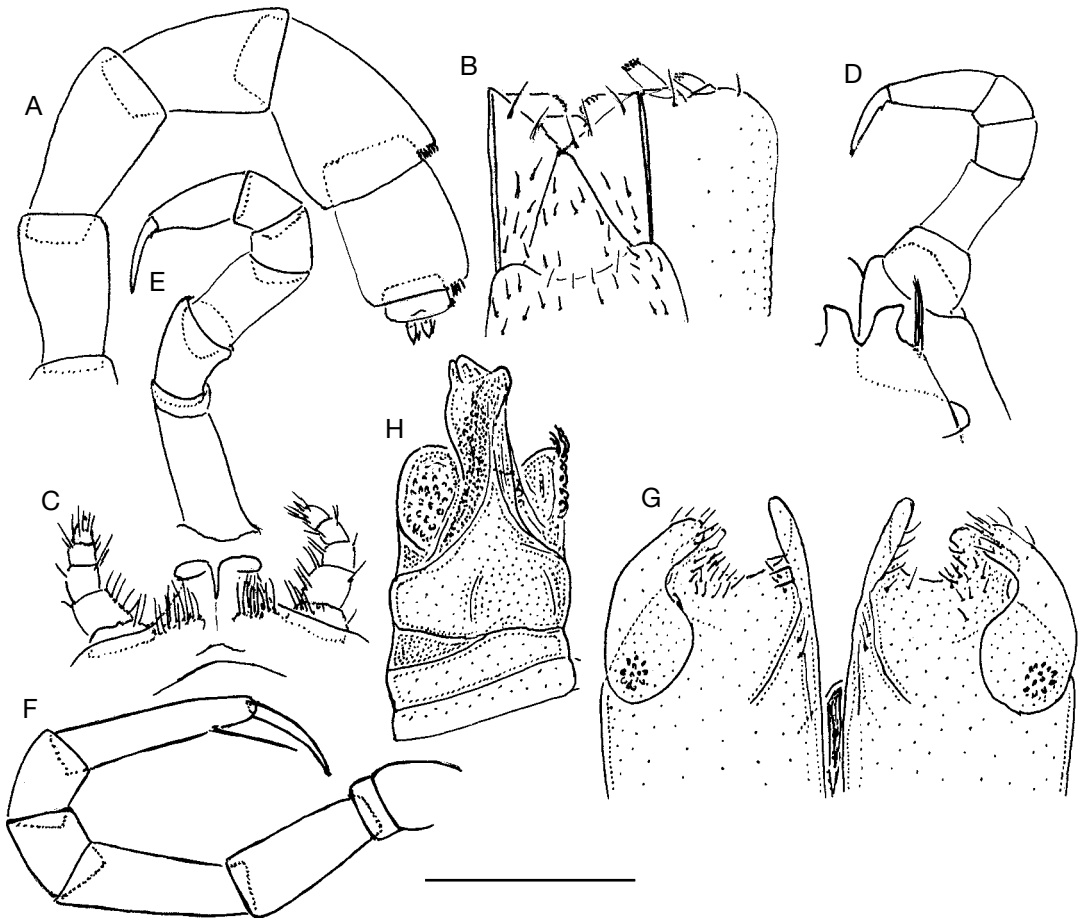


FIG. 11. — *Glyphiulus obliteratoides* n. sp., paratype ♂: **A**, antenna; **B**, gnathochilarium; **C**, leg 1, frontal view; **D**, leg 2, caudal view; **E**, leg 3; **F**, leg 9; **G**, anterior gonopods, caudal view; **H**, right posterior gonopod, frontal view. Scale bar: A-F, 0.3 mm; G, H, 0.4 mm.

legs 2 and 3 only (Fig. 11D), onward nearly missing (Figs 10B; 11F); legs about as long as body diameter (Fig. 10B); male leg 1 with 5-segmented but shortened telopodites (Fig. 11C).

Head width = segment 2 = 6 < collum = 7(8) > segment 3 = 5 < 7 < 8 < 9 < 10 < 11 = midbody segments; body gradually tapering toward telson. Postcollar constriction evident (Fig. 9B).

#### REMARKS

The samples contain five haplopodous juveniles with 30-33p+1-3a+T, each with the ozoporiferous tubercles fully developed only on segments 5 and

6. In general, even juveniles of later, diplopodous, stadia are easily recognised due to the ozoporiferous cones being especially well developed on segments 5 and 6 only.

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

#### *Glyphiulus parobliteratus* n. sp. (Figs 12; 13)

TYPE MATERIAL. — **China**. Guizhou Prov., Zhuanyankong, 107°18'55.0"E, 28°14'30.9"N, emergence porch, 750 m,

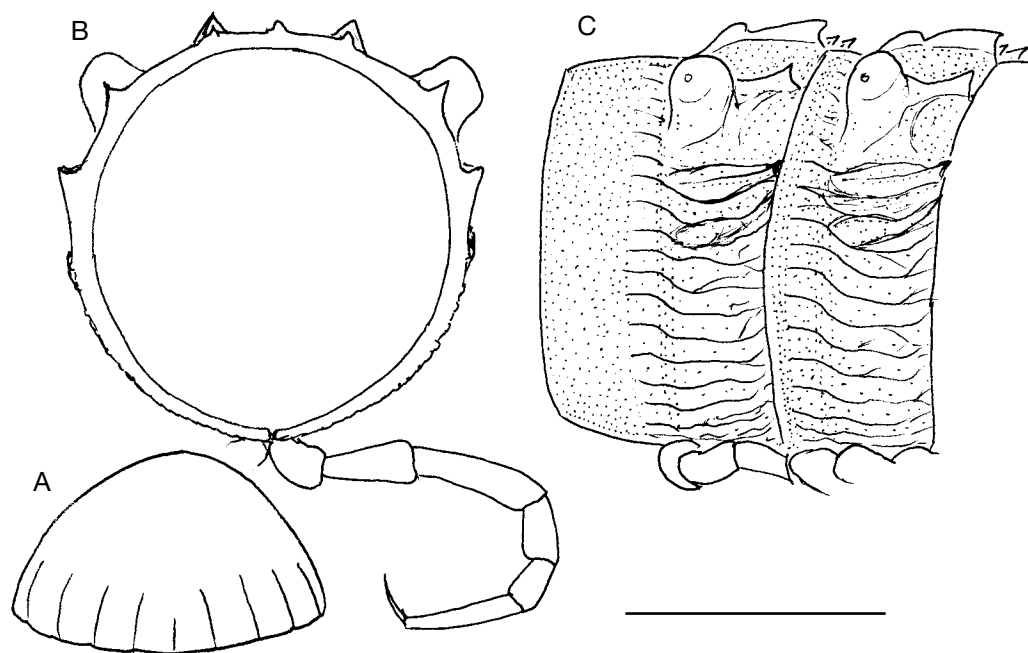


FIG. 12. — *Glyphiulus parobliteratus* n. sp., holotype ♂: **A**, schematic presentation of carinotaxy pattern of collum; **B**, midbody segment section; **C**, midbody segments, lateral view. Scale bar: A, not to scale; B, C, 1.0 mm.

1.III.2003, leg. M. Pouilly (CHI-Pouilly4), holotype ♂ (MNHN GA 048).

OTHER MATERIAL. — **China**. Guizhou Prov., Shuanghe River, Wenquan, Dafen Dong Cave, 107°18'44"E, 28°14'25.4"N, 680 m, 20.II.2003, leg. M. Pouilly (CHI-Pouilly6), 1 ♂ (MNHN GA 048).

ETYMOLOGY. — To again emphasize the very close resemblance to *G. obliteratus* n. sp.

DIAGNOSIS. — Differs from congeners by the unpigmented ocelli, coupled with the particularly polytrichous gnathochilarium, as well as certain details of gonopod structure (see also key below).

#### DESCRIPTION

Holotype with 41p+5a+T, about 26 mm long and 1.3 mm wide; non-type ♂ with 44p+5a+T, length about 22 mm, width 1.2 mm.

Coloration light grey-brown with contrastingly dark brown ozoporiferous cones, with head, antennae, legs and venter light yellow-brown (holotype), or rather uniformly dark grey-brown to brown (non-type). Ocelli barely discernible as slightly convex

tubercles, unpigmented, two or three in eye patch on each side of head.

Antennae (Fig. 13A), collum with 1a-4a+ma+4a-1a undulations at caudal margin, undulation ma being shortest (Fig. 12A), tergal crests (including ozoporiferous ones) (Fig. 12B, C), postcollar constriction, telson, segment shape (Fig. 12B), male legs 2 and 3 (Fig. 13D, E), other legs (Figs 12B; 13F) generally as in *G. obliteratus* n. sp., but gnathochilarium (mentum divided, n = 2) (Fig. 13B) even more polytrichous; conspicuous pleurosternal crests on segments 2-4 wanting (Fig. 9A); tergal crests divided, second lateral crest below ozoporiferous one barely traceable as a low anterior tubercle, carinotaxy pattern thus 1/0+1+1/i+3/3+1/i+1+1/0 (Fig. 12B, C); legs slightly longer than body diameter (Fig. 12B); male leg 1 with 5-segmented, normal telopodites (Fig. 13C).

Anterior gonopod coxosternum (Fig. 13G) with still longer paramedian processes. Posterior gonopods (Fig. 13H) with long, distally plumose flagella.

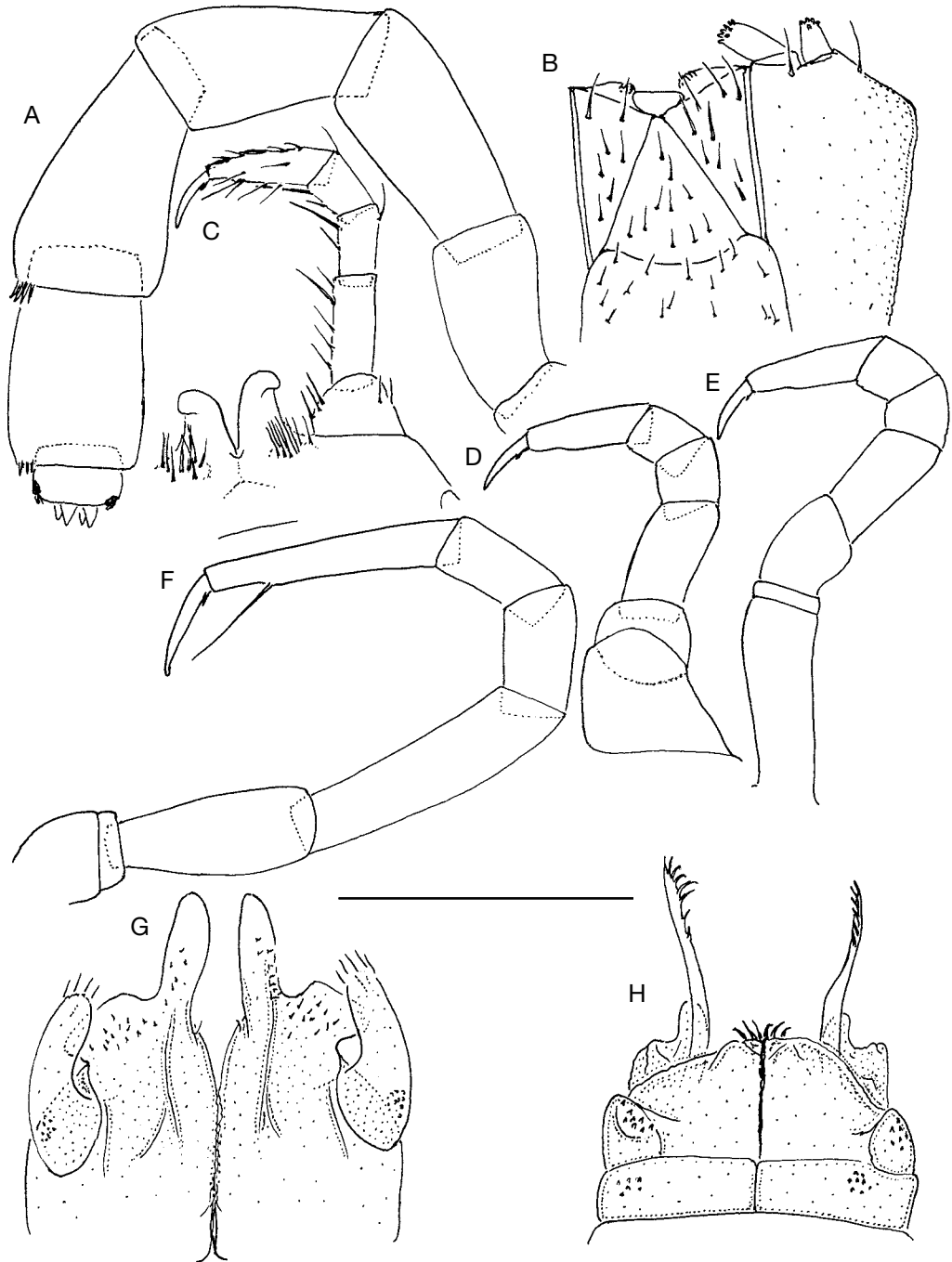


FIG. 13. — *Glyphiulus parobliteratus* n. sp., holotype  $\sigma$ : **A**, antenna; **B**, gnathochilarium; **C**, leg 1, frontal view; **D**, leg 2; **E**, leg 3; **F**, leg 13; **G**, anterior gonopods, caudal view; **H**, posterior gonopods caudal view, respectively. Scale bar: A-F, 0.3 mm; G, H, 0.4 mm.

