Fossil harvestmen (Arachnida, Opiliones) from Bitterfeld amber

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Abstract

Fossil harvestmen (Arachnida, Opiliones, Dyspnoi and Eupnoi) are described from Bitterfeld amber, Sachsen-Anhalt, Germany deposited in the Museum für Naturkunde, Berlin. The exact age of this amber has been in dispute, but recent work suggests it is youngest Palaeogene (Oligocene: Chattian). *Histricostoma tuberculatum* (Koch & Berendt, 1854), *Caddo dentipalpus* (Koch & Berendt, 1854), *Dicranopalpus ramiger* (Koch & Berendt, 1854) and *Leiobunum longipes* Menge, 1854 – all of which are also known from Eocene Baltic amber – are reported from Bitterfeld amber for the first time. They support the idea that both ambers sampled a similar terrestrial arthropod fauna: irrespective of any difference in age. *Mitostoma gruberi* **sp. n.** and *Amilenus deltshevi* **sp. n.** are described as new. One fossil is, in our opinion, morphologically indistinguishable from the extant species *Lacinius erinaceus* Staręga, 1966 from the Caucuses, and is tentatively assigned to this taxon. The Bitterfeld material thus includes the first fossil record of the extant genera *Amilenus* Martens, 1969 and *Lacinius* Thorell, 1876 respectively.

Keywords

Eupnoi, Dyspnoi, Oligocene, Sachsen-Anhalt, biogeography

Introduction

Most of the known fossil harvestmen (Arachnida: Opiliones) comprise inclusions in Baltic amber which are usually assigned to an Eocene (ca. 44-49 Ma) age. These Baltic amber species were described by Koch and Berendt (1854), Menge (1854) and Roewer (1939). Their affinities were reviewed by Bishop and Crosby (1924) and Staręga (1976a, 2002) with formal redescriptions and synonymy lists in Ubick and Dunlop (2005) and Dunlop (2006). Excluding synonyms and *nomina dubia*, nine valid harvestman species in Baltic amber can currently be recognised: four eupnoids, four dyspnoids and one laniatorid. A less familiar source of amber is the Bitterfeld deposit from the Sachsen-Anhalt region of eastern Germany, sometimes referred to in the literature as 'Sächsischer Bernstein'. Barthel and Hetzer (1982) illustrated some Bitterfeld inclusions, including a juvenile harvestmen held in what is now the Deutsches Bernsteinmuseum, Ribnitz-Damgarten, Germany. The first fossil cyphophthalmid harvestman (a basal clade) was described as *Siro platypedibus* Dunlop & Giribet, 2003 from Bitterfeld material in the Museum für Naturkunde Berlin (MfN). Here, we complement this initial study by describing further well-preserved Bitterfeld inclusions assignable to Eupnoi and Dyspnoi. Four of the taxa recorded here appear to be conspecific with species already known from Baltic amber (Dunlop 2006). Two species from Bitterfeld are interpreted as new, and another one can even be tentatively assigned to an extant harvestman species. The material includes the first fossil record of the extant genera *Lacinius* Thorell, 1876 and *Amilenus* Martens, 1969.

Material and methods

Bitterfeld amber originates from the site of the Goitsche [or Goitzsche] opencast 'Braunkohle' mine, near the town of Bitterfeld, Sachsen-Anhalt, Germany. Actively collected from the mid 1970s to the late 1990s, the mine is now flooded and no longer accessible (see e.g. Hoffeins and Hoffeins 2003). Bitterfeld inclusions held in the MfN arrived largely under the supervision of the palaeobotanist Prof. Manfred Barthel; see e.g. Barthel and Hetzer (1982) for an initial overview. The material came to Berlin as part of an agreement with the 'Volkseigener Betrieb Ostseeschmuck' (i.e. the GDR's state-owned Baltic Sea jewellery company), now the Deutsches Bernsteinmuseum in Ribnitz-Damgarten. In the 1980s the animal inclusions in Berlin were distributed to the relevant zoological curators of the MfN for sorting and provisional identification; the results of which were summarised by Schumann and Wendt (1989). The harvestmen (and other arachnids) were examined by Manfred Moritz, who assigned taxa where possible, but did not formally publish these identifications. In fact Schumann and Wendt (1989: 38) only listed "Phalangidae (subfamily Gyanthinae)" as present, without further details, and some of the provisional identifications by Moritz on the associated labels appear to

post-date this publication; see also Dunlop and Giribet's (2003) discussion of the cyphophthalmid.

All specimens described here are held in the palaeontological collections of the MfN, where they have been assigned MB.A. numbers (for Museum Berlin, Arthropoda). Sequential series of 10-30 images at different focal planes through the specimen were taken with a Leica stereomicroscope using the Leica Application Suite© software. Stacks of images were assembled into a single final picture using Auto Montage©. Specimens were drawn with a *camera lucida* attachment on a Leica MZ12 stereomicroscope. Fossils were compared to the literature – especially Šilhavý (1956) and Martens (1978, 2006) – and to extant material in the arachnological collections of the following institutions: MfN, Muséum d'Histoire naturelle, Genèva, Switzerland (MHNG), Museum and Institute of Zoology in Warszawa, Poland (MIZW), National Museum of Natural History, Sofia, Bulgaria (NMNHS) and the collection of Plamen Mitov (PMC). For comparative purposes photographs of the following Recent harvestmen species are also included here:

Mitostoma chrysomelas (Hermann, 1804). Material: Bulgaria, Sofia, Loven Park, housing complex "Dianabad", 10 m from Dragalevska River, under *Pinus*-bark, 10.IV.2004, leg. and det. P. Mitov (PMC). – 2 juv. (body length: 1.37 mm) (Fig. 4).

Mitostoma patrizii Roewer, 1953. Material: Italy, Sardinia, Village Domusnovas, Grotta di San Giovanni, 12.X.1980, leg. P. Beron, det. P. Mitov (NMNHS: museum inventory No. 84). – 1 male (body length: 2.1 mm) (Fig. 5).

Amilenus aurantiacus (Simon, 1881). Material: FYR of Macedonia: Šar planina (Šar Mountains), North of Tetovo, 800-1000 m altitude, *Fagus*-forest, on slopes, 11.IX.1986, leg. C. L. Deeleman and P. R. Deeleman, det. P. Mitov (MHNG). – 2 juv. (body length: 3.1 mm) (Fig. 22).

Lacinius erinaceus Staręga, 1966. Material: Caucasus: Abkhazia, region of Sukhumi, by the second bridge on Gumista River, on brushy limestone hillock, 21.XI.1963, leg. B. Pisarski (MIZW: museum inventory number 108/63). – 1 male (Holotype) (Figs 28-29).

Age of the inclusions

Considerable literature has been generated arguing both for and against a Miocene age for the Bitterfeld inclusions. Earlier studies generally supported a younger date and the uniqueness of the amber (Barthel and Hetzer 1982; Führman and Barsdorf 1986; Weitschat 1997). However, subsequent work (e.g. Röschmann 1997) recognised that both ambers appear to contain common arthropod species. Expanding this theme, Hoffeins and Hoffeins (2003) concluded that Baltic and Bitterfeld amber yield very similar faunal compositions and were thus probably of the same age – but perhaps with some regional differences. For spiders, Wunderlich (2004: 246-251) listed at least 17 species common to both ambers; with the comment that many other species are known only from single specimens and may be recovered from both localities in future. Wunderlich

thus regarded these amber deposits as probably being similar in age, but perhaps (as per Hoffeins and Hoffeins) involving an independent Bitterfeld amber forest.

A general problem with these arguments is that it is not at all clear how long a 'typical' species of terrestrial arthropod can survive essentially unchanged (see also Schmidt and Dörfeld 2007). For example, Sellnick (1919, 1931) effectively assigned a number of oribatid mites from Baltic amber to living species, albeit distinguished by the subspecies name '*fossilis*'. From the ca. 16 Ma Dominican Republic amber there is at least one fossil pseudoscorpion which is indistinguishable from – and indeed assigned to – an extant species (Judson 1998). In a similar vein, Armas (1988) synonymised a Dominican amber scorpion species described by Schawaller (1979) with an extant scorpion from the Caribbean region. Schawaller (1982) himself noted that a Dominican amber whip scorpion (Amblypygi) was morphologically almost identical to a modern Caribbean form; maintaining a distinct species name for the fossil based on little more than the difference in age.

We identify a comparable situation among Opiliones from Bitterfeld amber here (see *Lacinius* below). Indeed another Baltic (and now also Bitterfeld) amber harvestman, *Caddo dentipalpus* (Koch & Berendt, 1854), has been closely compared to the extant species *C. agilis* Banks, 1892, found disjunctly in North America and Japan. Transferred by Crosby and Bishop (1924: 83), they explicitly noted "It is very closely related to *C. agilis*.", while to quote Shear (1975: 73) on these same fossil and Recent taxa: "There is a strong possibility that they really are the same species, and this indicates a much wider previous distribution for *Caddo*." Further discussion of this fossil harvestman's affinities can be found below.

Thus it is unclear to what extent terrestrial arthropods in amber (individually or generally) are stratigraphically relevant as 'index fossils' and how, in the absence of absolute radiometric dates, this can be tested independently without circular reasoning. Baltic and Bitterfeld amber clearly do yield morphologically very similar harvestmen (see below), as well as other arachnid species. This could be interpreted either as evidence for a similar age for the ambers, or as evidence for a continuum of long-lived (morpho-) taxa throughout the Palaeogene of north–central Europe. The strong similarity of many of these fossils to extant taxa would tend to favour the latter interpretation, and it is interesting to observe that the closest living matches to some northern European amber arachnids are distributed in warmer latitudes today.

Recent studies on the age and provenance of Bitterfeld amber have concluded that it should indeed be treated as independent of the better known Baltic amber (Knuth et al. 2002; Führman 2004; Schmidt and Dörfeld 2007). These papers suggest a youngest Palaeogene (Oligocene: Chattian) age, whereby the amber-bearing sediment has a suggested absolute age of 25.3-23.8 Ma; i.e. about 20 million years younger than Baltic amber. Further details of the geological setting and debates about the age of the Bitterfeld deposit can be found in these publications, and references therein. An Oligocene age is adopted in the present paper.

