

***Heteropoda parva* n. sp. and *H. martusa* n. sp.
primitive or derived *Heteropoda* species?
(Araneae: Sparassidae: Heteropodinae)**

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Abstract: Two new *Heteropoda* species are described from Malaysia and Sumatra: *H. parva* n. sp. and *H. martusa* n. sp. Male genital characters show intermediate forms between known genera. The systematic position of the new species is discussed.

Kurzfassung: Zwei neue *Heteropoda*-Arten aus Malaysia und Sumatra werden beschrieben: *H. parva* n. sp. and *H. martusa* n. sp. Merkmale der männlichen Genitalien besitzen intermediäre Ausprägungen zwischen bekannten Gattungen. Die systematische Stellung der neuen Arten wird diskutiert.

Introduction

Heteropoda Latreille 1804 is the largest genus within the subfamily Heteropodinae. It contains about 150 nominal species; many more species are yet undescribed (JÄGER pers. observ.). Individuals are large nocturnal hunters and occur in Asia and Australia. Exceptions are the cosmopolitan *H. venatoria* (Linnaeus, 1767), which inhabits warm regions all over the world, and the east mediterranean, cave-dwelling *H. variegata* (Simon, 1874). Recent revisions were published by SETHI & TIKADER (1988) for India and by DAVIES (1994) for Australia. DAVIES (1994) recently described one new genus (*Yiinthi*) and JÄGER (1999, 2000a) three new genera (*Sinopoda*, *Bhutaniella* and *Pseudopoda*), which contain species previously placed in *Heteropoda*. All five genera are mainly based on genital characters.

Two species in particular came to my attention, because they appear to be interesting from a systematic point of view. Their characters point to a generically intermediate systematic position or in other words: they cannot be clearly associated with anyone genus at first look. Both species are described here and their systematic position is discussed.

Abbreviations ALE – anterior lateral eyes, AME – anterior median eyes, AW – anterior width of prosoma, CH – clypeus height, Fe – femur, Mt – metatarsus, NHMG – Natural History Museum, Geneva (Switzerland), OL – opisthosoma length, OW – opisthosoma width, Pa – patella, PH – prosoma height, PJ – consecutive number of Sparassidae, examined by Peter JÄGER, PL – prosoma length, PLE – posterior lateral eyes, PME – posterior median eyes, Pp – palpus, PW – prosoma width, RTA – retrolateral tibial apophysis, Tar – tarsus, Ti – tibia; I, II, III, IV – leg I etc.

Taxonomy

Heteropoda parva n. sp. (Figs 1–12)

Type material: 1♂ holotype (PJ 369, with label: Malaysia, Perak, Chenderiang, 290–330m, 22.–31.1.94. Coll. Peter SCHWENDINGER), 1 ♀ paratype (PJ 370, dito); both deposited in NHMG.

Derivatio nominis: The specific name refers to the small size of the species (Latin: *parvus* – small; adj.).

Diagnosis: Small *Heteropoda* species. ♂ with only indistinctly sheath-like conductor, filiform embolus with apical appendix (figs 1–4, 6). ♀ vulva with short copulatory ducts and large spermathecae, the latter with one large cavity (in contrast to spermathecae consisting of twisted ducts within in other *Heteropoda* spp.) (figs 8–9).

Description: ♂: PL 3.1, PW 2.7, AW 1.4, PH 1.0, OL 3.0, OW 1.8. Eye measurements/interdistances: AME 0.18, ALE 0.29, PME 0.24, PLE 0.31, AME–AME 0.09, AME–ALE 0.04, PME–PME 0.17, PME–PLE 0.24, AME–PME 0.24, ALE–PLE 0.26, CH AME 0.32, CH ALE 0.21.

Leg formula: 2413. Spination: Pp 131,101,2121, Fe I–II 323, III 322, IV 321, Pa I 000, II–IV 001, Ti I–II 2226, III–IV 2126, Mt I–II 201(2)4, III 2026, IV 3036. Chelicerae with 2 (left) and 3 (right) anterior and 4 posterior teeth and with denticles in cheliceral furrow.

Embolus thin, originating from a 7'o'clock-position on the tegulum, running nearly a semicircle; tip embedded in conductor. Conductor anvil-shaped, slightly sheath-like with margins bent to the inner side, originat-

ing from prolateral tegulum. Sperm-duct visible in ventral view, with one broad „?“-shaped part and another narrow part with a small loop in front of embolic base (figs 2, 4). Tibial apophysis with a slightly curved and pointed dorsal part; ventral part shaped like a large tooth (figs 3, 5).

