

# An enigmatic spiny harvestman from Baltic amber

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## Abstract

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## Key Words

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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 Sabaconidae, 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.

## Introduction

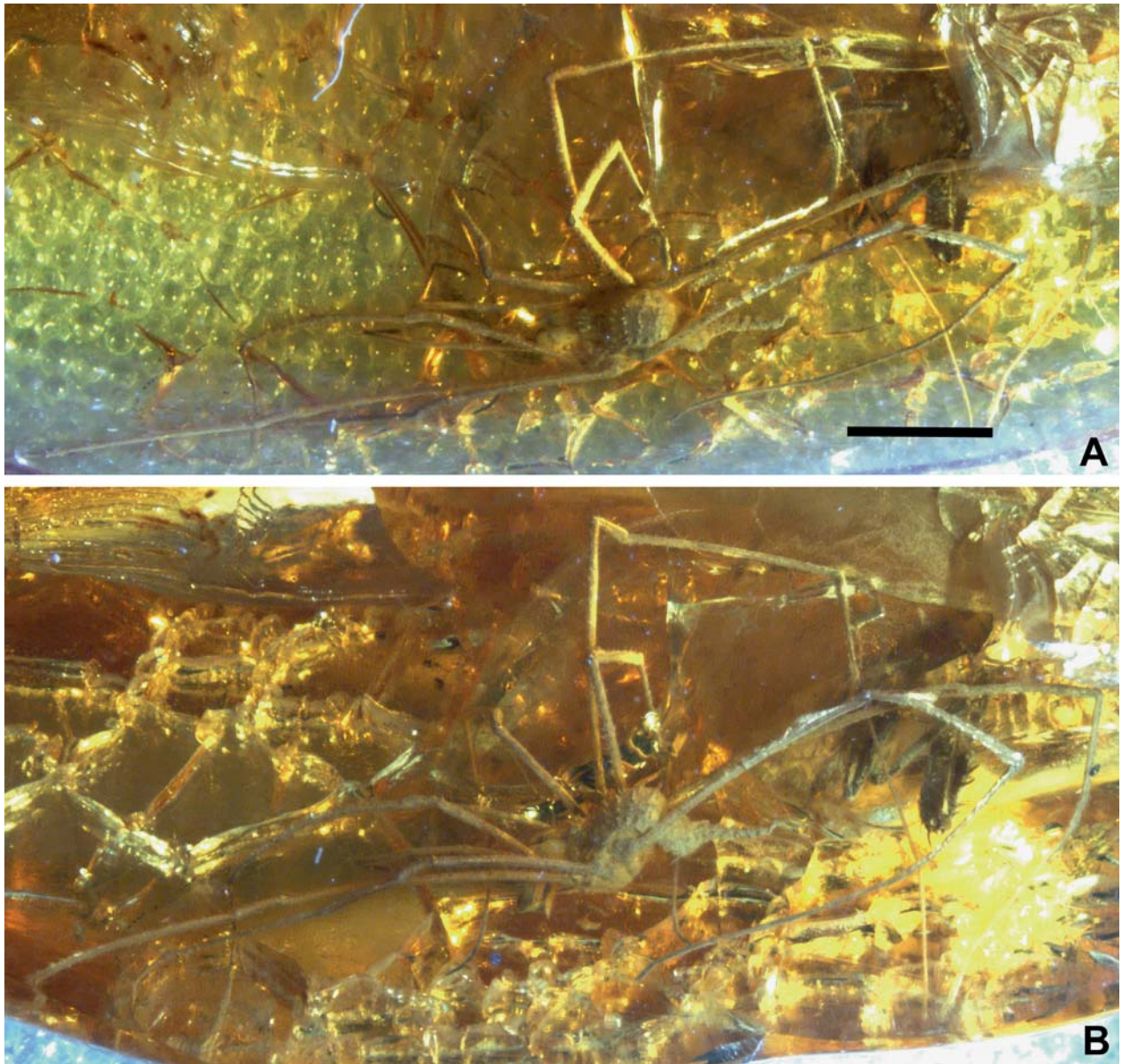
Harvestman (Arachnida: Opiliones) are a diverse group of arthropods in modern terrestrial ecosystems, with nearly 6,500 living species described thus far (Kury 2000; data as of March 2011). By contrast only thirty valid fossil species of harvestman are known, albeit with a record going back some 410 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 Starega (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 MB.A.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

