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The millipede tribe Nedyopodini, with special reference to the fauna of Taiwan (Diplopoda: Polydesmida: Paradoxosomatidae)

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The millipede tribe Nedyopodini, with special reference to the fauna of Taiwan (Diplopoda: Polydesmida: Paradoxosomatidae)

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Abstract

The east and southeast Asian millipede tribe Nedyopodini is here restricted to a single genus, *Nedyopus* Attems, 1914; the following genera are here considered to be junior subjective synonyms: *Vaulogerodesmus* Brölemann, 1916, *Nesodyopus* Verhoeff, 1940, n. syn., and *Varyomorpha* Wang, 1957, n. syn. This taxonomically confused tribe/genus is reviewed and redefined. Based on new collections, the fauna of Taiwan currently contains five *Nedyopus* species including the redescribed *N. hsientienensis* (Wang, 1957) and *N. pectinatus* (Wang, 1957), both n. comb. ex *Varyomorpha*, as well as the newly described *N. caudatus* n. sp., *N. latus* n. sp., and *N. wui* n. sp. A key to these five species is provided.

Keywords: Millipede, *Nedyopus*, tribe Nedyopodini, Taiwan

Introduction

The tribe Nedyopodini is one of the most characteristic elements in the paradoxosomatid fauna of east and southeast Asia. It is defined by the parabasally enlarged gonopod femorite that, due to its torsion, supports the seminal groove on the lateral side (Jeekel 1968). Hoffman (1980) considered the tribe as encompassing the following genera: *Nedyopus* Attems, 1914, with eight to nine species from Japan, China, and Korea; *Nesodyopus* Verhoeff, 1940, with one species from Bonin Islands, Japan; *Vaulogerodesmus* Brölemann, 1916, with two species from Indochina; and *Varyomorpha* Wang, 1957, with two species from Taiwan. However, the latter genus was incorporated into this tribe with some reservation.

Since then, only *Vaulogerodesmus* has been reviewed (Golovatch et al. 2003), with three species reported from Vietnam and two others from southern China.

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Korsós (2004), in a recent review of the diplopod fauna of Taiwan, referred to one relatively widespread species of *Nedyopus*, as well as to two endemic species of *Varyomorpha* as occurring on the island.

Taxonomically, the Nedyopodini is perhaps one of the most confused tribes of Paradoxosomatidae (Jeekel 1968). The distinctions between the genera, species, and subspecies as presented in the available descriptions are often very poor, most of the illustrations, when given at all, are imperfect or misleading, and many types are lost. Even the few relevant keys (Attems 1914, 1937; Takakuwa 1954; Miyosi 1959) are too superficial to be of any use.

The present paper aims to provide solutions to some of the numerous taxonomic problems in the tribe. A starting point has been provided by the abundant material of Paradoxosomatidae recently accumulated for study from all over Taiwan. Since the fauna of Taiwan is very confused taxonomically, with nearly all types of the species or subspecies described by Yu-Hsi Moltze Wang being lost, this step of amassing new, often topotypic material became absolutely mandatory. Because representatives of Nedyopodini appear to be quite diverse and unusual in the new samples, the occasion is taken here to review this tribe.

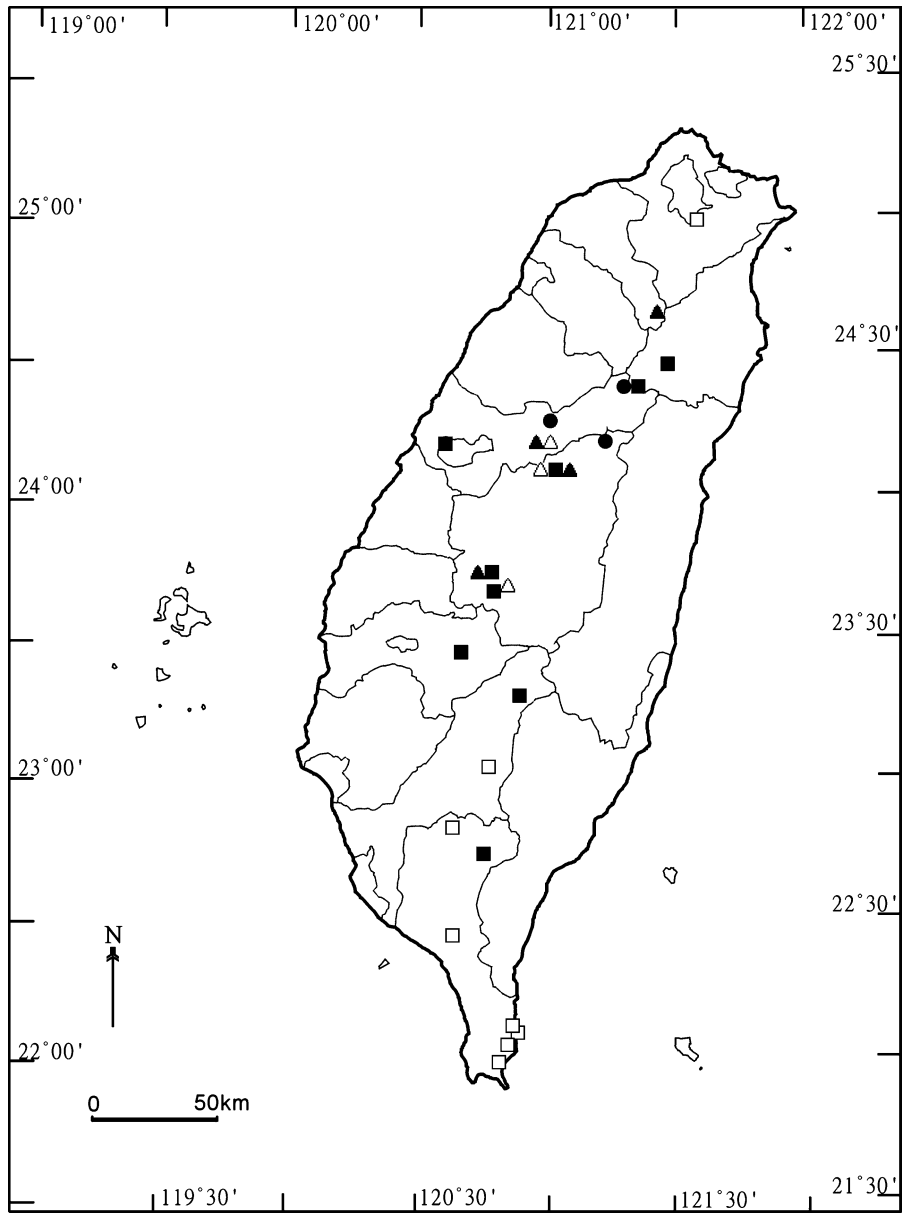
Material and methods

Extensive new collections of millipedes, covering most parts of Taiwan (see Map 1), were made between 1991 and 2003, by hand-sorting of soil and litter. Specimens were preserved in 70% ethanol. External characters were examined and drawn with a Leica MZ 16 stereomicroscope, as well as being studied with a Hitachi S2400 scanning electron microscope. Coloration of the specimens is described from alcohol material. This material has been shared between the collections of the Department of Life Sciences, National Chung Hsing University (NCHUL); Department of Biological Sciences, National Sun Yat-Sen University (NSYSUB); Department of Life Science, National Taiwan Normal University (NTNUL); National Museum of Natural Science (NMNS); Taiwan Forestry Research Institute (TFRI); and the Zoological Museum of the State University of Moscow (ZMUM).

Taxonomic review

Nedyopus Attems, 1914 is certainly a genus central to the classification of the Nedyopodini, being both the oldest available genus-group name and highly diverse. Originally, *Nedyopus* was established for three Japanese species, with *Strongylosoma cingulatum* Attems, 1898 chosen as type species (Attems 1914). Since then, *Nedyopus* has become one of the most speciose and characteristic groups of the family Paradoxosomatidae occurring in east and southeast Asia. The following species, subspecies or varieties have hitherto been referred to *Nedyopus*:

- *Nedyopus cingulatus* (Attems, 1898), the type species, sometimes synonymized with *N. patrioticus* (Attems, 1898) (Wang 1955; Korsós 2004), reported only from Japan (Takashima 1949; Takashima and Haga 1952; Takakuwa 1954; Miyosi 1959; Jeekel 1968).
- *Nedyopus patrioticus* (Attems, 1898), described as *Strongylosoma patrioticum* Attems, 1898, at present known from different parts of Japan and Korea (Attems 1898, 1914,



Map 1. Distribution of species of the genus *Nedyopus* in Taiwan. (□) *Nedyopus hsientienensis* (Wang, 1957); (■) *Nedyopus caudatus* n. sp.; (▲) *Nedyopus pectinatus* (Wang, 1957); (△) *Nedyopus latus* n. sp.; (●) *Nedyopus wui* n. sp. Borders between counties are shown.

1937; Takashima 1949; Takakuwa 1954; Takashima and Haga 1956; Paik 1958; Miyosi 1959; Jeekel 1968; Nishikawa and Murakami 1991; Mikhaljova et al. 2000), and previously reported from Taiwan (Wang 1955). It is sometimes considered to be a senior subjective synonym of *N. cingulatus* (see above), and even as the valid name to be accepted instead of the much older *Oxyurus flavolimbatus* L. Koch, 1878 (cf. Koch 1878), a *nomen oblitum* (Shinohara 1985). If Korsós (2004) is correct in synonymizing

N. cingulatus with *N. patrioticus*, his choice of suppressing the type species can hardly be considered as fortunate. It would seem more appropriate to keep *cingulatus* as the valid name.

- *Nedyopus patrioticus* var. *unicolor* (Carl, 1902), described without illustrations as *Strongylosoma patrioticus* var. *unicolor* Carl, 1902, from Sumatra, a variety said to be very close to the typical form (Carl 1902), but Attems (1937) doubted its conspecificity with *N. patrioticus*.
- *Nedyopus tambanus* (Attems, 1901), described as *Strongylosoma tambanum* Attems, 1901, currently known from various places in Japan (Attems 1901, 1914, 1937; Takashima 1949; Takakuwa 1954; Takashima and Haga 1956; Miyosi 1959; Shinohara 1958, 1974; Jeekel 1968; Nishikawa and Murakami 1991).
- *Nedyopus tambanus ikaonus* (Attems, 1909), described as *Strongylosoma tambanum ikaonum* Attems, 1909, and only known from Japan (Attems 1909, 1914, 1937; Takashima 1949; Takakuwa 1954; Miyosi 1959; Jeekel 1968).
- *Nedyopus tambanus mangaesinus* (Attems, 1909), also described in *Strongylosoma* and known only from Japan (Attems 1909, 1914, 1937; Verhoeff 1936; Takashima 1949; Takakuwa 1954; Miyosi 1959; Jeekel 1968).
- *Nedyopus koreanus* Verhoeff, 1936, described from Korea (Verhoeff 1936), but relegated to the status of a subspecies, *N. patrioticus koreanus*, by most subsequent authors (Attems 1937; Takakuwa 1954; Paik 1958). Jeekel (1968) listed *koreanus* as a *bona fide* species.
- *Nedyopus koreanus niponianus* Verhoeff, 1940, only known from Japan (Verhoeff 1940; Jeekel 1968); often referred to as *N. patrioticus niponianus* (cf. Takashima 1949; Takakuwa 1954 [as *p. nipponicus*, lapsus]; Miyosi 1959).
- *Nedyopus*. (*Nesodyopus*) *boninensis* Verhoeff, 1940, described and only known from the Bonin Islands, Japan; at present this monobasic taxon is considered to be a full genus (Jeekel 1968; Hoffman 1980).
- *Nedyopus hiburizimensis* Miyosi, 1955, only known from Japan (Miyosi 1955, 1959; Jeekel 1968).
- *Nedyopus hiburizimensis aquilus* Haga, 1968, described without illustrations, only known from Japan (Haga 1968).
- *Nedyopus venustus* Shinohara, 1963, only known from Japan (Shinohara 1963; Jeekel 1968).

There have also been three other species described in *Nedyopus*, but later moved to other genera:

- *Nedyopus variatus* Attems, 1953, from Vietnam, currently placed in *Sellachuneza* Enghoff, Golovatch, and Nguyen, 2004 (cf. Hoffman 1963; Jeekel 1968; Enghoff et al. 2004).
- *Nedyopus jeanae* Wang, 1957, described from Taiwan (Wang 1957b), transferred to *Aponedyopus* Verhoeff, 1939 (Jeekel 1968; Wang and Mauriès 1996), downgraded by Wang (1963, 1964) to the status of a subspecies of *Aponedyopus montanus* Verhoeff, 1939, but now considered as a strict junior subjective synonym of *A. montanus* (Korsós 2004).
- *Nedyopus reesi* Wang, 1957, also described from Taiwan (Wang 1957a), transferred to *Aponedyopus* (Wang 1964; Jeekel 1968; Wang and Mauriès 1996) and now also considered a junior subjective synonym of *A. montanus* (Korsós 2004).

The genus *Vaulogerodesmus* Brölemann, 1916 was synonymized with *Nedyopus* by Attems (1937), but revalidated by Jeekel (1968) and currently contains the following species (Golovatch et al. 2003):

- *Vaulogerodesmus pictus* Brölemann, 1916, type-species, endemic to Vietnam (Brölemann 1916; Golovatch et al. 2003; Enghoff et al. 2004).
- *Vaulogerodesmus dawydoffiae* (Attems, 1953), described as *Helicorthomorpha dawydoffiae* Attems, 1953, from Vietnam (Attems 1953), transferred to *Vaulogerodesmus* by Hoffman (1973), considered endemic to Vietnam (Enghoff et al. 2004).
- *Vaulogerodesmus mahunkai* Korsós and Golovatch, 1989, described from Vietnam (Korsós and Golovatch 1989), where it is considered endemic (Enghoff et al. 2004).
- *Vaulogerodesmus beroni* Golovatch, 1995 and *V. picturatus* Golovatch, 1995, both described and still known only from southeastern China (Golovatch 1995).

Varyomorpha Wang, 1957 was first proposed as a subgenus of *Oxidus* Cook, 1911 and later treated as full genus (Wang 1964), but still remaining of unclear status (Jeekel 1968; Hoffman 1980; Korsós 2004). The following species are currently referred to this genus:

- *Varyomorpha hsientienensis* (Wang, 1957), first described as *Oxidus (Varyomorpha) hsientienensis* Wang, 1957, from Taiwan (Wang 1957a, 1958), currently referred to as *V. hsientienensis* (Jeekel 1968; Korsós 2004);
- *Varyomorpha pectinata* (Wang, 1957), described as *Oxidus (Varyomorpha) pectinatus* Wang, 1957, from Taiwan (Wang 1957b, 1958), at present referred to as *V. pectinata* (Jeekel 1968; Korsós 2004).

