New Middle Eocene Formicid Species from Germany and the Evolution of Weaver Ants

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GENNADY M. DLUSSKY, TORSTEN WAPPLER, and SONJA WEDMANN

Two new species of weaver ant are described from the Eocene of Germany. Males and gynes of *Oecophylla longiceps* Dlussky sp. nov. are found in the middle Eocene (about 47 Ma) of Grube Messel, Germany. Males, gynes and two workers of *O. eckfeldiana* Dlussky sp. nov. are recorded from the middle Eocene (about 43 Ma) of Eckfeld maar, Germany. The two new species are among the oldest records of the extant genus *Oecophylla*. First adaptations for moving in the forest canopy are present in the workers of *O. eckfeldiana*. Even more specialized adaptations for arboreal life are found in the workers of *O. brischkei* from Baltic amber. The coexistence of two species in Baltic amber and in the Bembridge marls suggests that in these cases different ecological niches were realised by sympatric species. Comparisons of the queens from different fossil and extant species indicate morphological trends, partly connected with increasing fertility. Most likely *Oecophylla* originated in the early Paleogene in the Palaearctic realm, radiating strongly during the climatic changes of the Eocene–Oligocene transition.

Key words: Insecta, Hymenoptera, Formicidae, *Oecophylla*, Eocene, Paleogene, Messel, Eckfeld.

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Introduction

Weaver ants are famous for constructing their nests from clusters of green leaves which are bound together with silk produced by their mature larvae (e.g., Hölldobler and Wilson 1990). Weaver ants constitute the genus *Oecophylla* (Formicidae, Formicinae) which consists of only two extant species, *O. longinoda* and *O. smaragdina* (Bolton et al. 2006). *O. longinoda* (Latreille, 1802) is widespread in the forested regions of tropical Africa, and *O. smaragdina* (Fabricius, 1775) ranges from India across almost all of tropical Asia to the Solomon Islands and northern Australia (Fig. 1). Both species are very similar in morphology and behaviour. Over most of their ranges these species tend to be common, and in many localities they are among the several most abundant and ecologically dominant elements of the arboreal ant fauna (e.g., Hölldobler 1983; Blüthgen and Fiedler 2002).

However, in the past weaver ants were more widespread and diverse (Fig. 1). Until now, 13 fossil species of weaver ants have been described, the most ancient originating from the middle to late Eocene: *Oecophylla brischkei* Mayr, 1868 and *O. crassinoda* Wheeler, 1922 (= *O. brevinodis* Wheeler, 1915) from the Baltic amber and *O. bartoniana* Cockerell, 1920 from the Eocene Bagshot Beds, Bournemouth, UK. The first two species are also present in Bitterfeld amber (also called Saxonian amber) (GMD personal observations). The

Bitterfeld amber is considered to be contemporaneous with Baltic amber and both are similar in chemical composition and inclusions of the fauna and flora (e.g., Schumann and Wendt 1989; Röschmann and Mohrig 1995; Hoffeins and Hoffeins 2003). Although now located in Miocene deposits, Bitterfeld amber has been shown to be Baltic amber that had been eroded and been redeposited in Miocene sediments (Weitschat 1997). However, geological studies by Knuth et al. (2002) and Fuhrmann (2005) indicate an independent origin and an Oligocene age of the Bitterfeld amber. Until this discussion is definitively resolved, we follow the former assumption that Bitterfeld amber is, in essence, Baltic amber that has been eroded and redeposited in younger strata. Six species of *Oecophylla* were described from European Oligocene deposits: *O. atavina* Cockerell, 1915, *O. perdita* Cockerell, 1915, *O. megarche* Cockerell, 1915 (Bembridge Marls, Isle of Wight, UK, Lower Oligocene or possibly Upper Eocene age, Hooker et al. 2007), *O. praeclara* Förster, 1891 (Brunstatt, France), *O. superba* Théobald, 1937 (Kleinkembs, Haut-Rhin, France), and *O. sicula* Emery, 1891 (Sicilian amber). Also four species were described from Miocene deposits: *O. obesa* (Heer, 1849) (Radoboj, Croatia), *O. leakeyi* Wilson and Taylor, 1964 (Mfwangano Island, Lake Victoria, Kenya), *O. xiejiaheensis* (Hong, 1984) (Shanwang, China) and *O. grandimandibula* Riou, 1999 (Montagne d'Andance, Ardeche, France).

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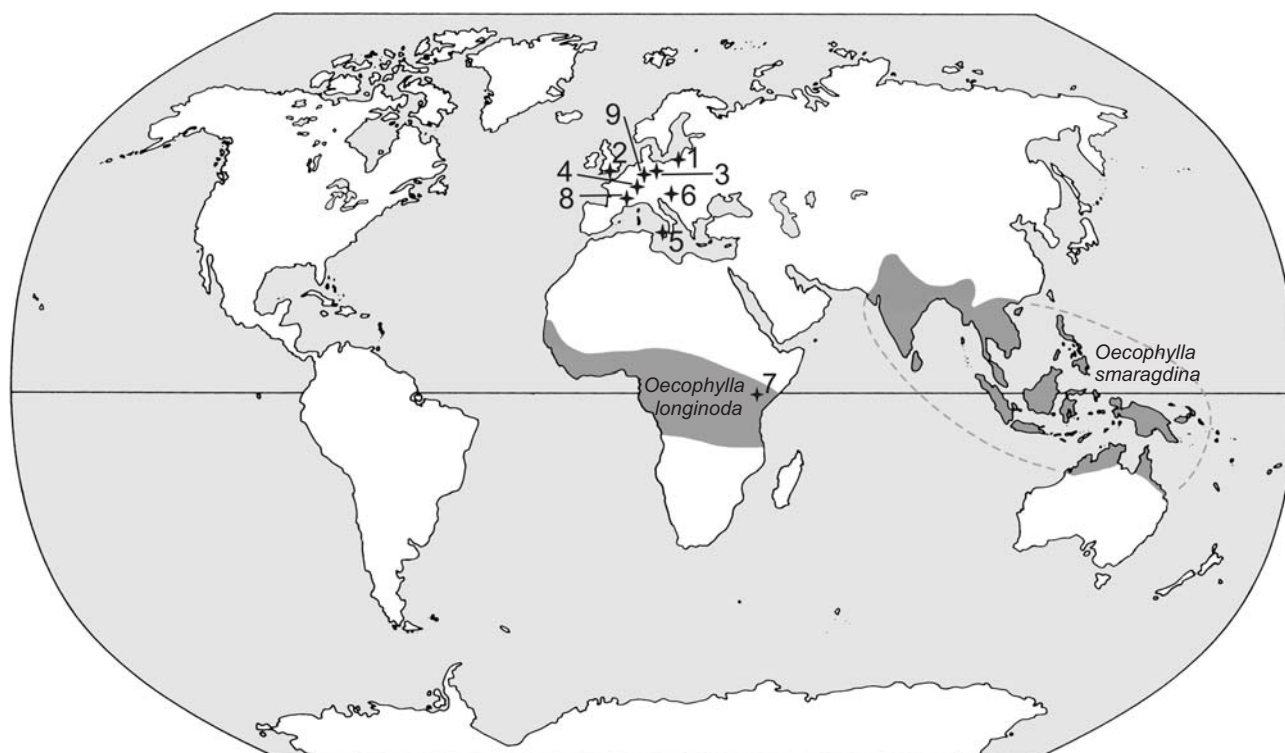http://app.pan.pl/acta53/app53-615.pdf

Fig. 1. Distribution of extant and fossil weaver ants. Extant ranges are shaded grey, fossil sites are marked with an asterisk. Abbreviations: 1, Baltic amber; 2, Bournemouth and Isle of Wight; 3, Saxonian amber; 4, Brunstatt and Kleinkembs; 5, Sicilian amber; 6, Radoboj; 7, Mfwangano Island; 8, Montagne d'Andance; 9, Messel and Eckfeld. Distribution of extant species modified after Lokkers (1986).

