



New fossil ants of the subfamily Myrmicinae (Hymenoptera, Formicidae) from the Upper Oligocene of Enspel (Westerwald Mountains, Rhineland Palatinate, Germany)

Karla Jessen¹

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Abstract

New species of the subfamily Myrmicinae are described from the fossil volcanogenic Lake Enspel, Westerwald, Germany. This Fossil-Lagerstätte comprises lake sediments, which essentially consist of intercalated “oilshales” and volcanoclastics. The sediments were dated to be of late Oligocene age. Out of the 287 fossil ants from Enspel examined, 96.5% ($n = 277$) belong to the formicoid clade (Formicinae, Dolichoderinae, Myrmicinae), and only 3.5% ($n = 10$) to the poneroid clade (Ponerinae, Agroecomyrmecinae). The high proportion of Myrmicinae (36.6%) indicates that this subfamily was already strongly represented in Central Europe in the late Oligocene. However, it should be noted that the large number of specimens are alate reproductives. The number of workers is low: $n = 19$, or 6.1% of 312 specimens when 25 isolated wings are included. Ten new species, belonging to the genera *Paraphaenogaster*, *Aphaenogaster*, *Goniomma* and *Myrmica* are named. Taxonomic questions regarding the separation of the two genera *Aphaenogaster* and *Paraphaenogaster* as well as aspects of biogeography, palaeoenvironment and palaeobiology in Enspel are discussed.

Keywords Upper Oligocene · Formicidae · Myrmicinae · Taxonomy · Biodiversity · Palaeoecology · Palaeoenvironment · Enspel

Introduction

Regarding their biodiversity and ecological position, the success story of ants has been elaborated by Hölldobler and Wilson (1990, 2010) and since then repeatedly mentioned by many other authors (e.g. Dlussky and Wedmann 2012; LaPolla et al. 2013). According to AntCat (Bolton 2019), there are 13,575 extant valid species described.

The study of the evolutionary history of ants is a challenge. The reconstruction of the evolutionary steps from the very beginning of ant evolution up to the status we have today can only be solved by a combination of taxonomic, genetic and palaeontological research (Ward 2007; LaPolla et al. 2013; Barden 2017).

The earliest fossil records of ants are from the Upper Cretaceous of France (99–100 Ma) and Burmese amber (99 Ma) (LaPolla et al. 2013; Barden 2017). Recently, one ant fossil has been documented from the Paleocene of Alberta (Canada) (LaPolla and Barden 2018). The Eocene is comparatively well represented by 12 fossil sites: In Baltic amber, Bitterfeld (Germany), Denmark, Rovno (Ukraine), Sakhalin (Russia), Cambay (India), Oise (France) and Fushun (China), or in former lacustrine sediments from the Okanagan Highlands (Canada/USA), Green River (USA), Messel (Germany), Bembridge (UK), Florissant (USA, shale) and in marine sediments of the Isle of Fur (Denmark). In contrast, only six fossil sites are known from the Oligocene: Fonseca Formation (Brazil), Aix-en-Provence, Cereste (both France), Kleinkems, Enspel and Rott (all Germany). Ants from Miocene have been reported from numerous fossil sites, i.e. Stavropol (Russia), Radoboj (Croatia), Shanwang (China), Öhningen (Germany), Dominican Republic and Crete (Greece). With regard to the fossils found in Sicilian amber (Italy), no exact geological age is known; the data range from Eocene to Miocene (Ragazzi and Roghi 2014). The former Paleocene ants from Sakhalin amber (Russia) and Isle of Fur (Denmark) have been redated as Eocene (Kodrul 1999; Larsen et al. 2003), whereas the Fur Formation represents the

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✉ Karla Jessen
karla.jessen@gmx.de

¹ August-Bebel-Straße 62, Griesheim 64347, Germany

transition from Paleocene to Eocene. Fossil Pliocene ants are known from Willershausen (Germany) (Dlussky et al. 2011).

Hypotheses on myrmicine evolution vary. In the “Dynastic Succession Hypothesis” by Wilson and Hölldobler (2005), tropical forest soils and ground litter in the angiosperm forest are interpreted as the “headquarters” of ant evolution. While living in soil litter, they supported nitrogen production, which had a beneficial effect on the growth of angiosperms (Berendse and Scheffer 2009). The authors assume that the Myrmicinae living in these habitats radiated in the early Eocene and surpassed the Ponerinae in biodiversity and biomass. In addition, Myrmicinae were able to add seeds and elaiosomes to their diet and were able to expand into dry habitats such as grasslands and deserts later on.

The “African Origin Hypothesis” (Dlussky et al. 2004; Radchenko and Dlussky 2013) is primarily based on the early fossil record (genus *Afromyrma*) from Late Cretaceous mudstones in Botswana (Africa). According to this hypothesis, the subfamily Myrmicinae evolved in Africa. When they invaded Europe (possibly via the Tethys Sea by rafting), an adaptive radiation led to a relative high number of genera (25). At that time, myrmicine ants were very likely arboreal dwellers or at least foraging on trees, because the number of workers found in amber is relatively high, compared to the number of workers belonging to real epigaeic living taxa. Although the proportion of myrmicine specimens in European Eocene amber is low (Dlussky and Rasnitsyn 2009), Radchenko and Dlussky (2013) stress the increase of new myrmicine genera in late Eocene amber as possibly being the cause of the decrease of poneroid taxa in amber, compared to their high number found in mid-Eocene Messel deposits (Dlussky and Wedmann 2012). As most of the Eocene myrmicine genera are extinct, the authors suppose that they could not compete with other myrmicine taxa or with taxa from other subfamilies invading Europe.

The “New World Tropic Hypothesis” by Ward et al. (2015) is based on DNA-sequencing and sequence annotation. In their study, the subfamily Myrmicinae is consistently recovered as monophyletic, with the exception of the ant genus *Ankylomyrma* Bolton 1973. The authors reduced the number of tribes from 25 down to 6 crown groups of Myrmicinae. Their results indicate that the diversification of crown-group Myrmicinae began about 100 Ma ago and was initially concentrated in the New World tropics. These tribes range in age from 52.3 to 71.1 Ma. Their divergence dating estimates show that the early and mid-Eocene (55–40 Ma) was an important period of diversification for myrmicine ants. The earliest fossil records on Myrmicinae are from early-middle Eocene and they show a considerable taxonomic diversity (Perkovsky 1915; Dlussky and Rasnitsyn 2002; Radchenko and Perkovsky 2016). The fossil record supports the authors’ inference that the major lineages of Myrmicinae had already originated by this time.

The main difference between the first two hypotheses is the early habitat of Myrmicinae. Radchenko and Dlussky (2013)

interpret early Myrmicinae as arboreal dwellers, whereas Wilson and Hölldobler (2005) assume the forest soil and ground litter as the early habitat of the myrmicine ants. The study of Ward et al. (2015) does not support the African Origin Hypothesis either. The African genus *Afromyrma* (Dlussky et al. 2004), however, was not used as an a priori calibration in their dating analysis, because it is not accepted by other myrmicologists (Wilson and Hölldobler 2005; Archibald et al. 2006).

According to Wilson and Hölldobler (2005) and Ward et al. (2015), myrmicine ant diversification took place in early to mid-Eocene. This, however, is not reflected in the fossil record. The number of myrmicine specimens from all Eocene and Oligocene deposits in Eurasia and North America do not make more than 5–6% (Radchenko and Dlussky 2013). The proportion of myrmicine specimens from European amber is only 2.1–13.2%, while the proportion of myrmicine genera is relatively high at 38% (Dlussky and Rasnitsyn 2009; Radchenko and Dlussky 2013). Only during the Late Oligocene to mid Miocene do the number of myrmicine ants specimens increase to contemporary percentages, i.e. Kleinkems 36% (early Oligocene), Enspel 36.6% (Upper Oligocene MP 28, this paper), Rott 50% (late Oligocene, MP 30), Radoboj 22% (early Miocene) and Vishnevaya balka, Stavropol 40% (mid Miocene) (Dlussky and Wedmann 2012). These findings, however, are in accordance with earlier statements by Ward (2000), according to whom the numbers of fossil myrmicine ant specimens became similar to the modern ones (about 74%) by the mid Miocene.

The volcanogenic Lake Enspel is an oil shale deposit with abundant and diverse fossil insects. According to Wedmann (2000), there is a predominance of Coleoptera (53%), followed by Diptera (24%) and Hymenoptera (12%). Six percent of the fossils belong to Trichoptera, mainly represented as larvae ($n = 4222$). Among the Hymenoptera, ants make about 50%.

Wedmann et al. (2010) give a preliminary study on ant fossils from Enspel. In this study, subfamilies were identified but not quantified. A high proportion of Myrmicinae was found, mainly belonging to the morphogenus *Paraphaenogaster* (personal communication G. Dlussky, cited in Wedmann et al. 2010).

The essential goal of the paper is to describe the myrmicine fauna of Lake Enspel. Additionally, the fossil ants of Lake Enspel are allocated down to the subfamily level, and their different percentages are stated. The other subfamilies will be described elsewhere. As geological and palaeobotanical data on Enspel are published, palaeoenvironmental aspects can be discussed.

Material und methods

All fossils are currently stored in the Directorate General for Cultural Heritage Rhineland-Palatinate, Directorate Archaeology, Department Earth History, Mainz, Germany. In the long

term, they will be deposited in the “Typothek” of the State Collection of Natural History Rhineland-Palatinate/Museum of Natural History Mainz, Mainz, Germany (NHMM).

Fossil ants were found during yearly excavation campaigns between 1995 and 2013 conducted by the Directorate General for Cultural Heritage Rhineland-Palatinate, Directorate Archaeology, Department of Earth History.

In Enspel, the quality of preservation of ants is often exceptional, as shown by chitin preserved in its primary organic molecular structure (Stankiewicz et al. 1997; Colleary et al. 2015) and by original colours of insects (McNamara 2013). The amount of melanin in the chitin determines the darkness of an insect. For the fossil deposit Messel (Germany), it has been shown that melanin is preserved (Vinther 2015). Since it is not systematically demonstrated for Enspel, colour cannot be considered as a taxonomic characteristic. Deviations in the preservation of structural colours from sample to sample within the same fossil location were documented by McNamara et al. (2012).

Abbreviation of specimen numbers: NHMM = Naturhistorisches Museum Mainz; PE = Palaeontology Entomology; 2009 = found in 2009; 6281 = running inventory number of the year; LS = Landessammlung (State Collection). Information on the layer is given. They refer to the standard profile in Felder et al. (1998). Photographs were taken with a photomicroscope Leica M205C DFC500. Enlarged prints were hand traced by pen, and drawings were scanned and redone/improved by standard graphical software (Photoshop, Inkscape). Details were elaborated by examination with a Binocular M7 Wild Heerbrugg.

Full lines indicate sclerite boundaries, dashed lines indicate supposed sclerite boundaries or supposed veins, short strokes with rounded corners indicate visible sclerite margins. Preserved sclerites are coloured grey, preserved wings are coloured slightly less grey.

Remark

It is important to *always* keep both plates (A and B) of the insect body fossil while excavating. When sedimentary rocks are split, parts of the fossil insect can be found on each plate. As an example: propodeal spines or the number of antenna segments are of high taxonomic value. Unfortunately, these fragile body parts break off easily and might be left on the opposite plate.

Terminology

Morphological terminology follows Bolton (1994), and in its expansion the Morphological Terms in Antwiki. According to Antwiki, the term “node” is ...*A rounded or knob-like structure, commonly used to refer to the dorsal nodes of the petiole or postpetiole.* The term “peduncle” is used for a more or less

slender anterior section of the petiole, which begins immediately posterior to the propodeal-petiole articulation and extends back to the petiole node. It is very variable in length and thickness, but when present in any form, the petiole is termed pedunculate.

Nomenclature of the wing venation follows Dlussky and Perfilieva (2014) and Perfilieva et al. (2017) (Fig. 1).

The sculpture of the sclerites often is well preserved, as are sometimes fragile parts, like bristles and tibial spurs. Normally in papers dealing with fossil ants, the terms “imprint fossil” or “impression fossil” are used. For ants from Enspel, these terms are not appropriate. It has been shown by Stankiewicz et al. (1997) that the original chitin molecular structure has been preserved in insect body fossils from Enspel. In addition, for fossil weevils from Enspel Gupta et al. (2007) showed that the aliphatic polymer in the insect fossils did not derive from migration from the organic-rich host sediment. Therefore, the terms *insect body fossil* or *compression fossil* are more appropriate and will be used in this paper.

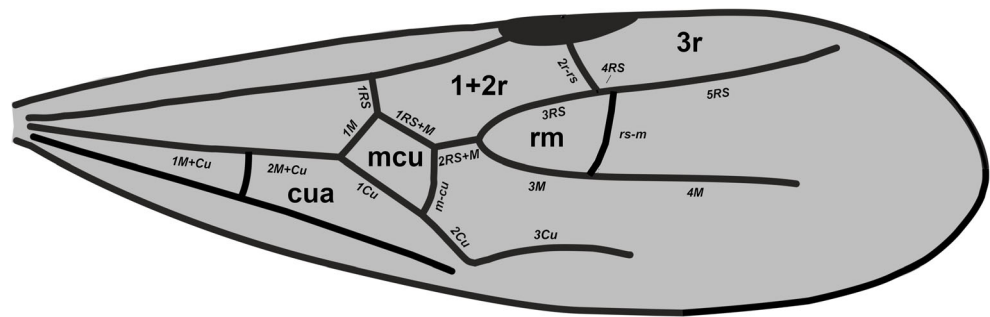
Posteriorly to the pars stridens of the stridulation organ, there are integumentary foldings on the presclerite of the first gastral tergite. These foldings are preserved in some specimens described here. They are most likely functionally linked to the stridulation organ. When the gaster moves back and forth, the male produces a sound. Studies on extant species show that the sound differs between the species (Castro et al. 2015). Álvarez (2009) named these structures “pillars”. The term “pillars” will also be used here, although “furrows and ridges” would often describe their morphology better. Most likely they evolved from the girdling constriction respectively “cinctus3” (see Serna and Mackay 2010).

Measurements

Measurements on compression fossils can only be approximations because of perspective distortion or deformation. Significant deformation mainly happens to softly sclerotized parts; other parts with stronger sclerotization show little or no deformation. To support the validity of the measurements, body parts positions are mentioned. Measurements are taken as seen, deviations from reality due to perspective distortions are considered exceptional. Where a measurement cannot be taken precisely because the start or ending point is not seen, the measurement is noted as being an estimate (est.). The gaster is often incomplete or damaged. In addition, gaster length can vary because of its telescoping variability (Tschinkel 2013). This makes the dimension BL only an approximate value. For this reason, the value BL without gaster (BLw/oG) is given additionally.

Measurements are given in mm. BL: addition of MML, HL, AL, PL, PPL and GL, completed by estimations where needed; BLw/o G: addition of MML, HL, AL, PL and PPL; THL: HL including mandibles; HL: head length, without mandibles; HW: maximum head width excluding eyes; HW* measured from mid

Fig. 1 Stylized forewing, nomenclature of veins shown here is based on Dlussky and Perfilieva (2014, Fig. 65) and Perfilieva et al. (2017, Fig. 1b)



ocellum to mid eye x2 (for specimens which are embedded strongly dorsolateral to overcome foreshortening); ED: eye diameter; GeL: Gena length; SL: scape length; ML: mandibles length; MML: length of masticatory margin of mandibles; AL: alitrunk length, measured from head connection to the most posteroventral point of alitrunk; AH: alitrunk height, measured from the ventral margin of mesopleuron to highest point of mesonotum; AW: alitrunk width; ScuL: scutum length; ScutL: scutellum length; MesoL: length of mesonotum (worker); PL: petiole length (ventral dimensions, measured from most anterior ventral point to most posterior ventral point); PH: petiole height; PPL: postpetiole length (ventral dimensions, measured from most anterior ventral point to most posterior ventral point); PPH: postpetiole height; PPW: postpetiole width; HeH: helcium height; HeW: helcium width; G1L: length of first gastral segment, measured from medio-anterior margin of first gastral tergite to medio posterior margin of first gastral tergite; G1W: width of first gastral tergite; GL: gaster length (in most cases estimated, because of incompleteness); FWL: forewing length; 2M+Cu: length of vein 2M+Cu (inner dimensions); 1Cu: length of vein 1Cu (inner dimensions); 1M: length of vein 1M (inner dimensions); m-cu: length of vein m-cu (inner dimensions); 1RS+M: length of vein 1RS+M (inner dimensions); 2RS+M: length of vein 2RS+M (inner dimensions).

Indices: $CI = (HW \cdot 100) / HL$; $SI = (SL \cdot 100) / HW$; $IED / HL = (ED \cdot 100) / HL$; $IHL / AL = (HL \cdot 100) / AL$; $Imcu = (1RS+M / 1Cu) \cdot 100$; $I2RS+M / 1RS+M = (2RS+M / 1RS+M) \cdot 100$; $I2RS+M / m-cu = (2RS+M / m-cu) \cdot 100$; $I2RS+M / 2M+Cu = (2RS+M / 2M+Cu) \cdot 100$.

Geological and palaeoenvironmental background

Lake Enspel, a fossil volcanic crater lake, is part of the Cenozoic Volcanic Field of the High Westerwald Mountains (Germany), marked by the solid line in Fig. 2. This locality represents a late Oligocene deep, limnologically closed lake, which developed in a small volcanotectonic trachytic caldera located about 35 km NE of Koblenz, Germany. The crater was probably formed by an initial phreatomagmatic eruption around 24.79 ± 0.05 Ma ago (Mertz et al. 2007). A closed lake basin developed with an original depth of 240 m, and a diameter of 1.7×1.3 km (Pirrung 1998; Pirrung et al. 2001), which existed for up to 200–220 Kyr

(Mertz et al. 2007; Herrmann 2010). Afterwards, sedimentation was stopped by a huge basaltic inflow. The sedimentary infill of the crater lake, mainly debrites and turbidites and minor diatomitic black pelites (“oil shale”), is defined as the Enspel Formation (Schäfer et al. 2011). This kind of sedimentation lasted throughout its entire existence (Schindler and Wuttke 2015). The age brackets for the Enspel lacustrine sediments are between 24.56 ± 0.04 and 24.79 ± 0.05 Ma (Mertz et al. 2007). As the fossils were found close to the upper basal flow, their age is close to 24.56 ± 0.04 Ma years.

A highly diverse flora and fauna is exceptionally well preserved, displayed by primary organic molecules (i.e. chitin) or organelles (Stankievics et al. 1997; Colleary et al. 2015), preservation of primary colours of insects (McNamara 2013) and crop and/or stomach content of, e.g. frogs and birds (Wuttke and Poschmann 2010; Mayr 2013; Smith and Wuttke 2015).

Lake Enspel was surrounded by a relatively high crater rim (Pirrung 1998). During the duration of sedimentation, the rim was episodically eroded, deposited in part temporarily on alluvial fans, and then episodically resedimented on the lake floor. Gullies formed on the subaerial part of the steep inner crater rim, and mudflows occurred in the local gullies (Schindler and Wuttke 2015). The walls and the ground of the gullies were lightly vegetated, displayed by subaerially dessicated owl pellets that were washed episodically into the lake by flowing water (Smith and Wuttke 2015).

The late Oligocene was characterised by pronounced climatic changes that were accompanied by vast vegetational changes. The mean annual temperature of this terrestrial environment was estimated at about 15–17 °C, the warmest month about 25 °C, the coldest one about 5–7 °C and the mean annual precipitation was between 900 and 1355 mm/year (Uhl and Herrmann 2010). Compared to the “World Map of the Köppen-Geiger Climate Classification”, temperature in Enspel was similar to the contemporary Mediterranean, but humidity was significantly higher.

The vegetation was dominated by zonal assemblages of a mesophytic forest with a strong East Asian influence. Based on the fossil macroflora found in Enspel, four communities of plants have been described by Köhler and Uhl (2014): water plants, azonal riparian vegetation (of the lake shore), azonal riparian forest, zonal mesophytic forest/mixed mesophytic forest. The forest consisted of four storeys and reached the

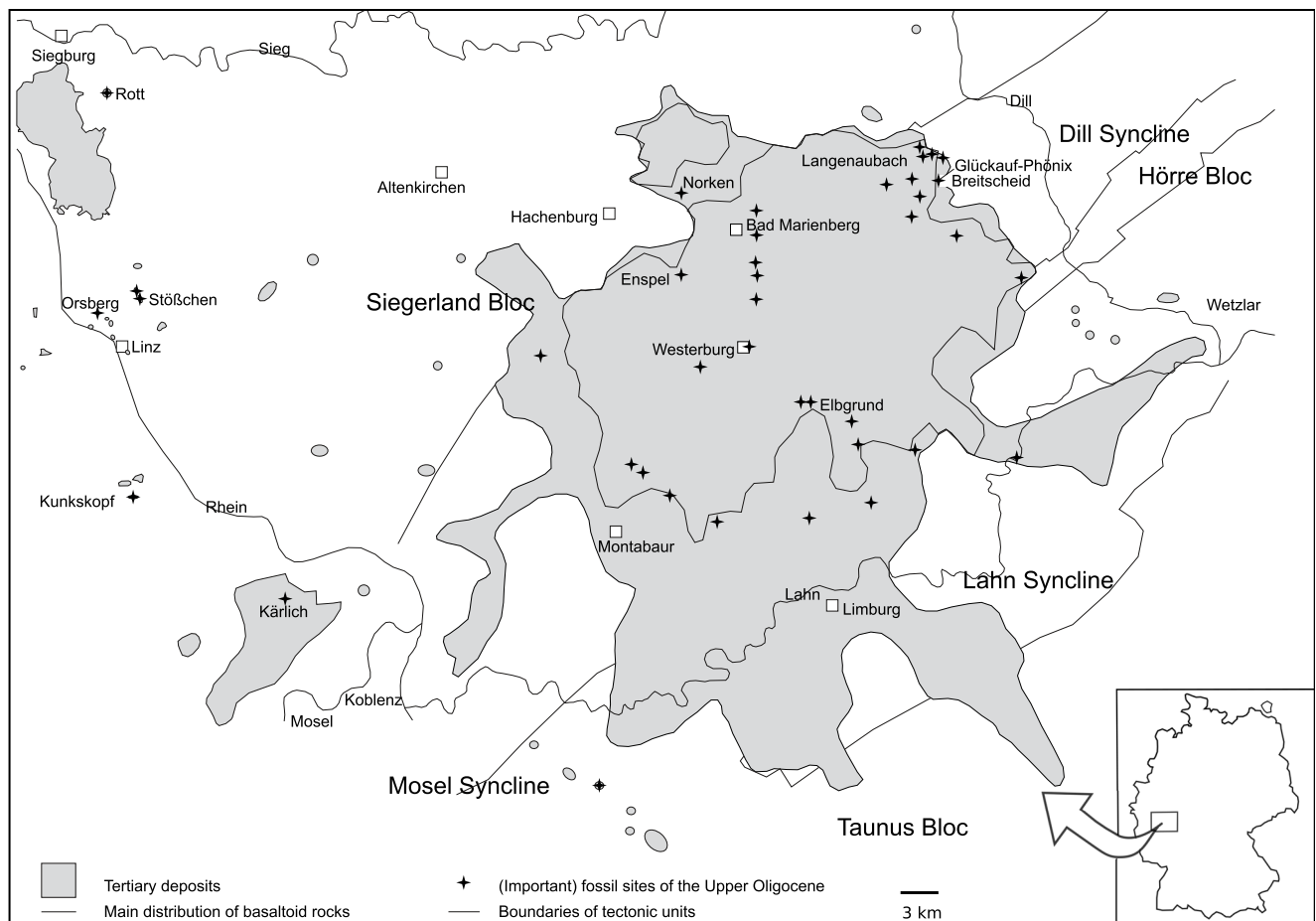


Fig. 2 Tectonic and geographical map of the Westerwald Mountains, showing the location of the Fossil-Lagerstätte Lake Enspel (adapted from Schindler and Wuttke 2010)

lake in non-disturbed parts of the crater rim that was characterised by mostly steep margins. Azonal elements (aquatic and semi-aquatic plants, riparian forest) are only represented based on approximately 15 % of the taphoflora (Köhler and Uhl 2014). Banks of the supposed gullies or streamlets feeding into the lake or shallow marginal areas can also be assumed as the potential growth areas of these plants (Schindler and Wuttke 2015).