Colour: Yellowish-brown with red-brown markings. Chelicerae with three thin longitudinal frontal stripes. Dorsal prosoma medially brighter, laterally with radial markings, with a dark margin in posterior half and with a bright transversal band on its steep posterior part. Sternum, coxae, labium and gnathocoxae pale yellow. Opisthosoma with a light median zone above the heart, ventrally with an irregular dark pattern and a dark patch in front of the spinnerets. Spinnerets dorsally red-brown, ventrally pale yellow. Legs pale yellow, slightly mottled with dark patches, femoral spines originating from these patches. Femora with slightly iridescent hairs.

Leg and palp measurements:

♂	Fe	Pa	Ti	Mt	Tar	Total	♀	Fe	Pa	Ti	Mt	Tar	Total
Pp	1.6	0.7	1.1		1.3	4.7		1.5	0.8	1.3		1.5	5.1
I	4.0	1.4	4.3	3.8	0.9	14.4		3.5	1.5	3.4	3.0	1.2	12.6
II	4.7	1.4	5.1	4.7	1.6	17.5		4.1	1.2	3.9	3.4	1.2	13.8
III	3.9	1.3	3.7	3.5	1.1	13.5		3.5	1.3	3.2	2.9	1.0	11.9
IV	4.2	1.1	4.1	4.3	1.5	15.2		3.9	1.3	3.6	3.8	1.4	14.0

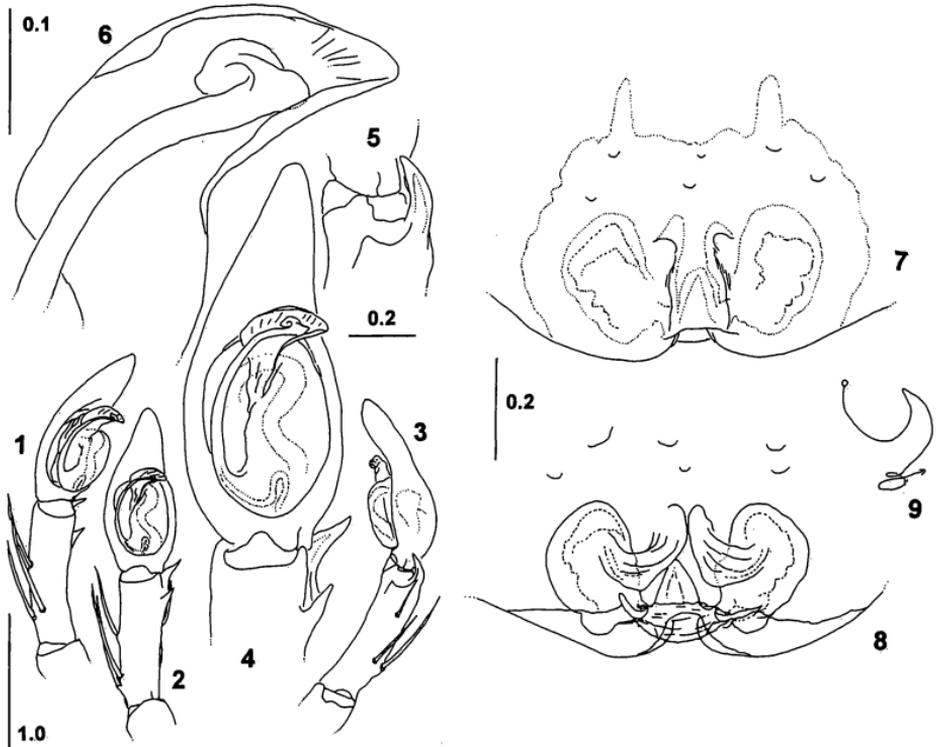
♀: PL 3.4, PW 3.0, AW 1.6, PH 1.1, OL 3.2, OW 2.2. Eye measurements/interdistances: AME 0.21, ALE 0.34, PME 0.27, PLE 0.35, AME-AME 0.13, AME-ALE 0.04, PME-PME 0.19, PME-PLE 0.28, AME-PME 0.27, ALE-PLE 0.29, CH AME 0.39, CH ALE 0.28 (fig. 12). Leg formula: 4213. Spination: Pp 131,101,2121,1013, Fe I-II 323, III 322, IV 321, Pa I-III 000, IV 001, Ti I-III 2026, IV 2126, Mt I-II 0004, III 2024, IV 3036. Palpal claw with 6 (+ 1 small) teeth. Chelicerae with 3 anterior and 4 posterior teeth and with denticles in cheliceral furrow (fig. 11).