Oecophylla brischkei, *O. crassinoda*, and *O. sicula* are known from worker caste. *O. leakeyi* is known from a fossil nest with numerous pupae, larvae and fragments of workers. Imprints of alate queens and males represent the other species.

The real number of fossil species of *Oecophylla* is less than given above. *Oecophylla perdita* perhaps is a junior synonym of *O. atavina*. Judging from the figure of *O. xiejiaheensis* in Zhang (1989) this species does not represent an *Oecophylla* and is transferred here to the genus *Camponotites* Dlussky, 1981. *O. bartoniana* and *O. praeclara* were described from forewings only, so they may be conspecific with other species, known from complete imprints. But in any case the fossil *Oecophylla* species demonstrate that in the past the weaver ants were more widely distributed than nowadays. Noteworthy also is the coexistence of two different species in deposits of the Eocene (Baltic and Bitterfeld amber) and upper Eocene/lower Oligocene (Bembridge Marls).

During recent taxonomic work on the ant fauna from the middle Eocene of Germany two new species of *Oecophylla* were recognized in material from Messel and Eckfeld. These species are described herein (vide infra). They are of exceptional interest for two reasons: (i) these two species are among the oldest known representatives of the genus and (ii) they shed new light on the evolution of weaver ants.

Institutional abbreviations.—FIS, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main (Abteilung Messelforschung), Germany; NHMM, Naturhistorisches Museum Mainz (Landessammlung für Naturkunde Rheinland-Pfalz), Germany.

Other abbreviations.—AL, alitrunk (mesosoma) length from junction with head to that with petiole; AW, alitrunk width; BL, total body length; ED, maximum eye diameter; FWL, fore wing length; HL, head length without mandibles; HW, maximum head width; MdL, mandible length; PtL, petiole length; PtW, maximum petiole width; SL, scape length. Wing terminology (only terms not illustrated in Fig. 2): mcu, discoidal cell; rm, submarginal cell; rs-m, radio-medial crossvein. ♀, gyne; ♀♀, gynes; ♂, male; ♂♂, males.

Material and methods

The slabs with the fossils are stored permanently in glycerin to prevent damage by desiccation. The fossil specimens were photographed using a digital camera, and enlarged prints were hand traced by pen. The resulting draft drawing was scanned and improved finally using a standard graphic software. In the line drawings, full lines indicate visible sclerite boundaries, dashed lines indicate inferred sclerite boundaries, and dotted lines indicate visible margins of incomplete sclerites.

Impression fossils of ants are significantly deformed. The compaction strongly affected the estimated ant dimensions. Our experience shows that some measurements are less af-
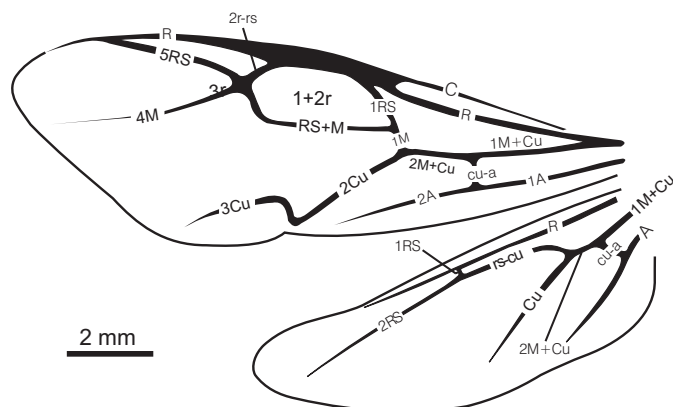
Fig. 2. Wings of weaver ant *Oecophylla longiceps* Dlussky sp. nov., drawing with nomenclature of wing venation.

fected by the deformation than the others, this especially concerns the length of the alitrunk in comparison to its width and height.

Nomenclature of the wing venation (Fig. 2) follows Dlussky (1983) and Dlussky and Rasnitsyn (2003). Other terminology is adopted from Bolton (1994).

Geological setting

The Fossillagerstätten Grube Messel and Eckfeld Maar (both in Germany) are former maar lakes of middle Eocene age. Besides plants, the insects are the most common fossils in these localities. The fossils are embedded in finely laminated bituminous claystones (so-called "oil shale").

Messel is located on the eastern side of the Rhine rift valley, about 8 km northeast of Darmstadt. The sediments of the Messel Formation are biostratigraphically dated as lower middle Eocene (Geiseltalian) (Franzen 2005). Absolute dating shows that the sediments have an age of about 47 Ma (Mertz et al 2004; Mertz and Renne 2005). The crater of former Lake Messel had a diameter of about 1.5 km and initially a depth of about 300–400 m (Harms 2002; Felder and Harms 2004). The fossil insects represent a highly diverse fauna which is mostly terrestrial (e.g., Lutz 1986, 1990; Hörnschemeyer and Wedmann 1994; Tröster 1991, 1993, 1994, 1999; Wappler 2003b, 2006; Wappler and Engel 2003; Wappler and Andersen 2004; Wedmann and Hörnschemeyer 1994; Wedmann 2005, 2007; Wedmann and Makarkin 2007; Wedmann et al. 2007; Wedmann and Yeates 2008). But although there are few body fossils of aquatic insects, a rich aquatic food web was detected (e.g,. Richter and Baszio 2001; Wedmann and Richter 2007).

Thus far more than 30,000 macrofossils have been excavated from the Eckfeld maar, documenting a highly diverse terrestrial flora and fauna (e.g., Neuffer et al. 1996; Lutz et al. 1998; Lutz and Neuffer 2000; Wappler 2002, 2003a; Wappler and Andersen 2004; Wappler and Engel 2003, 2006; Wappler et al. 2004; Wilde and Frankenhäuser 1998). This volcanic crater was filled by a freshwater lake with an origi-

nal diameter of 900 m and a depth exceeding 110 m (Pirrung et al. 2001). ^{40}Ar/^{39}Ar dating of basalt from the diatreme breccia underlying the lake sediments indicates an age of 44.3±0.4 Ma for Eckfeld (Mertz et al. 2000). With respect to the insect taphocoenosis it must be mentioned that approximately 84% of all specimens recovered are beetles (Coleoptera) (e.g., Lutz 1993; Wappler 2003a).

Systematic paleontology

Formicidae Latreille, 1809

Formicinae Latreille, 1809

Genus *Oecophylla* Smith, 1860

Type species: *Oecophylla virescens* (Fabricius, 1775), junior synonym of *Oecophylla smaragdina* (Fabricius, 1775), Recent.

Remarks.—Based on the following features the fossil ants presented here can be affiliated to Formicinae: *Oecophylla*. Characters of Formicinae are as follows: Waist consisting of one segment (petiole). Gaster without constriction between first and second segments. Antenna of male geniculate. Forewing without closed cell rm; usually sections 5RS and 4M with joint start (rs-m lost). Characters of *Oecophylla*: Forewing with narrow pterostigma and with closed cells 1+2r, 3r, closed cell and mcu absent; posterior margin of cell 3r (formed by RS) concave. Scape attached at some distance from clypeus. Mandibles large, triangular, with sharp teeth on the masticatory margin and long apical teeth. Petiole without scale.

