An enigmatic spiny harvestman from Baltic amber

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Introduction

Harvestman (Arachnida: Opiliones) are a diverse group of arthropods in modern terrestrial ecosystems, with nearly 6,500 living species described thus far (Kury 2000; data as of March 2011). By contrast only thirty valid fossil species of harvestman are known, albeit with a record going back some 410 million years to the Early Devonian. A general review of the harvestman fossil record can be found in Dunlop (2007). The most productive locality for fossils of these arachnids is Baltic amber, which dates from the Eocene (ca. 44–49 Ma) of north-central Europe. Four suborders of Opiliones are conventionally recognised: Cyphophthalmi, Eupnoi, Dyspnoi and Laniatores. All have now been recorded from Baltic amber (cf. Koch & Berendt 1854; Menge 1854; Roewer 1939; Dunlop & Mammitzsch 2010; Dunlop & Mitov 2011). Further comments on this amber fauna, and partial revisions of some species, have also been published by Stareńga (1976, 2002), Ubick & Dunlop (2005) and Dunlop (2006). Here, we describe a new specimen from Baltic amber which immediately caught our attention for having long, spiny legs, elongate and slender pedipalps, and multiple rows of short spines across the body (Figs 1–4). Compared to previous descriptions, this is evidently something new for the amber fauna. Further study revealed that it preserves an unusual combination of characters, raising questions about its familial affinities. It is formally described as a new genus and species below.

Materials and methods

The type and only known specimen originates from the private collection of Dr Michael Steiner (Free University Berlin) and has now been formally deposited in the amber collections of the Museum für Naturkunde Berlin (MfN) under the repository number MBA.1878 (for Museum Berlin Arthropoda). The specimen was originally obtained over ten years ago from Polish traders and may originate from the Polish coast of the Baltic Sea (M. Steiner, pers. comm. 2011). The fossil was photographed using a Leica stereomicroscope running the software package Leica Application Suite. Stacks of in most cases ca. 30 images were assembled into a single final picture using the software package Auto Montage. Brightness, contrast, etc. were adjusted

Abstract

A new harvestman (Arachnida: Opiliones) from Baltic amber (Palaeogene: Eocene; ca. 44–49 Ma) is described as Piankhi steineri n. gen., n. sp. This enigmatic fossil expresses long, slender pedipalps without a tarsal claw, which is characteristic for the suborder Dyspnoi. The chelicerae are notably enlarged and the dorsal body surface is formed from a carapace with a separate prosomatic tergite (metapeltidium), plus a large opisthosomal scute (or scutum parvum). However these characters, combined with the distinctly spiny limbs and further rows of spines across the fossil’s opisthosoma, have no parallel among the modern dyspnoid harvestmen that we are aware of. The fossil resolves features reminiscent of modern members of the dyspnoid families Ceratolasmatidae, Nipponopsalididae, Ischyropsalididae and Sabacoonidae, but does not show unequivocal apomorphies of any one particular family. We must entertain the possibility that this is an extinct body plan from the Eocene of north-central Europe, and we tentatively refer the fossil to a new genus in an unresolved position among the Ischyropsalidoidea (Dyspnoi). An amorphous triangular structure behind the anal region is assumed to be faecal matter, rather than part of the original anatomy.

Key Words

Arachnida
Dyspnoi
Eocene
Opiliones
systematics

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Comparative material studied and photographed: *Hesperonemastoma modestum* (Banks, 1894) (Figs 5A, B). – 1 male (body length 1.17); USA, California, Monterey County, 28.X.1982, leg. Roy John-son, Jr., det. J. C. Cokendolpher, (PM); *Taracus birsteini* Ljovushkin, 1971 (Figs 5C–G). – 1 male (body length 4.2), 1 female (body length 4.6); Russia, Maritime Province, NW part of Vladivostok City, cata-combs, 21.VIII.1998, coll. Yu. M. Marusik, det. A. N. Chemeris, (PM). Note that we accept here the conclusions of Giribet et al. (2010) and Shear (2010b) in placing *Hesperonemastoma* Gruber, 1970 in Sabaconidae rather than Ceratolasmatidae. Scutum combination terminology follow Martens (1969a, fig. 10; 1972, fig. 2; 1978), and Shultz & Pinto-da-Rocha (2007, fig. 2.4).