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**Figure 1.** *Piankhi steineri* n. gen, n. sp. Overview of the complete animal (holotype and only known specimen: MB.A.1878) from Eocene Baltic amber (ca. 44–49 Ma). **A.** Dorsal view; **B.** Dorso-lateral view. Scale bar equals 2 mm.

manually in Adobe Photoshop. Drawings were prepared using a Leica MZ12 stereomicroscope with a *camera lucida* attachment. The amber fossil was compared to descriptions of living species in the literature – initially Roewer (1923) then also Sato & Suzuki (1939), Šilhavý (1956), Martens & Suzuki (1966), Gruber (1970, 1978), Ljovushkin (1971), Suzuki (1974), Shear (1975, 1986, 2010a) and Martens (1978, 1983, 1989) – and to extant, alcohol-preserved material in the Museum für Naturkunde Berlin and in the P. Mitov collection (PM). All measurements are in mm.

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 Johnson, Jr., det. J. C. Cokendolpher, (PM); *Taracus birsteini* Ljovuschkin, 1971 (Figs 5C–G). – 1 male (body length 4.2), 1 female (body length 4.6); Russia, Maritime Province, NW part of Vladivostok City, catacombs, 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 combina-

tion terminology follow Martens (1969a, fig. 10; 1972, fig. 2; 1978), and Shultz & Pinto-da-Rocha (2007, fig. 2.4).

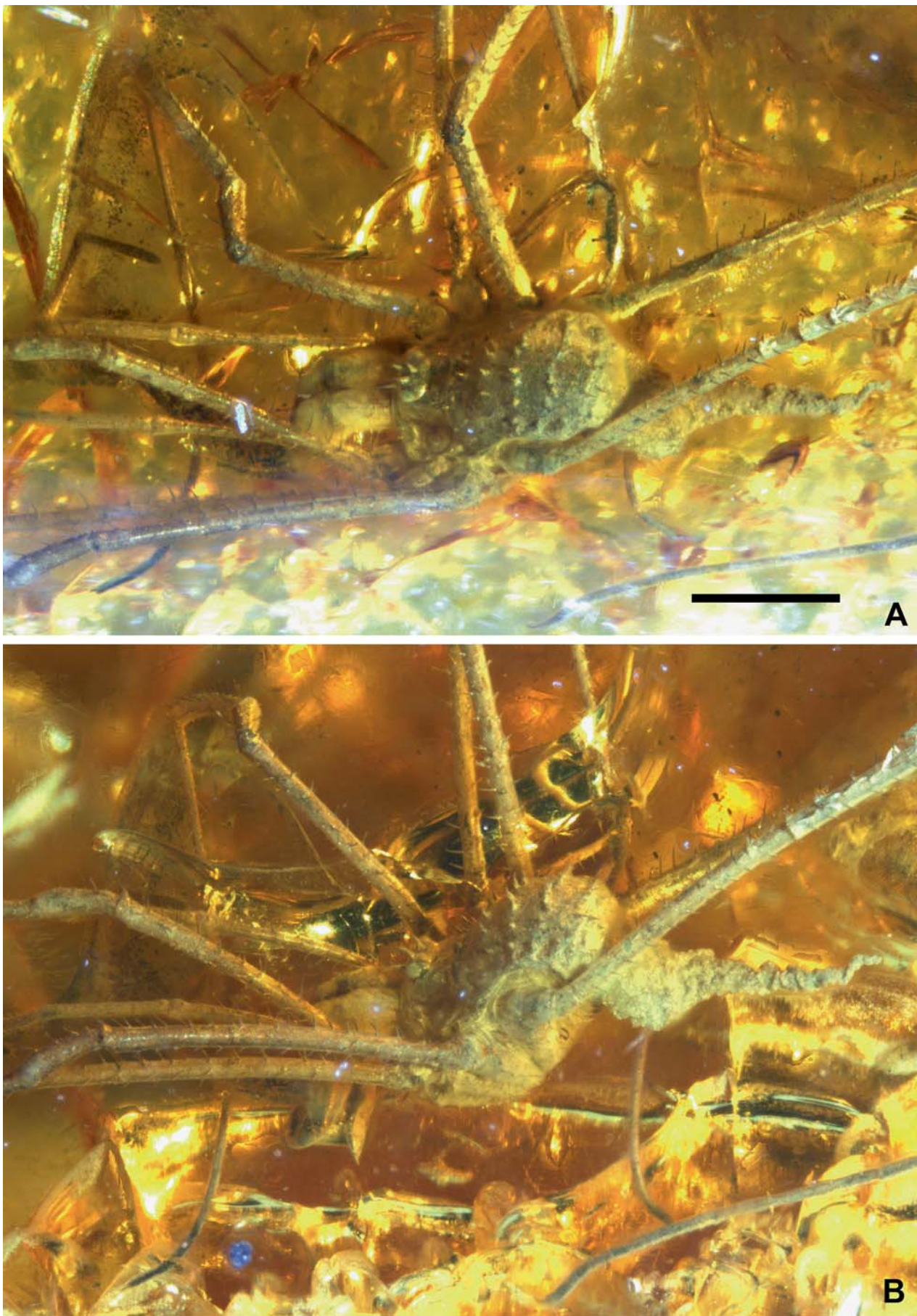
Baltic amber is conventionally dated to an Eocene (Lutetian) age of about 44–49 Ma. Details of the geological setting, other faunal elements and the presumably warm palaeoenvironment can be found in Weitschat & Wichard (2010) and references therein.

