Pacific Insects 17 (2–3): 247-255 31 August 1977

THE SYSTEMATIC POSITION OF THE DIPLOPOD FAMILY DORATODESMIDAE, AND DESCRIPTION OF A NEW GENUS FROM MALAYA (POLYDESMIDA)

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Abstract: Ascetophacus macclurei is described as a new genus and species of doratodesmid milliped from the Batu Caves near Kuala Lumpur, Malaya. The literature pertaining to the family Doratodesmidae is reviewed, and the status of this family with respect to other polydesmoids discussed. It is concluded that closest affinities lie probably with the Holarctic family Polydesmidae on the basis of gonopod anatomy, and that previous allocations of doratodesmids to the family Oniscodesmidae were based upon overemphasis of purely convergent adaptive characters. A checklist of the presently known taxa of the family is provided.

Many widely diverse forms of animals have developed the ability to enroll the body as a passive defense mechanism, but the phenomenon of volvation is especially well exploited by various members of the class Diplopoda. In most species of the subclass Pentazonia, and in the polydesmoid families Sphaeriodesmidae, Cyrtodesmidae, and Oniscodesmidae, the body form has become generally broadened and strongly convex, with the paranota depressed and apically acuminate, and 1 or more of the anteriormost segments greatly enlarged laterally to function as a centrum against which the remaining paranota fit snugly. When enrolled, most of these animals form a compact sphere of unquestionable effectiveness against many predators. Although a superficial similarity in the body form of the various volvatory polydesmoids induced Verhoeff in 1941 to group them all into a suborder, Sphaerosomita, a study of the male genitalia and of peripheral characters leaves little doubt that such a grouping is based upon the misapprehension of a purely adaptive character. It is, however, notable that polydesmoid volvation is dominantly a phenomenon of the New World tropics. A few rare species only have been recorded from West Africa and Southeast Asia.

Although most volvating millipeds tend to present a smooth and polished surface when enrolled, there are occasional exceptions. The glomerid genus *Trachysphaera* of Europe is notable for the high and heavily sculptured transverse crests of most body segments, and some Neotropical sphaeriodesmids in the genera *Hybocestus* and *Cyphodesmus* have a transverse series of high conical tubercles across the terga of all except the anteriormost segments. Species of the family Cyrtodesmidae tend to be irregularly tuberculate and roughened dorsally, sometimes hairy as well.

A totally different and singular variety of dorsal ornamentation occurs in a small and poorly-known group of polydesmoids ranging from Java to Malaya, most species of which have a prominent conic to styliform median process on most of the metaterga. When such animals are enrolled, their bodies form not a sphere, but rather a flattened or lenticular shape, with a row of spoke-like projections radiating from its periphery (FIG. 1). These millipeds have been referred to a somewhat apocryphal family, Doratodesmidae, the status of which has been in doubt and confusion ever since 1896.

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Some years ago, during a survey of the fauna of the Batu Caves at Kuala Lumpur, Malaya, Dr H. Elliott McClure obtained a large series of a doratodesmid which is manifestly of a different generic type than the species so far known from Java and Sumatra. Upon having the opportunity to study this material, entrusted to my care by the authorities of the Bishop Museum, I was able to consider the systematic position of the group and the status of the family name Doratodesmidae proposed for it by Cook in 1896a.

HISTORICAL SUMMARY

The first known species of this group was taken in Java by the noted Dutch zoologist Max Weber and was named by Pocock (1894) as *Doratonotus armatus*. Silvestri (1895) published the brief diagnosis of *D. beccarii* from Mt Singalang, Sumatra, and Cook proposed the new generic name *Doratodesmus* to replace the preoccupied *Doratonotus*. In 1896(b), Cook very briefly diagnosed 2 new species (*D. vestitus* and *D. muralis* from Java), and established the family Doratodesmidae.

In 1901, Sinclair described *Doratonotus cavernicola* from specimens taken in caves in south-central Malaya. Attems listed the genus and its 5 species in several papers (1914, 1926, 1940), referring it to the family Oniscodesmidae, and in 1930 recorded *D. armatus* from southern Sumatra. No further additions to the group were made until 1945, when Chamberlin published the new taxa *Hoplitesmus enoplus* from West Java and *Pauroplus analdes* from Sumatra.