Composition of the fossil ant record of Lake Enspel

Between 1995 and 2013, 354 ant fossils were found in Enspel. For 287 of these, the subfamily could be identified (for 42 specimens the subfamily was indeterminable, and in addition there are 25 isolated wings). Myrmicinae make up 36.6% ($n = 105$) of the specimens, and Formicinae and Dolichoderinae combined 59.9% ($n = 172$). The distinction of the latter two subfamilies is difficult; 80 fossils could be identified with quite high probability as Formicinae, only 4 as Dolichoderinae, and the remainder were not clearly assignable to either of the two subfamilies. Ponerinae make about 2.1% ($n = 6$), Agroecomyrmecinae 1.4% ($n = 4$).

At the present stage, it can be stated that fossil ants from the formicoid clade (Formicinae, Dolichoderinae, Myrmicinae) comprise 96.5% of the total. Specimens belonging to the poneroid clade are represented by 3.5% ($n = 10$). By far the majority of the specimens are males and alate females, and the number of workers is low: $n = 19$. This is equivalent to 6.1%, when 25 isolated ant wings are included ($n = 312$ in total). Fourteen of the 25 isolated wings show the typical “Paraphaenogaster wing venation pattern”.

Systematic palaeontology

Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1835
Tribus Stenammini Ashmead, 1905

Genus *Paraphaenogaster* Dlussky, 1981

Type species: *Paraphaenogaster microphthalma* Dlussky, 1981

The genus *Paraphaenogaster* originally was described by Dlussky (1981), based on males originating from Miocene sediments in Vishnevaya balka, Stavropol in Russia.

Gyne: BL between 9 and 12 mm. Head usually longer than wide. The occipital corners vary from flattened to well developed. Mandibles sub-triangular to triangular with more than 6 triangular teeth. Apical and sub-apical tooth larger, can be slightly curved. Antenna 12-segmented, no distinct club. High alitrunk with arched mesonotum. Wing venation with closed cells mcu and 1+2r. The vein 5RS reaches far to the distal edge of the forewing, it rarely reaches it completely. So in most species, cell 3r remains open. Cell rm is not developed, because vein rs-m is absent. Sometimes an unsclerotized, thin residue of the vein rs-m can still be detected. Vein 2r-rs short. The distal section of vein M does not branch off from vein RS near the junction 2r-rs/RS, but much further proximal. Thus, the free distal ends of veins M and RS do not branch off from a common node (see also Radchenko and Perkovsky 2016; Perfilieva et al. 2017). Proximal part of vein M with distinct lumen, towards distal vein turns into a stronger sclerotized line. The distal part seems to be just a stronger sclerotized line, possibly to improve the wings stability, without having any supply function. This also applies for vein 2Cu and 3Cu. Only the proximal part of 2Cu has a distinct lumen.

Propodeum armed. Petiole with distinct peduncle, posteriorly ending in a high petiolar node. Petiolar node slightly tapered, rounded. Postpetiole with gradually arising and descending node, not pedunculate. Solid, high helcium articulates higher than mid length at posterior face of petiole. Constriction of postpetiole towards gaster differs, postpetiole can be wider than petiole.

Male: BL 7–12 mm (length of male *P. microphthalma* was given as 12 mm. The males found in Enspel are between 7 and 10 mm long.) Eye diameter between 0.27 and 0.50 mm. (Eye diameter of 0.27 mm is an estimation for *P. microphthalma* based on the drawing, the eye diameter of the Enspel males are between 0.35 and 0.50 mm). High and arched mesonotum, moderate descending propodeum. Well-developed sub-triangular mandibles with 4–6 triangular-shaped teeth. For all species described here, the petiole is pedunculate without a high, distinct node. Petiole is slightly ascending towards distal. Postpetiole is mostly elongate with a more or less constricted helcium. Postpetiole can dorsally be dome-shaped. Petiole and postpetiole can be regularly or irregularly striated. Wing venation as gyne.

Worker: BL about 6–8 mm. Head elongate oval, CI around 90. Mandibles triangular with 7–8 teeth. Outer margin of mandible is evenly curved. Alitrunk elongate. In profile, promesonotum can be significantly higher than propodeum, pronotum can be separated from mesonotum by a clear promesonotal suture. Propodeal spines present. Petiole pedunculate, with rounded node.

Differential diagnosis: *Paraphaenogaster* resembles *Aphaenogaster* to a great extent, i.e. elongate head, 12-segmented antenna, high and arched alitrunk, pedunculate and high-noded petiole. The only criteria to separate *Paraphaenogaster* from *Aphaenogaster* are the lack or strong reduction of the cell rm.

Fig. 3 *Paraphaenogaster loosi* sp. nov., gyne, holotype NHMM-PE1995/5503-LS a+b. **a** Photomontage, plate a and b combined (photograph of plate a, see Supplementary Data 1: Fig. 1, photograph of plate b, see Supplementary Data 1: Fig. 2). **b** Line drawing; *Paraphaenogaster* cf. *loosi*, gyne, NHMM-PE2013/5037-LS. **c** Photograph. **d** Line drawing; *Paraphaenogaster* cf. *loosi* gyne, NHMM-PE1995/7896-LS a+b. **e** Photograph of plate a. **f** Photomontage of plate a and b combined (see also Supplementary Data 1: Fig. 3; photograph of plate b, see Supplementary Data 1: Fig. 4). **g** Line drawing

Remarks: Since the workers and dealate females lack the fore wings, the main distinguishing feature between the genera *Aphaenogaster* and *Paraphaenogaster* is not present. Strictly spoken, it is impossible to allocate worker or dealate females to one or the other genera. This is the weakest point of creating a morphogenus based on the wing venation pattern. However, since the genus *Paraphaenogaster* is much more represented in Enspel than *Aphaenogaster*, the worker specimens are assigned to the genus *Paraphaenogaster*.

Dlussky and Wedmann (2012) stated that it is almost impossible to prove the conspecificity of gynes and males of fossil ants. This is also the case here. There are no specific morphological characteristics that would allow me to state a conspecificity of male and gyne.

Paraphaenogaster loosi sp. nov.

(Fig. 3a, b)

Etymology: Honouring former munipale mayor Gerhard Loos (Westerburg, Germany), in place of all town mayors, local authorities and the county council, who all were engaged to develop the Fossil-Lagerstätte Enspel to the main touristic centrum Stöffel-Park (Enspel, Westerwald Mountains, Germany) by fundraising political and financial support from the state Rhineland-Palatinate and the European Union.

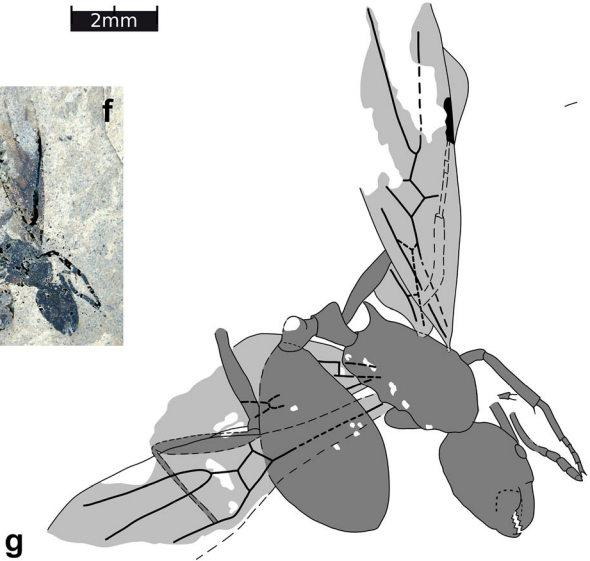
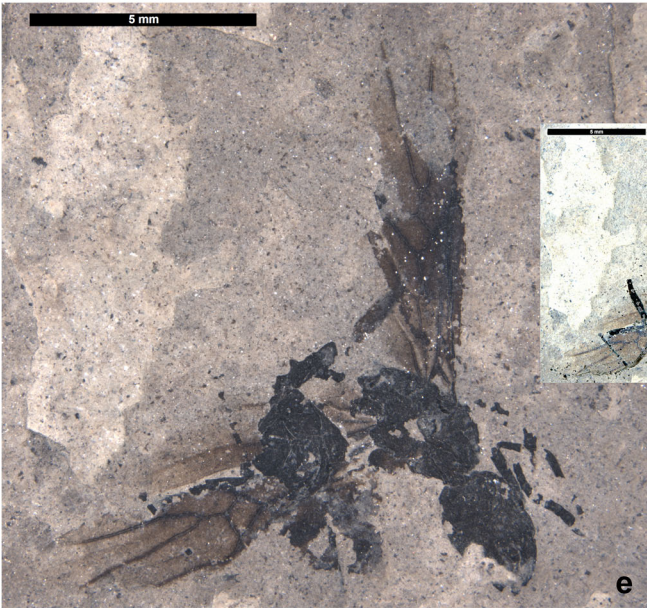
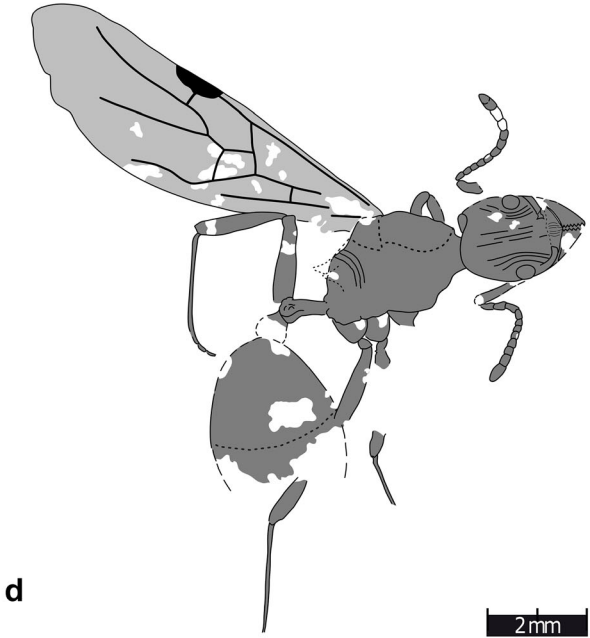
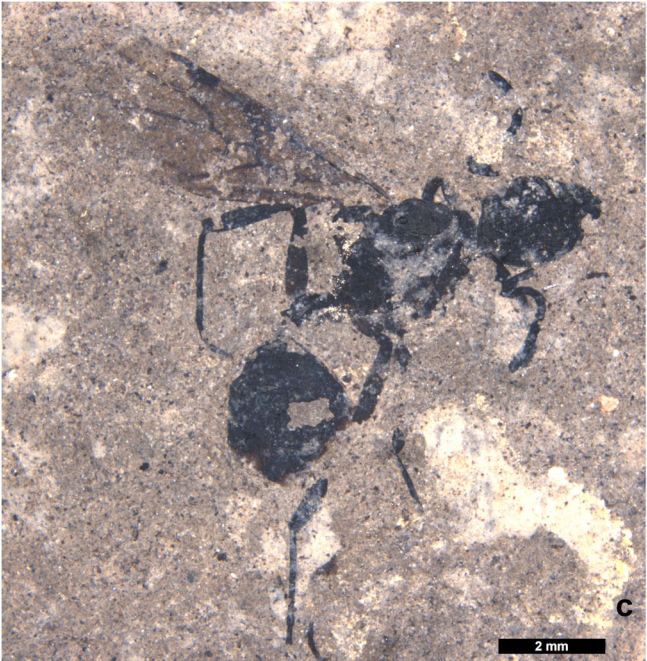
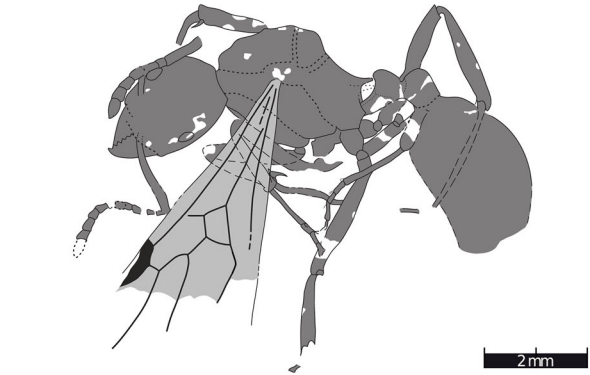
Holotype: NHMM-PE1995/5503-LS a+b, winged gyne.

Position: Head dorsal, alitrunk, petiole, postpetiole, gaster (partly) lateral.

Colour: Brown, both plates a and b existing.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL about 9.73. Head distinctly longer than wide, with feebly concave sides, smoothly rounded occipital corners. Head length is about 68% of alitrunk length. Anterior margin of clypeus smooth. Eyes slightly longer than wide, located at mid length of head, eye diameter is about 22.3% of head length. Gena well developed. Mandibles sub-triangular, with eight well-developed triangular-shaped teeth; the two first apical teeth larger than the others. Twelve-segmented



antenna, no distinct club. Scape just protrudes beyond occipital margin. Surface of the head is sculptured with wide striae. At the occiput striae are also combined with transversal structures, resulting in a reticulate pattern. Alitrunk high, mesonotum arched. Scutum anteriorly covers pronotum. Scutellum thickened and distinctly upraised. It is transverse oval shaped with tapered ends. Propodeal slope steep, propodeum armed with two long spines, directed straight backwards. No propodeal lobes developed. Tibial spurs combed at fore leg, simple at hind leg; for the mid leg it is not clear. Pronotum, propleuren striated, propodeum with transversal strong striae, other parts of alitrunk unspecificly rugose. Mesopleuron large. Posteroventral margin of metasternum almost forms a right angle. Wing venation as in genus description. Apical part of vein 5RS is not preserved, so it is uncertain if cell 3r is closed here. Petiole with long peduncle and distinct node. Peduncle anteroventral with small protrusion. Petiole dorsally with distinct sutures, along peduncles midline and marking the transition from peduncle to node. Node with steep ascending anterior face and steep descending posterior face, dorsally structured rugose. Postpetiole with rounded node. Helcium articulates with petiole at about mid length of posterior face of petiole. Gaster is damaged. However, two continuous break lines prove that the first gastral tergite is the longest one, which is typical for myrmicine ants. Sculpture on first gastral tergite is unspecific rugose, not shiny.

Measurements: Holotype NHMM-PE1995/5503-LS a+b; BLw/oG: 6.87, HL: 1.98, HW: 1.58 (est.), ED: 0.44, GeL: 0.59, ML: 0.96, MML: 0.59 SL: 1.56, AL: 2.91, FWL: 7.69 (est.), ScuL: 1.52, ScutL: 0.62, HiTL: 2.02, PL: 0.90, PH: 0.71, PPL: 0.5, PPH: 0.69, HeH: 0.43, GIL: 1.68 (est.), GIH: 1.53. Wing venation: 2M+Cu: 0.75, 1Cu: 0.71, 1M: 0.38, m-cu: 0.47, 1RS+M: 0.38, 2RS+M: 0.49. Indices: CI: 79.98, SI: 98.85, IED/HL: 22.32, IHL/AL: 67.98, Imcu: 54.17, I2RS+M/1RS+M: 126.92, I2RS+M/m-cu: 95.62, I2RS+M/2M+Cu: 64.71.

Differential diagnosis: *P. loosi* is characterised by its combination of BL > 9 mm, an arched promesonotum with a protruding scutellum, straight and well-developed propodeal spines, a high, steeply ascending petiolar node, and a nodular postpetiole. As an essential difference to *P. tertiaria*, this species has a convexly curved clypeus margin and does not show any median indentation (see Dlussky and Putyatina 2014). The clypeus of *P. tertiaria* is not convexly curved but horizontal in itself, and has a median depression at the anterior clypeus margin.

Paraphaenogaster cf. *loosi*
(Fig. 3c, d)

Specimen: NHMM-PE2013/5037-LS, winged gyne

Position: Head dorsal, alitrunk, petiole, postpetiole (partly), first gastral tergite dorsolateral.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S14.

Description: BL about 9.03. Head oval, slightly longer than wide, at the sides feebly convex. Smoothly rounded occipital corners, posterior margin median slightly concave, with a distinct small groove. Head length is about 66% of alitrunk length. All dorsal parts of head, including gena, are completely sculptured with distinct widely spaced striae. Towards posterior part of head striation turns to be also combined with transversal structures so it turns to a kind of reticulate pattern. Anterior margin of clypeus convex, median part of clypeus with distinct longitudinal striae. Frontal carinae reaching back to about anterior margin of eyes. Frontal lobes hardly developed. Frons fairly wide. Mandibles sub-triangular. Masticatory margin with about 7 triangular-shaped teeth, all about same size. The apical tooth seems to be slightly bigger but it is not claw-like curved. Eyes located slightly below midlength of head. Eye diameter is about 21.6% of head length. Antenna 12-segmented, no distinct club. Funiculus is not filiform or slender. The top of the apical funicular segment is separated by an additional suture. This apical top is not valued as a separate funicular segment, but is seen as a taphonomic feature, see also chapter: Taphonomic aspects. First funicular segment longer than second, third and forth; the second funicular segment is slightly longer than wide. Scape overtrudes slightly occipital margin of head. Scape is widely curved at base, at bend distinctly narrower than at its distal part. Scutum, scutellum and pronotum with longitudinal rugae, propodeum transversely striated. Scutellum is protruding. Posterior margin of metanotum not distinctly thickened. Propodeal spines unclear, but according to imprint of sediment seen on the photograph, short propodeal spines are very likely. Propodeum with transversal striation at posterior declivity. These are continuing vertical at lateral parts of propodeum. Petiole equipped with long peduncle. Node most likely has been tilted forward and appears flattened due to the caudal-dorsolateral perspective. Postpetiole not preserved but imprints in the sediment indicate the existence of a medium size node. Wing venation with closed cells m-cu, 1+2r, open 3r. Shape of cell m-cu sub-trapezoid. 1RS comparably long, distinctly inclining distal. Wing venation pattern follows in all other aspects the description of the genus. First gastral tergite large, with homogenous, slightly rugose sculpturing, it is not shining.

Measurements: NHMM-PE2013/5037-LS; BLw/oG: 6.18, HL: 1.82, HW: 1.73, ED: 0.41, GeL: 0.44, ML: 0.91, MML: 0.41, SL: 1.58, AL: 2.76, FWL: 8.23, ScuL: 1.07, ScutL: 0.46, HiTL: 1.79, PL: 0.75, PPL: 0.43 (est.), HeW: 0.32, GIL: 1.93. Wing venation: 2M+Cu: 0.65, 1Cu: 0.65, 1M: 0.28, m-cu: 0.50, 1RS+M: 0.46, 2RS+M: 0.38. Indices: CI: 94.98, SI: 91.58, IED/HL: 22.65, IHL/AL: 65.95, Imcu: 70.45, I2RS+M/1RS+M: 83.87, I2RS+M/m-cu: 88.26, I2RS+M/2M+Cu: 59.09.

Remarks: This specimen has not been classified as the paratype of *P. loosi* sp. nov., because the morphology of its petiole and postpetiole is not clear. It differs from *P. loosi* in its colour. As mentioned above, the colour has no taxonomic value, see Chapter: Material and Methods.

Paraphaenogaster cf. *loosi*
(Fig. 3e–g)

Specimen: NHMM-PE1995/7896-LS a+b, winged gyne.

Position: Head from ventral, alitrunk from ventrolateral, petiole, postpetiole, and gaster from lateral.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S12.

Description: BL about 11.89 (see also remark). Head distinctly longer than wide, with smoothly rounded posterior corners. Head length is about 62.3% of alitrunk length. Side parts where eyes are located seem to be slightly concave. Gena convex. Eyes located slightly below mid length of head, eye diameter is about 18.7% of head length. Elongate, subtriangular mandibles with 6–7 triangular-shaped teeth. First apical tooth bigger than second apical tooth, second apical tooth slightly bigger than the other teeth. Apical tooth is bended. Antenna most likely 12-segmented. Scape protrudes beyond the occipital margin of the head. Alitrunk elongate, relatively flat. Scutum anteriorly covers pronotum; Propleuren irregular longitudinally sculptured. Dorsolateral and lateral parts of propodeum densely striated. Propodeum dorsally with transversal bulgy striae. Propodeal lobes weakly developed, not as distinct as specimen in NHMM PE2010/5496-LS. Length of propodeal spines 0.4 mm, slightly curved downwards. Spine's base fairly wide. Tibial spurs distinct and combed at fore leg, not clear at middle and hind leg. Wing venation with closed cells m-cu and 1+2r. Shape of cell m-cu trapezoid. Apical part of vein 5RS does not reach apical margin of forewing. So cell 3r is open. In other respects, the description of the wing venation of the genus applies. Petiole with peduncle and distinct tapered node. In profile, the anterior face of the petiole shows a concave line, the transition from peduncle to node appears slightly smoother here than in *P. loosi*. Node's sculpture rugose. Postpetiole with smoothly arising and descending node. Postpetioles node less high than petioles node (according to marks in the sediment), top rounded. Solid and high helcium articulates at mid length at posterior face of petiole. First gastral segment clearly longer than the others and stronger sclerotized, but without any specific sculpture. In this specimen, sculpture and sutures are comparatively poorly preserved.

Measurements: NHMM-PE1995/7896-LS a+b; BLw/oG: 7.43, HL: 2.05, HW: 1.82, ED: 0.38, GeL: 0.62, ML: 1.09,

MML: 0.71, SL: 1.87 (est.), AL: 3.28, HiTL: 2.05, FWL: 9.0, PL: 0.93, PH: 0.85, PPL: 0.47, PPH: 0.69 (est.), HeH: 0.43. Wing venation: 1Cu: 0.87, 1M: 0.53, m-cu: 0.56, 1RS+M: 0.47, 2RS+M: 0.51. Indices: CI: 88.8, SI: 102.95; IED/HL: 18.7, IHL/AL: 62.33, Imcu: 54.24, I2RS+M/1RS+M: 109.38, I2RS+M/m-cu: 107.38.

Remarks: The big difference in body length to *P. loosi* is due to the low degree of telescoping of its gaster. If one compares the values of BLw/oG, the difference in size is smaller and more realistic. The preserved propodeal spine appears slightly bent downwards. This can be caused by taphonomic influences. Colour differences are not assessed as taxonomic characteristics, see Chapter: Material and Methods.

Paraphaenogaster schindleri sp. nov.
(Fig. 4a, b)

Etymology: Honouring Dr. Thomas Schindler, who developed essential models for the formation and sedimentological development of Lake Enspel and other Oligocene Lagerstätten in the Westerwald Mountains through time.

Holotype: NHMM-PE2001/5065-LS, winged gyne.