## Systematic paleontology

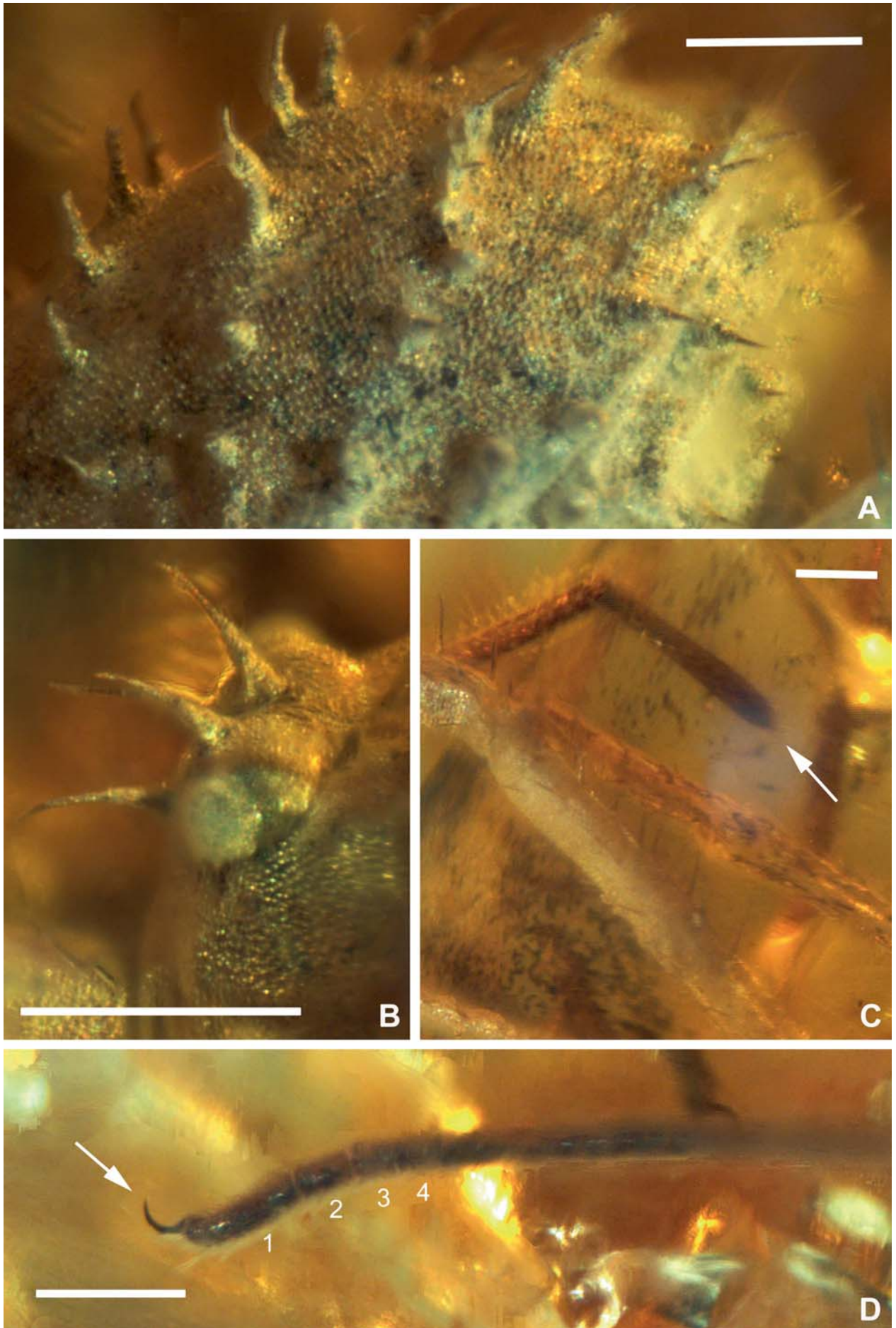
Order **Opiliones** Sundevall, 1833

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.



palp (Figs 3C, 4C) clearly points towards Dyspnoi; particularly the fact the tarsus is the shortest article and that it lacks an obvious tarsal claw. By contrast, in Eupnoi 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 dyspnooid families (as reviewed by Gruber 2007).

#### Superfamily ?*Ischyropsalidoidea* Simon, 1879

*Remarks.* Dyspnoi is traditionally divided into two superfamilies: Troguloidea 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 troguloid families Trogulidae, Dicranolasmatidae and Nemastomatidae all have highly characteristic body shapes (see also figures in Martens 1978) which differ substantially from the new amber fossil. For example dicranolasmatids 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 tergite(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 shorter 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 harvestmen 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