Finally, a redescription of *D. armatus* from the original type material was published by Jeekel (1955) who noted that *H. enoplus* is a strict synonym of Pocock's species. In the same paper, Jeekel provided an excellent drawing of the genitalia, making the comprehension of these appendages possible for the first time, and incidentally pointed out that the Sumatra record by Attems was unquestionably based on a different and so far undescribed species.

TAXONOMY

Superfamily POLYDESMOIDEA

Family DORATODESMIDAE

A group of small (body length to 15 mm) tropical polydesmoids in which the paranota of the 2nd body segment are flabellately enlarged and function as a basis upon which most of the following paranota rest when the animal is enrolled; some of the metaterga (generally of segments 5 through 19) are provided with conspicuous, upright, median projections (FIG. 1). Gonopods of the polydesmoid type: coxae large, subtriangular, in contact medially and fairly rigidly attached to the aperture, their main axis parallel to that of the body, at least the distal 1/3 exserted, dorsal surface with a concavity; telopodites relatively large, prefemora small and so hinged as to permit movement only in the direction of the median body axis.

In proposing this family, Cook (1896a, b) did not go into details about its affinities. Chiefly on the basis of the modified 2nd segment, Attems consistently referred *Doratodesmus* to the family Oniscodesmidae, a taxon which in his usage was defined largely on the basis of the animals' ability to roll up into a sphere. It is indeed strange that not only Attems, but to an even greater extent Verhoeff, placed such emphasis upon what is obviously an adaptive character, one capable of recurring in a variety of small humus-dwelling polydesmoids. Of the various genera placed in this "family" in his last and most detailed treatment, Attems (1940) included members of at least 4 groups which I think warrant family status: Oniscodesmidae and Sphaeriodesmidae which are related to the chelodesmoid complex of families, and Cyrtodesmidae and Doratodesmidae which seem allied to the pyrgodesmoids and polydesmoids, respectively, on the basis of gonopodal characters.

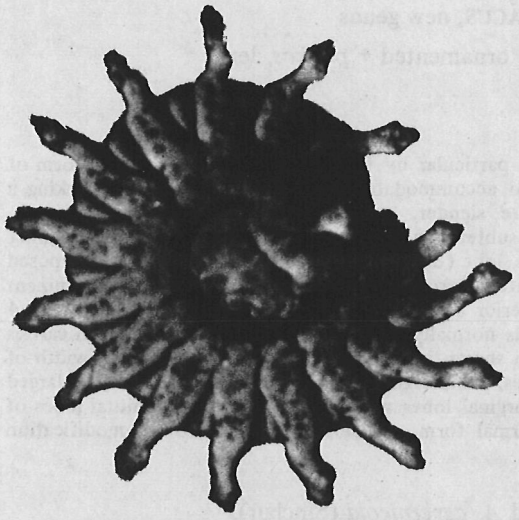

FIG. 1. *Ascetophacus macclurei,* n. sp. Paratype, shown in the enrolled condition. (Photograph by S. D. Chalgren.)

The major point unsettled at this moment is the degree of relationship between the last 2 families mentioned above. Admittedly there is a considerable external resemblance between *Cyrtodesmus* and *Doratodesmus,* and there is plenty of evidence of relictual biogeographic affinities between the millipeds of South America and Southeast Asia. But on the basis of what I can determine about gonopod structure, the coxae in the latter genus (and in the new one here proposed) are built closely along the lines of those of typical polydesmids, that is to say, with the major axis extending in a longitudinal direction, and with the telopodites hinged thereupon in such a way as to be capable only of movement in the same plane. Cyrtodesmids on the other hand have the coxae subglobosely enlarged in a more transverse direction, with a quite different mode of telopodite articulation; and in general facies suggesting the plan typical of pyrgodesmoid (=stylodesmoid) groups.

My preference at the present time is to regard the Doratodesmidae as a valid family within the superfamily Polydesmoidea, having only a remote affinity with the Neotropical family Cyrtodesmidae.

At least 3 very distinct genera can be recognized in the handful of species so far on record, as indicated in the following key. There is little doubt in my mind that the future holds the promise of a number of interesting discoveries in this family, especially to be expected from Sumatra from which so far only 2 doratodesmids have been recorded.

