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## Review of the dragon millipedes, genus *Desmoxytes* Chamberlin, 1923 (Diplopoda, Polydesmida, Paradoxosomatidae)

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The tribe Hylomini is formally suppressed, and all its constituents united in a single genus, *Desmoxytes* Chamberlin, 1923 (with *Hylomus* Cook & Loomis, 1924, and *Pteroxytes* Jeekel, 1980, as new subjective junior synonyms), of the tribe Orthomorphini. A key is given to the 19 currently known species, of which six are described as new (*D. acantherpestes*, *D. gigas*, *D. jeekeli*, *D. pterygota*, *D. rubra*, all from Thailand, and *D. hostilis*, from Vietnam), and one (*D. taurina* (Pocock, 1895), from Burma) is redescribed from cotypes. In addition, new records are given of *D. terae* (Jeekel, 1964) and *D. planata* (Pocock, 1895) (with *D. rastrituberus* (Zhang, 1986) as a new subjective junior synonym) in Thailand, and of *D. pilosa* (Attems, 1937) in Vietnam. The phylogenetic relationships between the species are analyzed by means of J.S. Farris' program Hennig86. The resulting cladogram is not very well substantiated but the analysis at least emphasizes that the correlation between gonopodal and somatic (in particular paratergal) characters is very poor.

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### INTRODUCTION

Very few millipedes have received English names. However, *Hylomus draco* Cook & Loomis, 1924b, struck its authors as being so extraordinary that it was not only placed in a new family, Hylomidae, but was also given the vernacular name "dragon millipede" (Cook & Loomis 1924a). Subsequent studies by several authors have revealed a handful of species related to *H. draco*, all to a greater or lesser extent sharing its peculiar somatic features. These species, all except one pantropical "tramp" species occurring in Southeast Asia, have hitherto been referred to a separate tribe, Hylomini ("dragon millipedes" in the wider sense), in the family Paradoxosomatidae (see Jeekel 1968, 1980; Hoffman 1980). The beautifully ornamented, often brightly coloured

"dragon millipedes" (see Fig. 80) form a distinctive and conspicuous element in the incredibly rich paradoxosomatid fauna of that region.

The previously described species of Hylomini mainly occur in Burma, China, and Vietnam. As is often the case, older materials show a conspicuous lacuna in Thailand, certainly because of the independence of this country from colonial European influence. However, Zoologisk Museum, Copenhagen, has amassed a considerable collection of Thai millipedes over the last decades, including several undescribed Hylomini. Incidentally, Zoologisk Museum also possesses male cotypes of a poorly known species. During the first author's stay in Copenhagen in November, 1992, the opportunity was therefore taken to review the entire group of dragon millipedes, as well as to present a cladistic analysis of interspecific relationships.

### Historical review

Jeekel (1980) included 3 genera and 11 species in the Hylomini: *Hylomus draco* Cook & Loomis, 1924 (type-species of *Hylomus* Cook & Loomis, 1924), *H. cervarius* (Attems, 1953), *H. spectabilis* (Attems, 1937), *H. longispinus* (Loksa, 1960), *H. pilosus* (Attems, 1937), *H. asper* (Attems, 1937), *Desmoxytes cervina* (Pocock, 1895), *D. planata* (Pocock, 1895), *D. delfae* (Jeekel, 1964), *D. taurina* (Pocock, 1895), and *Pteroxytes terae* (Jeekel, 1964) (type and only species of *Pteroxytes* Jeekel, 1980). Three further species, all from China, were described subsequent to Jeekel's review, but none of them within a valid genus sensu Jeekel (1980): *Centrodemus cornutus* Zhang & Li, 1982, *Pratinus minutuberculus* Zhang, 1986, and *Pratinus rastrituberus* Zhang, 1986.

In addition, H. Lohmander proposed a nomen nudum, *Pratinus lindbergi*, which was never described (see Lindberg, 1961). We have seen the pertinent specimens (Natural History Museum, Gothenburg, Sweden, courtesy of T. von Proschwitz), one ♂ and several ♀♀. Although the male lacks the gonopods this species is obviously not a member of the group treated here: its paraterga are very narrow, not at all wing-, antler- or spinelike; furthermore, there are no femoral modifications in the ♂, as found in the majority of *Desmoxytes* species.

When proposing and, later, substantiating this tribe, Jeekel (1968, 1980) noted its very clear affinities with the huge, Australasian tribe Orthomorphini and even stated that "very little new evidence is needed for the suppression of the Hylomini and the transfer of its members to the Orthomorphini" (1980: 652). With the new evidence at hand, we are now inclined to formally synonymize the Hylomini under the Orthomorphini. Furthermore, the nature of the character variation within the group leads us to merge all former Hylomini in a single genus, *Desmoxytes* by priority. This decision is in better agreement with the earlier ideas of Jeekel (1963, 1964) than with his more recent ones (Jeekel 1980).

### Material, acknowledgements, and methods

The bulk of the studied material belongs to the Zoological Museum Copenhagen (ZMUC). Additional specimens derive from the Zoological

Museum of the State University of Moscow (ZMUM, K. Mikhailov), the Senckenberg Museum, Frankfurt/M. (SMF, M. Grasshoff), and the Hungarian Natural History Museum, Budapest (HNMB, Z. Korsós), with which collections part of the ZMUC and ZMUM material has been shared. We thank the mentioned curators for making specimens available to us. We also thank Richard L. Hoffman (Virginia Museum of Natural History) for helpful comments to the manuscript. SG's stay in Copenhagen was made possible through a grant from the Danish Natural Science Research Council.

The phylogenetic analysis was made with the help of the computer program Hennig86 (Farris 1988).

## TAXONOMY

### Genus *Desmoxytes* Chamberlin, 1923

*Prionopeltis* Pocock, 1895: 828 (preoccupied).

*Desmoxytes* Chamberlin, 1923: 165.

*Hylomus* Cook & Loomis, 1924: 105 (syn. n.)

*Pratinus* Attems, 1937: 113 (replacement name for *Prionopeltis* Pocock, 1895, synonymized by Jeekel 1980).

*Ceylonemus* Chamberlin, 1941: 33 (synonymized by Jeekel 1980).

*Pteroxytes* Jeekel, 1980: 655 (syn. n.).

### Diagnosis

Medium-sized to large Orthomorphini (12-35 mm long), often brightly coloured. Paraterga very strongly to exceedingly well-developed, wing-, spine- or antler-shaped. Surface of metazona often more or less roughly granulate, more seldom smooth. Epiproct normal in most species but sometimes unusual in having hypertrophied setiferous tubercles near tip. Certain ♂ femora (5, 6, 7 and/or 9) very often inflated to humped ventrally. Gonopod usually suberect, seldom subfalcate, with postfemoral region invariably strongly demarcated by a sulcus or cingulum. Solenophore and solenomerite usually strongly reduced in size and condensed, more seldom *Orthomorpha*-like, i.e. relatively long and slender.

Type-species: *Desmoxytes coniger* Chamberlin, 1923 (junior synonym of *Prionopeltis planatus* Pocock, 1895).

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### Remarks

The combination of (mostly) conspicuously enlarged paraterga and (mostly) relatively condensed gonopod postfemoral region has hitherto served as the decisive distinguishing characters first of a separate family, Hylomidae (Cook & Loomis 1924a), and later of a separate tribe, Hylomini, of the Paradoxosomatidae (Jeekel 1968, 1980; Hoffman 1980). However, as noted above, Jeekel (1968, 1980) continuously felt that even tribal rank of Hylomini might prove to be overestimated, and that it perhaps ought to be merged in the tribe Orthomorphini. Indeed, with the new evidence presented below in the species descriptions and phylogenetic discussion, Jeekel's prediction appears to be fully borne out, and we herewith make the synonymy formal.

As in several other examples of species-rich genera, e.g. *Tylopus* (Paradoxosomatidae, Golovatch & Enghoff 1993), Hylomini seems to display "... no correlation between gonopod structure, shape of the paranota [=paraterga] and femoral modifications in the leg of the males" (Jeekel 1980: 657). More specifically, the obvious evolutionary trend from plesiomorphous, i.e. relatively simple, winglike paraterga (observed in *D. acantherpestes*, *D. cervina*, *D. delfae*, *D. planata*, *D. pterygota*, *D. rubra*, *D. taurina*, and *D. terae*), to apomorphic, antler-shaped (in *D. aspera*, *D. cervaria*, *D. cornuta*, *D. draco*, *D. hostilis*, *D. jeekeli*, *D. pilosa*, and *D. spectabilis*) or spiniform (in *D. gigas*, *D. longispina*, and *D. minutubercula*) ones does not correlate with the trend in gonopod morphology: from the more plesiomorphous, *Orthomorpha*-like gonopod conformation (especially well-expressed in *D. jeekeli*, to a somewhat lesser degree also in *D. spectabilis* and *D. cervaria*), via some intermediates (*D. draco*, *D. taurina*, *D. terae*, etc., in which the solenophore lies somewhat more distally than the base of the solenomerite), up to the clearly apomorphic pattern of a highly condensed gonopostfemoral region (*D. delfae*, *D. planata*, *D. pterygota*, *D. rubra*, etc.). Male femoral modifications vary from naught via inflations to hump-like protuberances and can likewise be stated to be scattered randomly amongst the species concerned. Table 1 shows this clearly. The mosaic-like distribution of character states will be further discussed under the

phylogenetic analysis. Suffice it here to say that we, unlike Jeekel (1980), have found it impossible to delimit genera and species-groups of dragon millipedes and therefore unite all its nominal genera within *Desmoxytes*, allocated in Orthomorphini.

Considering the lumping of "hylomine" genera proposed here, the status of *Centrodesmus* Pocock, 1894 deserves mention. This genus has enlarged paranota quite as conspicuous as the most extreme ones found in *Desmoxytes*. The genus was based on *C. typicus* Pocock, 1894, from Sumatra, of which the male is unknown; therefore the relationships of the genus remain unsettled. Only study of male topotypes can reveal whether *Centrodesmus* is a senior synonym of *Desmoxytes*.

### A key to the species of *Desmoxytes*

1. All metaterga with three transverse rows of numerous setae, one in front of and the other two behind the middorsal sulcus (Figs. 49-50) ..... 2
- All metaterga (but not collum) with fewer (usually two) transverse rows of less numerous setae ..... 3
2. Coloration castaneous brown. Body ca. 35 mm long. Head considerably narrower than collum, paraterga of collum neither particularly elevated above dorsum nor spiniform (Fig. 49) ..... *D. gigas*
- Coloration pallid. Body 25-27 mm long. Head somewhat wider than collum, particularly due to almost vertical and spiniform paraterga of the latter ..... *D. minutubercula*
3. Postcollar metaterga either (?fully) devoid of traceable rows of setae/tubercles or only with a single, caudal traceable row of such tubercles ..... 4
- Postcollar metaterga always with two traceable rows of setae/tubercles/spines, one in front of and the other behind middorsal sulcus (e.g. Figs. 2, 12, 30, 33, 55, 71) ..... 5
4. Metaterga not spinose, setation/tuberculation pattern untraceable, only paraterga spiniform. Epiproct with unusually hypertrophied setiferous tubercles near tip. Male femur 7 with a big distoventral protuberance. Gonopod lamina medialis subequal in height to remaining solenophore ..... *D. longispina*
- Metatergal setation/tuberculation pattern traceable at least as a caudal row of two huge lateral and two small paramedian spines (Figs. 21-23). Epiproct normal. Legs unmodified. Gonopod lamina medialis considerably higher than remaining solenophore (Figs. 26-28, m) ..... *D. acantherpestes*
5. Metatergal surface smooth, more or less shining, at best quite finely shagreened (Figs. 30, 33, 42, 69, 71). Axial line often traceable on metaterga (Figs. 42, 71). Paraterga largely wing-shaped, almost never antler-like. Epiproct always normal ..... 6
- Metatergal surface more rough, granulate/tuberculate/spinulate (e.g. Figs. 12, 13, 55, 56, 66, 67). Axial line almost entirely missing. Paraterga mostly antler-shaped