Epigynal field broader than long, with two short longitudinal bands originating from the anterior margin of the field. Median septum short, with anterior margins curved sideways and with subseptal cavity (fig. 7). Spermathecae irregularly oval (figs 7-8).

Colour: As in male, but generally darker and with pattern more distinct. Legs darker, with yellow patches, dorsally brighter (fig. 10). Iridescence of femoral hairs more pronounced.

Distribution: Known only from the type locality.

Relationships: The reduced conductor indicates a close relationship with *H. martusa* n. sp. and distinguishes both species from all other known *Heteropoda* species. Whether both new species are closely related, or structures in their male bulbs have convergently evolved, has to be investigated from material of further species and from the unknown female of *H. martusa* n. sp.



Figs 1–9: *Heteropoda parva* n. sp., 1–4 ♂ palp (1 prolateral, 2+4 ventral, 3 retrolateral), 5 tibial apophysis (retrolateral), 6 tip of embolus and conductor (ventral), 7 epigyne (ventral), 8 vulva (dorsal), 9 schematical course of ♀-copulatory ducts (dorsal).

***Heteropoda martusa* n. sp.** (Figs 13–16)

Type material: 1♂ holotype (PJ 64, with label: W.Sumatra, Bungar-Bondar, 14. IV. 1914, SCHULTZ, s. v.), SMF.

Derivatio nominis: The specific name is an arbitrary combination of letters taken from the word „Sumatra“ (noun in apposition).

Diagnosis: ♂ Embolus filiform, distally corkscrew-like coiled, a feature unique within the whole genus (figs 14–15). Dorsal part of RTA large, its tip reaching basal third of tegulum (figs 13–14).

Description: ♂: PL 6.5, PW 6.3, AW 3.3, PH 1.5, OL 6.2, OW 4.1. Eye measurements/interdistances: AME 0.52, ALE 0.64, PME 0.41, PLE 0.64, AME–AME 0.24, AME–ALE 0.03, PME–PME 0.46, PME–PLE 0.71, AME–PME 0.71, ALE–PLE 0.39, CH AME 0.51, CH ALE 0.36.

Leg formula: 2134 ? [the third pair of leg is usually shortest in the Sparassidae. Probably the left fourth leg (the right fourth leg is missing) was lost and regenerated in a younger individual stage, so that this is not recognizable any more in the adult]. Spination: Pp 131,101,2120, Fe I–III 323, IV 321, Pa I 001, II 101(0), III 001, IV 000, Ti I–II 2326, III 22(1)26, IV 2126, Mt I–II 1014, III 2024, IV 3036. Chelicerae with 3 anterior and 4 posterior teeth and with denticles in cheliceral furrow.

Embolus originating from a 7'o'clock-position on the tegulum. Tip of embolus distally knob-like as in *H. bellendenker* Davies, 1994 (fig. 16), lying in conductor (figs 14–15). Conductor short, originating from pro-lateral to distal tegulum, with a start of a sheath-like shape. Sperm-duct visible in ventral view, straight, without loop (fig. 14). Tibial apophysis with very large dorsal part, this – seen in lateral view – apically broadened and with a small tip (figs 13–14).

Colour: Red-brown with light hairs. Chelicerae with three slight longitudinal stripes running together into a patch in distal half. Dorsal prosoma with dark red-brown fovea and marble-like lateral pattern, marginally with light hairs (other hairs apparently rubbed off). Sternum red-brown. Coxae, labium and gnathocoxae yellow-brown with darker pattern. Opisthosoma dorsally with irregular pattern and a dark transversal band in posterior half, laterally with long hairs, ventrally with short hairs and four longitudinal lines. Spinnerets dorsally darker than ventrally. Legs yellow-brown, with dark spine-patches, small dots – especially ventrally – and with dark dorsal longitudinal stripe on femora.