One more species from Taiwan, described as *Oxidus (Varyomorpha) kosingai* Wang, 1958, has since been synonymized with *Helicorthomorpha orthogona* (Silvestri, 1898) (Jeekel 1980).

Systematic part

Because the taxonomy of the Nedyopodini is so badly confused, and given that the available material derives only from Taiwan, a full revision is not attempted here. It is necessary to amass and study much more material, including the existing types and new collections, to clarify the status of the Japanese, Korean, and Sumatran members. Instead, we focus on the fauna of Taiwan, which alone is sufficiently diverse to justify several important changes to the classification of the tribe. This group currently comprises a single, highly variable and quite speciose genus, for which the name *Nedyopus* has priority. Following Attems (1937), we consider *Vaulogerodesmus* as a subjective junior synonym of *Nedyopus*. Furthermore, since *Nesodyopus* and *Varyomorpha* are also synonyms of *Nedyopus*, the whole tribe Nedyopodini becomes monogeneric. Hence the diagnosis presented below holds for both the Nedyopodini and *Nedyopus*.

The fauna of Taiwan contains at least five species of *Nedyopus*. Based on their characteristics, this genus (and tribe) can be redefined as follows (cf. Jeekel 1968; Hoffman 1973).

Tribe NEDYOPODINI Jeekel, 1968

Genus *Nedyopus* Attems, 1914

Type-species: *Strongylosoma cingulatum* Attems, 1898.

Vaulogerodesmus Brölemann, 1916 (type-species: *Vaulogerodesmus pictus* Brölemann, 1916), synonymized by Attems (1937).

Nesodyopus Verhoeff, 1940 (type-species: *Nedyopus boninensis* Verhoeff, 1940), n. syn.

Varyomorpha Wang, 1957 (type-species: *Oxidus hsientienensis* Wang, 1957), n. syn.

Diagnosis

Usually medium-sized Paradoxosomatidae (12–48 mm long, 1.4–5.0 mm wide) with 20 body segments, a normal pore formula, modestly to poorly developed paraterga, a deep and strongly beaded stricture between pro- and metazona, short to relatively long antennae and legs, and a more or less distinct, often contrasting colour pattern. Teguments smooth to rugulose, only seldom rugose-granular in places. Tergal setae usually missing or nearly so, only rarely conspicuously dense. Pleurosternal carinae usually present, especially on segments 2–7. Male legs, especially pregonopodial ones, usually with tarsal brushes, in some species the brushes cover the distoventral parts of the tibiae. A more or less evident sternal structure between male coxae 4, ranging from a long tongue-shaped process to two small paramedian tubercles.

Gonopods with long and subcylindrical coxae, latter usually sparsely setose distoventrally. Telopodite only slightly longer than coxa; prefemoral part small, as usual densely setose and clearly delimited. Femorite elongate, strongly twisted so that seminal groove runs entirely on its lateral face, with a short, stalk-shaped basis; medial face with a more (usually) or less (seldom) strongly developed groove/excavation parabasally, demarcating a more (usually) or less (some “*Vaulogerodesmus*” species) prominent lobe/expansion (**e**); medial face of femorite with a more (usually) or less (some “*Vaulogerodesmus*” species) evident lobe (**l**) situated from about midway to distoventrally; this lobe is often irregularly shaped and denticulate, sometimes broken into two parts (**l'** and **l''**) near its middle; solenomere rather short, flagelliform, usually with a more or less evident lobe (**m**) near base on dorsolateral side of femorite; solenophore (=tibiotarsus) complex, more or less strongly coiled, normally only vaguely demarcated at base from femorite, without a postfemoral sulcus, usually consisting of several hyaline lobes (up to four: **A**, **B**, **C** and **D**) nearly completely sheathing and supporting the solenomere, lobe **B** normally the largest and recognizable due to longitudinal ribs/rugulosity.

Remarks

The synonymy of *Vaulogerodesmus* is supported by the fact that several of the species studied here show a modestly enlarged gonofemorite, combined with various degrees of development of the demarcation sulcus between the femorite and the solenophore. Until recently, *Vaulogerodesmus* was believed to be confined to Indochina and the adjacent parts of China, comprising species with a relatively poorly grooved and modestly expanded gonopod femorite, as opposed to the particularly deeply grooved and dorsolaterally strongly expanded one observed in the *Nedyopus* species or subspecies from Japan and Korea. The vast geographical gap in between (i.e. central and northeastern China, as well as Taiwan) also seemed to support the separation of these two genera. However, Golovatch et al. (2003) suggested that if transitional forms were found as a result of progress in the knowledge of Nedyopodini, both *Nedyopus* and *Vaulogerodesmus* would have to be merged. The new material from Taiwan allows us to confirm that this is the case.

The synonymy of *Nesodyopus* stems from the very unreliable diagnosis of this subgenus originally given by Verhoeff (1940). In contrast to other *Nedyopus*, *N. boninensis* shows a considerably narrower **e**, a non-demarcated gonopostfemoral portion and a simple solenophore, consisting of only two lobes. This condition is strikingly similar to that observed in typical *Vaulogerodesmus* species. Although both Jeekel (1968) and Hoffman (1980) assigned full generic status to *Nesodyopus*, they emphasized that this was only

provisional. Moreover, both Takakuwa (1954) and Miyosi (1959) treated *N. boninensis* as a typical *Nedyopus*, omitting *Nesodyopus* altogether as a genus-level taxon.

The synonymy of *Varyomorpha* could only be established with fresh topotypic material to hand. Because the types of Wang's species *V. hsientienensis* and *V. pectinata* are lost, it appears necessary to designate neotypes from among the available near-topotypes in order to stabilize the nomenclature and fix these names.

Like Jeekel (1968), we refrain from using the terms “*lamina lateralis*” and “*lamina medialis*” to designate certain parts of the solenophore in describing the gonopod conformation of *Nedyopodini*. Firstly, the solenophore of *Nedyopus* is usually a highly complex structure, consisting of several (two to four) lobes. Secondly, the remarkably twisted gonofemurite, coupled with a no less strongly coiled solenophore, not only makes homologization difficult, but also renders the above positional terminology pointless. We entirely agree with Hoffman (1973) that, fundamentally, the solenophore in *Nedyopus* shows both the laminae well developed, but the correspondence between them remains unclear.

Below we provide descriptions of all five *Nedyopus* species that are securely documented in the fauna of Taiwan and give a key for their separation. Wang's (1955) record of *N. patrioticus*, like most others by this author, is regarded too dubious to be considered seriously.

Species descriptions

Nedyopus hsientienensis (Wang, 1957), comb. n.

(Figures 1–10, 53–61, 97–102)

Neotype (here designated): ♂ (NSYSUB-DI 216), Taiwan (R.O.C.), Taipei City, JhihNanGong, 206 m a.s.l., March 2002, leg. C.-C. Chen and C.-E. Yang.

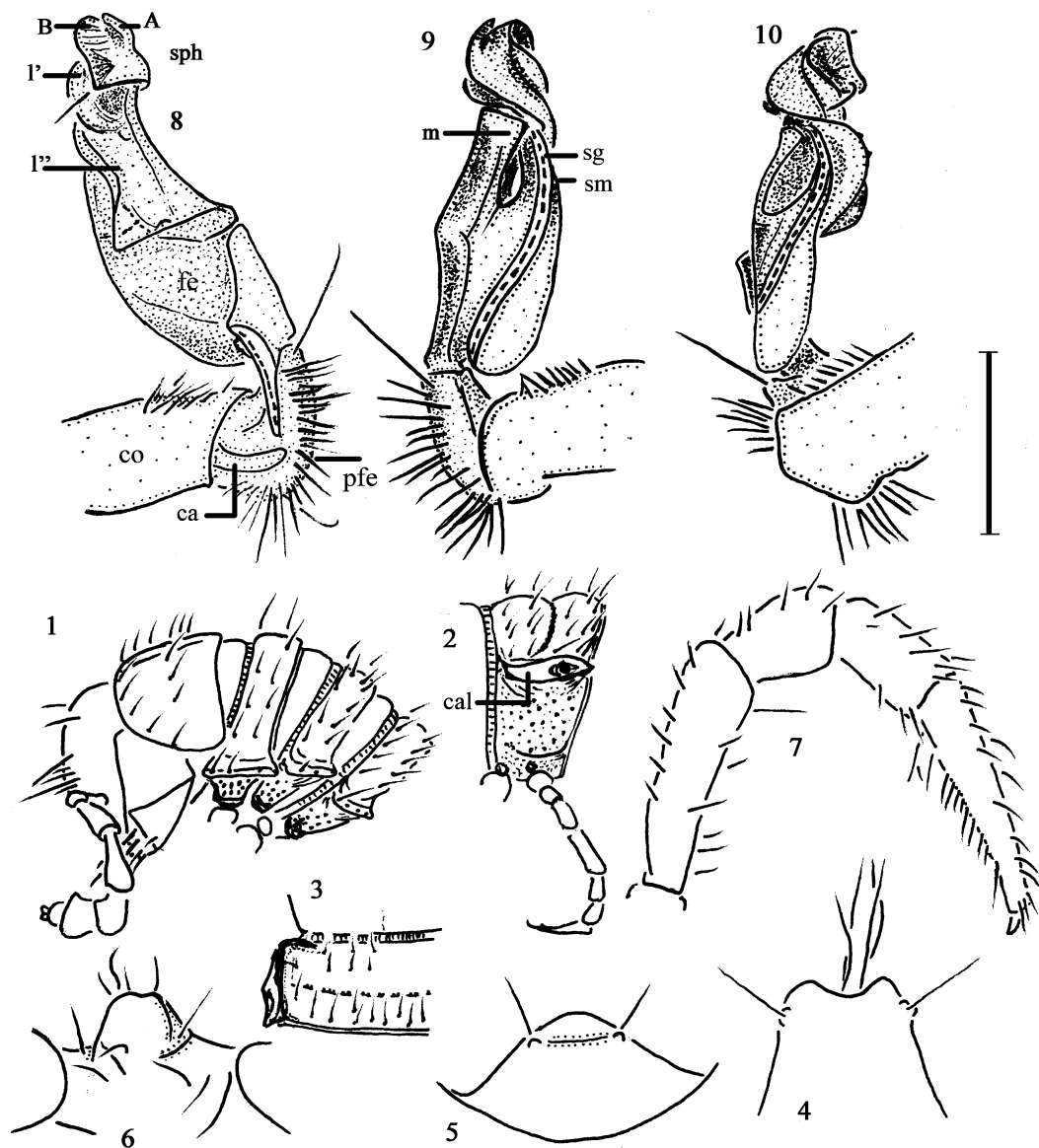
Other material. 6♂, 7♀, one juvenile (NSYSUB-DI 198–211), 2♂, 2♀ (ZMUM), Pingtung County, SanDiMen, CingShan, ca 190 m a.s.l., under stones, 19 August 1999, leg. H.-W. Chang. 10♀ (NSYSUB-DI 380–389), same county, ManJhou, JiuPeng, 20 m a.s.l., 28 April 1999, same collector. 1♂ (NSYSUB-DI 217), Kaohsiung County, TaoYuan, MaLiShau river, ChuYunShau forest path, ca 750 m a.s.l., 22 February 2000, same collector. 1♂ (NSYSUB-DI 218), Pingtung County, ManRen, GangKou river estuary, ca 30 m a.s.l., 21 April 1999, same collector. 1♂ (NSYSUB-DI 219), same locality, NanRen Road, Police Office, under trees, below stones but above soil, ca 10 m a.s.l., 19 November 2001, leg. C.-C. Chen. 1♂ (NSYSUB-DI 220), same county, LaiYi, NanHe, ca 90 m a.s.l., 19 August 1999, leg. H.-W. Chang. 1♂, 1♀ (NSYSUB-DI 221–222), same county, KenTin, LanRen River, 63 m a.s.l., 23 March 2002, leg. C.-C. Chen.

Diagnosis

Differs from congeners by a contrasting colour pattern, combined with the relatively well-developed paraterga, the densely setose postcollar metaterga, and the gonopod-telopodite tip consisting of only two lobes.

Description

Length 12–15 (♂, $n=6$) or 17–18 mm (♀, $n=6$); width of midbody metazona 1.2–1.4 (♂) or 1.8–2.0 mm (♀). Neotype ca 14 mm long and 1.2 mm wide.



Figures 1–10. *Nedyopus hsientienensis* (Wang, 1957), male from CingShan. (1) Anterior body portion, lateral view. (2) Segment 10, lateral view. (3) Left half of metatergum 10, dorsal view. (4) Epiproct, dorsal view. (5) Hypoproct, ventral view. (6) Sternal lobe between coxae 4, ventral view. (7) Leg 16. (8–10) Left gonopod, medial, lateral, and dorsal views, respectively. ca, cannula; cal, callus; co, coxite; fe, femorite; pfe, prefemoral part; sg, seminal groove; sm, solenomere; sph, solenophore; l, l', l'', A, B, lobes of solenophore; m, lobe at base of solenomere. Scale bar: 1.0 mm (1–3); 0.3 mm (4–10).

Coloration in alcohol brown to dark brown in both sexes; sometimes head and antennae slightly lighter brown, antennae increasingly blackish distally, but tip contrastingly pallid, epiproct very light brown to light brown; a wide, very light brown to light brown, moniliform axial stripe, narrowed-subtrapeziform on proterga and broadened-subtrapeziform on metaterga; pleurosternal region, sterna, and legs pallid, sometimes distal podomeres pale brown (only in ♂).