## REMARKS

Because the non-type ♂ shows some minor differences from the holotype – the slightly better developed crests on the collum and subsequent terga, thus showing two crests, not one, below the ozoporiferous cones – the conspecificity of these samples remains to be verified.

Such troglomorphic traits as the unpigmented ocelli and the elongated appendages allow this species to be considered as troglobitic.

*Glyphiulus costulifer* n. sp.

(Figs 14-16)

TYPE MATERIAL. — Laos. Luang Prabang Prov., Nong Kiaw (Muang Ngoy), Tham Pha Kouang Cave, 102.68°E, 20.72°N, 29.XII.2000, leg. A. Bedos & L. Deharveng (LAO-099), holotype ♂ (MNHN GA 049); paratypes 3 ♂♂, 2 ♀♀ (MNHN GA 049); 1 ♂ (SEM); 1 ♂, 1 ♀ (ZMUM); 1 ♂, 1 ♀ (ZMUC); 1 ♀ (NMNHS).

ETYMOLOGY. — To emphasize the normally carinate collum.

DIAGNOSIS. — Differs from congeners by the nearly typical carinotaxy pattern of the collum, coupled with highly unusual traces of both ventrolateral crests, the very little modified male coxae 1, the long but bare flagellum of the posterior gonopods, etc. (see also key below).

## DESCRIPTION

Holotype with 56p+1a+T, about 28 mm long and 1.8 mm wide; paratypes (♂, ♀) with 48-62p+3-1a+T, length 23-35 mm, width 1.5-1.9 mm.

Coloration light yellow-brown to red-brown, tergal crests often dark castaneous brown. Greyish to red-brown, subtriangular eye patches with 7-9 ocelli each. Antennae usual (Figs 14A; 16A), gnathochilarium (mentum divided, n = 3) oligotrichous (Fig. 16B).

Head width = segment 2 = 6 < collum = 7(8) > segment 3 = 5 < 7 < 8 < 9 < 10 < 11 = midbody segments; body gradually tapering toward telson. Postcollar constriction evident (Fig. 14B).

Collum almost typically crested, only median crest (ma) unusually abbreviated; carinotaxy pattern typical of the *granulatus*-group (I-VI+7a+pc+ma+pc+7a+VI-I) (Fig. 14A, B). Subsequent metaterga evidently crested as well (Fig. 14A-E). Carinotaxy formula 2+I/

i+3/3+I/i+2, i.e. all dorsal crests subdivided (Fig. 14C, D), while both ventrolateral crests undivided, barely traceable as ribbons of micropunctate/shagreened texture (Fig. 15B). Ozoporiferous tubercles round, only slightly wider than high (Fig. 15A, B).

Tegument delicately alveolate-areolate, dull throughout. Fine longitudinal striations in front of stricture between pro- and metazona ventrolaterally, laterally and dorsally, remaining surface of prozona very delicately shagreened. Segments round in cross-section (Fig. 15A). Epiproct with a distinct, hump-like ridge dorsally in distal 3/4 extent (Fig. 14E), in ventral view rounded and subtriangular in caudal part (Fig. 14F). Paraprocts flattened ventrally, with only a shallow but evident submarginal depression beside caudal edge, each with a row of about a dozen setae at medial margin (Fig. 14F). Hypoproct sublanceolate, very delicately and broadly emarginate caudomedially (Fig. 14F).

Ventral flaps behind gonopod opening on male segment 7 distinguishable as a low but clear transverse ridge (Fig. 15C).

Legs long, those on midbody segments about as long as segment diameter (Fig. 14C). Claw with a short but evident accessory spine at base (Fig. 16C-F).

Male legs 1 highly characteristic (Fig. 16C) in showing only slightly modified coxae with two low, paramedian, contiguous cones; telopodites 5-segmented, normal. Male legs 2 and 3 modified as usual (Fig. 16D, E).

Anterior gonopods (Figs 15D; 16G) not notched, paramedian processes (d) high, telopodites evidently curved. Posterior gonopods (Figs 15E, F; 16H) highly compact, typical of the group, flagella (f) high and bare.

## REMARKS

Due to the nearly unmodified male legs 1, this species is probably among the basalmost in the genus.

In the absence of any troglomorphic traits, this species can only be considered troglomorphic at most. This cave is known to support another congener, *G. bedosae* Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2007 (see Golovatch *et al.* 2007). Interestingly, both species share the same, rather conspicuous structure of the telson.

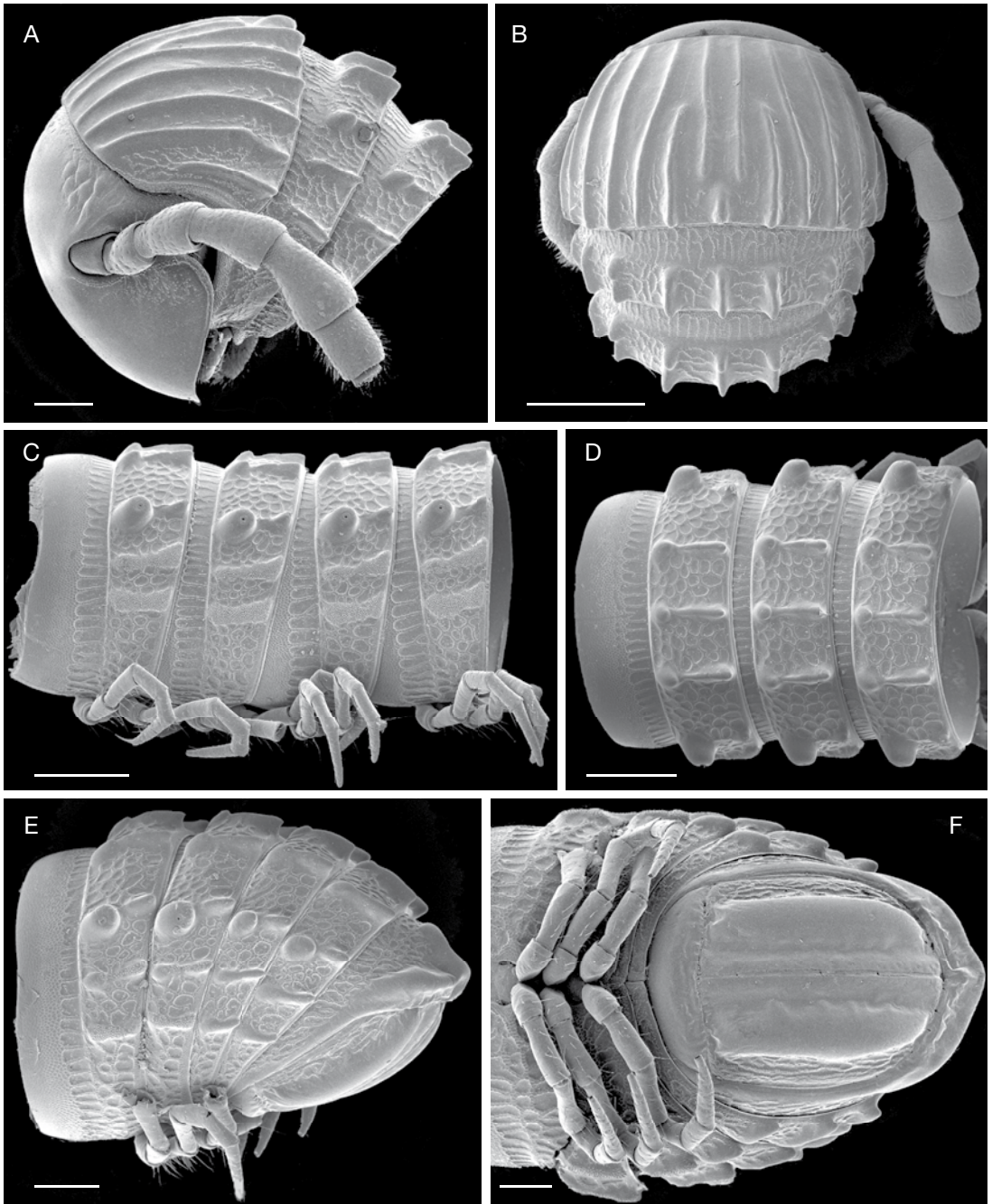


FIG. 14. — *Glyphiulus costulifer* n. sp., paratype ♂: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal body end, lateral view; **F**, same, ventral view. Scale bars: A, E, F, 0.2 mm; B-D, 0.5 mm.

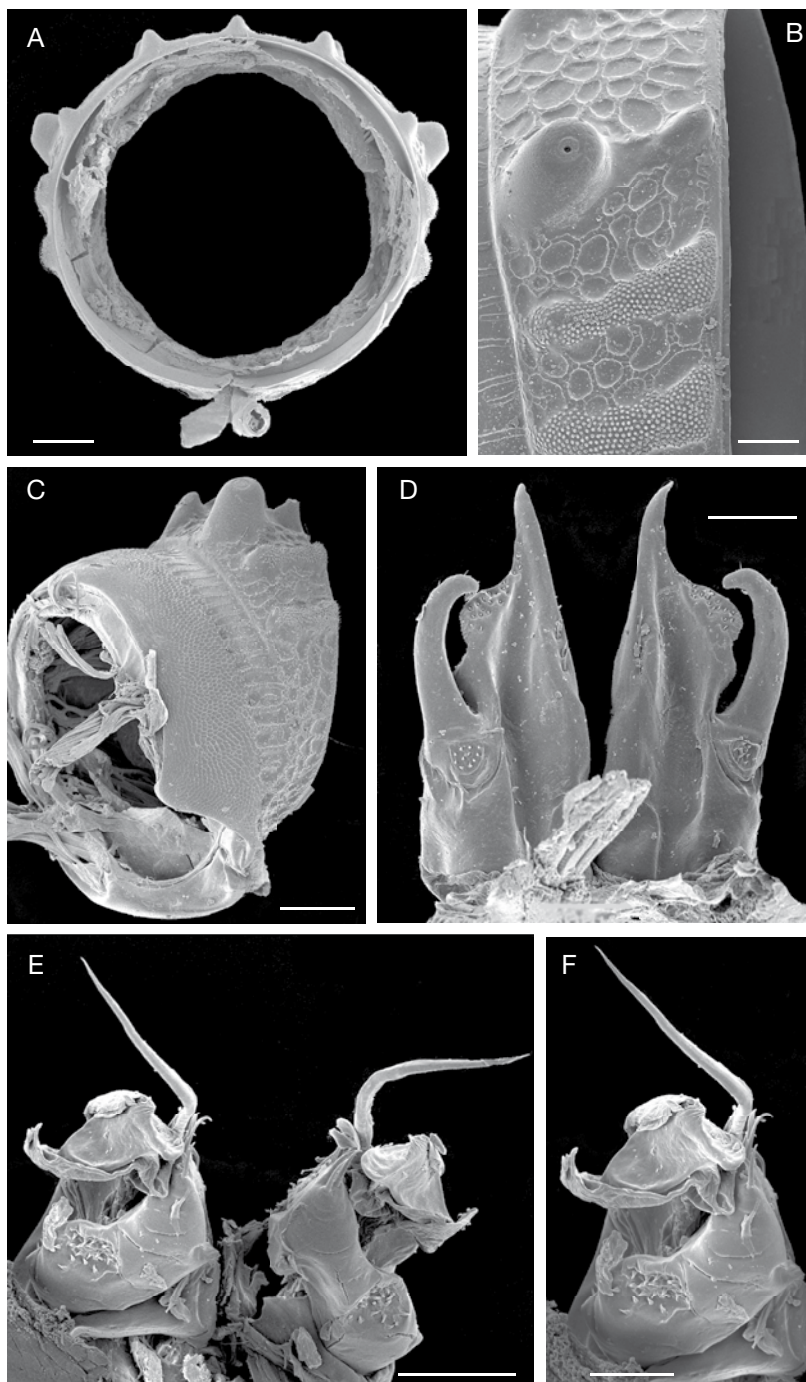


FIG. 15. — *Glyphiulus costulifer* n. sp., paratype ♂: **A**, midbody segment section; **B**, midbody metazonite enlarged, lateral view; **C**, segment 7, frontolateral view; **D**, anterior gonopod, caudal view; **E**, posterior gonopod, caudal view; **F**, posterior gonopod, enlarged caudal view. Scale bars: A, C, 0.2 mm; B, D, E, 0.1 mm; F, 0.05 mm.