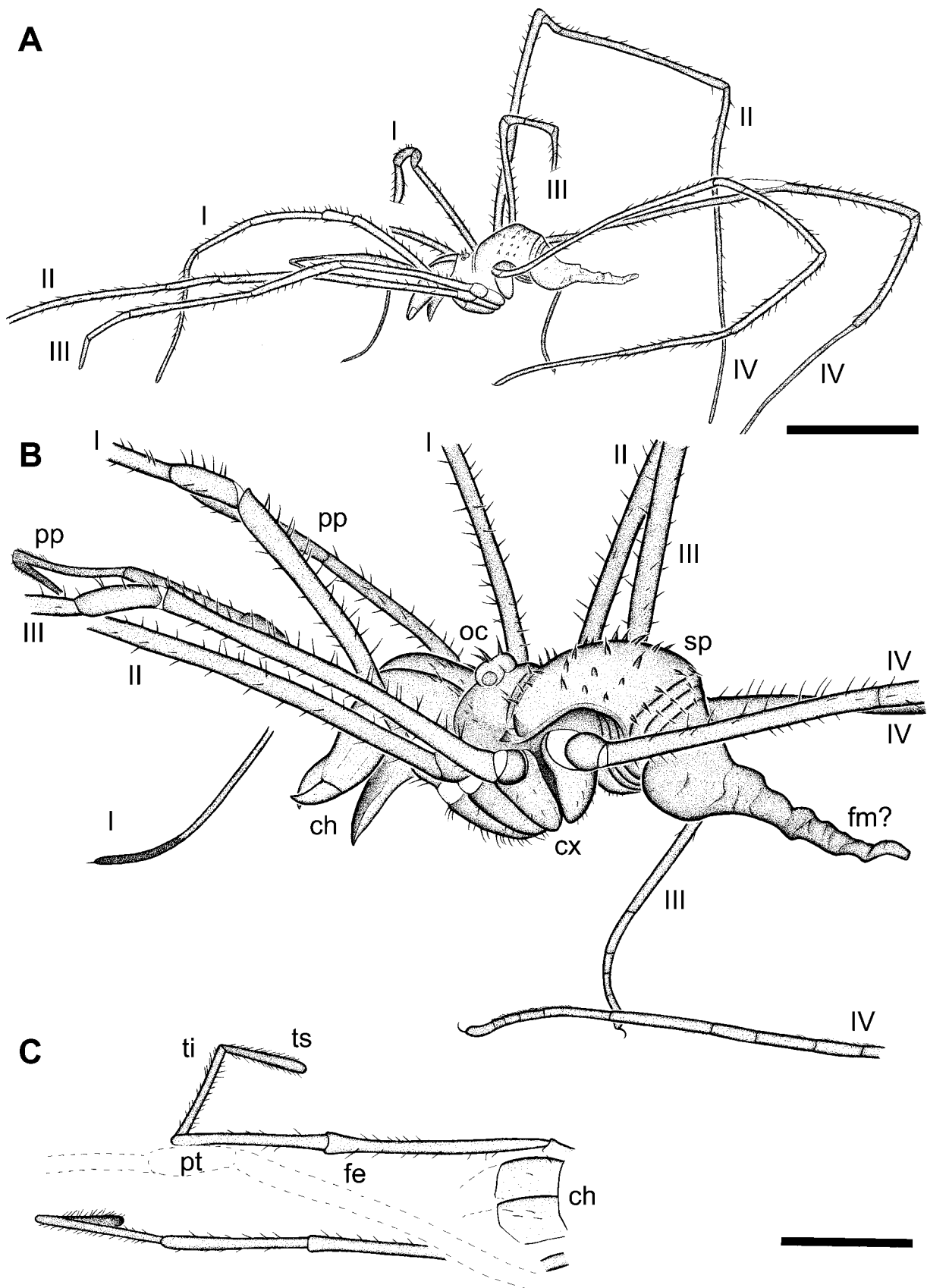
(Gruber 2007). However, unlike our fossil there are no robust spines on the ocularium, on the appendages or on the body in general. The chelicerae of nipponopsalidids are also proportionally much larger than those of the fossil, and further differences are elucidated below.

Superficially similar to Nipponopsalididae is the family Ischyropsalididae although this group apparently belongs in the second superfamily, Ischyropsalidoidea. This resemblance is thus considered convergent (Gruber 2007) and Ischyropsalididae is currently represented by a single genus, *Ischyropsalis* C. L. Koch, 1839, found in Central Europe and the Pyrenees, including the Carpathians, 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 material 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* species are not well known. As with nipponopsalidids, extant ischyropsalidids have not been recorded with all the characters seen in our fossil; namely stout spines on the ocularium, legs and body. What is worth mentioning here is that Martens’ (1978, p. 186) diagnosis of the ischyropsalidids 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 chelicerae can be up to ca. 1½ 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 dyspnooid harvestmen in general.