Descriptions

Suborder Dyspnoi Hansen & Sørensen, 1904
Family Nemastomatidae Simon, 1879

Genus ?*Histricostoma* Kratochvíl, 1958

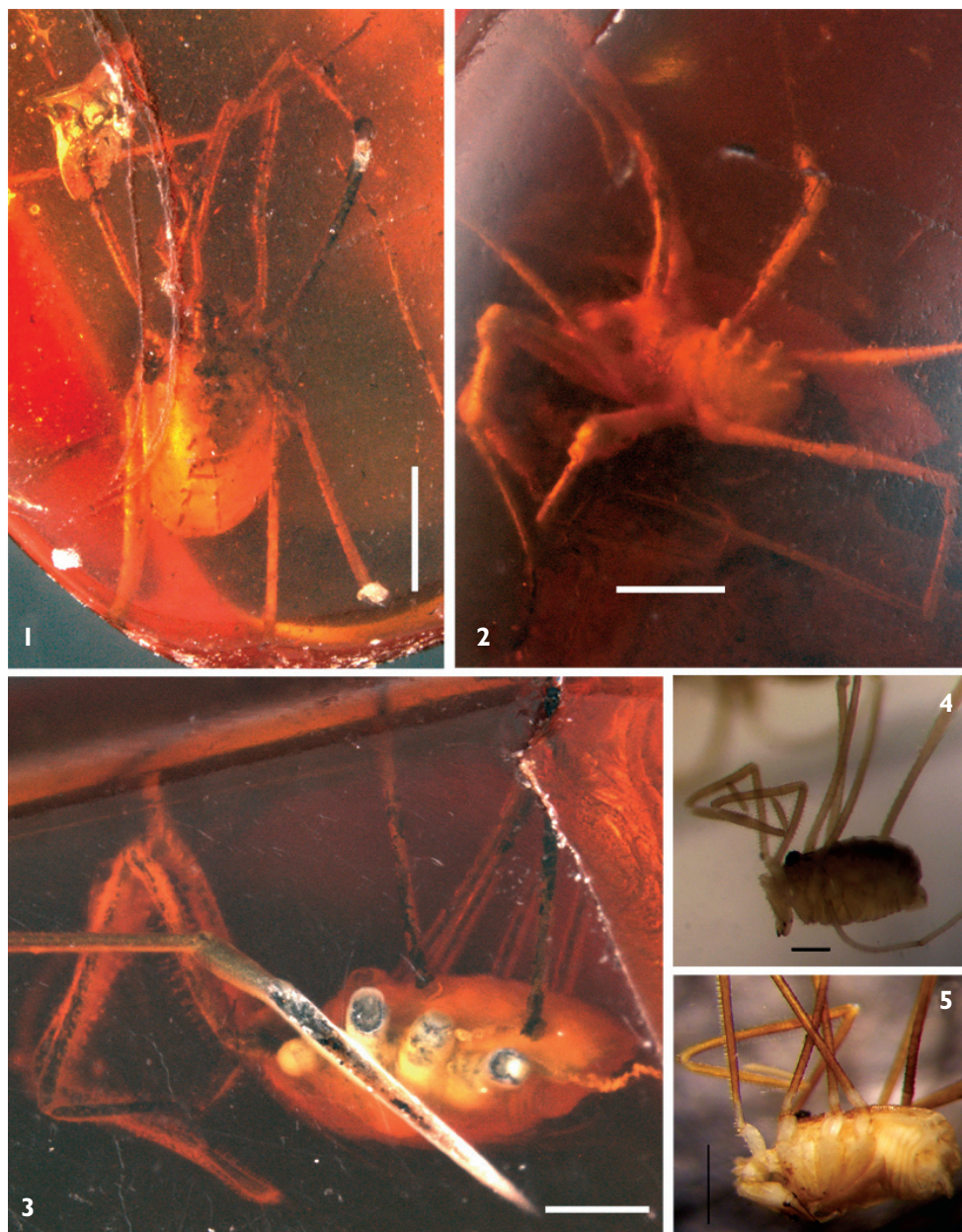**?*Histricostoma tuberculatum* (Koch & Berendt, 1854)**
Figs 1-2, 6-8

**Synonymy.** See Dunlop (2006, p. 179).

Holotype. MfN, Berendt collection, repository nr. 7248, redescribed by Dunlop (2006), from Baltic amber (Palaeogene, Eocene); precise locality unclear.

Additional material. MfN, MB.A. 1652 (also bears a label "Ser. 8/11") and MB.A. 1653. Bitterfeld amber, probably from the site of the Goitsche open-cast Mine near Bitterfeld, Sachsen-Anhalt, Germany; Palaeogene (Oligocene: Chattian).

Description. MB.A. 1652 (Figs 1, 6) is a fairly complete specimen in dorsal view. Body compact, smoothly oval, length 1.48 mm; maximum width ca. 1.0 mm. Prosoma and opisthosoma completely fused together with little or no evidence of tagmosis between these body regions, of divisions of the prosomal dorsal shield and/or of opisthosomal segmentation. Ocular tubercle flattened, diameter of each lens c. 0.1 mm. Slight bilobation to the anterior margin of the prosomal dorsal shield. Basal article of chelicera projects forwards, maximum length 0.26 mm, more distal articles largely tucked under body obscuring details, but quite setose on their anterior margin. Basal article distally with a globular and setose apophysis (Fig. 7). Pedipalps elongate and slender. Palpal coxae project forwards up to 0.19 mm. Subsequent articles with lengths (in mm) of trochanter, 0.28; femur, 0.85; patella, 0.70; tibia, 0.78; tarsus, 0.33; giving a total post-coxal length of 2.94. Palpal trochanter oval, bearing numerous very short setae. Femur longer, curving mesally slightly and widening distally, and with longer inward-pointing setae; especially on the mesal surface. Patella and tibia also with some longer setae. Tarsus slightly swollen and quite densely setose. Leg 1 almost complete, other legs attached to body as femora only; with leg 4 quite poorly preserved. Leg 1 article lengths (in mm): trochanter, 0.22; femur, 1.59; patella, 0.26; tibia, 0.69; metatarsus, 1.50; tarsus at least 0.56. Tarsus with at least one long and one short distal article but distal end and any claw equivocal. Femora 2 and 3 with lengths of 1.87 and 1.44 mm respectively. Most leg articles elongate, slender and widening slightly distally, but patella short and globular. Femora typically with three pseudo-articulations, revealed as concavities in the limb outline and/or as paler bands about a third to a half of the way along the article. Trochanters often with short hairs (as in the pedipalps) and femora with a mixture of short hairs and robust, but very short spines along the length of the article. Setation seemingly weak or absent on more distal leg articles, but reappearing as a few longer setae towards the distal end. At least two disarticulated distal limb regions also cross the body, presumably deriving

Figures 1-5. Nemastomatids. **1** ?*Histricostoma tuberculatum* (Koch & Berendt, 1854), MB.A. 1652 **2** ?*H. tuberculatum*, MB.A. 1653 **3** *Mitostoma gruberi* sp. n. MB.A. 1654 (holotype) [all from Bitterfeld amber (Palaeogene: Oligocene)] **4** Juvenile *Mitostoma chrysomelas* (Recent harvestman for comparison) **5** Male *Mitostoma patrizii* (Recent harvestman for comparison). Scale bars equal 1.0 mm (**1-2**, **5**), 0.5 mm (**3**) and 0.35 mm (**4**).
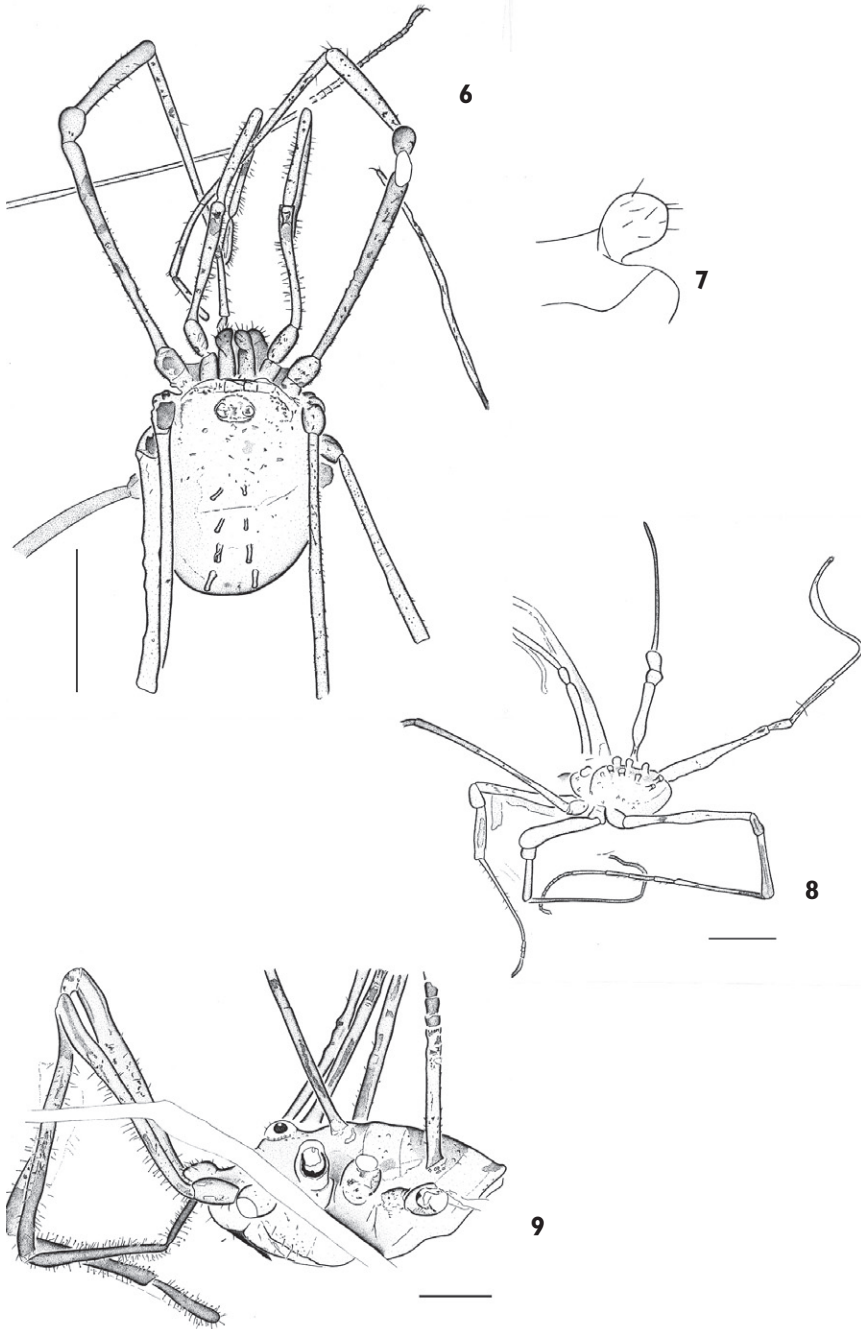
Figures 6-9. *Camera lucida* drawings of the specimens shown in **1-3**. **6** ?*Histricostoma tuberculatum* (Koch & Berendt, 1854), MB.A. 1652 **7** the same – detail of the apophysis at the tip of the first cheliceral segment (right chelicerae, dorso-lateral view) **8** ?*H. tuberculatum*, MB.A. 1653 **9** *Mitostoma gruberi* sp. n. MB.A. 1654 (holotype). All from Bitterfeld amber (Palaeogene: Oligocene). Scale bars equal 1.0 mm (**6**, **8**) and 0.5 mm (**9**).

from the same animal. Both end in a single curved claw and one is clearly an annulate tarsus with at least 15 individual elements. Opisthosoma smooth, without ornament save for four pairs of prominent spines standing perpendicular to the body surface. Spines c. 0.2 mm high, ending in slightly swollen and rounded tips. Anterior three pairs more or less parallel, c. 0.2 mm apart, posterior (fourth) pair a little larger and more widely separated, c. 0.3 mm apart. Ventral surface of body unknown.