Position: Head dorsal, alitrunk dorsolateral, petiole lateral, postpetiole dorsolateral, gaster dorsolateral.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: Gyne. BL about 11.74. Head longer than wide, with almost parallel sides, and distinct occipital corners. Head does not get narrower towards the front. Posterior margin of head median with a smooth depression. Long straight frontal carinae reaches beyond the median ocellus. All dorsal parts of head completely sculptured with constant longitudinal striae. Eyes located at about midlength of head. Eyes relatively small, head more than five times longer than maximum eye diameter. Gena striated. Anterior clypeal margin smooth, median convexly shaped. Clypeus densely striated. Fronto-clypeal-suture median convex, frontal triangle distinctly reaching beyond frontal lobes. Mandibles triangular. Masticatory margin with 6–8 triangular-shaped teeth. Teeth 5 and 6 seem to be slightly smaller than the others. Most apical parts of mandibles hidden in the sediment. Therefore there is no evidence for the existence of one or two distinctly enlarged and curved apical teeth. Scape just reaches posterior margin of head. Scape widely curved at base. Funiculus 11-segmented. The six proximal segments are almost as long as wide, slightly increasing in size towards apex. The six apical funicular segments continuously slightly increasing length towards apex, but they do not form a differentiated club. Alitrunk high, not arched. Scutum large, flat, overlaps pronotum anteriorly, antero-lateral corners of pronotum not visible from dorsal.

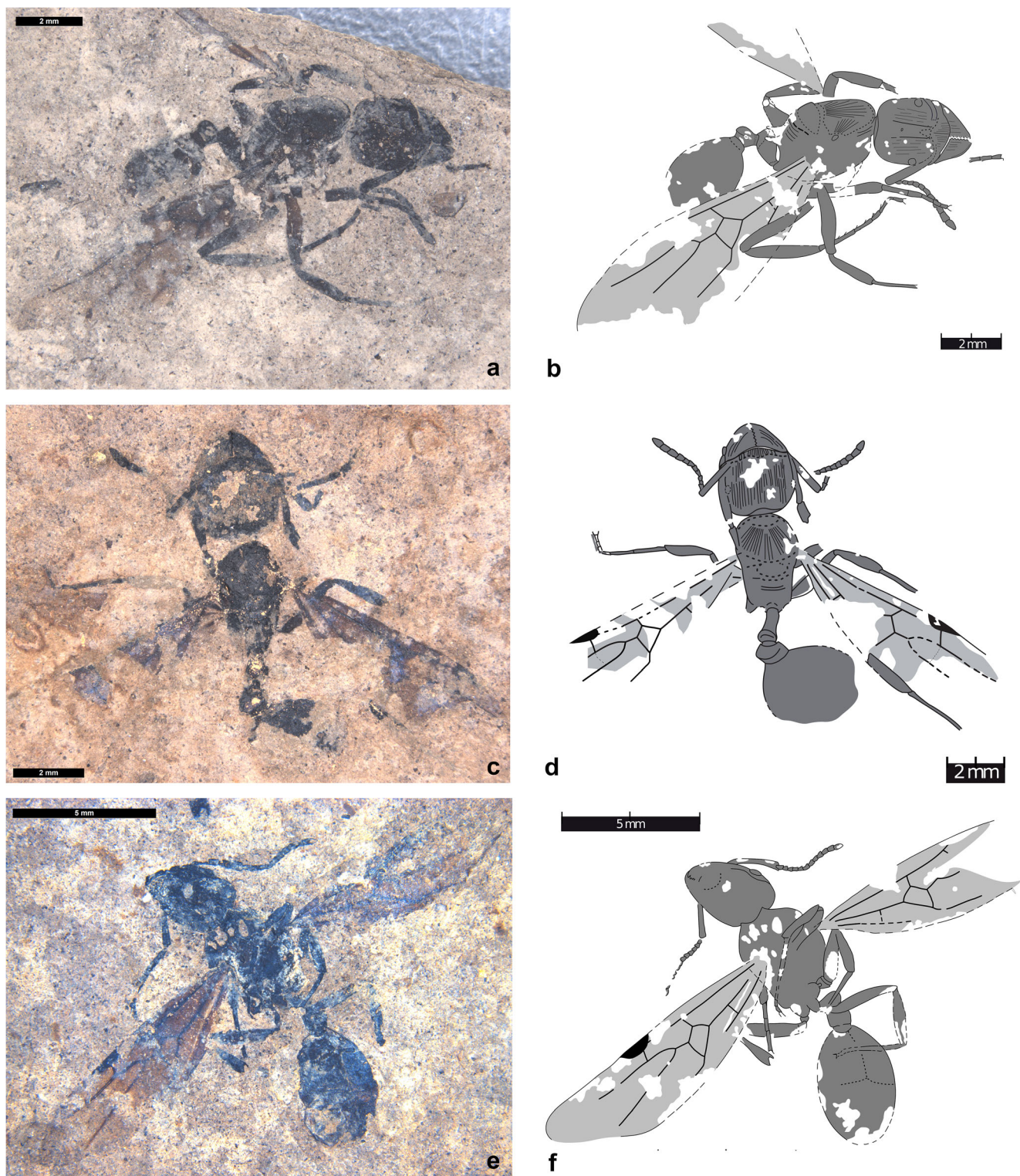


Fig. 4 *Paraphaenogaster schindleri* sp. nov., gyne, holotype NHMM-PE20001/5065-LS. **a** Photograph, **b** Line drawing; *Paraphaenogaster* cf. *schindleri*, gyne, NHMM-PE2010/5462-LS. **c** Photograph, **d** Line

drawing; *Paraphaenogaster* cf. *schindleri*, gyne, NHMM-PE2002/5019-LS. **e** Photograph, **f** Line drawing; detail: head with left antenna, see Supplementary Data 1: Fig. 5.

Scutellum is transversely oval shaped with tapered ends. Its anterior margin is upraised (could also be caused by taphonomic processes). Propodeal declivity fairly steep. Well-

developed metanotum, its posterior margin is distinctly thickened. Propodeal spines only recognisable as outlines. Propodeum could be slightly angled, provided with small

pointed corners. Scutum is striated, straight in the middle, slantwise to both sides. Latter converge towards tegula. Scutellum also with coarse longitudinal ridges. Signs of tibial spurs found at all legs, simple at mid and hind legs, broader and probably brushed at foreleg. Tarsal segments of all legs with bristles. Wing venation with closed cells mcu and 1+2r. Shape of cell mcu distinctly trapezoid. Vein 1Cu almost double length of 1RS + M. In other respects, the description of the wing venation of the genus applies. Propodeum with transversal striation at posterior declivity, continuing vertical at lateral parts of propodeum. Solid, round propodeal-petiolar articulation, protrudes from alitrunk. Petiole pedunculate, very stout. In profile, it appears dorsally convex. Dorsal part of petiolar node is incomplete. Postpetiole with distinct node. Ascent and descent of node medium. The node's top seems to have another surface structure; it stands out from the rest of the postpetiole. This probably also applies for the petiole top. Helcium projects ventrally at less than mid length of petiole's anterior face. Maximum height of petiole and postpetiole is about equal. Gaster is not complete. Posterior margins of first gastral tergite and sternite are not clear because of break lines.

Measurements: Holotype NHMM-PE20001/5065-LS; BLw/oG: 8.61, HL: 2.51, HW: 2.15, ED: 0.35, GeL: 0.68, ML: 1.47, MML: 0.76, SL: 2.02, AL: 3.74, ScuL: 1.75, ScutL: 0.68, FWL: 10.08, HiTL: 2.14, PL: 1.03, PH: 0.69, PPL: 0.56, PPH: 0.78, HeH: 0.35, Wing venation: 2M+Cu: 0.90, 1Cu: 0.93, 1M: 0.63, m-cu: 0.78, 1RS+M: 0.50, 2RS+M: 0.56. Indices: CI: 85.71, SI: 93.7, IED/HL: 14.05, IHL/AL: 67.17, Imcu: 53.97, I2RS+M/1RS+M: 111.76, I2RS+M/m-cu: 133.86, I2RS+M/2M+Cu: 62.30.

Differential diagnosis: *P. schindleri* differs from *P. loosi* by its well defined occipital corners and its long, almost parallel running frontal carinae. It is not allocated to the genus *Messor* because CI in *Messor* gyne is in most species distinctly above 100. (Measurements on images from the Antweb of ten gynes from ten different extant *Messor* species showed an average CI of more than 106.) Also the outer line of the mandibles is not nearly as strongly bent as with the extant *Messor* gyne. In addition, the central backward area of the clypeus and the frontal triangle do not reach the width seen with the extant *Messor* gynes. Therefore, there is no strong reason to assign this sample to the genus *Messor*. Comparisons with fossil *Messor* species are hardly possible. So far, only one fossil *Messor* species has been described: *Messor sculpturatus*, Carpenter 1930 from the late Eocene deposit in Florissant, USA. This assignment, however, is equivocal and it has been generally questioned by Bolton (1982: p. 341), later Bolton (1995: p. 257) classified it as insertae sedis in *Messor*.

Paraphaenogaster cf. *schindleri*
(Fig. 4c, d)

Specimen: NHMM-PE2010/5462-LS, winged gyne.

Position: Head, alitrunk, and petiole dorsal, postpetiole and first gastral segment dorsolateral. **Colour:** ?Dark brown to black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S6-10.

Description: BL about 11.41. Head slightly longer than wide. Median anterior margin of clypeus smooth, convex shaped. Head sides almost parallel. Posterior margin of head is not well preserved; it is visible only as a shadow. Location of eyes is about mid length of head. Mandibles triangular; masticatory margin with 6–8 triangular teeth of subequal size. There is no evidence for the existence of longer apical curved teeth. Scape just reaches posterior margin of head. Dorsal parts of head that are preserved are completely sculptured with regular longitudinal striae. Towards occiput it turns into a reticulate pattern. Antenna with 12 segments, with a weak 4-segmented club. Alitrunk slender. Medioanterior part of scutum slightly rugose, rest of scutum with fine striae, slantwise to both sides, straight in the middle. Scutellum oval shaped with tapered ends; its sculpture is punctated and roughly rugose. Prescutellum distinct, with longitudinal striae. Well-developed metanotum. Propodeum with horizontal striae. Cuticle of propodeum shows triangle-like acute structures. As these do not follow any pattern, they are most likely caused by taphonomic processes. Propodeal spines unclear. No tibial spurs found at fore and mid leg. Preservation of wings poor. Wing venation with closed cells mcu and 1+2r. Shape of cell mcu trapezoid. Distal parts of forewings not well preserved. Therefore, cell 3r remains unclear. Vein rs-m very thin, sclerotization lacking. As other veins are preserved, it is likely that the vein rs-m is primarily strongly reduced. Petiole elongate with long peduncle ending in a petiolar node. Due to the caudo-dorsolateral perspective on the petiolar node and the fractures it contains, its shape cannot be clearly determined. Postpetiole with distinct node. Anterior face of its node steeply ascending, node distinctly tapered transversely to the body axis, forming a ridge. Posterior face of node much shorter, gradually descending. Helcium projects from low down of the anterior face of the postpetiole. Only first gastral tergite preserved, its sculpture is rugose.

Measurements: NHMM-PE2010/5462-LS; BLw/oG: 8.09; HL: 2.41, HW: 2.31, ED: 0.31 (?), GeL: 0.31, ML: 1.55, MML: 0.76, SL: 1.86, AL: 3.03, AW: 1.84, ScuL: 1.49, ScutL: 0.47, FWL: 9.0, HiTL: 1, 98, PL: 1.15, PPL: 0.74, GIL: 2.48. Indices: CI 95.74, SI: 80.77, IED/HL: 13.43(?), IHL/AL: 79.54.

Remarks: Unfortunately, central parts of the head, like posteriorly extending area of the clypeus and the frontal

triangle, are not preserved. Also, it is not clear if this species has two almost parallel running long carinae like *P. schindleri*. As this specimen has some characteristics, like body size, shapes of head, mandibles, petiole and postpetiole in common with *P. schindleri*, it is specified as *Paraphaenogaster* cf. *schindleri*. It is not allocated to the genus *Messor* because CI in extant *Messor* gyne is in most species distinctly above 100. Also, outer lines of mandibles are not strongly bend. An assignment to the genus *Aphaenogaster* is not strongly supported. Neither by the relatively high CI nor by its petiole shape, nor by its wing venation pattern. Vein rs-m is very weak.

Paraphaenogaster cf. *schindleri*
(Fig. 4e, f)

Specimen: NHMM-PE2002/5019-LS, winged gyne.

Position: Head, alitrunk petioli, and gaster from lateroventral.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S14.

Description: Gyne. BL about 12.65. Head elongate, with well-developed occipital corners. Head parallel at sides, eyes appear slightly sunken at about mid length of head. Mandibles triangular, more than six teeth. Apical and preapical teeth clearly bigger than the others, sharp and claw-like curved. Other teeth are shaped triangular and of almost equal size. Antenna with 12 segments. Funiculus slender without distinct club. Pedicellus erroneously appears two-segmented. Scape just reaches occipital margin of head. Scape with continuously increasing width towards distal. Anterior part of laterocervical plates of the propleura well preserved. Wing venation with closed cells mcu and 1+2r. Shape of cell mcu is strongly trapezoid. Vein 1Cu twice as long as 1RS + M. In all other respects, the description of the wing venation of the genus applies. Due to the dorsoventral position of the fossil, it is not clear if there are propodeal spines developed. Tarsal segments of mid and hind legs with bristles. Petiole partly hidden in sediment, visible parts indicate a stout pedunculate petiole. Postpetiole seen from lateroventral elongate, most likely with flat node. It is broadly connected with petiole. Gaster elongate, first gastral segment distinctly longer than the others, reaches half-length of gaster. Gastral tergites covering lateral and lateroventral parts of gaster. However, this impression could also be caused by deformation.

Measurements: NHMM-PE2002-5019-LS; BLw/oG: 8.56; HL: 2.56, HW: 2.36, ED: 0.56, ML: 1.16, MML: 0.68, SL: 1.93, AL: 3.44, FWL: 10.31, HiTL: 2.31, PL: 1.10, PH: 0.81, PPL: 0.78, HeH: 0.54, G1L: 2.49, G1W: 2.56. Wing venation: 2M+Cu: 1.01, 1Cu: 1.04, 1M: 0.54, m-cu: 0.71, 1RS+M: 0.51, 2RS+M: 0.56. Indices: CI: 92.0, SI: 81.91, IED/HL: 21.8; IHL/AL:

74.64, Imcu: 49.3, 12RS+M/1RS+M: 108.57, 12RS+M/m-cu: 126.51, 12RS+M/2M+Cu: 55.07.

Remarks: This specimen resembles *P. schindleri* in body length, head size and head shape, the latter especially with regard to the occipital corners. Although dorsal side of head cannot be seen, an assignment as *Paraphaenogaster* cf. *schindleri* appears to be appropriate.

Paraphaenogaster bizeri sp. nov.
(Fig. 5a, b)

Etymology: Honouring Thomas Bizer, Mainz, Germany, who managed the photographic repository of the Enspel excavations and did the image processing for many Enspel papers, published by the staff of the General Department for the Conservation of the Cultural Heritage of Rhineland Palatinate, Department Archaeology/History of the Earth, Mainz (Germany).

Holotype: NHMM-PE1997/5991-LS, winged gyne.

Position: Head, alitrunk, petiole, postpetiole, first gastral tergite dorsal. Worth mentioning is the fact that left mandible is extremely arched because of a surface distortion in the sediment.

Colour: Black. Alitrunk, petiole, postpetiole, and gaster pyritized.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S14 o.

Description: BL about 11.5. Head slightly wider than long, with rounded occipital corners. Head tapers anteriorly. Median part of anterior clypeus margin is smooth and follows strongly convex curve. Ridges of striae are reaching anterior margin. The posterior margin of the head shows median a small pointed depression. Frontal carinae reaching back to about mid length of eyes. Frontal lobes do not cover antennal condyle completely. All dorsal parts of head, completely sculptured with constant longitudinal, fairly fine striae, at occiput it turns to a reticulate pattern. Frons wide. Mandibles sub-triangular. Masticatory margin with about 8 triangular shaped teeth, all about the same size. Apical tooth not preserved, but signs in the sediment indicate a bigger apical tooth. Eyes located at midlength of head. Eyes diameter is only about 17% of head length. Scape reaches posterior margin of head. Antenna with 12 segments. No differentiated club. Alitrunk partly pyritized. Scutellum is transverse oval with tapered ends. Well-developed metanotum. Posterior margin of metanotum distinctly thickened. Scutum longitudinally striated. Scutellum with coarse longitudinal ridges. Propodeum with transversal striation at posterior declivity continuing vertical at lateral parts of propodeum. Propodeal spines not preserved, but according to photograph analysis very likely.

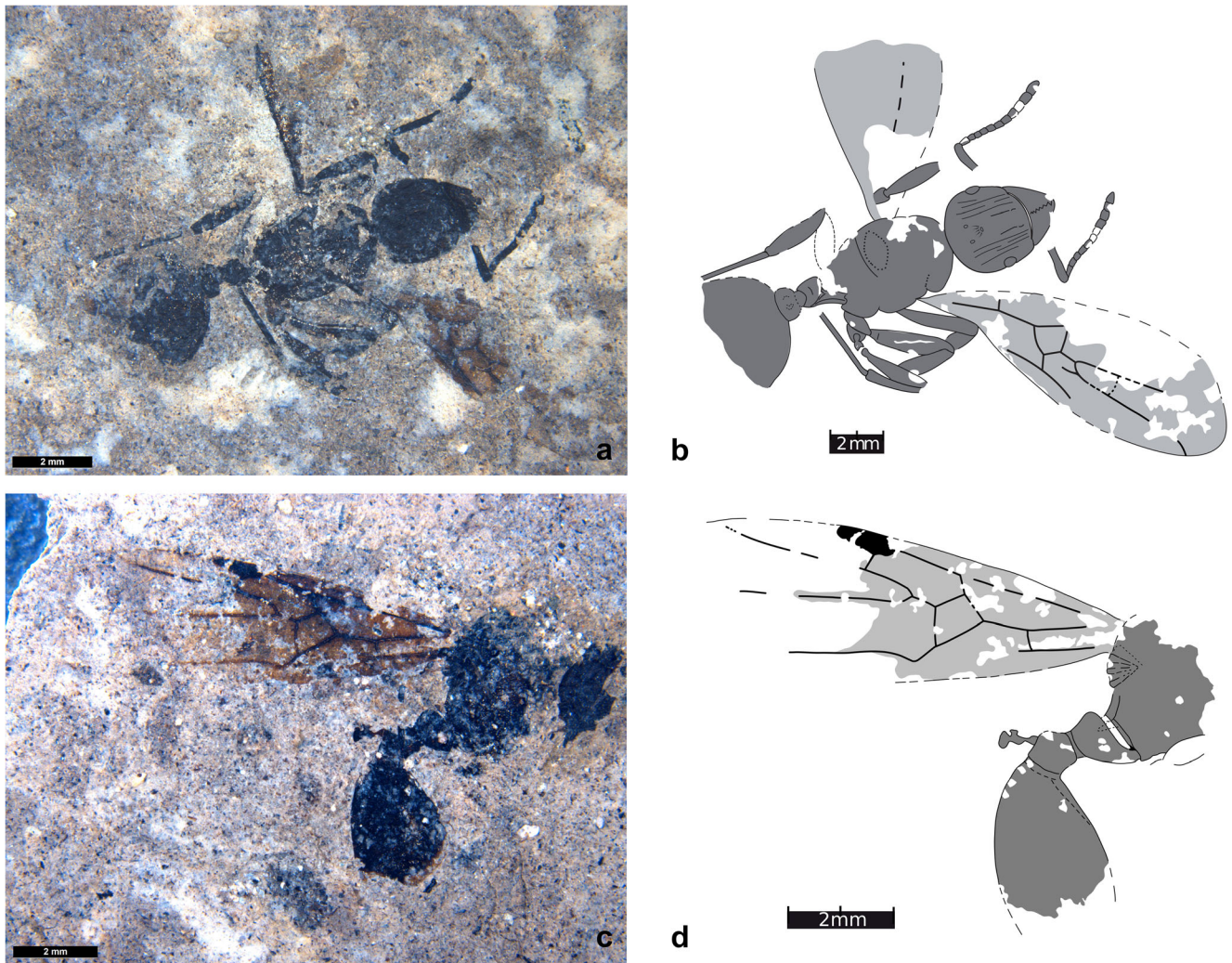


Fig. 5 *Paraphaenogaster bizeri* sp. nov., gyne, holotype NHMM-PE1997/5991-LS. **a** Photograph, **b** Line drawing, detail: head, see Supplementary Data 1: Fig. 6; *Paraphaenogaster incertae sedis*, gyne,

NHMM-PE1995/5175-LS. **c** Photograph, **d** Line drawing, detail: petiole and postpetiole, see Supplementary Data 1: Fig. 7

Petiole with long, stout peduncle and a distinct high petiolar node. Peduncle appears ventrally and laterally slightly concave. Peduncle lateral with two long ridges and a groove in between. Postpetiole wide, with distinct node. Anterior face of node moderately ascending, rounded top. Posterior face of node much shorter, gradually descending. Helcium articulates ventrally at less than mid length of posterior face of petiole. Wing venation with closed cells mcu, 1+2r, and 3r. Vein rs-m weak, not distinct, sclerotization at junction with vein 4M only. Shape of cell mcu trapezoid. Vein 5RS does reach the apical margin of wing, but it is very weakly sclerotized in its distal part. Additional incomplete vein is leaving proximally from 2-3rs. In all other respects, the description of the genus applies. First gastral tergite large, with homogenous slightly rugose surface sculpturing. **Measurements:** Holotype NHMM-PE1997/5991-LS; BLw/oG: 7.80, HL: 2.05, HW: 2.14, ED: 0.35, GeL: 0.85, ML: 1.18, MML: 0.74, SL: 1.73, AL: 3.12, FWL: 8.23, ScuL: 1.36, ScutL:

0.56, HiTL: 2.08, PL: 1.15, PPL: 0.75, PPW: 0.88, G1W: 3.06. Wing venation: 2M+Cu: 0.91, 1Cu: 0.82, 1M: 0.62, m-cu: 0.62, 1RS+M: 0.49, 2RS+M: 0.47. Indices: CI: 104.44. SI: 80.83, IED/HL: 17.26, IHL/AL: 65.55, Imcu: 58.93, I2RS+M/1RS+M: 96.97, I2RS+M/m-cu: 108.85, I2RS+M/2M+Cu: 51.61.

Differential diagnosis: *P. bizeri* is characterised by its combination of BL 11–12 mm, its posteriorly wide head, narrowing towards the front, its rounded and distinct occipital corners, and its relatively small eyes. Its head is sculptured with regular, relatively fine striae, including the clypeus. It differs from *P. tertiaria* by its head shape, eyes position and shape of the lateral parts of the anterior clypeal margin. The head shape of *P. tertiaria* is characterised by “...parallel sides and rounded occipital margin, without occipital angles” (Dlussky and Putyatina 2014, p: 273). It differs from *P. jurei* (Heer 1849) regarding its size and head shape (see also Dlussky and Putyatina 2014, p. 271).

Paraphaenogaster incertae sedis
(Fig. 5c, d)

Specimen: NHMM-PE1995/5175-LS, winged gyne. Formicidae indet. Wedmann 2000: 68, Fig. 23 (wing).