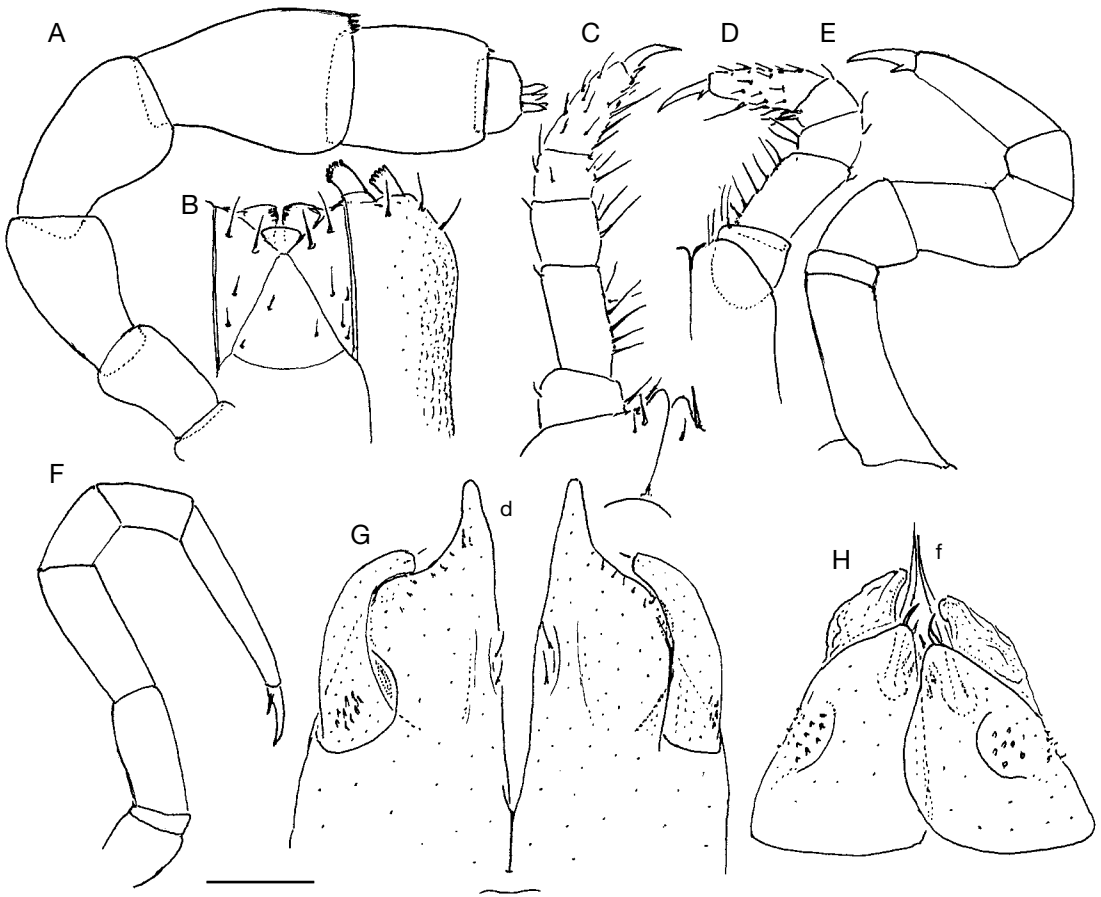


FIG. 16. — *Glyphiulus costulifer* n. sp., paratype ♂: **A**, antenna; **B**, gnathochilarium; **C**, leg 1, frontal view; **D**, leg 2; **E**, leg 3; **F**, leg 13; **G**, anterior gonopods, caudal view; **H**, posterior gonopods, caudal view. Abbreviations: **d**, digitiform process; **f**, flagellum. Scale bar: A-F, 0.2 mm; G, H, 0.1 mm.

*Glyphiulus subcostulifer* n. sp.  
(Figs 17-19)

TYPE MATERIAL. — Laos, Vang Vieng, Tham None, 102.4338°E, 18.9513°N, cave, 1.I.2000, leg. A. Bedos & L. Deharveng (LAO-111), holotype ♂ (MNH GA 050), paratype ♂ (SEM).

ETYMOLOGY. — To emphasize the very close resemblance to *G. costulifer* n. sp.

DIAGNOSIS. — Differs from congeners by the unique carinotaxy formulae, coupled with certain details of leg and gonopod structure (see also key below).

DESCRIPTION

Holotype with 50p+2a+T, about 29 mm long and

1.7 mm wide; paratype 1.3 mm wide.

Coloration uniformly light brownish. Only three or four slightly infuscate and convex ocelli in each eye patch (Fig. 17A).

Antennae (Fig. 19A), postcollar constriction, dorsal crests (including ozoporiferous ones) and carinotaxy pattern on postcollar terga (Fig. 17C-E), segment's texture and cross-section (Figs 17C, D; 18A, B), paraprocts and hypoproct (Fig. 17F), ventral flaps of male segment 7 (Fig. 18B), male legs 2 and 3 (Fig. 19D, E) generally as in *G. costulifer* n. sp., but gnathochilarium (mentum divided,  $n = 3$ ) (Fig. 19B) slightly more polytrichous; collum (Fig. 17B) with five, not three, anteriorly

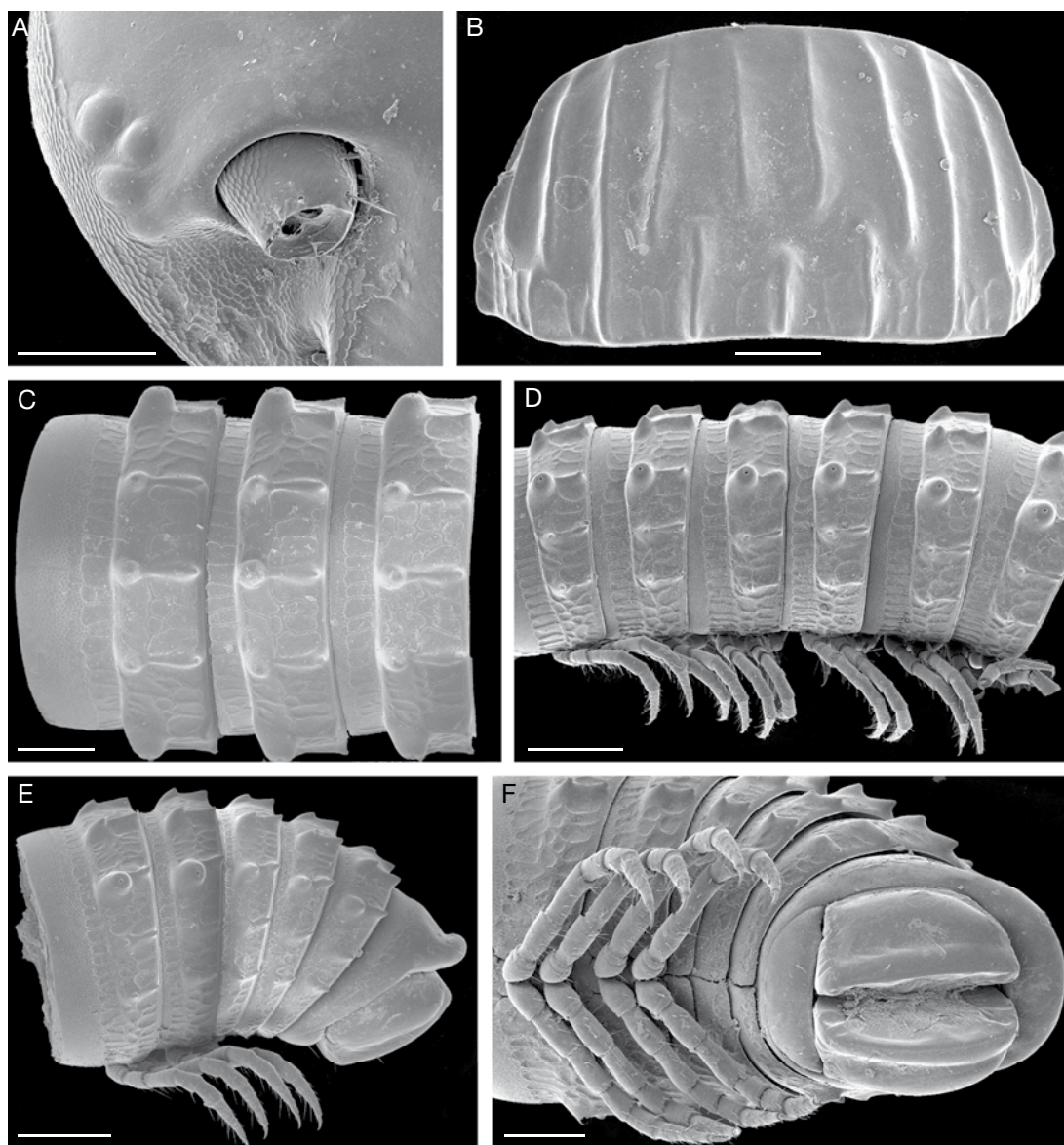


FIG. 17. — *Glyphiulus subcostulifer* n. sp., paratype ♂: **A**, ocellarium; **B**, collum, dorsal view; **C**, midbody segments, dorsal view; **D**, same, lateral view; **E**, caudal body end, lateral view; **F**, same, ventral view. Scale bars: A, 0.1 mm; B, C, F, 0.2 mm; D, E, 0.5 mm.

and six, not two, posteriorly abbreviated crests, median crest (ma) only scarcely shorter than both flanking ones (I-II+3c+4a+5c+VI+7c+8a+pc+ma+pc+8a+7c+VI+5c+4a+3c+II-I); all tergal crests (Figs 17A-E; 18A, B) on subsequent body seg-

ments subdivided, but anterior tooth on dorsal crests more rounded, and both lateral crests below ozoporiferous cone normal (2/2+I/i+3/3+I/i+2/2); epiproct (Fig. 17E, F) upturned and very broadly rounded in caudal part; legs slightly shorter than



body diameter (Fig. 18A), always with an evident but short accessory spine at base of claw (Fig. 19D-F); male leg 1 with 4-segmented, considerably shortened telopodites and large paramedian coxal processes (Fig. 19C); each anterior gonopod coxosternal plate subsecuriform (Fig. 19G); posterior gonopods with distally slightly plumose flagella (Fig. 19H).

#### REMARKS

In the absence of any troglomorphic traits, except perhaps for the slightly reduced eyes, this species can only be considered troglophilic at most.