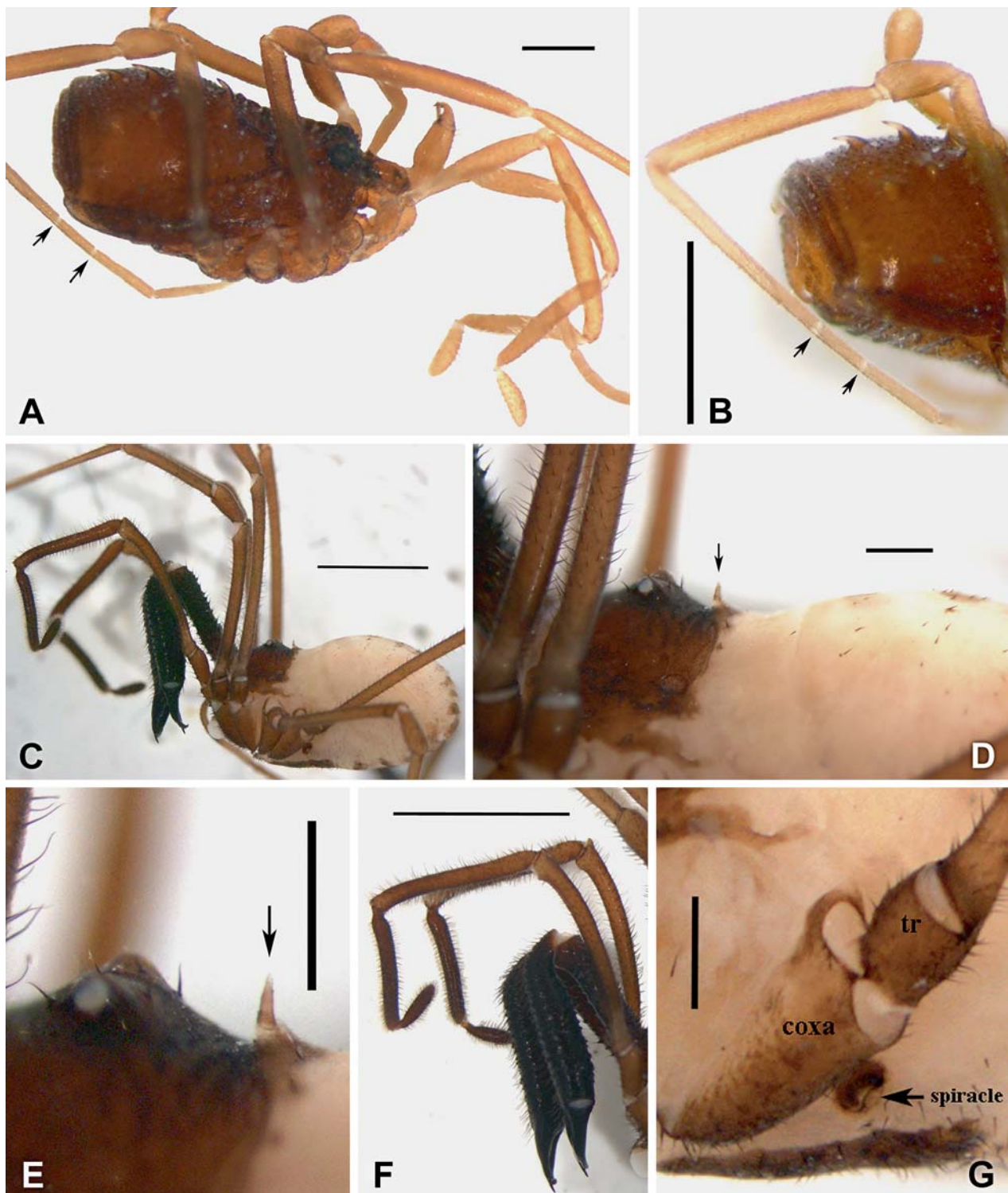
There are two further families in Ischyropsalidoidea to consider: Ceratolasmatidae and Sabaconidae. In some ceratolasmatids the pedipalps are elongate and thin (cf. *Crosbycus* Roewer, 1914) like those of the fossil. However, in other genera the pedipalps are short and moderately stout (cf. *Acuclavella* Shear, 1986 and *Ceratolasma* Goodnight & Goodnight, 1942). For comparative 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 ceratolasmatid. 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: “Ischyropsalidoids 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, **cx** – 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,  $T_s/T_i = 0.42$ ;  $T_i/P_t = 0.91$ ; 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  $T_s/T_i = 0.46$ ,  $T_i/P_t = 0.70$ ; **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).

scutum heavily ornamented with microsculpture of warts, fine denticles, or anvil shaped tubercles”.