Postcollar constriction rather faint, particularly in ♀, width of head <segments 5–16>4>2>3>collum in ♂, head<segments 5–17>4>2>3>collum in ♀; further on toward telson trunk gradually and gently tapering both in width and height. Antennae short, clavate, reaching from stricture to end of segment 2 dorsally in ♂ (Figures 1, 54), a little shorter in ♀, only reaching from end of collum to prozonum 2. Paraterga relatively well developed (Figures 1–3, 54–58), calluses (**cal**) with three to four minute denticles at lateral margin (Figures 1–3) on segments 2–19; calluses delimited by a sulcus both dorsally and ventrally, though ventral sulcus is finer than dorsal one, more evident on pore-bearing segments; paraterga like low ridges, slightly surpassing caudal tergal contour on segments 2 (Figures 1, 54), 18, and 19, spiniform caudally. Axial line usually wanting, only poorly visible in places. Transverse sulcus evident on segments 5–18, reaching base of paraterga, wanting on segment 19, generally deep, slightly deeper in ♂, lineiform, clearly beaded at bottom (Figures 2, 3, 55, 56). Surface generally shiny and rather smooth, sometimes rugulose on posterior metaterga only of ♂, sometimes rugulose on metazonum 19 below paraterga; metazona below paraterga evidently and densely granular, contrastingly smooth to finely rugulose on segment 19. Limbus thin, caudal margin entire. Stricture between pro- and metaterga roughly beaded, particularly in ♂, general appearance of body submoniliform. Tergal setae long, pattern 5+5(6) anteriorly and 3+3(4) in the middle on collum in ♂, 4+5 and 3+3 in ♀, setae of anterior row on collum seldom abraded; numerous setae on all postcollar metaterga, two setae on each lateral callus of paraterga 2 and 19, and a single seta on paraterga 3–18, these lateral setae only seldom abraded. Ozopores lateral, lying on callus ca one-third metatergal length from caudal edge (Figures 2, 56). Pleurosternal carinae present, having the form of wide, straight (segments 2, 5–7) or rounded (segments 3 and 4) ridges on pregonopodial segments, with a distinct, granular, narrowly rounded, subtriangular tooth that nearly reaches the caudal metazonal margin on each of segments 6 and 7 (♂), or in the form of narrow ridges on segments 2–4 (♀), onward increasingly poorly developed, reduced to low bosses visible up to segment 17 in ♂ (Figures 1, 2, 54, 56) or to segment 16 or 17 in ♀, thereafter virtually absent. Epiproct digitiform, flattened dorsoventrally, long in lateral view, ratio of epiproct length to pre-epiproct length of telson 1:2.9 in ♂ (Figure 58), slightly shorter in ♀; subtruncate and emarginate in dorsal view; pre-apical papillae evident, close to apex (Figures 4, 57). Hypoproct more (♂) (Figures 5, 59) or less (♀) roundly subtriangular, 1+1 setae at caudal corners situated on well-separated knobs, sides concave at base.

Sterna modestly setose, not modified except for a linguiform, slightly emarginate, setose lamina between ♂ coxae 4 (Figures 6, 60); each cross-impression with an evident transverse sulcus but with a poorly developed, shallow axial groove.

Male legs 1–7 with tarsal brushes (Figure 61), thereafter tarsal setation thinning out, without brushes (Figure 7). Legs long, ca 1.5 times (♂) (Figures 2, 56) to almost as long as midbody height (♀).

Gonopods (Figures 8–10, 97–102) complex. Coxite elongate, subcylindrical, strongly setose distoventrally; cannula normal. Telopodite strongly twisted; prefemoral part rather short, as usual densely setose; femorite with a short stalk basally, followed by a modestly broadened, elongate, distal portion carrying a peculiar hyaline lamella (**I**) on medial side, with a smooth or sometimes denticulate margin; **I** divided in distal third into two lobes (**I'** and **I''**); solenophore (**sph**) hyaline, twisted, nearly as long as femorite, with two apical lobes (a small lobe **A** and a large, hyaline, ribbed/rugulose lobe **B**), nearly completely sheathing a mostly flagelliform and rather short solenomere; seminal groove running medially on stalk of femorite, then directed abruptly laterally to follow subdorsal side of remaining portion of

femorite, finally changing course ventrad onto solenomere at end of **l** and at base of **sph**; a small lamina (**m**) near base of solenomere on lateral side.

Remarks

This material, including the near-topotypic neotype, has been chosen as representing *N. hsientienensis* because it does not contradict in any way the original description (Wang 1957a), even though the latter is extremely poor. Amongst the characters that tally are the relatively small body, the dark brown coloration with a markedly light pattern, the short antennae, the poorly developed paraterga with the transverse sulcus starting from segment 5, and the complex gonopod configuration. The characteristic dense tergal setation was not mentioned by Wang (1957a), but he could have easily overlooked this, as he did for other distinctive features of this species, or else the type material might have been in too poor condition to retain the tergal setae.

Nedyopus pectinatus (Wang, 1957), comb. n.

(Figures 11–21, 62–72, 103–108)

Neotype: ♂ (NSYSUB-DI 192), Taiwan (R.O.C.), Taoyuan County, FuSiing, SihLeng, 1244 m a.s.l., 19 April 2003, leg. S.-I. Wu.

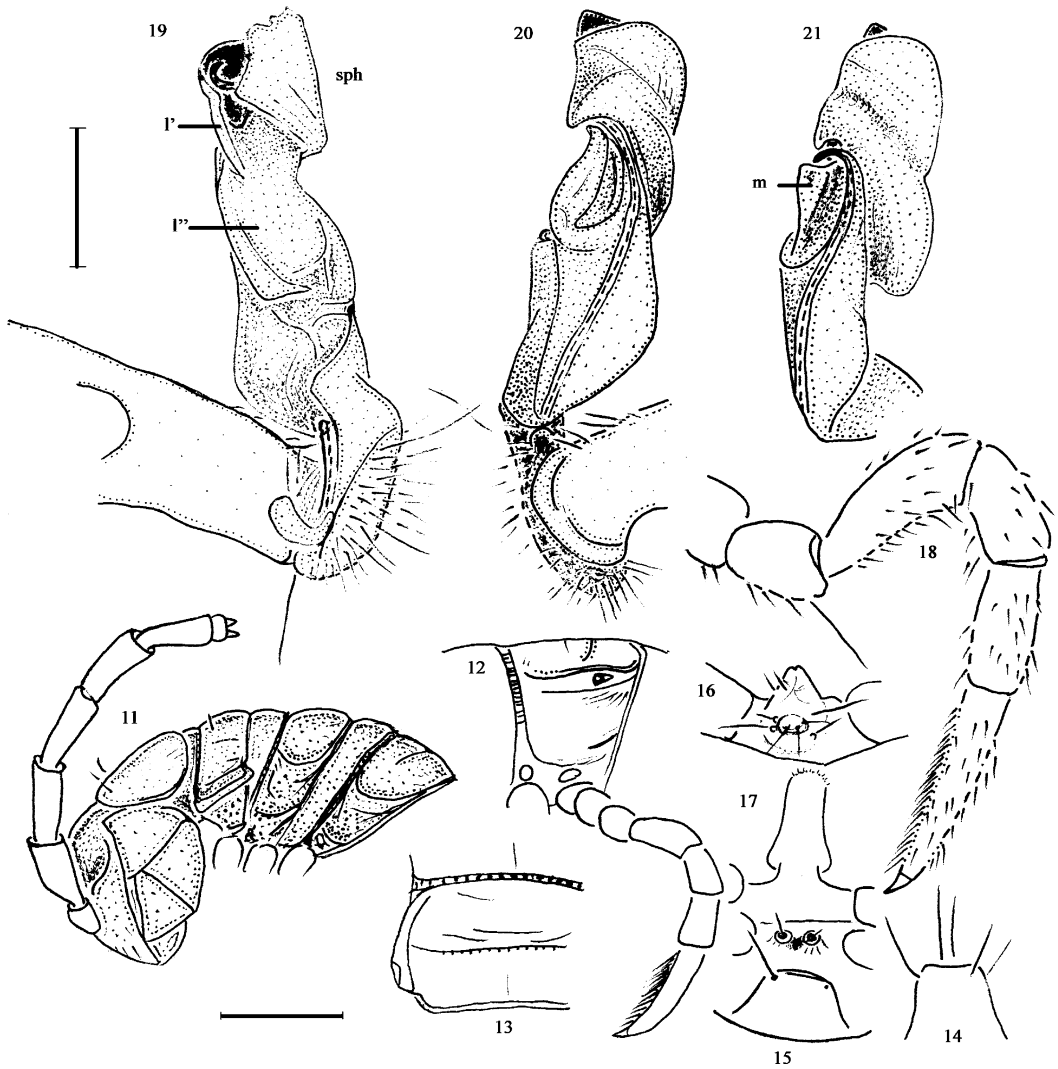
Other material. 1♂, 2♀ (NSYSUB-DI 193–195), 1♂, 1♀ (ZMUM), same locality and date, together with holotype. 2♂, 1♀ (NMNS 4418-002), Nantou County, LuGu, FengHuangGu, at bamboo forests in birds garden, ca 734 m a.s.l., 29 April 1996, leg. W.-H. Chou. 7♂, 2♀ (NMNS 4418-003), Nantou County, LuGu, FengHuangGu, lawn region behind the administration building, 734 m a.s.l., 27 January 1996, same collector. 3♀ (NMNS 4418-004), same locality, 29 April 1996, same collector. 1♂ (NMNS 4418-005), same locality, 29 May 1996, same collector. 6♂, 4♀ (NMNS 4418-006), same locality, YinTan, natural forests, February 1997, same collector. 8♂ (NCHUL), Nantou County, RenAi, HueiSun, 1664 m a.s.l., 7 April 1998, leg. S.-H. Wu. 1♀ (NCHUL), same locality, at decayed wood in natural forest, 27 December 1997, same collector. 4♂, 1♀ (NTNUL-My 36–40), Taichung County, HePing, GuGuan, JiaBaoTai, ca 1000–1406 m a.s.l., 25 January 1988, leg. S.-H. Chen. 1♀ (NTNUL-My 45), same locality, date, and collector.

Diagnosis

Differs from congeners by the black-brown coloration, combined with the long antennae, the metatergal transverse sulcus on segments 4–19, some other peculiar somatic characters (see below and key), and the gonopod telopodite tip consisting of only one large lobe with up to three marginal, shallow lobules.

Description

Length ca 19–25 (♂, *n*=10) or 22–29 mm (♀, *n*=6); width of metazonite 10 ca 1.5–2.0 (♂) or 2.0–2.5 mm (♀). Neotype ca 22 mm long and 1.7 mm wide. Coloration in alcohol black-brown; usually a wide, dark brown, axial, moniliform stripe broadened subtrapeziform on metaterga, sometimes visible only on metatergum 19; calluses in ozopore region, pleurosternal region and epiproct similarly dark brown; antennae increasingly blackish



Figures 11–21. *Nedyopus pectinatus* (Wang, 1957), male near-topotype from SihLeng (11–16, 18–21) and male from HueiSun Farm (17). (11) Anterior body portion, lateral view. (12) Segment 10, lateral view. (13) Left half of metatergum 10, dorsal view. (14) Epiproct, dorsal view. (15) Hypoproct, ventral view. (16, 17) Sternal lobe between coxae 4, ventral view. (18) Leg 15. (19–21) Left gonopod, medial, lateral, and dorsal views, respectively. sph, solenophore; l', l'', lobes of solenophore; m, lobe at base of solenomere. Scale bars: 1.0 mm (11–13); 0.5 mm (14–18); 0.3 mm (19–21).

distally, but tip contrastingly pallid; hypoproct, sterna and distal podomeres light to light brown; basal podomeres lighter, yellow to yellow-brown. Coloration faded to milky yellow-brown upon long preservation in alcohol. Coloration of ♀ usually somewhat lighter, but paraterga, tergal parts adjacent to paraterga, pleurosternal region and epiproct brown; basal podomeres pallid to light yellow-brown.

Main somatic and gonopod characters as in *N. hsientienensis*, but width of head=" segments 5–16 >> collum = 4 > 2 > 3 in ♂, or head (broadest) >> collum = 2 = 4 > 3 < 5 < 6 < 7–16 in ♀. Antennae relatively long, slender, reaching from stricture to end of segment 4 dorsally in ♂ (Figures 11, 64), a little shorter in ♀, reaching from stricture of segment 3

dorsally. Paraterga very poorly developed (Figures 11–13, 64–67), calluses virtually without denticles; calluses delimited by a sulcus both dorsally and ventrally, though ventral sulcus much finer than dorsal one, only present on segments 5, 7, 9–19, sometimes visible also on segment 8, a little more evident on pore-bearing segments; paraterga like more (pore-bearing segments) or less (poreless segments) evident ridges, slightly surpassing caudal tergal contour only on segment 2 (Figures 11, 64). Axial line from visible in places (♂) or wanting (♀) to evident from anterior part of collum to end of segment 19. Transverse sulcus on segments 4–19 in ♂, on segments 5–19 in ♀, usually only traceable, but sometimes wanting on segment 19, nearly reaching base of paraterga 4, 6, and 19, reaching the base on other segments (Figures 11–13, 65–67) in ♂, but only reaching base of paraterga 9, 10, 12, 13, and 15 in ♀. Surface of anterior halves of metaterga transversely rugose to rugulose (Figures 12, 13, 65–67); rear halves of metaterga 18 and 19 in ♂ smooth to rugose, collum and anterior metaterga rugulose; rear halves of metaterga rugose from midbody segments to segment 19 in ♀; metazona below paraterga rugulose sublongitudinally over posterior halves, evidently granular until segment 7, thereafter increasingly poorly granulose subcaudally on segments 8–18, the grains remaining only on, but not above, pleurosternal carinae on segments 5 and 6, sometimes evidently granular only until segment 5 in ♂, evidently granular only until segment 4 in ♀. Tergal setae short, pattern 2+2 anteriorly on collum and 1+1 also anteriorly on segment 2, onward abraded. Pleurosternal carinae evident on segments 2–7, like narrow rounded ridges on segments 2–4 (Figures 11, 64), like wider ridges on segments 5 and 6, with small but evident teeth caudally on segments 2 and 6, like a particularly prominent caudal tooth still failing to surpass rear contour on segment 7; thereafter carinae increasingly poorly developed, expressed like low rugulose bosses, until segment 10 more or less clearly delimited dorsally by a curved shallow sulcus or line, devoid of caudal teeth (Figures 12, 67); sometimes carinae rather well visible on segments 2–7, like narrow rounded ridges on segment 2, like wider ridges on segments 3 and 6, without teeth caudally on segments 2 and 6, but always with a particularly prominent caudal tooth on segment 7 in ♂, evident and like narrow rounded ridges on segments 2–4 in ♀. Epiproct very long in lateral view, ratio of epiproct length to pre-epiproct length of telson 1:1.9 (Figure 69), very faintly emarginate in dorsal view; pre-apical papillae evident to nearly wanting (Figures 14, 68). Hypoproct (Figures 15, 70) roundly subtrapeziform, 1+1 setae at caudal corners situated on very small, well-separated knobs.

Sterna not modified except for a subtriangular, very narrowly notched to rather broad, more or less long, linguiform, setose lamina between ♂ coxae 4 (Figures 16, 17, 71, 72) and a paramedian pair of strong setae between ♂ coxae 5 (Figures 17, 72); subsequent pregonopodial sterna with traces of paramedian pairs of bunches of long setae.

Legs 1 to those of segments 14–17 with tarsal brushes (Figure 18), setation gradually thinning out toward telson, usually replaced by relatively modest setation after segment 15 in ♂. Legs long, mostly >2 (♂) (Figures 12, 67) or ca 1.5 times (♀) as long as midbody height.