#### *Glyphiulus percostulifer* n. sp. (Figs 20; 21)

TYPE MATERIAL. — Laos. Khammouan Prov., Ban Nakok (= Nakhok), Tham Thê, 104.49°E, 17.90°N, cave, hand collection, 11.II.1998, leg. A. Bedos & L. Deharveng (LAO-016), holotype ♂ (MNHN GA 051); paratypes 1 ♂, 1 ♀, 1 subad. ♂ (MNHN GA 051); 1 ♀ (ZMUM/SEM).

ETYMOLOGY. — To emphasize the very close resemblance to *G. costulifer* n. sp., but with more strongly developed tergal crests.

DIAGNOSIS. — Differs from congeners in the small size, the completely unpigmented tegument and ocelli, coupled with certain details of leg and gonopod structure (see also key below).

#### DESCRIPTION

Holotype with 34p+2a+T, about 14 mm long and 1.0 mm wide; adult paratypes with 36p+2a+T, about 14 mm long and 1.0 mm wide (♂), with 40p+1a+T or 38p+1a-T, about 17 mm long and 1.0 mm wide (♀); subadult ♂ with 31p+2a+T.

Coloration uniformly pallid, ocelli not visible (Fig. 20A).

Postcollar constriction, dorsal crests and carinotaxy pattern on postcollar terga (Fig. 20A-E), segment's texture and cross-section (Fig. 20B-D), paraprocts and hypoproct (Fig. 20F), ventral flaps of male segment 7, male legs 2 and 3 (Fig. 21D, E), penes (Fig. 21D) generally as in *G. costulifer* n. sp., but antennae elongate, antennomeres 5-7 richer in sensilla (Fig. 21A), gnathochilarium (mentum

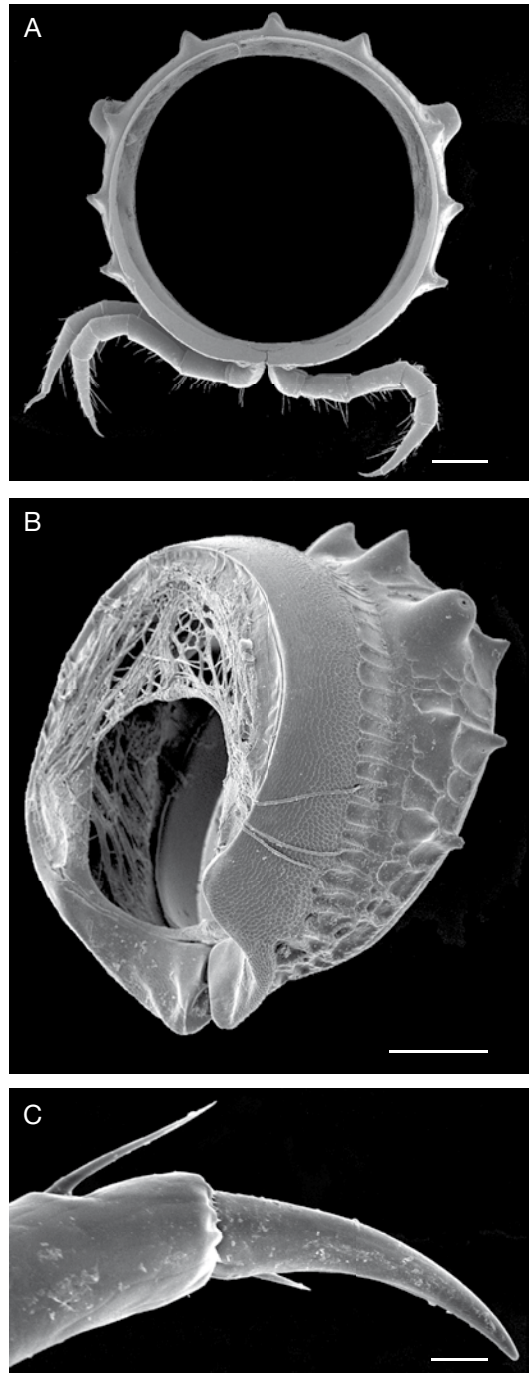


FIG. 18. — *Glyphiulus subcostulifer* n. sp., paratype ♂: **A**, midbody segment section; **B**, segment 7, frontolateral view; **C**, claw. Scale bars: A, B, 0.2 mm; C, 0.01 mm.

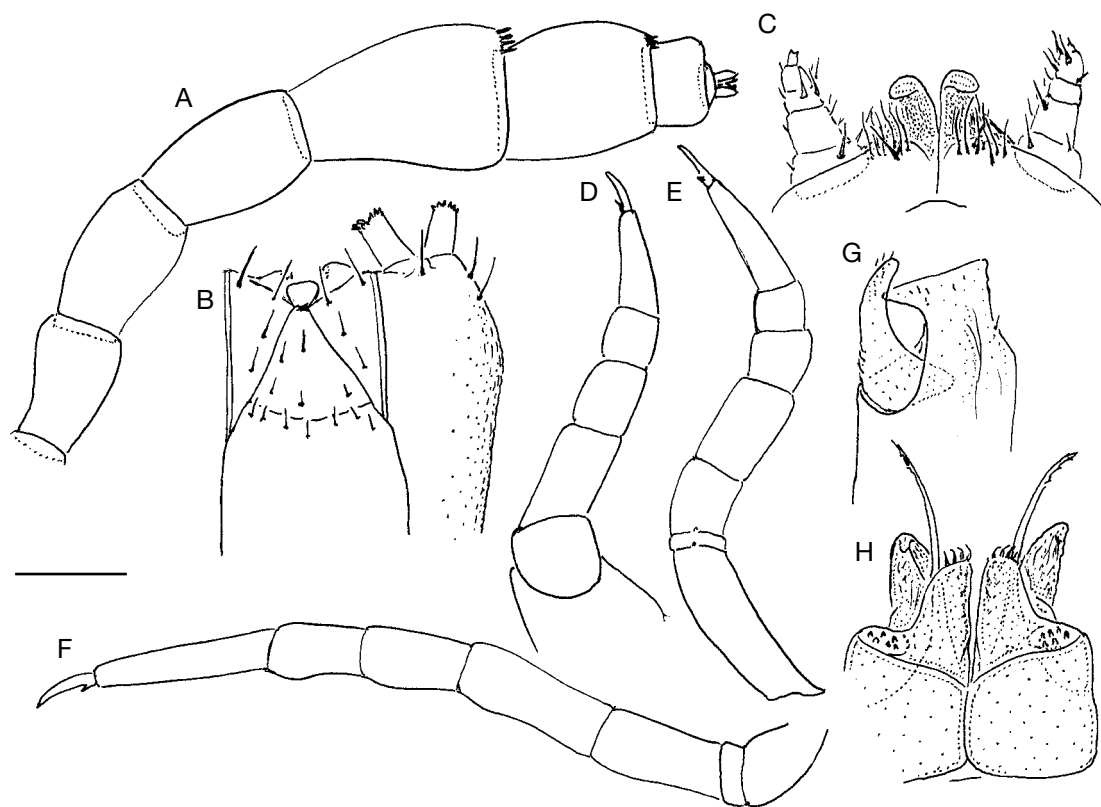


FIG. 19. — *Glyphiulus subcostulifer* n. sp., paratype ♂: **A**, antenna; **B**, gnathochilarium; **C**, leg 1, frontal view; **D**, leg 2; **E**, leg 3; **F**, leg 11; **G**, right anterior gonopod, frontal view; **H**, posterior gonopods, frontal view. Scale bar: 0.2 mm.

divided,  $n = 2$ ) (Fig. 21B) slightly even more oligotrichous; collum (Fig. 20A) with a nearly typical carinotaxy formula (I-IV+5a+pc+ma+pc+5a+IV-I); all tergal crests (Fig. 20A-E) on subsequent body segments higher, subdivided ( $2/2+1/i+3/3+1/i+2/2$ ), ozoporiferous cones about as high as wide; epiproct (Fig. 20E, F) upturned and broadly rounded in caudal part, with one median and two paramedian crests; legs slightly longer than body diameter (Fig. 20B), always with an accessory filament/spine at base of claw, which is usually slightly more than half as long as claw (Fig. 21D-F); male leg 1 with normal, 5-segmented telopodites and large, paramedian, coxal processes (Fig. 21C); each anterior gonopod plate with a high and subsecuriform distomedial process (Fig. 21G); posterior gonopods with distally slightly plumose flagella (Fig. 21H).

#### REMARKS

Based on several troglomorphic traits, such as the completely unpigmented body and ocelli, as well as the elongated antennae and legs, this species seems to be troglobitic, although the small size may also be evidence of its being an inhabitant of the MSS ("milieu souterrain superficiel").

#### *Glyphiulus paracostulifer* n. sp. (Figs 22-24)

TYPE MATERIAL. — **China**. Guizhou Prov., Qianxy, Hong Lin Town, Lao Hu Dong Cave, 21.XI.2003, leg. L. Latella & S. Meggiorini, holotype ♂ (MNHN GA 052); paratypes 1 ♀ (MNHN GA 052); 1 ♀ (ZMUM); 1 ♀ (MCSNV/SEM).

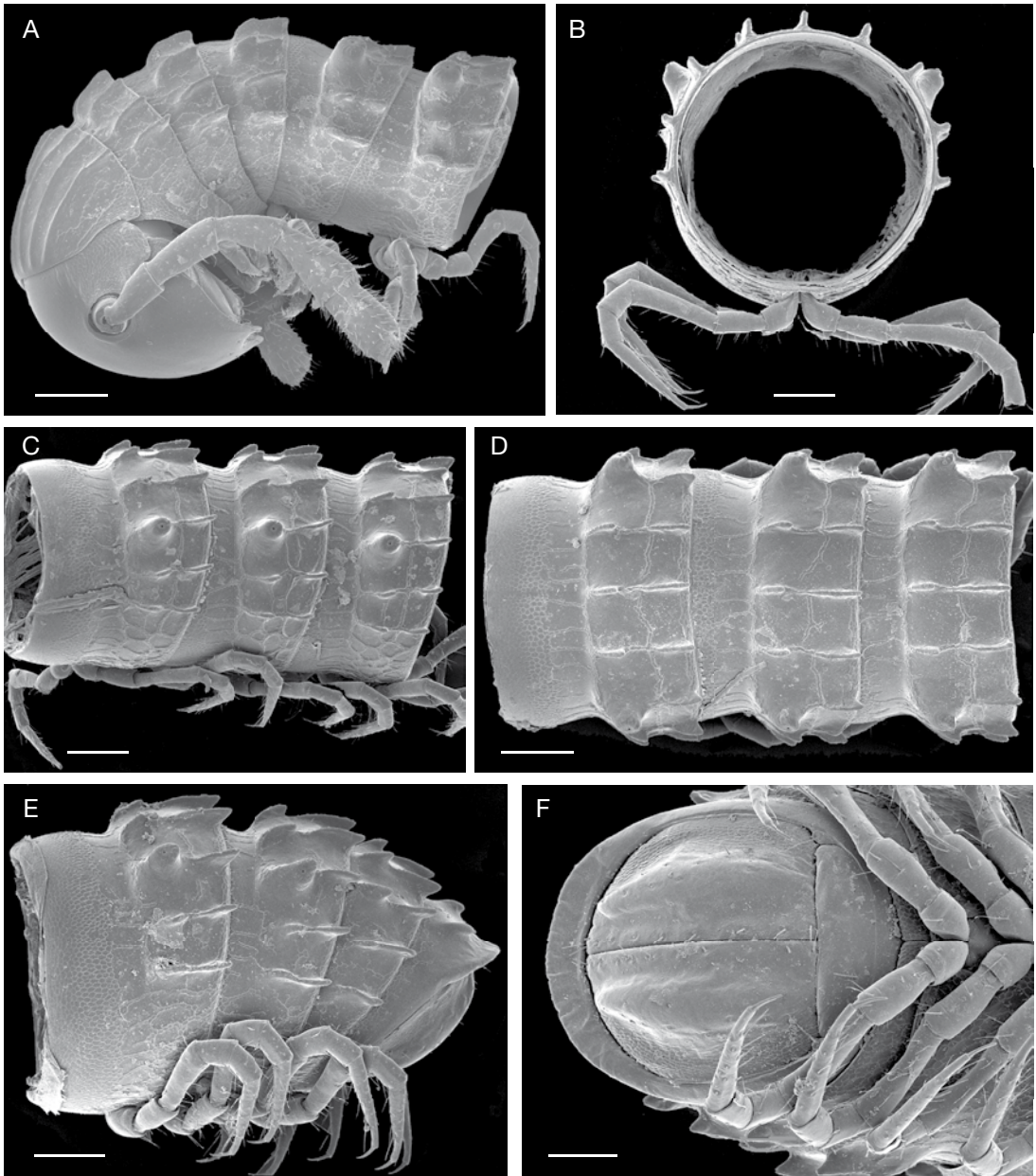


FIG. 20. — *Glyphiulus percostulifer* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, midbody segment section; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal body end, lateral view; **F**, same, ventral view. Scale bars: A-E, 0.2 mm; F, 0.1 mm.