Oecophylla longiceps Dlussky sp. nov.

Figs. 2, 3, 6A.

Etymology: *Longiceps* from the Latin "having a long head".

Type material: Holotype: Mel 3643 (♀). Paratypes: Mel 890 (♀), Mel 6220 (♀), Mel 6441 (♀), Mel 6803 (♀), Mel 7636 (♂). Other specimens: Mel 56, MeI 468, MeI 923, MeI 953, MeI 2404, MeI 3276, MeI 3344, MeI 3928, MeI 5889, MeI 6174, MeI 6282, MeI 6371, MeI 6585, MeI 6988, MeI 7165, MeI 7638, MeI 7654, MeI 8016, MeI 8657, MeI 8742, MeI 11113, MeI 11492, MeI 11661, MeI 12686, MeI 12686, MeI 12939 (♀♀);MeI 4997, MeI 5393, MeI 7865, MeI 10461, MeI 11073 (♂♂) (all FIS).

Type locality: Grube Messel, Hesse, Germany.

Type horizon: Messel Formation, middle Eocene, ca. 47 Ma (Mertz and Renne 2005).

Diagnosis.—Gynes of *O. longiceps* differ from gynes of other known species of the genus by their elongate head: the head is 1.2 times as long as wide, whereas in other species the head is as long as wide or wider than long.

Description.—Gyne. BL 12–16 mm, AL 4–5 mm, FWL 10–14 mm. Head longer than wide, narrower at its base than apically, with feebly convex sides and rounded occipital margin. Anterior margin of clypeus rounded. Eyes comparatively small, oval, situated slightly ahead midlength of head; maximum eye diameter about one-fifth of head length. Mandibles large, triangular, with large sharp apical tooth. Antennae geniculate. Scape attached at some distance from clypeus, protrudes beyond the occipital margin
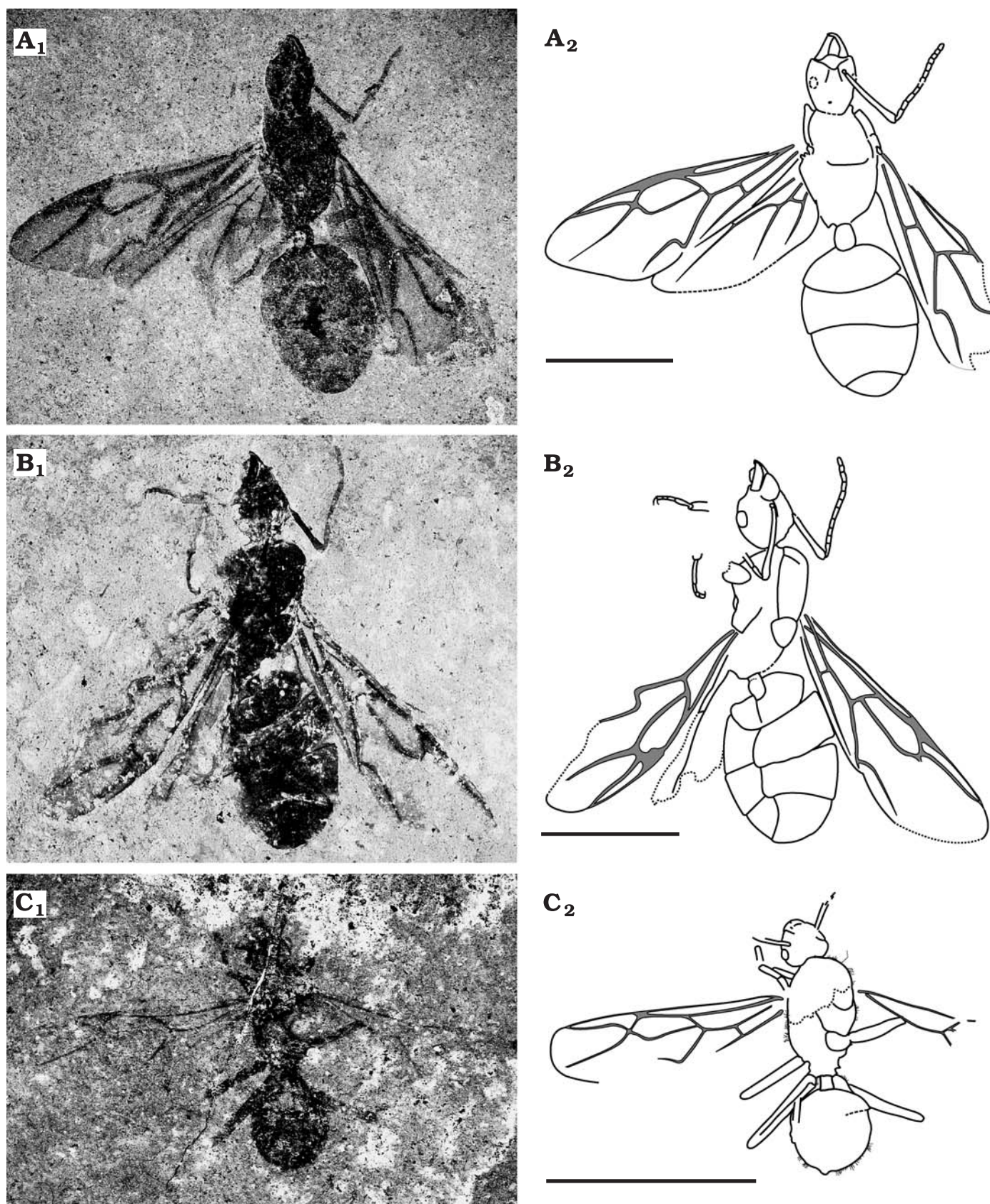
Fig. 3. Weaver ant *Oecophylla longiceps* Dlussky sp. nov., Grube Messel, middle Eocene. **A**. Gyne, holotype MeI 3643. **B**. Gyne, paratype MeI 890. **C**. Male, paratype MeI 7636. Photographs (A_1–C_1) and drawings (A_2–C_2). Scale bars 5 mm.

of the head, about 1.2 times as long as head. Joints of funiculus about twice as long than thick. Alitrunk a little wider than head. Scutum in side view feebly convex above and rounded anteriorly, not over-hanging pronotum in dorsal view. Propodeum feebly convex in side view. Legs rather short and thick. Petiole without scale or node, narrowed anteriorly and posteriorly, a little longer than wide and high. Gaster oval.

Wing venation typical for *Oecophylla*. Forewing with closed cells 1+2r, 3r, with no closed rm and mcu. Pterostigma narrow. Usually sections 5RS and 4M with joint start (rs-m lost). Cell 3r comparatively narrow, 5RS bent into 3r. 1RS and 1M form united transverse vein; 1M shorter than 1RS. 1RS inclined, forming acute angle with R; 2r-rs inclined. Section RS+M (delimiting cell 1+2r from below) bent. 3Cu convex. Hind wing with two longitudinal veins 2RS and Cu. 1RS distinct, short. Section rs-cu concave, much longer than 2M+Cu. Crossvein cu-a about as long as 2M+Cu.

Male.—BL 6–7 mm, AL about 3 mm, FWL about 6 mm. Head comparatively small, considerably narrower than alitrunk, a little wider than long. Eyes convex. Alitrunk less than twice longer than high. Legs rather long and thin. Petiole without scale or node, narrowed anteriorly, a little longer than wide. Gaster oviform. In some places on the perimeter of the paratype numerous outstanding hairs are visible, so evidently in the living specimen the complete body was coated with numerous hairs. Wing venation as in gyne.