KEY TO THE GENERA OF DORATODESMIDAE

1. Only the antepenultimate segment with a prominent median dorsal process, other metaterga with usually 3 transverse rows of rounded tubercles; telopodite of gonopod apparently short, curved mesad, without distal lobes or processes ..... **Pauroplus** Chamberlin
   – Segments 4 or 5 through penultimate with conspicuous median dorsal processes; telopodite relatively large, nearly straight or curved in median plane of body axis, terminating in several distinct processes . . . 2
2. Dorsal processes distally acuminate, conical, recurved posteriad; paranota acuminate laterally, the pores located near front margin basally; edges of paranota of segment 2 not notched and lobed; gonopods (known only for the type-species) with medioapical coxal process; telopodite enlarged distally, with 5 lobes or processes, prostatic groove running out to end of the terminalmost process ..... **Doratodesmus** Cook
   – Dorsal processes apically enlarged and bilobed on each side, not sloped posteriad; paranota with rounded lateral lobes, the pores located in the median lobe; gonopods lacking coxal process, telopodite slender and curved (in the type-species) with 3 apical processes, prostatic groove terminating in a small cluster of setae near base of 1 apical process ..... **Ascetophacus, n. gen.**

Genus ASCETOPHACUS, new genus

(Gk. *asketos,* curiously made, ornamented + *phakos,* lens)

Type-species: *A. macclurei,* n. sp.

Diagnosis: A doratodesmid genus characterized in particular by the distinctly polydesmid-like form of the gonopods: coxae concave on the ventral side to accommodate the retracted telopodites, lacking a distomedian projection near the cannula; telopodite slender, arcuate, cingulate near the midlength, terminating in 2 apical branches (*b, c*) and an erect subterminal process (*a*), the prostatic groove running out the lateral side to terminate at a small setose lobe (*d*) near base of process *c*. Body composed of 20 segments, the first 4 ornamented with low seriate tubercles dorsally, segments 5–19 with prominent erect median dorsal processes, these highest on anterior segments, enlarged apically and usually with 4 rounded lobes. Paranota wide, slender, the outer ends normally with 3 lobes of which the median carries the ozopore. Modified anterior segments of the form shown in FIG. 2; the collum small, about width of head, set with 3 transverse rows of small tubercles; metatergum of segment 2 with greatly enlarged paranota, the edge of which is incised to form 7 marginal lobes which interlock with paranotal lobes of segments 3–9 when animal is enrolled. Legs of normal form, set close together, without modification in the ♂ sex.

Referred species: 2, *A. macclurei,* n. sp., and *A. cavernicola* (Sinclair).

Distribution: Known so far only from the central part of the Malay Peninsula.

Ascetophacus macclurei Hoffman, n. sp. FIG. 1–8

Material examined: ♂ holotype (BISHOP 10,472), 2♂, 2♀ topoparatypes, from Cavern C, Batu Caves, ±10 km N of Kuala Lumpur, Selangor, Malaysia, 20.X.1959; also numerous ♀ and ♂ paratypes from the Batu Caves dated 27.X., 10.XI., 15.XII., and 28.XII.1959; 8.III., 17.VI., 3.V., 19.VII., 18.X., 16.IX. 1960, all by H. E. McClure; deposited in Bishop Museum except some duplicates retained in my collection.

Diagnosis: With the characteristics of the genus; apparently to be distinguished from the poorly-described *A. cavernicola* in that the paranota are laterally 3-lobed instead of 5-lobed as stated for the other species.