- (c.g. Figs. 12, 13, 66, 67), less often wing-shaped. Epiproct normal or with hypertrophied setiferous tubercles near tip ..... 11
6. Metaterga with a caudal row of very distinct spines. Metatergal surface a little more coarsely shagreened and almost dull. Paraterga either wing- or antler-shaped ..... 7
- Metaterga not spinose, at best with poorly developed knobs. Metatergal surface more delicately shagreened, shining. Paraterga always wing-shaped ..... 8
7. Paraterga antler-shaped. Caudal edge of metaterga with 3(4)+3(4) spines. Sternal lamina between male coxae 4 simple, low, rounded. Legs unmodified ..... *D. aspera*
- Paraterga cariniform (Figs. 70-72). Caudal edge of metaterga with 2+2 spines (Fig. 71). Sternal lamina between male coxae 4 with a prominent, rounded, caudal protuberance (Fig. 73). Male femora 5 and 6 distinctly inflated ..... *D. planata*
8. Coloration of living animals red, in alcohol mostly pinkish. Paraterga relatively little elevated above dorsum (Figs. 31-32). Male femora 5 and 6 humped (Figs. 34-35) ..... 9
- Colour brown to piceous, never pink. Paraterga much projecting higher above dorsum (Figs. 42, 43, 62, 53). Male femora 5-6 either unmodified or only moderately inflated (Fig. 45) ..... 10
9. Metatergal tubercles: 1+1 anterior, 2+2 posterior. Axial line traceable (Figs. 30, 33). Sternal lamina between male coxae 4 roundly subtriangular (figs. 34-35). Gonopod lamina medialis more strongly produced mesally than dorsally (Figs. 37-40, *m*) ..... *D. rubra*
- Metatergal tubercles: 2+2 anterior, 2+2 posterior. Axial line untraceable. Sternal lamina between male coxae 4 roundly subtrapeziform. Gonopod lamina medialis (*m*) more strongly produced dorsally than mesally ..... *D. delfae*
10. No particular colour pattern. Paraterga relatively high and narrow (Figs. 42-43). Sternal lamina between male coxae 4 relatively high (Fig. 44). Gonopod solenophore relatively complex (Figs. 46-48) ..... *D. pterygota*
- Colour pattern: ground colour piceous, contrasting with whitish/yellowish patches at base, at edges, and just below paraterga (Figs. 62-63). Paraterga wider and lower (Figs. 62-63). Sternal lamina between male coxae 4 relatively low. Gonopod solenophore simpler (Figs. 46-48) ..... *D. terae*
11. Paraterga wing-shaped (Figs. 54-56). Male femora 5 and 6 inflated (Fig. 58) ..... 12
- Paraterga antler-shaped (e.g., Figs. 2, 12, 66, 67). Male femora 5 and 6 either unmodified or strongly humped (Figs. 6, 16, 17) ..... 13
12. Metatergal tubercles very poorly developed, 1+1 anterior, 2+2 posterior. Paraterga surpassing rear tergal contour already from midbody somites. Sternal lamina between male coxae 4 about twice as high as broad ..... *D. cervina*
- Metatergal tubercles: 2+2 anterior, 3+3 posterior, posterior tubercles relatively high (Figs. 55-56). Paraterga surpassing rear tergal contour only on a few posteriormost somites. Sternal lamina between male coxae 4 much lower, slightly transverse (Fig. 57) ... *D. taurina*
13. 3+3 or more spine-shaped posterior tubercles at least on some midbody metaterga (e.g. Figs. 2, 66) ..... 14
- No more than 2+2, sometimes spiniform posterior metatergal tubercles (e.g. Fig. 12) ..... 16
14. Epiproct normal. Male femora 6, 7, and 9 ventrally humped ..... *D. cervaria*
- Epiproct with hypertrophied setiferous tubercles near tip. Legs either unmodified or only male femur 6 humped ..... 15
15. Colour red-pinkish. 4+4 spiniform posterior tubercles at least on some midbody metaterga (Fig. 66). Metazona finely and sparsely pilose. Sternal lamina between male coxae 4 divided into two independent cones (Fig. 68). Legs unmodified. Gonopod suberect, postfemoral region strongly condensed, solenomerite short (Fig. 69) ..... *D. pilosa*
- Colour pallid to brownish, never pinkish. No more than 3+3 posterior metatergal tubercles (Fig. 2). Metazona not pilose. Sternal lamina between male coxae 4 bifid, with a conspicuous caudal protuberance (Fig. 5). Gonopod subfalcate, postfemoral region far less condensed, *Orthomorpha*-like, solenomerite relatively long (Figs. 8-10) ..... *D. jeekeli*
16. Larger, ca. 35 mm long. Epiproct with hypertrophied setiferous tubercles near tip. 1+1 poorly developed posterior metatergal tubercles. Only male femur 7 inflated. Gonopod postfemoral region relatively less condensed, solenomerite relatively long ..... *D. spectabilis*
- Smaller, 25 mm long. Epiproct normal. 2+2 posterior metatergal spines. Modified male femora always ventrally humped. Gonopod postfemoral region strongly condensed, solenomerite short ..... 17
17. Antennae relatively short, stout (Fig. 11). Paraterga short, stout, setose (Figs. 11-13). Subanal scale caudally rather deeply emarginate (Fig. 14). Male femora 6 and 7 humped (Figs. 16-17). Gonopod solenophore terminally pointed (Figs. 19-20) ..... *D. hostilis*
- Antennae extremely long and slender. Paraterga very long and high, naked. Subanal scale caudally straight or only slightly concave. Either only male femur 6 or male femora 5-7 humped. Gonopod solenophore terminally blunt ..... 18
18. Colour purple to pink. Paraterga mostly 4-branched. Sternal lamina between male coxae 4 fungiform. Male femora 5-7 humped ..... *D. draco*
- Colour pallid. Paraterga at best 3-branched. Sternal lamina between male coxae 4 very deeply notched. Only male femur 6 humped ..... *D. cornuta*

Below follow descriptions of the new species, followed by comments on previously described species of which we have seen material, and a catalogue of the remaining species.

***Desmoxytes jeekeli* sp. n.**

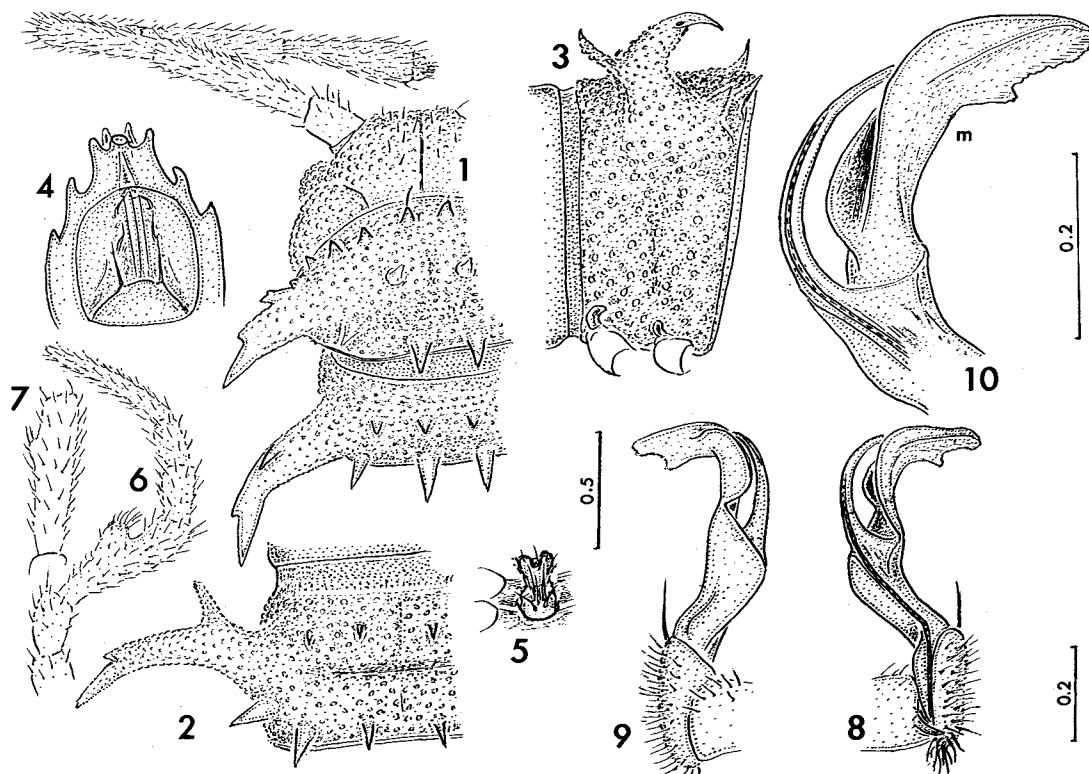
Figs. 1-10.

Material studied: HOLOTYPE ♂ Thailand, Chiang Mai Province, Doi Suthep, 1400-1500 m, 2.x.1981; Zool. Mus. Copenhagen leg. (ZMUC). - PARATYPES: 1 ♂, 1 ♀, 1 juv.

tubercles at least on 2, 66) ..... 14  
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 7, and 9 ventrally ..... *D. cervaria*  
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 Fig. 11). Paraterga .....  
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 caudally straight or .....  
 male femur 6 or male .....  
 enophore terminally .....  
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 mostly 4-branched.  
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Figs. 1-10: *Desmoxytes jeekeli* sp. n., ♂ paratype. - 1: anterior body end, dorsal. - 2-3: somite 10, dorsal (2) and lateral (3). - 4: telson, ventral. - 5: sternal lamina between coxae 4, subventral. - 6: leg 6. - 7: femur 7. - 8-9: left gonopod, mesal (8) and lateral (9). - 10: distal part of gonopod, mesal. - Scales in mm. - m: lamina medialis.

(ZMUC), data as holotype. - 2 ♂ (ZMUC), 1 ♂ (SMF), same locality, 1000 m, 17.v.1958; B. Degerbøl leg. - 1 ♂, 2 ♂ (ZMUC), same locality, 1100 m, 22.vi.1958; B. Degerbøl leg. - 1 ♂ (ZMUC), same locality, 30.x.1958; B. Degerbøl leg. - 1 ♂ (HNMB), same locality, 31.x.1958; B. Degerbøl leg. - 1 ♂ (ZMUC), same locality, 1000 m, 3.xi.1958; B. Degerbøl leg. - 1 ♂, 1 ♀ (ZMUM), same locality, 1000 m, forest along stream, 5.xi.1958; B. Degerbøl leg. - 1 ♂ (ZMUC), same locality, 6.xi.1958; B. Degerbøl leg. - 1 ♂ (ZMUC), same locality, 1300 m, evergreen valley forest, 10.ii.1959; B. Degerbøl leg. - 1 ♂ (ZMUC), Doi Suthep National Park, Doi Pui → Chang Khian, 1400 m, 17.ix.1981; Zool. Mus. Copenhagen leg. - 1 juv. (ZMUC), Chieng Mai Province, Doi Chiang Dao, limestone area, 1300 m, 18.x.1981; Zool. Mus. Copenhagen leg.

Derivatio nominis: Named after the prominent Dutch specialist in Diplopoda, Dr. C. A. W. Jeekel.

#### Diagnosis

Paraterga antler-like (Fig. 2). Gonopods not condensed (Figs. 8-10). Male femora 6 and 7 modified. Similar in these respects to *cervaria* but

differing in unmodified male femur 9 and modified epiproct (Fig. 4).

#### Description

Length 15-16 (♂)/ 18-20 mm (♀), width of mid-body pro- and metazona 1.0-1.2 and 2.8-3.0 (♂)/ 1.4-1.6 and 3.0-3.5 mm (♀). Colour in alcohol entirely pallid to rusty or castaneous brown; often most of antennomere 7, sometimes also distal parts of antennomere 6 (and 5) dark brown to piceous; proximal podomeres, venter and paraterga invariably pallid, sometimes yellowish. Anterior body part sometimes darker.

*Head* rather sparsely setose, much narrower than collum. Epicranial suture distinct. Antennae very long, in situ usually surpassing somite 4 (♂) or 3 (♀), rarely somewhat shorter, but invariably slender, only antennomere 6 relatively clavate (Fig. 1).

*Collum* a little narrower than subequal somites 2 and 4, and a bit narrower than somite 3; with three transverse rows of setiferous cones/spines: 3(4)+3(4), 1+1, and 1+1 (Fig. 1).

*Body* parallel-sided on somites 5-17, onward quite abruptly tapering. Metaterga with a pattern of two rows of similar cones/spines, on somites 2-5 always 2+2 and 2+2, on subsequent metaterga always 2+2 and 3+3 (Figs. 1-2). Axial line practically missing, sometimes barely traceable on metaterga as very thin brownish stripe. Paraterga antler-shaped, prominently ( $\sigma$ ) to less prominently elevated above, or almost level to, dorsum ( $\varphi$ ), directed more laterad than dorsad, strictly spiniform and directed caudally only on somite 19, bispinose on fore edges, tips directed increasingly caudally, surpassing rear tergal contour only on somites 17-19. Surface invariably dull, prozona very finely shagreened, metazona relatively coarsely granulate both dorsally (Figs. 1-3) and laterally (Fig. 3), sterna delicately microgranulate. Suture between pro- and metazona deep, distinctly beaded. Ozopores invisible from above, lying laterally just at base of ultimate incision of paraterga. Sulcus on metaterga poorly expressed on somites 3 and 4, fully developed and quite deep on somites 5-18, missing on somite 19. Pleurosternal carinae absent.

*Epiproct* short, unusual in having several prominent setiferous cones both at and removed from tip (Fig. 4). *Subanal scale* subsemicircular, with setae at caudal edge practically devoid of supporting knobs (Fig. 4).

*Sterna* sparsely setose, between  $\sigma$  coxae 4 with a strongly bilobed, sparsely setose lamina carrying a big, caudal, setiferous swelling (Fig. 5).

*Legs* not particularly long, relatively stout,  $\sigma$  femur 6 always distinctly humped on ventral side, femur 7 often a little inflated, seldom with an inconspicuous ventral protuberance (Figs. 6-7).

*Gonopods* (Figs. 8-10) subfalcate, femorite relatively short, subequal in length to solenophore and solenomerite, postfemoral part far from condensed, tip of solenophoral lamina medialis (*m*) serrulate.

***Desmoxytes hostilis* sp. n.**

Figs. 11-20.

Material studied: HOLOTYPE  $\sigma$  North Vietnam, Vinh Phu

Province, Tamdao, 1200 m, primary forest, 12-22.iv.1986; S. Golovatch, L. Medvedev et al. leg. (ZMUM). -PARATYPES: 3  $\sigma$  (ZMUM), 1  $\sigma$ , 1  $\varphi$  (ZMUC), 1  $\sigma$  (SMF), data as holotype.

Derivatio nominis: Named after its very spiny, unfriendly, even hostile appearance.

**Diagnosis**

Paraterga antler-like, although relatively short (Fig. 12). Gonopods somewhat condensed (Figs. 18-20). Male femora 6 and 7 modified. Similar in these respects to *draco* but differing in unmodified male femur 5 and much shorter paraterga.

**Description**

Length ca. 14 ( $\sigma$ )/16-18 mm ( $\varphi$ ), width of mid-body pro- and metazona 0.8-0.9 and 1.6 mm ( $\sigma$ )/1.2-1.4 and 1.9-2.1 mm ( $\varphi$ ). Colour rusty brown; most of antennomere 7, sometimes also antennomere 6 and frons dark brown; proximal podomeres, venter and paraterga yellowish-brown.

*Head* densely setose, a bit narrower than collum and subequal in width to subequal somites 2 and 4; epicranial suture distinct. Antennae relatively short and stout (Fig. 11), in situ reaching to end ( $\sigma$ ) or midlength ( $\varphi$ ) of somite 3.

*Collum* with bispinose paraterga and in addition 3 transverse rows of setiferous spines: 4+4, 1+1, and 2+2 (Fig. 11).

*Body* parallel-sided on somites 5-17, onward gently and gradually tapering; somites 2 and 4 a little narrower than somite 5. Metaterga with two rows of similar cones/spines: 2+2 shorter and 2+2 longer, (not counting paratergal spines, Figs. 11-12). Axial line practically missing. Paraterga coniform, tri- to quadrispinose, setiferous, well elevated above dorsum (a little less so in  $\varphi$ ), directed dorsolaterad until somite 17, onward increasingly caudolaterad, on somites 5-18 each with a conspicuous caudal knob opposing a similar knob on caudolateral metatergal spine. Surface invariably dull, prozona finely shagreened, metaterga relatively coarsely spinulate/tuberculate/granulate (Figs. 11-13), metazonal sides coarsely granulate (Fig. 13), sterna delicately granulate. Suture between pro- and metazona deep, distinctly beaded. Ozopores invisible from above, lying laterally just at base of three apical spines/cones crowning paraterga. Sulcus on metaterga evident and rather deep on somites 5-18, shallow on somite 19. Pleurosternal carinae absent.

st, 12-22.iv.1986; S. M). - PARATYPES: (F), data as holotype. ry spiny, unfriendly,

relatively short condensed (Figs. modified. Similar in ng in unmodified paraterga.