Gonopods (Figures 19–21, 103–108) complex, much as in *N. hsientienensis*, but lamella **1** with a smooth margin, divided in the middle into two similarly sized parts, end of **sph** either not divided into distinct lobes (Figure 19) or consisting of three lobules: **A** and an emarginate **B**, latter forming a separate **D** (Figures 103–105); a small lamina (**m**) present at base of solenomere on dorsal side.

Remarks

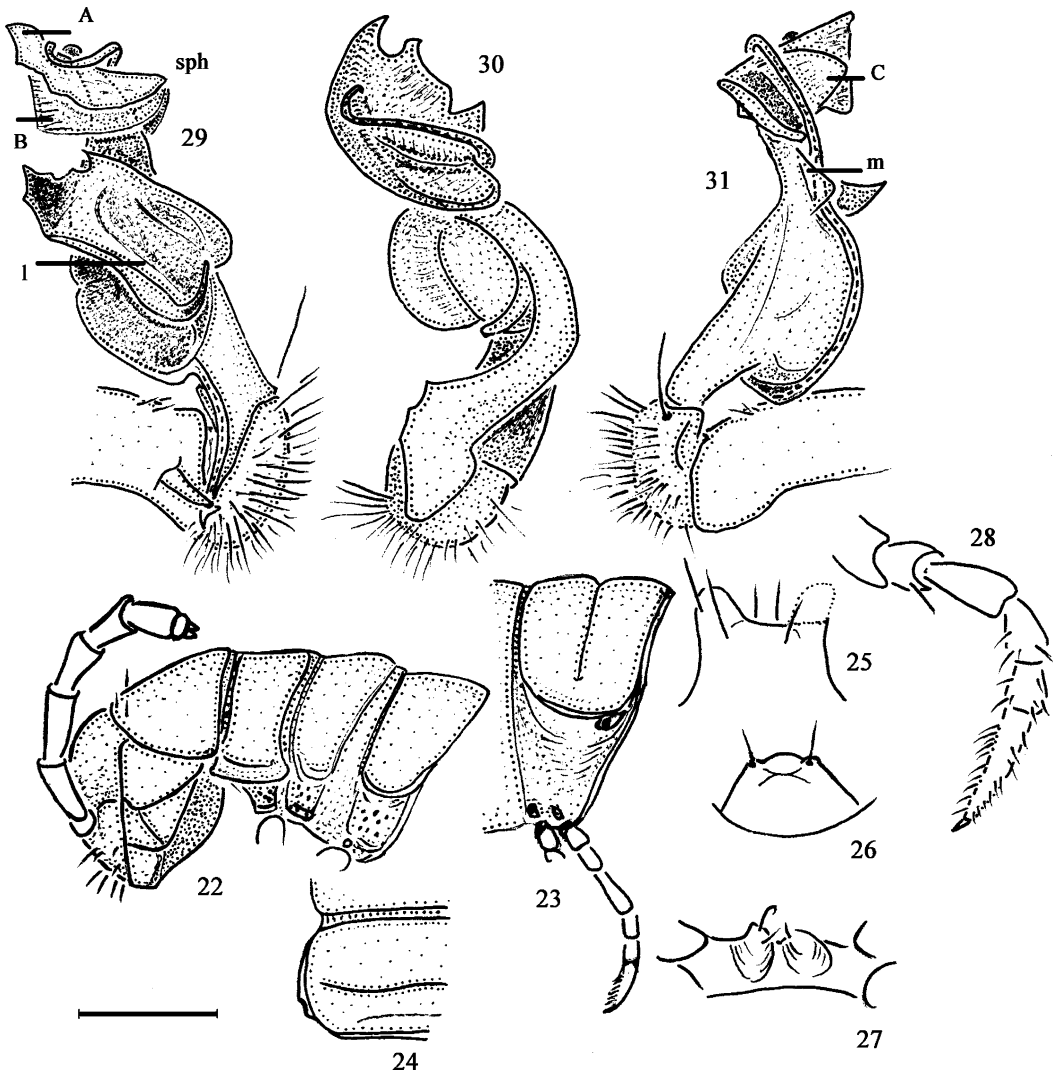
The neotype was collected from about 30 km south of the type locality. Although the original description of this species (Wang 1957b) is even poorer than that of the previous

species, all of the characters that are mentioned or illustrated tally, such as body size, the dark brown coloration with a non-contrasting lighter pattern, and even the gonopod outlines, with an easily recognizable lobe I'.

Nedyopus caudatus, new species

(Figures 22–31, 73–80, 109–114)

Holotype: ♂ (NSYSUB-DI 390), Taiwan (R.O.C.), PingTung County, UTai, ALi, 1600 m a.s.l., 19 January 2005, leg. M.-H. Syu. Paratypes: 1♂, 5♀ (NSYSUB-DI 391–396), 1♂, 1♀



Figures 22–31. *Nedyopus caudatus* n. sp., male paratype from Syuan. (22) Anterior body portion, lateral view. (23) Segment 12, lateral view. (24) Left half of metatergum 12, dorsal view. (25) Epiproct, dorsal view. (26) Hypoproct, ventral view. (27) Sternal cones between coxae 4, ventral view. (28) Leg 19. (29–31) Left gonopod, medial, ventral, and lateral views, respectively. sph, solenophore; l, A, B, C, lobes of solenophore; m, lobe at base of solenomere. Scale bar: 1.0 mm (22–24); 0.5 mm (25–28); 0.25 mm (29–31).

(ZMUM), same place, date, and collectors as the holotype. 1♀ (NSYSUB-DI 229), Kaohsiung County, TaoYuan, JhongJhihGuan 2024 m a.s.l., 19 October 2002, leg. H.-W. Chang. 1♂ (JDLee 20021114001), NanTou County, LuGu, SiiTou, ShenMu walking path, 1058 m a.s.l., 15 November 2002, leg. J.-D. Lee. 2♀ (NMNS 4418-007), same county FengHuangGu, lawn region behind the administration building, 1698 m a.s.l., 24 August to 25 September 1996, leg. W.-H. Chou. 3♀ (NMNS 4418-008), same locality, YinTan, natural forest, ca 750 m a.s.l., 25 August to 26 September 1996, same collector. 2♀ (NMNS 4418-009), same locality and collector, February 1997. 3♂, 2♀ (NCHUL), same county, RenAi, HueiSun Farm, 1664 m a.s.l., 27 November 1997, leg. S.-H. Wu. 2♂ (NCHUL), same locality, in decayed wood in natural forest, 1664 m a.s.l., 27 December 1997, same collector. 1♀ (NMNS 4418-010), Taichung City, TungHai University, in decayed branches and leaves, ca. 100 m a.s.l., 26 March 2000, collector unknown. 1♀ (NSYSUB-DI 231), Chia-I County, ALiShan, ALiShan, LongTou, in bamboo forest, 1300 m a.s.l., 21 April 2002, leg. J.-L. Chao. 1♀ (TFRI), Ilan County, DaTong, SihJi forest path, JiaLuo Lake, 2000 m a.s.l., date unknown, leg. W.-C. Ye. 1♂, 4♀ (NSYSUB-DI 223–227), Taichung County, HePing, Syuan, no. 710 forest path, ca 2050–2100 m a.s.l., 21 August 2002, leg. C.-C. Chen and Y.-H. Lin. Non-type: one juvenile (NSYSUB-DI 228), same place, date, and collector as for holotype, five juveniles (NSYSUB-DI 399–403).

Diagnosis

Differs from congeners by the widely bifid epiproct, the pleurosternal carinae only on segments 2–4, the sternum between ♂ coxae 4 with two cones, the tarsal brushes missing, as well as in some more somatic and gonopod characters (see below and key).

Description

Length ca 21–30 (♂, $n=5$) or 19–32 mm (♀, $n=10$); width of midbody metazona 1.5–3.0 (♂) or 2.0–3.5 mm (♀). Holotype ca 30 mm long and 2.8 mm wide.

Coloration in alcohol light brown, marbled; antennae increasingly blackish distally, but tip contrastingly pallid; head, collum, segments 2–4 slightly darker brown; a wide, yellow to whitish, axial stripe moniliform, broadened subtrapeziform on metaterga; paraterga and entire region below, including sterna and legs, rather light brown to pallid. Coloration of ♀ usually much lighter brown to pale brown, colour pattern same in both sexes.

Main somatic and gonopod characters as in *N. hsientienensis*, but width of head = segment 5 > 2 > collum = 4 > 3 < 6–16 in ♂, or either head ≥ collum = 4 < 2 > 3 < 5 ≤ 6 ≤ 7–15 or head = 3 < collum > 2 > 4 < 5 ≤ 6 ≤ 7–15 in ♀, segments (6)7–15(16) always being broadest. Antennae short but slender, reaching midway of metatergum 2 dorsally in ♂ (Figures 22, 73, 74). Paraterga very poorly developed (Figures 22–24, 74–76); calluses only delimited by a clear-cut sulcus dorsally; starting from segment 6, sometimes a more or less poorly developed line in place of a ventral sulcus; calluses mostly like low ridges (poreless segments) or flat discs (pore-bearing segments), slightly surpassing caudal tergal contour only on segment 2 (Figures 22, 74). Paraterga with two to three minute denticles at lateral margin. Axial line evidently visible on anterior metaterga, onward poorly visible in places, usually present in ♂, sometimes wanting to just traceable (on midbody metaterga) in ♂. Transverse sulcus sometimes present up to segment 17 in ♀, very finely beaded at bottom, not reaching base of paraterga (Figures 23, 24, 75, 76). Surface rugulose in places;

metazona below paraterga usually evidently and densely granulose on segments 2–19 (♂) or 2–18 (♀), particularly on segments 2–7 (Figure 22) (♂) or only on segments 2–3 in (♀), thereafter granulation sometimes barely traceable until segment 13 (♀) or 14 (♂, ♀). Stricture between pro- and metaterga evidently but not very strongly beaded. Tergal setae short, pattern 2+2 anteriorly on collum, sometimes abraded (usually in ♀), onward always abraded. Ozopores lateral, lying on callus ca one-quarter metatergal length from caudal edge (♂) (Figures 23, 24, 75, 76). Pleurosternal carinae present, slightly reduced in ♀, like wide rounded ridges on segments 2–4, thereafter increasingly poorly developed, like low bosses traceable until segments 7 (♂) (Figures 22, 23, 74, 76) or 5 (♀), further on virtually missing; sometimes the carinae like narrow ridges on segments 2–4, like rounded ridges on segments 5–7, with small but evident teeth caudally only in ♂. Epiproct very long in lateral view, ratio of epiproct length to pre-epiproct length of telson 1:1.9 in ♂ (Figure 78), in dorsal view widely bifid; pre-apical papillae wanting (Figures 25, 77). Hypoproct roundly (♂) or straightly (♀) subtrapeziform (Figures 26, 79), sides straight (♂) or concave (♀) at base.

Sterna sparsely setose, not modified except for two setose cones between ♂ coxae 4 (Figures 27, 80).

Male legs without tarsal brushes (Figure 28). Legs short, nearly as long as midbody height (♀), slightly longer in ♂ (Figures 23, 76).

Gonopods (Figures 29–31, 109–114) complex, much as in *N. hsientienensis*, but lamella **1** larger and carrying a smooth to denticulate margin in distal part, not divided into two parts, end of **sph** divided into three distinct lobes: a denticulate **A**, and rugulose **B** and **C**.

Etymology

To emphasize the particular tip of the epiproct.

Nedyopus latus, new species

(Figures 32–41, 81–88, 115–120)

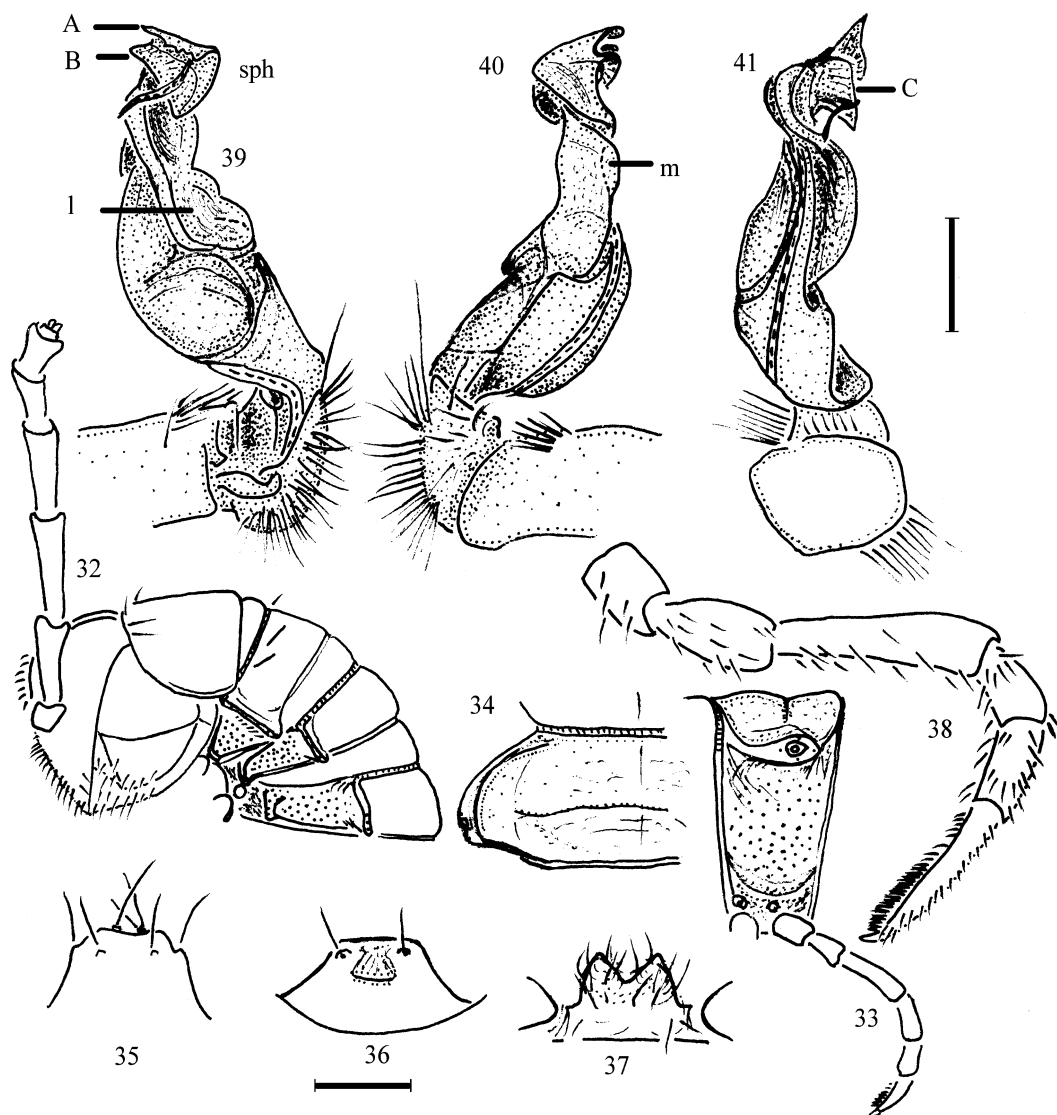
Holotype: ♂ (NCHUL), Taiwan (R.O.C.), NanTou County, LuGu, SiiTou, bamboo forest, ca 1160–1398 m a.s.l., 31 October 1997, leg. S.-H. Wu. Paratypes: 2♂, 9♀ (NCHUL), same locality and date, together with holotype. 4♂, 4♀ (NCHUL), same county, RenAi, HueiSun, decayed wood in natural forest, 1664 m a.s.l., 27 December 1997, same collector. 2♂, 1♀ (NTNUL-My 46–48), Taichung County, HePing, GuGuan, JiiaBaoTai, ca 1000–1406 m a.s.l., 25 January 1988, leg. S.-H. Chen. 1♀ (JDLee20021114010), same county, LuGu, SiiTou, TuDiGongLun walk path, ca 1160–1398 m a.s.l., 15 November 2002, leg. J.-D. Lee.