Baltic amber is conventionally dated to an Eocene (Lutetian) age of about 44–49 Ma. Details of the geological setting, other faunal elements and the presumably warm palaeoenvironment can be found in Weitschat & Wichard (2010) and references therein.

**Systematic paleontology**

**Order Opiliones** Sundevall, 1833

**Suborder Dyspnoi** Hansen & Sørensen, 1904

**Remarks.** The position of this new fossil is challenging. The long legs (Figs 1, 4A) evidently exclude the suborder Cyphophthalmi, while the fact that the pedipalps are not raptorial precludes an assignment to Laniatores. This leaves Eupnoi and Dyspnoi. The shape of the pedi-
Figure 2. *Piankhi steineri* n. gen, n. sp. Body and proximal limb region. A. Dorsal view; B. Dorso-lateral view. Scale bar equals 1 mm.
pulp (Figs 3C, 4C) clearly points towards Dyspnoid; particularly the fact the tarsus is the shortest article and that it lacks an obvious tarsal claw. By contrast, in Eu- pnoi the tarsus of the pedipalp is usually the longest article and ends in a single, curved and clearly visible claw. However, the new fossil, with its spiny legs and body, does not appear to fall neatly into any of the known dyspnoid families (as reviewed by Gruber 2007).

Superfamily ?Ischyropsalidoidea Simon, 1879

Remarks. Dyspnoid is traditionally divided into two superfamilies: Troguloididae and Ischyropsalidoidea. Cladistic studies (Shultz & Regier 2001; Giribet et al. 2002, 2010) have largely supported this basic scheme; with Giribet et al. (2010) estimating a split between these groups as far back as the late Carboniferous. The trogu- loid families Trogulidae, Dicranolasmatidae and Ne- mastomatidae all have highly characteristic body shapes (see also figures in Martens 1978) which differ substantially from the new amber fossil. For example di- cranolasmatids have eyes borne on a forward-projecting ‘hood’ while in trogulids the eyes are at the very tip of the prosoma close to the basis of the two hood arms. In all of these three families the carapace region merges smoothly into the dorsal opisthosoma forming the so-called scutum magnum. By contrast, in the new fossil the carapace appears to be differentiated from the opisthosoma and is not fused to the succeeding ter- gite(s). In fact the carapace of the fossil even shows a division line towards its posterior margin (Figs 2, 4B), interpreted here as a separate prosomatic tergite; or free metapeltidium in some terminologies. Furthermore, the opisthosoma of the fossil expresses a scutum parvum; i.e. a large scute formed from a series of fused tergites (Figs 3A, 4B). Since it bears five rows of spines, it seems reasonable to assume that it is derived from five tergites. In any case this scute is followed by two short- er free tergites. Such a body plan is reminiscent of the eupnoid family Sclerosomatidae (cf. Tourinho 2007), but as noted above the morphology of the pedipalp argues strongly against such affinities. Also, as figured by, e.g., Tourinho-Davis (2004, figs 1–4) the venter of typical sclerosomatids differs from that of this amber specimen.

Of particular interest is the fourth troguloid family, Nipponopsalididae, which is currently restricted to East Asia. Like the amber fossil (Figs 2, 4B) these har- vestmen have enlarged chelicerae with spines on the proximal article, slender pedipalps longer than the body, a carapace with a free metapeltidium and (at least in males) a scutum parvum covering the opisthosoma (Gruber 2007). However, unlike our fossil there are no robust spines on the ocularium, on the appendages or on the body in general. The chelicerae of nipponopsalil- dids are also proportionally much larger that those of the fossil, and further differences are elucidated below.