), width of mid- and 1.6 mm (♂)/ our rusty brown; mes also anten- proximal podom- wish-brown.

rrower than col- lequal somites 2 . Antennae rela- situ reaching to site 3.

rga and in addi- sional spines: 4+4,

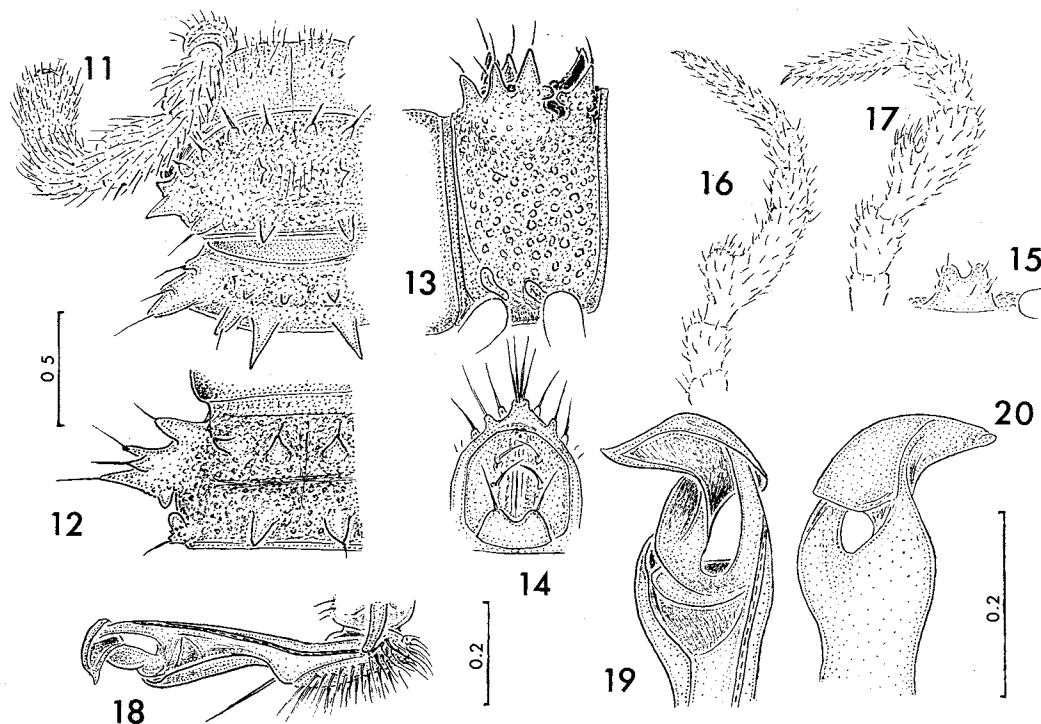
es 5-17, onward omites 2 and 4 a ataterga with two shorter and 2+2 spines, Figs. 11-

sing. Paraterga setigerous, well less so in ♀), e 17, onward in-

nites 5-18 each opposing a simi- al spine. Surface agreed, meta-

late/tuberculate/ tal sides coarsely ately granulate. a deep, distinctly m above, lying cal spines/cones

etaterga evident 18, shallow on absent.



Figs. 11-20: *Desmoxytes hostilis* sp. n., ♂ paratype. - 11: anterior body end, dorsal. - 12-13: somite 10, dorsal (12) and lateral (13). - 14: telson, ventral. - 15: sternal lamina between coxae 4, ventral. - 16-17: legs 6 (16) and 7 (17). - 18: right gonopod, mesal. - 19-20: distal part of gonopod, mesal (19) and lateral (20). - Scales in mm.

*Epiproct* short, with 3+3 setiferous knobs near tip (Fig. 14). *Subanal scale* more or less deeply emarginate at caudal edge (Fig. 14).

*Sterna* sparsely setose, with a bilobed lamina between ♂ coxae 4 (Fig. 15).

*Legs* not very long, relatively stout, ♂ femora 6 and 7 conspicuously inflated, each with a ventral hump (Figs. 16-17); the hump seldom bifid.

*Gonopods* (Figs. 18-20) suberect, postfemoral part relatively condensed, solenophore characteristically tortiled, apically pointed.

#### *Desmoxytes acantherpestes* sp. n.

Figs. 21-28.

Material studied: HOLOTYPE ♂ Thailand, western coast of Siam Gulf, Hua Hin, 8.viii.1979; B. Petersen leg. (ZMUC).

Derivatio nominis: Named in commemoration of the similarly armed, giant Paleozoic millipede genus *Acantherpestes*.

#### Diagnosis

Paraterga winglike. Gonopods strongly condensed. Male femora unarmed.

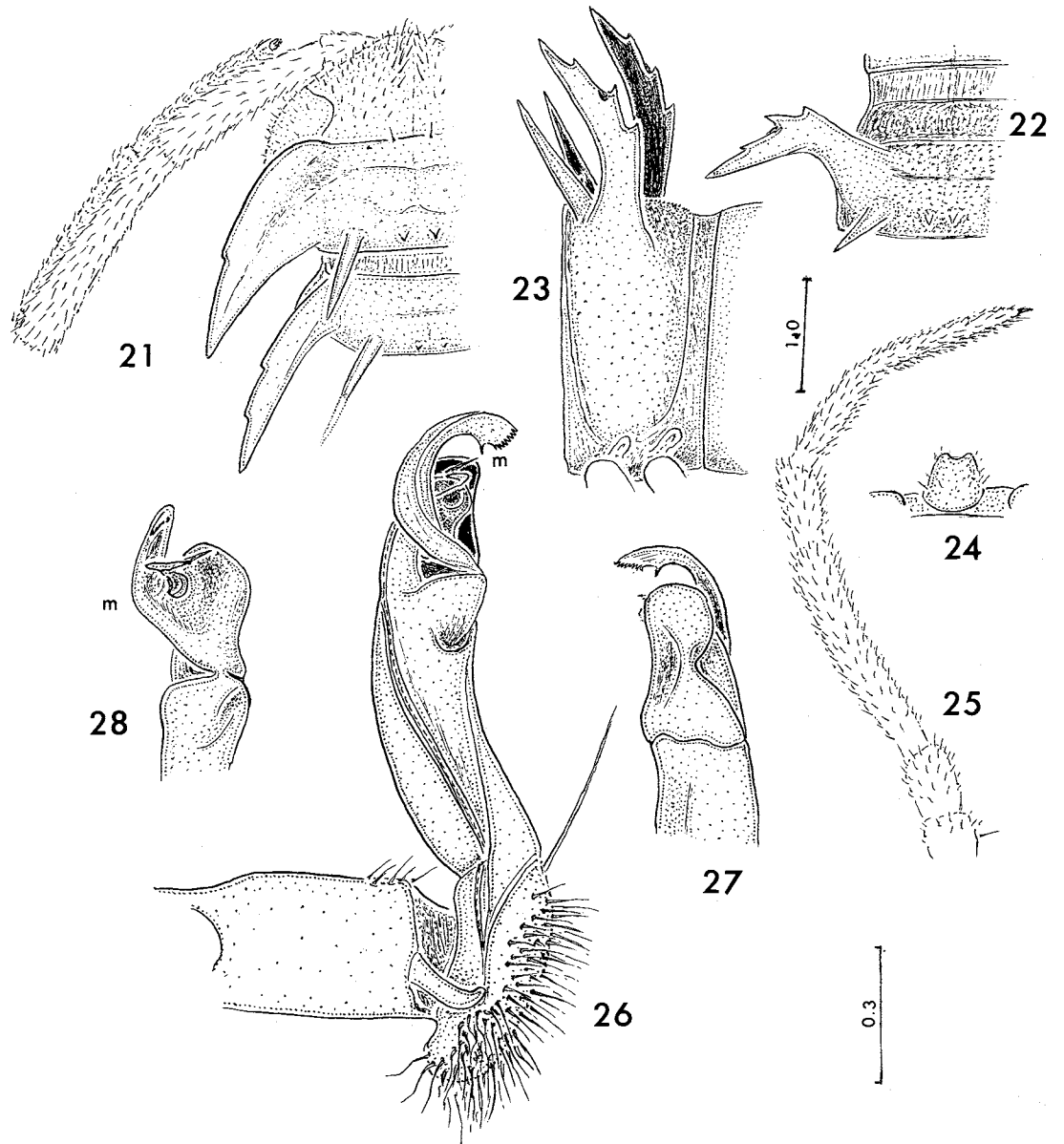
#### Description (♂)

Length ca. 32 mm, width of midbody pro- and metazona 2.0 and 3.7 mm. Colour pale brownish; most of antennomere 7 dark brown; sides below paraterga and sulcus region on metaterga brown; venter, proximal podomeres, paraterga and tergal spines yellowish.

*Head* modestly setose, considerably narrower than collum. Epicranial suture distinct. Antennae exceedingly long and slender, in situ surpassing somite 5 (Fig. 21).

*Collum* subequal in width to somite 5, significantly broader than narrowest somite 3, a little broader than somite 2 and a bit broader than somite 4; with two transverse rows of setae (2+2 and 1+1) without supporting knobs, and 2+2 spines caudally, lateral spines huge (Fig. 21).

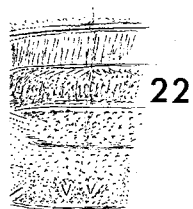
*Body* parallel-sided on somites 5-16, onward gently and gradually tapering. Metaterga with a row of barely traceable ?1+?1 setae (insertions) and 2+2 spines, lateral spines huge (Figs. 21-22).



Figs. 21-28: *Desmoxytes acantherpestes* sp. n., ♂ holotype. - 21: anterior body end, dorsal. - 22-23: somite 10, dorsal (22) and lateral (23). - 24: sternal lamina between coxae 4, ventral. - 25: leg 6. - 26: left gonopod, mesal. - 27-28: distal part of gonopod, lateral (27) and ventromesal (28). - Scales in mm. - m: lamina medialis.

Axial line practically missing. Paraterga wing-shaped, extremely long and well elevated above dorsum, directed dorsolaterad until somite 18, much shorter and directed practically caudad on somite 19, on midbody somites not protruding

caudally beyond tergal rear margin, each with 2-3 distinct incisions along frontal edge (Figs. 22-23). Surface relatively smooth, prozona and sterna very finely shagreened and slightly shining, metaterga relatively coarsely shagreened and practically



24



25

dull, metazonital sides coarsely shagreened to microgranulate and dull, suture dividing pro- and metazona particularly smooth (Figs. 21-23). Ozopores small, hardly visible from above, lying dorso-laterally just at base of penultimate incision. Sulcus on metaterga evident and rather deep on somites 5-16, poorly developed on somite 17 and especially 18, entirely missing on somite 19. Pleurosternal carinae absent.

*Epiproct* short, with a pair of big setiferous knobs rather removed from straight and narrow tip. *Subanal scale* subsemicircular, with caudal setae almost devoid of supporting knobs.

*Sterna* rather delicately and densely setose, with a simple, sparsely setose, roundly subtrapeziform, apically bilobed lamina between ♂ coxae 4 (Fig. 24).

*Legs* extremely long and slender, entirely unmodified (Fig. 25).

*Gonopods* (Figs. 26-28) suberect, postfemoral part rather condensed, solenophore characteristically tortiled, lamina medialis (*m*) subfalcate and apically fringed, higher than lamina lateralis.

#### *Desmoxytes rubra* sp. n.

Figs. 29-40.

Material studied: HOLOTYPE ♂ Thailand, Satun Province, Thale Ban National Park (6°42'N, 100°10'E), lowland rainforest, <400 m, on vegetation & under bark, 20.x.1991; M. Andersen, O. Martin & N. Scharff leg. (ZMUC). - PARATYPES: 6 ♂, 3 ♀ (ZMUC), 1 ♂, 1 ♀ (ZMUM), 1 ♂ (SMF), 1 ♀ (HNMB), data as holotype. - 1 ♂ (ZMUC), Yala Province, Bang Lang National Park (6°04'N, 101°11'E), lowland rainforest, <400 m, 20.x.1991; M. Andersen, O. Martin & N. Scharff leg. (ZMUC).

Derivatio nominis: Named after its bright red colour *in vivo*.

#### Diagnosis

Paraterga wing-like. Gonopods strongly condensed. Male femora 5 and 6 modified. Similar in these respects to *pterygota*, *cervina*, *planata*, and *delfae*; particularly similar to *delfae* by virtue of its bright red colouration and spineless metaterga but differing as specified in couplet 9 of the key.

#### Description

Length 18-20 (♂)/ 22-24 mm (♀), width of mid-body pro- and metazona 1.3-1.4 and 2.1-2.4 (♂)/ 1.8-2.0 and 2.5-2.9 mm (♀). Colour in alcohol usually bright pinkish, especially on rear halves of

metaterga, often faded to entirely yellowish with brown patches below paraterga; only antennae (except tip) dark brown to piceous; distal podomeres pale brownish to grey. Live colour bright red (M. Andersen, O. Martin & N. Scharff, personal communication).

*Head* very modestly setose only on frons, labrum and genae, elsewhere bare, a little narrower than or almost equal to collum. Epicranial suture distinct. Antennae exceedingly long and slender, *in situ* well surpassing somite 5 (♂) or 4 (♀) (Fig. 29).

*Collum* a little narrower than somite 2; at least with two transverse rows of setae, 3+3 and 1+1 (insertions) without supporting knobs; a third, caudal row, if present, barely traceable as insertion points.

*Body* parallel-sided on somites 5-16, anteriorly and posteriorly gently and gradually tapering. Metaterga with a row of barely traceable 1+1 setae on very poorly developed knobs, and 2+2 very small tubercles (Figs. 29, 30, 33). Axial line traceable only on rear halves of metaterga. Paraterga wing-shaped, rather well (♂, Fig. 32) to slightly (♀, Fig. 31) elevated above dorsum, directed mainly laterad until somite 18, much shorter and directed practically caudad on somite 19, always somewhat protruding caudally beyond tergal rear margin, each with 2-3 distinct incisions along frontal edge (Figs. 29-33). Surface smooth, mostly polished; prozona extremely finely shagreened, dorsally slightly shining, ventrally distinctly shining like sterna; metaterga finely shagreened, shining, on rear halves very faintly rugulose; metazonital sides a little more coarsely shagreened and dull; suture dividing pro- and metazona smooth (Fig. 29-33). Ozopores small, visible from above, lying dorso-laterally just at base of ultimate incision in a groove. Sulcus on metaterga evident and rather deep on somites 3-18, missing on somite 19. Pleurosternal carinae absent.