ETYMOLOGY. — To emphasize the close resemblance to *G. costulifer* n. sp.

DIAGNOSIS. — Differs from congeners in the relatively

large size, the completely unpigmented tegument and ocelli, the undivided tergal crests, coupled with certain details of leg and gonopod structure (see also key below).

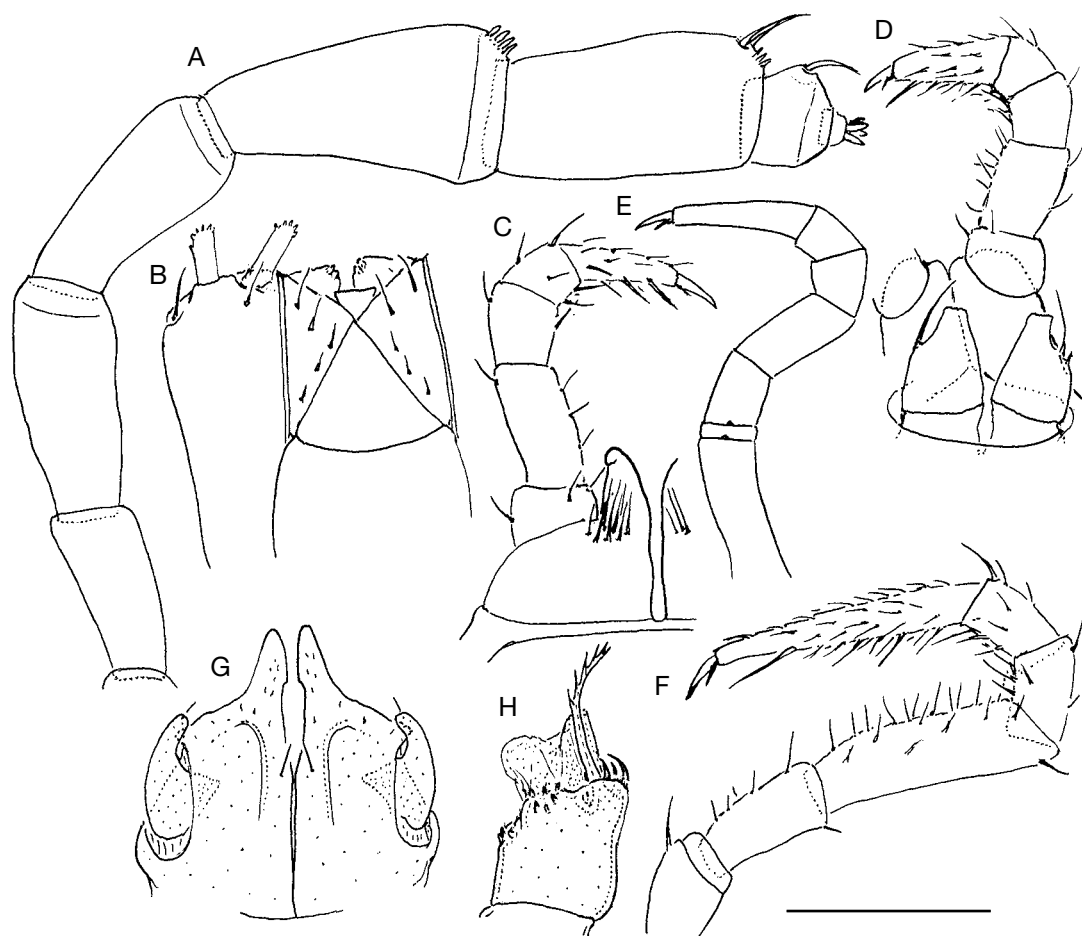


FIG. 21. — *Glyphiulus percostulifer* n. sp., paratype  $\sigma$ : A, antenna; B, gnathochilarium, ventral view; C, leg 1, caudal view; D, leg 2, caudal view; E, leg 3; F, leg 13; G, anterior gonopods, caudal view; H, right posterior gonopod, frontal view. Scale bar: 0.2 mm.

#### DESCRIPTION

Holotype with 65p+1a+T, about 43 mm long and 2.0 mm wide; adult paratypes with 52p+2a+T, 55p+3a+T or 57p+1a+T, all about 36 mm long and 2.0 mm wide.

Coloration rather uniformly pale yellowish to brownish, only some ozoporiferous cones a little darker; ocelli unpigmented, a few barely discernible per eye patch.

Gnathochilarium (mentum divided,  $n = 1$ ), post-collar constriction (Fig. 22B), segment's texture and cross-section (Fig. 22A-E), most of telson (Fig. 22E, F), ventral flaps of male segment 7, male legs 2 and 3

(Fig. 24C, D), posterior gonopods (Fig. 24G) generally as in *G. subcostulifer* n. sp., but antennae slightly more elongate and less rich in sensilla (Figs 22A; 23D; 24A); collum (Fig. 22A, B) with a nearly typical carinotaxy formula (I-III+4c+5a+pc+ma+pc+5a+4c+III-I), crests evident; all tergal crests (Figs 22A-E; 23A) on subsequent body segments higher, especially so until about segment 9 or 10, virtually not divided (2+I/i+3+I/i+2), ozoporiferous cones only barely lower than wide; epiproct with an evident dorsal rib (Fig. 22E); legs about as long as body diameter (Fig. 23A, B), at most with only a vestigial spine at claw base (Figs 23C; 24E); male leg 1 with reduced

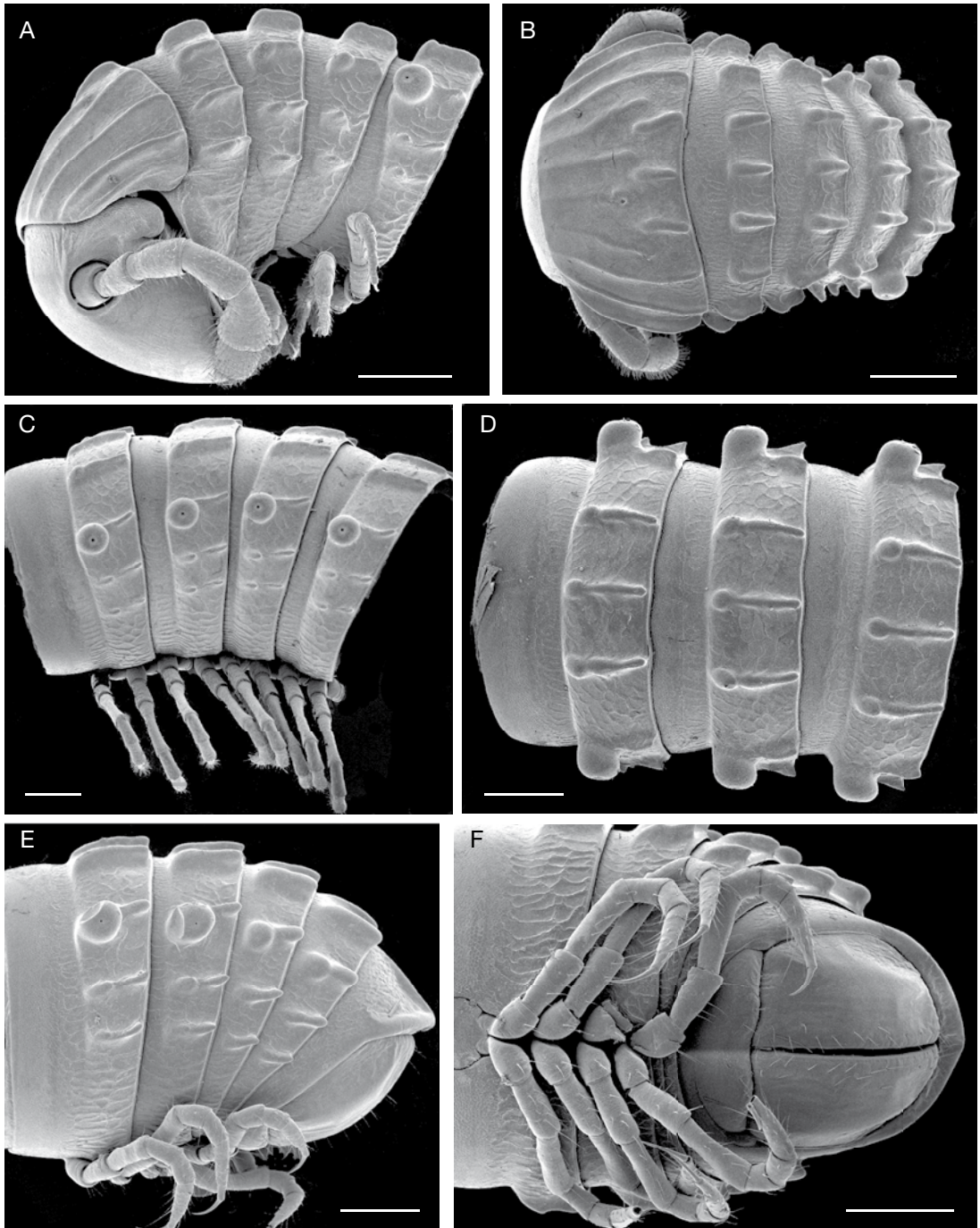


FIG. 22. — *Glyphiulus paracostulifer* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal body end, lateral view; **F**, same, ventral view. Scale bars: 0.5 mm.

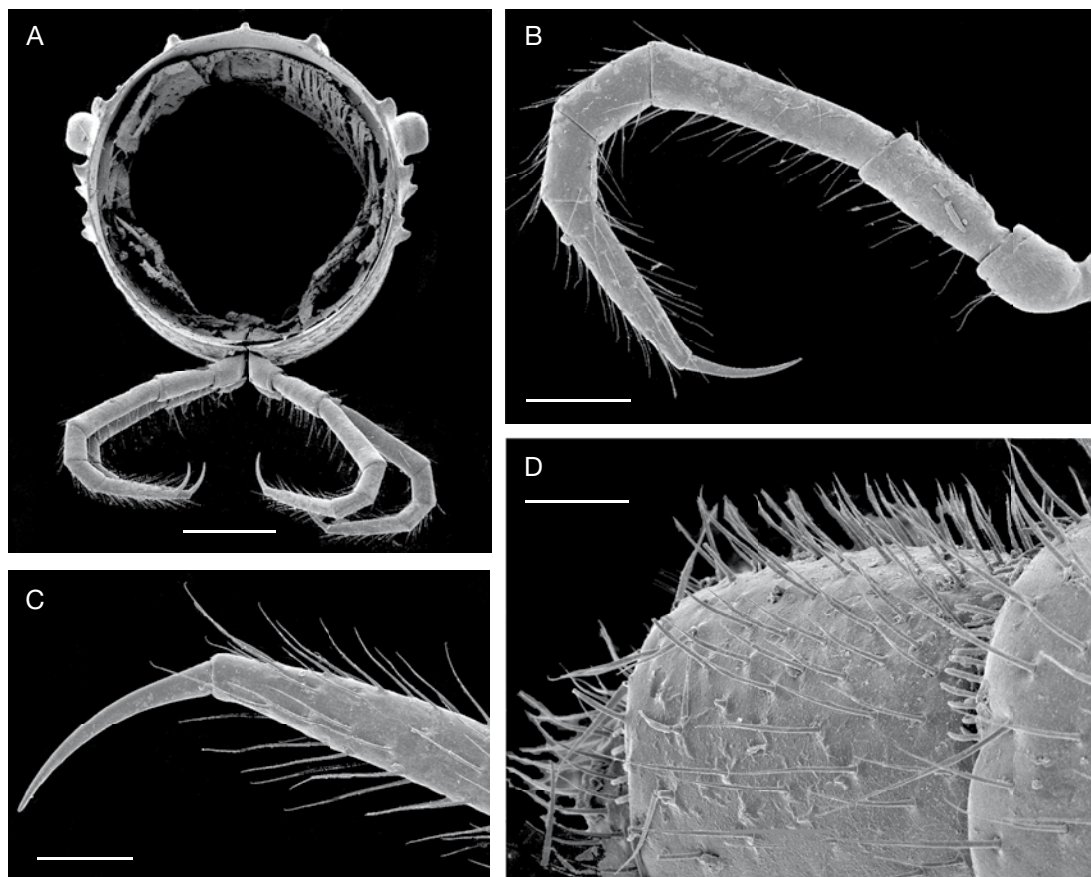


FIG. 23. — *Glyphiulus paracostulifer* n. sp., paratype ♀: **A**, midbody segment section; **B**, midbody leg; **C**, claw; **D**, antennal sensilla. Scale bars: A, 0.5 mm; B, 0.2 mm; C, 0.1 mm; D, 0.05 mm.