MB.A. 1653 (Figs 2, 8) is an almost complete specimen, but one which is largely covered with a white emulsion, which makes features of the body and especially the proximal regions of the legs appear much thicker than they would have been in life. Body oval, length 1.52 mm. Eye tubercle distinct, but lacking details, while differentiation into a prosoma and opisthosoma unusually clearly expressed for a nemastomatid harvestman. Opisthosoma bears four pairs of erect spines arranged in two sub-parallel rows. Chelicerae and pedipalps largely equivocal. Legs relatively complete. Leg 1 with article lengths (in mm) of: femur, ca. 1.2; patella, 0.37; tibia, 0.77; metatarsus and tarsus, ca. 1.8. Total length ca. 4.1 mm. Metatarsus–tarsus boundary indistinct, but tarsus with some degree of distal division into tarsomeres. Leg 2 incomplete, lengths of trochanter 0.28 and femur 2.62 mm. Femur noticeably slender. Leg with article lengths (in mm) of: trochanter, 0.23; femur, 1.23; patella preserved at an angle which prevents measurement; tibia, 0.63; metatarsus and tarsus, ca. 2.77. Metatarsus–tarsus boundary indistinct. Leg 4 especially well preserved with article lengths (in mm) of: trochanter, 0.33; femur, 1.90; patella, 0.35; tibia, 0.80; metatarsus, 1.4; tarsus, ca. 2.3. Total length ca. 7 mm. Tarsus subdivided into four long and ten short tarsomeres; tarsus ends in a single claw.

Remarks. ?*Histricostoma tuberculatum* (Koch & Berendt, 1854) has now been recorded from both Baltic and Bitterfeld amber. All these fossils are tentatively assignable to *Histricostoma* Kratochvíl, 1958 based on the pillar-like opisthosomal spines. However, other nematostomid genera can show similar armature, thus the slight uncertainty about this referral. Unfortunately without penis morphology, which has so far not been recorded in amber fossils, an unequivocal referral to *Histricostoma*, or any other genus remains difficult. An alternative could be *Mediostoma* Kratochvíl, 1958, although for us ?*H. tuberculatum* is more '*Histricostoma*' like than '*Mediostoma*' like in term of the form and position of the thorns; the absence of specific microsculpture elements on the leg femora and scutum, and the position of the ocular tubercle. We concede that the shape of the apophysis matches the *Mediostoma* type, but this in isolation is insufficient – some other nemastomatid gerera express a similar shape (e.g. *Vestiferum* Martens, 2006, *Nemastomella* Mello-Leitão, 1936) – and variation in apophysis shape within *Mediostoma* species can be high (Martens 2006: 186).

Interestingly the opisthosomal spines are less pronounced in the holotype from Baltic amber (Dunlop 2006: fig. 6C) – which also has a slightly broader, somewhat pear-shaped, opisthosoma – when compared to the new Bitterfeld material. However, as Martens (1978) noted, in Recent species spination is less pronounced in females compared to males. Minor differences in the degree of spination would thus be a poor species character to adopt and it is conceivable that the differences observed here are principally sexually dimorphic. The unusually clear dividing line between the pro- and

opisthosoma in MB.A. 1653 may result from the emulsion layer highlighting a furrow between the prosoma and opisthosoma, which is normally present in many adult nemastomatids. In juveniles such tagmosis is also clearly present since the scutum magnum remains divided into two parts (e.g. Rambla 1968: fig. 4), although here they are clearly separate sclerites. This cannot be resolved in the emulsion-covered MB.A. 1653.

Also of note is the fact that in this fossil species the legs and pedipalps are elongate and slender. This is untypical for males of Recent species, where the female pedipalp is usually the more slender (cf. Martens 2006: fig. 26). However, the presence of an apophysis on the chelicera of MB.A. 1652 (Fig. 7) is characteristic for males. It is conceivable that we could be dealing with an andromorphic female; see e.g. Chemini (1984) for an example of this phenomenon in Recent nemastomatids. Further support for this hypothesis comes from the absence of any thorns on the distal end of the pedipalp patella (Fig. 6) which are normally present in *Histricostoma* males (Staręga 1976b; Martens 1978, 2006; P. Mitov pers. obs.). In any case, the distal end of the pedipalp femur bears concavities – something typical for Recent *Histricostoma* species and provides further grounds for referring these fossils to this genus. Other potentially useful characters, such as the form and concavity of the secretion area of the cheliceral gland, are equivocal in these fossils.

Mitostoma gruberi sp. n.

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Figs 3, 9

Material. MfN, MB.A. 1654. Bitterfeld amber. Probably from the site of the Goitsche Open Cast Mine near Bitterfeld, Sachsen-Anhalt, Germany; Palaeogene (Oligocene: Chattian).

Diagnosis. Fossil *Mitostoma* with a specific form of the apophysis on the first cheliceral segment and specific form of the palpal tarsal segment.

Etymology. In honour of Dr Jürgen Gruber (Vienna) in recognition of his extensive studies on harvestmen, and nemastomatids in particular.

Description. MB.A. 1654 comprises a well-preserved body and pedipalps in lateral view, with a number of slightly disarticulated leg femora. Body length, 1.5 mm. Ocular tubercle distinct, eye diameter 0.20 mm. Opisthosoma with hints of segmentation and slight tuberculation on the dorsal surface towards the posterior half of the body. Chelicerae largely obscured, but dorsal part of first segment appears inflated forming an apophysis whose form is close to that of the Italian endemic *Mitostoma orobicum* (Caporiacco, 1949) (see Tedeschi and Sciaky 1997: fig. 11). Pedipalps long and slender, article lengths in mm: trochanter, 0.27; femur, 1.42; patella, 1.63; tibia, 0.80; tarsus, 0.48. Tarsus slightly swollen at its distal end. Pedipalps setose, many palpal setae, particularly towards the distal end, with rounded tips (i.e. clavate setae). Trochanters of legs oval, femora long and slender, but more distal parts of the legs equivocal. Femora with scattering of short, thorn-like spines and one femur (femur 4?) with at least three short pseudoannulations, beginning about 0.8 mm along its length.

Remarks. This fossil can be assigned to *Mitostoma*, as opposed to *Nemastoma* C. L. Koch, 1836, on the basis of the proportions of the pedipalp articles, while the cheliceral apophysis indicates a male specimen. Whether it is juvenile or adult is less clear, but strong parallels can be drawn with the widespread European species *M. chrysomelas* (Hermann, 1804) if the fossil is juvenile, or with the Sardinian troglobitic endemic *M. patrizii* Roewer, 1953 if adult (cf. Fig. 5). Juveniles of the former and adults of the latter have small tubercles on the scutum – see especially Roewer (1953: fig. 1) and Tedeschi and Sciaky (1997: fig. 1) for *M. patrizii* – although the scutum of the fossil specimen is better developed than in comparable juveniles of *M. chrysomelas* (cf. Fig. 4).

Note that an existing fossil from Baltic amber has already been assigned to *Mitostoma – M. denticulatum* (Koch & Berendt, 1854) – transferred here from *Nemastoma* by Staręga (1976a); an interpretation followed by Dunlop (2006). On reflection, this assignment to *Mitostoma* may be incorrect and the situation is not helped by the dorsal surface of the holotype being partially broken and the apparent loss of the type material of its putative junior synonym *N. succineum* Roewer, 1939. In our revised opinion, the legs of *M. denticulatum* express lengths more consistent with modern *Carinostoma* Kratochvíl, 1958 or *Mediostoma* Kratochvíl, 1958 species. These (and other) nemastomatid genera with comparable dorsal ornament may be closer to the Baltic amber fossils. The status of *M. denticulatum* will be reassessed in a future study of Baltic amber harvestmen. Thus for the reasons outlined above we are confident that our new Bitterfeld species can be assigned to *Mitostoma* and is probably not conspecific with Koch and Berendt's Baltic amber taxon.

Suborder Eupnoi Hansen & Sørensen, 1904
Family Caddidae Banks, 1893
Subfamily Caddinae Banks, 1893

Genus *Caddo* Banks, 1892

***Caddo dentipalpus* (Koch & Berendt, 1854)**
Figs 10-14

Synonymy. See Dunlop (2006, p. 169).
Holotype. MfN, Berendt collection nr. 7340, redescribed by Dunlop (2006), from Baltic amber (Palaeogene, Eocene); precise locality unclear.
**Additional material.** MfN, MB.A. 1655 (also bears the label "Ser. 12/13") and MB.A. 1656 (also bears the label "Ser. 8"), from Bitterfeld amber, probably from the site of the Goitsche open-cast Mine near Bitterfeld, Sachsen-Anhalt, Germany; Palaeogene (Oligocene: Chattian).
Description. MB.A. 1655 (Figs 10, 12) is a relatively complete specimen in lateral view. Body compact, length ca. 1.5 mm. Prosoma dominated dorsally by massive, oval eyes, maximum width 0.58 mm, in the form of a bilobed ocular tubercle. Further details of carapace morphology concealed beneath eyes. Chelicerae and sternal region cannot be

seen. Pedipalps stout, femur particularly robust with at least eleven stout setae on the inferior lateral surface opposing the more distal articles. Femoral dentition equivocal in this specimen. Palpal article lengths (in mm): femur, 0.46; patella, 0.40; tibia, 0.23; tarsus 0.42. Some setal positions on femur revealed as sockets only. More distal palpal articles also setose; tarsus ends in a single, gently curving claw. All legs elongate and slender, femora and patellae sometimes with a short, stout seta near the distal end; patella noticeably shorter than adjacent articles. Right legs 1, 2 and probably 4 relatively complete. Articles of leg 2 noticeably longer than corresponding articles of leg 1, e.g. patellae 0.26. and 0.29 mm, tibiae 1.02 and 1.29 mm and metatarsi 1.36 and 1.91 mm respectively. Right leg 1 ends in a distally annulate tarsus with at least 11 annulations; distal annulus bears a single, hook-shaped claw. Left leg 3 relatively complete, other legs on left side truncated. A disarticulated leg fragment, probably a distal region bearing an annulate tarsus, crosses the distal part of left leg 3. Opisthosoma covered dorsally with a shield-like sclerite, length 0.67 mm, lacking obvious segmental divisions. Ventral region equivocal, but some hints of up to four sternites towards the posterior end of opisthosoma preserved.