Holotype. Adult ♂, ca 10.0 mm in length (difficult to determine with accuracy), maximum width, 2.1 mm. Coloration after 15 years in spirit uniform pale testaceous to grayish white, perhaps nearly the color in life. General appearance when enrolled as shown in FIG. 1. The ultimate segment rests on the tergum of segment 4 so that the dorsal processes form a complete circuit of radiating spokes; the enrolled body appears distinctly lenticular or discoid as formalized in the generic name. Body with 20 segments. Head normal in appearance, similar to that of *Polydesmus,* the labrum similarly projecting slightly ventrad; front flat and glabrous; interantennal space wide; a low rounded-ovoid tubercle each side just above antennal socket. Antennae long and relatively slender, without peculiarities. Collum small, narrower than head, trapezoidal in shape, widest across front edge, latter with a median series of 4 small contiguous lobes, then with 3 larger and distinctly separated lobes on each side, lateral end rounded. Disc of collum nearly flat, with about 8 tubercles on each side arranged in an irregular triangle, the lateralmost tubercle largest and slightly inclined laterad. Segment 2 (FIG. 2, 3) with greatly enlarged and depressed paranota; dorsum of metazonum virtually flat, with about 3 irregular transverse series of 6 to 8 small tubercles each, the posterior series most prominent; paranotal base deeply concave posteriorly, the concavity accommodating a prominent boss at anterior base of following patanota when animal is straightened. Anterolateral edge of paranota continuous, evenly arcuate, divided into 6 prominent lobes; lateral surface concave with a median elevation surmounted by a tubercle; posterior edge thickened, with an elongate flange near base, forming an elongated groove into which anterior edge of following paranota fit during volvation. Segments 3 and 4 similar, but dorsal tuberculation somewhat more distinct and paranota narrowed laterad, dorsolateral boss at base of paranota prominent, on segment 3 projecting forward; paranota of both segments with deep grooves on posterior edges, and elongate marginal flanges similar to that of segment 2. Segments 5–19 similar in structure, prozona slightly longer than metazona, surface of prozona and stricture microscopically areolated, surface of metazona roughened, with traces of transverse series of tubercles; surface of middorsum produced into high median projections, each apically expanded and bilobed on each side, some also with smaller subapical lateral lobes (probably homologous to tubercles