Position: Parts of alitrunk, petiole, postpetiole, and parts of gaster from lateral, one forewing. Head and legs are missing.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL > 11. Head is missing. Alitrunk stout, high, arched. Scutum strongly arched. Scutellum thickened, and distinctly upraised. Metanotum distinct. Marks of propodeal spines existing, fractures of broken spine can be identified. Petiole with stout peduncle. Peduncle not bar-like; there is a smooth transition from peduncle to node. Node is continuously ascending, anterior face shaped slightly convexly. Node slightly tapered, with rounded top. Postpetiole stout, with gradually arising and descending node. Its node is less high than the petiole's node. Solid, high helcium articulates higher than mid length at posterior face of petiole. Wing venation with closed cells m-cu and 1+2r. Cell m-cu trapezoid shaped. Vein 5RS does reach the apical margin of wing, but it is very weakly sclerotized in its distal part. 1RS distinctly inclining distad. Wing venation pattern follows in all other aspects the description of the genus. First gaster distinctly longer than the others, with homogenous sculpture, probably not shiny.

Measurements: NHMM-PE1995/5175-LS; AL: 3.7, AH: 2.9, FWL: 10.38, PL: 1.18, PH: 0.96, PPL: 0.66, PPH: 0.9, HeH: 0.51, G1L: 2.91, G1H: 2.23. Wing venation: 2M+Cu: 0.93, 1Cu: 0.97, 1M: 0.65, m-cu: 0.72, 1RS+M: 0.54, 2RS+M: 0.47. Indices: Imcu: 56.06; I2RS+M/1RS+M: 86.49, I2RS+M/m-cu: 119.15, I2RS+M/2M+Cu: 50.79.

Remarks: This specimen most probably has a BL > 11. Based on the combination of an arched mesonotum, protruding scutellum, its petiole and postpetiole shape and its wing venation pattern; this specimen is allocated to the genus *Paraphaenogaster*. As the head is completely missing, specimen cannot be assigned more precisely.

Paraphaenogaster freihauti sp. nov.
(Fig. 6a, b)

Etymology: Honouring Bernd Freihaut, Darmstadt, a distinguished architect, who run the project to develop the Fossil-Lagerstätte Enspel and an industrial heritage of basalt mining to the famous touristic site Stöffel-Park (Enspel, Westerwald Mountains, Germany).

Holotype: NHMM-PE1995/8758-LS, worker.

Position: Head, alitrunk from dorsolateral, petiole, postpetiole and gaster from lateral.

Colour: Head, alitrunk and first gastral segment dark brown to black, petiole and postpetiole, gastral segments 2–4, and legs medium brown.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S14.

Diagnosis: BL about 6.14. Head longer than wide, with smoothly rounded occipital corners. Head sides are slightly convex. Strong gena. Eyes located behind mid length of head. Eyes diameter is about 14.3% of head length. Mandibles stout, sub-triangular, with 7–8 teeth. Teeth have approximately the same size. Antenna hardly preserved, only some funicular segments preserved. The anterior margin of clypeus is smooth. Head with distinct longitudinal striae. Alitrunk elongate, slender. Promesonotum dome-shaped, pronotum sculptured longitudinal rugose. Along the middle of the pronotum, there is a deep longitudinal groove, but it is not clear if this is a morphological or a taphonomical feature. Dorsal profile line of propodeum distinctly lower than arched promesonotum. Propodeal spines short, acute, triangular, widened at base. Petiole with distinct peduncle that gradually develops into a tapered rounded node. Although link between peduncle and propodeum is partly disarticulated and morphology gets unclear, a small projection at anteroventral part of peduncle is indicated. Postpetiole in profile with smoothly rounded node. Postpetioles node not as high as petioles node. Helcium articulates at more than half of posterior face of petiole. Gaster complete. First gastral segment far the longest of all gastral segments, reaches slightly more than half-length of gaster.

Measurements: Holotype NHMM-PE1995/8758-LS, BLw/oG: 4.25, HL: 1.34, HW: 1.24, ED: 0.19, GeL: 0.60, ML: 0.63, MML: 0.32, AL: 1.7, AH: 0.98, HiTL: 1.55, PL: 0.54, PH: 0.37, PPL: 0.34, PPH: 0.34, HeH: 0.22, G1L: 1.28, GL: 1.89. Indices: CI 92.31, IED/HL: 14.29, IHL/AL: 78.52.

Differential diagnosis: There are no fossil *Paraphaenogaster* nor *Aphaenogaster* worker from Oligocene known yet. The two *Aphaenogaster* species *A. maculate* (Theobald 1937) and *A. maculipes* (Theobald 1937), known from the late Oligocene, are gynes. Radchenko and Perkovsky (2016) informally allocated these species to the genus *Paraphaenogaster*. Since worker do not have wings, the main differentiating feature to allocate the genus is missing. So genus allocation is based on an assumption. For completeness and as a precaution, a comparison with all known *Aphaenogaster* workers is done herein. This species resembles *A. sommerfeldti* Mayr 1868 in its body contours. But sculpture of head differs. Head sculpture of *A. sommerfeldti* Mayr 1868 is described as fine wrinkled dots. *P. freihauti* shows distinct longitudinal striae at head. It clearly differs from *A. oligocenica* Wheeler 1915 and *A. mersa* Wheeler 1915 because their promesonotum is not raised. In addition, head and alitrunk sculpture differs in *A. mersa* and *P. freihauti*. *A. amphioceanica* De Andrade 1995 is characterised by an elongated head and neck which are missing

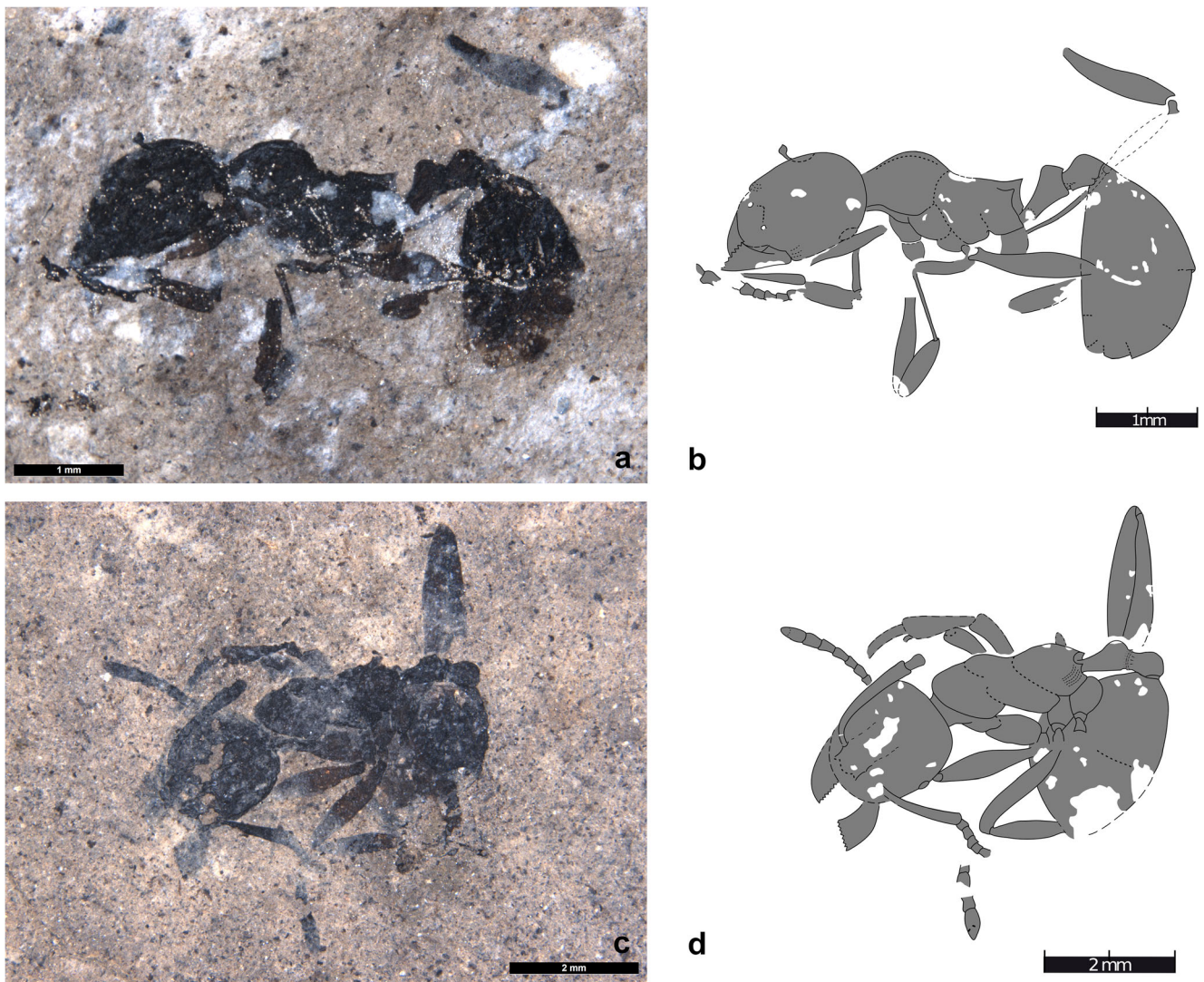


Fig. 6 *Paraphaenogaster freihauti* sp. nov., worker, holotype NHMM-PE1995/8758-LS. **a** Photograph, **b** Line drawing; *Paraphaenogaster wettauferi* sp. nov., worker, holotype NHMM-PE1995/5604-LS. **c** Photograph, **d** Line drawing

here. *A. dluskyana* Radchenko and Perkovsky 2016 is bearing elongate-triangular mandibles and long spines in contrast to *P. freihauti*. Also *A. praerelicta* De Andrade 1995 from the Mexican amber shows long propodeal spines. In *A. antiqua* (in Dlussky and Perkovsky 2002), propodeal spines are not widened at base, additionally, antennal segments 2–7 seem to be very short compared to those in *P. freihauti*.

Paraphaenogaster wettauferi sp. nov.
(Fig. 6c, d)

Etymology: Honouring Michaela Wettlaufer, Alsfeld (Germany), who treated conservatively most of the fossil insects from Lake Enspel.

Holotype: NHMM-PE1995/5604-LS, worker.

Position: Head dorsal, alitrunk dorsolateral, petiole, postpetiole from lateral, gaster from lateroventral.

Colour: Body black, well sclerotized; legs dark brown.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Diagnosis: BL about 8.18. Head slightly elongated, wider posteriorly than anteriorly. Occipital corners rounded. Head sides slightly convex. Eyes located above mid length of head. Eyes small, their diameter is about 8.4% of head length. Mandibles stout, triangular, with approximately eight small teeth, subequal in size. There is no clear evidence for a big apical tooth. Scape exceeds occipital margin of head. Scape bended at base. Funiculus most likely with 11 segments, 3–4 apical segments somehow larger, forming a weak club. Anterior margin of clypeus median smoothly convex.

Irregularities are interpreted as being caused by fossilization processes. Frontal lobes flat, weakly convex. Head sculptured with longitudinal rugae. Alitrunk elongate, slender. Pronotum and mesonotum clearly separated by promesonotal suture. Mesonotum convex in profile and higher than pronotum. Metanotal groove present. Short, relatively blunt spines project from the posterior face of the propodeum. Petiole with long peduncle and distinct node. Top of node irregularly coarsely sculptured. Posterior margin of the petiole is thickened. Postpetiole with elongate helcium and a distinctly rounded node. Nodes sculpture coarsely hammered/dotted. First gastral segment is the most sclerotized, and it is the longest.

Measurements: Holotype NHMM-PE1995/5604-LS, BLw/oG: 6.07, HL: 1.92, HW: 1.75, ED: 0.16, GeL: 0.71, ML: 0.97, MML: 0.69, SL: 1.4, AL: 2.39, AH: 0.96, MesoL: 0.72, HiTL: 1.64, PL: 0.63, PH: 0.44, PPL: 0.44, PPH: 0.43, HeH: 0.26, G1L: 1.64. Indices: CI: 90.76, SI: 80.21, IED/HL: 8.41, IHL/AL: 80.57.

Differential diagnosis: *P. wettlauferi* is distinguished from all other known fossil *Aphaenogaster* species by its very small eyes.

Ten males were examined more closely. All show the typical *Paraphaenogaster* wing venation pattern. Males show slight differences in shape and sculpture of head, pronotal neck, alitrunk, petiole and postpetiole. However, these differences are considered too small to exist as an independent species under consideration of possible taphonomic influences. Only one new species is described from this variety of conservation images.

Paraphaenogaster wuttkei sp. nov.

(Fig. 7a–c)

Etymology: Honouring Dr. Michael Wuttke, former head of the Section History of the Earth at the General Department of the Cultural Heritage of Rhineland Palatinate, Department Archaeology/Section History of the Earth, Mainz (Germany), who initiated and headed the scientific excavations through 26 years at the Fossil-Lagerstätte Enspel.

Holotype: NHMM-PE1997/5513-LS, winged male.

Position: Head: dorsal, alitrunk: dorsolateral, petiole: dorsolateral, gaster: dorsal.

Colour: Dark brown to black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL about 9.23. Head longer than wide, with smoothly rounded posterior corners. Mandibles subtriangular with six teeth. Last two apical teeth bigger than the others, which are of about the same size. Eyes are about 33.7% of head length. Eyes located laterally at about mid

length of head. It looks as if the compound eye is not only oval in shape, but also has a small anterior bulge. However, this impression may also have been caused by the compaction. Further specimens of this species would be needed to verify this morphological interpretation. Antenna with short scape and filiform funiculus, 12- or 13-segmented. Funicular segment 6 and 7 almost two times longer than wide. Funiculus about 3.3 times longer than scape. Anterior clypeal margin smooth and distinctly convex. Irregularities along the margin are interpreted to be due to taphonomic influences. Along and parallel to the anterior margin, there are a few long transverse striae. Posterior margin of clypeus projects backwards. The frontal triangle is structured with short, semicircularly arranged striae and forms a rosette-like pattern. Posterior part of the rosette is raised like a ridge with rounded top. Anteriorly to this ridge, semicircular concentric circles are arranged (Fig. 7c). Frontal lobes are hardly covering base of scape. Head striated, particularly at gena and at frontal carina. Posterolateral parts of head reticulated. Alitrunk large and arched as a whole. It is sculptured almost all over with fine and dense striae. Straight striae extend obliquely at lateral and posterior parts of scutum. The anterior part of scutum shows no distinct striae. The striation pattern could follow notauli. Anterior part of scutellum slightly protruding. Proscutellum distinct, slightly recessed. Propodeum longitudinally densely striated. There is no evidence for the existence of spines. Petiole with elongate stout peduncle, increasing height towards distal, rounded top posteriorly. Ventral part of peduncle expands anteriorly so alitrunk-petiole connection seems to be particularly wide and solid. This anterior ventral extension, however, could also have been caused by extreme flattening during the fossilization process. Postpetiole disarticulated from petiole and incomplete. Two longitudinal ridges can be identified on postpetiole's node. Forewing with closed cells: mcu and 1+2r. Pterostigma well developed. Cell mcu triangular. Wing venation pattern follows in all other aspects the description of the genus. Parts of first gastral segment preserved. Sculpture of first gastral tergite not specific, shiny.

Measurements: Holotype NHMM-PE1997/5513-LS; BLw/oG: 6.2, HL: 1.44, HW: 1.34, ED: 0.49, GeL: 0.29, ML: 0.66, MML: 0.29, AL: 3.15, ScuL: 1.27, ScutL: 0.44, HiTL: 2.64, FWL: 9.08, PL: 0.82, PH: 0.5, G1L: 1.53. Wing venation: 2M+Cu: 0.69, 1Cu: 0.84, 1M: 0.47, m-cu: 0.62, 1RS+M: 0.56, 2RS+M: 0.31. Indices: CI: 92.86, IED/HL: 33.67, IHL/AL: 45.75, Imcu: 66.67, I2RS+M/1RS+M: 55.26, I2RS+M/m-cu: 92.67, I2RS+M/2M+Cu: 44.68.

Differential diagnosis: *P. wuttkei* is characterised by its complex sculpture in the central part of the clypeus and the frontal triangle. With regard to combination with its body length (BLw/oG: 6.34) and its forewing length (FWL < 0.9), this species differs from the other *Paraphaenogaster* males described here. As it is not clear, if the remarkable wide anterior part of the petiole is natural or caused by taphonomic

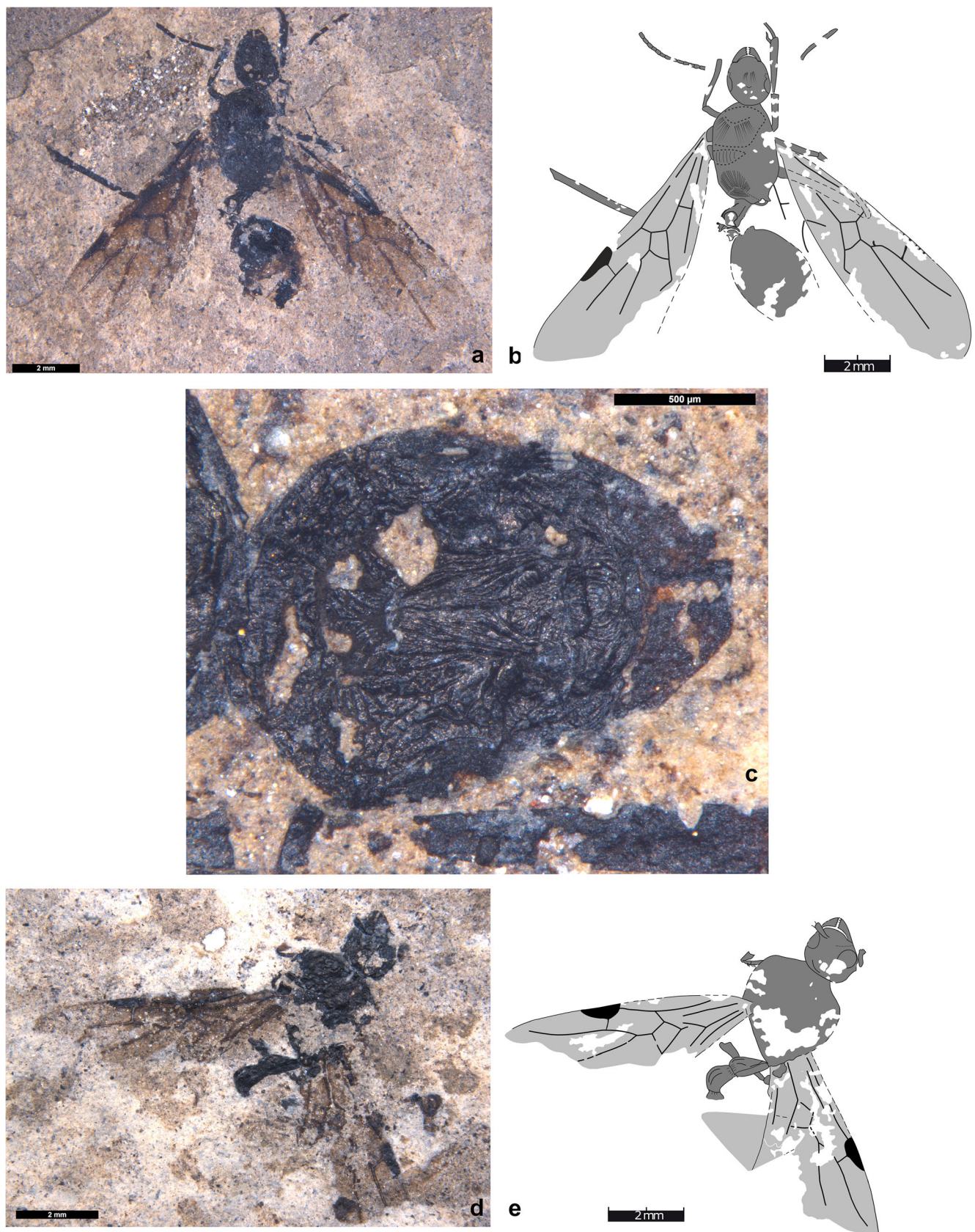


Fig. 7 *Paraphaenogaster wuttkei* sp. nov., male, holotype NHMM- PE1997/5513-LS. **a** Photograph. **b** Line drawing. **c** Detail: head; *Paraphaenogaster* cf. *wuttkei*, male, NHMM-PE1995/6227-LS. **d** Photograph. **e** Line drawing

processes, it will not be taken as a specific morphologic feature. Since the alitrunk is seen from dorsal, it is not clear if the pronotum is anteriorly extended into a neck-like shape.

Paraphaenogaster cf. *wuttkei*
(Fig. 7d, e)

Specimen: NHMM-PE1995/6227-LS, winged male.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Position: Head, alitrunk dorsal, petiole lateroventral; postpetiole dorsolateral, parts of alitrunk and complete gaster missing.

Colour: Dark brown to black.

Description: BL about 8.9 (estimated, because gaster is missing). Head slightly wider than long, with rounded posterior corners. Mandibles sub-triangular with 6–7 teeth at masticatory margin. First two apical teeth bigger than the others, slightly curved. Other 4–5 teeth decrease slightly in size towards basal angle of mandible, on right mandible; however, the third apical tooth is smaller than the following ones. Eyes big, oval, located below mid length of head. Eye diameter is about 40% of head length. Anterior clypeal margin smooth, convex. Posterior clypeal margin projecting backwards. Antennal sockets are close together. Between antennal sockets a transverse clypeal beal ascends. Additional sculpture of the median part of the clypeus seems to be complex; it is striated and sculptured but the exact pattern cannot be identified. Frontal lobes straight, just covering base of scape. Scape short and relatively wide, reducing width only at base. All preserved dorsal parts of head are striated, particularly strong at gena. Alitrunk strongly deformed, only parts of scutum, pronotum and propodeum are preserved. Preserved parts of scutum partly with fine dense striae. Preserved parts of propodeum are striated as well. Petiole pedunculate, the anterior face of petiole is continuously rising straight up ending in a node. Anterior part of petiole slightly widened (width about 0.22 mm). Ventral part of petiole flat, slightly concave. Almost complete posterior face of petiole is connected with helcium of postpetiole. Helcium shows thick longitudinal striae. Postpetiole elongate, flat node with rounded top. Postpetiole shorter, but slightly higher than petiole. Petiole and postpetiole are longitudinally striated, petiole also shows laterally oblique ridges. Postpetiole's top notched longitudinally, with thickened ridges on both sides. Forewing with closed cells: mcu and 1+2r. Cell 3r open. Pterostigma well developed. Wing venation pattern follows in all other aspects the description of the genus. Gaster almost completely missing. Preserved parts of the presclerite of the 4th abdominal

tergite show radially arranged ridges. These integumentary foldings, so called “pillars”, are interpreted as being associated with the stridulation organ.

Measurements: NHMM-PE1995/6227-LS; BLw/oG: 5.76, HL: 1.25, HW: 1.27 (head flattened), ED: 0.5, GeL: 0.24, ML: 0.60, MML: 0.29, SL: 0.59, AL: 2.67, FWL: 8.46, PL: 0.88, PH: 0.51 PPL: 0.66, PPH: 0.54 (positioned dorsolateral, measured as seen); HeH: 0.37. Wing venation: 2M+Cu: 0.69, 1Cu: 0.59, 1M: 0.41, m-cu: 0.50, 1RS+M: 0.29, 2RS+M: 0.46. Indices: CI: 101.18, IED/HL: 40.0, IHL/AL: 46.89, Imcu: 50.0, I2RS+M/1RS+M: 155.0, I2RS+M/m-cu: 95.62, I2RS+M/2M+Cu: 65.96. The following male specimens also belong to the genus *Paraphaenogaster*, but do not have sufficiently distinct characteristics to warrant the designation of a new species.