MB.A. 1656 (Figs 13-14) is another excellent specimen, also in lateral view, and preserving the mouthparts in some detail. Body compact, length c. 1.5 mm. Prosoma with large eyes, maximum diameter 0.56 mm, remainder of carapace obscured. Chelicerae robust, composed of three articles. First cheliceral article tubular, total length not preserved, ornamented with sparse setae. Second cheliceral article somewhat swollen and globose proximally, tapering distally and becoming recurved at the very end to form the fixed finger of the claw (= chela). Total length 0.57 mm. Movable finger short, length 0.16, forming the free finger of the claw. Pedipalps robust. Right trochanter bears one thorn medially. One femur preserves a prominent, dentate thorn on the inferior surface (hence the name *dentipalpus*) and both femora exhibit a blunt, mesal protuberance at the distal end of the article, bearing setae. Patella, tibia and tarsus of pedipalp strongly setose. Leg 1 complete, folded across the body, with podomere lengths (in mm) of femur, 0.60; patella, 0.32; tibia, 0.79; metatarsus, 1.79; and tarsus, 0.59. Total length 4.09. Tarsus multi-articulate, composed of ten elements with the longest located proximally, and ending in a single tarsal claw. Remaining legs incomplete, but longer than leg 1. Dorsal opisthosoma with evidence for at least five tergites. Ventral surface equivocal.

Remarks. *Caddo dentipalpus* (Koch & Berendt, 1854) is present in both Baltic and Bitterfeld amber. It is of particular interest given that there are no Recent records of caddids in Europe, or much of Asia for that matter. According to Shear (1975), Caddidae is currently restricted to North America, Mexico, Chile, Japan, Australia, New Zealand and South Africa. Like these amber inclusions, the genus *Caddo* is restricted today to the northern hemisphere. The amber shows that it used to occur more widely, being present in north-central Europe during the Palaeogene, but subsequently became extinct in this region. The Bitterfeld specimens described here are probably juveniles. Their body lengths of 1.5 mm are shorter than the 2.3 mm of the holotype in Baltic amber and are slightly outside the published minimum ranges for adults of the very similar extant species *Caddo agilis*: 1.64 mm for females, 1.9 mm for males (cf. Suzuki et al. 1977; Suzuki 1986). Minor differences in morphology can be observed in the Bitterfeld fossils, but compared to
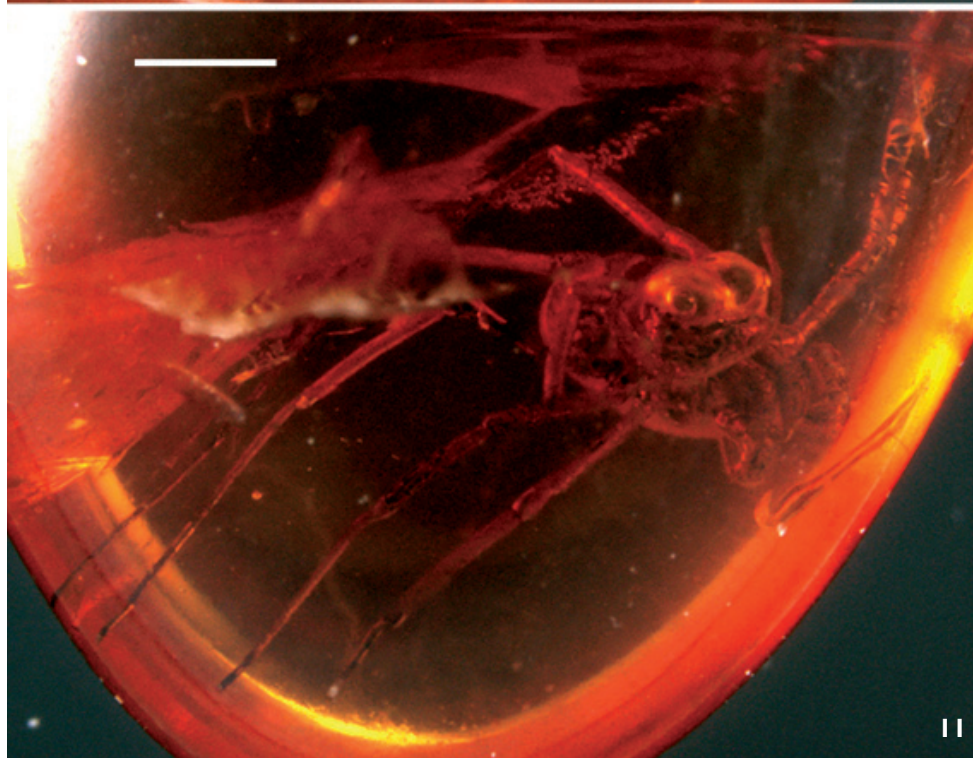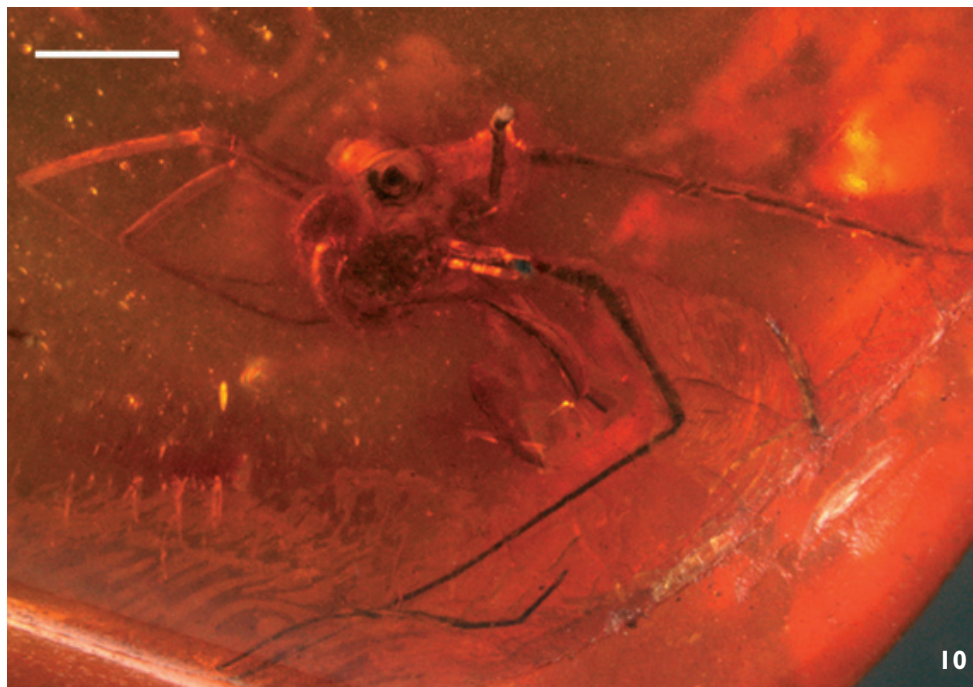
Figures 10-11. *Caddo dentipalpus* (Koch & Berendt, 1854) from Bitterfeld amber (Palaeogene: Oligocene). **10** MB.A. 1655 **11** MB.A. 1656. Scale bars equal 1.0 mm.
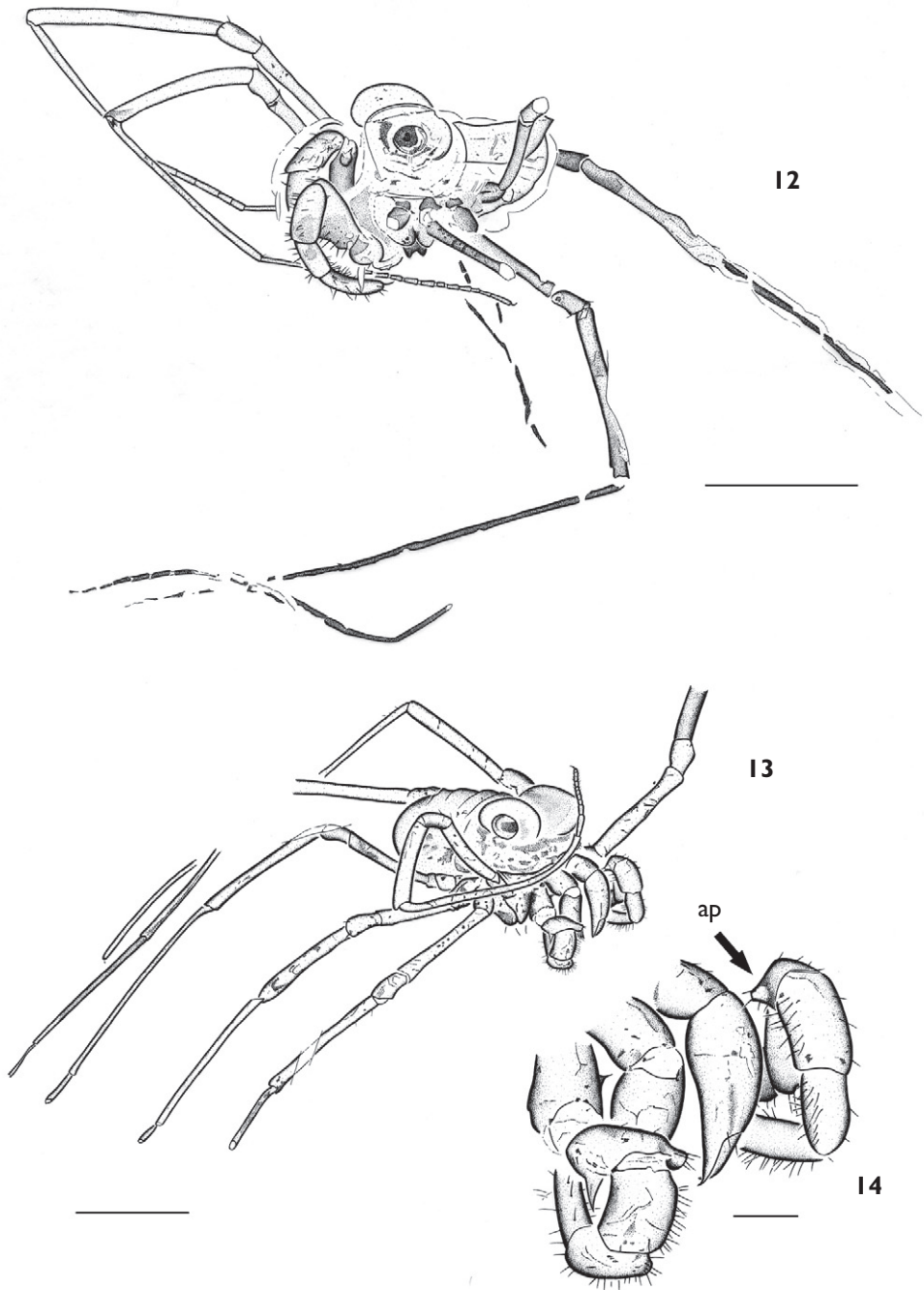
Figures 12-14. *Caddo dentipalpus* (Koch & Berendt, 1854). *Camera lucida* drawings of the specimens shown in **10-11**. **12** MB.A. 1655 **13** MB.A 1656 **14** the same, detail of the mouthparts showing the distal median apophysis of the pedipalp femur (ap). All from Bitterfeld amber (Palaeogene: Oligocene). Scale bars equal 1.0 mm (**12-13**) and 0.2 mm (**14**).