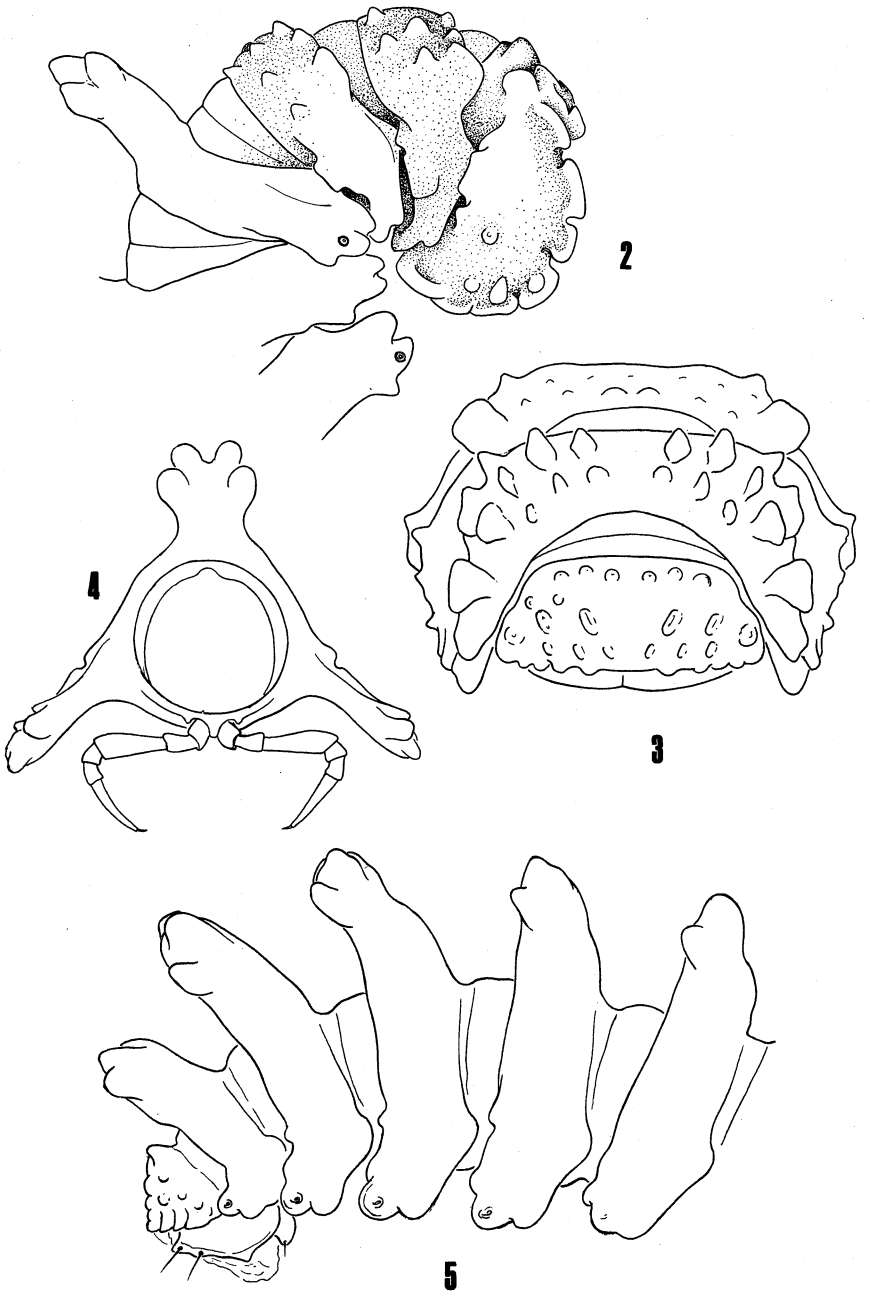

FIG. 2–5. *Ascetophacus macclurei,* n. sp., external structural features. (2) Segments 2–5 and parts of 6 and 7, lateral aspect. (3) Segments 1–3, anterior-dorsal aspect (the head and collum deflexed). (4) Midbody segment, posterior aspect. (5) Segments 15–20, lateral aspect. Drawings from ♂ topoparatype.

in the transverse series of anterior segments), caudal side of the projections concave. Paranota continuing slope of dorsum, depressed at about a 45° angle from the horizontal (FIG. 4), laterally trilobed with ozopores (on segments 5, 7, 9, 10, 12, 13, 15–19) centered in the median lobe; posterior lobe becoming smaller on posterior segments, obsolete on segments 18 and 19. Segment 20 small, transversely trapezoidal, with 3 series of tubercles, not produced medially; paraprocts normal in appearance, flattened, the marginal setae set fairly close to dorsal end. Hypoproct small, transverse, smooth, not produced medially. Sterna small, elevated, very narrow on most segments, intercoxal space less than ½ coxal length; legs of the form shown in FIG. 4, all are similar, without secondary sexual modifications; vasa deferentia open flush on surface of coxae of 2nd pair. Legs of segments 5 and 6 set progressively further apart in going posteriad, thus forming a deep triangular area into which the gonopod telopodites are accommodated during volvation. Gonopod aperture large, transversely oval, its sides elevated laterally; coxae large and prominent, firmly fixed in position with about ½ the length exposed, broadly in contact medially and basically similar in form to those of the Polydesmidae. In profile, coxae (FIG. 7, 8) subtriangular, broadest at midlength; sternal apodemes long, distinct from coxae, a small median sternal remnant present (FIG. 6, *h*). Dorsal side of coxa with concavity (FIG. 6, *g*) for retraction of telopodite and a dorsolateral field of macrosetae laterad to it. Cannula present, not subtended by an apical coxal projection as in *Doratodesmus*. Telopodite elongate, hinged to move in a plane parallel to median body axis as in the Polydesmidae, relatively large for size of the animal, arcuately curved posteriad. Prefemur heavily setose on lateral side, sparsely so on median, cannula inserted into a small basal depression which gives rise to the prostatic groove; latter running up median side of telopodite to about its midlength where, marked by a prominent cingulum it then moves around to the lateral side and continues out to a small setose knob (FIG. 7, 8, *d*) perhaps homologous to the endomerite of Polydesmidae. Postcingular region of telopodite with distinct flange on lateral side, and 3 terminal processes, 1 (*a*) laminate and erect, the other 2 (*b* and *c*) apical and parallel to each other. End of prefemur (or base of acropodite region) with a prominent spiniform process (*e*).

Remarks: The opportunity to examine the sexual characters of a 2nd species of doratodesmid naturally invites comparison with the corresponding appendages of *Doratodesmus armatus*. Despite the general overall agreement in body form between the 2 species, there is a disappointing lack of any close similarity in gonopod structure, compelling the conclusions that either (1) the family is highly diverse and the 2 species under consideration represent anatomical extremes (different subfamilies?), or (2) 2 families are involved, externally similar by virtue of convergent evolution, after the manner of the Sphaeriodesmidae and Oniscodesmidae in the neotropics.