Paraphaenogaster incertae sedis
(Fig. 8a)

Specimen: NHMM-PE2001/5194-LS, male.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S12.

Position: Head ventral, alitrunk lateral, petiole dorsolateral, postpetiole dorsal, disarticulated, gaster partly missing.

Colour: black.

Description: BL about 8.65. Head wider than long, to both sides from ventral midline distinct longitudinal striae are running from median anterior part of the head to its lateroposterior parts. Eyes large and oval. Head and alitrunk slightly elongated forming a neck. Alitrunk large, strongly arched, scutum with distinct fine dense striae. Scutellum slightly convex. Propodeum steeply descending and densely striated. Petiole and postpetiole elongate, both without a distinct node. Postpetiole not narrowed at helcium. Petiole with long regular fine striae, postpetiole irregularly striated, rugose. Densely arranged integument foldings on presclerite of first gastral tergite, so called “pillars” preserved. First gastral tergite shiny.

Measurements: NHMM-PE2001/5194-LS; BLw/oG: 5.52 (including THL, instead of HL and MML), HL: 1.06, HW: 1.0 (est.), ED: 0.35; AL: 2.76, FWL: 6.13, ScuL: 1.49, ScutL: 0.37, PL: 0.78, PH: 0.32, PPL: 0.63, PPH: 0.40, HeH: 0.31, Wing venation: 1M: 0.38, 1Cu: 0.69, m-cu: 0.49, 1RS+M: 0.35, 2RS+M: 0.35. Indices: CI: 94.44, IED/HL: 33.33, IHL/AL: 38.41, Imcu: 51.06, I2RS+M/1RS+M: 100.0, I2RS+M/m-cu: 83.85.

Remarks: This specimen is characterised by its indication of a pronotal neck. It differs from *P. wuttkei* in BLw/oG (5.5 vs. 6.2 in *P. wuttkei*) and FWL (6.1 vs. 9.1 in *P. wuttkei*). The strong parallel striation on the petiole has this specimen in common with the sample NHMM-PE2001/5160-LS. The latter, however, does not show any indication of a neck.

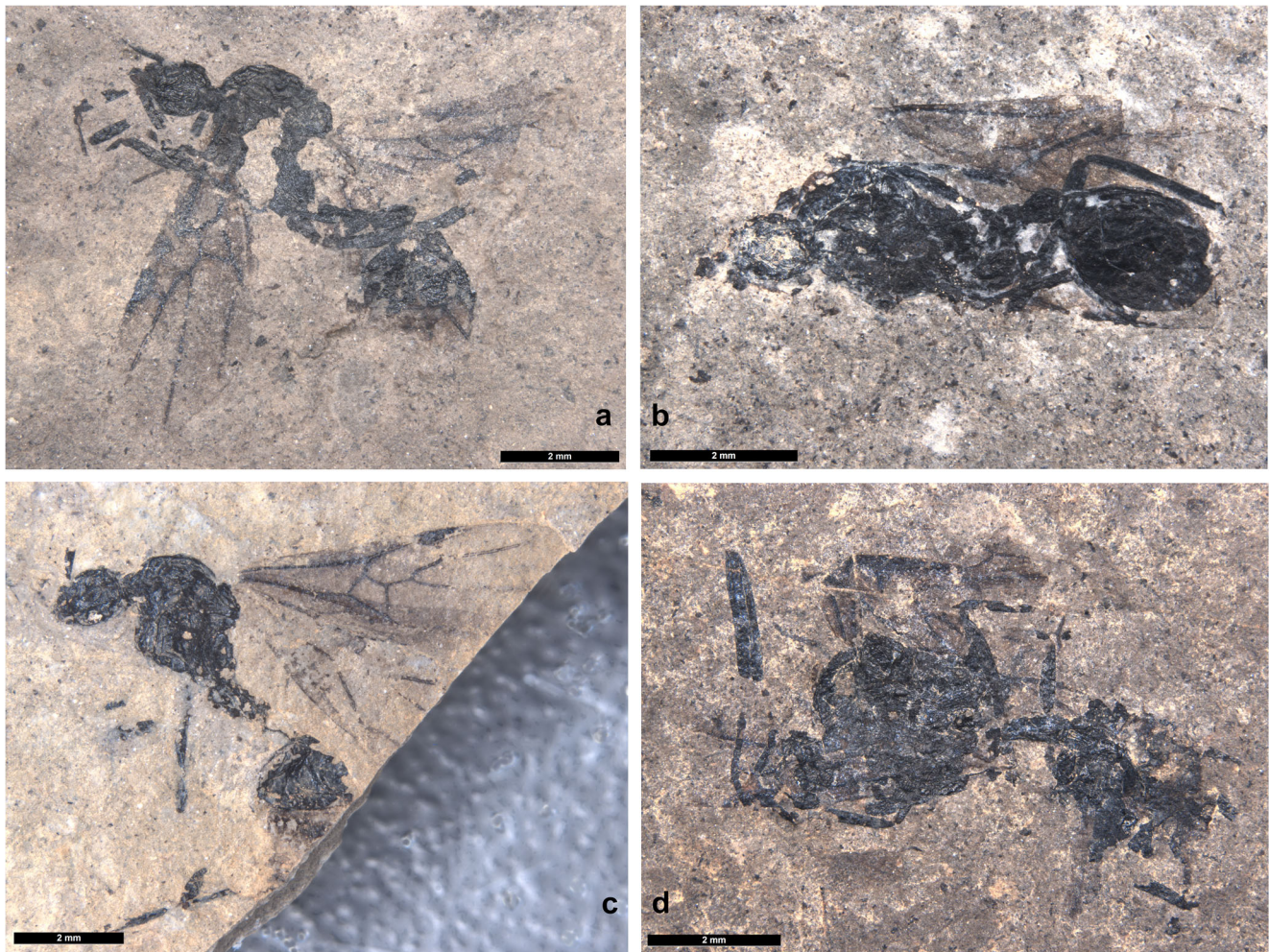


Fig. 8 *Paraphaenogaster incertae sedis*, male, NHMM- PE2001/5194-LS. **a** Photograph; *Paraphaenogaster incertae sedis*, male, NHMM-PE2010/5697-LS. **b** Photograph; *Paraphaenogaster incertae sedis*, male,

NHMM- PE2010/5576-LS. **c** Photograph, detail: head, alitrunk, see Supplementary Data 2: Fig. 1; *Paraphaenogaster incertae sedis*, male, NHMM-PE2001/5160-LS. **d** Photograph

Paraphaenogaster incertae sedis
(Fig. 8b)

Specimen: NHMM-PE2010/5697-LS, male.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Position: Head ventral, alitrunk lateroventral, petiole lateral, gaster dorsal.

Colour: Black.

Description: BL about 7.79. Head longer than wide, without distinct occipital corners. Long striae starting from ventral midline heading posteriorly towards occiput. Sharp corners at the posterior part of head are being interpreted as fractures. Comparatively small eyes. Alitrunk well developed, mesonotum arched. Propodeum smoothly descending. All visible parts of alitrunk are

striated, scutum shows very fine striae. Petiole's peduncle stout, smoothly ascending towards distal, node with rounded top. Anterior part of petiole hidden; its length can therefore only be estimated. Petiole and postpetiole show dense fine longitudinally striae. Helcium narrowed, showing a distinct constriction between petiole and postpetiole. Postpetiole slightly nodiform, without a distinct dorsal notch. Gastral tergites with unspecific sculpture, not shiny. Either two or three gastral tergites are preserved. It is not clear, because the posterior margins of the tergites are not sharp. The presclerite of the 4th abdominal tergite shows a semicircled structure with radially arranged ridges. This structure, named "pillars", is part of the stridulation organ. Semicircle's diameter is 0.32 mm.

Measurements: NHMM-PE2010/5697-LS; BLw/oG: 5.05 (including THL, instead of HL and MML), HL: 1.10, HW: 0.9,

ED: 0.38, AL: 2.51, FWL: 5.73, PL: 0.69, PH: 0.41, PPL: 0.47, PPH: 0.46, HeH: 0.26. Wing venation: 2M+Cu: 0.53, 1Cu: 0.56, 1M: 0.31, m-cu: 0.38, 1RS+M: 0.24, 2RS+M: 0.40. Indices: CI: 81.33, IED/HL: 34.67, IHL/AL: 43.87, Imcu: 42.11, I2RS+M/1RS+M: 168.75, I2RS+M/m-cu: 77.97, I2RS+M/2M+Cu: 75.0.

Remarks: The specimen NHMM-PE2010/5697-LS is characterised by its comparably nodiform postpetiole with a narrowed helcium. Postpetiole constricted towards gaster. Both petioles with fine dense striae. Postpetiole without dorsal notch. In addition, size and forewing length is comparably small (BLw/oG: 5.05, FWL: 5.7).

Paraphaenogaster incertae sedis
(Fig. 8c)

Specimen: NHMM-PE2010/5576-LS, male (photograph, see Supplementary Data 2: Fig. 1)

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S14 u.

Position: Head dorsal, alitrunk lateral, petiole lateroventral, only remnants of the postpetiole are preserved, only first gastral segment and the second gaster sternite are preserved.

Colour: Black, appears shiny.

Description: BL about 8.58. Head oval, with occipital corners. Head sculptured with medium dense striae. Eyes large and oval. Three ocelli preserved. Anterior margin of clypeus smooth. Frontoclypeal suture is projecting backwards between antennal sockets. Mandibles large, triangular, number of teeth unclear. The pronotum appears slightly stretched forward, but there are no clear signs of a pronotal neck. Alitrunk large, high, strongly arched, scutum with distinct fine dense striae, scutellum is not protruding. The propodeum is steeply sloping; its central dorsal part has dense, fine striae in the longitudinal direction, while they are arranged transversely at the rear of the propodeum. Petiole with long peduncle, increasing height posteriorly, no distinct node. Wing venation with closed cells m-cu and 1+2r, cell 3r open. Wing venation pattern follows in all other aspects the description of the genus. Alitrunk-petiole connection is wide and solid. Postpetiole unclear. First gastral segment shiny, not much longer than the second gastral segment.

Measurements: NHMM-PE2010/5576-LS; BLw/oG: 5.7 (including THL, instead of HL and MML), HL: 1.18, HW: 1.24*, ED: 0.44, AL: 2.73, AH: 1.93, ScuL: 1.44, ScutL: 0.6, FWL: 6.27, PL: 0.94, PH: 0.44, GIL: 1.43. Wing venation: 2M+Cu: 0.56, 1Cu: 0.75, 1M: 0.41, m-cu: 0.53, 1RS + M: 0.43, 2RS + M: 0.46. Indices: CI: 105.0, IED/HL: 37.5, IHL/AL: 43.15, Imcu: 56.86, I2RS+M/1RS+M: 106.9, I2RS+M/m-cu: 98.56, I2RS+M/2M+Cu: 81.58.

Remarks: In this specimen, the pronotum seems to be stretched forward so that it gets a neck-shaped impression, but no distinct pronotal neck seems to be developed. The head is also not extended to the back.

Paraphaenogaster incertae sedis
(Fig. 8d)

Specimen: NHMM-PE2001/5160-LS, male.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S12.

Position: Head dorsal, alitrunk lateral, petiole and postpetiole dorsolateral, gaster strongly damaged, wings only partly preserved.

Colour: Black.

Description: BL about 7.76. Head shaped triangular, wider than long. Eyes large and oval. There is no clear indication for a neck. Alitrunk high and large. Scutum strongly arched. Scutellum not protruding. Propodeum with moderate slope. No spines. Each preserved part of alitrunk with fine striae. Wings only partly preserved. However, veins 2RS+M, 2-3RS and 3M can be clearly identified and show the proportions typical for *Paraphaenogaster*. Cell rm is not present. Petiole elongate, flat node. Anterior part of petiole not widened. Posterior margins of petiole and postpetiole seem to be thickened. Postpetiole broadly connected with petiole, only weak constriction at helcium. Postpetiole shorter than petiole, slightly increasing height towards distal. Petiole and postpetiole with strongly pronounced regular striae. Postpetiole's top with an indication of two ridges. At anterior margin of first gastral tergite so called "pillar" preserved.

Measurements: NHMM-PE2001/5160-LS; BLw/oG: 5.03(including THL, instead of HL and MML), HW: 1.15, AL: 2, 58, AH: 1.67, ScuL: 1.22, PL: 0.87, PH: 0.47, PPL: 0.47, PPH: 0.51, HeH: 0.37.

Remarks: This specimen differs from all other *Paraphaenogaster* males by a combination of its slender petiole, which ends posteriorly in a flat node, the barely constricted helcium, the strong regular striation and the thickened posterior margins of both petioles.

Paraphaenogaster incertae sedis

Specimen: NHMM-PE1995/7286-LS, male; (photograph, see Supplementary Data 2: Fig. 2).

Position: Body parts are preserved in different positions: head lateroventral, alitrunk lateral (deformed), petiole and postpetiole lateroventral, gaster dorsal.

Colour: Dark brown to black.

Description: BL estimated 8.75. Alitrunk with steep descending propodeum. No spines. All visible parts of alitrunk show medium fine striae. There is no indication for a neck.

Measurements: NHMM-PE1995/7286-LS; BLw/oG: 5.7 (including THL, instead of HL and MML), HL: 1.16, HW: 1.18 (head deformed, measured as seen), ED: 0.43, AL: 2.82, FWL: 7.0, PL: 0.88, PH: 0.53, PPL: 0.54, PPH: 0.53, HeH: 0.38. Wing venation: 2M+Cu: 0.82, 1Cu: 0.76, 1M: 0.43, m-cu: 0.53, 1RS+M: 0.46; 2RS+M: 0.47. Indices: CI: 101.3, IED/HL: 36.71, IHL/AL: 41.24, Imcu: 59.62, I2RS+M/1RS+M: 103.23, I2RS+M/m-cu: 100.03, I2RS+M/2M+Cu: 57.14.

Remarks: Petiole and postpetiole of this specimen are similar to those of the sample NHMM-PE1995/6227-LS. Clypeus and frontal triangle unfortunately cannot be seen.

Paraphaenogaster incertae sedis

Specimen: NHMM-PE1997/6133-LS, winged male (photograph, see Supplementary Data 2: Fig. 3).

Position: Head missing, alitrunk lateral, petiole and postpetiole dorsolateral, gaster lateral.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: Alitrunk well developed, strongly arched. Steep descending propodeum. Well-developed mesopleura. All visible parts of alitrunk show fine striae. Anterior part of petiole missing; its length therefore can only be estimated. Postpetiole elongate. Helcium disarticulated from petiole. Helcium not narrowed. Therefore, there is no distinct constriction between petiole and postpetiole as it can be seen in NHMM-PE1995/6227-LS or even better in NHMM-PE2001/5160-LS. Petioles are not regularly striated. Petioles and postpetioles dorsal depressions and their lateral ridges are well preserved. Wing venation with closed cell m-cu and 1+2r. Cell 3r open. Only vein 3M is showing a distinct lumen, vein 4M appears without. Postpetiole seems to be posteriorly extended and overlapping the presclerite of first gastral tergite. This extension is most likely part of the stridulation organ. “Pillars” are partly covered by the extension (for more information, see chapter *Terminology*). Sculpture of first gastral tergite is unspecific, but shiny.

Measurements: NHMM-PE1997/6133-LS; AL: 3.09, AH: 2.46, PL: 0.99, PH: 0.49, PPL: 0.51, PPH: 0.43, HeH: 0.37. Wing venation: 2M+Cu: 0.78, 1M: 0.37, 1RS+M: 0.32; 2RS+M: 0.31. Indices: I2RS+M/1RS+M: 95.45, I2RS+M/2M+Cu: 39.62.

Paraphaenogaster incertae sedis

Specimen: NHMM-PE2001/5139-LS, male (photograph, see Supplementary Data 2: Fig. 4)

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S12.

Positions: BL about 7.89. Head dorsolateral, alitrunk lateral, petiole and postpetiole lateral, gaster dorsal.

Colour: Black, partly pyritized.

Description: Alitrunk appears massiv, including propodeum. All visible parts of alitrunk show medium fine striae. Anterior part of petiole not preserved. However, petiole seems to be pedunculate, posterior part of petiole with rounded top, no pronounced node. Postpetiole slightly nodiform, its rounded top has a notch.

Measurements: NHMM-PE2001/5139-LS; BLw/oG: 5.73 (including THL, instead of HL and MML), HL: 1.21, HW: 1.03 (est.), ED: 0.44, AL: 2.70, AH: 2.21, FWL: 7.33, ScuL: 1.55, ScutL: 0.60, PL: 0.88, PH: 0.47, PPL: 0.68. Wing venation: 2M+Cu: 0.74, 1Cu: 0.60, 1M: 0.41, m-cu: 0.44, 1RS+M: 0.37, 2RS+M: 0.37. Indices: IED/HL: 36.59, IHL/AL: 44.73, Imcu: 60.98, I2RS+M/1RS+M: 100.0, I2RS+M/m-cu: 80.91, I2RS+M/2M+Cu: 50.0.

Paraphaenogaster incertae sedis

Specimen: NHMM-PE1995/9490-LS, male (photograph, see Supplementary Data 2: Fig. 5)

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S12.

Position: Head ventral, alitrunk dorsolateral, petiole and postpetiole missing, gaster partly missing. **Colour:** Black.

Description: Head oval, no distinct occipital corners. To both sides from ventral midline distinct longitudinal striae are running in a slightly curved way from median anterior part of the head to its lateroposterior parts. Eyes large and oval. Alitrunk large, sculptured with medium fine striae all over. Mesonotum arched, scutum projecting. Propodeum long, descending moderate, dorsally sculptured with dense transvers striae. Only first gastral tergite partly preserved. Its sculpture is unspecific, not shiny.

Measurements: NHMM-PE1995/9490-LS; HW: 1.18, ED: 0.44, AL: 2.88, AH: 2.21, FWL: 6.88, ScuL: 1.38. Wing venation: 2M + Cu: 0.65, 1Cu: 0.65, 1M: 0.38, m-cu: 0.43, 1RS+M: 0.37, 2RS+M: 0.44. Indices: Imcu: 56.82, I2RS+M/1RS+M: 120.0, I2RS+M/m-cu: 86.79, I2RS+M/2M+Cu: 68.18.

Genus *Aphaenogaster* Mayr, 1853

Type species: *Aphaenogaster sardoa* Mayr, 1853

Diagnosis: Gyne. BL 7–12. Head longer than wide. Teeth are all about the same size, apical tooth can be slightly bigger. Alitrunk high and arched. Propodeal spines present. Wing venation with closed cells m-cu, 1+2r, and a distinct cell rm.

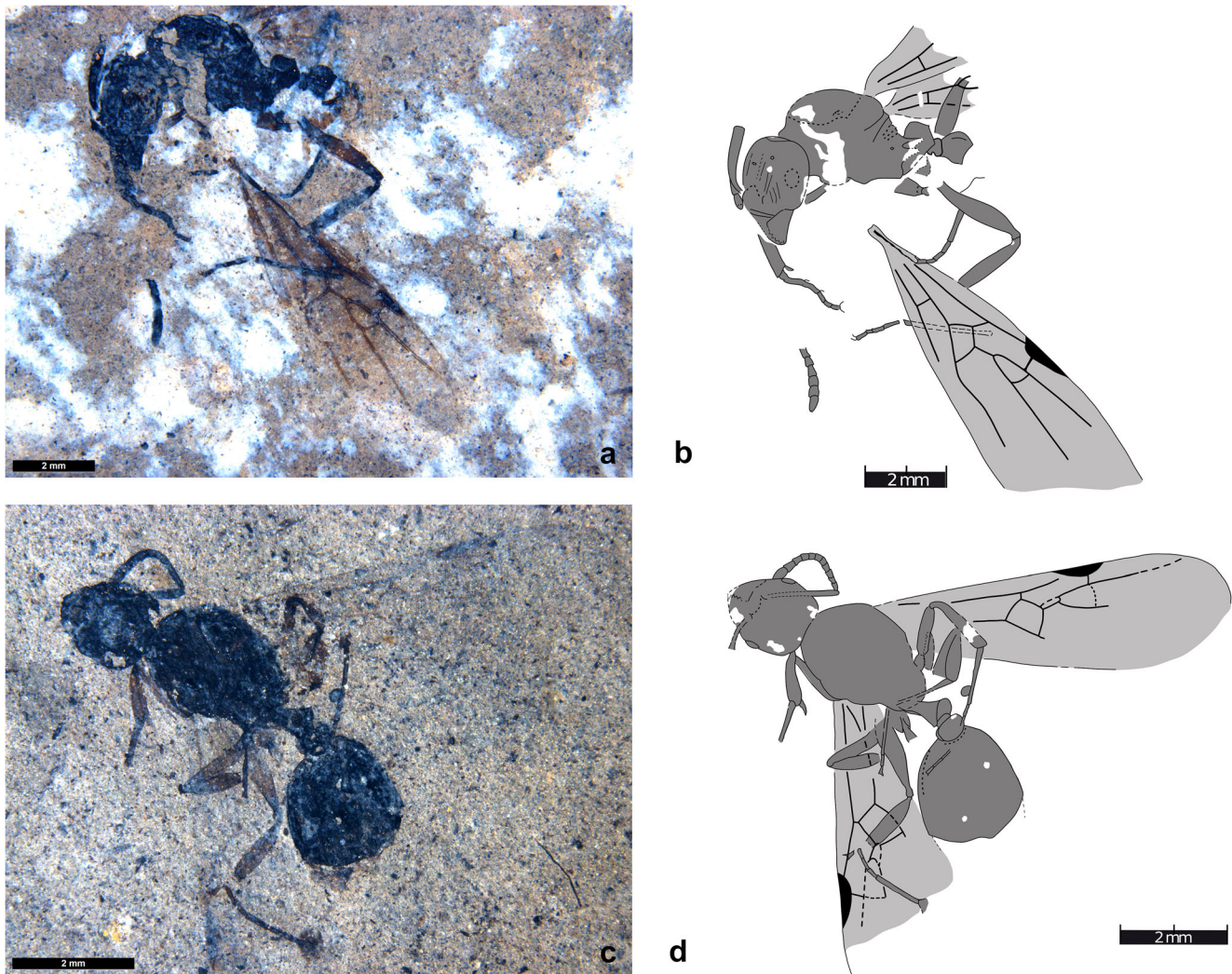


Fig. 9 *Aphaenogaster enspelensis* sp. nov., gyne, holotype NHMM-PE1997/5555-LS. **a** Photograph, **b** Line drawing, detail: head, alitrunk, petiole, and postpetiole, see Supplementary Data 3: Fig. 1.; *Goniomma*

poschmanni sp. nov., gyne, holotype NHMM-PE2009/6281-LS. **c** Photograph, **d** Line drawing, detail: head with antenna, see Supplementary Data 3: Fig. 2

Vein 2r-rs short. Vein 5RS is in reduction. At its distal end, sclerotization becomes extremely weak. It is a matter of interpretation, if cell 3r is seen as open or closed. The distal section of vein M does not branch off from vein RS near the junction 2r-rs/RS, but much further proximal. Thus, the free distal ends of M and RS do not branch off from a common node. With the exception of a well-developed cell rm, the venation pattern is similar to the one described for the morphogenus *Paraphaenogaster* (Radchenko and Perkovsky 2016; Perfilieva et al. 2017). Vein M3 and the proximal part of vein M4 show an intervening lumen; it is lacking in the distal part of M4. The latter part seems to be just a stronger sclerotized line to possibly improve the wings stability, without having any supply function. This also applies for the distal part of vein Cu. Petiole pedunculate with distinct node. Postpetiole shorter than petiole.