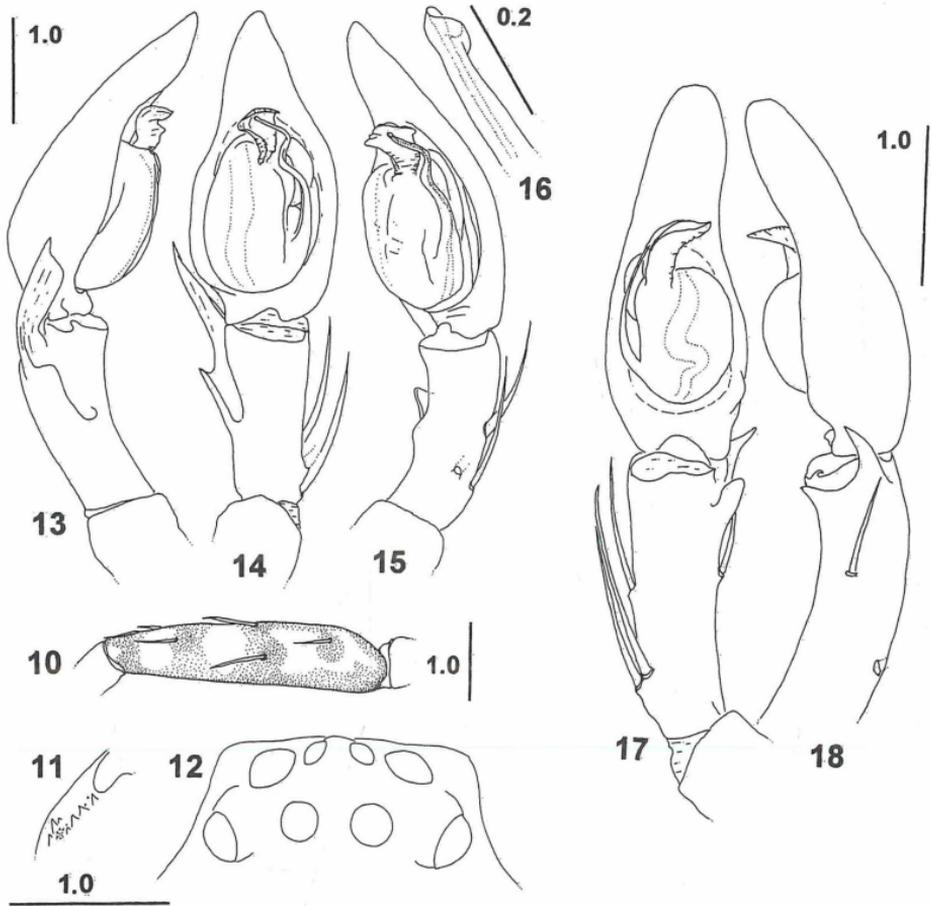
Leg and palp measurements:

♂	Fe	Pa	Ti	Mt	Tar	Total
Pp	3.2	1.5	2.2	—	3.4	10.3
I	8.8	3.7	8.9	8.4	2.5	32.3
II	10.1	4.0	10.5	10.1	2.9	37.6
III	8.7	3.3	8.2	7.3	2.1	29.6
IV	8.0	2.7	7.5	7.7	2.2	28.1

♀: unknown.

Distribution: Only known from the type locality.

Relationships: see *H. parva* n. sp.



Figs 10–12: *Heteropoda parva* n. sp., 10 femur of first right leg of ♀ (prolateral), 11 cheliceral dentition of ♀ (ventral), 12 eye position of ♀ (dorsal).

Figs 13–16: *Heteropoda martusa* n. sp., 13–15 ♂ palp (13 retrolateral, 14 ventral, 15 prolateral), 16 tip of embolus (prolateral).

Figs 17–18: *Heteropoda* sp. ♂ palp (17 ventral, 18 retrolateral).

Systematics

Three questions arise, regarding the systematic positions of *Heteropoda parva* n. sp. and *H. martusa* n. sp.:

1. If both species possess intermediate characters, as suggested in the introduction, between which genera do they stand?
2. Can they be assigned to a certain genus at all? If so, to which genus do they belong?
3. Do intermediate characters allow phylogenetic statements, i.e. are these intermediate forms primitive or derived?

Conclusions can only be drawn from male genital organs, as they allow more meaningful statements on phylogeny. To answer the first question raised above, the five genera mentioned earlier have to be compared. *Heteropoda* Latreille possesses a sheath-like conductor, arising prolaterally from the tegulum, and a filiform embolus, which is embedded in the conductor with its apical half (figs 17–18; compare also DAVIES 1994, JÄGER 2000b). The conductor of *Yiinthi* Davies is spoon-shaped and arises prolaterally as in *Heteropoda* (DAVIES 1994). The embedding of the embolus tip into the conductor in *Yiinthi* spp. is not as distinct as in *Heteropoda* spp., but very similar. The embolus in *Yiinthi* spp. has a subterminal flagellum. The retrolateral apophysis of both latter genera arises distally from the tibia and it is divided into a longer dorsal part and a short, tooth-like ventral part. In *Sinopoda* Jäger, *Pseudopoda* Jäger and *Bhutaniella* Jäger, the conductors are membranous, strongly reduced and arise distally from the tegulum (JÄGER 1999, 2000a). The embolus tip is near the conductor, but not embedded. Emboli are modified: in *Sinopoda* they are divided into two parts (JÄGER 1999), in *Pseudopoda* flattened and widened, and in *Bhutaniella* modified to complex structures (JÄGER 2000a).