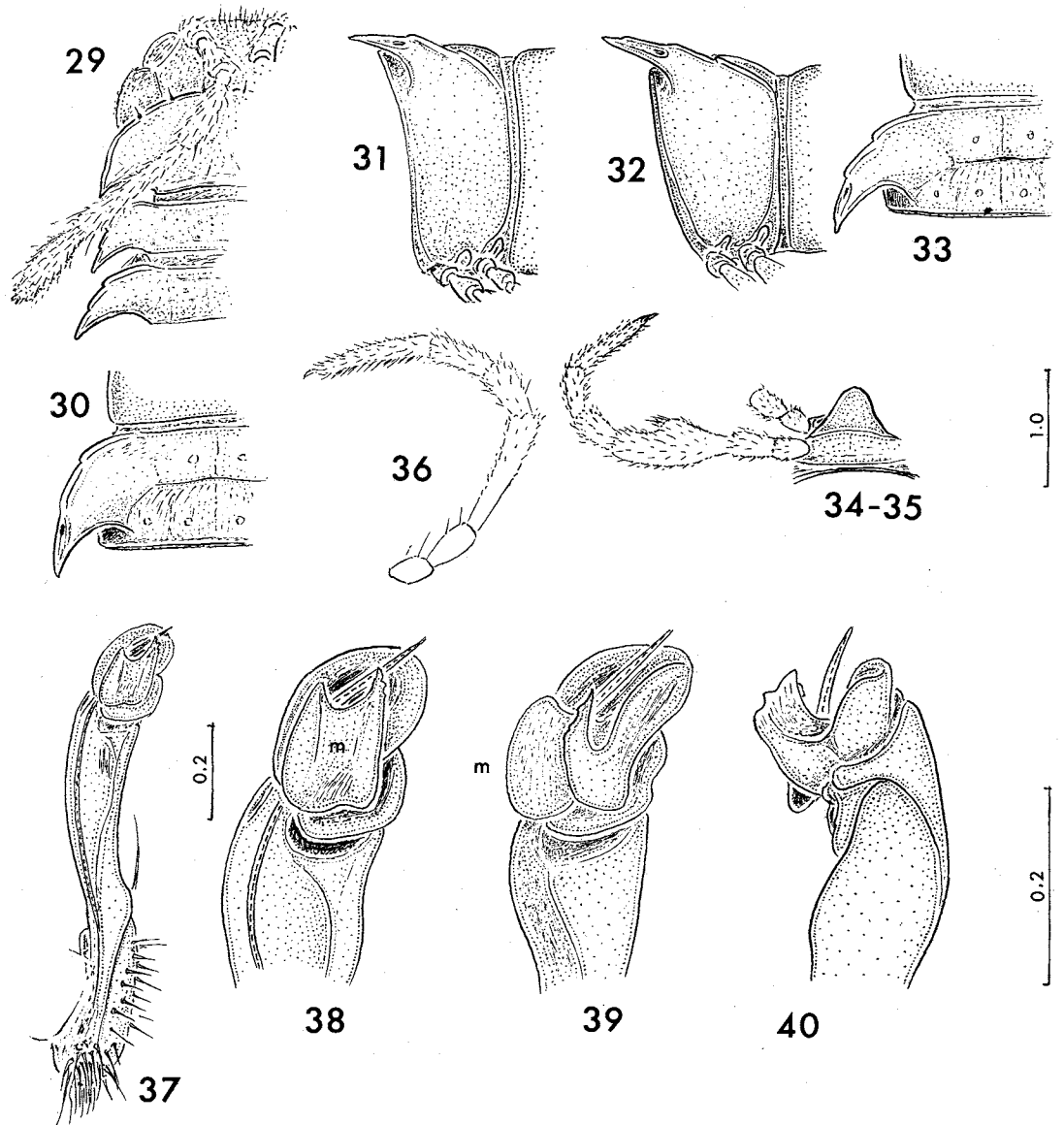
*Epiproct* short, with a pair of small, setiferous, lateral knobs quite close to straight and very narrow tip. *Subanal scale* roundly subtriangular, with caudal setae almost devoid of supporting knobs.

*Sterna* rather delicately and sparsely setose, with a simple, sparsely setose, roundly subtrapeziform lamina between ♂ coxae 4 (Fig. 34).

*Legs* extremely long and slender (Fig. 36), ♂

Fig. 10, dorsal (22) and distal part of gonopod,

Fig. 22, dorsal (22) and distal part of gonopod, n, each with 2-3 setae (Figs. 22-23). a and sterna very shining, metaterga and practically



Figs. 29-40: *Desmoxytes rubra* sp. n., ♀ (29-31, 36) and ♂ paratype (32-35, 37-40). - 29: anterior body end, dorsal. - 30-33: somite 10, dorsal (30, 33) and lateral (31-32). - 34-35: sternal lamina between coxae 4 and leg 5, ventrocaudal. - 36: last leg. - 37: left gonopod, submesal. - 38-40: distal part of gonopod, mesal (38), ventromesal (39), and ventrolateral (40). - Scales in mm. - m: lamina medialis.

femora 5 and 6 subequally distinctly inflated and humped ventrally (Fig. 35).

*Gonopods* (Figs. 37-40) suberect, postfemoral part highly condensed, solenophore characteristically tortiled, lamina medialis (*m*) apically bilobed and distinctly protruding mesally.

#### Note

This bright red species was observed climbing the vegetation in considerable numbers (M. Andersen, O. Martin & N. Scharff, personal communication). This strongly suggests that the bright colour is aposematic. The similarly coloured, and

apparently closely related *D. delfae* was likewise collected "crawling on low foliage" (Jeekel 1964).

***Desmoxytes pterygota* sp. n.**

Figs. 41-48.

Material studied: HOLOTYPE ♂ Thailand, western coast, in forest at big waterfalls south of Kapoe, 15.xi.1990; M. Andersen & A.R. Rasmussen leg. (ZMUC). - PARATYPES: 2 ♂ (ZMUC), 1 ♂ (ZMUM), data as holotype.

Derivatio nominis: Named after its wing-like paraterga.

**Diagnosis**

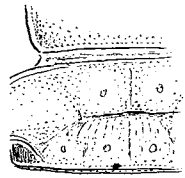
Paraterga wing-like. Gonopods strongly condensed. Male femora 5 and 6 modified. Similar in these respects to *cervina*, *planata*, *rubra* and *delfae*, differing from *cervina* by smooth surface and from the three others by much larger paraterga.

**Description (♂)**

Length 20-22 mm, width of midbody pro- and metazona 1.5-1.6 and 2.6-2.7 mm. Colour pale brownish; antennae (except tip) and head always piceous to blackish-brown, sometimes several anteriormost metaterga dark brown, forming a transition to paler rest of body; proximal podomeres, venter and paraterga yellowish.

*Head* modestly setose, considerably narrower than collum. Epicranial suture distinct. Antennae very long and slender, in situ reaching beyond somite 4 (Fig. 41).

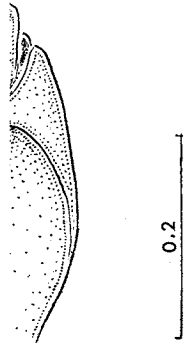
*Collum* a bit broader than narrowest somite 3, but a bit narrower than subequal somites 2 and 4; devoid of knobs, at least with two transverse rows



33

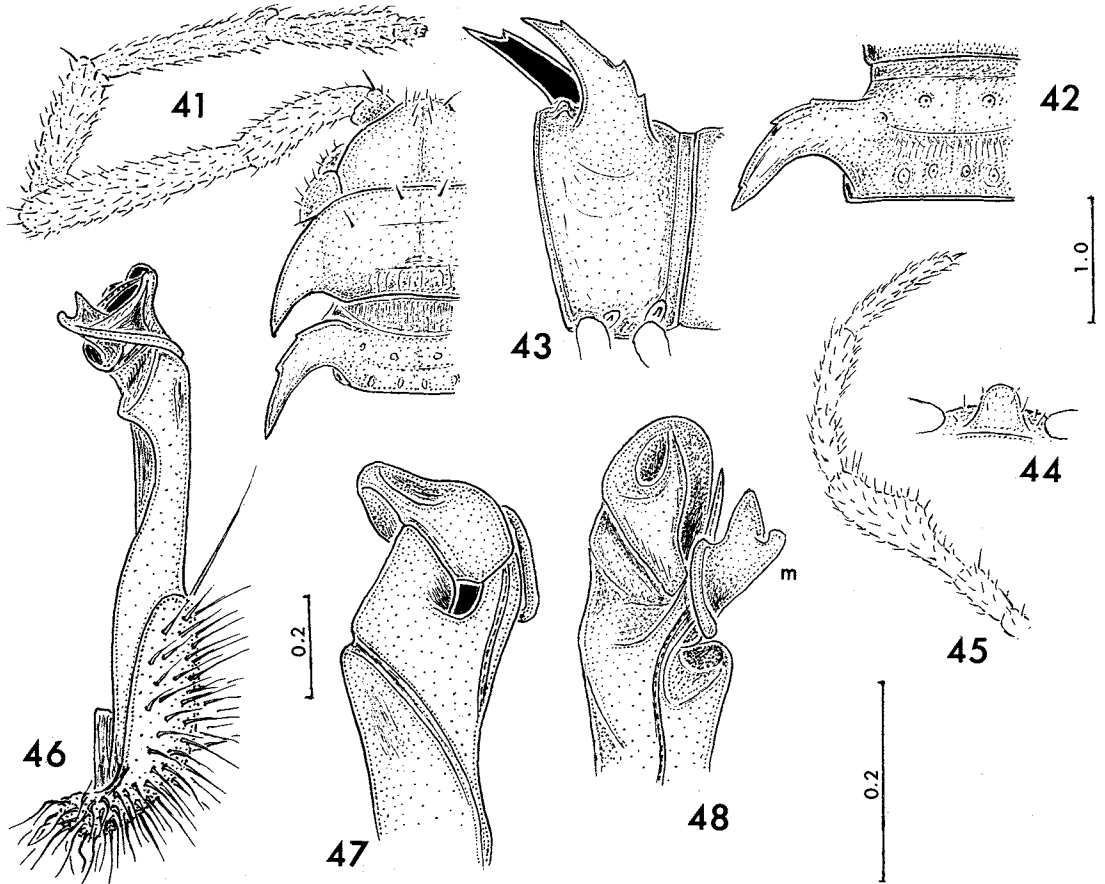


35



36: last leg. - 37: left  
- Scales in mm. - m:

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ly coloured, and



Figs. 41-48: *Desmoxytes pterygota* sp. n., ♂ paratype. - 41: anterior body end, dorsal. - 42-43: somite 10, dorsal (42) and lateral (43). - 44: sternal lamina between coxae 4, ventrocaudal. - 45: leg 5. - 46: left gonopod, submesal. - 47-48: distal part of gonopod, sublateral (47) and dorsal (48). - Scales in mm. - m: lamina medialis.

of setae: 3+3 and 1+1; a third, caudalmost row, if present, barely traceable (Fig. 41).

*Body* parallel-sided on somites 5-16, onward gently and gradually tapering. Metaterga with two rows of little cones: 2+2 mostly setiferous and shorter, and 2+2 a bit bigger (Figs. 41-42). Axial line practically missing. Paraterga wing-shaped, well elevated above dorsum, directed dorsolaterad until somite 17, onward practically caudolaterad, invariably protruding caudally beyond tergal rear margin, each with 2-3 distinct incisions along frontal edge (Figs. 41-43). Surface relatively smooth, prozona and sterna very finely shagreened and slightly shining, metaterga relatively coarsely shagreened and shining, metazonital sides coarsely shagreened to microgranulate and dull, suture dividing pro- and metazona especially shining and smooth (Figs. 42-43). Ozopores barely visible from above, lying dorsolaterally just at base of penultimate incision. Sulcus on metaterga evident and rather deep on somites 3-18, missing on somite 19. Pleurosternal carinae absent.

*Epiproct* rather short, with a pair of small setiferous knobs well removed from a slightly concave tip bearing a pair of apical papillae. *Subanal scale* subsemicircular, with caudal setae almost devoid of supporting knobs.

*Sterna* rather delicately and sparsely setose, with a simple, barely setose, roundly subtrapeziform lamina between ♂ coxae 4 (Fig. 44).

*Legs* extremely long and slender, ♂ femora 5 and 6 equally conspicuously inflated, each with an indistinct ventral protuberance (Fig. 45).

*Gonopods* (Figs. 46-48) suberect, postfemoral part highly condensed, solenophore characteristically tortiled, lamina medialis (*m*) apically bilobed.

#### *Desmoxytes gigas* sp. n.

Figs. 49-52.

Material studied: HOLOTYPE ♀ Thailand, Krabi Province, road between Krabi and Phuket, 10 km south of Krabi (8°09'N, 98°50'E), lowland rainforest, <200 m, 13.x.1991; M. Andersen, O. Martin & N. Scharff leg. (ZMUC).

Derivatio nominis: Named after its relatively big size.

#### *Diagnosis*

Although the ♂ is not known, this species can be distinguished from all congeners except *minu-*

*tubercula* by the combination of big size, subspiniiform paraterga, and three rows of tubercles on all metaterga. From *minutubercula* it differs as specified in couplet 2 of the key.

#### *Description* (♀)

Length ca. 35 mm, width of midbody pro- and metazona 2.8 and 6.4 mm. Colour in alcohol castaneous brown, with a paramedian pair of relatively wide, pale brownish, obscure, dorsal stripes accompanied by a pair of brown stripes level and somewhat below paraterga; lower parts of sides and venter contrastingly whitish-yellow; antennae (except tip) dark brown, head and most of collum brown; legs very pale brown (proximal podomeres) to brownish (distal podomeres), like tergal spines and paraterga.

*Head* modestly and delicately setose, considerably narrower than collum. Epicranial suture distinct. Antennae exceedingly long and slender, in situ well surpassing somite 4 (Fig. 49).

*Collum* somewhat narrower than subequal somites 2 and 4, a bit more so than somite 3; with three rows of 5+5, 5+5 and 3+3 setiferous tubercles (Fig. 49).