Worker.—Unknown.

Dimensions (mm).—MeI 3643 (♀, holotype): AL = 4.5, HL = 2,3, HW = 1.9, SL = 2.7, PtL = 1.05, PtW = 0.82, FWL = 10.9; MeI MeI 890 (♀, paratype): AL = 5.0, HL = 2.5, ED = 0.57, SL = 2.6, PtL = 0.94, FWL = 10.3; MeI MeI 6220 (♀, paratype); AL = 4.0, HL = 2.2, HW = 1.8, SL = 2.6, PtL = 0.94, PtW = 0.90, FWL = 11.6; MeI 6803 (♀, paratype): AL = 4.45, HL = 2.6, FWL = 11.6; MeI 7636 (♂, paratype): BL = 6.1, AL = 2.9, HL = 0.95, HW = 1.05, PtL = 0.35, PtW = 0.29; FWL = 5.8.

Oecophylla eckfeldiana Dlussky sp. nov.

Fig. 4.

Etymology: After the type locality.

Type material: Holotype: PE-2000/8 (♀). Paratypes: PE-1992/253 (♀), PE-1994/159 (♀), PE-2000/1948 (minor worker), PE-2000/1947 (head of major worker), PE-2000/1951 (♀). Other specimens (♀♀): PE-1994/160, PE-1994/162, PE-1994/186, PE-1997/26, PE-1998/3, PE-1998/5, PE-1998/8, PE-1998/14, PE-1998/16, PE-2000/9, PE-2000/11, PE-2000/12 (all NHMM).

Type locality: Eckfeld, Germany.

Type horizon: Middle Eocene, ca. 44 Ma (Mertz et al. 2000).

Diagnosis.—Head of gynes of *O. eckfeldiana* is about as long as wide as in *O. atavina* (longer than wide in *O. longiceps*, and wider than long in fossil *O. superba* and both living species), but in *O. atavina* the head is distinctly narrower in front than behind, and the petiole is longer (twice as long as

wide and high in *O. atavina* and a little longer than wide and high in *O. eckfeldiana*).

Description.—Gyne. BL 10–14 mm, AL 3–4 mm, FWL 10–13 mm. Head about as long as wide, with convex sides, smoothly rounded occipital corners and feebly convex occipital margin. Anterior margin of clypeus rounded. Eyes comparatively small, oval, situated on the midlength of head; maximum eye diameter about 0.3–0.4 times head length. Mandibles triangular, teeth are not visible. Antennae geniculate. Scape attached at some distance from clypeus, protrudes far beyond the occipital margin of the head, 1.1–1.4 times as long as head. Joints of funiculus about 2.5 times longer than thick. Alitrunk a little wider than head. Scutum in side view feebly convex above and rounded anteriorly, not over-hanging pronotum in dorsal view. Propodeum seems to be flat in side view (it is not visible in side view in any specimens). Legs rather short and thick. Petiole without scale or node, a little longer than wide and high. Gaster oval.

Forewing with closed cells 1+2r, 3r, with no closed rm and mcu. Pterostigma narrow. Sections 5RS and 4M with joint start (rs-m lost). Cell 3r comparatively narrow, 5RS bent into 3r. 1RS and 1M form united transverse vein; 1M shorter than 1RS. 1RS inclined, forming acute angle with R; 2r-rs inclined. Section RS+M (delimiting cell 1+2r from below) bent.

Major worker (Fig. 4C).—Only one head is preserved. HL = 1.3 mm. Head as long as wide, narrower in front than behind, with rounded occipital corners and feebly convex occipital margin. Eyes oval, convex, 0.3 times as long as head. Anterior margin of clypeus rounded. Mandibles elongate, dentate. Scape attached at some distance from clypeus, far protrudes beyond the occipital margin of the head, 1.15 times as long as head.

Minor worker (Fig. 4D).—BL = 5 mm, HL = 0.5 mm. Head about as long as wide, with convex sides, smoothly rounded occipital corners and feebly convex occipital margin. Anterior margin of clypeus rounded. Frontal lobes parallel. Eyes oval, situated on the midlength of head; maximum eye diameter about one fourthhead length. Mandibles long, about half head length, triangular, with long apical teeth and more short acute teeth on the masticatory margin. Scape attached at some distance from clypeus, protrudes far beyond the occipital margin of the head, 1.5 times longer than head. Joints of funiculus about 2.5 times longer than thick. Dorsal part of alitrunk and part of petiole destroyed. Legs rather short and thick, shorter than alitrunk. Petiole seems to be without scale or node, narrower in front than behind. Presumably these workers were able to elevate their gaster, but not as good as living species and fossil *O. brischkei*. Gaster oval.

Dimensions (mm).—PE-2000/8 (♀, holotype): AL = 4.2, HL = 2.0, SL = 2.2, FWL = 10.6; PE-1992/253 (♀, paratype): AL = 3.1; HL = 1.7, HW = 1.7, SL = 2.4; PE-1994/159 (♀, paratype): AL = 3.9, HL = 2.0, HW = 2.1, FWL = 11.4; PE-2000/1947 (major worker, paratype): HL = 1.3, HW = 1.3, SL = 1.5, MdL = 0.67, ED = 0.36; PE-2000/1948 (minor worker, paratype): AL = 1.5, HL = 0.5, MdL = 0.51, SL =
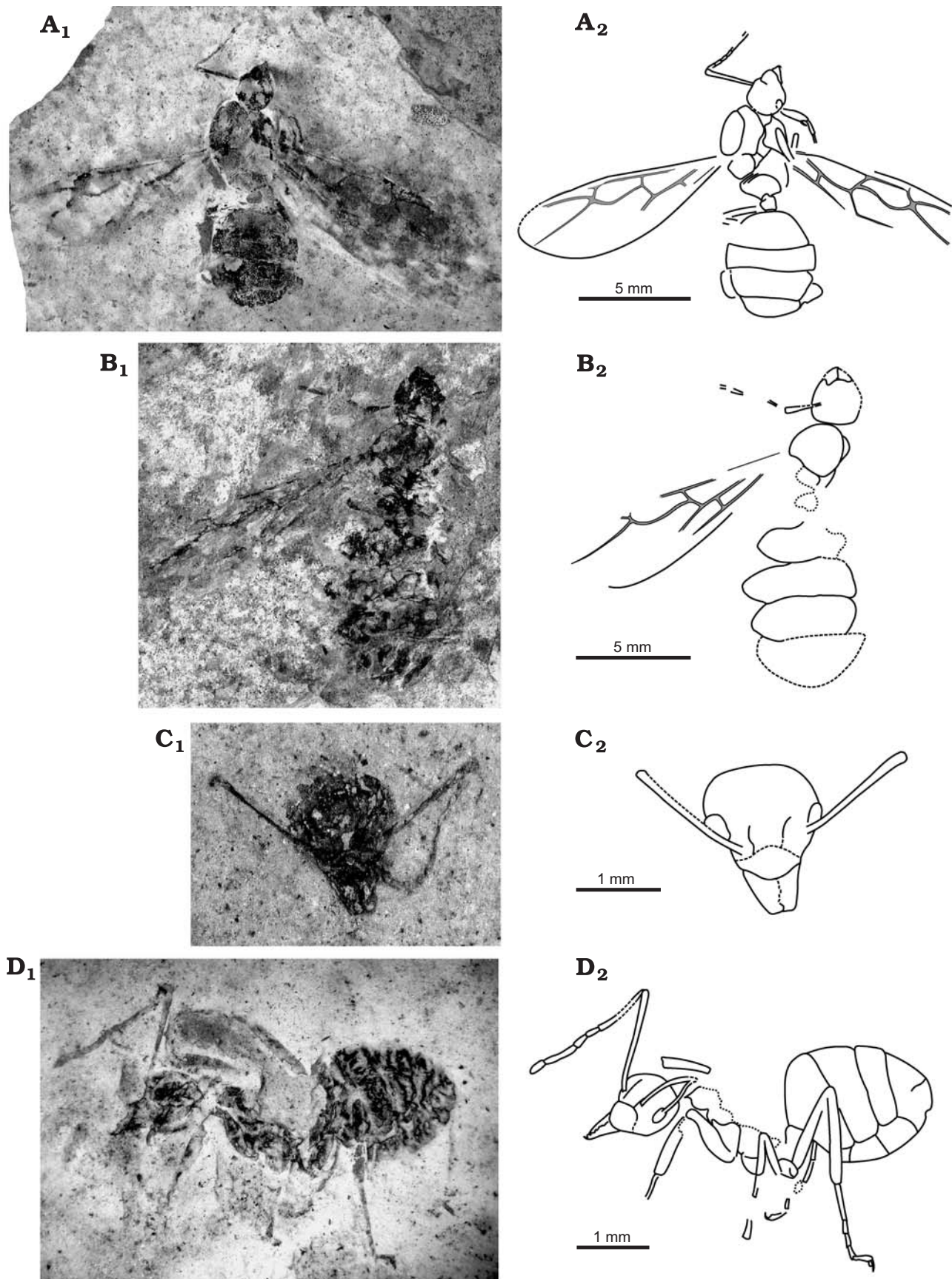
Fig. 4. Weaver ant *Oecophylla eckfeldiana* Dlussky sp. nov., Eckfeld, middle Eocene. **A**. Gyne, holotype PE-2000/8. **B**. Gyne, paratype PE-1994/159. **C**. Head of major worker, paratype PE-2000/1947. **D**. Minor worker, paratype PE-2000/1948. Photographs (A₁–D₁) and drawings (A₂–D₂).