In the very broadest of terms, the gonopod of *Ascetophacus* bears a striking resemblance to that of a typical polydesmid, while that of *Doratodesmus* looks as though it should be attached to a member of the cryptodesmid subfamily Pterodesminae. To be sure, this state of things is not necessarily a contradiction, since in my view the Polydesmidae, Cryptodesmidae, and Doratodesmidae make up, with some other groups, a superfamily Polydesmoidea (Hoffman 1975).

The status of the curious taxon *Pauroplus analdes* (Chamberlin, 1945) cannot be estimated in the want of actual material. If Chamberlin's drawings are to be trusted, the organism appears to be some sort of doratodesmid, but with highly disjunct gonopods. Considering the diversity exhibited by the handful of species so far known, one is encouraged to anticipate that a rich fauna of the group exists in Sumatra particularly, hopefully to be revealed by refined techniques of sampling for soil animals.

About the same remarks can be made for the Malayan species *A. cavernicola* described by Sinclair (1901) from several caves in the south-central part of that peninsula. It is entirely possible that I may have redescribed this species, although it would be highly presumptuous to make such an assumption, particularly considering the high degree of local endemism that characterizes the majority of small diplopods. I have so far been unable to determine the location of the type material of *A. cavernicola;* it might still be at Cambridge (England).

SUMMARY OF KNOWN DORATODESMIDAE

Genus *Doratodesmus* Cook, 1896(b) (syns. *Doratonotus* Pocock, 1894, preoccupied; *Hoplitesmus* Chamberlin, 1945)

1. *D. armatus* (Pocock, 1894) (syn. *Hoplitesmus enoplus* Chamberlin, 1945). This species,