*Body* parallel-sided on somites 5-16, onward gently and gradually tapering. Metaterga with three transverse rows of setiferous tubercles, on metaterga 2 and 3 4+4, 3+3, and 3+3 tubercles, from somites 4 and 5 already 5+5, 3+3, and 3(4)+3(4), number of tubercles further increasing toward telson to 6+6, 4+4, and 5(6)+5(6), not counting the pair of particularly long caudolateral spines (Figs. 50-51); these spines reduced in size toward somite 17, wanting on somites 18 and 19. Axial line practically wanting. Paraterga subspiniiform, rather well elevated above dorsum, directed mainly laterad until somite 17, much shorter and directed practically caudad on somites 18 and 19, only on a few caudalmost somites somewhat protruding caudally beyond tergal rear margin, each with 2-3 distinct incisions along frontal edge (Figs. 49-51). Surface entirely dull; prozona finely shagreened; metazona delicately granulate/spiculate dorsally, more delicately so on sides below paraterga and on sterna; suture dividing pro- and metazona smooth (Figs. 49-51). Ozopores small, invisible from above, lying laterally just at base of ultimate incision. Sulcus on metaterga poorly de-

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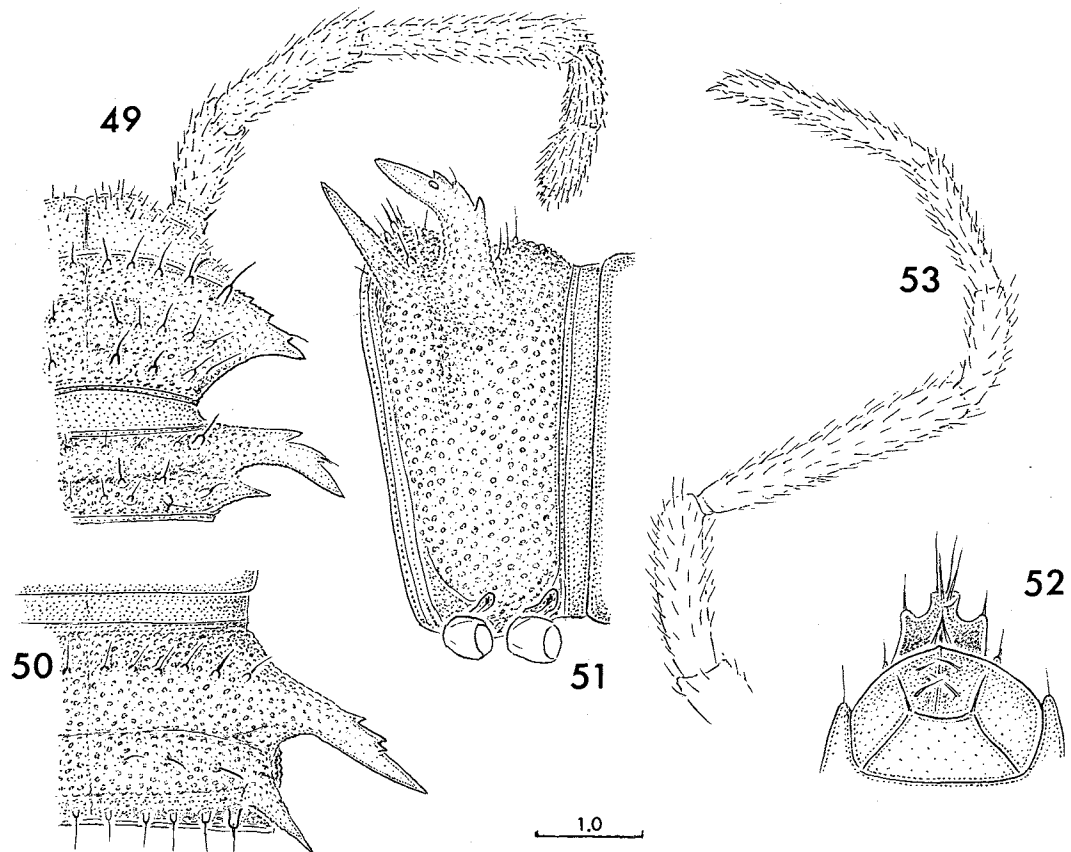
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Ozopores small,  
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terga poorly de-



Figs. 49-53: *Desmoxytes gigas* sp. n., ♀ holotype. - 49: anterior body end, dorsal. - 50-51: somite 10, dorsal (50) and lateral (51). - 52: telson, ventral. - 53: leg of somite 12. - Scale in mm.

veloped on somites 2-4, fully evident and rather  
deep on somites 5-18, missing on somite 19.  
Pleurosternal carinae absent.

*Epipect* short, with a pair of prominent, seti-  
ferous, lateral knobs quite close to straight tip (Fig.  
52). *Subanalscale* caudally slightly concave, setae  
practically without supporting knobs (Fig. 52).

*Sterna* rather delicately and sparsely setose.  
Legs extremely long and slender (Fig. 53).

#### *Desmoxytes taurina* (Pocock, 1895)

Figs. 54-61.

*Prionopeltis taurinus* Pocock, 1895: 830. - Burma: Rangoon;  
Pegu (Taikkyii and Palon).

*Pratinus taurinus*: Jeekel 1964: 63; Jeekel 1968: 61.

*Desmoxytes taurina*: Jeekel 1980: 655.

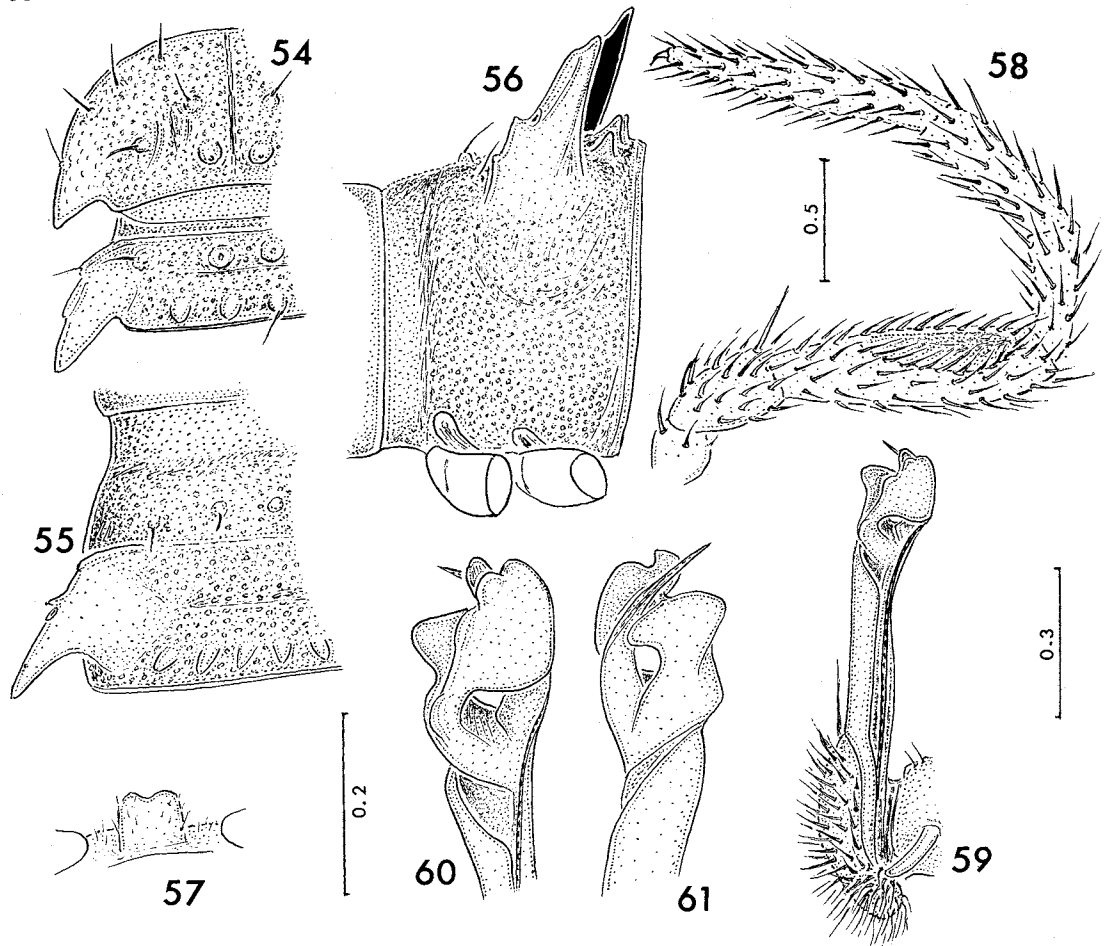
Material studied: 2 ♂ cotypes "*Prionopeltis taurinus* Poc.  
ex. typ., Palon Birma Fea" (ZMUC).

#### *Descriptive remarks* (♂)

The two males at hand are in very poor condition,  
one very incomplete, with gonopod tips broken off;  
the other better preserved, almost complete, on an  
insect pin; both males are in alcohol. The short  
redescription below finally allows to properly  
allocate this species, which has never been  
revised since its quite insufficient original  
description (Pocock 1895).

Length ca. 15 mm, width of midbody pro- and  
metazona 1.2 and 2.0 mm. Colour, originally  
stated as being castaneous brown (?), is now rather  
rusty brown, with a greenish tinge perhaps due to  
metallic oxides from the pin.

*Head* rather densely setose, epicranial suture  
well-developed, antennae broken off, but prob-  
ably very long.

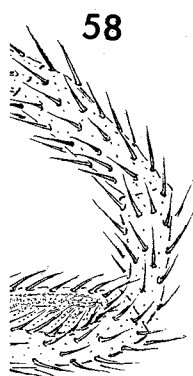


Figs. 54-61: *Desmoxytes taurina* (Pocock, 1895), ♂ cotype. - 54: collum and somite 2, dorsal. - 55-56: somite 9, dorsal (55) and lateral (56). - 57: sternal lamina between coxae 4, ventrocaudal. - 58: leg 5. - 59: right gonopod, mesal. - 60-61: distal part of gonopod, mesal (60) and lateral (61). - Scales in mm.

*Collum* subequal in width to subequal somites 2-4, but a little narrower than somite 5, with three transverse rows of setiferous tubercles/cones: 3(?4)+3(?4), 1+1, and 2+2 (Fig. 54).

*Body* parallel-sided on somites 5-17, onward gently and gradually tapering. Metaterga 2-6 with two rows of cones/spines: 2+2 very short and 2+2 longer. Metatergum 8 with 2+2 and 3+2, metatergum 9 (Fig. 55) with 2+2 and 3+3 similar tubercles/cones, metatergum 10 again with 2+2 and 2+2, pattern gradually changing back to 2+2 and 3+3 at least toward somites 17-19. Axial line practically missing. Paraterga wing-shaped, well elevated above dorsum, directed strongly dorso-

laterad until somite 17, onward directed increasingly caudolaterad, with 2-3 well-expressed incisions at fore edge (Figs. 55-56). Surface invariably dull, prozona finely shagreened, metazona relatively coarsely shagreened to microgranulate throughout (Figs. 54-56), sterna delicately microgranulate. Suture between pro- and metazona deep, distinctly beaded. Ozopores barely visible from above, lying dorsolaterally just at base of penultimate incision in a groove. Sulcus on metaterga very poorly expressed on somites 4 and 18, somewhat more evident and relatively deep in between, missing on somite 19. Pleurosternal carinae absent.



*Epiproct* short, with a broadly truncate tip and a pair of lateral preterminal incisions, both very small, inconspicuous, lying very close to tip. *Subanal scale* subtrapeziform, with setiferous knobs at caudal edge barely visible.

*Sterna* rather densely setose, with a slightly concave, slightly setose, subquadrate lamina between ♂ coxae 4 (Fig. 57).

*Legs* very long, slender, ♂ femora 5 and 6 conspicuously inflated (Fig. 58).

*Gonopods* (Figs. 59-61) suberect, postfemoral part relatively condensed, solenophore characteristically tortiled, distoventrally with a bulge, lamina medialis (*m*) apically somewhat trilobate.

#### *Desmoxytes terae* (Jeekel, 1964)

Figs. 62-65.

*Pratinus terae* Jeekel 1964: 69; Jeekel 1968: 51. - Malaya: Perlis, Kaki Bukit, near Kampong Wang Tongga.

*Pteroxytes terae*: Jeekel 1980: 655.

Material examined: 1 ♂ Thailand, Satun Province, Thale Ban National Park (6°42'N, 100°10'E), in logs, litter, under stones, 8.xi.1990; M. Andersen & A. R. Rasmussen leg. (ZMUC).

#### *Descriptive remarks* (♂)

Very little can be added to the exhaustive original description given by Jeekel (1964). The drawings presented here are mainly included to illustrate the highly characteristic colour pattern, with a piceous background colour contrasting against whitish (not yellowish) patches at base and along the edges of the paraterga (Figs. 62-63). The lobe between the ♂ coxae 4 is very low, semicircular in outline, almost naked, with two pores on the caudal side (Fig. 64). The gonopod tip (Fig. 65) is practically identical to the one depicted by Jeekel (1964) for his Malayan specimens, showing the pattern of a still not extremely condensed postfemoral part. The only male at hand is 2.1 and 3.8 mm in width on midbody pro- and metazona, respectively.

#### *Desmoxytes pilosa* (Attems, 1937)

Figs. 66-69.

*Centrodesmus pilosus* Attems 1937: 124; Attems 1938: 238.

- Central Vietnam, Col des Nuages, Phanrang.