extant taxa these are probably sexually dimorphic. For example, MB.A. 1655 (Fig. 12), without obvious spines or thorns on the pedipalp femur, is probably male, whereas MB.A. 1656 (Fig. 14), which has such spination, is probably female. The holotype of *C. dentipalpus* clearly has three femoral thorns (Bishop and Crosby 1924: fig. 1). By comparison there are three such thorns in *Caddo agilis* females, whereas males have only one strong, finger-like protuberance (e.g. Gruber 1974: figs 18-22; Suzuki and Tsurusaki, 1983).

A distal mesal protuberance of the femur – as in MB.A. 1656 (Fig 14: ap) – is of some significance. Visible in both Bishop and Crosby's (1924: fig. 1) and Dunlop's (2006: fig 2A) drawings of the *C. dentipalpus* holotype too, this apophysis has also been reported in *C. agilis*. In detail, Bishop (1949) reported this structure at the distal mesal angle of the pedipalp femur in juveniles from North America. Suzuki (1958) reported it from his (Japanese) females and Gruber (1974) figured it in adult females from North America. It appears to be generally absent from males (Gruber 1974; Suzuki and Tsurusaki 1983). This femoral protuberance again emphasises the similarities – if not the conspecificity *sensu* Shear (1975) – between fossil and living *Caddo* harvestmen. The question of whether the amber examples merit a separate species is difficult to answer and further fossils would be welcome to test the stability of characters both between genders and instars. Bishop and Crosby's (1924: fig. 1) illustrations also hint at a protuberance on the mesal side of the patella and a rather poorly defined feature in this area – or at least a group of setae – was observed here in MB.A. 1655 (Fig. 12). If this character could be confirmed in other specimens it would offer a possible diagnostic character compared to Recent species.

Conceivably, Eocene–Oligocene populations of European *Caddo* occupied specialized habitats and expressed subtle differences from modern Asian and North American forms which are difficult to assess in the available fossils. To complicate matters further, some modern *Caddo* species are thought to have arisen through neotony of isolated populations (Shear 1975; Rambla 1980) and there are also frequent reports of parthenogenesis among the Recent fauna (e.g. Gruber 1974; Shear 1975; Suzuki 1976; Suzuki and Tsurusaki 1983) all of which may hinder the resolution of unequivocal apomorphies for the amber species. Shultz and Regier (2009) recently argued that *C. agilis* and its potential neonate *C. peperella* Shear, 1975 – both of which occur disjunctly in North America and Japan – evolved as distinct species, prior to their separation into American and Asian populations. Questioning the neotony hypothesis, they further discussed the potential role of paedo- and peramorphosis in understanding *Caddo* evolution and noted the need for further data from ancestral *Caddo* populations. With these provisions in mind, we prefer to retain *C. dentipalpus* as a separate taxon for the time being.

Family Phalangiidae Latreille, 1802
Dicranopalpus genus group

Remarks. The following two genera are clearly related, but their position has been debated. For example Martens (1978) referred them to Gyantinae [= Gyinae]. Crawford (1992, p. 4) disputed this and recognised an informal '*Dicranopalpus* genus group'

comprising *Dicranopalpus*, *Amelinus* and *Lanthanopilio* Cokendolpher & Cokendolpher, 1984; which he suggested could eventually merit family status. In the absence of further revision, Crawford's term is adopted here.

Genus *Dicranopalpus* Doleschall, 1852

Dicranopalpus ramiger (Koch & Berendt, 1854)
Figs 15-19

Synonymy. See Dunlop (2006: 170).

Holotype. MfN, Berendt collection, repository number 7250, from Baltic amber (Palaeogene, Eocene); precise locality unclear.

Additional material. MfN, MB.A. 1657 (also bears label "Ser. 12/14) and MB.A. 1658 (also bears label "Ser. 8"), from Bitterfeld amber, probably from the site of the Goitsche open-cast Mine near Bitterfeld, Sachsen-Anhalt, Germany; Palaeogene (Oligocene: Chattian).

Description. MB.A. 1657 (Figs 15, 17) is a fairly complete specimen in dorsal view. Body oval to quadrate, length 1.22 mm, maximum width 0.90 mm. Prosoma with semicircular propeltidium bearing ocularium; length 0.125 mm, width 0.325 mm, distance from ocular tubercle to the front of prosoma 0.1 mm. Opisthosoma with hints of weak segmentation, largely obscured by an imperfection in the matrix. Chelicerae indistinct, as are proximal articles of pedipalp. Patella of pedipalp, length 0.18 mm, with characteristic *Dicranopalpus* setose apophysis on mesal side, length 0.25 mm, extending about three-quarters of the way down the adjacent tibia. Tibia of pedipalp with length 0.27 mm, terminating in a further blunt, short setose apophysis. Pedipalpal tarsus widens slightly distally and ends in a single claw. Legs long and slender, but full lengths not preserved. Leg 2 longest, at least 8.6 mm. Measurable articles preserved in their entirety are (in mm) as follows. Leg 1: femur, 1.05; patella, 0.29; tibia, 1.02. Leg 2: femur, 2.24; patella, 0.33; tibia, 2.37. Leg 3: femur, 1.04; patella, 0.25; tibia 0.92. Ventral surface of the body not visible.