1.4, ED = 0.24, F3L = 1.2; PE-2000/1951 (♀, paratype): AL = 3.2, HL = 1.7, HW = 1.6, SL = 1.8.

Remarks.—Described workers are different in size and proportions. However, similar differences between major and minor workers from the same colony are known in both Recent species and Miocene *Oecophylla leakeyi* (Wilson and Taylor 1964).

Discussion

Our data permit us to draw conclusions about the evolution of weaver ants from the middle Eocene to Recent. Based on detailed comparisons with the closely related extant species of *Oecophylla* we can draw inferences on on their former behaviour from the morphology of the fossil *Oecophylla* species. Therefore, we give here a short introduction to the biology of Recent weaver ants and discuss which morphological characters of these insects are connected with specific patterns of their behaviour.

Extant *Oecophylla smaragdina* and *O. longinoda* are very similar in morphology and behaviour. Their worker caste is moderately polymorphic, with allometry affecting mainly the thorax and petiole. The frequency distribution of individuals of the minor and major worker castes in both Recent species is unusual in that the majors outnumber the minors (Wilson and Taylor 1964). The major workers do most of the foraging and nest construction, while the minors remain in and around the nest, caring for the brood and queen and holding the larvae during the weaving operation in nest building (Weber 1949; Ledoux 1950).

Extant weaver ants are extremely abundant, aggressive, and territorial. Individual colonies, which are mutually antagonistic, may have a range of up to 1600 m² including about 20 trees and comprise approximately 500,000 workers (Way 1954; Hölldobler 1979, 1983). Highly organized aggressive predatory behaviour of weaver ants, combined with extensive foraging throughout the area occupied by a colony, explains their success in killing or driving away many pests or potential pests, notably Heteroptera and foliar-feeding Coleoptera. They have achieved a position of exceptional ecological importance in the rain forests, and in plantations of cacao, citrus, coconut palm, coffee, and other trees (e.g., Way and Kahoo 1992). At the same time the ants collect honeydew from coccids and other Sternorrhyncha, protect these sternorrhynchans from predators, carry them to the appropriate part of the food plant at the correct stage of the trophobionts' development. Way (1954) in particular documented such interrelations between *Oecophylla longinoda* and *Saissetia zanzibarensis* (Coccidae), and Blüthgen and Fiedler (2002) recorded a wide range of interactions between *O. smaragdina*, plants and honeydew-producing trophobionts.

Both Recent weaver ant species are wholly arboreal, living in the canopy of tropical forests. Workers move on branches, twigs and leaves and very rarely go down to the ground. They build pendulous bag-like nests with a diameter up to 0.5 m from green leaves, fastened together with silk. Ants are able to construct nests from leaves of various form and size. For example, in East Africa the nests of *O. longinoda* have been found on 89 species of tree belonging to 35 families, all evergreen, some of them by no means specialized as ant-plants (Way 1954). The silk that these ants use comes from glands of the last instar larvae which generally provide silk for the cocoon. It is interesting that larvae of *Oecophylla* and some species of *Polyrhachis*, which also make silk nests, do not spin cocoons at pupation, although most of the Formicinae do so. Both extant species of *Oecophylla* construct their nests like this: in order to make a nest wall, it is necessary for groups of workers to pull leaves together simultaneously while others hold larvae between their mandibles and move them back and forth. The process of nest construction and cooperation of workers was studied in detail by Ledoux (1949, 1950), Chauvin (1952) and other authors and reviewed by Sudd (1967).

General morphology of Recent weaver ants is determined by their mode of life. Long legs permit them to step from leaf to leaf, long antennae permit them to touch the ground, and comparatively large convex eyes provide stereoscopic vision for evaluation of distance between leaves. A similar habitus is characteristic of arboreal ants moving in tree crowns, belonging to different subfamilies, for example *Dendromyrmex* and some species of *Polyrhachis* and *Camponotus* from Formicinae, *Leptomyrmex fragilis* (F.Smith, 1859) and *Dolichoderus atellaboides* (Fabricius, 1775) from Dolichoderinae, *Aphaenogaster swammerdami* Forel, 1886 and some *Pheidole* from Myrmicinae. Some of these ants (*Oecophylla, Leptomyrmex*) also are able to pull up the gaster (Fig. 5E) like some rapidly running desert ants (some *Cataglyphis* and *Dorymyrmex*). The biomechanics and morphological changes connected with such capability were analyzed by Dlussky (1981). As a result of the elevation of the gaster the body's centre of gravity drifts forward. There are two consequences of such drifting. First, the load on the hind legs decreases. Second, the movements of the insect become more precise, especially during jumping and rotation. Rapidly running desert ants use the displacement of the centre of gravity to increase their speed of running. These ants also have enlarged hind coxae and correspondingly enlarged coxal muscles. In contrast, the hind coxae of arboreal ants which are able to lift their gaster are not increased, so these arboreal ants use the displacement of the centre of gravity not for increasing of their speed of running but only for greater precision of movement.

The elongated propodeum and petiole of *Oecophylla* are related to the capacity to pull up the gaster. Vertical movements of the gaster of ants with a one-segmented waist are realized by two articulations (one between propodeum and petiole and the other between petiole and gaster) and four pairs (elevators and depressors) of muscles (two in the propodeum and two in the petiole). The bases of the elevator muscles fasten on the anterior parts of the propodeum and petiole, and the bases of the depressor muscles fasten on the dorsal part of

these segments. Improvement of gaster elevation is related to lengthening of the elevators and correspondingly increased distance between origin and base of these muscles. Such ants have an elongated propodeum and petiole. Their petioles are pedunculate or triangular in profile view. By contrast, ants that intensively tuck their gaster (most Formicinae) have lengthened depressors and correspondingly convex propodeal dorsum and a high petiole with a scale.