Diagnosis

Differs from congeners by the larger size, combined with the rather well-developed paraterga; an axial line is evident from the collum to the tip of the epiproct, and the gonopod femorite is rather narrow basally (see below and key).

Description

Length ca 26–29 (♂, $n=5$) or 29–31 mm (♀, $n=5$); width of midbody metazona 3.5–4.0 (♂) or 4.0–4.8 mm (♀). Holotype ca 27 mm long and 3.5 mm wide.



Figures 32–41. *Nedyopus latus* n. sp., male paratype from SiiTou. (32) Anterior body portion, lateral view. (33) Segment 10, lateral view. (34) Left half of metatergum 10, dorsal view. (35) Epiproct, dorsal view. (36) Hypoproct, ventral view. (37) Sternal cones between coxae 4, ventral view. (38) Leg 14. (39–41) Left gonopod, medial, lateral, and dorsal views, respectively. sph, solenophore; l, A, B, C, lobes of solenophore; m, lobe at base of solenomere. Scale bars: 1.0 mm (32–34); 0.5 mm (35–38); 0.3 mm (39–41).

Coloration in alcohol dark brown to grey-brown in both sexes, prozona light grey-brown to grey-brown, with posterior parts near stricture darker grey-brown; sometimes axial line light brown to blackish; epiproct light grey-brown to light brown; paraterga light grey-brown to light brown, pleurotergal region lighter grey-brown to brown, pleurosternal region lighter grey-brown to light brown, sterna light grey-brown, basal segments of legs lighter grey-brown, distal podomeres dark brown to brown.

Main somatic and gonopod characters as in *N. caudatus*, but width of head=segment 3=4<collum<2≤6=8=11=14<5=7=9=10=12–15 in ♂, or head<collum=3=4<2<5=6<7–15 in ♀. Antennae long, slender, reaching stricture of metatergum 4 dorsally in ♂ (Figures 32, 81, 82), a little shorter in ♀, reaching anterior part of metatergum 3. Paraterga rather well developed (Figures 32–34, 81–86), slightly declined, narrowed distad; calluses with four minute pits (insertion points of abraded setae) at lateral margin (Figures 32–34) on collum and pore-bearing segments, three pits on segments 2, 3, and poreless segments, sometimes poorly expressed on segment 19; calluses delimited by a sulcus both dorsally and ventrally, but a line in place of ventral sulcus on poreless segments; calluses mostly like high ridges (poreless segments) or flat but evident discs (pore-bearing segments), never spiniform caudally. Axial line evident on collum to end of segment 19 or even up to end of epiproct. Transverse sulcus reaching base of paraterga, visible on segment 19, beaded at bottom on segments 5–17, especially poorly beaded on segment 18 (Figures 33, 34, 83, 84). Surface sometimes transversely rugulose on metaterga (Figure 34), longitudinally rugulose at posterior end of metaterga and on metazona below paraterga, where also evidently and densely granular (Figures 32, 33, 82). Stricture between pro- and metaterga evidently but not very strongly beaded, general appearance of body non-moniliform; stricture slightly wider and deeper in ♂. Tergal setae short, pattern 2+2 anteriorly on collum, 2+2 anteriorly on segment 2, 1+1 on segment 3 (often the setae abraded), onward always abraded. Ozopores lateral, lying on callus ca one-third metatergal length from caudal edge (Figures 33, 34, 83, 84). Pleurosternal carinae present, like wide rounded ridges on pregonopodial segments (♂), with a small caudal tooth on segment 5, with a larger one on segment 6 and a particularly prominent one on segment 7, all granular, sharp and triangular, nearly reaching caudal metazonal margin (♂), or like narrow ridges on segments 2–4 (♀), onward increasingly poorly developed, like low bosses traceable until segment 15 or 16 in ♂ (Figures 32, 33, 82, 84) or until segment 9 in ♀, thereafter virtually missing. Epiproct long in lateral view, ratio of epiproct length to pre-epiproct length of telson 1:2.6 in ♂ (Figure 86), in dorsal view subtruncate, slightly emarginate; pre-apical papillae evident, rather close to apex (Figures 35, 85). Hypoproct straightly to roundly subtrapeziform (Figures 36, 87), 1+1 setae at caudal corners situated on very small knobs, sides concave.

Sterna sparsely setose, more sparsely in ♀, not modified except for a deeply notched, setose, rather high lamina between ♂ coxae 4 (Figures 37, 88), as well as paramedian bunches of strong setae between ♂ coxae 5–7.

Male legs 1 to those of segment 14 or 15 with tarsal brushes (Figure 38), setation gradually thinning out toward telson, becoming relatively modest after segments 15 or 16. Legs relatively long, ca 1.5 (♂) (Figures 33, 84) or 1.2 times (♀) longer than midbody height.

Gonopods (Figures 39–41, 115–120) complex, much as in *N. caudatus*, but femorite narrower at base, and distal part of 1 not denticulate.

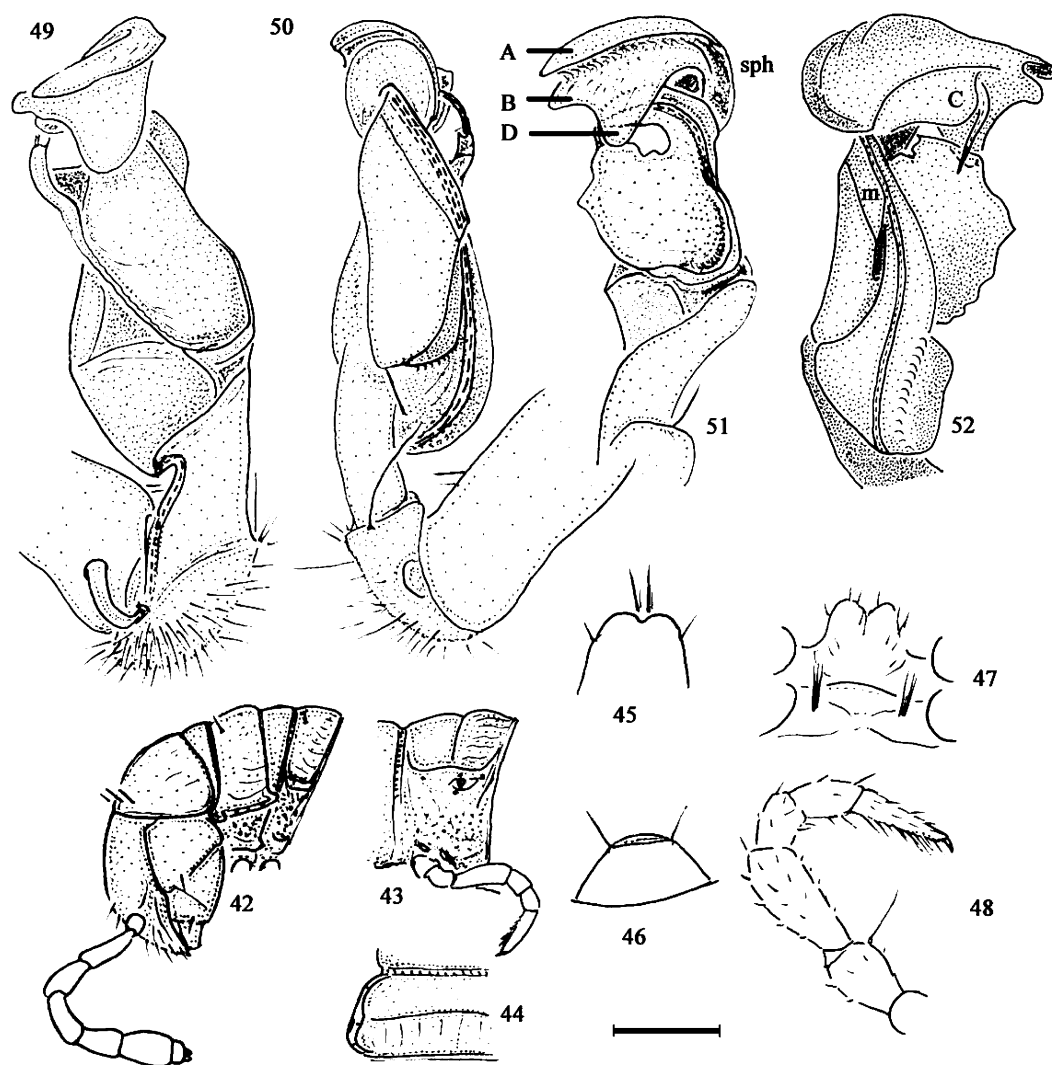
Etymology

To emphasize the relatively wide paraterga.

Nedyopus wui, new species

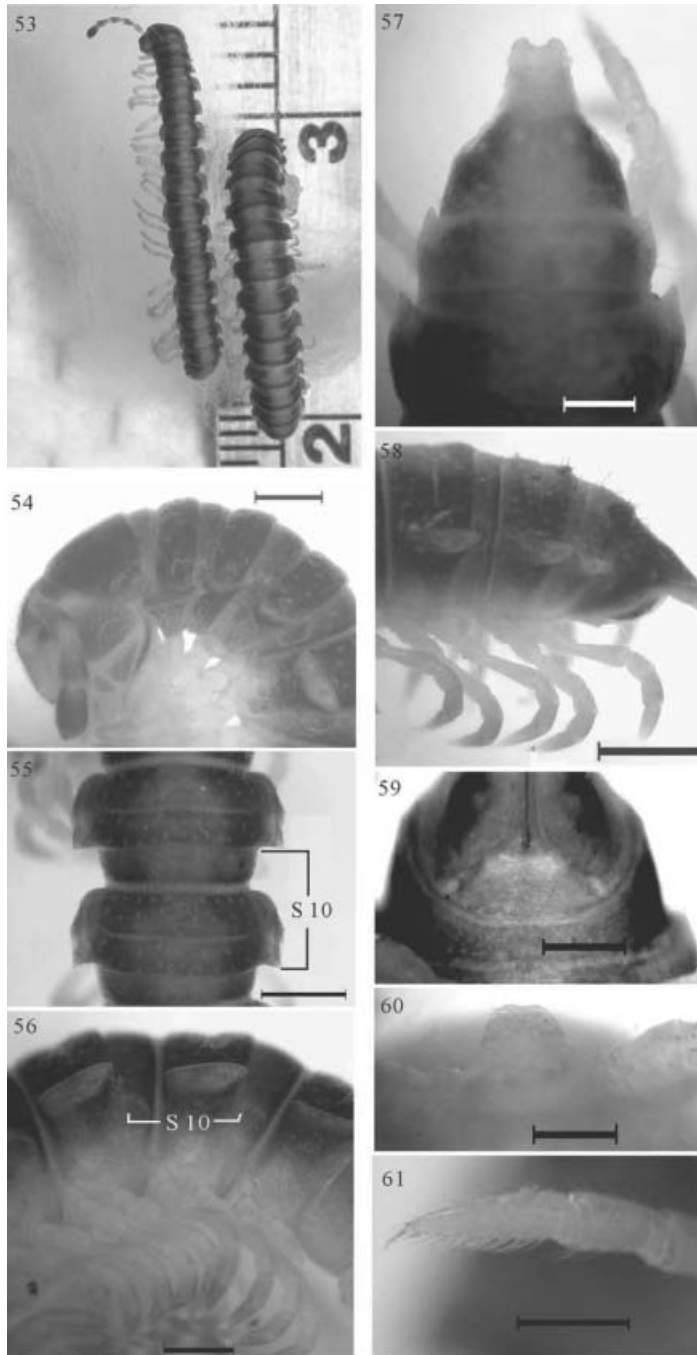
(Figures 42–52, 89–96, 121–126)

Holotype: ♂ (NSYSUB-DI 232), Taiwan (R.O.C.), Nantou County, RenAi, HuaGer water source, 2553 m a.s.l., under stones, 22 August 2002, leg. C.-C. Chen and Y.-H. Lin.