MB.A 1658 (Figs 16, 18-19) is a fairly complete specimen in dorsal view. Body oval and compact, length 1.32 mm. Prosoma with semicircular propeltidium, length 0.44 mm, dominated by prominent, heart-shaped ocularium, length 0.20, width 0.225, distance from ocular tubercle to front of prosoma 0.1 mm. Ocular tubercle bears multiple short, forward-pointing setae in a band across the dorsal region between the eyes. Dorsal surface behind propeltidium, including all opisthosomal tergites, missing. Lateral regions of body only preserved in outline. Chelicerae fairly robust, but folded under the body with few details. Pedipalpal trochanter short, length 0.12 mm, and quadrate. Palpal femur long, length 0.72 mm, with slight curvature and distal widening. Palpal femur setose, especially on its inferior surface. Palpal patella short, length 0.19 mm, but with prominent and characteristic *Dicranopalpus* mesal apophysis. Length of apophysis 0.33 mm, bearing multiple setae towards the distal end in particular and
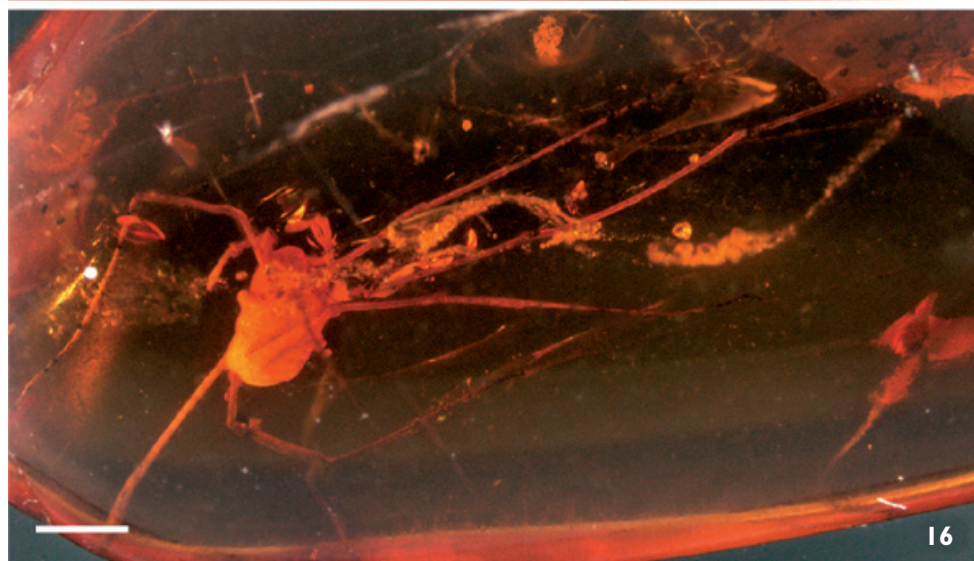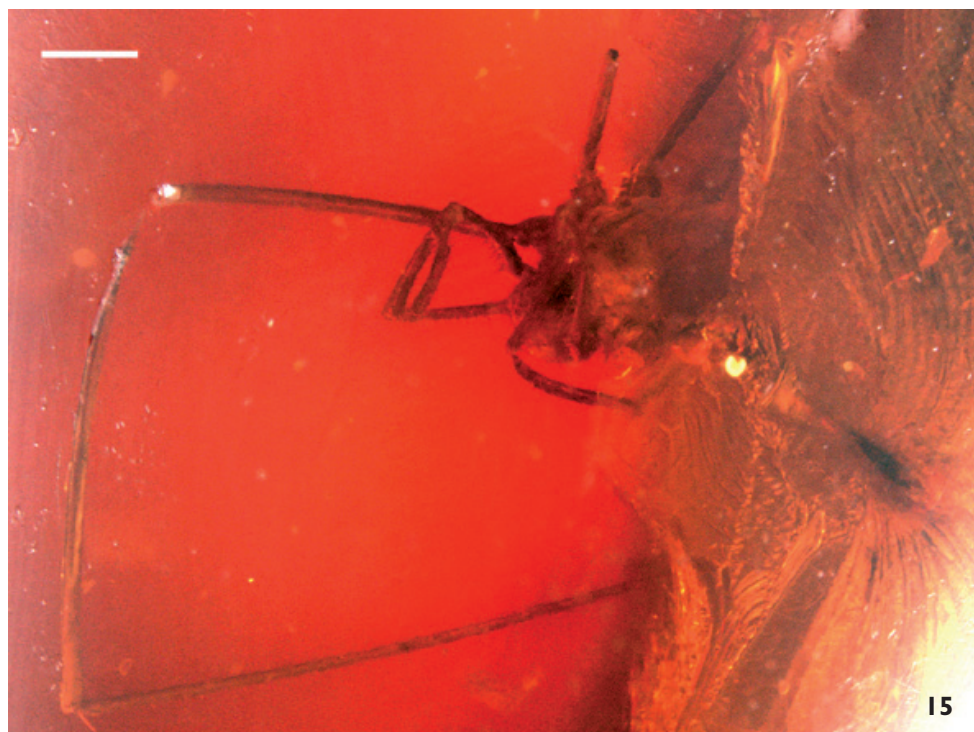
Figures 15-16. *Dicranopalpus ramiger* (Koch & Berendt, 1854) from Bitterfeld amber (Eocene: Oligocene). **15** MB.A. 1657 **16** MB.A. 1658. Scale bars equal 0.5 mm (**15**) and 1.0 mm (**16**).
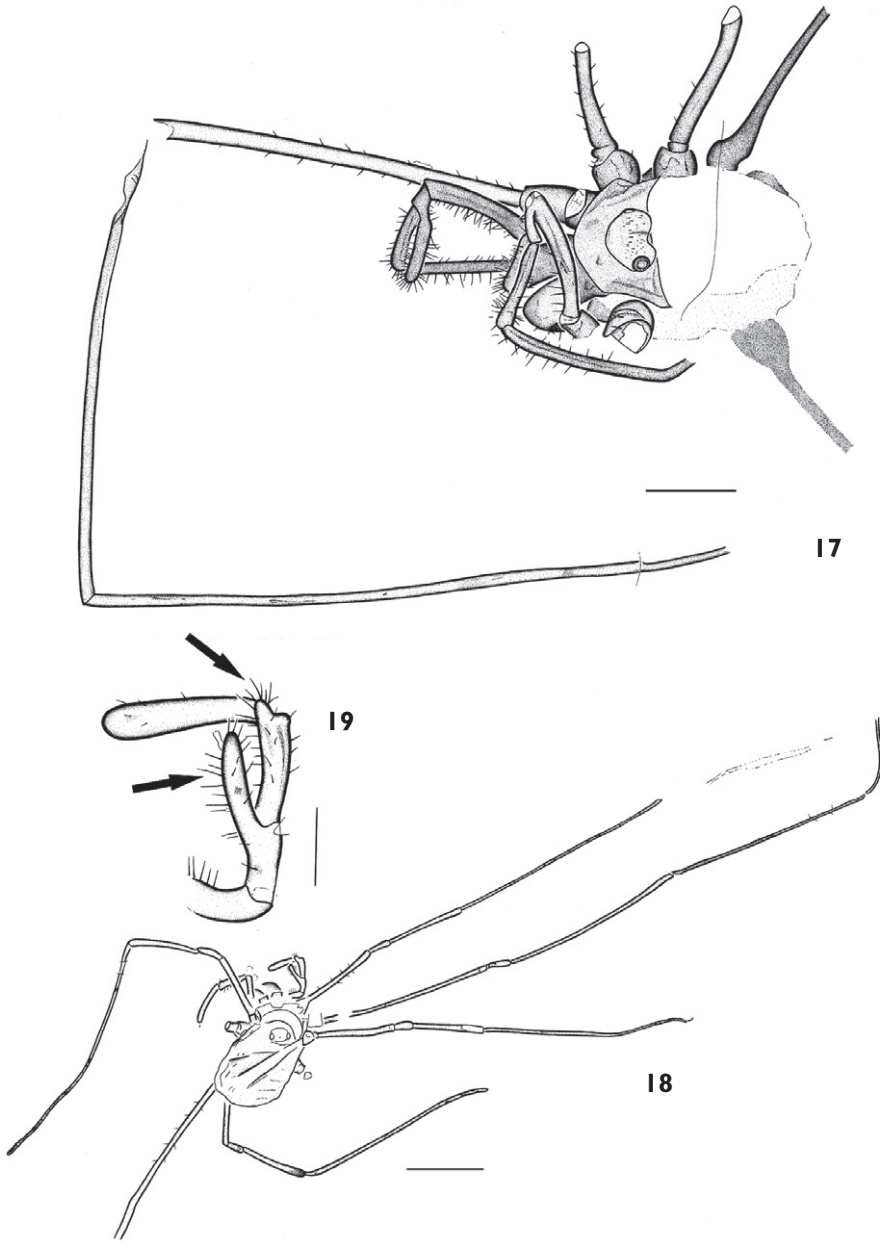
Figures 17-19. *Dicranopalpus ramiger* (Koch & Berendt, 1854) from Bitterfeld amber (Eocene: Oligocene). *Camera lucida* drawings of the specimens shown in **15-16**. **17** MB.A. 1657 **18** MB.A 1658 **19** the same, detail of the long patella and short tibial apophyses (arrowed) characteristic for the genus. Scale bars equal 0.5 mm (**17**), 1.0 mm (**18**) and 0.2 mm (**19**).

extending almost two-thirds of the way down the length of the adjacent tibia. Palpal tibia itself elongate, length 0.51 mm, and widening distally. Palpal tarsus incomplete, but elongate, length at least 1.0, with hints of distal curvature; although terminal end is obscured. Tibia and tarsus also setose. Leg trochanters globose. Femora elongate, but incomplete in legs 2-4. Femora bear a few short setae. Femora of legs 2 and 3 preserve a proximal pseudoarticulation close to the trochanter. Leg 1 fairly complete, elongate and slender; total length at least 8.0 mm. Femur length ca. 2.0 mm. Patella not clearly preserved. Tibia length 2.60 mm. Setation on more distal podomeres indistinct, as is expected metatarsus–tarsus boundary. Ventral surface of body unknown.

Remarks. *Dicranopalpus ramiger* (Koch & Berendt, 1854) is present in both Baltic and Bitterfeld amber. Both the Bitterfeld specimens described here are quite small with relatively large eye tubercles (e.g. Fig. 17) compared to other described fossil and Recent material in this genus. For this reason we suspect they might be juveniles. Dunlop (2006) discussed the second apophysis on the tibia – clearly preserved in MB.A 1658 (Fig. 19) – which was used by Menge (1854) to define a new species. Given the poor state of preservation in the holotype of Koch and Berendt's (1854) species, this character is regarded as unreliable and all Baltic (and now Bitterfeld) examples can probably be referred to a single taxon: *D. ramiger*. Note that the Bitterfeld specimen figured by Barthel and Hetzer (1982, fig. 9) from the Deutsches Bernsteinmuseum (repository number 5/2) was provisionally referred by these authors to *Dicranolasma* Sørensen, 1873. This is almost certainly a *lapsus* since this Recent genus belongs to the dyspnoid family Dicranolasmatidae. Their figured specimen clearly bears the long patellar apophysis typical for *Dicranopalpus* Doleschall, 1852 (Phalangiidae).

Genus *Amilenus* Martens, 1969

Amilenus deltshevi sp. n.
urn:lsid:zoobank.org:act:FE124EB4-D388-4C05-B1F4-B648AC935329
Figs 20-21, 23-26

Holotype. MB.A 1659. Bitterfeld amber, probably from the site of the Goitsche opencast Mine near Bitterfeld, Sachsen-Anhalt, Germany; Palaeogene (Oligocene: Chattian).

Additional material. MB.A. 1660 (paratype). From the same locality as the holotype.

Diagnosis. Fossil *Amilenus* species with a distinct form of the apophysis on the pedipalpal patella.

Etymology. In honour of Prof. Christo Deltshev (Sofia) in recognition of his extensive contributions to arachnology and on the occasion of his 70th birthday.

Description. The holotype (MB.A. 1659, Figs 20, 23-24) is an almost complete specimen in lateral view. Body ovoid, length ca. 0.8 mm; details of body, ocular tubercle and mouthparts equivocal. Pedipalps well-preserved, with article lengths (in mm) of: femur, 0.21; patella, 0.14; tibia, 0.16; tarsus, 0.4. Patella with a distinct, bluntly-

pointed, mesal apophysis bearing a number of stout spines. Tibia slightly inflated distally and also bearing stout mesal spines in this distal region. Tarsus slightly expanded distally; apotele present as a short, curving, distal claw. Legs relatively complete; all elongate and slender, and when preserved at their full length ending in a single, claw like apotele. Leg 1 with article lengths in (mm) of: femur, 0.56; patella, 0.19, tibia, 0.47; metatarsus and tarsus (boundary indistinct) 1.75. Leg 2 with article lengths in (mm) of: femur, 1.19; patella, 0.22; tibia 1.72, metatarsus and tarsus (boundary indistinct) at least 1.47, but full length not preserved. Leg 3 less completely known, patella 1.1 mm; tibia 0.58 mm. Leg 4 with article length in mm of: femur c. 0.8; patella, 0.19; tibia, 0.75, metatarsus and tarsus (boundary indistinct), 3.0.

The paratype MB.A. 1660 (Figs 21, 25-26) is an almost complete specimen best seen in dorsal view, but missing the second pair of legs and the dorsal surface of the opisthosoma. Body oval to rectangular, length c. 1 mm; width of prosoma 0.7; width of opisthosoma 0.75. Ocularium present on the propeltidium, fairly large in proportion to the rest of the body; possibly hinting at a juvenile. Length 0.174 mm, width 0.215 mm, distance from ocular tubercle to the front of prosoma 0.110 mm. Meso- and metapeltidium, together with the tergal region of the opisthosoma equivocal. Pedipalps quite well-preserved. Both patella and to a lesser extent tibia express mesal apophyses, with fairly dense setation along the entire mesal surface of these articles. Leg 1 with article lengths (in mm) of: femur, 0.95; patella, 0.23; tibia, 1.02; metatarsus, 0.79; tarsus, 1.44. Some annulation of the tarsus preserved, but details lacking. Leg 2 only known from an incomplete femur on the left side. Leg 3 with article lengths (in mm) of: femur, 0.78; patella, 0.20; tibia, 1.02; metatarsal-tarsal division, indistinct but length together 2.8. Annulation of the tarsus into at least 12 elements and the distal apotele in the form of a single curving claw also visible in this limb. Leg 4 with article lengths (in mm) of: femur, 0.1.42; patella, 0.21; tibia, 1.28; metatarsal-tarsal division, indistinct but length together at least 1.8.