5-segmented telopodites and large paramedian coxal processes (Fig. 24B); each anterior gonopod plate with a high distomedial process (Fig. 24F).

REMARKS

Based on several troglomorphic traits, such as the unpigmented body and ocelli, as well as the somewhat elongated antennae and legs, this species seems to be troglobitic.

*Glyphiulus intermedius* n. sp.  
(Figs 25; 26)

TYPE MATERIAL. — China. Sichuan Prov., Chengdu County, Huan Long Dong Cave (No. 593), 26.VIII.1999,

leg. J. & B. Lips, holotype ♂ (MNHN GA 053); paratypes 1 ♂, 2 ♀♀, 1 juv (MNHN GA 053); 1 ♀ (SEM); 1 ♀ (ZMUM).

ETYMOLOGY. — To emphasize a somewhat intermediate position between *Podoglyphiulus* species and the remaining species of the *javanicus*-group.

DIAGNOSIS. — Differs from congeners in the particularly long ozoporiferous tubercles, the special carinotaxy formula on the collum, coupled with certain details of gonopod structure (see also key below).

DESCRIPTION

Holotype with 43p+4a+T, about 26 mm long and 1.6 mm wide; adult paratypes with 38p+4a+T, about 22 mm long and 1.5 mm wide (♂), or with

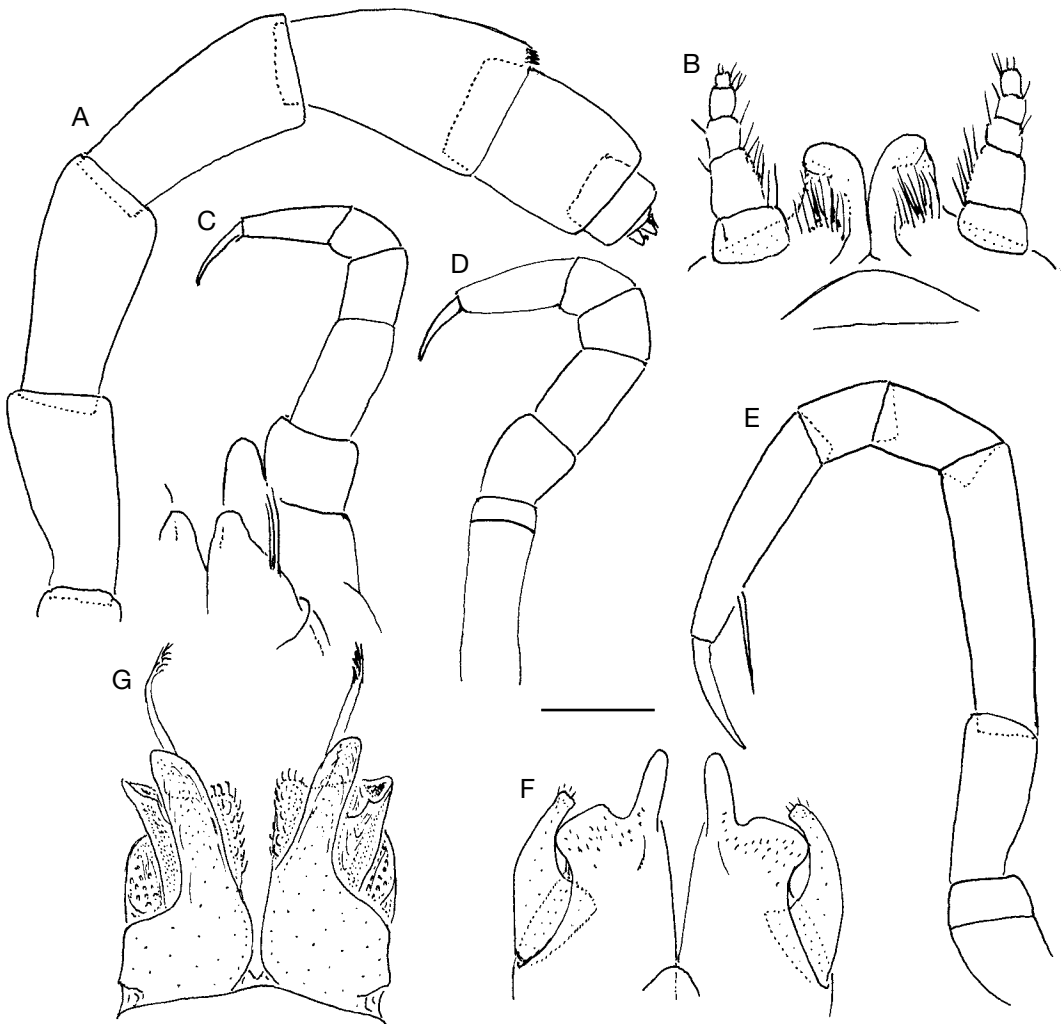


FIG. 24. — *Glyphiulus paracostulifer* n. sp., paratype ♂: **A**, antenna; **B**, leg 1, frontal view; **C**, leg 2, caudal view; **D**, leg 3; **E**, leg 11; **F**, anterior gonopods, caudal view; **G**, posterior gonopods, frontal view. Scale bar: 0.2 mm.

43p+4a+T, about 26 mm long and 1.6 mm wide (♀); with 53p+2a+T, about 37 mm long and 2.0 mm wide (♀); with 56p+1a+T, about 36 mm long and 2.2 mm wide (♀).

Coloration from uniformly pallid to marbled light yellow- or grey-brown, ozoporiferous cones often contrastingly dark brown; antennae, legs and venter yellowish to light yellow-brown; in adults, 8-12 blackish ocelli in a subtriangular eye patch

on each side of head.

Antennae (Fig. 26A), gnathochilarium (Fig. 26B), postcollar constriction (Fig. 25B), dorsal crests and carinotaxy pattern on postcollar segments (Fig. 25), segment's texture and cross-section (Fig. 25F), paraprocts, ventral flaps of male segment 7, male legs 1-3 (Fig. 26C-E), penes (Fig. 26D) generally as in *G. percostulifer* n. sp., but collum (Fig. 25A, B) with a slightly

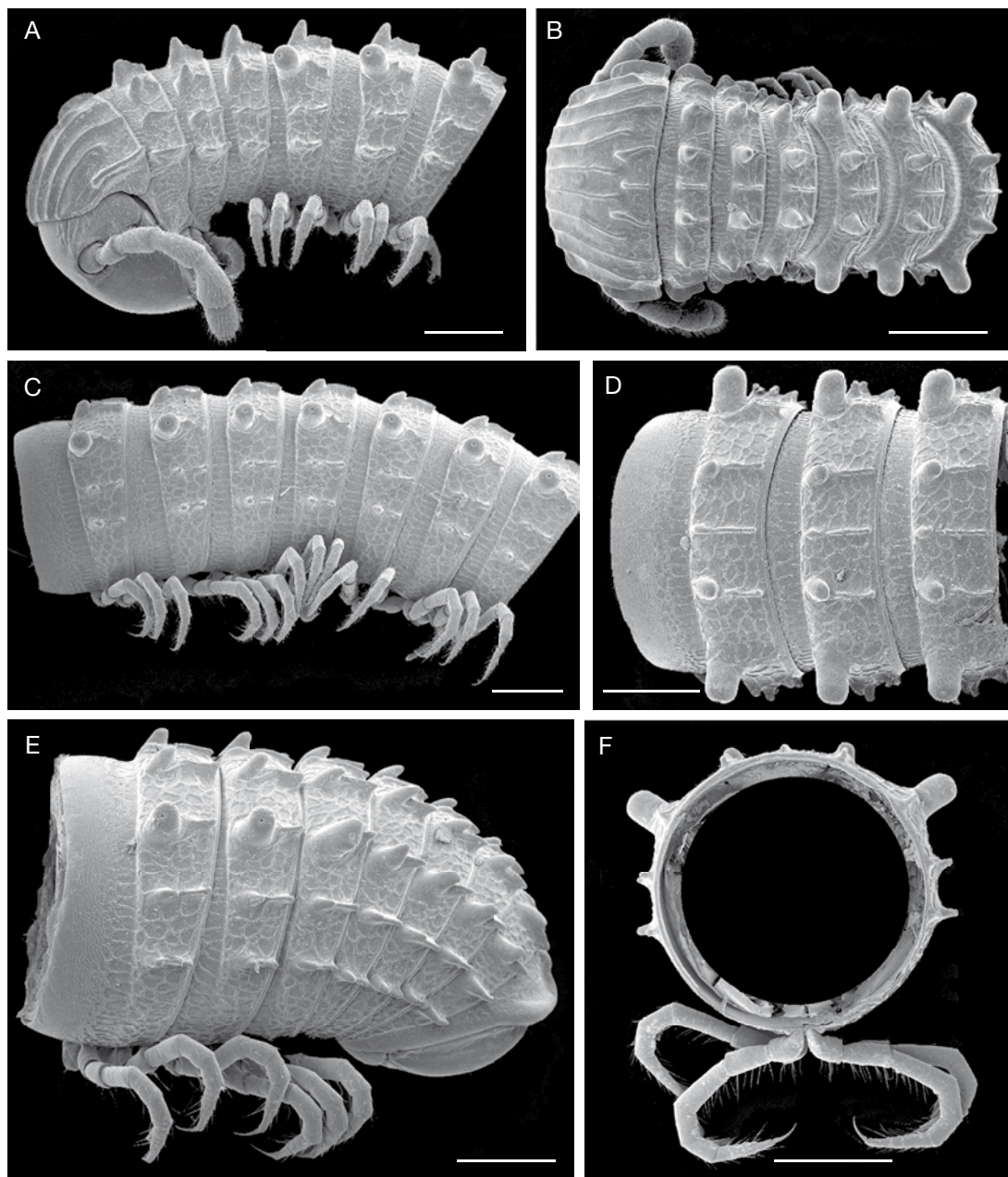


FIG. 25. — *Glyphiulus intermedius* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal body end, lateral view; **F**, midbody segment section. Scale bars: 0.5 mm.

deviating carinotaxy formula (I+2c+III-IV+5c+6a+pc+ma+pc+6a+5c+IV-III+2c+I); all tergal crests (Fig. 25A-E) on subsequent body seg-

ments higher, subdivided (2/2+I/i+3/3+I/i+2/2), ozoporiferous cones higher than wide; anterior half of paramedian dorsal crests particularly