Superficially similar to Nipponopsalididae is the fa- mily Ischyropsalidae although this group apparently belongs in the second superfamily, Ischyropsalidoidea. This resemblance is thus considered convergent (Gruber 2007) and Ischyropsalidae is currently represented by a single genus, Ischyropsalis C. L. Koch, 1839, found in Central Europe and the Pyrenees, including the Car- pathians, the northern Iberian Peninsula and the Italian Peninsula. A putative record of Ischyropsalis hellwigi (Panzer, 1794) in Turkey (Central Anatolia region) (see Kurt et al. 2008) requires confirmation whereby materi- alis merits revision. These are also distinctive harvestmen with long and spiny chelicerae. Ischyropsalis hellwigi is known to be a specialist predator on gastropods and the especially enlarged and powerful mouthparts are used here to crack snail shells (Martens 1965; Nyffeler & Symondson 2001). The diets of other Ischyropsalis spec- ies are not well known. As with nipponopsalidids, ex- tant ischyropsalids have not been recorded with all the characters seen in our fossil; namely stout spines on the ocularium, legs and body. What is worth mention- ing here is that Martens’ (1978, p. 186) diagnosis of the ischyropsalids includes the fact that – as in the amber specimen – the abdominal tergites can be fused into a scutum parvum. The large chelicerae of the fossil are also worth reiterating. In Ischyropsalis the chelicera- ce can be up to ca. ½ to 2 times body length. In our new fossil the chelicerae are marginally shorter than the body, but still noticeably large compared to those of dyspnoid harvestmen in general.

There are two further families in Ischyropsalidoidea to consider: Ceratolasmatidae and Sabaconidae. In some ceratolasmatis the pedipalps are elongate and thin (cf. Croshycus Roewer, 1914) like those of the fos- sil. However, in other genera the pedipalps are short and moderately stout (cf. Acuclavela Shear, 1986 and Ceratolasma Goodnight & Goodnight, 1942). For compara- tive illustrations see e.g. Shear (1986, figs 21, 40) or Gruber (1978, figs 19, 26; 2007, figs 4.12f, 4.13h). On balance, the amber fossil is probably not a ceratol- asmatid. While having a light micro-ornament on the carapace and scutum parvum (Fig. 3A), it lacks heavy sculpture on the dorsal body surface and also retains a separate metapeltidium. It thus differs from Ceratolasmatidae as defined by Shear (1986, p. 19), namely: “Ischyropsaloids with very heavy sclerotization, scutum parvum to magnum; metapeltidium not separate sclerite, with two sensory cones or none; carapace and

Figure 3. Piankhi steineri n. gen, n. sp. Details of body and legs. A. Scutum parvum showing cuticle micro-ornament and rows of discrete spines; B. Ocularium bearing four prominent spines; C. Pedipalp showing apparent absence of a tarsal claw (arrowed); D. Distal end of leg IV showing annulation of the tarsus (four numbered tarsomeres) and a single tarsal claw (arrowed). Scale bars equal 0.2 mm.
Figure 4. Camera lucida drawing of the specimen shown in Figures 1–3. A. Lateral-dorsal overview showing length and proportion of the entire legs; B. Lateral-dorsal details of the body and the proximal limbs and their ornament; C. Dorsal view specifically highlighting the pedipalps showing their proportions (including a long patella) and absence of a tarsal claw. Abbreviations: ch – chelicerae, ex – coxa, fe – femur, fm? – possible faecal material, oc – ocularium, pp – pedipalp, pt – patella, sp – scutum parvum (with ornament), ti – tibia, ts – tarsus. Legs numbered from I–IV. Scale bar equals 2 mm (A) and 1 mm (B–C).
Figure 5. Comparative images of two modern harvestmen: both Dyspnoi: Sabaconidae. 