Remarks. The key character in both these specimens is the mesal apophysis on the patella of the pedipalp (Figs 24, 26, arrowed). Not as long as the apophysis of *Dicranopalpus* (see above), it closely matches the gross morphology of extant species such as *Amilenus aurantiacus* (Simon, 1881) (Fig. 22, arrowed) where even juveniles – the fossils could also be subadult – express such an apophysis. Based on this we recognise these Bitterfeld fossils as a new species, and the first fossil example of *Amilenus*. However, some expected details compared to extant members of this genus, like pseudoannulation of tibiae 2 and 4 or teeth on the pedipalp claw, could not be resolved; although the latter may not be present in modern juveniles of this size (i.e. body length). In the holotype the ocular tubercle is probably hidden behind the legs and is rather small in extant species. Also of note is the fact that the tibia of leg 2 in modern juveniles is longer than femur; a situation paralleled by the holotype.

One of our initial suspicions was that this new material could be conspecific with the Baltic amber species *Opilio ovalis* Koch & Berendt, 1854. Its holotype could not be traced in its expected repository in Berlin (cf. Dunlop 2006), but the original illustration implies the presence of a somewhat distally thickened and mesally rather setose
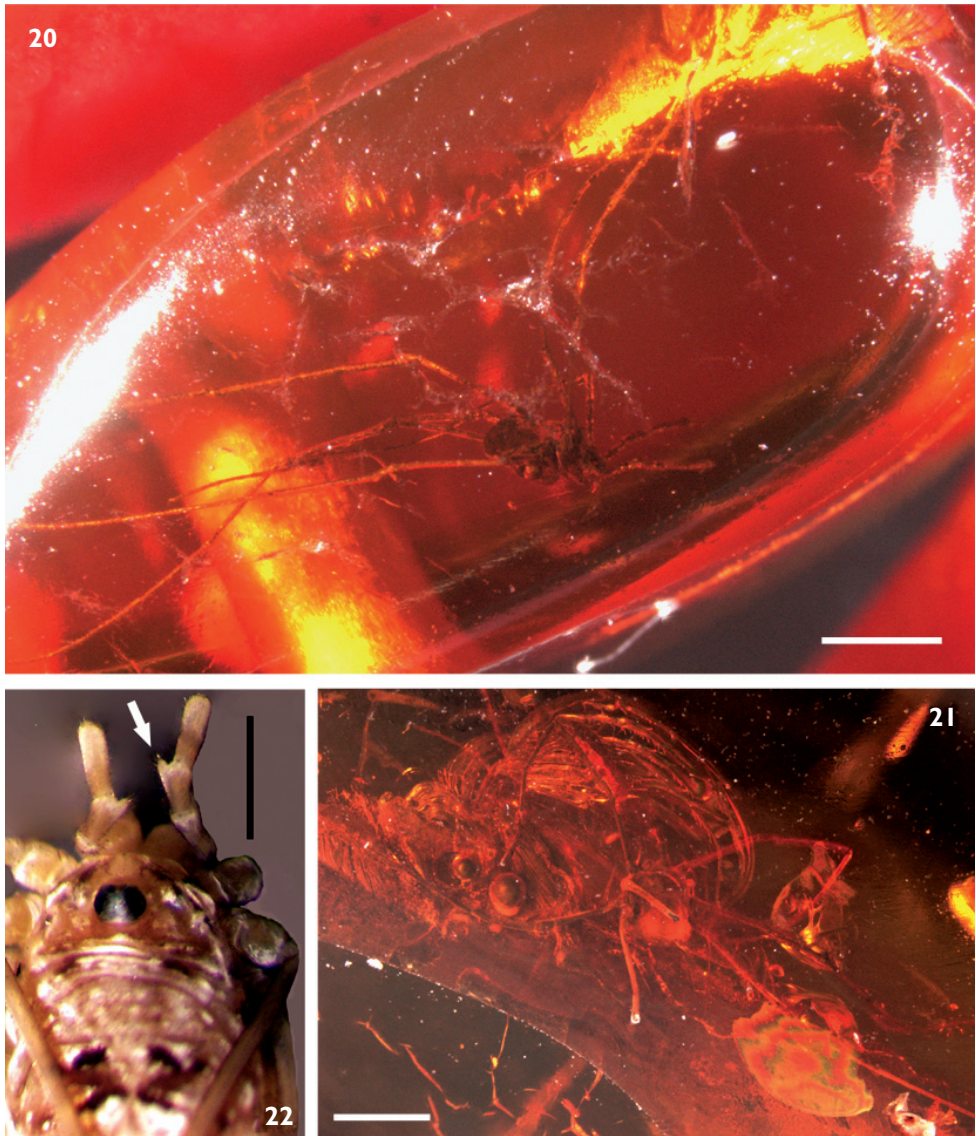
Figure 20-22. Fossil and Recent *Amilenus*. **20** *Amilenus deltshevi* sp. n., M.BA 1659 (holotype), from Bitterfeld amber (Palaeogene: Oligocene) **21** *A. deltshevi* sp. n. M.BA 1660 (paratype), also from Bitterfeld amber **22** Juvenile *Amilenus aurantiacus* (Simon, 1881) (Recent harvestman for comparison), note the medial apophysis on the patella (arrowed). Scale bars equal 1.0 mm.

pedipalp patella. However, the Bitterfeld material differs from the *O. ovalis* illustration in having a distinct, projecting apophysis on the patella and strong setae on the tibia too. We are fairly certain that *O. ovalis* is misplaced at the genus level, but since the focus of the present paper is the Bitterfeld deposit, we will address this question fully in future work on Baltic amber harvestmen.
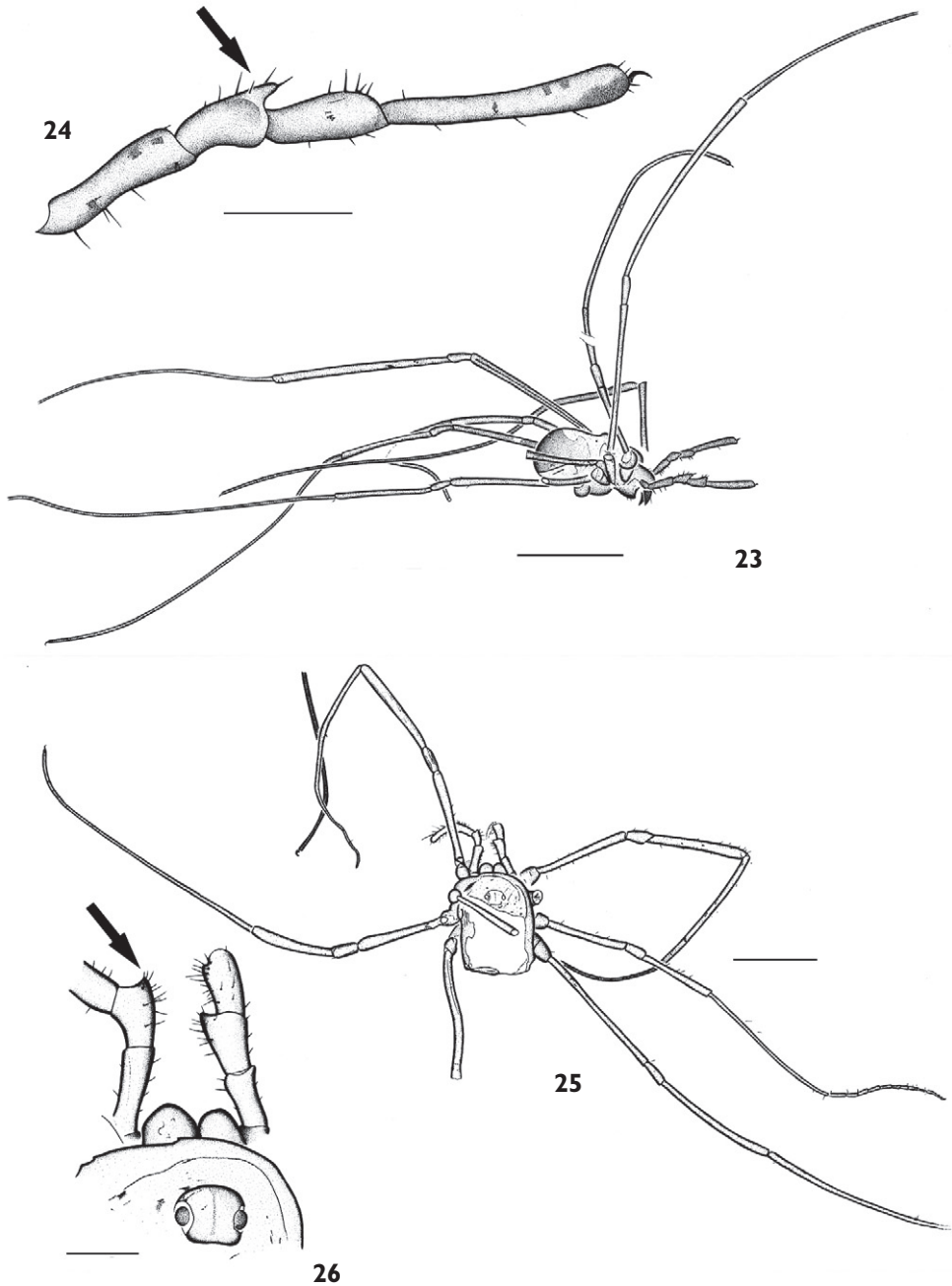
Figures 23-26. *Amilenus deltshevi* sp. n. *Camera lucida* drawings of the specimens shown in **20-21**. **23** MB.A 1659 (holotype), from Bitterfeld amber (Eocene: Oligocene) **24** the same, detail of the pedipalp showing the patellar apophysis (arrowed) **25** MB.A 1660 (paratype) **26** the same, detail of the anterior prosoma and pedipalps showing the patella apophysis (arrowed). Scale bars equal 1.0 mm (**23**, **25**), 0.2 mm (**24**, **26**).