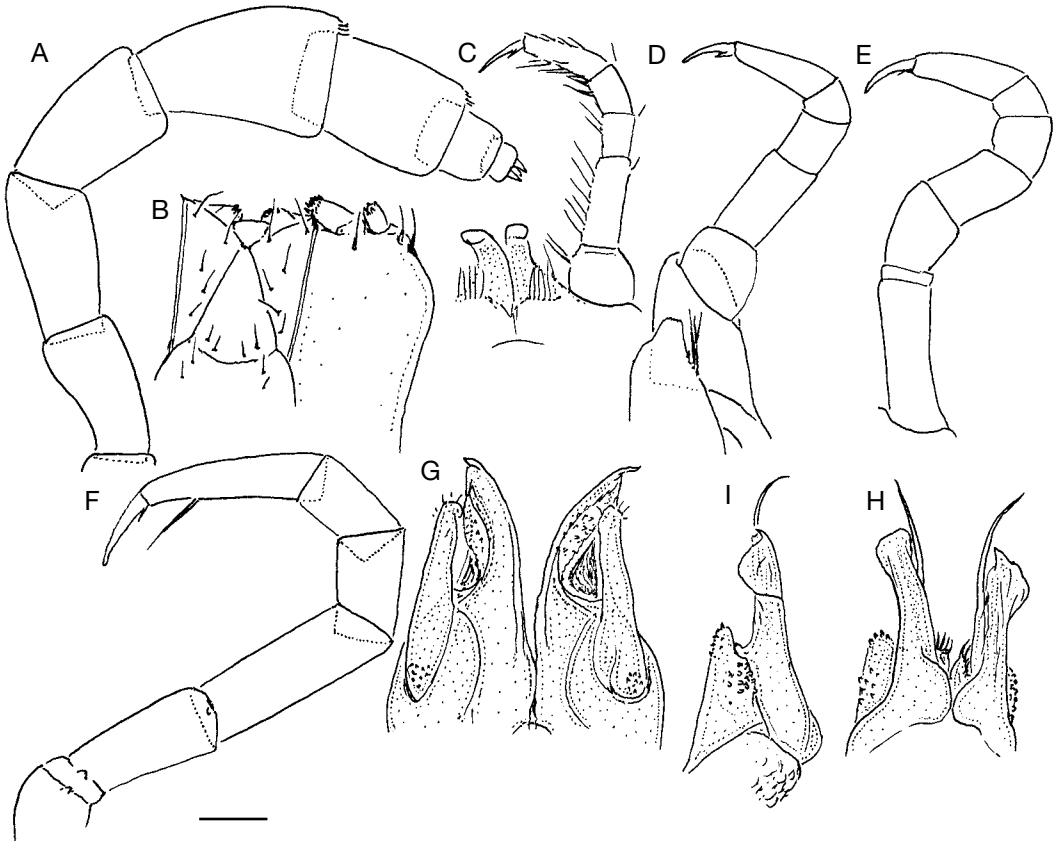


FIG. 26. — *Glyphiulus intermedius* n. sp., ♂ paratype: **A**, antenna; **B**, gnathochilarium, ventral view; **C**, leg 1, caudal view; **D**, leg 2, caudal view; **E**, leg 3; **F**, leg 11; **G**, anterior gonopods, caudal view; **H**, posterior gonopods, caudal view; **I**, left posterior gonopod, lateral view. Scale bar: 0.1 mm.

high, subtriangular on first 10–11 postcollar segments (Fig. 25A, B), thereafter somewhat lower (Fig. 25C–F); epiproct with a small but distinct tubercle at midway dorsally (Fig. 25E), very broadly rounded in caudal part in ventral view; hypoproct slightly but evidently emarginate mediocaudally; legs about as long as body diameter (Fig. 25F), always with a short accessory spine at base of claw (Fig. 26C–F).

Anterior gonopods (Fig. 26G) with coxosternum not plate-shaped but narrowed/elongate distally; telopodites straight. Posterior gonopods (Fig. 26H, I) also slightly elongate, flagella long and bare.

#### REMARKS

The juvenile paratype is haplopodous, with 32p+2a+T. As usual, the ozoporiferous cones on segments 5 and 6 are considerably larger than the others.

In the absence of clear troglomorphic traits, this species seems to be trogliphilic at most. In addition, the cave is described as being “very small, full of bats and guano” (J. Lips *in litt.*).

Even though the gonopods of this new species are not very typical of the group concerned, their similarity to, and ready derivation from, the basic patterns is unquestionable. An assignment to *Podoglyphiulus* can be excluded on both morphological and zoogeographical grounds (see above).

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

1. At least some crests on collum more or less obliterated (Figs 1A, B; 3A, B; 6A, B; 10A, B; 12A) ..... 2  
 — Crests on collum fully developed, no significant parts of collum smooth (Figs 14A, B; 17B; 20A; 22A, B; 25A, B) ..... 8
2. Pleurosternal (= lowest) crests on segments 2-4 very prominent, arcuate (Figs 1A; 3A); flagella of posterior gonopods missing; southern China ..... 3  
 — Pleurosternal crests on segments 2-4 not particularly prominent, as on subsequent segments (Figs 6A; 10A); flagella of posterior gonopods present or absent ..... 5
3. Body of adults 1.1-1.4 mm wide; carinotaxy formula of midbody segments  $1/1+I/i+3+I/i+1/1$  (Fig. 1A-E); male telopodites 1 slightly reduced, 4-segmented (Fig. 2C); cave in Yunnan Province, China ..... *G. obliteratus* n. sp.  
 — Body of adults 1.6-2.2 mm wide; two divided crests below ozoporiferous cone; male telopodites 1 slightly reduced in size but 5-segmented ..... 4
4. Carinotaxy formula of midbody segments  $2/2+I/i+3+I/i+2/2$ ; body unpigmented, only ocelli black; cave in Guizhou Province, China ..... *G. zorzini*  
 — Carinotaxy formula of midbody segments  $2/2+I/i+3/3+I/i+2/2$  (Fig. 3A, B); body and ocelli pigmented, at least partly dark; cave in Yunnan Province .... *G. subobliteratus* n. sp.
5. Axial crest on midbody segments strongly reduced, carinotaxy formula  $2/2+I/i+1/1+m+1/1+I/i+2/2$  (Fig. 6); legs slightly shorter than body diameter (Fig. 6F); anterior gonopod coxosternum with particularly high median outgrowths, devoid of a notch at distal margin (Fig. 8G); cave in North Vietnam ..... *G. mediobliteratus* n. sp.  
 — Axial crest on midbody segments not so strikingly reduced; legs subequal to or even longer than body diameter; anterior gonopod coxosternum deeply notched at distal margin; caves in Guizhou Province, China ..... 6
6. Carinotaxy formula of midbody segments  $1/0+1+I/i+3/3+I/i+1+1/0$  (Fig. 12B, C); male telopodites 1 normal, 5-segmented (Fig. 13C); anterior gonopods as in Figure 13G, posterior gonopods as in Figure 13H ..... *G. parobliteratus* n. sp.  
 — Carinotaxy formula of midbody segments different; male telopodites 1 reduced in size but 5-segmented (Fig. 11C); anterior gonopods and posterior gonopods not as above ..... 7
7. Carinotaxy formula of midbody segments  $1/0+1+I/i+3+I/i+1+1/0$  (Fig. 9A-E); body and ocelli pigmented; medial outgrowth of anterior gonopod coxosternum folded (Fig. 11G) ..... *G. obliteratoides* n. sp.  
 — Carinotaxy formula of midbody segments  $2/2+I/i+3/3+I/i+2/2$ ; body and ocelli unpigmented; medial outgrowth of anterior gonopod coxosternum not folded .... *G. sinensis* n. comb.
8. Carinotaxy formula of collum typical for the *granulatus*-group, I-VI+7a+pc+ma+pc+7a+VI-I, that of midbody segments  $2+I/i+3/3+I/i+2$  (Fig. 14A-E), texture of both lateralmost crests unusually micropunctate (Fig. 15B); male legs 1 and gonopods as in Figure 16C, G, H; cave in Laos ..... *G. costulifer* n. sp.  
 — Carinotaxy formula of collum not as above, both lateralmost crests usual, smooth; male legs 1 and gonopods not as above ..... 9
9. Carinotaxy formula of collum I-III+P+M+P+IV-I (i.e. all crests complete), that of midbody segments  $2/2+I/i+3/3+I/i+2/2$ ; anterior gonopod coxosternum without a deep notch at distal margin (unknown in *G. formosus*); male telopodites 1 strongly reduced,

- 1-3-segmented (unknown in *G. formosus*); flagella of posterior gonopods plumose distally (unknown in *G. formosus*) ..... 10
- Carinotaxy formula of collum not as above, at least some of the crests being abbreviated; carinotaxy formula of midbody segments as above or different; anterior gonopod coxosternum often deeply notched at distal margin; male telopodites 1 usually less reduced; flagella of posterior gonopods, when present, bare or plumose ..... 13
10. Adult body about 1.5 mm wide; male femora 6 and 7 with a glandular adenostyle distoventrally; Zhejiang Province, China ..... *G. reticulatus*
- Body width at least 1.8 mm; male femora without adenostyles ..... 11
11. Coloration light yellow-brown; only 12 ocelli in a subtriangular patch, black; adult body 1.8 mm wide; cave in Guangxi Province, China ..... *G. pulcher*
- Coloration darker, epigeic species; fewer ocelli per eye patch; body about 2.5-2.6 mm wide ..... 12
12. Nine ocelli in two rows per patch; Hong Kong (♀) ..... *G. formosus*
- Seven ocelli in three rows per patch; male telopodites reduced, 3-segmented; half-anterior gonopod with a subsecuriform coxosternum; Mt. Bana, Danang Province, Vietnam ..... *G. mediator*
13. Carinotaxy formula of collum I-V+P+ma+P+V-I, that of midbody segments 3/3+I/i+3+I/i+3/3; not only male coxa 1 but also femur 1 with a median outgrowth; northern Thailand ..... *G. siamensis*
- Carinotaxy formulae not as above; only male coxae 1 with a pair of paramedian processes ..... 14
14. Carinotaxy formula of midbody segments 2+I/i+3+I/i+2 ..... 15
- Carinotaxy formula of midbody segments 2/2+I/i+3/3+I/i+2/2 ..... 16
15. Carinotaxy formula of collum I-III+4c+5a+pc+ma+pc+5a+4c+III-I (Fig. 22A, B); male telopodites 1 reduced in size (Fig. 24B); half-anterior gonopod coxosternum narrowly notched at distal margin (Fig. 24F); cave in Guizhou Province, China ..... *G. paracostulifer* n. sp.
- Carinotaxy formula of collum I-IV+P+ma+P+IV-I; male telopodites 1 not reduced in size; half-anterior gonopod coxosternum broadly and barely emarginate at distal margin; cave in northern Vietnam ..... *G. vietnamicus*
16. Coloration entirely pallid, ocelli not visible; adult body up to about 1.0 mm wide; paramedian outgrowths of anterior gonopod half-coxosternum especially high and large (e.g., Fig. 21G) ..... 17
- Coloration usually darker, ocelli always dark and discernible; body at least 1.3 mm wide; paramedian outgrowths of anterior gonopod half-coxosternum less conspicuous ..... 18
17. Ozoporiferous cones much wider than high; epiproct normal, smooth dorsally; male telopodites 1 reduced, 2-segmented; half-anterior gonopod with a particularly deep notch, such that both distal outgrowths are extremely prominent; posterior gonopods without flagella; Java, Indonesia (introduction from continental Southeast Asia?) ... *G. javanicus*
- Ozoporiferous cones about as high as wide (Fig. 20A-E); epiproct unusual in showing two paramedian crests (Fig. 20E); male telopodites 1 normal, 5-segmented (Fig. 21C); half-anterior gonopod weakly emarginated at distal margin, only paramedian outgrowths prominent (Fig. 21G); posterior gonopods with flagella (Fig. 21H); cave in Laos ..... *G. percostulifer* n. sp.