Remarks: The fact that in *Aphaenogaster* the proximal part of the vein section M4 is also equipped with a pronounced lumen shows that the lumen is developed according to functional needs. The presence or absence of a lumen does not necessarily correspond to the vein sections M3 and M4.

Aphaenogaster enspelensis sp. nov.
(Fig. 9a, b)

Etymology: Named after the village Enspel in the Westerwald Mountains (Rhineland-Palatinate, Germany), territory of the Lake Enspel Fossil-Lagerstätte.

Holotype: NHMM-PE1997/5555-LS, winged gyne.

Position: Head, alitrunk from dorsolateral, petiole and postpetiole from anterolateral. Gaster missing.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S14.

Description: Gyne. BL about 11.32. Head longer than wide, with distinct, rounded occipital corners. Posterior margin of head is indicating a median depression. Clypeus slightly convex in profile. Median part of clypeus with longitudinal striae, anterior clypeus margin here smooth. Eyes located slightly below mid length of head. Mandibles strongly developed, sub-triangular. Apex of left mandible missing. Due to compaction masticatory margin is bended downwards, only three triangle-shaped teeth can be identified. Based on estimation, there should be more than six triangular-shaped teeth. Shape and size of apical tooth is not clear either. Scape slightly surpasses head posteriorly. Head sculpture with wide coarse striae, visible at frons, at clypeus, between antennal sockets and eyes, and at gena. Alitrunk robust, high, arched. Metanotum well developed. Propodeal spines stout with broad base. Gradually descending posterior face of propodeum transversely striated. Scutum and scutellum sculptured rugosely. Tibial spurs on foreleg brushed or combed. At first and second tarsal, segment of protarsus bristles preserved. Wing venation with closed cells mcu, 1+2r and rm. Shape of cell mcu is trapezoid. The vein rs-m does not appear as a direct vertical extension of vein 2r-rs, but branches distally slightly offset from the vein RS. The results is a very short vein 4RS (see Fig. 65 in Dlussky and Perfilieva 2014, and Fig. 1a in Perfilieva et al. 2017). In all other aspects, the description of the wing venation of the genus applies. Petiole stout with round bar-like peduncle and high distinct node. Petiole's position is not clear; the node might have been twisted. Anterior face of node steep, tapered and rounded at top. Top of node with longitudinal respectively transverse grooves, depending whether the petiole has been twisted or not. Posterior face of node less steep. Peduncle broadly connected with alitrunk. Postpetiole disarticulated from petiole. Helcium almost round in cross section, its anterior margin is thickened, ventrally with a little invers notch. Node of postpetiole round, domeshaped, not tapered, slightly constricted towards gaster.

Measurements: Holotype NHMM-PE1997/5555-LS: BLw/oG: 7.50, HL: 1.98, HW*: 1.82, ED: 0.54, GeL: 0.51, ML: 1.07, MML: 0.75, SL: 1.84, AL: 3.36, AH: 2.42, FWL: 9.15, ScuL: 2.05, ScutL: 0.64, HiTL: 2.11, PH: 0.87, PPL: 0.46 (excl. helcium), PPH: 0.78, HeH: 0.44. Wing venation: 2M-Cu: 0.84, 1Cu: 0.84, 1M: 0.47, m-cu: 0.57, 1RS+M: 0.47, RS+M: 0.51. Indices: CI: 92.0, SI: 101.0, IED/HL: 27.52, IHL/AL: 58.87, Imcu: 56.14, I2RS+M/1RS+M: 109.38, I2RS+M/m-cu: 108.85, I2RS+M/2M+Cu: 61.40. (Because of perspective shift, no measurement is given for PL; it has only been estimated for calculating BL).

Differential diagnosis: *A. enspelensis* is the only *Aphaenogaster* species deriving from Oligocene deposits.

All other *Aphaenogaster* reproductives found in Oligocene deposits, like *A. maculate*, *A. maculipes* and *A. archaica* have been informally allocated to the genus *Paraphaenogaster* (Radchenko and Perkovsky 2016). None of these three species were found to have propodeal spines. Gyne of the species *A. mayri* and *A. donisthorpei* found in Eocene sediments in Florissant are smaller; their BL is only 7–8 mm (Carpenter 1930). In *A. mayri*, short but distinct spines are reported; in *A. donisthorpei*, they were not seen. Thus, gynes of *A. enspelensis* are characterised by the combination of broad-based, large propodal spines and a body length of more than 11 mm.

Genus: *Goniomma* Emery, 1895

Type species: *Goniomma collingwoodi*

Diagnosis: For fossil *Goniomma* only: Gyne. Description: BL 7–8 mm. Head wider than long, it becomes narrower towards the front. Antenna 12-segmented with weak 4-segmented club. Scape hardly bended at base, clearly extending occipital margin. Mandibles triangular, with 6–7 triangular-shaped teeth. Apical tooth bigger and curved. Eyes located below heads mid length. Anterior clypeal margin fairly straight; it shows no distinct convex line. Alitrunk large, wide and arched. Propodeal spines unclear. Wing venation with closed cell mcu, and 1+2r. Cell mcu barely trapezoid, almost square. Vein 1RS remarkably short. Veins rs-m, 2RS+M, 2-3RS and 5RS and 3M are thin and weakly sclerotized. Therefore cell rm is strongly reduced. Sclerotization of veins in general weak. Legs brown. Body darker than legs. Petioles anterior face is continuously ascending, posteriorly it is steeply descending. Top of petiolar node is not rounded. Helcium low, postpetiole wide, only slightly constricted towards gaster. First gastral tergite distinctly longer than the others.

Differential diagnosis: Fossil *Goniomma* species are not known yet. Extant *Goniomma* gyne are smaller, BL about 4–5 mm (Espadaler 1986), and their funiculus is significantly shorter, not extending the occipital margin of head. The fossil specimens have not been assigned to the genera *Aphaenogaster* or *Paraphaenogaster* because of their combination of a CI well over 100, their wing venation pattern, their weak veining and their unarmed (most likely) or slightly armed propodeum. They are not assigned to the genus *Messor*, since the head in this genus narrows towards the front (clearly visible in the paratype). In most extant *Messor* species, the head width is not reduced towards the front. In addition, the outer margins of the mandibles are not strongly curved—as it is typical for extant *Messor* species.

Goniomma poschmanni sp. nov.
(Fig. 9c, d)

Ethymology: Honouring Markus Poschmann, Koblenz,

specialist in the discovery, study and publication of fossil arthropods, and supervisor at the scientific excavations in the oil shale of Lake Ensipel.

Holotype: NHMM-PE2009/6281-LS, winged gyne.

Position: Head from dorsal, alitrunk, petiole, postpetiole and first gastral segment from dorsolateral.

Colour: Body dark brown-black, legs brown.

Type locality and horizon: Ensipel Oilshale, Rhineland-Palatinate, Germany. Ensipel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL about 7.37. Head clearly wider than long, with rounded occipital corners. Head tapers towards the front. Head length just reaches half length of alitrunk. Eyes are clearly located below mid length of head. Lateroventrally drawn out eyes cannot be stated. Anterior margin of clypeus smooth, slightly convex. Mandibles triangular equipped with 6–7 well-developed triangular teeth, slightly increasing in size towards apex. Marks in the sediment indicate an apical tooth which is bigger than the others and slightly curved. Antenna 12-segmented, funicular segments gradually increasing in size

toward the apex. Scape distinctly protrudes beyond the occipital margin of head. Scape hardly bended at base; it looks even straight. Frontal lobes do not cover antennal condyle. Frons wide, with longitudinal striae. Alitrunk high, wide and arched. Sculpture and sutures of alitrunk not well preserved or not strongly developed. There are no indications for distinct propodeal spines. However, blunt short teeth cannot be clearly excluded because propodeum is covered by tarsi. Sclerotization of wing venation seems to be weak primarily. Cell m_{cu} is slightly trapezoidal in shape. Veins 4M, 2Cu and 3Cu are strongly reduced respectively not well preserved. Another vein is running parallel to vein 2RS+M. It is not clear if this vein is definitely belonging to the same forewing. In all other aspects, description of the wing venation of the genus applies. Legs medium brown, they are less sclerotized or coloured. They appear almost transparent. Petiole is continuously ascending, at its highest point it shows an acute transverse ridge, top is not rounded. Descending face of petiole steep. Postpetiole wider than long, with rounded top. Helcium articulates slightly below its mid length. First gastral

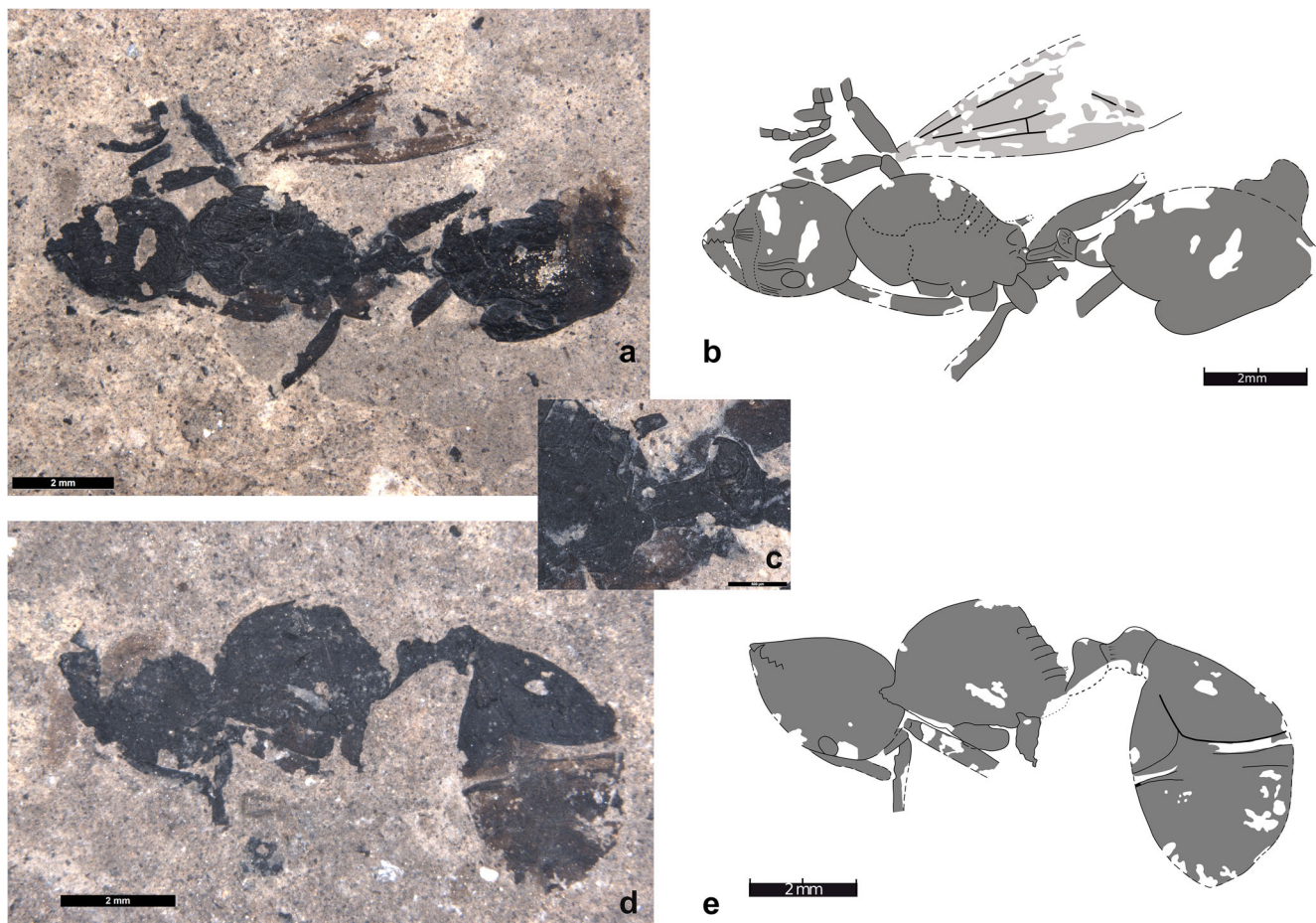


Fig. 10 *Stenammini incertae sedis*, gyne, NHMM- PE2010/5496-LS. **a** Photograph. **b** Line drawing. **c** Detail: petiole, also Supplementary Data 3: Fig. 4. *Stenammini incertae sedis*, gyne, NHMM-PE1995/9611-LS. **d**

Photograph. **e** Line drawing, detail: propodeum, petiole, and postpetiole, see also Supplementary Data 3: Fig. 5

tergite distinctly larger than the others, with homogenous and slightly rugose surface sculpturing. Its presclerite shows integumentary foldings arranged in a semicircle. These so-called pillars are most likely part of the stridulation organ.

Measurements: Holotype NHMM-PE2009/6281-LS; BLw/oG: 5.07, HL: 1.21, HW: 1.44, ED: 0.35, GeL: 0.29, ML: 0.66, MML: 0.41, SL: 1.4, AL: 2.32, AW: 1.62 (est.), HiTL: 1.13, FWL: 6.67, PL: 0.79, PH: 0.57, PPL: 0.34, PPW: 0.6, HeW: 0.23, G1L: 1.86, G1W: 1.89. Wing venation: 2M+Cu: 0.59, 1Cu: 0.66, 1M: 0.47, m-cu: 0.51, 1RS+M: 0.46, 2RS+M: 0.26. Indices: CI: 119.51, SI: 96.94, IED/HL: 29.27, IHL/AL: 52.03, Imcu: 68.89, I2RS+M/1RS+M: 58.06, I2RS+M/m-cu: 77.96, I2RS+M/2M+Cu: 45.0.

Paratype: NHMM-PE2005/5162-LS (photograph, see Supplementary Data 3: Fig. 3)

Position: All preserved body parts from dorsal.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S14.

Description paratype: BL about 7.65. General habitus like holotype. Mandibles triangular, apical tooth here well preserved; it is longer than the others and curved. Eyes located below mid length of head. Seen from dorsal anterior half of alitrunk wide, narrows posteriorly. Legs also brown and less sclerotized than body, appearing transparent. Tibial spines at hind leg not combed. There is no distinct sculpture identifiable, sutures on alitrunk weak as in holotype. Wing venation very similar to holotype. Vein 2Cu is preserved, vein 3Cu very thin and weak. There is no clear indication for an armed propodeum.

Measurements paratype: NHMM-PE2005/5162-LS; BLw/oG: 5.02, HL: 1.21, HW: 1.43, ED: 0.35, GeL: 0.29, ML: 0.69, MML: 0.41, AL: 2.05, AW: 1.64, HiTL: 1.25, FWL: 7.40, PPL: 0.51, PPW: 0.59, G1L: 1.82, G1W: 2.07. Wing venation: 2M+Cu: 0.69, 1Cu: 0.69, 1M: 0.50, m-cu: 0.50, 1RS+M: 0.46, 2RS+M: 0.34. Indices: CI: 118.3, IED/HL: 29.27, IHL/AL: 58.96, Imcu: 65.96, I2RS+M/1RS+M: 74.19, I2RS+M/m-cu: 83.85, I2RS+M/2M+Cu: 48, 94.

Stenammini incertae sedis
(Fig. 10a–c)

Specimen: NHMM-PE2010/5496-LS, winged gyne.

Position: Head, alitrunk, petiole, postpetiole (partly), gaster (partly) dorsolateral.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S12.

Description: BL about 12.17. Head is slightly deformed. It appears longer than wide, oval shaped, with convex sides and

flattened occipital corners. Anterior clypeus margin with some fracture edges, also exactly at the middle part. This could be misinterpreted as a primarily concave indentation. Additional little spikes visible at left anterior clypeus margin are valued as subsequent damaging; they are missing on the right side. Five to six distinct longitudinal striae at median part of clypeus, lateral parts of clypeus strongly developed, slightly uplifted, they do not show any specific sculpture. At gena, lateral anterior margin of clypeus thickened. Frontal carinae reaching back to about anterior margin of eyes. Frons, antennal sockets and gena sculptured with wide striae, whereas posterior parts of head and occiput are reticulated. Frons fairly wide. Mandibles triangular. Masticatory margin with about eight triangular-shaped teeth, most of them about of the same size. Apical tooth slightly bigger. Eyes located at about midlength of head. Scape reaches posterior margin of head. Alitrunk high, arched, scutum and scutellum strongly developed, propodeal declivity fairly moderate. Scutellum transversely oval shaped with rounded curves laterally, not striated. Scutellum strongly sclerotized and slightly protruding from alitrunk. Propodeum armed with stout spines. Propodeal lobes, round and well developed. Suture between pronotum and episternum very distinct. Scutum and pronotum is irregularly longitudinally sculptured, not distinctly striated. Scutellum and metanotum strongly sculptured but not striated. Scutellum does not tapering laterally to a point. Anterior margin of scutellum thickened. Propodeum transversally striated, striation continues vertically on metasternum. Mesosternum hardly sculptured. Petiole with long, bar-like peduncle and a distinct high node. Node with steep ascending anterior face and steep descending posterior face (see Fig. 10c). Peduncle with longitudinal unspecific sculpture, dorsally with distinct suture in the middle. Top of node rugose. Node and peduncle clearly separated by triangular-shaped suture, as it also can be seen in *Paraphaenogaster loosi*. Helcium articulates very deep at posterior face of petiole. Postpetiole only partly preserved, most likely with moderately ascending, medium high node (based on photograph). One forewing purely preserved. Only veins A, M + Cu and cu-a preserved. The existence of cell m-cu is not proved, but likely. First gastral tergite large, with homogenous, slightly rugose surface sculpturing.

Measurements: NHMM-PE2010/5496-LS; BLw/oG: 8.28, HL: 2.36, HW: 2.11, ED: 0.49, GeL: 0.60, ML: 1.25, MML: 0.65, AL: 3.59, ScuL: 1.38, ScutL: 0.65, PL: 1.0, PH: 0.81, PPL: 0.68, HeW: 0.37, G1L: 2.36. Indices: CI: 89.44, IED/HL: 20.54, IHL/AL: 65.87.

Remarks: The wing venation pattern is not preserved. The head is slightly deformed, so its head shape and CI are not clear. It is similar to *Paraphaenogaster bizeri* in size and general habitus, but there is no clear evidence to distinguish it clearly between the two genera: *Paraphaenogaster* or

Aphaenogaster. This specimen is characterised by its well developed, rounded propodeal lobes. This definitely makes it different from *P. loosi*; in *P. bizeri*, the potential propodeal lobes cannot be assessed. It is not assigned to *Messor*, because shapes of head and mandibles do not support this. It is not assigned to *Stenammina*, because antennal sockets are not close and there is no indication for the existence of neither two distinct ridges nor for a long finger-like projection of the median part of the clypeus that extends backwards between the antennal sockets.

Stenammini incertae sedis

(Fig. 10d, e)

Specimen: NHMM-PE1995/9611-LS, gyne.

This specimen is lacking information on taxonomically important body parts, like clypeus, antenna, spines and forewings. Based on some characteristic features, like pedunculate petiole, highly arched mesonotum, triangular-shaped mandibles, it could be allocated to the genus *Aphaenogaster* or *Paraphaenogaster*.

Position: Head from ventrolateral, alitrunk, petiole, postpetiole, and parts of gaster lateral.

Colour: Black.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S6-8.

Description: BL about 12.27. Head almost as long as wide, with convex sides and rounded occipital corners. Head narrows anteriorly. The head is big in relation to the alitrunk, approximate head length is about 77.5% of alitrunk length. Triangular mandibles with long masticatory margin, 8–10 teeth, last two apical teeth larger and strongly curved. Scape reaches posterior margin of head. Alitrunk high and short. The outer shape of the alitrunk is intact, but sutures between the sclerites cannot be identified. Generally, the fossil ants from Enspel do not show strong deformation caused by compression. As this ant is strongly sclerotized, it is assumed that the relatively short alitrunk reflects the original shape. Propodeal spines are not preserved. But the photographic analysis indicates break points posteroventral just above the petiole's insertion. Along the descending face of the propodeum, very distinct, transverse, slightly protruding stripes are developed. Petiole is pedunculate, gradually arising and descending node. Postpetiolar node less high, with distinct rounded top. Petiole and postpetiole are firmly connected via high helcium. Ventral missing parts of petiole and postpetiole (incl. helcium) can be reconstructed by marks in the sediment (photographic analysis). No wings preserved. First gastral segment black, due to stronger sclerotization. The posterolateral margins of its tergite and sternite follow distinct flat curves. Following gastral segments brownish in colour due to less sclerotisation.

Measurements: NHMM-PE1995/9611-LS; BLw/oG: 7.82, HL: 2.45 HW: 2.05, ED: 0.57, ML: 1.47, MML: 0.61, SL: 1.69; AL: 3.17, AH: 2.45, PL: 0.97, PH: 0.81(est.), PPL: 0.62, PPH: 0.88 (est.); HeH: 0.51 (est.), G1L: 2.73. Indices: CI: 83.58, SI: 82.5, IED/HL: 23.37, IHL/AL: 77.47.

Remarks: This specimen is characterised by its combination of BL > 12; its big head in relation to the length of the alitrunk, a remarkably high and short alitrunk, its dorsally rounded, dome-shaped petiolar node and its thick transverse stripes at the posterior face of the propodeum. Further specimens are needed to give a valid species diagnosis.

Tribus Myrmicini Lepeletier de Saint-Fargeau, 1835

Genus *Myrmica* Latreille 1804

Diagnosis: Gyne. BL < 7 mm, colour light brown; antenna, and tarsi dark brown. Mandibles elongate to subtriangular, with 5–6 teeth. Apical and sub-apical teeth bigger than the others. Clypeus anterior margin smooth, tapered in the middle. Antennal sockets widely separated. Antenna 12-segmented with distinct 3–4 segmented club, scape widely bended at base. Segments 3 to 7 of funiculus not slender, rather short and wide. Frontal carina diverging to both sides. The dark ring around the eyes is interpreted as a stronger sclerotized circumocular sulcus, clearly visible in light brown specimens. Scutum and scutellum remarkably flat. Scutum does not overlap pronotum anteriorly or laterally. Scutums anterior margin appears slightly arched and stepped. Scutellum is not oval-shaped with tapered ends. Scutellums posterior margin is strongly curved backwards. Front legs with combed tibial spurs. Steeply descending propodeum, almost vertically. As these specimens are less sclerotized, propodeal spines may break off easily. Only in one specimen they are preserved. Petiole with very short peduncle and dorsally rounded petiolar node. Postpetiole nodiform, constriction towards gaster weak or absent. Suture between dorsal and ventral sclerites of postpetiole distinct, partly open posteriorly (this could also have been caused by taphonomic effects).

Differential diagnosis: All fossil *Myrmica* species known, originating from Eocene were described based on worker specimens. According to Radchenko et al. (2007) with only one exception, they mostly have long propodeal spines, head and alitrunk show very coarse sinuous rugosity and reticulation. Only *M. paradoxa* has short blunt propodeal teeth and a fine reticulation. In *Myrmica* species from Enspel, the alitrunk appears primarily widely and slightly irregularly striated. There is no evidence of an additional reticulation on the alitrunk.