A. Hesperonemastoma modestum (Banks, 1894), male. (USA, California). Body, dorso-lateral view; dorsal scutum with rows of anvil-shaped tubercles and four pairs of pointed, curved thorns. Note that patellar fe, pt, ti, almost equal in length, Ts/Ti = 0.42; Ti/Pt = 0.91; two pseudoarticulations (arrowed) on left leg IV metatarsus. (Abbreviations as in Figure 4); 

B. The same, closer view. Note again the thorns and pseudoarticulations; 

C. Taracus birsteini Ljovuschkin, 1971, male. (Russia, Maritime Province). Body, lateral view; 

D. The same, closer view showing rows of black spines on dorsum, and position of a metapeltidial sensory cone (arrowed); 

E. Detail of D, showing ocularium, furnished with six black spines, and the metapeltidial sensory cone (height 0.2) (arrowed); 

F. The same, chelicerae and pedipalps; palpal Ts/Ti = 0.46, Ti/Pt = 0.70; 

G. Detail of body, showing spiracle opening specifically behind the left fourth leg coxa, lateral view. Note the excentric joint of the trochanter (tr), especially pronounced in fourth leg coxa in sabaconids and ischyropsalidids. Scale bars equal 0.5 mm (A–B, D–E, G); 2 mm (C) or 2.5 mm (F).
sclerotized areas having a microsculpture of spinous ridges
and tubercles, the opisthosoma being more or less domed
and bearing a fine hair at its apex. Taking all this together,
we tend towards ischyropsalid/sabaconid affinities of our
fossil (see below). Nevertheless, Gruber (2007) noted that
the pedipalp tibia and tarsus in Taracus is densely setose and
the tarsus is strongly bent backwards under the tibia (as in Sabac-
on). In this sense the amber fossil, with light setation
differs from Taracus. Flexion at the end of the pedipalp
is more problematic as a character, since it is possible
that this bend is no longer expressed in amber speci-
mens after death; as it occurs in (relaxed) modern ma-
terial stored in alcohol (PM, pers. obs.). Overall, the
amber fossil is however close to Taracus in terms of the
absence of pseudoarticulation in the leg femora, and
in the form and proportions of the pedipalp in
which the patella is noticeably long (cf. Figs 4C and
5C, F). Compare this with Ischyropsalis (cf. Dresco
1967, fig. 22; Gruber 2007, fig. 4.15e) where the patel-
la is shorter as compared to the remaining limb articles.
A long palpal patella is a general feature of, e.g., the
sabaconids Hesperonemastoma (Fig. 5A) and Taracus
(Fig. 5F), the ceratolomatid Crosbycus, and the new
fossil (see below). Nevertheless, the rather elongate pal-
pal tarsus in the fossil is closer to the condition in
Ischyropsalis. In modern sabaconids the tarsus tends to
be shorter. As an aside, we should note Shear’s (1975,
p. 8) comments concerning food preferences and thus
(ecological) similarities between Taracus and snail-eat-
ing ischyropsalisids: “There is no direct evidence about
the dietary habits of Taracus. H. W. Levi, personal
communication, could not induce a Colorado species of
Taracus to eat snails.”

In conclusion, pedipalp morphology clearly indicates
a dyspnoid harvestman, but we prefer to leave the exact
position of this amber fossil open. A similar approach
was taken by Giribet & Dunlop (2005) for an unusual-
looking dyspnoid harvestman from the Cretaceous
Myanmar (Burmese) amber. The new Baltic amber fos-
sil shows some similarities in its dorsal anatomy, long
pedipalps and enlarged chelicerae to the modern East
Asian Nipponopsalididae, the European Ischyropsalidi-
da, some North American Ceratolasmatidae, and the
Asian to North American genus Taracus among the
Sabaconidae. Note that the ocularium in the new fossil
is near the front edge of the prosoma as in some cera-
tolomatids, sabaconids (Fig. 5), and nemastomatids;
while in habitus the scutum of the fossil resembles that of
Sabacon okadai Suzuki, 1941 (Suzuki 1941, fig. 1),
Tomicomerus (sensu Shear 1975); and Ischyropsalis
(after Martens 1969b). Although not strictly speaking
spiny, the scutum of Sabacon dentipalpe Suzuki, 1949
cf. Suzuki 1949, figs 1–2) have minute humps each
bearing a fine hair at its apex. Taking all this together,
we tend towards ischyropsalid/sabaconid affinities and
tentatively refer the new amber fossil to Ischyropsal-
idoidea.