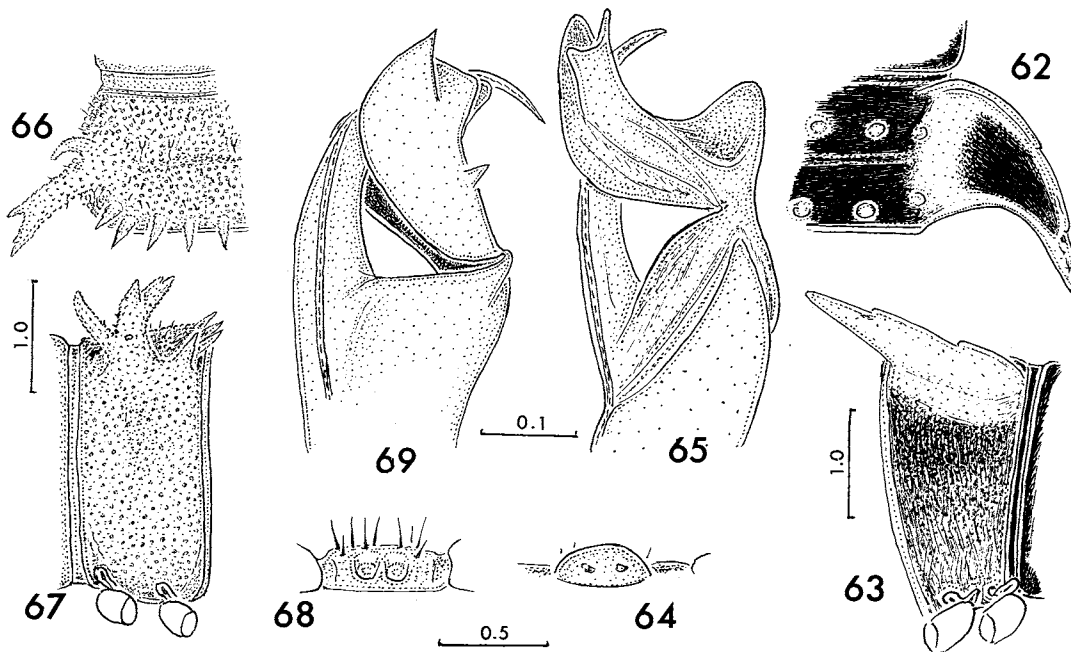
*Pratinus pilosus*: Jeekel 1964: 63; Jeekel 1968: 61.

*Hylomus pilosus*: Jeekel 1980: 658.

59

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50-61: distal part of

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Figs. 62-65: *Desmoxytes terae* (Jeekel, 1964), ♂. - 62-63: somite 10, dorsal (62) and lateral (63). - 64: sternal lamina between coxae 4, ventrocaudal. - 65: distal part of left gonopod, submesal. - 66-69: *Desmoxytes pilosa* (Attems, 1937), ♂. - 66-67: somite 10, dorsal (66) and lateral (67). - 68: sternal lamina between coxae 4, ventrocaudal. - 69: distal part of left gonopod, mesal. - Scales in mm.

Material examined: 1 ♂, 1 ♀ Central Vietnam, Daklak Province, ca. 40 km NW of Buon Ma Thuot, Buon Ya Wam, 450 m, 2-3.v.1986; S. Golovatch, L. Medvedev et al. leg. (ZMUM).

#### *Descriptive remarks*

This species was described quite satisfactorily (Attems 1937, 1938) from several specimens deriving from more or less the same area. The only discrepancy is that our material is rather pinkish, perhaps more strongly faded than Attems' bright red specimens. The few drawings presented here are included mainly to illustrate the highly conspicuous tergal sculpture and position of the ozopores ventrally close to base of the paratergum (Figs. 66-67); the sternal lamina between the ♂ coxae 4 composed of two independent cones (Fig. 68), and the gonopod distal part displays quite a condensed pattern of the postfemoral region (Fig. 69).

#### *Desmoxytes planata* (Pocock, 1895)

Figs. 70-75.

*Prionopeltis planatus* Pocock 1895: 829. - Andamans: Great Cocos Island.

*Desmoxytes coniger* Chamberlin 1923: 165. - in soil about plants from Java.

*Euphyodesmus greeni* Attems 1936: 213. - Ceylon: Paradenyia.

*Euphyodesmus (Ceylonemus) vector* Chamberlin 1941: 33. - Honolulu, Hawaii, in soil about plants from Ceylon.

*Pratinus planatus*: Jeekel 1964: 63; Jeekel 1968: 61. - Mauriès 1980: 161. - Seychelles: Mahé, Silhouette, Praslin.

*Pratinus greeni*: Jeekel 1964: 63.

*Pratinus vector*: Jeekel 1964: 63.

*Desmoxytes planata*: Jeekel 1980: 652. - Golovatch & Korsós, 1992: 25. - Seychelles: Mahé, Silhouette, Praslin.

*Pratinus rastrituberus* Zhang, 1986: 255 (syn. n.). - South China, Yunnan Prov., Luxi County, Mangshi.

Material studied: 2 ♂, 6 ♀ Northern Thailand, Chiang Mai Province, Chiang Mai, 300 m, in garden, 26.ix.1981; Zool. Mus. Copenhagen leg. (ZMUC). - 1 ♂, 1 ♀, same data, 2.x.1981; Zool. Mus. Copenhagen leg. (ZMUC). - 1 ♀ Chiang Mai Province, Doi Inthanon National Park, Siripum, 1200-1300 m, 7.x.1981; Zool. Mus. Copenhagen leg. (ZMUC). - 1 ♀ Chiang Mai Province, Fang Horticultural Station, 550-600 m, 21.x.1981; Zool. Mus. Copenhagen leg. (ZMUC).

#### *Descriptive remarks*

The live colour of the above specimens was purplish pink (H.E. personal observations), alcohol has changed it drastically into brown to dark brown, with both antennae and head sometimes piceous. In this connection, Zhang's (1986) de-

scription of *Pratinus rastrituberus* fully agrees with the studied material of *D. planata*, as well as with Jeekel's (1980) redescription. The few drawings here, prepared from material deriving from the Seychelles (s. Golovatch & Korsós 1992), are included to facilitate recognition of the species and to substantiate the new synonymy. None of the characters mentioned in Zhang's description of *Pratinus rastrituberus* lies outside the individual variation range of *D. planata*: the metazona are rather finely shagreened, but considerably more coarsely so than the prozona (Figs. 70-71), the sternal lamina between the ♂ coxae 4 is characteristically expanded caudad into a prominent swelling (Fig. 73), and the gonopod tip is highly condensed, typical for the species in question (Fig. 75). We therefore formally synonymize *Pratinus rastrituberus* Zhang, 1986, with *Desmoxytes planata* (Pocock, 1895).

#### *Desmoxytes* sp.

Material examined: 1 ♂ (badly damaged), Thailand, Phuket Province, Phuket, Ton Sai Waterfalls (8°01'N, 98°25'E), forest, <200 m, 12.x.1991; M. Andersen, O. Martin & N. Scharff leg. (ZMUC).

#### *Remarks*

The only specimen at hand being badly damaged, with most somites/paraterga broken and legs largely missing, we refrain from describing it at the moment until more material becomes available. Both superficially and on the basis of gonopod conformation, it strongly resembles *D. rubra* sp. n. However, judged both from the details of gonopod structure and from the considerably more elevated paraterga, it seems to represent still another, yet undescribed form.

#### *Desmoxytes aspera* (Attems, 1937) (comb. n.)

*Centrodesmus asper* Attems 1937: 125; Attems 1938: 240. - Central Vietnam, Bana, Col des Nuages.

*Pratinus asper*: Jeekel 1964: 63; Jeekel 1968: 61.

*Hylomus asper*: Jeekel 1980: 658.

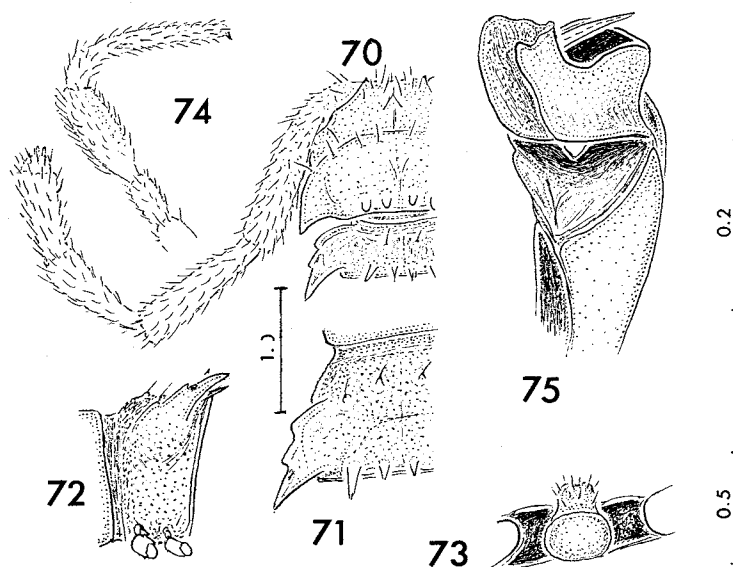
#### *Desmoxytes cervaria* (Attems, 1953) (comb. n.)

*Centrodesmus cervarius* Attems 1953: 175. - North Vietnam, Fan-Si-Pan, Chapa.

*Pratinus cervarius*: Jeekel 1964: 63; Jeekel 1968: 61.

*Hylomus cervarius*: Jeekel 1980: 657.

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Figs. 70-75: *Desmoxyles planata* (Pocock, 1895), ♀ from Silhouette (70-72) and ♂ from Mahé (73-75). - 70: anterior body end, dorsal. - 71-72: somite 10, dorsal (71) and lateral (72). - 73: sternal lamina between coxae 4, ventrocaudal. - 74: leg 6. - 75: left gonopod, submesal. - Scales in mm.

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Attems 1938: 240.-  
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1968: 61.

953) (comb. n.)  
75. - North Vietnam,  
kel 1968: 61.

***Desmoxyles cervina* (Pocock, 1895)**

*Prionopeltis cervinus* Pocock 1895: 831. - Burma, Tenasserim: Malewoon; southern Tenasserim.

*Pratinus cervinus*: Jeekel 1964: 63; Jeekel 1968: 61.

*Desmoxyles cervina*: Jeekel 1980: 654.

***Desmoxyles cornutus* (Zhang & Li, 1982)**

(comb. n.)

*Centrodesmus cornutus* Zhang & Li, 1982: 37. - China, Guangxi.

***Desmoxyles delfae* (Jeekel, 1964)**

*Pratinus delfae* Jeekel 1964: 66; Jeekel 1968: 51. - Thailand: Bukit Besar; Bukit Besar, Nawnchila.

*Desmoxyles delfae*: Jeekel 1980: 654.

***Desmoxyles draco* (Cook & Loomis, 1924)**

(comb. n.)

*Hylomus draco* Cook & Loomis 1924a: 106; Cook & Loomis

1924b: 50; Jeekel 1980: 656. - Central China, Kiang-si Prov., Lu Shan Distr., Kuling, south of Kiukiang.

***Desmoxyles longispina* (Loksa, 1960) (comb. n.)**

*Centrodesmus longispinus* Loksa, 1960: 135. - South China, Central Kuloui, Pien-Ja.

*Hylomus longispinus*: Jeekel 1980: 658.

***Desmoxyles minutubercula* (Zhang, 1986)**

(comb. n.)

*Pratinus minutuberculus* Zhang, 1986: 253. - China, Guanxi Zhuang Autonomous Region, Tianlin County.

***Desmoxyles spectabilis* (Attems, 1937)**

(comb. n.)

*Centrodesmus spectabilis* Attems 1937: 124; Attems 1938: 238. - Central Vietnam, Bana.

*Pratinus spectabilis*: Jeekel 1964: 62; Jeekel 1968: 61.

*Hylomus spectabilis*: Jeekel 1980: 658.

MONOPHYLY AND RELATIONSHIPS  
OF *DESMOXYTES*

As will be clear from the remarks under the generic heading, the definition of *Desmoxytes* is somewhat fragile: Although several characters (paraterga, gonopods, ♂ femora) show striking modifications within the group, the distribution of apomorphic states is pronouncedly mosaic-like (Table 1) such that neither of these characters can easily be selected as an autapomorphy at the generic level.

The best candidate for a generic autapomorphy seems to be that the paraterga of all species are at least somewhat pointed and laterally and/or dorsally expanded in comparison with the normal state seen within Paradoxosomatidae: rather narrow, keel-like paraterga, projecting only modestly laterad. Although this apomorphy may appear weak (several other paradoxosomatid genera have paraterga approaching the shape seen in the least modified *Desmoxytes*), no other characters counterindicate monophyly of the genus.

As also mentioned under the generic heading, *Desmoxytes* belongs to the tribe Orthomorphiini. However, its phylogenetic relationships with the other members of this tribe (eight genera according to Hoffman 1980) remains an open question for the time being.

RELATIONSHIPS BETWEEN SPECIES  
OF *DESMOXYTES*

**Procedure of analysis**

Being confident, in spite of what is stated above, that *Desmoxytes* constitutes a monophyletic group, we have attempted a phylogenetic analysis of its species. Fortunately, the descriptions of most of the species we have not been able to study ourselves are sufficiently detailed to allow extraction of character states.

A total of 24 characters were therefore scored for each species. Multistate characters were converted to binary ones by character splitting. The defining autapomorphy of *Desmoxytes* (at least somewhat pointed and expanded paraterga) was not included in the analysis, and nor were autapomorphies of single species, such as the relatively short antennae of *hostilis*, the dense metatergal pilosity of *pilosus*, and the humped ♂ femur 9 of *cervaria*. Table 2 shows the analyzed characters. The outgroup ("ancestor") was coded with character states known to be prevalent in other Paradoxosomatidae. For two characters, 1: colour, and 12 (lamina between ♂ coxae IV) we could not decide the state in the outgroup and therefore ran all analyses with each of the possible four combinations. The characters matrix is shown in Table 3.

Table 1. Gonopod types, paratergal and femoral modifications in *Desmoxytes* (excluding *gigas*, of which the ♂ is unknown). Modifications on ♂ femora 5-7 and 9 are indicated as + = inflated, ++ = humped. Species abbreviations, see Table 3.

GONOPODS	PARATERGA		
	Wing-like	Antler-like	Spine-like
<i>Orthomopha</i> -like	-	CEA 6++, 7++, 9++ JEE 6++, 7+ SPE 7+	-
Somewhat condensed	TER TAU 5+, 6+	DRA 5++, 6++, 7++ HOS 6++, 7++	MIN 6++
Strongly condensed	ACA PTE 5+, 6+ CEI 5+, 6+ PLA 5+, 6+ DEL 5++, 6++ RUB 5++, 6++	ASP PIL COR 6++	LON 6?, 7++

## N SPECIES

Table 2. The characters used for phylogenetic analysis, and their coding for the analysis. Multistate characters have been coded as two binary characters.