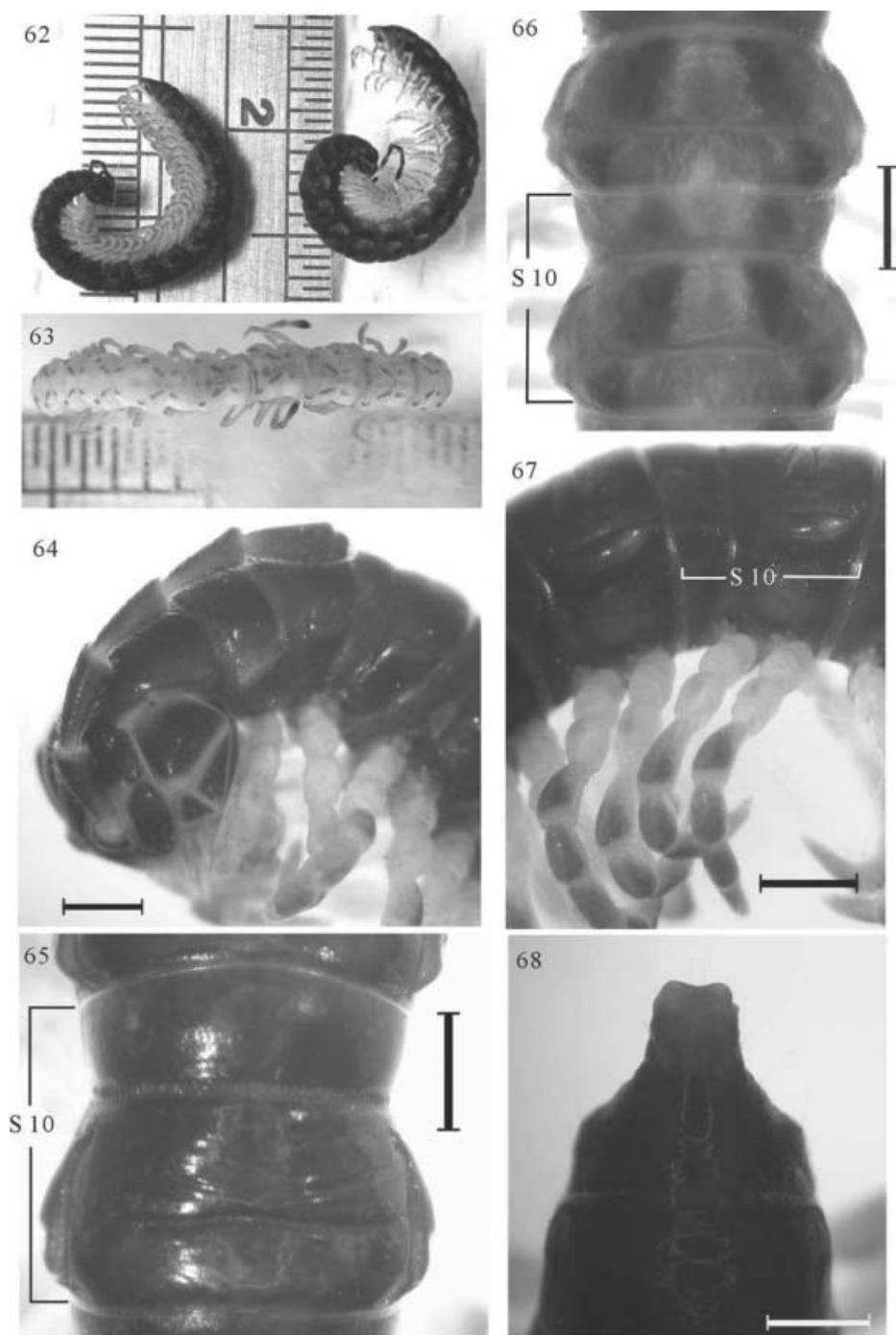


Figures 42–52. *Nedyopus wui* n. sp., male paratype from Syuan. (42) Anterior body portion, lateral view. (43) Segment 10, lateral view. (44) Left half of metatergum 10, dorsal view. (45) Epiproct, dorsal view. (46) Hypoproct, ventral view. (47) Sternal structures between coxae 4 and 5, ventral view. (48) Leg 13. (49–52) Left gonopod, medial, lateral, ventral, and dorsal views, respectively. sph, solenophore; A, B, C, D, lobes of solenophore; m, lobe at base of solenomere. Scale bar: 1.0 mm (42–44); 0.5 mm (45–48); 0.2 mm (49–52).

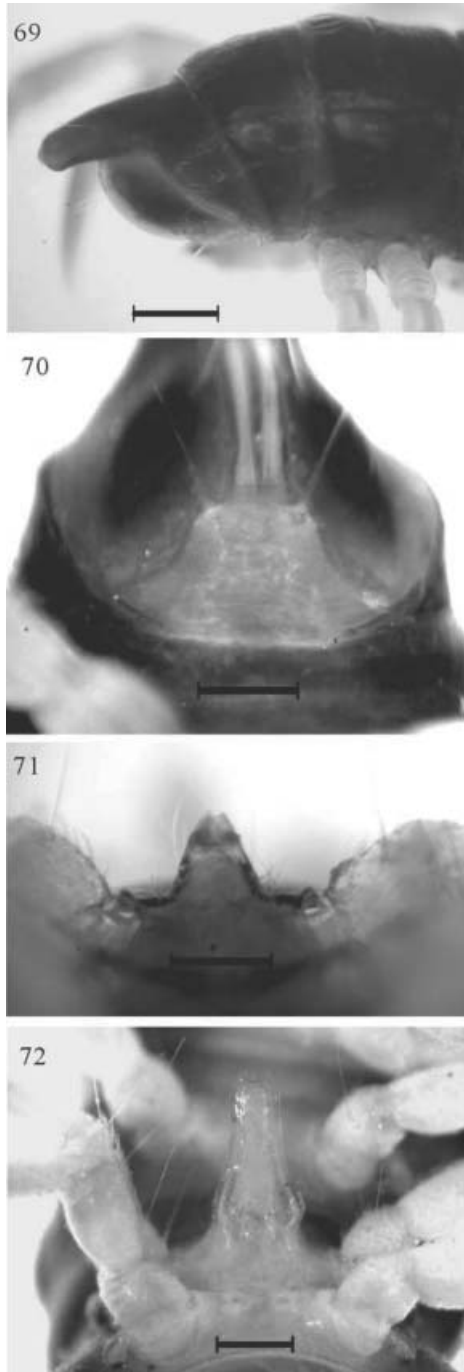
Paratypes: 1♂, 2♀ (NSYSUB-DI 233–235), 1♂, 1♀ (ZMUM), same locality and date, together with holotype. 2♂ (NSYSUB-DI 238–239), Taichung County, HePing, Syuan, no. 710 forest path, ca 2050–2100 m a.s.l., 21 August 2002, same collector. 1♂ (NMNS 4418-011), same county, AnMaShan, no. 1, fresh wood, 5–10 cm depth, 2000 m a.s.l., 28 May 1996, leg. R.-F. Chao. 1♂ (NMNS 4418-012), same locality, no. 3, rotting wood, 10–15 cm depth, 13 January 1996, same collector. 1♂ (NSYSUB-DI 240), same locality, forested entertainment zone, 7 May 2003, leg. S.-I. Wu.



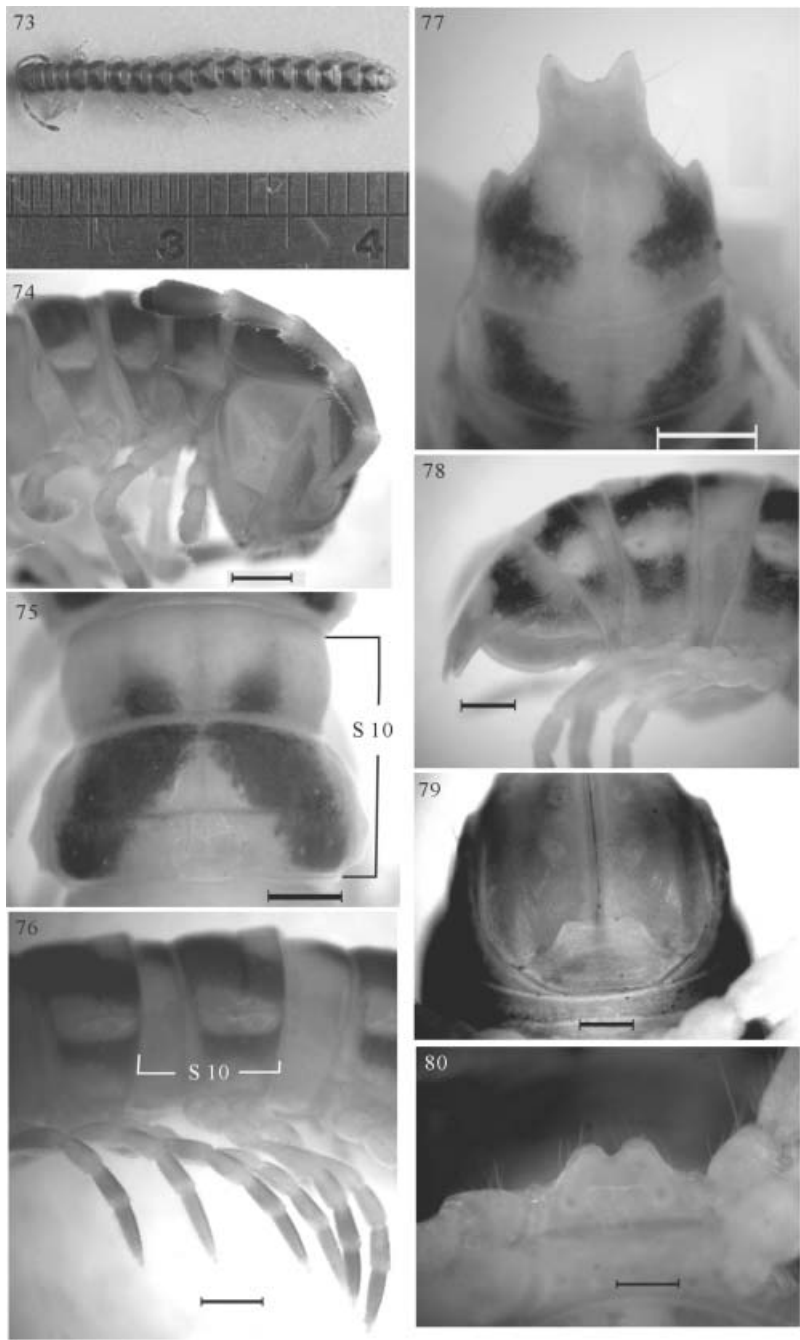
Figures 53–61. *Nedyopus hsientienensis* (Wang, 1957), male from CingShan. (53) Entire body, dorsal view. (54) Anterior body portion, lateral view. (55, 56) Segment 10 (S 10), dorsal and lateral views, respectively. (57, 58) Epiproct, lateral and dorsal views, respectively. (59) Hypoproct, ventral view. (60) Sternal lobe between coxae 4, ventral view. (61) Tarsal brush of right leg 4. Scale bars: 0.4 mm (54–56); 0.3 mm (57); 0.7 mm (58); 0.2 mm (59, 60); 0.2 mm (61).



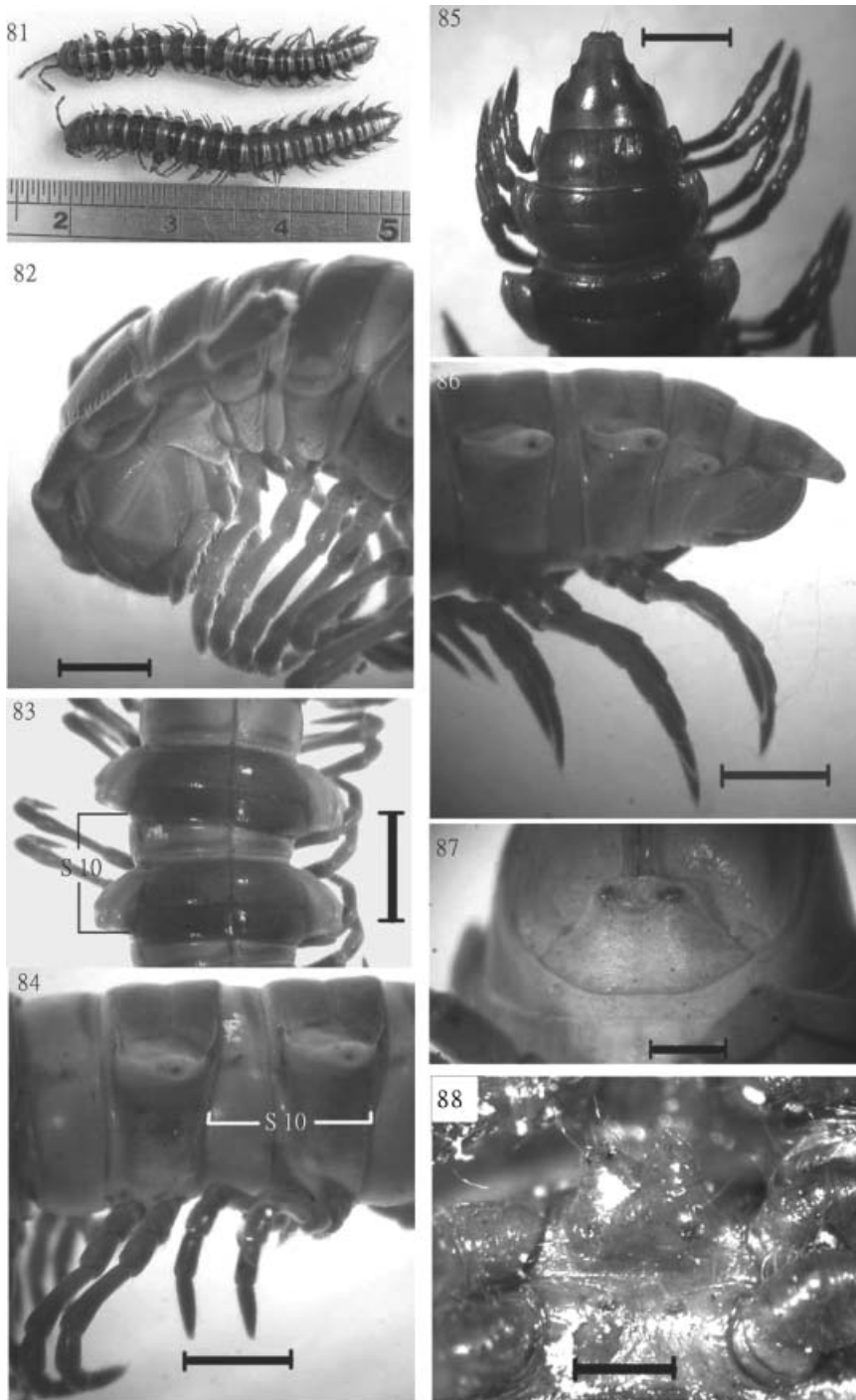
Figures 62–72. *Nedyopus pectinatus* (Wang, 1957), male near-topotype from SihLeng (62, 64, 65, 67–70, 72) and male from FengHuangGu (63), and HuiSun Farm (66, 71). (62, 63) Entire body, dorsal view. (64) Anterior body portion, lateral view. (65, 66) Segment 10 (S 10), dorsal view. (67) Segment 10 (S 10), lateral view. (68, 69) Epiproct, dorsal and lateral views, respectively. (70) Hypoproct, ventral view. (71, 72) Sternal lobe between coxae 4, ventral view. Scale bars: 0.5 mm (64); 0.4 mm (65, 69); 0.7 mm (67); 0.3 mm (66, 68, 71, 72); 0.2 mm (70).