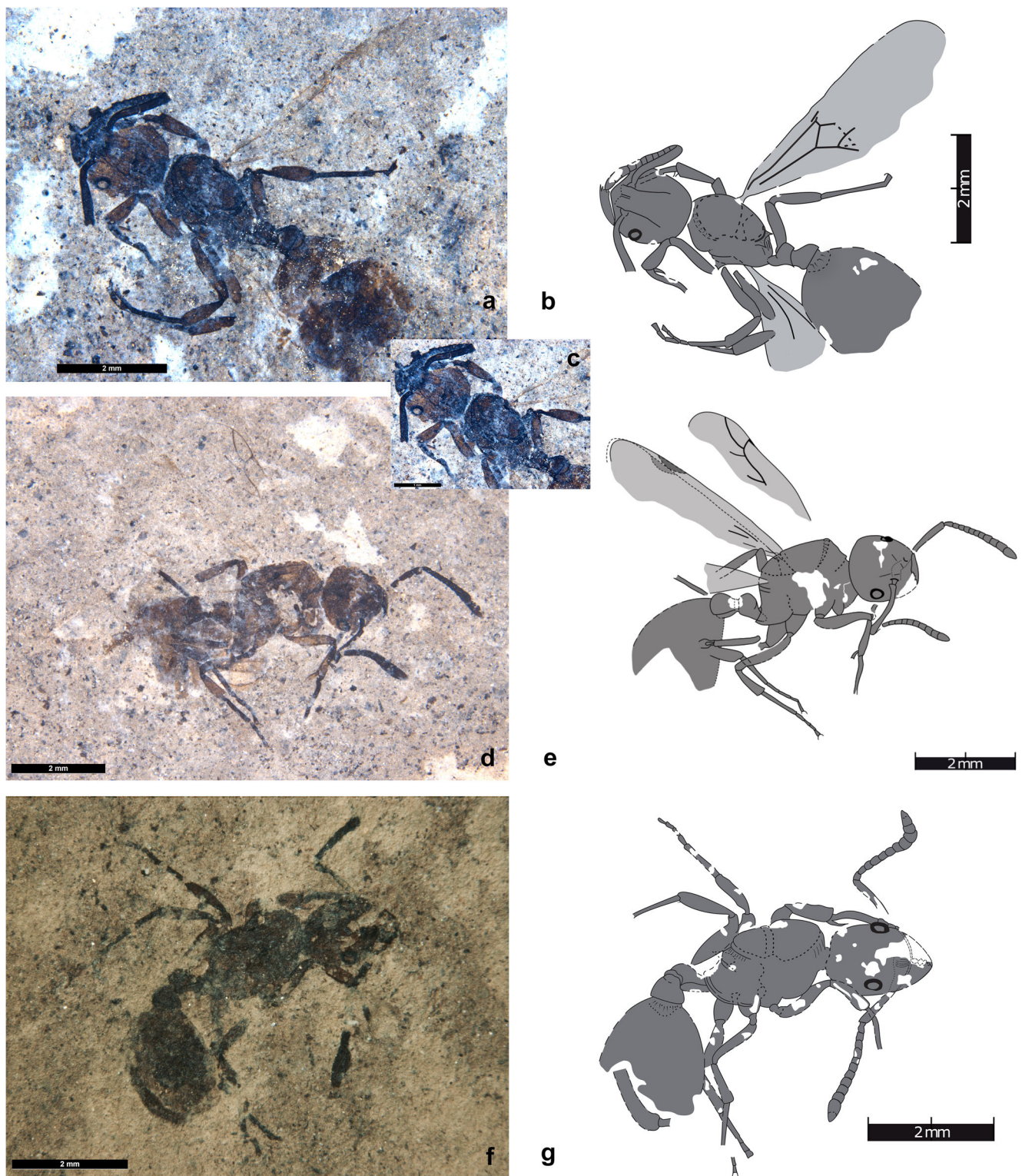


Fig. 11 *Myrmica schaeferi* sp. nov., gyne, holotype NHMM-PE2009/5826-LS. **a** Photograph. **b** Line drawing. **c** Detail: head, alitrunk, petiole and postpetiole; *Myrmica cf. schaeferi*, gyne, specimen NHMM-PE2010/5676-LS. **d** Photograph. **e** Line drawing, detail: head, alitrunk,

petiole and postpetiole, see Supplementary Data 3, Fig. 6; *Myrmica nungesseri* sp. nov., gyne, holotype NHMM-PE2001/5066-LS. **f** Photograph. **g** Line drawing

Myrmica schaeferi sp. nov.
(Fig. 11a–c)

Etymology: Honouring Petra Schaefer, Mainz, specialist for the “not preparable”, and who was one of the supervisors of the former scientific excavations in the oilshales of Lake Enspel.

Holotype: NHMM-PE2009/5826-LS, winged gyne.

Position: Head, alitrunk, petiole, postpetiole and parts of gaster from dorsolateral, part of forewing and hind wing.

Colour: Medium brown; clypeus, mandibles, antenna, and tarsi dark brown.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL about 6.95. Head slightly longer than wide. Relatively small eyes are located below head's mid length. Head is about 8.7 times longer than maximum inner eye diameter. The middle parts of the eyes are missing. Circumocular sulcus strongly sclerotized. Dark brown. Mandibles elongate, not triangular, slightly curved like a flat shovel. Masticatory margin with 5–6 teeth. Apical and sub-apical teeth can only be identified by marks in the sediment. Apical tooth distinctly longer than sub-apical tooth. Other teeth smaller than apical and sub-apical teeth. Antennal sockets widely separated. Anterior clypeus margin smooth, gradually pointed in the middle. Median portion of clypeus with longitudinal wide striae. In addition, a pair of distinct ridges can be identified in the middle of the clypeus and one on both sides starting from the frontal lobe running anteriorly, reaching anterior margin of clypeus. Frontal carinae diverging towards both sides; they clearly project beyond the posterior eyes margin. Frontal triangle is missing or not apparent. Scape reaches posterior margin of head. Scape stout and widely curved at base. Apical and sub-apical funicular segments of antenna partly missing. Antenna is 12-segmented with a 4-segmented club. Funicular segments 6 to 9 wider and shorter than the others. Condylar bulb well preserved, half covered by frontal lobes. Head sculptured with longitudinal, slightly irregular widely spaced striae, posteriorly sculpturing turns more into a reticulate pattern. Alitrunk seems to be fairly high, with flat scutum, prescutellum and scutellum. Scutum does not extend towards anterior and lateral parts of alitrunk. Around the anterior margin, scutum appears arched and stepped. Prescutellum at sides distinctly longer than in the middle. Metanotum strongly sclerotized, dark brown in colour. Propodeum fairly steeply descending. Two propodeal spines widened at base can be identified, slightly diverging posteriorly. Scutum with distinct longitudinal striae. Promesonotal suture is strongly sculptured. Propodeum with longitudinally widely spaced striae. Wing venation poorly preserved. One forewing with closed cell mcu and one hind wing can be identified. Fore

legs with well-developed combed tibial spurs. Petiole with a very short, dorsally slightly concave peduncle forms posteriorly into a round node. Postpetiole slightly elongate with gradually ascending anterior face and rounded node. Helcium starts at about half-length of petiole's posterior face. Postpetiole's tergite and sternite do not appear to have grown together firmly. Posterior face of postpetiole short; it is broadly connected with first gastral segment. Gaster not complete, sclerites are weakly sclerotized. At postpetiole-gaster articulation first gastral tergite is thickened. Posterior to this articulation a semicircle structure can be identified. These structures are interpreted as so-called “pillars”, being associated with the stridulation organ.

Measurements: Holotype NHMM-PE2009/5826-LS; BLw/oG: 4.53, HL: 1.56, HW: 1.40, ED: 0.26, GeL: 0.29 (est.), ML: 0.79, MML: 0.34, SL: 1.18, AL: 1.82, ScuL: 0.84, ScutL: 0.47 (incl. prescutellum), FWL: 4.89, HiTL: 1.01, PL: 0.51, PH: 0.40, PPL: 0.29, PPH: 0.54, HeH: 0.28. Wing venation 1Cu: 0.71, 1M: 0.41, m-cu: 0.43, 1RS+M: 0.25. Indices: CI: 89.62, SI: 84.21, IED/HL: 16.98, IHL/AL: 85.75, Imcu: 35.42.

Differential diagnosis: *M. schaeferi* differs from *M. nungesseri* sp. nov., described hereafter, mainly in its wide head shape with its distinct and rounded occipital corners. Additionally, the mandible seems to be more elongate in *M. schaeferi* than in *M. nungesseri*.

Myrmica cf. *schaeferi*
Fig. 11d,e

Specimen: NHMM-PE2010/5676-LS, winged gyne.

Position: Head, alitrunk, petiole, postpetiole and parts of gaster from dorsolateral.

Colour: Medium brown; mandible basal margin, antenna, and tarsi dark brown.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL about 6.97. Head appears almost round. It has partly been transversally crushed. Relatively small eyes are located below head's mid length. Head is about 5.1 times longer than eye diameter. Left compound eye is preserved. The middle part of the right eye is missing, circumocular sulcus strongly sclerotized. Mandibles elongate, not triangular, slightly curved like a flat shovel. Masticatory margin with five teeth, basal tooth excluded. Apical tooth is distinctly longer than second sub-apical tooth. Third and fourth tooth smaller than first, second and fifth tooth. Fifth tooth with wide base, but it is less high than sub-apical tooth. Basal margin of mandible thickened, darker in colour. Anterior clypeus margin smooth, tapered in the middle. Clypeus regularly densely striated. Frontal carinae diverging to both sides reaches about mid eyes level.

Scape overtrudes posterior margin of head. Scape widely curved at base, and at bend slightly narrower than at its midlength. Antenna with 12 segments, funiculus ends with a 4-segmented club. First and second funicular segments are distinctly longer than wide. Antenna condyle are partly covered by frontal lobes. Antennal sockets widely separated. Head is sculptured with longitudinal striae, posteriorly parts of head slightly reticulate. Alitrunk well developed, with remarkably flat scutum and scutellum, steeply ascending pronotum and steeply descending short propodeum. The anterior margin of scutum appears slightly bulbously arched and stepped. Scutum longitudinal rugose. Posteriorly, scutum seems to be covered by proximal parts of a wing. Most likely both forewings lying on top of each other. Parts of both hind wings can be identified. Wing venation is most likely very weak. Very close to the fossil another insect wing with partly good preservation can be identified. It does not belong to the fossil. Prescutellum at sides distinctly longer than in the middle. Tibial spurs with comb at fore legs well developed. Propodeum is steeply descending. Propodeal spines are not preserved. Their existence cannot be excluded, they may have been demolished. Petiole almost sessile. However, a very short, dorsally slightly concave peduncle transforms to a distinct round node. Node is not tapered. Postpetiole slightly elongate with gradually ascending anterior face and rounded node. Helcium starts at about half-length of petiole's posterior face. Postpetiole's tergite and sternite separated. Posterior

face of postpetiole short; it is broadly connected with first gastral segment. Gaster is not complete, damaged.

Measurements: NHMM-PE2010/5676-LS; BLw/oG: 4.79, HL: 1.32, HW: 1.32, ED: 0.26, GeL: 0.32, ML: 0.62, MML: 0.29, SL: 1.10, AL: 2.07, AH: 1.36, ScuL: 0.96, ScutL: 0.46, FWL: 4.27, HiTL: 1.04, PL: 0.66, PH: 0.47, PPL: 0.44, PPH: 0.56, HeH: 0.31. Indices: CI: 100.0, SI: 83.33, IED/HL: 20.0, IHL/AL: 64.01.

Remarks: The colour of the clypeus is not darkened as with *M. schaeferi*. This may reflect a natural diversity of colouration, or it may have been caused by various taphonomic processes. The clypeus is clearly striated in this specimen, but the two strong ridges running in *M. schaeferi* from the frontal lobe to the front edge of the clypeus are not visible here. The absence of the two ridges and the larger CI do not provide sufficient evidence for the creation of a separate species, as both characteristics may be different due to conservation. Apical funicular segment shows an additional suture. This is not valued as a separate segment, as it most likely may be caused by taphonomic processes.

Myrmica nungesseri sp. nov.
(Fig. 11f, g)

Etymology: Honouring Kai Nungesser, who supervised the scientific collections of the Enspel fossils.

Holotype: NHMM-PE2001/5066-LS, gyne.

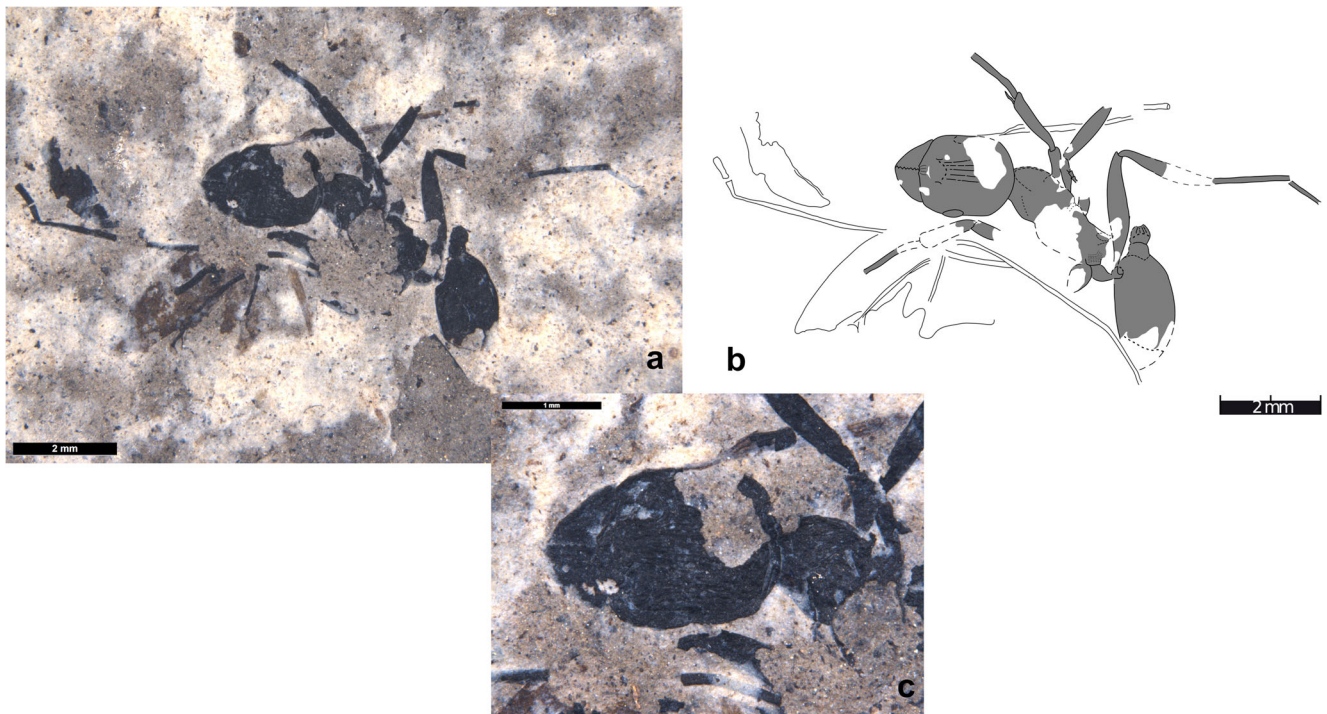


Fig. 12 Myrmicinae incertae sedis, worker, NHMM-PE2011/5020-LS. **a** Photograph. **b** Line drawing. **c** Detail: head

Position: Head from dorsal, alitrunk, petiole from dorso-lateral, postpetiole and parts of gaster from dorsal. No wings.

Colour: Medium brown; clypeus, mandibles, antenna, tarsi dark brown.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL about 6.92. Head longer than wide. Relatively small eyes are located below head mid length. The middle parts of the eyes are missing. Circumocular sulcus strongly sclerotized. Median part of clypeus seems to be convex, with longitudinal striae following the convex shape. Clypeus anterior margin smooth, median slightly tapered. Mandibles only partly preserved. Shape is elongated to almost triangular, with approximately five teeth. Apical and sub-apical tooth slightly curved and longer than the others. Apical tooth longer than sub-apical tooth. Scape reaches posterior margin of head. Scape slightly curved at base. Antenna with 12 segments, funiculus with 4-segmented club. Basal funicular segment longer than funicular segments 2–5. Head sculptured with longitudinal widely spaced striae. Alitrunk with flat scutum, prescutellum and scutellum. Posterior margin of scutellum and metanotum are strongly sclerotized, dark brown in colour. Scutum, prescutellum and scutellum with distinct wide apart longitudinal striae respectively longitudinal rugose. Propodeal spines are not obtained, but due to photographic analysis; there is strong evidence of the existence of long spines. Distinct transverse striae posteriorly at descending face of propodeum. Tibial spurs with long comb at fore legs, another simple tibial spur also preserved at left hind leg. Petiole almost sessile, with short peduncle. Node with rounded top, not tapered. The impression of a subpetiolar spine could be caused by other body parts lying below petiole. Postpetiolar node wide. Helcium broadly connected almost with complete petiole posterior face. Postpetiole is broadly connected with first gastral segment. Postpetiole widest at posterior margin. Sutures between petiole and postpetiole tergites and sternites distinct. Gaster is not complete. A wing is wrapped around gaster. First gastral sternite is disarticulated from postpetiole. First gastral segment seems to be relatively longer than in *M. schaeferi*. Ridges arranged in a semicircle can be identified at the anterior margin of the first gastral tergite. This structure is associated with the stridulation organ.

Measurements: Holotype NHMM-PE2001/5066-LS; BLw/oG: 4.83, HL: 1.34, HW: 1.18*, ED: 0.26, GeL: 0.29, ML: 0.76, MML: 0.38, SL: 1.0, AL: 2.09, ScuL: 0.75, ScutL: 0.66 (incl. prescutellum), HiTL: 0.99, PL: 0.51, PH: 0.47, PPL: 0.50, PPW: 0.51, HeH: 0.32, G1W: 1.46. Indices: CI: 87.91, SI: 85.0, IED/HL: 19.78, IHL/AL: 64.01.

Differential diagnosis: *M. nungesseri* differs from the other *Myrmica* species described here mainly by the combination of its oval head shape with flattened occipital corners, and its sub-triangular mandibles. In addition, the prescutellum is consistent in length without any median constriction, as it is the case in *M. schaeferi*. Metapleura are posteriorly formed slightly bell-bottomed, covering partly hind coxae.

Myrmicinae incertae sedis

(Fig. 12a–c)

Specimen: NHMM-PE2011/5020-LS, worker.

Position: Head dorsal, alitrunk dorsolateral, petiole, postpetiole and gaster most likely from dorsolateral.

Colour: Black, well sclerotized.

Type locality and horizon: Enspel Oilshale, Rhineland-Palatinate, Germany. Enspel Formation, Upper Oligocene, MP 28; (24.56–24.79 Ma, Mertz et al. 2007), layer S16.

Description: BL approximately 8.27 (estimated because petiole are not complete). Head distinctly longer than wide, sub-rectangular shaped, with distinct occipital corners. Head sides straight, on eye level slightly concave. Eyes located before mid length of head. Head widest here. Fairly large eyes. Eyes diameter is about 25.9% of head length. Mandibles stout, triangular, with 8–10 triangular shaped teeth. Teeth have all almost the same size. There is no clear evidence for a distinctly bigger apical bended tooth. Antennas not preserved. The anterior margin of the clypeus is not smooth. Irregularities are interpreted as changes caused by fossilization processes, including a putative weak concave depression in the central part of the clypeus margin. Head all over with distinct longitudinal striae. Median part of clypeus strongly striated, probably convex. Distance between antennal sockets wide. Alitrunk only partly preserved, particularly slender. Promesonotum slightly arched. Metanotal groove present. Foreleg with long tibial spurs. Break edges at propodeum and marks in the sediment do indicate the existence of propodeal spines. Petiole and postpetiole only partly preserved. A reconstruction is not possible. Only first gastral tergite preserved. It shows an unspecific structure and it is the far longest tergite of all.

Measurements: NHMM-PE2011/5020-LS, BLw/oG: 5.99, HL: 1.82, HW: 1.58, ED: 0.47, GeL: 0.38, ML: 1.13, MML: 0.66, AL: 2.51, AH: 1.02, HiTL: 1.93, G1L: 1.93. Indices: CI: 87.0, IED/HL: 25.89, IHL/AL: 72.35.

Remarks: This specimen differs from all known fossil worker of the genera *Paraphaenogaster* or *Aphaenogaster* by its almost rectangular head shape and its comparable large eyes. Because this worker specimen is lacking antenna and the complete petiole, an allocation on genus level is not appropriate. Even the assignment to the subfamily Myrmicinae is based on an assumption.

Identification key for myrmicine gynes from Enspel

1. BL > 9, petiole pedunculate, anterior face of petiole more or less steeply ascending, mandibles triangular..... 2
 - BL < 9, CI > 110, petiole pedunculate, mandibles triangular, eyes below mid length of head..... 3
 - BL ≤ 7 mm, petiole with short peduncle, scutum and scutellum remarkably flat, funiculus with 3–4 segmented club, body brown, mandibles elongate or sub-triangular, not triangular, with 5–6 teeth, postpetiole without any constriction towards gaster..... 4
2. Head elongate, occipital corners rather flat, petiole pedunculate with steeply ascending high node, apical and sub-apical teeth slightly bigger than the others, alitrunk arched, scutellum distinctly protruding, postpetiole nodular, propodeal spine distinct, no cell rm, Fig. 3a, b..... *Paraphaenogaster loosi*
 - Head elongate with almost parallel sides and well developed occipital corners, straight, almost parallel running frontal carinae, reaching beyond medium ocellum, alitrunk high with flat mesonotum, petiole with stout, not bar-like peduncle, anterior face of petiole slightly convex, posterior face of petiole steeply descending, no cell rm, Fig. 4a, b..... *Paraphaenogaster schindleri*
 - Head with distinct relatively fine striae, including clypeus, at occiput reticulate, head wide posteriorly, narrows towards the front, fairly small eyes, teeth have more or less the same shape and size, apical tooth (?) not preserved, alitrunk arched, cell rm not present, Fig. 5a, b..... *Paraphaenogaster bizeri*
 - Alitrunk arched, stout spines that are wide at base, forewing with distinct cell rm, petiole pedunculate, ascending face of node concave, postpetiole with rounded, domed node, Fig. 9a, b..... *Aphaenogaster enspelensis*
3. CI > 100, head narrows towards anterior. Mandibles triangular. Alitrunk massiv. All veins of forewing weakly sclerotized, vein rs-m visible but even less sclerotized than the others. Petiole pedunculate, transition from peduncle to node fluent. Node is not rounded at top; it has a distinct transverse crest instead, posterior face of petiole steeply descending. Postpetiole wide and nodiform. Figure 9c, d..... *Goniomma poschmanni*
4. Occipital corners rounded, median part of clypeus with distinctive ridges in the middle of the clypeus and one on both sides starting from the frontal lobe running anteriorly, reaching anterior margin of clypeus, head sculptured with

wide striae, towards occiput it turns more into a reticulate pattern, along anterior margin, scutum seems slightly arched and stepped, prescutellum flat, at sides distinctly longer than in the middle, Fig. 11a–c..... *Myrmica schaeferi*

- Head oval, occipital corners fairly flat, anterior margin of clypeus smooth, shaped oval, tapered, but not distinctly pointed in the middle; median part of clypeus convex with distinct striae following convex shape; mandibles shape sub-triangular; sculptured with wide striae, anterior margin of scutum is not slightly bulgingly, prescutellum flat, consistent in length, at sides as long as in the middle, without any median constriction; metapleuron posteriorly formed slightly bell-bottomed, covering partly hind coxa. Figure 11f, g..... *Myrmica nungesseri*

Identification key for myrmicine worker from Enspel

- CI > 90, alitrunk with domed promesonotum, propodeum lower level. Figure 6a, b..... *Paraphaenogaster freihauti*
- CI > 90, small eyes, alitrunk with distinctly separated pronotum and mesonotum, propodeum not distinctly on lower level. Figure 6c, d..... *Paraphaenogaster wettlauferi*

Discussion

Taxonomic questions

The majority of the fossil ant species described here belong to the tribe Stenammini. This tribe is well represented in the fossil record, especially by the genera *Aphaenogaster* with 19 species, and *Paraphaenogaster* with 4 species (referring to Antwiki, August, 2019). According to Branstetter et al. (2016, p. 8) “... this richness belies the fact that the placement of many of these fossil taxa within the tribe, or within genera in the tribe, is dubious, largely due to uncertainty in both diagnostic characters and generic boundaries”. This statement also applies to some extent to the species of the genera *Aphaenogaster* and *Paraphaenogaster* described here.