One of the main patterns of *Oecophylla* nest construction is drawing the leaves together. Perhaps a speciality of the mandible construction of these ants is connected with such behaviour. Their mandibles have very large acute apical teeth (Fig. 5F), which permit the ants to hold the leaves and draw them together.

Oecophylla longinoda produces sexuals throughout the year under West African forest conditions. After the nuptial flight, the fecundated gyne attempts to establish a colony. She lays eggs that develop into workers. At a temperature of 30° C larvae hatch in 10 days, and 18 days later first workers appear. At the beginning the queen and her offspring live on leaves without any nest. When the first mature larvae have developed the queen uses their silk to construct an awning. Only the first workers construct the first chamber from leaves. In nature, very few of the attempts to start colonies in this way meet with success (Ledoux 1949, 1950). More successful is a cooperative foundation of colony by several queens (pleometrosis), described in both *O. longinoda* and *O. smaragdina* (Peeters and Andersen 1989). The general advantages of pleometrosis include a faster increase in the number of workers in a colony, thus producing a foraging workforce more rapidly. This is important, because dealate queens do not forage and thus feed the first brood on their metabolized wing muscles and fat reserves. Cooperation of young queens also guarantees a better protection of the young colony from various insect enemies. Later only one of these founder queens remains.

A mature *Oecophylla* colony possesses many (up to 150) nests, however, the colonies are monogynous so the queen is present only in the main nest (Way 1954; Vanderplank 1960). The complete worker population of the colony (up to 500,000) is the offspring of one queen. So queens of Recent *Oecophylla* are very fecund. The queen may produce hundreds of eggs a day (Hölldobler and Wilson 1977). Gynes of Recent *Oecophylla* have a large heavy gaster that contains many ovarioles, which is related to their high fertility and other morphological characters. First, these gynes have a wide and massive alitrunk which houses their large flying muscles. The scutum is particularly large (connected with the muscles of the forewings), it overhangs the pronotum in dorsal view. Second, the main function of the petiolar muscles is not the elevation of the gaster (as in workers), but the fixing of the heavy gaster in a horizontal position. This task demands not lengthening, but strengthening of the gaster elevators. So the gyne's petiole of Recent species is wide with massive knolls where the gaster elevators originate (Fig. 6C).

The comparison of Recent and fossil species demonstrates gradual changes of the afore-mentioned characters.

Wilson and Taylor (1964) pointed out a morphocline in the increase of length of the legs, antennae and petiole, and the narrowing of the metathoracic constriction of *Oecophylla* workers in the row: *O. crassinoda* (Baltic amber) ÷ *O. brischkei* (Baltic amber) ÷ *O. sicula* (Sicilian amber) ÷ *O. longinoda* + *O. smaragdina* (Recent). They concluded that the fossil species exhibit the approximate phylogenetic succession that must have occurred in the evolution of the modern species of *Oecophylla*. Wilson and Taylor (1964) also demonstrated that Miocene *O. leakeyi* had a polymorphism of workers like in Recent species.

Good indices of body gracility are the ratio of length versus width of alitrunk (AI = AL/AW) and the ratio of scape length versus head length (SI = SL/HL). In major workers of recent *O. longinoda* and *O. smaragdina* AI = 3.1–3.4 and SI = 1.4–1.6. Ants which move mainly on the ground and on tree trunks usually have a more compact alitrunk and a shorter scape. For example in *Formica* Linnaeus, 1758 AI = 2.0–2.7 and SI = 0.9–1.2, and in *Lasius* Fabricius, 1804 AI = 1.8–2.05 and SI = 0.7–1.05. Some fast running desert ants have an elongate alitrunk, however, their scape is comparatively shorter than in recent *Oecophylla*. For example in *Cataglyphis* Förster, 1850 AI = 2.5–3.0 and SI = 0.95–1.2.

Fossil *Oecophylla* differ from Recent species in their proportions. In the holotype *O. crassinoda* AI = 2.3 and SI = 0.9 and in *O. brischkei* AI = 2.7–2.8 and SI = 1.1–1.2. The alitrunk of workers of *O. eckfeldiana* described in this paper is partially destroyed, so calculation of AI is impossible for this species but its SI = 1.15 as in *O. brischkei*. So middle Eocene *O. eckfeldiana* (Fig. 4D) demonstrate first adaptation for moving in foliage canopy (lengthening legs and antennas, construction of petiole for elevation of the gaster). More specialized adaptations for an arboreal life (specialized construction of petiole for more intensive elevation of the gaster than in *O. eckfeldiana*) are found in middle to late Eocene *O. brischkei* (Fig. 5C). In Recent *O. longinoda* and *O. smaragdina* (Fig. 5E) these arboreal adaptations are even more extreme.

O. crassinoda differs from this line. It had a comparative short alitrunk and antennas (AI = 2.3, SI = 0.9) and a short nodiform petiole (Fig. 5B), so it was not able to elevate its gaster. Also the apical tooth of the mandible of *O. crassinoda* (Fig. 5A) is comparatively shorter and thicker than in Recent species (Fig. 5F) and Eocene *O. brischkei* (Fig. 5D) (a character which we connect with behaviour during nest construction).