Turning to Sabaconidae, the Holarctic genus *Sabacon* Simon, 1879 has long been known from Baltic amber (Menge 1854; Roewer 1939; Dunlop 2006). *Sabacon* comprises harvestmen with highly distinctive inflated distal tips of the pedipalps covered in a dense coat of fine setae. Some *Sabacon* species can – like the amber inclusion – express rows of spines across the dorsal opisthosoma (see below). At least one example of another sabaconid genus, *Hesperonemastoma modestum* (Fig. 5A, B), also has a dorsal spination pattern reminiscent of our fossil, but we can exclude the amber specimen from this genus which is defined (Gruber 1970) by a *Nemastoma*-like body, without a clear distinction between the carapace and dorsal opisthosoma. Furthermore, the amber fossil, in which the pedipalps are slender along their entire length and not distally inflated (Figs 3C, 4C), can also be excluded from *Sabacon*. Note that while some members of this genus – including the Baltic amber species (Dunlop 2006, fig. 4a) – have fairly small chelicerae, certain male *Sabacon* species also have much enlarged and more massive chelicerae, similar to the new fossil. For example, this is seen in *Sabacon imamurai* Suzuki, 1964 (cf. Suzuki 1964, fig. 1; 1974, fig. 9a, b) or *Tomicomerus bryanti* (Banks, 1898) (see Shear 1975, fig. 36). Note that Shear (1986) subsequently considered *Tomicomerus Pavesi*, 1899 to be a synonym of *Sabacon*; it appears somewhat intermediate between *Sabacon* and another genus which merits consideration: *Taracus* Simon, 1879 (see Shear 1975, p. 6).

*Taracus* occurs today in North America, and the Russian Far East (Ljovushkin 1971; Tchemeris 2000). Note that in the Tchemeris paper it was misidentified it as a species of *Nipponopsalis* Martens and Suzuki 1966 (cf. Gruber 2007). However, careful study yields sufficient characters to differentiate *Taracus* from nipponopsalidids. For example, Nipponopsalididae have a scutum parvum, scutum laminatum, scutum dissectum; a free metapeltidium, and a domed carapace with a large and low ocularium and low, rather large eyes. Nipponopsalidid palps are typically very long and slender with sparse simple setae (clavate setae occur only in juveniles on the tibia and tarsus), the leg femora have pseudoarticulations, the spiracles are hidden in a furrow behind the leg IV coxae and there is a characteristic penis structure and sternal-coxogenital region; see e.g. Sato & Suzuki (1939, figs 1–3), Martens & Suzuki (1966, figs 1–3) and Gruber (2007) for details. Some of these features (low ocularium, very slender pedipalps, pseudoarticulations on the legs) again help exclude our new amber fossil from Nipponopsalididae.

As figured by Tchemeris (facsimile copy also in Gruber), at least the Russian species of *Taracus* (see also Figs 5C–G) has quite prominent hairs on the appendages and a somewhat domed opisthosoma reminiscent of our fossil, while the tips of the pedipalps (Figs 5C, F) are not so inflated as in *Sabacon*. Never-

theless, 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 *Sabacon*). 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 specimens after death; as it occurs in (relaxed) modern material 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 patella 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 ceratolasmatid *Crosbycus*, and the new fossil (see below). Nevertheless, the rather elongate palpal 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-eating ischyropsalids: “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 fossil shows some similarities in its dorsal anatomy, long pedipalps and enlarged chelicerae to the modern East Asian Nipponopsalididae, the European Ischyropsalididae, 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 ceratolasmatids, 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) has minute humps each bearing a fine hair at its apex. Taking all this together, we tend towards ischyropsalidid/sabaconid affinities and tentatively refer the new amber fossil to Ischyropsalidoidea.

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 amber dyspnoid. Since even among the modern dyspnoids



gross morphology can be homoplastic (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 dyspnoid 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.** Dyspnoid 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 dyspnoid 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 micro-ornament. 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: M.B.A.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 *Crosbycus dasychnemus* (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 clavate setae on the palps; clavate setae are thus typical only for juveniles of these taxa. Our fossil specimen lacks clavate 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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