Both new species show filiform emboli and distally arising tibial apophyses. This points to congenity with *Heteropoda*. However, the conductors are not distinct sheath-like, as mentioned in diagnoses of *Heteropoda* by DAVIES (1994) and JÄGER (1999, 2000b). The new species show transitional forms between the typical conductor of *Heteropoda* (fig. 17) and the membranous conductors of, e.g., *Pseudopoda*. Moreover, the filiform emboli are modified: in *H. parva* n. sp. with a subterminal appendix (fig. 6), whose position is similar to that of the flagellum in *Yiinthi*. A similar appendix is found also in another *Heteropoda* species:

Heteropoda gordonensis Davies 1994. The appendices in all three cases are considered convergently developed, since no other relevant characters support a close relationship between these species. The filiform embolus in *H. martusa* n. sp. shows a characteristic corkscrew-shape (fig. 14), which is unique in the genus *Heteropoda*. Embolus modifications in both new species may be associated with the non-sheath-like conductor, since in the three genera without a sheath-like conductor (*Sinopoda*, *Pseudopoda* and *Bhutaniella*) the emboli are also modified (see above). These changes may have developed in connexion with copulatory mechanisms, which are poorly known, except for the functioning of the sheath-like conductor in *Heteropoda venatoria*. During copulation of this species the embolus slides through the conductor, whose tip is set near to the copulatory orifice (JÄGER pers. observ.). The lack of mechanical stability during copulation may be compensated by modifications of the embolus. No observations on copulations in genera without an sheath-like conductor are reported so far. These would be helpful to determine mechanisms and functions of single genital structures and thus, systematic positions of both new species could become clearer.

Female genitalia of *H. parva* n. sp. are similar to those of typical *Heteropoda*: the first windings of the copulatory ducts are directed medio-laterad, distinct spermathecae are present (figs 8–9).

The second question cannot be answered sufficiently. Several characters of male genital organs (filiform embolus, distally arising tibial apopysis) and female genital organs point to congenity with *Heteropoda*, although single characters are not conform (emboli, conductors). Prior to a revision of the genus *Heteropoda* and the discovery of the female of *H. martusa* n. sp., both new species are placed in *Heteropoda*.

Three alternatives may be considered for answering the third question:

- I. Both species occupy a basal position within *Heteropoda*, i.e. their characters shared with, e.g., *Pseudopoda* spp. are plesiomorphic (fig. 19).
- II. The species are highly derived within „*Heteropoda*“ and represent a transition to other derived genera (e.g. *Pseudopoda*). This would imply that the special characters of the two new species are apomorphic and thus characterize a new taxon. The here proposed „*Heteropoda*“ would then be paraphyletic).
- III. The two species belong to the *Heteropoda*-clade and show (spontaneous) convergent developments of structures, as they

also appear in other genera, which are not closely related to the new species.

In order to answer this question we have to look into other heteropodine genera. One central character is the conductor with its different character states. The plesiomorphic state within the Heteropodinae seems to be a membranous conductor without a distinct sheath-like shape, as in species of *Pandercetes*, *Barylestis*, *Spariolemus*, *Sinopoda*, *Pseudopoda* and *Bhutaniella*. This assumption is supported by membranous conductors in many species of the Sparassinae, Palystinae, primitive Deleninae and some Sparianthinae. Convergent development of a similar (*Heteropoda*-) type of conductor appears, for example, in *Damastes* spp. (Madagascar) and *Gnathopalystes* spp. (SE Asia, Melanesia). The conductor of *Heteropoda* spp. represents a specialized and thus apomorphic form: the embolus, or at least its distal part, is embedded in a sheath-like distal part of the conductor in the resting position (copulatory mechanism, see above). *Yiinthe* has a spoon-shaped conductor, which is generally very similar to that of *Heteropoda*. Whether both states are convergently developed or derived from a common ancestor, remains an unsolved question. Additional characters of female genitalia are helpful to distinguish these taxa accurately (spermathecae: elongated in *Yiinthe*, distinctly separated from copulatory ducts in *Heteropoda*; first winding of copulatory ducts: orad or caudad in *Yiinthe*, medio-laterad in *Heteropoda*).