The presence of two species of *Oecophylla* in the Baltic amber documents that in the middle to late Eocene there were two different ecological niches realised to avoid competition between these species. Perhaps *O. brischkei* moved in the foliage canopy like Recent species and *O. crassinoda* (Fig. 5A, B) moved on the tree trunks and large branches. One of the authors (GMD.) observed such division between two endemic species of *Camponotus* in Tonga: *C. nigrifrons* Mayr, 1870 build their nests in tree trunks and rotten brunches, whereas *C. conicus* Mayr, 1876 live in the canopy and build their nests in lianas.
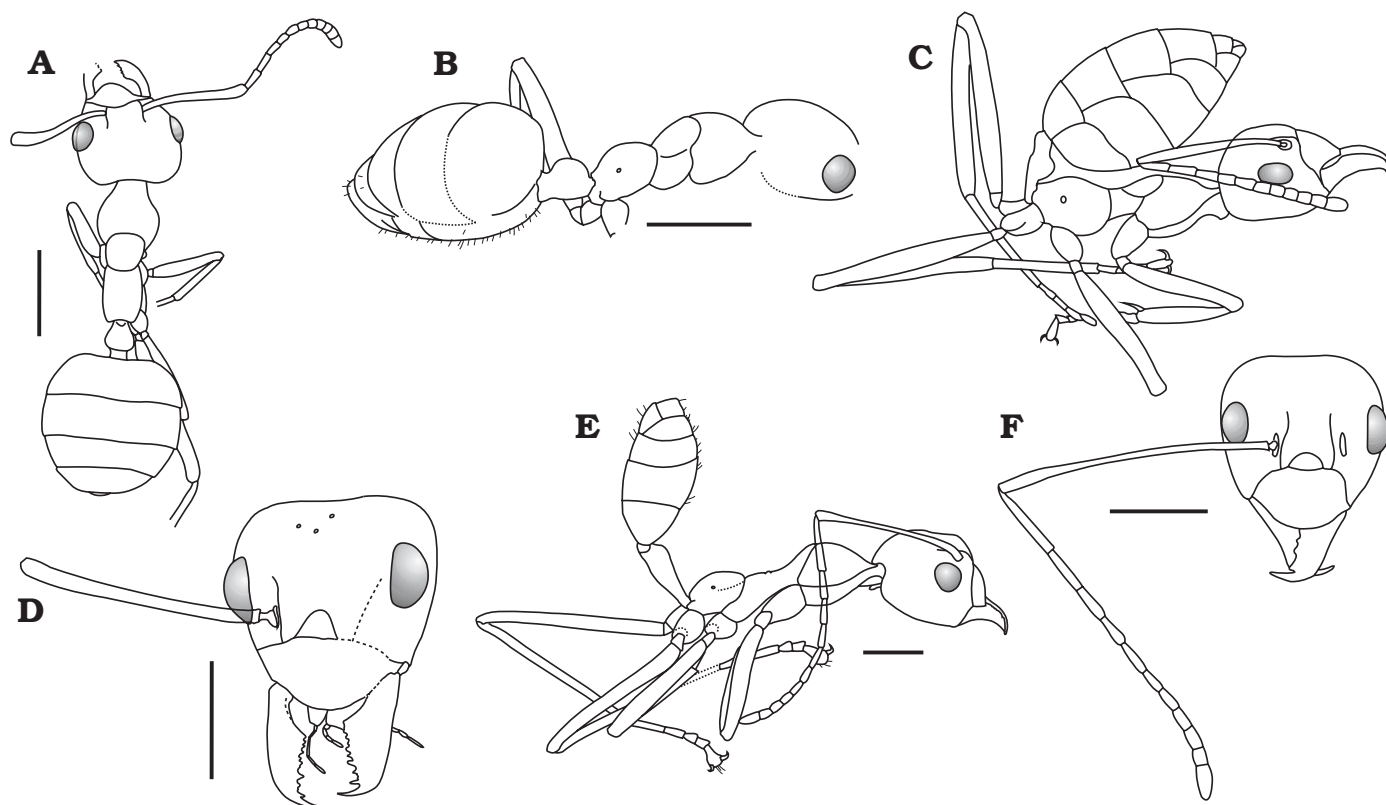
Fig. 5. Workers of different species of *Oecophylla* weaver ants. **A**. Dorsal view of *Oecophylla crassinoda* Wheeler, 1922, Baltic amber, middle to late Eocene, holotype GZG BST.4620. **B**. Side view of *O. crassinoda* Wheeler, 1922, Bitterfeld amber, middle to late Eocene, Humboldt Museum No 11/214. **C**. Side view of *Oecophylla brischkei* Mayr, 1868, Baltic amber, middle to late Eocene (from Wheeler 1915, with some changes). **D**. Head of *O. brischkei* Mayr, 1868, Baltic amber, middle to late Eocene, GZG.BST.04618. **E**. Side view of major worker of Recent *Oecophylla smaragdina* (Fabricius, 1775) from Vietnam. **F**. Frontal view of head of major worker of *O. smaragdina* (Fabricius, 1775). Scale bars 1 mm.

Two sympatric species of *Oecophylla* also exist in the late Eocene/early Oligocene deposits of Bembridge Marls. They differ by size: in *O. atavina* the forewing of gynes is 9–13 mm long, in *O. megarche* the forewings have a length of 20–24 mm. However, we cannot say anything about differences in biology of these species, as only wings and small fragments of bodies of gynes of *O. megarche* are preserved.

Concerning the morphology of the gynes (Fig. 6), an evolutionary trend towards the elongation of the petiole seems to be detectable. The petiole is a little longer than wide and high in middle Eocene *O. longiceps* and *O. eckfeldiana* and it is twice as long as wide and high in Oligocene *O. atavina*. The petiole of *O. longiceps* is the most plesiomorphic. It is narrowed anteriorly and posteriorly in dorsal view like in *Eoformica pinguis* (Scudder, 1877) from the middle Eocene of North America (Dlussky and Rasnitsyn 2003). The petiole of *O. eckfeldiana* is about rectangular. The petiole of *O. atavina* is trapezoidal, like in workers of Recent species. It seems that changes in gyne petiole construction reflect the evolution of the petiole in workers, which is probably connected with the improvement of elevation of the gaster. It is known that in ants with primitive colony organization the gynes are similar to workers and differ mostly by the construction of alitrunk and the presence of ocelli, which is con-

nected with their ability to fly. The morphological divergence of gynes seems to become more pronounced in species in which the behaviour is different from the behaviour of the workers. This seems to be mostly connected with increasing fertility of the gyne. The gynes' petioles of Recent weaver ant species and Oligocene *O. superba* are different from that of the associated workers. We have not seen *O. superba* but infer information on this species on the base of drawing by Théobald (1937). In the gynes of that species the petiole is wider than long in dorsal view and in *O. smaragdina*; it has a pair of massive knolls where the gaster elevators originate. Such construction is connected with increasing of gyne fertility and correspondingly with increasing of weight of the gaster (see above). Also these gynes had a wider and massive alitrunk connected with the enlarged flying muscles. Thus we can conclude that gynes of *O. longiceps, O. eckfeldiana,* and *O. atavina* were not so fertile, and their colony populations were not as numerous as those of Recent species.

Another tendency in the *Oecophylla* gynes' evolution is expressed in the changes of the head form. In *O. longiceps* it is longer than wide, without developed occipital corners. The head of *O. eckfeldiana* is squarish, about as long as wide, with convex sides and smoothly rounded occipital corners. In *O. atavina* and *O. megarche* it is subtrapezoid, with dis-
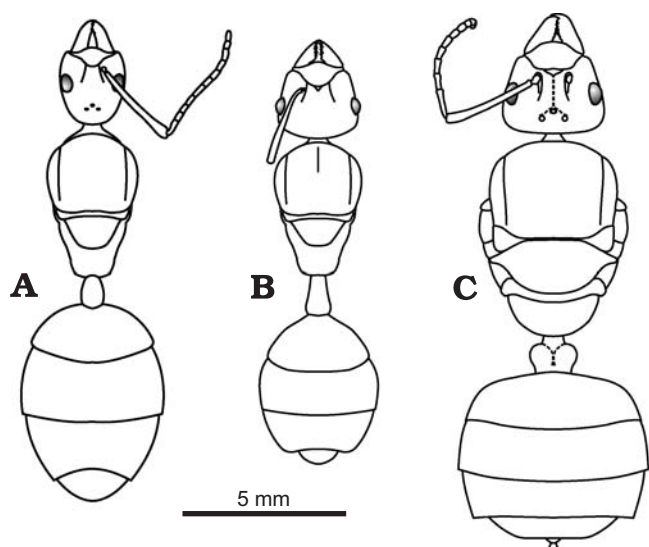
Fig. 6. Gynes of different species of *Oecophylla* weaver ants. **A**. Reconstruction of *Oecophylla longiceps* sp. nov., Grube Messel, middle Eocene. **B**. Reconstruction of *Oecophylla atavina* Cockerell, 1915, Bembridge Marls, Oligocene. **C**. *Oecophylla smaragdina* (Fabricius, 1775), Recent, Vietnam.

tinct occipital corners, about as long as wide, and in Recent *Oecophylla smaragdina* it is distinctly trapezoid, wider than long. Such changes are related to the strengthening (increasing of muscle bulk) of the mandibular compressors, which bases fasten in the occipital corners (Dlussky and Fedoseeva 1988). We cannot explain the reason for these changes. Queens of *Oecophylla* neither hunt nor construct nests. Also these changes are not connected with changes in workers. The heads of workers of middle Eocene *O. eckfeldiana*, late Eocene *O. brischkei*, Miocene *O. leakeyi* and Recent species have a similar form, about as long as wide or a little longer than wide (HL/HW = 1.0–1.05).