<p><b>Char. 1-2</b> Colour 00. pallid 01. red-pink 10. brown-piceous</p> <p><b>Char. 3</b> Body length 0. medium (12-25 mm) 1. larger (&gt;25 mm)</p> <p><b>Char. 4</b> Metatergal setal tubercles 0. 2 rows 1. 3 rows</p> <p><b>Char. 5-6</b> Anterior row of metatergal tubercles 00. 2+2 10. 1+1 01. 3+3 or more</p> <p><b>Char. 7-8</b> Posterior row of metatergal tubercles 00. 2+2 10. 1+1 01. 3+3 or more</p> <p><b>Char. 9</b> Metatergal surface texture 0. smooth 1. granulate-tuberculate-spinulate</p> <p><b>Char. 10</b> Suture between pro- and metazona 0. normal 1. distinctly beaded</p> <p><b>Char. 11-12</b> Shape of paraterga 00. wing 01. spine 10. antler</p>	<p><b>Char. 13</b> Shape of epiproct 0. normal 1. subapical setiferous tubercles greatly hypertrophied</p> <p><b>Char. 14</b> Subanal scale 0. subsemicircular-subtrapeziform 1. caudal margin more or less distinctly concave</p> <p><b>Char. 15-16</b> Shape of lamina between <math>\sigma</math> cxIV 00. two separate knobs 01. a subquadrate-subtrapeziform lobe 11. as 1, but with strong caudal protuberance 10. complex configuration</p> <p><b>Char. 17-18</b> Modification of <math>\sigma</math> feV 00. none 01. inflation 11. hump</p> <p><b>Char. 19-20</b> Modification of <math>\sigma</math> feVI 00. none 01. inflation 11. hump</p> <p><b>Char. 21-22</b> Modification of <math>\sigma</math> feVII 00. none 01. inflation 11. hump</p> <p><b>Char. 23-24</b> Gonopod tibiotarsus and solenomerite 00. <i>Orthomorpha</i>-like: both relatively long 01. both considerably shortened but not fully condensed 11. extremely condensed, much shorter than femorite.</p>
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As the matrix shows, there are two species of which many characters are unknown: *gigas*, because the  $\sigma$  has not been described, and *longispina* because the original description is incomplete. The analyses were run both with all species and with these two species excluded.

Characters 10 (suture) and 14 (subanal scale) are unknown in two species in addition to *gigas* and *longispina*. Therefore, analysis were run both with all characters and without these two characters.

All in all, 16 combinations were thus tried. All were analyzed with Hennig86 (Farris 1988), a computer program for finding most parsimonious trees, using the mhennig\*;bb\* commands. Numbers of trees obtained varied from 6-105. A strict consensus tree (Hennig86's nelsen command) was obtained for each of the 16 combinations. In addition to unweighted analysis, Hennig86's successive weighting procedure (Farris 1988) was applied. This yielded 1-43 trees, and strict consensus trees were obtained.

Table 3. The character matrix used for the computerized phylogenetic analysis. Abbreviations used in the text and in Table 1 are given after each species name. Ancestors 1-4 were used as outgroups, one at a time.

Character no.	1				2		
	0	12345	67890	12345	67890	1234	5
ANCESTOR1	0	00000	00000	00000	00000	00000	0000
ANCESTOR2	0	00000	00000	00000	00000	10000	0000
ANCESTOR3	0	10000	00000	00000	00000	00000	0000
ANCESTOR4	0	10000	00000	00000	10000	00000	0000
<i>acanthopestes</i> ACA	0	00101	00000	00000	10001	0011	
<i>aspera</i> ASP	0	10000	1010?	100?	10000	0011	
<i>cervaria</i> CEA	0	10000	00110	10000	00011	1100	
<i>cervina</i> CEI	0	10101	00010	00000	10101	0011	
<i>cornuta</i> COR	0	00000	0001?	100?	10001	0011	
<i>delfae</i> DEL	0	01000	00000	00000	11111	0011	
<i>draco</i> DRA	0	01000	00010	10011	01111	1101	
<i>gigas</i> GIG	0	10110	10110	0100?	?????	????	
<i>hostilis</i> HOS	0	10000	00011	10010	10011	1101	
<i>jeekeli</i> JEE	0	10000	00111	10101	10011	0100	
<i>longispina</i> LON	0	000??	???	011?	000??	1111	
<i>minutubercula</i> MIN	0	00110	1011?	010?	00011	0001	
<i>pilosa</i> PIL	0	01000	00110	10100	00000	0011	
<i>planata</i> PLA	0	01000	00000	00001	10101	0011	
<i>pterygota</i> PTE	0	00000	00000	00000	10101	0011	
<i>rubra</i> RUB	0	01001	00000	00000	11111	0011	
<i>spectabilis</i> SPE	0	10100	01011	10100	00000	0100	
<i>taurina</i> TAU	0	10000	00111	00000	10101	0001	
<i>terae</i> TER	0	10100	00000	00000	10000	0001	

### Result of the analysis

A total of 22 different clades was suggested in these 32 consensus trees.

The successive weighting procedure (Table 4) clearly divided the characters into good, mediocre and bad ones. Unanimously "good" characters (weight 10 throughout) are:

CHAR. 4. Metaternal setal tubercles (0. 2 rows, 1. 3 rows).

CHAR. 7. Second pair of metaternal tubercles in posterior row (0. present, 1. absent).

CHAR. 12. (see below, under char. 11-12)

CHAR. 14. Subanal scale (0. subsemicircular-subtrapeziform, 1. caudal margin more or less distinctly concave).

"Mediocre" characters (weights always 4 or variable from 3 to 10) include:

CHAR. 9. Metaternal surface texture (0. smooth, 1. granulate-tuberculate-spinulate).

CHAR. 11-12. Shape of paraterga (00. wing, 01. spine, 10. antler). (Char. 12 alone is "good").

CHAR. 18. Modification of ♂ feV (0. none, 1. inflation or hump).

Table 4. Weights ascribed to the characters by Hennig86's successive weighting procedure (character 0 = dummy character). Key to matrix designations: 1, 2, 3, 4: Ancestor 1, 2, 3 or 4 used as outgroup.

a = all species, b = without *gigas* and *longispina*.  
x = all characters, y = without char. 10 and 14.

Matrix	Character no.																							
	1										2													
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
1ax	0	1	0	10	0	2	10	0	4	1	4	10	1	10	1	1	2	4	2	2	3	4	1	3
2ax	0	1	0	10	0	2	10	0	4	1	4	10	1	10	1	2	2	4	2	2	3	4	1	3
3ax	0	1	0	10	0	2	10	0	4	1	4	10	1	10	1	1	2	4	2	2	3	4	1	3
4ax	0	1	0	10	0	2	10	0	4	1	4	10	1	10	1	2	2	4	2	2	3	4	1	3
1bx	0	1	0	10	0	0	10	0	4	1	4	10	2	10	0	1	2	4	2	2	10	10	2	1
2bx	0	1	0	10	0	0	10	0	4	1	4	10	2	10	0	2	2	4	2	2	10	10	2	1
3bx	1	1	0	10	0	0	10	0	4	0	4	10	2	10	1	1	2	4	4	4	2	3	1	1
4bx	1	1	0	10	0	0	10	0	4	0	4	10	2	10	1	2	2	4	4	4	2	3	1	1
1ay	1	1	1	10	0	2	10	0	4	-	4	10	1	-	1	1	2	4	2	2	1	4	1	3
2ay	1	1	1	10	0	2	10	0	4	-	4	10	1	-	1	2	2	4	2	2	1	4	1	3
3ay	1	1	1	10	0	2	10	0	4	-	4	10	1	-	1	1	2	4	2	2	1	4	1	3
4ay	1	1	1	10	0	2	10	0	4	-	4	10	1	-	1	2	2	4	2	2	1	4	1	3
1by	1	1	0	10	0	0	10	0	4	-	4	10	2	-	0	1	2	4	2	2	2	10	2	3
2by	1	1	0	10	0	0	10	0	4	-	4	10	2	-	0	2	2	4	2	2	2	10	2	3
3by	1	1	0	10	0	0	10	0	4	-	4	10	2	-	1	1	2	4	4	4	10	3	1	0
4by	1	1	0	10	0	0	10	0	4	-	4	10	2	-	1	2	2	4	4	4	10	3	1	0

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 edure (Table 4)  
 good, mediocre  
 "bad" characters  
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 bercles in posterior  
 -12)  
 ircular-subtrapezi-  
 distinctly concave).  
 lways 4 or vari-  
 (0. smooth, 1. gra-  
 wing, 01. spine, 10.  
 one, 1. inflation or  
 dummy character).

CHAR. 22. Modification of ♂ feVII (0. none, 1. inflation or hump).

Noticeably, the gonopodal characters (23-24) receive small weights (<4) throughout. Like other remaining characters, they must be characterized as "bad".

**Clades suggested by the analysis**

We have chosen for further consideration those clades which were included in all 16 consensus trees (with or without successive weighting), as well as those included in all four trees based on all species and all characters (with or without successive weighting).

Only three clades, two of which are overlapping, are included in all 16 consensus trees in the unweighted analysis, viz.:

- (PLA + (DEL + RUB))
- and:
- (MIN + GIG)

The four consensus trees based on analysis of all species and all characters, when considered alone, have an additional three, partly overlapping clades in common:

- ((MIN + GIG) + LON + COR + CEA + DRA + HOS + (JEE + SPE))

Successive weighting greatly improves the resolution. Eight clades are included in all 16 consensus trees, resulting in the cladogram shown in Fig. 76. The four trees based on all species and all characters, when considered alone, have an additional five clades in common, giving the more resolved tree, Fig. 77.

All clades suggested by the unweighted analysis, except (MIN + GIG) are also suggested by the weighted analysis.

**Character support of the suggested clades**

Neither Fig. 76 nor Fig. 77 can, however, be accepted as the preferred cladogram. Before a cladogram can be preferred, the character support of its constituent clades must be examined:

*Monophyly of Desmoxytes*

The clade containing all *Desmoxytes* species is

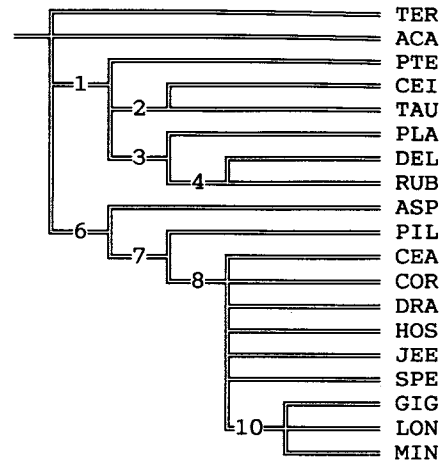


Fig. 76. Cladogram built from the clades included in all 16 consensus trees in the weighted analysis. Clade numbers refer to the text.

only supported by 2 equivocal, bad characters (char. 16, part of the composite character concerning the shape of the sternal lamina, and char. 24 (gonopods *Orthomorpha*-like or partly condensed in common ancestor of *Desmoxytes* + outgroup, partly condensed in ancestral *Desmo*-

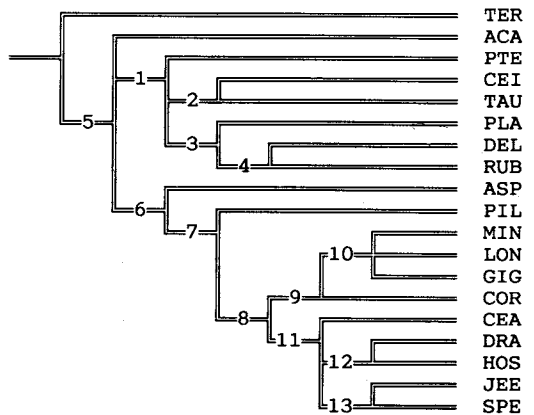


Fig. 77. Cladogram built from the clades included in all 4 consensus trees of the weighted analysis using all species and all characters. Clade numbers refer to the text.

	1	2	3	4
	3	4	1	3
	3	4	1	3
	3	4	1	3
	3	4	1	3
	10	10	2	1
	10	10	2	1
	2	3	1	1
	2	3	1	1
	1	4	1	3
	1	4	1	3
	1	4	1	3
	1	4	1	3
	2	10	2	3
	2	10	2	3
	10	3	1	0
	10	3	1	0

*xytes*). The monophyly of the genus is thus only poorly supported by the computerized analysis, but as mentioned above, the more or less modified paraterga *per se* do indicate that the genus is in fact monophyletic.

*Clade 1 (PTE + CEI + TAU + PLA + DEL + RUB)*  
Supported by one mediocre character (char. 18) and one bad (char. 20). Char. 18 concerns the modifications of ♂ femur V, and char. 20 similarly concerns ♂ femur VI. All the species in this clade have ♂ femora V and VI inflated or humped, but DRA also has got a humped ♂ femur V, and DRA like several other species have a humped ♂ femur VI.

*Clade 2 (CEI + TAU)*  
Supported by one mediocre character (char. 9) and one bad (char. 20). Char. 9 concerns the metatergal surface texture. These two species have a granulate-tuberculate spiculate texture, but the same is true of all the species in clade 7.

*Clade 3 (PLA + DEL + RUB)*  
Supported by one bad character (char. 2) concerning body colouration. These species are red, like a few others. This clade was found even by the unweighted analysis.

*Clade 4 (DEL + RUB)*  
Supported by one bad character (char. 17) concerning ♂ femur V. These species have ♂ femur V humped, like DRA. This clade was found even by the unweighted analysis.

*Clade 5 (all species except TER)*  
The notion of TER as sister-group of all other *Desmoxytes* species is supported by one bad character (char. 23): TER has an only somewhat condensed *Orthomorpha*-like gonopod configuration, but so have many other species.

*Clade 6 (ASP + PIL + MIN + LON + GIG + COR + CEA + DRA + HOS + JEE + SPE)*  
Supported by one mediocre character (char. 11) which, together with char. 12, concerns the shape of the paraterga. These species (except MIN, LON and GIG) have the paraterga antler-shaped (state 10), unlike any other species. The three exceptions have spine-shaped paraterga (state 01).

*Clade 7 (PIL + MIN + LON + GIG + COR + CEA + DRA + HOS + JEE + SPE)*

Supported by one mediocre character (char. 9, see discussion under clade 2) and one bad (char. 16, concerning the ♂ lamina between coxae IV).

*Clade 8 (MIN + LON + GIG + COR + CEA + DRA + HOS + JEE + SPE)*

Supported only by three bad characters (char. 19-20, ♂ femur V humped; char. 23, gonopods extremely condensed). This clade was found even by the unweighted analysis based on all species and all characters.

*Clade 9 (MIN + LON + GIG + COR)*

Supported only by one bad character (char. 15, concerning the ♂ lamina between coxae IV).

*Clade 10 (MIN + LON + GIG)*

The best substantiated clade, supported by two good characters (char. 12 and 4), one mediocre (char. 11), and one bad (char. 6, presence of three pairs of anterior metatergal tubercles). These three species are the only ones having spine-shaped paraterga (char. 11-12, cf. discussion under clade 6) and three rows of metatergal tubercles (char. 4, unknown for LON) however).