Together with those of *Heteropoda* spp., the conductors of the new species are considered synapomorphic (in combination with female genitalia). It appears to be unlikely that in the course of evolution the special function of the sheath-like conductor during copulation in all other *Heteropoda* spp. was given up in the new species. It seems to be a well-functioning mechanism. Thus a basal position of both species within *Heteropoda* is proposed.

The retrolateral tibial apophysis (RTA), arises distally in most species of all sparassid subfamilies and in other families of the RTA-clade. A median to basal position of RTA is found within the Heteropodinae in *Pseudopoda* and *Bhutaniella* and is considered apomorphic. Thus, the character „RTA“ is only useful to separate the latter genera from other heteropodine genera.

The embolus in its plesiomorphic state is filiform without appendages. The appendage in *H. parva* n. sp. seems to be evolved independently from similar structures in *Yiinthe* or other *Heteropoda* spp. (*H. gordonensis*). The corkscrew-shaped embolus in *H. martusa* n. sp. is an

autapomorphic structure. Although the different emboli in both species do not appear to be derived from a common ancestor, they are preliminary grouped together according to the similar shape of their conductor.

A basal position of the two new species within *Heteropoda* is supported by their short emboli. A short embolus with a 180° course is apparently the plesiomorphic state (e.g. fig. 17). Apomorphic, elongated emboli appear in different species groups of *Heteropoda*. In the elongated emboli the joint at the tegulum is moved from a proximal (figs 4, 14, 17) to a retrolateral or distal position (e.g. *H. marillana* Davies 1994: Fig. 13 F).

Considering all characters mentioned, the new species are preliminary placed in *Heteropoda*, since certain shared characters points to congenerity. Distinctions from other *Heteropoda* spp. are not pronounced enough to erect a new genus. Plesiomorphic characters (conductor not distinctly sheath-like, embolus short) point to a basal position within *Heteropoda* (fig. 19).

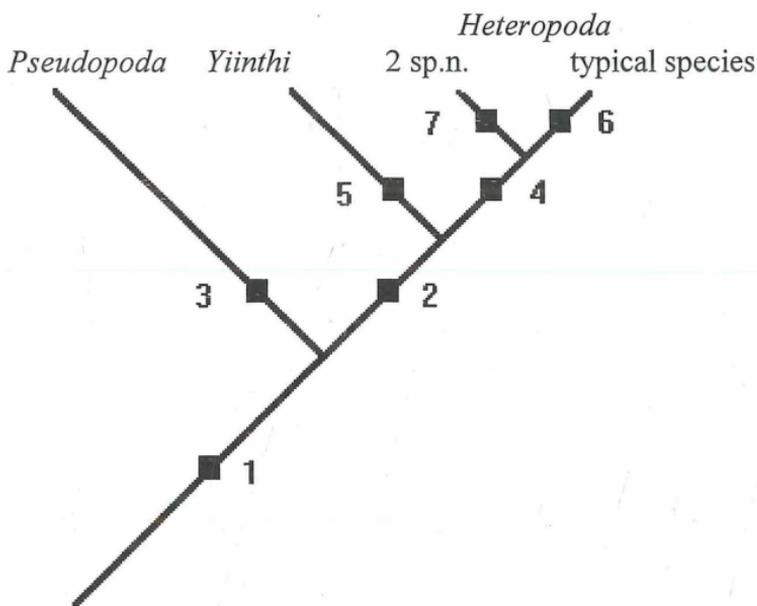


Fig 19: Proposed systematic position of *Heteropoda parva* n. sp. and *H. martusa* n. sp., in comparison to three heteropodine genera. 1 synapomorphies for Heteropodinae (denticles in cheliceral furrow, with majority of them near the three anterior teeth; long and curved teeth on female palpal claw). 2 conductor modified, aris-

ing prolaterally (plesiomorphically unmodified, arising distally). 3 RTA mesial to basal, embolus flattened. 4 synapomorphies for *Heteropoda* spp.: conductor more or less sheath-like (i.e. including transitional forms of the two new species), spermathecae distinctly separated from copulatory ducts. 5 subdistal embolic flagellum present, first winding of ♀ copulatory duct orad or caudad (not laterad), spermathecae elongated (DAVIES 1994). 6 conductor clearly sheath-like. 7 emboli modified.

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