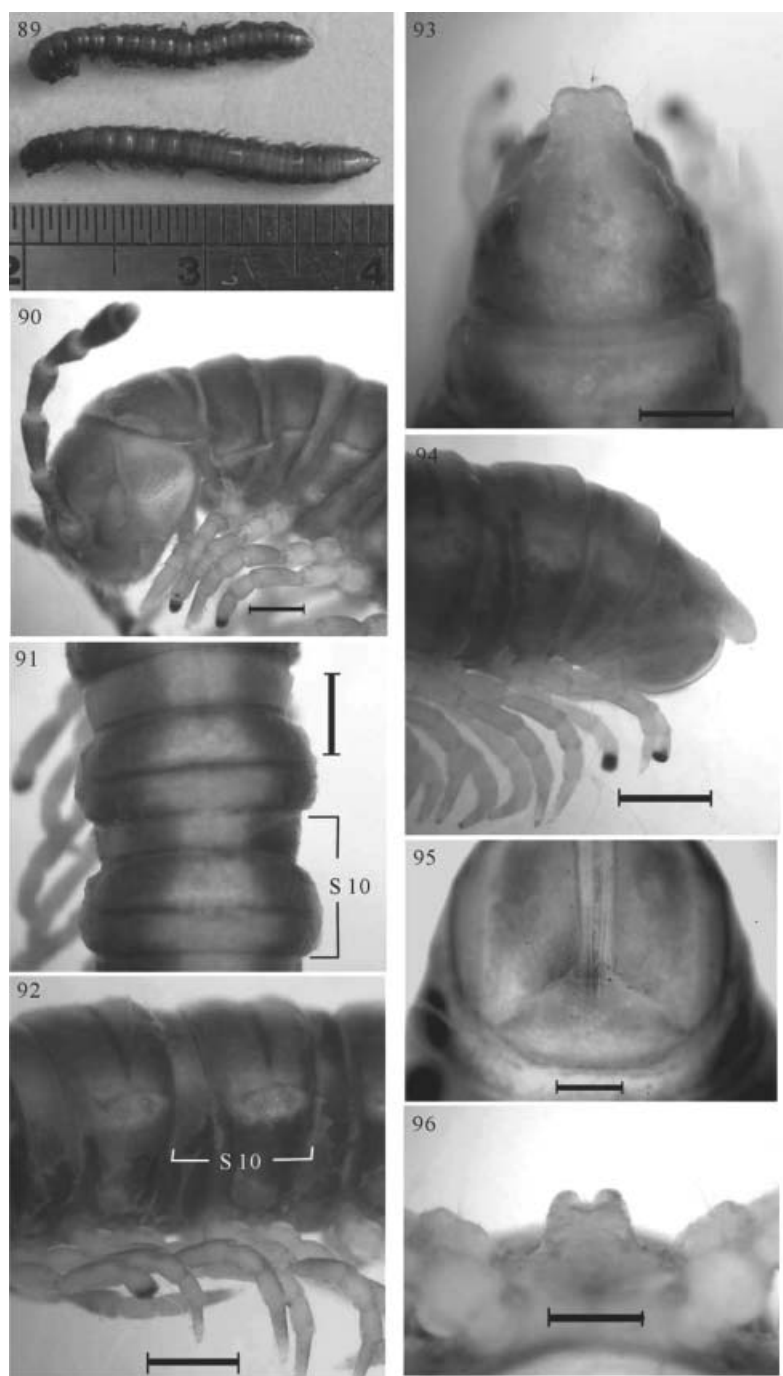
Figures 62–72. (Continued.)



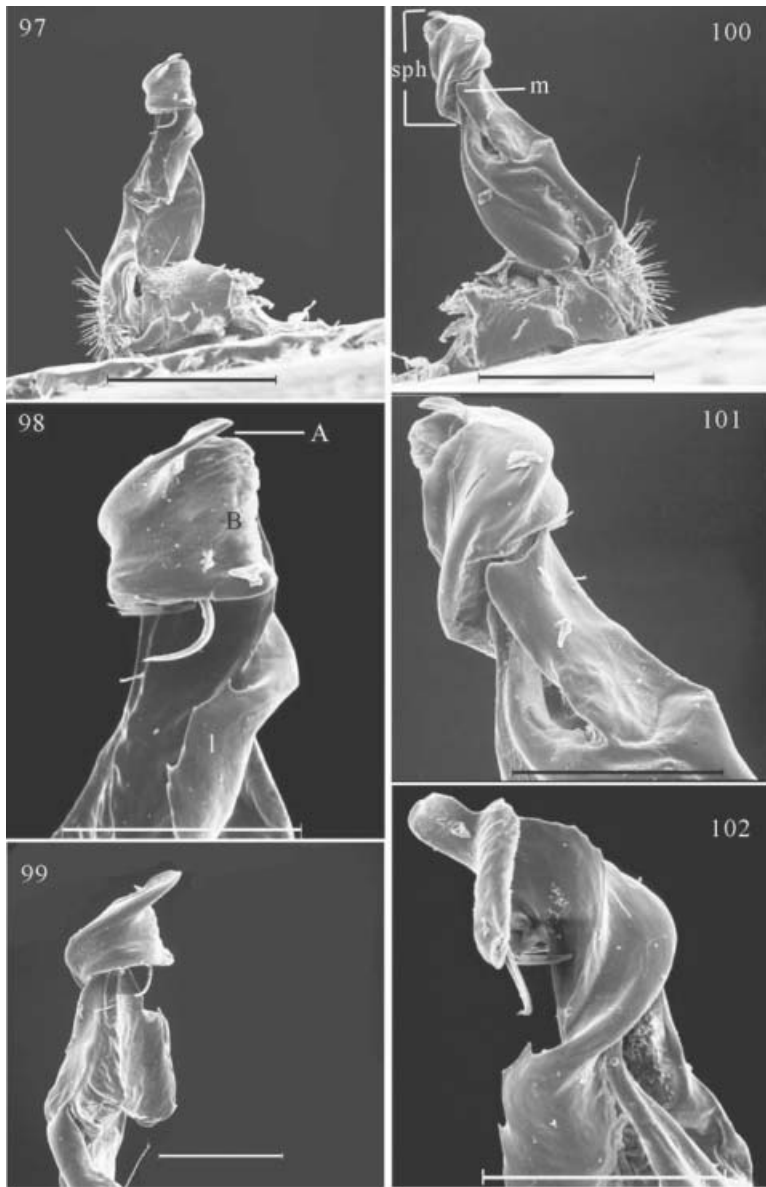
Figures 73–80. *Nedyopus caudatus* n. sp., male paratype from HueiSun Farm. (73) Entire body, dorsal view. (74) Anterior body portion, lateral view. (75, 76) Segment 10 (S 10), dorsal and lateral views, respectively. (77, 78) Epiproct, dorsal and lateral views, respectively. (79) Hypoproct, ventral view. (80) Sternal cones between coxae 4, ventral view. Scale bars: 0.5 mm (74, 76); 0.4 mm (75, 77, 78); 0.2 mm (79, 80).



Figures 81–88. *Nedyopus latus* n. sp., male paratype from SiiTou. (81) Entire body, dorsal view. (82) Anterior body portion, lateral view. (83, 84) Segment 10 (S 10), dorsal and lateral views, respectively. (85, 86) Epiproct, dorsal and lateral views, respectively. (87) Hypoproct, ventral view. (88) Sternal cones between coxae 4, ventral view. Scale bars: 0.8 mm (82); 1 mm (83); 0.7 mm (84–86); 0.3 mm (87); 0.2 mm (88).



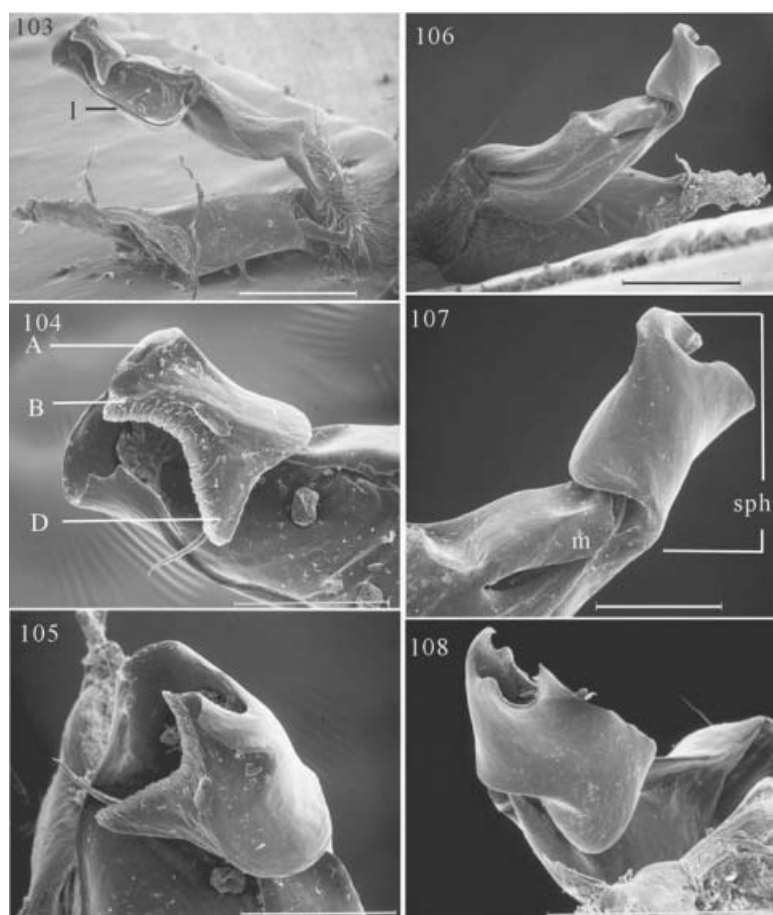
Figures 89–96. *Nedyopus wui* n. sp., male paratype from HuaGer water source. (89) Entire body, dorsal view. (90) Anterior body portion, lateral view. (91, 92) Segment 10 (S 10), dorsal and lateral views, respectively. (93, 94) Epiproct, dorsal and lateral views, respectively. (95) Hypoproct, ventral view. (96) Sternal structures between coxae 4, ventral view. Scale bars: 0.4 mm (90); 0.5 mm (91, 92, 94); 0.3 mm (93, 95, 96).



Figures 97–102. *Nedyopus hsientienensis* (Wang, 1957), male from CingShan, right gonopod. (97, 100) Entire, medial and lateral views, respectively. (98, 99, 101, 102) Telopodite tip, medial, ventral, lateral and dorsal views, respectively. sph, solenophore; l, A, B, lobes of solenophore; m, lobe at base of solenomere. Scale bars: 500 μ m (97, 100); 200 μ m (98, 99, 101, 102).

Diagnosis

Differs from congeners by the short antennae and epiproct, as well as in some other somatic and sexual characters (see below and key), with the tip of the gonotelopodite being supplied with four lobes.

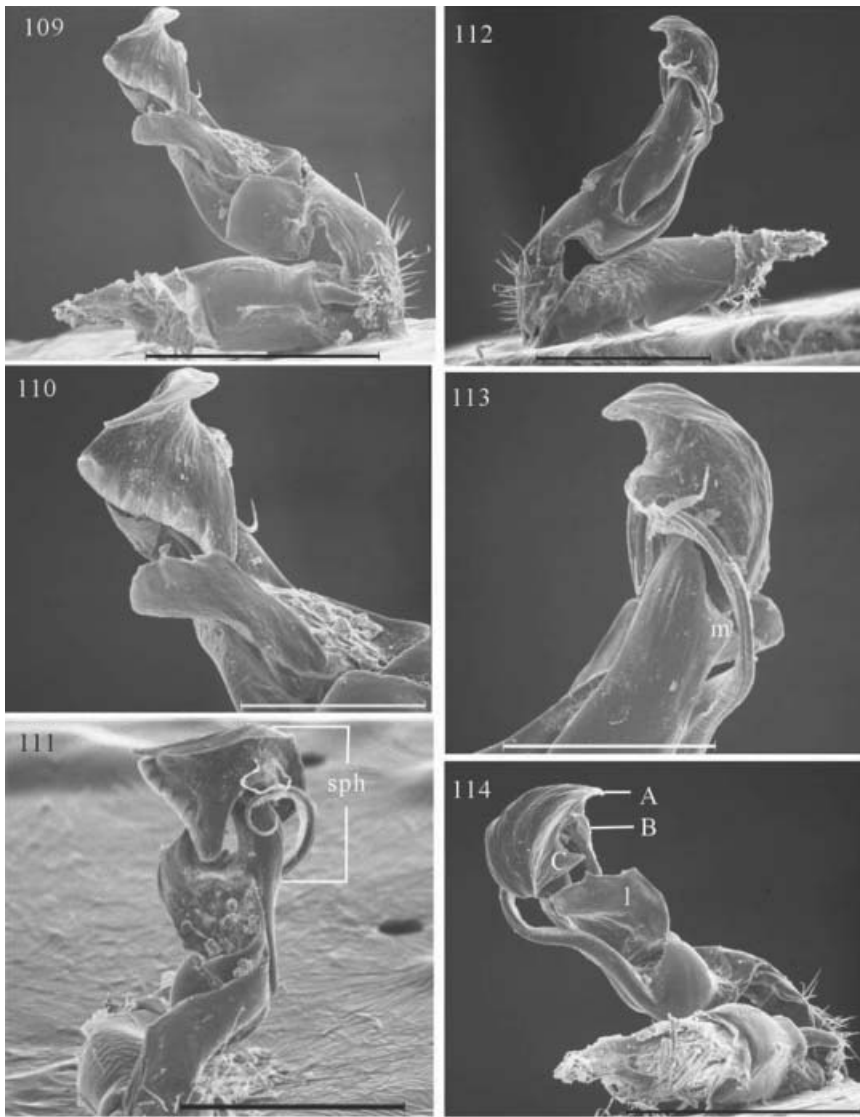


Figures 103–108. *Nedyopus pectinatus* (Wang, 1957), male from FengHuangGu, left gonopod. (103, 106) Entire, medial and lateral views, respectively. (104, 105, 107, 108) Telopodite tip, medial, ventral, lateral, and dorsal views, respectively. sph, solenophore; l, A, B, D, lobes of solenophore; m, lobe at base of solenophore. Scale bars: 500 μ m (103, 106); 200 μ m (104, 105, 107, 108).