*Clade 11 (CEA + DRA + HOS + JEE + SPE)*

Supported by one mediocre character (char. 22, ♂ femur V humped) and two bad (char. 1, colour brownish; char. 23, gonopods reversed to an *Orthomorpha*-like type).

*Clade 12 (DRA + HOS)*

Supported by one good character (char. 14, subanal scale more or less distinctly concave). Char. 14 is one of the characters which could not be scored for several species and therefore was excluded in some of the analyses. This clade could therefore not have been supported by all 16 consensus trees. On the other hand, the many missing entries for this character deprives it of some of its credibility.

*Clade 13 (JEE + SPE)*

Supported by one bad character (char. 13, epiproct with hypertrophied subapical tubercles). This clade was also found by the unweighted analysis based on all species and all characters.

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**Clade 14 (MIN + GIG)**

Whereas char. 4, 6, 11, and 12 support clade 10 (MIN + LON + GIG) after successive weighting, these characters support clade 14 in the unweighted analysis. Here, clade 14 is further supported by char. 3 (body large, as in some other species), and char. 8 (>2 tubercles in posterior metatergal row, unknown in LON).

**Conclusion of computerized analysis**

Among the clades discussed above, we have chosen to include two overlapping categories in our preferred cladogram 1) clades which in the weighted analysis were supported by at least one good or mediocre character, 2) clades which were suggested by the unweighted analysis.

These clades are nos. 1, 2, 3, 4, 6, 7, 8, 10, 11,

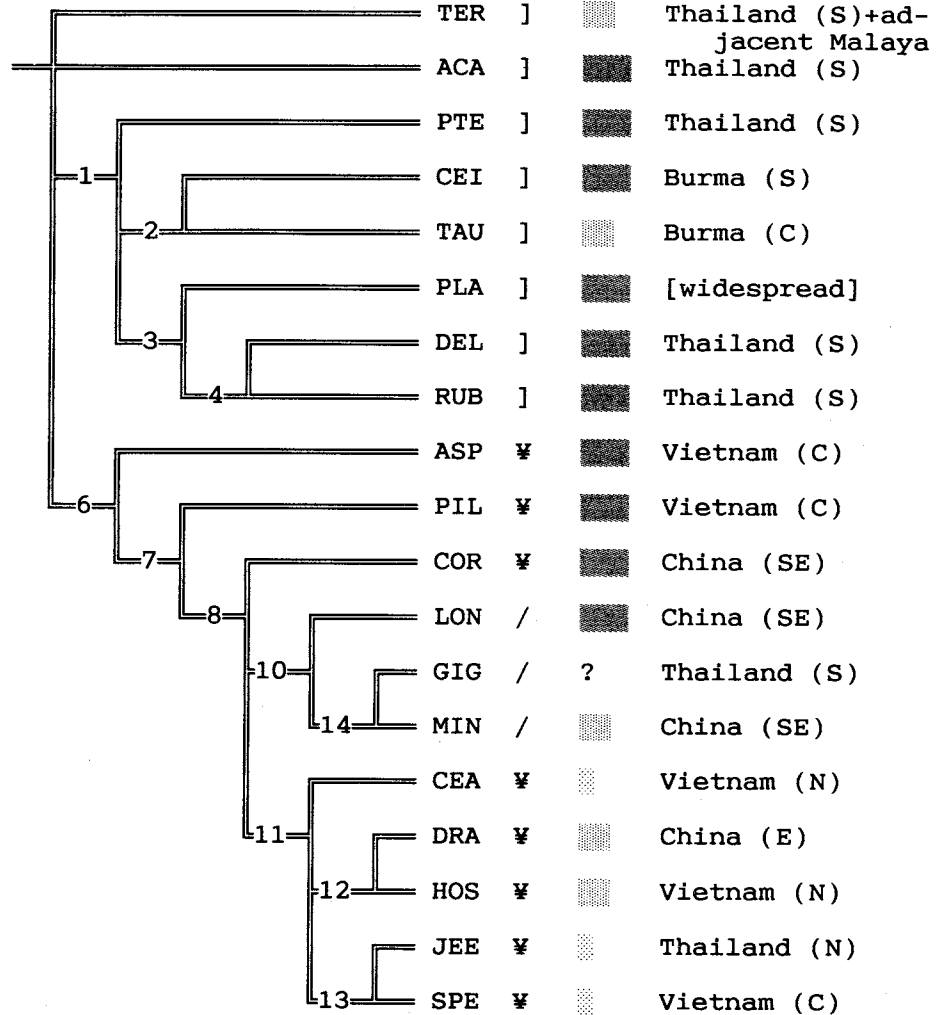


Fig. 78. The preferred cladogram, including clades suggested by the unweighted analysis as well as those supported by at least one good or mediocre character in the weighted analysis. Tree length: 81 steps, consistency index: 34, retention index: 51. Clade numbers refer to the text. Symbols to the right of species abbreviations indicate shape of paraterga (], wing; ¥, antler; /, spine) and degree of gonopod condensation (more condensed gonopods indicated by larger, more heavily shaded symbol). The known distribution of the species is shown to the right of the symbols.

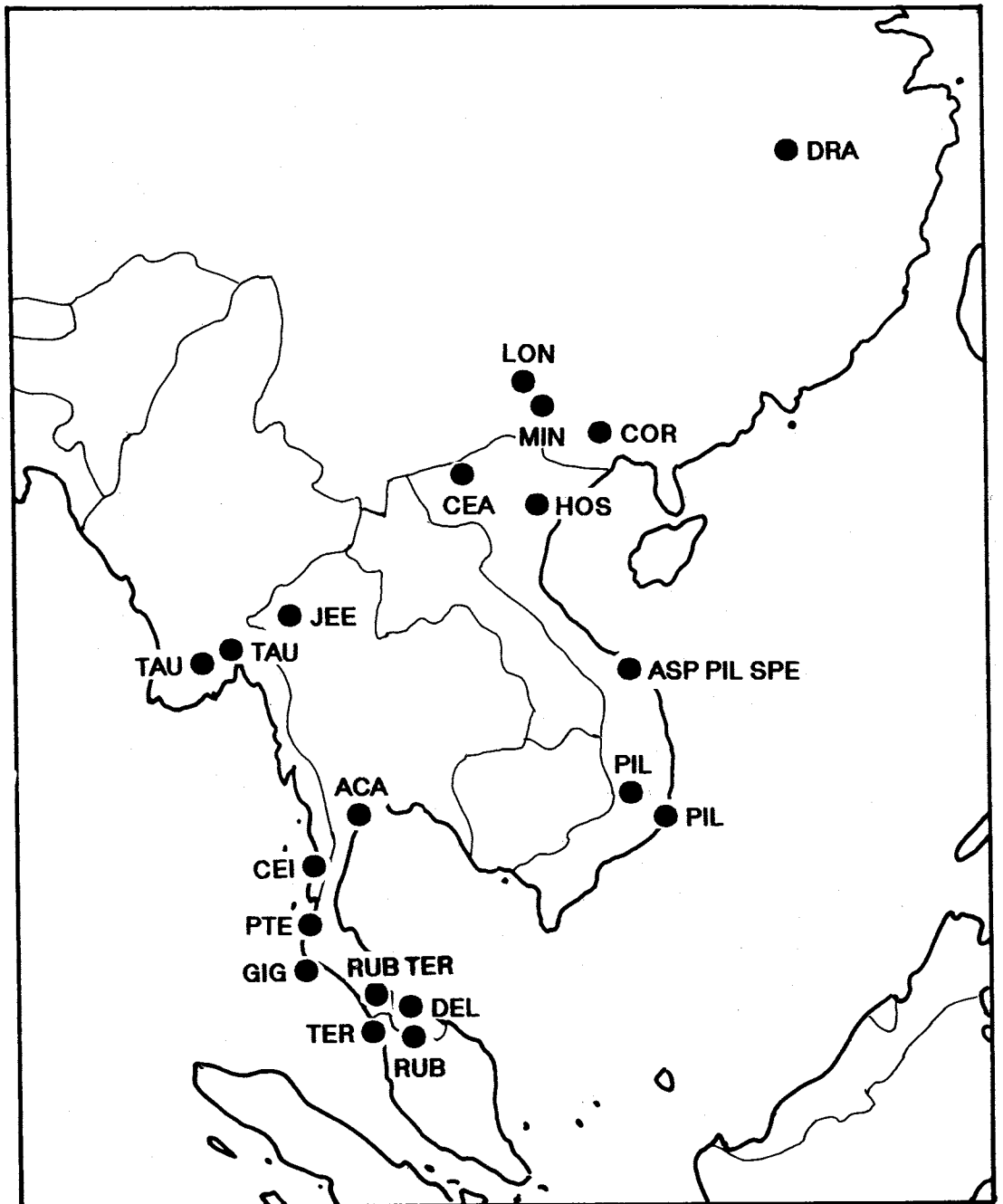


Fig. 79. Map of southeast Asia, showing records of *Desmoxytes* species, except the widespread *planata*.

12, 13, 14. It should be noted that only clade 10 (MIN + LON + GIG) is supported by a good character in the weighted analysis (of all species and all characters).

Fig. 78 shows the tree containing only these clades. This tree is 81 steps long, with a consistency index of only 34 and a retention index of 51. The state of the two most conspicuous characters, viz. shape of paraterga and degree of gonopod condensation, is shown to the right for each species. Although this tree cannot be regarded as final, it displays several interesting features.

Concerning the paraterga, it not surprisingly shows that the wing-like type, which approaches that found in other Paradoxosomatidae, is the original one within *Desmoxytes*, but it also indicates that the spinelike paraterga found in LON, MIN, and GIG seem to be derived from the more complex, antlerlike paraterga found in several other species.

As mentioned above, the gonopods correlate poorly with the paraterga. The overall pattern is that gonopods which are more or less close to the presumably ancestral *Orthomorpha*-type, are found in species with strongly modified paraterga, whereas strongly condensed gonopods are found both in "antlered" species and in "winged" ones. The most facile conclusion would be that the

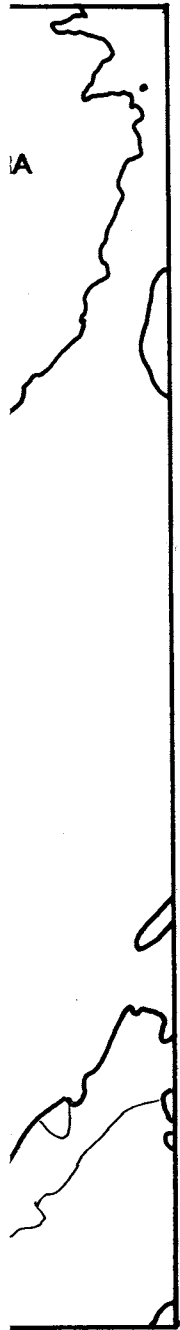
evolution of gonopodal structure in *Desmoxytes* has proceeded from the strongly condensed type towards a more *Orthomorpha*-like configuration. We are, however, not ready to subscribe to this idea: comparison with other Orthomorphini, and Paradoxosomatidae in general, strongly suggests that the very condensed gonopods found in several species of *Desmoxytes* have been derived from less condensed ones.

The conflict between paratergal and gonopodal structure in *Desmoxytes* is therefore still unsolved. We offer Fig. 78 as a preliminary hypothesis for relationships within the genus but will welcome any additional evidence that might shed further light on this riddle.

## BIOGEOGRAPHY

*Desmoxytes planata* has been recorded from widely scattered tropical localities. The other species of the genus are confined to SE Asia (Fig. 79).

The phylogenetic analysis yielded very little biogeographic information. The only structure which is evident from Fig. 78 is the indication of two sets of sister-species occurring in the same general area: CEI + TAU in southern Burma and DEL + RUB in southern Thailand.



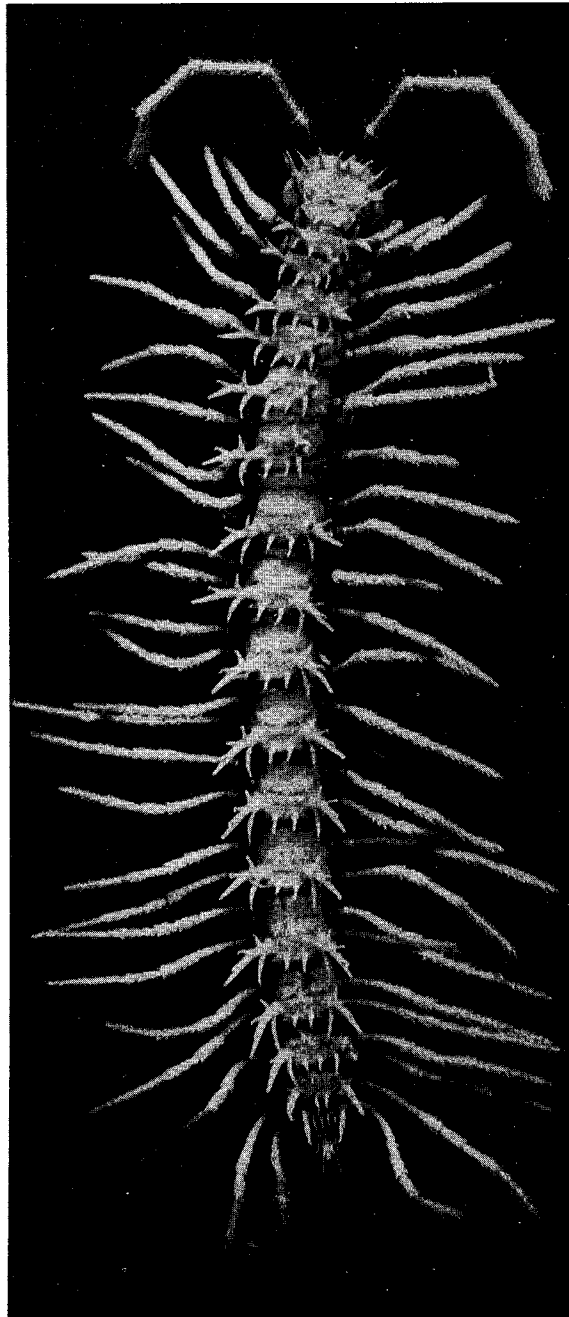


Fig. 80. *Desmoxytes draco*, 9 ×, from Cook & Loomis (1924a).

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