Gyne of the two genera *Aphaenogaster* Mayr, 1853 and morphogenus *Paraphaenogaster* Dlussky, 1981 are very similar in the following essential morphologic features: size, more or less elongate head, triangular mandibles, 12-segmented antenna without distinct club, high and arched mesonotum, pedunculate petiole, features for distinguishing between the two genera are poor. In *Aphaenogaster*, the cell rm is developed, in *Paraphaenogaster* it is not. The morphogenus *Paraphaenogaster* was established by Dlussky (1981), basically based on

males showing a specific wing venation pattern. Further species were established by Dlussky and Putyatina (2014), and by Dlussky and Perfilieva (2014). In both latter papers, the cell *rm* has been described as being present. Radchenko and Perkovsky (2016) and Perfilieva et al. (2017) provided an updated and corrected version of the wing venation. Because of the absence of cell *rm* in *A. maculipes* (Theobald 1937), *A. maculate* (Theobald 1937; both Céreste, France, Oligocene) and *A. pannonica* Bachmayer 1960, Austria), the authors consequently allocate these *Aphaenogaster* species to the morphotaxon *Paraphaenogaster*. This also applies for species of the former *Aphaenogaster*-subgenera *Deromyrma* and *Planimyrmica* which do not show cell *rm* either, such as *A. avita* Fujiyama, 1970, Japan, and *A. dumetorum* Lin, 1982, China (cited after Zhang et al. 1994).

The resulting question is: can the existence of the cell *rm* be valued as a taxonomic character? This topic has been discussed earlier. Smith (1961) reported that species of the subgenera *Aphaenogaster* and *Attomyrma* do have a closed cell 1+2r and a closed cell *rm*. Other *Aphaenogaster* species which are belonging to the former subgenera *Deromyrma* and *Planimyrmica* only have one cubital cell (cell 1+2r) and no cell *rm*. In this context, it is interesting to note that Branstetter et al. (2016) are confirming the separation of species belonging to the *Deromyrma* clade from the *Aphaenogaster* clade.

Regarding the differentiation between *Aphaenogaster* and *Messor* Forel 1890, Bolton (1982, p. 339) valued this feature "... as being just one step in a long gradual sequence of venation development in both *Aphaenogaster* and *Messor* and of no significance in genus-level discrimination among these ants". Moreover, Bolton (1982, p. 340) is assessing the vein *rs-m* as being a dynamic feature rather than a static one "... and that it is by no means rare to find specimens with different venation patterns on the left and right forewing, representing different stages in the sequence, and thus showing it to be a dynamic rather than a static system". According to this statement, the vein *rs-m* would not be a sufficient apomorphic feature to separate *Aphaenogaster* from *Paraphaenogaster*.

In order to estimate the taxonomic value of the feature vein *rs-m* for the Enspel myrmicine specimens, all wings of this type that were preserved well enough to show the existence of the vein *rs-m*, in case it would have been there—were analysed. Out of 69 myrmicine specimens with this specific wing venation pattern, only 1 had a distinct cell *rm*. Fifty-five specimens had no vein *rs-m*. In 13 specimens, non-sclerotized remains of the vein *rs-m* could be identified.

These data from Lake Enspel reveal a strong and stable trend for reducing vein *rs-m* in Stenammini. This morphological feature seems not as dynamic as it was described by Bolton (1982). Also non-sclerotized remains of *rs-m* reflect the evolutionary trend of losing *rs-m*. This could be used to derive the legitimacy for a genus of its own. This would be in accordance with the recommendation of Radchenko and

Perkovsky (2016) to allocate fossil *Aphaenogaster* species without vein *rs-m* to the genus *Paraphaenogaster*.

The genus *Aphaenogaster* is represented in Enspel by one species. Following the re-allocation suggested by Radchenko and Perkovsky (2016), all other *Aphaenogaster* species, originating from Oligocene deposits, like *A. archaica* Meunier 1915, *A. maculata*, Theobald (1937) and *A. maculipes*, Theobald (1937) would belong to the genus *Paraphaenogaster*. As a result, *A. enspelensis* is the only representative of the genus *Aphaenogaster* in Oligocene.

According to Ward et al. (2015), the genus *Aphaenogaster* is not monophyletic. Further taxonomic revision on this genus is expected. Until there is a complete understanding of the diverse genus *Aphaenogaster*, the two genera *Aphaenogaster* and *Paraphaenogaster* should be kept separate for the time being.

However, a weak point and big disadvantage of separating these two genera only by the wing venation pattern is the fact that the worker and dealate females cannot be assigned clearly. More distinctive features to separate these genera are required. Based on the numerous *Paraphaenogaster* species of Enspel, an enhanced description of this genus for all three castes can be given.

The "*Paraphaenogaster* wing venation pattern," however, occurs in many other myrmicine genera of the tribes Pheidolini, and Solenopsidini, the latter including the South-American species *Bariamyrmica hispidula* Lattke 1990 (Dlussky and Perfilieva 2014; Dlussky and Putyatina 2014).

Three specimens were allocated to the genus *Myrmica* (Tribe Myrmicini). They represent the first fossil record of the genus *Myrmica* in Oligocene. *Myrmica* species are known from Eocene, mainly from Baltic and Saxonian amber (Radchenko et al. 2007). As part of their revision of the genus *Myrmica*, the authors identified 16 described species from late Eocene, Oligocene and Miocene, that were mistaken *Myrmica*. Some of these were allocated to other genera and some, mainly originating from Miocene deposits, were titled to be *incertae sedis* in the genus *Myrmica*. Former *Myrmica archaica*, originating from Rott (Oligocene, Germany), has been informally allocated to *Aphaenogaster*. More recently, this was changed informally to *Paraphaenogaster* by Radchenko and Perkovsky (2016).

According to the results of Radchenko et al. (2007) and Ward et al. (2015), *Myrmica* species and their respective tribe Myrmicini arose in the late Eocene. The further evolutionary steps of *Myrmica* in Oligocene, Miocene and Pliocene are unknown, because of the big gap in the fossil record. Although the new *Myrmica* species described here are represented by gynes, they can be clearly differentiated from *Myrmica* species from Eocene amber, which were described based on worker specimens (Radchenko et al. 2007). Usually *Myrmica* species are characterised by distinct propodeal spines. Radchenko et al. (2007) described the new species, *M. paradoxa* with blunt short propodeal denticles. The authors highlight this as being very peculiar to the genus *Myrmica*, as is the very short dorsal part of its propodeum in relation to the propodeal declivity. The

Myrmica species from Enspel show that the propodeal spines were (still?) rather blunt and short in the Upper Oligocene.

Palaeoenvironmental and palaeobiological aspects

As *Paraphaenogaster* is most likely derived from *Aphaenogaster*, the latter genus is taken as a reference for the former.

Biogeography

According to Köhler and Uhl (2014), plant fossils originating from the mesophytic forest in Enspel do show a strong East Asian influence. These are clearly dominant in regards to the abundance and diversity of plant species found. Already during the early Eocene, a strong biotic European-Asiatic interaction has been documented for insects from Fushun amber by Wang et al. (2014), and some taxa show close phylogenetic relationships (“affinities”) to those from European amber. The studies by Guénard et al. (2015) also point to a strong affinity between the West Palearctic ant palaeofauna and modern Indomalayan and Australasian assemblages.

Possibly *Aphaenogaster* followed the plant migration from Asia to Europe. The oldest *Aphaenogaster* species *A. dluskyana* has been documented from Sakhalin amber (mid-Eocene, Russia) (Radchenko and Perkovsky 2016). The oldest *Paraphaenogaster* species, *P. hooleyana* (Dlussky and Perfilieva 2014), has been reported from the Isle of Wight (late Eocene). This record is only based on two forewings. Further *Aphaenogaster*-species, which should be assigned to the morphogenus *Paraphaenogaster* (Dlussky and Putyatina 2014; Radchenko and Perkovsky 2016), were found in Miocene deposits in East China and Japan (Fujiyama 1970; Hong 1984; Zhang et al. 1994). The numerous *Paraphaenogaster* species in the myrmicine fauna of Enspel indicate that this genus was well represented and diverse in the Upper Oligocene in Europe. In addition, the fact that this genus is still documented from Miocene and possibly Pliocene deposits, such as in Stavropol (Russia), Japan, East China and in Austria shows that it must have been very successful throughout the Palaeartic region.

Only the genus *Aphaenogaster* survived. Today in Europe, the species prefer Mediterranean climate, which means hot, dry summers and mild, rainy winters. From *Aphaenogaster picea* living in North America, we know that they can withstand temperatures of -0.5 to 42.5 °C (Warren and Chick 2013). In Enspel, the temperature range was less extreme, from 9° to 25 °C.

Goniomma is represented by only ten extant species also living in parts of the Mediterranean, such as Spain, France and Algeria. Extant *Myrmica* species inhabit the entire Holarctic. In Europe, the southernmost distribution area is the Mediterranean, but they are also known from the Caucasus,

North Africa and Iran. The occurrence of the genera *Goniomma*, and *Myrmica* in Enspel during late Oligocene corresponds to the southern distribution zone of the species occurring today.

Habitat of the Myrmicinae

Already Carroll (1975) revealed a high variety of habitats and diets for extant *Aphaenogaster* species in Florida. According to his studies, soil-dwelling species prefer well-drained habitats, while species nesting in rotting wood are most common in moist woodlands. Few species are arboreal. Thus, the palaeoecological conditions around Lake Enspel meet the requirements of existing *Aphaenogaster* species with regard to nesting and nutrition. Besides nesting in rotting woods, forest litter or even in living trees, more xeric habitats in well-drained sandy soil were also available around Lake Enspel. Schindler and Wuttke (2015) discuss the existence of dry areas within gullies of the crater wall with none or slight vegetation (see also Smith and Wuttke 2015). These dry areas could have been a suitable biotope for *Goniomma* species. Extant *Goniomma* are ground dwellers in the semi-arid and arid Mediterranean scrublands. Most extant *Myrmica* species are ground dwellers, foraging in litter and field layers. Few species are climbing up bushes or trees. In warm habitats, they prefer wet locations. Warm temperature with fairly high humidity made the area around Lake Enspel a suitable biotope for *Myrmica*.

In males of the genus *Paraphaenogaster* and in gynes of the genera *Myrmica* and *Goniomma*, so-called pillars were identified. These are integumentary foldings posteriorly associated with the stridulation organ. Their morphology varies between species and possibly affects the sound.

Stridulation organs are widespread in Myrmicinae (Castro et al. 2015). In earlier studies, three various functions were postulated for the stridulation organs: in the leaf-cutting ant *Atta* as an underground alarm system (Markl 1965, 1985) and as a recruitment signal to nestmates to exploit cutting sites (Roces and Hölldobler 1996); in *Pogonomyrmex* during mating by inseminated gynes, while escaping from males (Markl et al. 1977); and in *Novomessor* and *Messor* for enhancing the effectiveness of pheromones while recruiting nest mates to food sources (Markl and Hölldobler 1978; Hahn and Maschwitz 1985; Hölldobler and Wilson 1990, p. 257). In a more recent comparative study of the evolution of the stridulation organ in ants by Golden and Hill (2016), it is shown that this organ occurs in almost all myrmicine genera; most of them are nesting and foraging in and on the soil, respectively, but it also occurs in arboreal living myrmicine genera. The authors conclude that in ants, this organ must have evolved independently at least five times. Its function varies, and it does not give a clear indication on the way of life of the ant

genus. The earlier assumed origin function “as a burial/rescue signaling” is rejected by the authors.

Diet of the Myrmicinae

Investigations on extant *Aphaenogaster* species show that they feed on insects and other arthropods, seeds, petals, plant debris and on small invertebrates (Carroll 1975; Lubertazzi 2012).

Myrmecochory: *Aphaenogaster* is known as a relevant disperser of myrmecochorous seeds. The collection of elaiosome-bearing seeds by *Aphaenogaster rudis*-group is well documented, as is the high diversity of myrmecochorous plants used (Heithaus et al. 2005; Handel et al. 1981; Culver and Beattie 1978, cited after Lubertazzi 2012; Zelikova et al. 2008, 2011). *Aphaenogaster* spp. in Florida also feed on the free-growing fruiting bodies of fungi (Agaricales) of the Russulaceae, Tricholomataceae and Amanitaceae families, reports Carroll (1975). Today, myrmecochory mainly occurs in herbaceous plants in the northern hemisphere. More than 3000 plants have been identified to be myrmecochore. Is there any indication for the Enspel *Aphaenogaster* species having fed on elaiosomes? Studies on the rich and well-preserved macroflora from Enspel by Köhler and Uhl (2014) revealed 74 taxa. According to the authors, only 15% of the macroflora belonged to the herbaceous vegetation. Of these, 89% were evergreen. The authors point out that wind is the main carrier of the leaves, so a taphonomic filter could be the reason for the under-representation of shrubs (18%) and herbs (15%) in the Enspel flora. The degree of herbaceous vegetation could have been higher and with it the chance to have myrmecochore plants. In the Central European Oligocene, one would expect to find herbaceous plants carrying elaiosomes but these are chronically underrepresented in the fossil record, both as macrofossil and pollen (Uhl 2018, pers. communication).

Harvester ant: *Goniomma* is known as a granivore, living in small colonies (Espadaler 1986; Hensen 2002). Their diet can be very specific to special seeds (Bastida et al. 2008). In *Aphaenogaster*, there is no real harvesting ant represented. Partial seed harvesters, such as *Novomessor albisetosa* and *N. cockerelli* (Hölldobler et al. 1978; Hölldobler and Wilson 1990, p. 611; Johnson 2001) had earlier been allocated to the genus *Aphaenogaster* (Bolton 2003). The genus *Novomessor* Emery 1915 has recently been resurrected by Demarco and Cognato (2015). Real harvesting ants collect, store, transport, disperse and feed on seeds (Handel et al. 1981; Hahn and Maschwitz 1985; Hölldobler and Wilson 1990). In most cases, the habitats of harvester ants are xeric or semiarid. Harvester ants do not necessarily also predate on myrmecochore plants, but they could. Palyonological studies by Hermann (2010) identified essentially 80 taxa of angiosperms, 20 taxa of gymnosperms and 41 taxa of pteridophytes. Of the species found,

probably only the seeds of the families Poaceae and Cyperaceae served as food. Today, seeds of Poaceae are well documented as being collected and dispersed by harvester ants (Detrain and Pasteels 2000).

Animal diet

Numerous studies reveal a high variety on fossil arthropods found in Lake Enspel sediments (Wedmann 2000; Wedmann et al. 2010; Poschmann and Wedmann 2005; Poschmann 2006; Wappler and Heiss 2006; Poschmann et al. 2010). This indicates a good and sufficient food base for *Myrmica*, being mainly zoophagous, and also for additional feeding on small arthropods in *Aphaenogaster* and *Paraphaenogaster*.

Trophobiose

Extant *Myrmica* species are mainly zoophagous but they also feed on honeydew. It is not known whether this also applies to fossil *Myrmica*. However, several groups of Sternorrhyncha, such as aphids (Aphidoidea) and jumping plantlice (Psylloidea), were identified in Enspel layers (Wedmann 2000; Wedmann et al. 2010). Therefore, *Myrmica* could have partially fed on honeydew.

The palaeoenvironment of Lake Enspel met the requirements on myrmicine habitats in several ways. It offered habitats of a mesophytic forest, like rotting wood and litter as well as xeric, well-drained sandy soils—at average temperatures similar to those prevailing in the Mediterranean today. In addition, it offered a wide variety of animal and plant foods.

Mating behaviour

Paraphaenogaster males found in Enspel are not much smaller than the females (BL of males, 7.8–9.3 mm; females, 9.1–12.1 mm). In addition, their mandibles are well developed and their eyes are not extremely big. Based on knowledge of mating behaviour in ants, one can assume that mating took place close to the solid ground of a hilltop or a forest clearing. Males were competing directly against each other. In contrast when mating takes place in the air, males are much smaller than females and their mandibles are often strongly reduced, eyes and ocelli are well developed (Hölldobler and Wilson 1990; Helms 2018).

Taphonomic aspects

The majority of the ant fossils investigated were reproductives. Of the 312 specimens, only 19 belong to the worker caste (6.1%). Extant *Aphaenogaster* reproductives perform wedding flights in summer. For *A. treatae*, Forel 1886 Talbot (1966) described the conditions for the flight in more

detail (see also Helms 2018). The following scenario applies for complete insect body fossils: the winged reproductives were most likely transported by the wind out onto the lake. Having fallen onto the lake surface, they were fixed with their wings by adhesion. Because in Hymenoptera the ratio wing size and body mass is fairly low (Wagner et al. 1996) and, in addition, wettability of the hymenopteran wings is fairly high (Rust 1998), rain drops or waves enabled the insect bodies to break the water tension and to sink down before disarticulation of body parts took place (see also Lutz 1990). Compression fossils of workers are rare. They probably reach the lake surface via broken parts of plants that have fallen into the lake, drifted into the lake from the shore or flooded in via gullies originating from the crater wall. In specimen NHMM-2011/5020-LS, referred to Myrmicinae incertae sedis, plant remains can be seen very closely associated with the fossil (Fig. 12a–c).

Viewed dorsally, the masticatory margin of the mandible very often is bent downwards, so the teeth are pointing towards the sediment. This effect is caused most likely by compaction.

Apical funicular segment can show an additional distinct suture (e.g. NHMM-2013/5037-LS, NHMM-2010/5676-LS). This is not interpreted as a separate segment. Most likely, fossilization makes the internal structure of the apical funicular segment transparent. A similar effect can also occur at the pedicellus, so that it can erroneously appear as two funicular segments (see Supplementary Data 1, Fig. 5, left antenna of *Paraphaenogaster* cf. *schindleri*, specimen NHMM-2002/5019-LS).

Dorsal notches, which are often visible at the petiolar nodes, as well as lateral ridges along the petioles are not attributed to possible compression, since these structures occur only here.

All three *Myrmica* specimens lack the middle part of the compound eyes. The inner edge of the ring is smooth, not frayed. It is not clear if this loss was caused by taphonomic influence or by splitting of the sediment. In the latter case, the missing part adheres to the opposite plate (which has not been kept in most cases).

Evolutionary history

Today, the relative abundance of myrmicines is around 74% (Ward 2000). These data are based on the analysis of 110 Winkler samples collected from many localities in different regions (Nearctic, Neotropic, Malagasy, Australian and Oriental). Ward has proven that Myrmicinae are the dominant subfamily in forest leaf litter today.

According to Radchenko and Dlussky (2013), “Paleontological data demonstrate that for almost the entire evolutionary history of ants Myrmicinae took a subordinate position in the current territory of Eurasia and North America: the

proportion of their individuals in all investigated Eocene and Oligocene deposits, as a rule, does not exceed 5 to 6 percent”. (p. 1060). Dlussky and Wedmann (2012), however, stated an increase of myrmicine ants similar to the proportions of today during late Oligocene to Miocene (late Oligocene: Rott 50% (MP 30) and Vishnevaya balka, Stavropol (40%) (Dlussky and Wedmann 2012), and in Radoboj (22%) (Dlussky and Rasnitsyn 2009).

The proportion of myrmicine ants in Enspel (36.6%) corresponds well with these data. Although 94% of the fossils were reproductives, the ratio indicates that in the late Oligocene, Myrmicinae played a significant role in the ant fauna of Middle Europe. The myrmicine genera in Enspel mainly belonged to the tribes Stenammini and Myrmicini. There is a great diversity within the tribe Stenammini. The discovery of eight new species belonging to three different genera within this tribe, namely *Paraphaenogaster*, *Aphaenogaster* and *Goniomma*, impressively prove this. According to Branstetter et al. (2016) “The ‘*Goniomma*’ and ‘*Aphaenogaster*’ clades both originated in the Palearctic region 15 Ma and 17 Ma, respectively”. The results presented here show that diversification within the tribe Stenammini took place earlier, at least before 24.3 Ma.

The oldest described *Paraphaenogaster* is *P. hooleyana* Dlussky and Perfilieva (2014), based on two preserved forewings from Upper Eocene sediments of the Isle of Wight. The wings are not longer than 3.0 and 4.8 mm, possibly representing a female and a male. All other *Paraphaenogaster* males and females found have distinctly longer forewings (6.5–11.0 mm). Does this indicate that the earliest *Paraphaenogaster* from late Eocene were much smaller and they increased in size towards late Oligocene and Miocene? Since this specific wing venation pattern also occurs in other myrmicine tribes (Dlussky and Perfilieva 2014; Dlussky and Putyatina 2014), individual wings do not contain enough reliable information to discuss evolutionary trends.

The reason we do not find *Paraphaenogaster* today remains open. This morphogenus is known from deposits from late Eocene to Miocene—and even Pliocene. The climate in the Miocene still was warm, but it became cooler and drier during the Pliocene. If *Paraphaenogaster* was not widespread in the Mediterranean but limited to the northern and central part of Eurasia, this could indicate that it did not overcome the ice ages. Further studies on *Paraphaenogaster* from Pliocene deposits (and younger) are needed to find more precise answers to this question. This may also apply to *Paraphaenogaster* species from East Asia (China, Japan). In the relevant areas, aridity increased due to global cooling. Vegetation for Northeast China

and North Japan during the ice ages is described as “Main Taiga” and for South Japan as open boreal woodland (Ray and Adams 2001). Permafrost covered Asia as far south as Beijing (Rapp 2012, p. 12).

However, the genus *Aphaenogaster* survived the ice ages. This may be because they were more flexible (see existing *Aphaenogaster* in North America) or because populations extended to warmer areas that were not so strongly affected by the ice ages. According to the chronogram of Myrmicinae, the oldest *Aphaenogaster* specimen *Aphaenogaster araneoides* Emery 1890 evolved in the mid-Eocene (Ward et al. 2015). Radchenko and Perkovsky (2016) described the species *A. dluskyana*, as the oldest fossil record of an extant myrmicine genus from mid-Eocene Sakhalin amber. In Enspel, only one specimen has been allocated to the genus *Aphaenogaster*. Other fossil records of *Aphaenogaster* species are described from late Eocene, Oligocene, late Oligocene (Rott) and Miocene. Today in Europe, *Aphaenogaster* mainly occurs in the Mediterranean area. They prefer hot, dry summers and mild, rainy winters. In Germany, only one species (*A. subterranea*) survived, living in warm and dry areas (Seifert 2007).

The records of *Goniomma* are the earliest ones. *Goniomma* are harvester ants, and were probably able to survive the ice ages in southern warmer regions. Today, *Goniomma* is fairly limited in its distribution and represented by only ten species. *Myrmica* obviously also overcame the ice ages. This genus today is common and abundant, well represented with 188 species and 1 subspecies in the Holarctic (AntCat, Bolton 2019).

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Compliance with ethical standards

Conflict of interest The author declares that she has no conflict of interest.

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