Genus *Lacinius* Thorell, 1876

?*Lacinius erinaceus* Staręga, 1966
Figs 27, 31-32

Material. MB.A. 1661 (also bears the label "Ser. 12/12"), from Bitterfeld amber, probably from the site of the Goitsche open-cast Mine near Bitterfeld, Sachsen-Anhalt, Germany; Palaeogene (Oligocene: Chattian).

Description. An almost complete, juvenile specimen (Figs 27, 31-32) in anterolateral view, obscured in places by bubbles within the matrix. Body compact, length c. 1.75 mm, maximum width of prosoma 1.20, of opisthosoma 1.25. Division into pro- and opisthosoma, and any sclerites making up the prosomal dorsal shield, poorly resolved. Ocular tubercle pronounced, width 0.33 mm, bearing seven spines; immediately in front of it three fairly prominent spines present. Further, generally smaller, spines located behind the ocular tubercle. Anterior margin of prosomal dorsal shield slightly recurved to accommodate the chelicerae. Proximal article only of chelicerae preserved, lacking details. Pedipalps short and robust, again proximal articles only preserved. Right (?)patella of pedipalp with at least three denticle-like spines. Legs relatively short. Femur, patella and tibia quite robust, compared to the more slender distal articles, and heavily ornamented with rows of thorns. Each row can be up to ten thorns on the tibiae. Thorns take the form of conical, sometimes slightly curving, tubercles, length c. 0.1 mm; typically ending in a short bristle or seta. Metatarsus with one to three thorns proximally, but distal region generally bearing setae only. Legs most complete on right side, but leg 2 here missing, apart from a proximal stub (?trochanter). Metatarsal–tarsal division in leg 3 unclear; tarsus distally subdivided. Leg 4 well preserved with podomere lengths (in mm): patella, 0.41; tibia, 0.76; metatarsus, 1.12; tarsus, 1.21. Tarsus divided into one long and nine shorter elements, ending distally in a single, curved claw. Opisthosoma lacks clear segmentation, but is ornamented, like the legs, with conical spines, longest towards the posterior margin of the opisthosoma. The microsculture is granulated. The spines on the body do not appear to form any sort of regular pattern. Ventral surface largely covered by emulsion, but ventrally directed spines also observed here on the leg coxae and opisthosoma.

Remarks. This remarkable, spiny fossil is clearly something new for the European amber fauna. Two features (cf. Martens 1978) – the stout thorns ending in setae on the legs (and to a lesser extent the body) and the presence of three prominent spines in front of the eyes (Fig. 32) – indicate the extant genus *Lacinius* Thorell, 1876. The original hand-written note from Manfred Moritz provisionally assigned it to this genus. The probably closely-related *Odiellus* Roewer, 1923 lacks such well-developed thorns on the legs. Three Recent species of *Lacinius* occur in Germany today. All are distributed throughout much of the country, although somewhat rarer in the north (Blick and Komposch 2004). Interestingly, the extant central European species are notably less spiny than this Bitterfeld fossil. In gross morphology the new find is rather more like some extant species from the Mediterranean region (e.g. *Lacinius insularis*

Roewer, 1923), and especially *Lacinius erinaceus* Staręga, 1966 from the Caucasus. Indeed we were unable to recognise any reliable or non-trivial characters – other than age – which could distinguish MB.A. 166 from *L. erinaceus* (Figs 28-29). We concede that assigning older fossils to living species is controversial, but note again the precedent from the slightly younger Dominican Republic amber (see Age of the inclusions) and tentatively refer this new Bitterfeld harvestman to *L. erinaceus*. The highly spinose *Lacinius* morphs were clearly more widely distributed during the Oligocene and occurred further north than their distribution today.

Family Sclerosomatidae Simon, 1879

Genus *Leiobunum* C.L. Koch, 1839

Leiobunum longipes Menge, 1854
Figs 30, 33

Synonymy. See Dunlop (2006, pp. 172-173).

Holotype. Probably originally in Danzig (=Gdańsk, Poland), current whereabouts unknown (see also Dunlop 2006), from Baltic amber (Palaeogene, Eocene); precise locality unclear.

Additional material. MB.A. 1662 (series 15/10, provisionally labelled "Gyantinae cf. *Amilenus*" but not in fact referable to this genus; see above), probably from the site of the Goitsche open-cast Mine near Bitterfeld, Sachsen-Anhalt, Germany; Palaeogene (Oligocene: Chattian).

Description. MB.A. 1656 (Figs 30, 33) is an almost complete specimen of a fairly large harvestman in dorsal view. Body length: 2.1 mm; width of prosoma and opisthosoma 1.3 mm. Carapace procurved anteriorly, with clear division into pro-meso- and metapeltidium, and centrally located ocular tubercle. Length of ocularium 0.225 mm, width 0.275 mm, distance from ocular tubercle to front of prosoma 0.25 mm. Opisthosoma covered by scutum parvum bearing in places slightly granular ornament; posterior region and any segmentation here obscure. Body covered with small black dots and a subcuticular, silvery pigment. Chelicerae equivocal. Pedipalps short and pediform, but details lacking. Legs relatively complete, at least proximally, elongate and slender. Leg 1 femur length 1.83 mm, patella, 0.24. Leg 2 only known from incomplete femora. Leg 3 complete with podomere lengths (in mm) of femur, 1.79; patella, 0.45; tibia, 1.52; metatarsus, 1.86, tarsus, 3.20. Tarsus divided into 24 individual elements, becoming shorter distally, and ending in a single claw (apotele). Leg 4 only known from incomplete femora.

Remarks. *Leiobunum longipes* Menge, 1854 is present in both Baltic and Bitterfeld amber. Apparently quite common in Baltic amber (Staręga 2002), this fossil is fairly large compared to the other Bitterfeld finds. Nevertheless, it is probably still only a juvenile, although we see nothing which differentiates it from the species known from Baltic amber.

Figures 27-30. 27 Fossil ?*Lacinius erinaceus* Staręga, 1966, MB.A. 1661, from Bitterfeld amber (Palae-ogene: Oligocene) **28-29** Recent male *Lacinius erinaceus* Staręga, 1966 (Holotype) in dorsal and lateral view for comparison, revealing an almost identical morphology to the amber fossil **30** *Leiobunum longipes* Menge, 1854 from Bitterfeld amber, MB.A. 1662. Scale bars equal 1.0 mm.
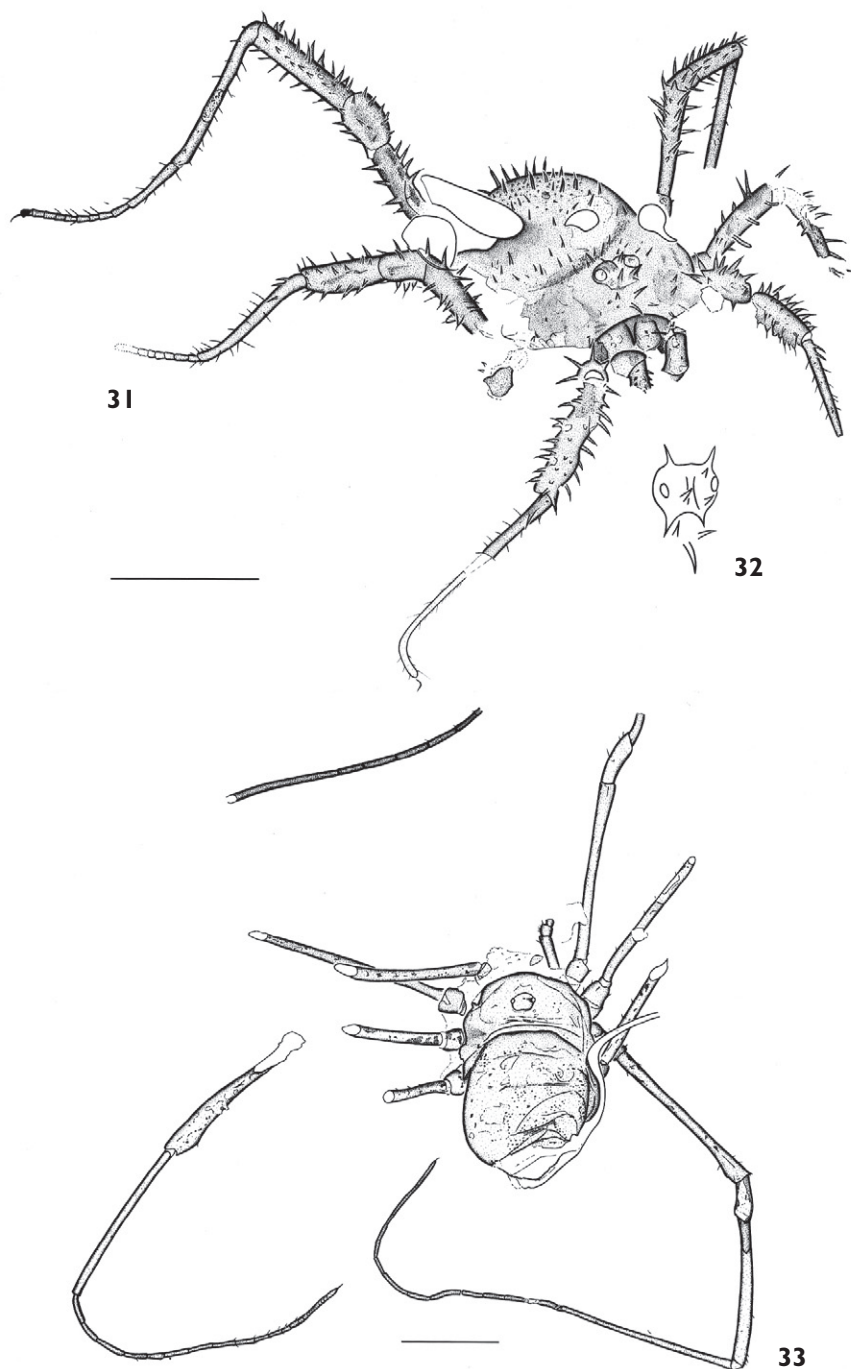
Figures 31-33. *Camera lucida* drawings of the specimens shown in **27** and **30**. **31** ?*Lacinius erinaceus* Staręga, 1966, MB.A. 1661 **32** the same detail of ocularium and its spination **33** *Leiobunum longipes* Menge, 1854, MB.A. 1662. Both from Bitterfeld amber (Palaeogene: Oligocene). Scale bars equal 1.0 mm (**31**, **33**).

Acknowledgements

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