All Cenozoic harvestmen discovered so far can be
assigned to living families, but given the fact that we
could not find an exact modern equivalent conceivably
we could be dealing with a new, extinct family here; as
suggested by Shear (2010a) for the older Myanmar am-
ber dyspnoid. Since even among the modern dyspnoids
gross morphology can be homoplasic (see especially comments in Shear 2010b) – with superficially similar-looking forms placed [and occasionally misplaced] in different superfamilies – we are reluctant to formally propose a fossil family at this stage for a single species represented by a single specimen. As with other amber records, genital characters are unfortunately not available, but we encourage scoring this fossil into future cladistic analyses of dyspodoid genera in the hope that this might help resolve its affinities.

**Piankhi** n. gen.

*Derivation of name.* Eugene Simon named two similar genera after transliterations of ancient Egyptian royalty, namely *Sabacon* [Shabaka] and *Taracus* [Tahrqua]. Continuing this theme, Piankhi the Nubian [Piye] was the father of Taracus and is chosen here as the name for this older (fossil) genus.

*Diagnosis.* Dyspodoid harvestmen with the following character combination: carapace bearing an ocularium with four large spines and a demarcated prosomatic tergite; chelicerae enlarged, nearly as long as body; pedipalps elongate and of typical dyspodoid morphology but without clavate setae; legs also elongate, at least proximally with robust patterns of spines and without pseudoarticulations on leg femora; opisthosoma with a single large scute (*scutum parvum*) bearing five rows of robust, thorn-like spines followed by two further short tergites each also with a spine row. Dorsal cuticle of pro- and opisthosoma generally with a granular microornament. Presence of sensory cones on the metapeltidium and supracheliceral lamellae equivocal. Genital characters equivocal.

*Remarks.* We were unable to resolve a modern genus of harvestmen expressing exactly this combination of features and thus feel obliged to create a new genus, diagnosed as above.

**Piankhi steineri** n. gen., n. sp.

*Derivation of name.* After Dr Michael Steiner (Free University Berlin), who originally acquired the specimen and subsequently made it available for study.

*Holotype.* MfN Berlin: MBA.1878.

*Type locality and horizon.* Baltic amber; possibly from the Polish coast. Palaeogene, Eocene (Lutetian).

*Diagnosis.* As for the genus.

*Description.* Body rounded, length ca. 1.6. Prosoma with bilobed ocularium, bearing four large spines – two per lobe (Fig. 3B). Carapace apparently divided into a pro- + mesopeltidium, plus a short, but demarcated metapeltidium forming the separate prosomatic tergite (Fig. 2). Pro- + mesopeltidium with anterolateral group of at least three small spines (Fig. 4B), but other ornament lacking. Metapeltidium ornamented with a row of short spines, angled slightly forwards. Presence/absence of sensory cones on metapeltidium equivocal. Sensory cones absent in *Croshyscus dasycnemus* (Crosby, 1911) (cf. Shear 1986) and *Hesperonemastoma* (cf. Giribet et al. 2010); in *Taracus* there is one (Figs 5D, E); in *Sabacon* two; in *Ischyropsalis* more than two (see also Gruber 2007). Presence/absence of supracheliceral lamellae equivocal (not distinct in *Ischyropsalis*; in *Hesperonemastoma* a median broad triangular sclerite, folded in the middle, separated from the carapace and directed downwards between the chelicerae; cf. Gruber 1970).

Chelicerae quite large and robust (Fig. 2), total length ca. 1.4, basal article lacks apophyses, but bears numerous short spines. All cheliceral articles otherwise unmodified, but second article with faint impression of a line, or two parallel lines, running along its length (Fig. 4B). Glandular (‘epigamic’) organs on chelicerae and presence/absence of diaphanous teeth equivocal.