Description

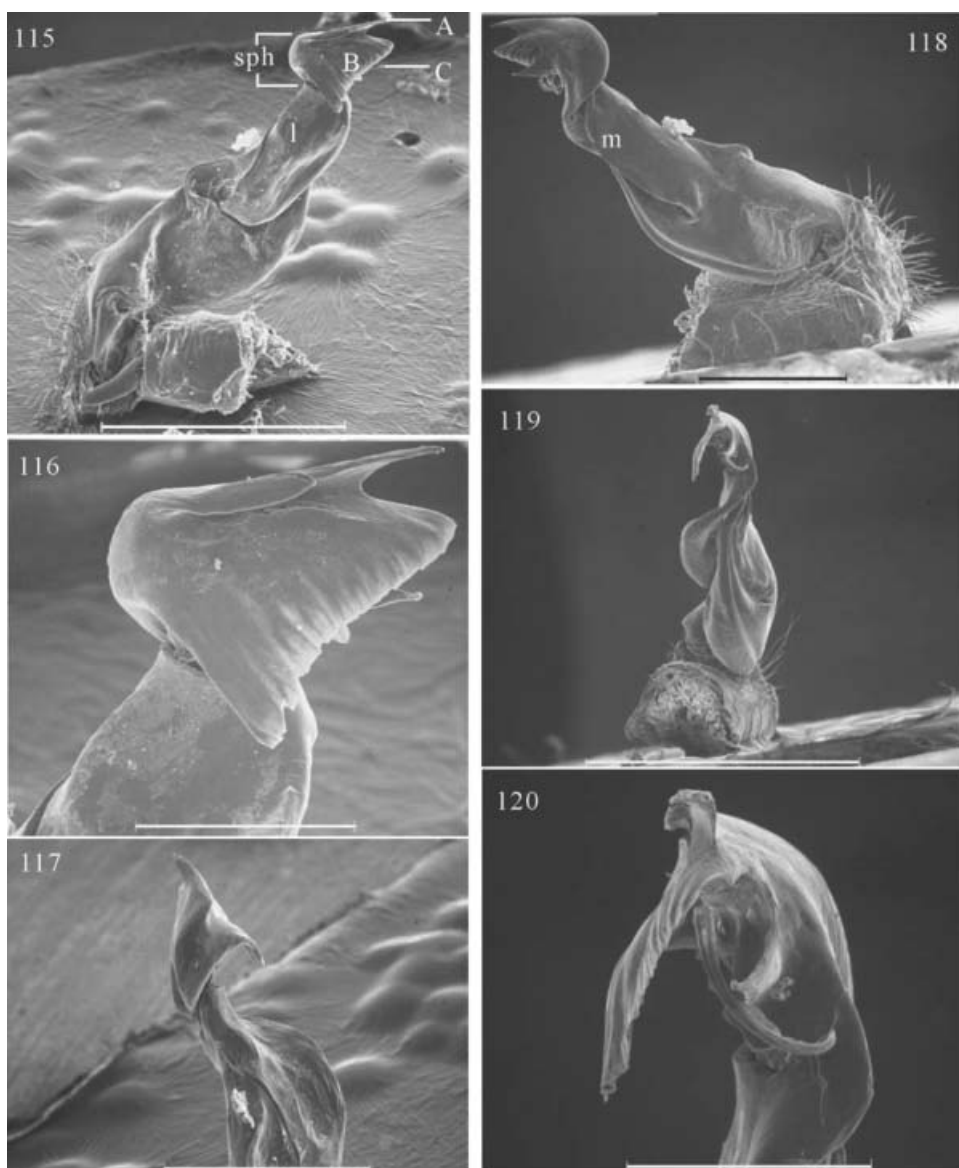
Length ca 16–17 (σ , $n=5$) or 17–19 mm (φ , $n=5$); width of midbody metazona 1.7–1.8 (σ) or 2.0 mm (φ). Holotype ca 16 mm long and 1.7 mm wide.

Coloration in alcohol light brown, sometimes slightly marbled; antennae darker brown, head, collum, segments 2–3 (4) and anterior part of telson brown; a wide, yellow to whitish, axial stripe, sometimes moniliform, broadened subtrapeziform on metaterga; sometimes paraterga similarly pallid also above and a little below calluses; pleurosternal region, sterna and basal segments of legs yellow-brown to light brown, distal podomeres up to basal third tarsi brown, distal third of tarsi pale brown. Coloration of φ usually slightly lighter brown, but axial stripe rather light brown, without being broadened subtrapeziform on metaterga, paraterga similarly lighter brown as body, sterna and basal segments of legs up to basal half of podomeres light brown, distal half of podomeres light yellow-brown, sometimes only distal third tarsi pale brown.



Figures 109–114. *Nedyopus caudatus* n. sp., male paratype from HueiSun Farm, left gonopod. (109, 112, 114) Entire, medial, lateral, and dorsal views, respectively. (110, 111, 113) Telopodite tip, medial, ventral, and lateral views, respectively. sph, solenophore; l, A, B, lobes of solenophore; m, lobe at base of solenomere. Scale bars: 500 μ m (109, 112, 114); 200 μ m (110, 111, 113).

Main somatic and gonopod characters as in *N. caudatus*, but width of head=segment 2=5–16>collum=4>3 in ♂, but head=2=5–16>collum=4>3, or head=2=5–16>collum=3=4 in ♀. Antennae relatively short, clavate, reaching from stricture to end of segment 2 dorsally in ♂ (Figures 42, 90), a little shorter in ♀, only reaching end of collum. Paraterga very poorly developed (Figures 42–44, 90–92), calluses with three to four minute denticles at lateral margin (Figures 42–44), on pore-bearing segments one of these lying just below ozopores, especially poorly expressed on segments 17–19, more evident in ♂ than in ♀; calluses delimited by a sulcus only dorsally, mostly like low ridges (poreless



Figures 115–120. *Nedyopus latus* n. sp., male paratype from SiiTou, left gonopod. (115, 118, 119) Entire, medial, lateral, and dorsal views, respectively. (116, 117, 120) Telopodite tip, medial, ventral, and dorsal views, respectively. sph, solenophore; l, A, B, C, lobes of solenophore; m, lobe at base of solenomere. Scale bars: 1.0 mm (115, 119); 500 μm (117, 118); 200 μm (116, 120).

segments) or flat discs (pore-bearing segments), slightly surpassing caudal tergal contour only on segment 2 (Figures 42, 90). Axial line poorly visible only in places, usually missing. Transverse sulcus clearly (♂) to finely (♀) beaded at bottom, nearly reaching base of paraterga (Figures 43, 44, 91, 92). Surface of only rear halves of metaterga longitudinally rugulose (Figures 42–44), sometimes rugulose only on posterior segments in ♂, metazona below paraterga rugose to rugulose and evidently granular to granulate. Stricture between



Figures 121–126. *Nedyopus wui* n. sp., male paratype from Syuan, left gonopod. (121, 124) Entire, medial and lateral views, respectively. (122) Telopodite tip, medial, ventral, lateral, and dorsal views, respectively. sph, solenophore; A, B, C, D, lobes of solenophore; m, lobe at base of solenomere. Scale bars: 500 μ m (121, 124); 200 μ m (122, 123, 125, 126).

pro- and metaterga roughly beaded, rather deep so that general appearance of body quite moniliform; stricture slightly wider and deeper in ♂. Tergal setae short, pattern 2+2 anteriorly on collum, sometimes abraded (♀), and 1+1 also anteriorly on segments 2 and 3, thereafter abraded. Ozopores more dorsolateral in ♀, lying on callus ca one-third metatergal length from caudal edge (Figures 43, 44). Pleurosternal carinae present, like wide rounded ridges on pregonopodial segments (♂) or on segments 2–4 (♀), thereafter increasingly

poorly developed, like low bosses traceable until segment 16 in ♂ (Figures 42, 43, 90, 92) or until segments 14–16 in ♀, onward missing. Epiproct short in lateral view (Figure 134), ratio of epiproct length to pre-epiproct length of telson 1:3.4 in ♂ (Figure 94), in dorsal view subtruncate, narrowly emarginate only in ♂; pre-apical papillae evident, sometimes nearly wanting in ♂, situated rather close to apex (Figures 45, 93). Hypoproct straightly to roundly subtrapeziform (Figures 46, 95), 1+1 setae at caudal corners situated on very small knobs, sides straight (♂, ♀) to slightly concave (♂).

Sterna modestly setose in ♂, more sparsely in ♀, not modified except for a narrowly notched, linguiform, setose lamina between ♂ coxae 4 and a paramedian pair of bunches of long setae between ♂ coxae 5 (Figures 47, 96).

Male legs 1 up to those of segment 13 with tarsal brushes (Figure 48), setation gradually thinning out toward telson, relatively modest after segment 14. Legs relatively short, about as long as midbody height in ♂ (Figures 43, 92), but only two-thirds midbody height in ♀.

Gonopods (Figures 49–52, 121–126) complex, much as in *N. caudatus*, but femorite with several folds on lateral side, I carrying a smooth to denticulate margin from midway distally; **sph** with four apical lobes (**A**, an emarginate **B** forming a separate lobe **D**, and **C**).

Etymology

Honours Dr Wu Sheng-Hai, Taichung, Taiwan, who provided much material for the present study.

Remarks on distribution and ecology

The island of Taiwan, a part of the island-arc system along the western edge of the Pacific Ocean, lies between the Asian continent and the Philippine Sea basin. The present elevation of Taiwan began ca 4 million years ago as a result of the collision of the Philippine and continental Asian tectonic plates (Page and Suppe 1981; Hsü 1990). Taiwan has an oceanic subtropical climate, being crossed in its middle by the Tropic of Cancer. However, with approximately 30% of its area lying between 1000 and 3000 m a.s.l., and more than 200 peaks above 3000 m in elevation, the mountains in Taiwan encompass a climatic range from subtropical to subarctic (Hsieh and Shen 1944). The tropical and subtropical virgin forests of lowland areas (<1000 m a.s.l.) are dominated by numerous species of *Ficus* and *Machilus*, although large areas of land have been converted to agriculture and plantations. Within the mid-montane belt (1000–2500 m a.s.l.), temperate and warm-temperate broad-leaved forests of *Castanopsis* and *Quercus* are widespread. These gradually give way to mixed montane coniferous forests of *Pinus*, *Chamaecyparis*, and *Taiwania* at higher elevations. The *Tsuga–Picea* forests that dominate the high altitudes of Taiwan (2500–3000 m a.s.l.) are slowly replaced by subalpine *Abies* woodlands toward the timber line, followed thereafter by dwarf bamboo stands of *Yushania miitakayamensis* above 3000 m. Alpine vegetation occurs above 3500 m, with a low scrub community of *Juniperus squamata* and rhododendrons, and a high herb community that is widespread in these barren, rocky areas.

The millipede *Nedyopus hsientienensis* occurs in both northern and southern Taiwan, more frequently in secondary forests dominated by *Acacia confuse*, but also in natural forests at altitudes lower than 750 m a.s.l. The species *Nedyopus pectinatus* inhabits secondary forests, bamboo plantations, and *Ficus–Machilus* woodlands, mainly at middle elevations (700–1700 m a.s.l.), in the mountains of northern and central Taiwan. In

contrast, *Nedyopus caudatus* is widespread in central and southern Taiwan, ranging from low to middle altitudes (100–2100 m a.s.l.). It frequently occurs in plantations, such as bamboo or *Cryptomeria japonica*, as well as in virgin montane forests. *Nedyopus latus* has only been found in central Taiwan, mostly in secondary forests at middle elevations (1000–1700 m a.s.l.), whereas *N. wui* seems to prefer virgin forest, at middle elevations, but still somewhat higher, between 2000–2550 m a.s.l., in central and northeastern Taiwan.

Such distributions show that, like the vast majority of Diplopoda, species of the genus *Nedyopus* are primarily forest-dwellers. In Taiwan at least, they tend to occur in mature primary stands in the mid-montane belt. Central Taiwan, the best-forested part of the island, appears to support most if not all of the *Nedyopus* species. This alone suggests a very high degree of endemism.

In Taiwan, most of the species of *Nedyopus* can tolerate some degree of anthropogenic pressure, also living in secondary forests or plantations. Unsurprisingly though, these tendencies are more typical of widely distributed congeners, e.g. *N. hsientienensis*. In contrast, the most restricted mid-montane species, like *N. latus* and *N. wui*, tend to prefer natural forest.

Key to the Taiwanese species of *Nedyopus*

1. Paraterga relatively to rather well developed (Figures 1–3, 32–34, 55, 56, 83, 84); metatergal transverse sulcus reaching base of paraterga 5–18; pleurosternal carinae with a caudal tooth on segments 5(6)–7; gonopod femorite narrowed to moderately broadened at base 2
- Paraterga very poorly developed (Figures 11–13, 22–24, 42–44, 65–67, 75, 76, 91, 92); metatergal transverse sulcus not reaching base of paraterga 5–18, or reaching the base only on some segments; pleurosternal carinae without caudal teeth; gonopod femorite always moderately broadened at base 3
2. Size larger: body length 26–31 mm, width 3.5–4.8 mm; colour pattern not contrasting; antennae long (reaching midpoint of metatergum 4); only few tergal setae until segment 3 (Figure 32); axial line evident from collum to end of epiproct; gonopod femorite narrow at base, lamella (I) not divided; telopodite tip with three lobes (Figures 39–41, 115, 116, 118–120). *N. latus*
- Body size smaller: length 12–18 mm, width 1.4–1.8 mm; colour pattern contrasting; antennae short (only reaching end of segment 2); numerous setae on all postcollar metaterga (Figures 1–3, 54, 55, 57, 58); axial line poorly visible or absent; gonopod femorite moderately broadened at base, lamella (I) divided; telopodite tip with two lobes (Figures 8–10, 97–102). *N. hsientienensis*
3. Coloration black-brown; antennae relatively long (reaching segment 4); calluses delimited by a sulcus both dorsally and ventrally; metatergal transverse sulcus on segments 4–19, reaching base of paraterga 5, 7–18; gonopod lamella (I) divided, without denticulation at margin; telopodite tip with only one lobe, bearing up to three lobules (Figures 19–21, 103–105). *N. pectinatus*
- Coloration light brown; antennae short (reaching segment 2); calluses delimited by a sulcus only dorsally; metatergal transverse sulcus on segments 5–18, not reaching base of paraterga; gonopod lamella (I) not divided, margin denticulate; telopodite tip with more than one lobe 4

4. Epiproct long and widely bifid (Figures 25, 77); pleurosternal carinae on segments 2–4 to segments 2–7, with caudal teeth on segments 5–7; two sternal cones between ♂ coxae 4 (Figures 27, 80); solenophore with three apical lobes (Figures 29–31, 109, 110, 114) *N. caudatus*
- Epiproct short and narrowly emarginate (Figures 45, 93, 94); pleurosternal carinae on segments 2–7; a narrowly notched, linguiform, sternal lamina between ♂ coxae 4 (Figures 47, 96); solenophore with four apical lobes (Figures 49–52, 121, 122, 126) *N. wui*

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