18. Carinotaxy formula of collum particularly complex, I-II+3c+4a+5c+VI+7c+8a+pc+ma+pc+8a+7c+VI+5c+4a+3c+II-I (Fig. 17B); male telopodites 1 reduced in size, but still 5-segmented (Fig. 19C); half-anterior gonopod coxosternum subsecuriform (Fig. 19G); flagella of posterior gonopods plumose (Fig. 19H); cave in Laos ..... *G. subcostulifer* n. sp.
- Carinotaxy formula of collum I+2c+III-IV+5c+6a+pc+ma+pc+6a+5c+IV-III+2c+I (Fig. 25A, B); male telopodites 1 normal, 5-segmented (Fig. 26C); half-anterior gonopod coxosternum as in Figure 26G; posterior gonopods as in Figure 26H, flagella bare; cave in Sichuan Province, China ..... *G. intermedius*

## CONCLUSION

With the *javanicus*-group treated here, comprising 19 species, our review of *Glyphiulus* can be considered accomplished. It therefore seems appropriate to provide brief analyses of the variation and distribution of its constituent species vis-à-vis the *granulatus*-group recently revised and containing another 20 species (Golovatch *et al.* 2007). Since both these species groups are clearly closely related, with the basic differences lying only in the conformation of male leg 1, the adoption of a broader concept of *Glyphiulus* seems warranted. Furthermore, these species groups do not show a clear-cut geographical separation from one another (Fig. 27). This contrasts with *Podoglyphiulus*, which forms a clearly delineated group both morphologically and zoogeographically (see above). The latter group is certainly coordinate in rank with *Glyphiulus*, thus allowing both to be treated as independent genera. On the contrary, the status of *Hypocambala* in relation to *Glyphiulus* still remains to be verified (see above).

Within the *granulatus*-group, there are several species that show infraspecific variation in the division of the mentum into a pro- and eumentum. Even though the mentum appears to be surprisingly stable and always divided within the *javanicus*-group, we can conclude 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 more than individual variation. In other words, the structure of the gnathochilarium is apparently 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 an evolutionary trend to be checked using adequate material (Golovatch *et al.* 2007).

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 classification, often allowing the grouping of species. The degrees of expression of the crests are 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 with that of the metaterga. In several cases at least, this correlation is less apparent 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* Mauriès & Nguyen Duy-Jacquemin, 1997 and, possibly, *G. sinensis*). 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* Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2007) even become enlarged against the background of the other strongly reduced crests. Reduction is especially evident due to loss of the ventrolateral crest, which becomes a stria similar to the several other striae located further ventrad.

Changes in the carinotaxy formulae of the collum in the *granulatus* and *javanicus* groups – from the typical I-VI+7a+pc+ma+pc+7a+VI-I (or even from more extreme cases such as *G. intermedius*

n. sp. or *G. subcostulifer* n. sp.), down to I-IV(V)+5(6)a+pc+ma+pc+5(6)a+(V)IV-I and then I-III+P+M(ma)+P+III-I, all apparently due to fusion/loss of several lateralmost crests – are rather common. The pattern shown by the paramedian and median crests, when these are visible, seems to be much more stable and important. Usually it is pc+ma+pc, more rarely P+M+P (*G. mediator*, *G. pulcher*, *G. recticollis*, *G. formosus*) or P+ma+P (*G. septentrionalis* Murakami, 1975, *G. siamensis*, *G. vietnamicus*). Only one species, *G. capucinus* Attems, 1938, has the crests strongly differentiated, but the formula is only slightly different from that of *G. superbus* Silvestri, 1923, which is only a derived case of the arrangement typical of the *granulatus* and, in part, *javanicus* groups.

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 anterior row tends to be smaller than the posterior one. In only one case – that of *G. beroni* Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2007 – are most of the crests divided transversely into three rows. In all other species the crests, except for the ozoporiferous ones, are totally undivided, as in *G. rayrouchi* and *G. latellai* Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2007 within the *granulatus*-group, as well as in *G. obliteratoides* n. sp., *G. paracostulifer* n. sp. and *G. vietnamicus* within the *javanicus*-group. The typical pattern for the *granulatus*-group is  $3(2)/3(2)+I/i+4/3+I/i+3(2)/3(2)$ , 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  $2/2+I/i+2/3+I/i+2/2$  (*G. adeloglyphus* Zhang & Li, 1982). Within the *javanicus*-group, however, the median crest is never doubled anteriorly, the typical formula being  $2(1)/2(1)+I/i+3/3+I/i+2(1)/2(1)$ . Only in *G. siamensis* is the arrangement  $3/3+I/i+3+I/i+3/3$ , while only *G. costulifer* n. sp. has the two lateralmost crests micropunctate, which is highly unusual.

Evolutionarily, however, it seems much easier to assume that a smooth collum and non-crested

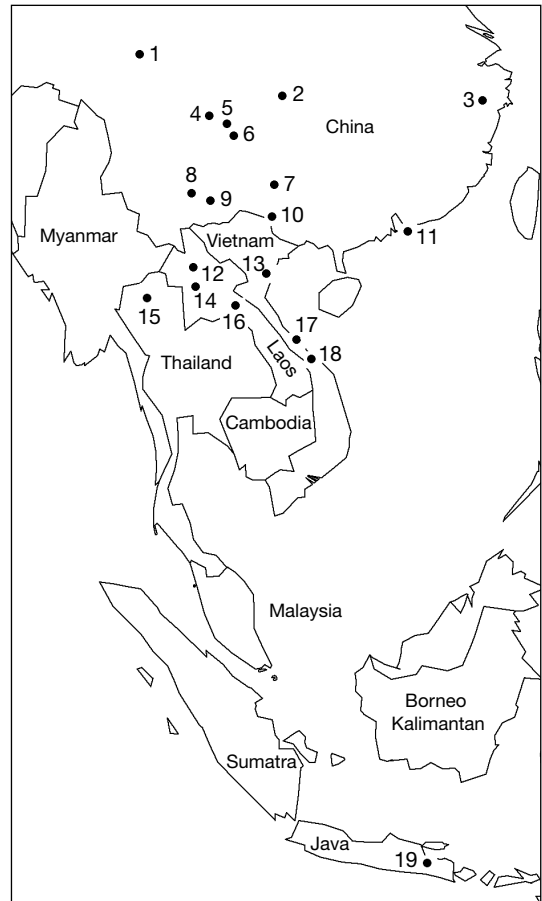


Fig. 27. — Distribution of species of the *javanicus*-group, and of *Glyphiulus* Gervais, 1847 in general (that of *G. granulatus* (Gervais, 1847) being pantropical, it is omitted here), shown more or less from north to south: 1, *G. intermedius* n. sp.; 2, *G. parobliteratus* n. sp.; 3, *G. recticollis* Zhang & Li, 1982; 4, *G. zorzini* Mauriès & Nguyen Duy-Jacquemin, 1997; 5, *G. paracostulifer* n. sp.; 6, *G. sinensis* (Meng & Zhang, 1993); 7, *G. obliteratoides* n. sp.; 8, *G. obliteratus* n. sp.; 9, *G. subobliteratus* n. sp.; 10, *G. pulcher* (Loksa, 1960); 11, *G. formosus* (Pocock, 1895); 12, *G. costulifer* n. sp.; 13, *G. mediobliteratus* n. sp.; 14, *G. subcostulifer* n. sp.; 15, *G. siamensis* Mauriès, 1983; 16, *G. percostulifer* n. sp.; 17, *G. vietnamicus* Mauriès, 1977; 18, *G. mediator* Attems, 1938; 19, *G. javanicus* Carl, 1911.

metaterga represent the plesiomorphic conditions. This at least is the case in *Hypocambala*, which seems to be a genus particularly closely related to *Glyphiulus*. Therefore, the especially multicarinate, complex formulae, like those observed in *G. intermedius* n. sp., *G. costulifer* n. sp., *G. paracostulifer* n. sp.,

*G. capucinus*, *G. granulatus* (Gervais, 1847) and many others, can be treated as (syn)apomorphic. The (nearly) smooth colla in numerous, primarily cave-dwelling congeners is therefore probably a symplesiomorphy.

Several species are presumed to be troglobites. Besides showing the typical traits of troglomorphy (general depigmentation, eye reduction, elongation of legs, claws and antennae, “gigantism”, although all relatively modestly expressed in comparison with certain examples in Polydesmida or even Julida), such species, belonging to both the *granulatus* and *javanicus* groups, tend not only to have more or less strongly obliterated crests on the collum, but also 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*, there seems to be no correlation between this feature and the size of the accessory spine at the claw base (Golovatch *et al.* 2007).

Legs 1 of the male are usually very strongly reduced within the *granulatus*-group, as opposed to being complete and little modified within the *javanicus*-group. In this respect, *G. basalis* seems to be especially primitive within the former group, whereas *G. costulifer* n. sp., *G. percosulifer* n. sp., *G. intermedius* n. sp., *G. vietnamicus* and some others are basal within the latter group. On balance, the particularly leg-like male telopodite 1 of *G. costulifer* n. sp. allows the *javanicus*-group to be considered as more basal in comparison with the *granulatus*-group.

Because the vulvae in *Glyphiulus* are surprisingly monotonous in structure, they are hardly of any use in systematics. 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 reliable sex and stadium matches. Unsurprisingly, there are many species of Cambalopsidae described solely from female material.

Based on all available evidence, an amended diagnosis of *Glyphiulus* would read as follows (*cf.* Mauriès 1977).

## Genus *Glyphiulus* Gervais, 1847

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

TYPE LOCALITY. — Mascarene Islands.

DIAGNOSIS. — Cambalopsidae with tergal crests evident at least on postcollar segments; similar crests often present also on collum, these not fragmented into more than two parts. Carinotaxy formulae of collum highly variable, often complex, but median crest, even if abbreviated anteriorly, usually clear. Carinotaxy formulae of postcollar segments usually  $2(1)/2(1)+I/i+4/3+I/i+2(1)/2(1)$  (*granulatus*-group) or  $2(1)/2(1)+I/i+3/3+I/i+2(1)/2(1)$  (*javanicus*-group), crests undivided or divided into three tubercles occurring only occasionally, same as three crests below *I/i*. Basalmost crests on ozoporiferous segments never hypertrophied, instead always being smallest, sometimes even abbreviated. Ozopores starting from segment 5, always lying on particularly prominent tubercles. Eyes usually present, though often reduced and sometimes unpigmented, especially so in cavernicoles.

Mentum of gnathochilarium usually divided. Male legs 1 from little modified to strongly reduced, either with coxal outgrowths contiguous but virtually never completely fused medially (*javanicus*-group) or with leg remains (more rarely, retaining a few segments) widely separated due to a sternum devoid of median strictures (*granulatus*-group). Male legs 2 nearly normal, not incrassate, coxae somewhat modified, and prefemora abbreviated frontally, for accommodation of penes. Male legs 3 with strongly elongated coxae.

Anterior gonopods usually with a shield-like coxosternum and a moveable, lateral, 1-segmented, often curved telopodite; flagella absent. Posterior gonopods compact, not elongated, often with apical flagelloid outgrowths.

## REMARKS

The general distribution of the *granulatus*-group shows a quite coherent pattern, occupying a region between Sichuan, Hubei and Shanghai in the North, and central Vietnam in the South. This matches very closely the distribution of the *javanicus*-group (Fig. 27), which ranges from between Sichuan and Zhejiang in the North to Java in the South. In other words, the distribution of the *granulatus*-group is somewhat more restricted and falls entirely within that of the *javanicus*-group, the latter thus fully reflecting the general range of *Glyphiulus*. Even after this review, there is no doubt that these generally subtropical to tropical, highly montane and often karstic areas contain many new species of this

widespread and large genus waiting to be found and described.

The only outlying member of the *javanicus*-group appears to be *G. javanicus* itself. The strong isolation of this species from the remaining bulk, which is restricted to continental Southeast Asia (Fig. 27), might well represent an accidental introduction from the mainland. Carl (1911) explicitly indicated a sugar cane plantation as the place whence the type series of *G. javanicus* had come.

The fact that the species of *Glyphiulus* are mostly highly local in distribution deserves attention. This can often be accounted for by their being troglobites, naturally restricted to one single cave or a limited group of caves. However, the impression that the majority of the species are scarcely more than troglolithes suggests that a wealthy, barely sampled fauna also exists epigeically. This undersampling is due to the fact that 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 the region. Summarising the poor state of current knowledge, we have still only touched the tip of the iceberg (Golovatch *et al.* 2007).

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