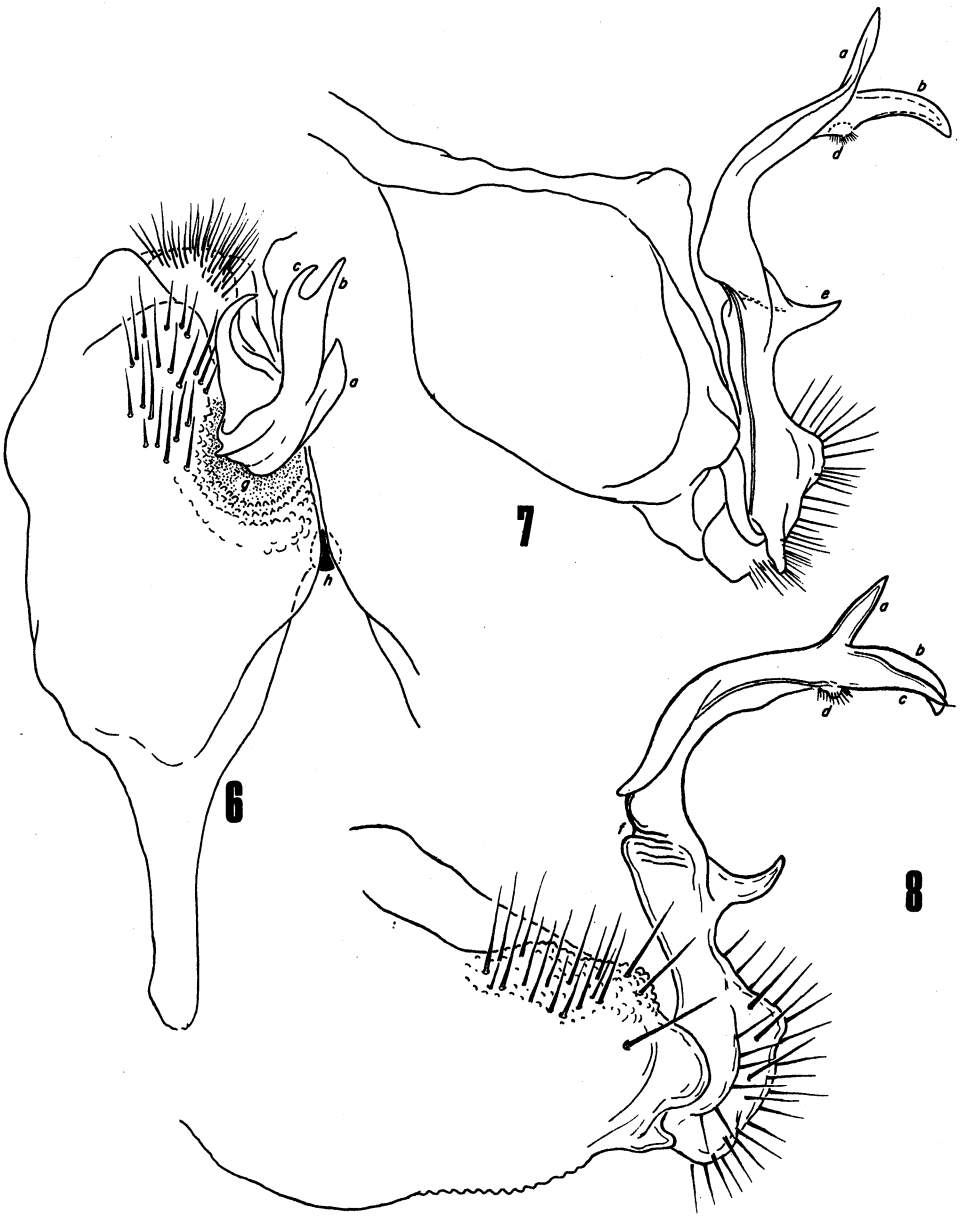

FIG. 6–8. *Ascetophacus macclurei,* n. sp., gonopod structure. (6) Left gonopod, dorsal aspect. (7) Left gonopod, mesal aspect. (8) Right gonopod, lateral aspect. Abbreviations: *a, b, c,* distal processes of telopodite; *d,* setiferous lobe terminating end of prostatic groove; *e,* femoral process; *f,* cingulum; *g,* concavity on dorsal side of coxa; *h,* sternal remnant. Drawings from topoparatype.

redescribed and illustrated by Jeekel (1955), is known from a number of localities in West Java.

2. *D. muralis* Cook, 1896(b). The surface of the metaterga is said to be areolated, the areas themselves light in color, separated by a dark network. Known only from the 2 syntypes, "Western Java," elevation about 1220 m (4000 ft).
3. *D. vestitus* Cook, 1896(b). Areolate like the preceding, but each area is provided with a median tubercle; even the dorsal processes are said to be tuberculate. "Gede, Western Java, 2745 m (9000 ft)."
4. *D. beccarii* (Silvestri, 1895). According to Silvestri's brief diagnosis, this species is red dorsally, with the legs and underparts ochraceus. A dorsal process is said to be present on segments 3 through 18, thus the distribution differs from all other known species. The type locality is Mt Singalang, in north-central Sumatra.
5. *D.* n. sp. (syn. *Doratodesmus armatus* Attems, 1930, nec Pocock, 1894). The female specimen reported under the name *armatus* by Attems (from the Kapala Tjurup waterfall, South Sumatra) clearly belongs, as noted by Jeekel (1955) ". . . to an unnamed species which may be easily distinguished from *armatus* by its much smaller size, different colour and the larger proportions and more vertical position of the middorsal processes of the metasomites."

Genus *Pauroplus* Chamberlin, 1945

6. *P. analdes* Chamberlin, 1945. This remarkable little species with only rudimentary dorsal processes on the last few segments is known only from the type-locality, Sumatra: Lompongs [Lampongs], Pedada Bay. This is at the south end of Sumatra (SW corner). A study of the gonopod structure is badly needed, as Chamberlin's drawings give no real impression of what they may be like.

Genus *Ascetophacus,* n. genus

7. *A. macclurei,* n. sp. Malaysia: Selangor State.
8. *A. cavernicola* (Sinclair, 1901), **n. comb.** This form was described from several cave collections (Gua Glaf, Raman District, and Gua Tana, Patani State) which I have been unable to locate on any maps available to me. [Patani River (Sungei) is located at lat. 5°39′ N, long. 100°27′ E (Ed.)].

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