Pedipalps long and slender, total length 3.1; individual article lengths: femur, 1.3; patella (Pt), 0.7; tibia (Ti), 0.6 and tarsus (Ts), 0.5; Ts/Ti = 0.83; Ti/Pt = 0.86. Pedipalp without obvious apophyses and without clavate setae; glandular tissue equivocal. Femur with large spines similar to the legs, patella not so spinose, and tibia and tarsus with more abundant coating of fine hairs. Tarsus shortest element in the pedipalp and lacking a terminal palpal claw (Figs 3C, 4C). Tarsus not noticeably inflated or with especially dense setation (as per *Sabacon*). Leg coxae subtriangular and with a few short setae.

Legs relatively long, approximate leg lengths: leg I, 6.6; leg II, at least 10.2; leg III, 6.5; leg IV, 10.1. All legs with prominent spines, angled slightly distally, along much of their length; apparently with four spines forming a cross-like pattern in transverse section. Femora without pseudoarticulations (present in nemastomatids and *Sabacon*, but not in *Taracus*). Metatarsi possibly subdivided, but unclear whether these constitute pseudoarticulations (as per *Hesperonemastoma*; Fig. 5A), or true segments (as per *Ischyropsalis*); areas of flexion can be resolved where the limb article seems to bend at certain points along its length. Tarsi clearly subdivided distally, where visible with a coating of fine hairs. Where leg tip is preserved, tarsus terminates in a single claw (Fig. 3D); smooth and without dentition.

Sternum equivocal. Opisthosoma somewhat domed (Fig. 2B), ornamented with multiple rows of short spines (Fig. 3A). At least four prominent rows visible, plus three further rows of slightly smaller spines towards the posterior end. First five spine rows occupy a single fused scute (a *scutum parvum*); the last two rows occupy two additional short, free tergites (NB: a plesiomorphic character in Shear [1986, tab. 1] for Ischyropsalidoidea is the presence of erect, acute spikes on the abdominal scutum). Some elements of the ventral sternites visible and with a few short setae, but details equivocal. Genital region not visible and penis/ovipositor equivocal. It is interesting to note that only one
sabaconid has a thorn on its ocularium – *Sabacon unicornis* Martens, 1972, from the Himalayas (Martens 1972, fig. 28) – and among the rest of the ischyropsalidoids, only *Hesperonemastoma modestum* has a similar scutum armament to the fossil; here including four pairs of sharp, curved and smooth/glazed thorns (Figs 5A, B).

Behind the opisthosoma lies a subtriangular, but rather poorly-defined element (Figs 2, 4A, B); length ca. 1.6; basal width ca. 0.5. This could conceivably be the terminal part of the opisthosoma – although this would be a very unusual feature compared to living harvestmen – and which we suspect it to be pressed out faecal material perhaps surrounded by the peritrophic membrane, as it appears to originate from the expected anal region.

Remarks. We cannot be certain whether the new fossil is male, female and/or immature (juvenile, nymph), since it is a unique species without an obvious Recent analogue. Furthermore, its body length (1.6 mm) is within the range of body sizes (0.89–22 mm) observed among Recent adult dyspnoid harvestmen (cf. Shear 1986; Gruber 2007). Note that in juvenile/immature dyspnoids the scutum is usually soft and formed from small, sclerotised areas which do not strongly express any armament and thus have a simpler sculpture (see e.g. Šilhavý 1948, 1956; Rambla 1968a, fig. 4, 1968b; Martens 1969a, figs 11–13). In some dyspnoid groups (Dicranolasmatidae, Nipponopsalididae) adults normally lack claveate setae on the palps; claveate setae are thus typical only for juveniles of these taxa. Our fossil specimen lacks claveate setae, the scutum appears robust and the spines on the body and ocularium are well developed. All of this tends to favour a more mature animal.

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