The most difficult problem is the origin and evolution of nest construction of weaver ants. Sudd (1967) pointed out that weaver ants build their nests in a way that cannot easily be brought into line with the methods ants use to build nests of soil. The strong dragging movements that weaver ants use to pull leaves together seems to have more in common with the transport of prey than with nest building. Several studies support the notion that weaving evolved separately at least four times in the Formicinae (Hölldobler and Wilson 1983; Johnson et al. 2003). This convergent evolution in other ant taxa gives possible examples for intermediate stages of the highly specialized weaving behaviour of *Oecophylla* (Hölldobler and Wilson 1983, 1990). The most primitive stage is the nest construction of *Dendromyrmex chartifex* (F. Smith, 1860); more specialized is behaviour of some *Polyrhachis* and *Camponotus senex* (F. Smith, 1858); and nest construction is most specialized in *Oecophylla*. Maybe some differences in mandible construction between *O. brischkei* and Recent species indicate some specialisation in nest-construction behaviour from the middle to late Eocene to modern time. Recent *Oecophylla* species have a more massive and stronger apical tooth

of mandible (perhaps used for dragging of leaves) than *O. brischkei* (Fig. 5D, F). Until now we can say that Miocene *O. leakeyi* constructed nests from leaves similar to Recent species. This is documented by the finding of a fossil nest of this species with numerous pupae and remains of leaves (Wilson and Taylor 1964). As far as the colony structure is concerned, colony structures seen in weaving ant species suggest an association between polydomy (that is, multiple nests for one colony) and weaving (Johnson et al. 2003). Nest construction with leaves limits the size of one nest; multiple nest sites allow the colony to grow. Therefore it seems reasonable to assume that *O. leakeyi* had a similar polydomous colony structure as the extant species of *Oecophylla*.

Thus, paleontological data demonstrate a gradual adaptation of *Oecophylla* to movement in the canopy foliage and an increasing fertility of their queens. When these ants began to construct nests from leaves and how their behaviour during nest construction evolved is obscure, but a polydomous colony structure at least since the Miocene is probable.

Fossil impressions of *Oecophylla* might also demonstrate a dynamic of participation of these ants in the ancient ant assemblages in Europe. Based on our data from the deposits of Messel (middle Eocene) they account 11% of all ants; in Eckfeld (also middle Eocene, but three million years younger than Messel)—15%; and in Bembridge Marls (Lower Oligocene, perhaps Upper Eocene)— 51%. Only one specimen of 241 (0.4%) was found in Oligocene deposits of Kleinkembs (Théobald, 1937), and only 4 of 136 (3%) in the Lower Miocene deposits of Radoboj (Mayr, 1867). We did not find these ants in the Upper Oligocene deposits of Rott (60 samples studied) and Enspel (47 samples studied).

The biogeographical distribution of fossil and extant species of *Oecophylla* is shown in Fig. 1. Already Wilson and Taylor (1964) commented on the absence of this taxon in the New World. It seems most likely that the genus was widely distributed and perhaps originated sometime during the early Tertiary in the Palaearctic realm, experiencing significant radiation during the climatic changes of the Eocene–Oligocene transition. This scenario fits with the results on the phylogeography of *O. smaragdina* (Azuma et al. 2006). Here it is proposed that the extant *O. smaragdina* and *O. longinoda* diverged between 13 to 11 Ma in the late Miocene. Subsequently *O. smaragdina* diverged into its seven extant subgroups between 7.8 and 3.6 Ma.

Clearly, numerous fossils of weaver ants await discovery and these will undoubtedly provide significant insights into the evolutionary history of this genus.

Acknowledgements

References

Azuma, N., Ogata, K., Kikuchi, T., and Higashi, S. 2006. Phylogeography of Asian weaver ants, *Oecophylla smaragdina*. *Ecological Research* 21: 126–136.

Blüthgen, N. and Fiedler, K. 2002. Interactions between weaver ants *Oecophylla smaragdina*, homopterans, trees and lianas in an Australian rain forest canopy. *Journal of Animal Ecology* 71: 793–801.

Bolton, B.A. 1994. *Identification Guide to the Ant Genera of the World*. 222 pp. Harvard University Press, Cambridge, Massachusetts.

Bolton, B., Alpert, G., Ward, P. S., and Nasrecki, P. 2006. *Bolton's Catalogue of Ants of the World*. Harvard University Press, Cambridge, Massachusetts, CD-ROM.

Chauvin, R. 1952. Sur la reconstruction du nid chez les fourmis Oecophylles (*Oecophylla longinoda* L.). *Behaviour* 4: 190–201.

Cockerell, T.D.A. 1915. British fossil insects. *Proceedings of the United States National Museum* 49: 469–499.

Cockerell, T.D.A. 1920. Fossil arthropods in the British Museum. 1. *Annals and Magazine of Natural History* 9: 273–279.

Dlussky, G.M. 1981. *Murav'i pustyn'*. 230 pp. Nauka, Moskva.

Dlussky, G.M. 1983. A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between the ants and scolioids [in Russian, English translation: *Paleontological Journal* 17: 63–76]. *Paleontologičeskij žurnal* 1983 (3): 65–78.

Dlussky, G.M. [Dlusskij, G.M.] and Fedoseeva, E.B. 1988. The origin and early evolutional steps of ants (Hymenoptera: Formicidae) [in Russian]. *In*: A.G. Ponomarenko (ed.), *Melovoj biocenotičeskij krisis i evoluciâ nasekomyh*, 70–144. Nauka, Moskva.

Dlussky G.M. and Rasnitsyn A.P. 2003. Ants (Hymenoptera: Formicidae) of Formation Green River and some other middle Eocene deposits of North America. *Russian Entomological Journal* 11 (for 2002): 411–436.

Emery, C. 1891. Le formiche dell'ambra Siciliana nel Museo Mineralogico dell'Università di Bologna. *Memorie della Reale Accademia delle Scienze dell'Istituto di Bologna* 5: 141–165.

Fabricius, J.C. 1775. *Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. 832 pp. Libraria Kortii, Flensburgi et Lipsiae.

Felder, M. and Harms, F.-J. 2004. Lithologie und genetische Interpretation der vulkano-sedimentären Ablagerungen aus der Grube Messel anhand der Forschungsbohrung Messel 2001 und weiterer Bohrungen. *Courier Forschungsinstitut Senckenberg* 252: 151–203.

Förster, B. 1891. Die Insekten des "Plattigen Steinmergels" von Brunstatt. *Abhandlungen zur Geologischen Spezialkarte von Elsass-Lothringen* 3: 333–594.

Franzen, J.L. 2005. The implications of the numerical dating of the Messel fossil deposit (Eocene, Germany) for mammalian biochronology. *Annales de Paléontologie* 91: 329–335.

Fuhrmann, R. 2005. Die Bernsteinlagerstätte Bitterfeld, nur ein Höhepunkt des Vorkommens von Bernstein (Succinit) im Tertiär Mitteldeutschlands. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* 156: 517–529.

Harms, F.-J. 2002. Steine erzählen Geschichte(n): Ursache für die Entstehung des Messel-Sees gefunden. *Natur und Museum* 132: 1–4.

Heer, O. 1849. *Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Zweiter Theil: Heuschrecken, Florfliegen, Aderflügler, Schmetterlinge und Fliegen*. vi + 264 pp. W. Engelmann, Leipzig.

Hölldobler, B. 1979. Territories of the African weaver ant (*Oecophylla longinoda* [Latreille]). *Zeitschrift fur Tierpsychologie* 51: 201–213.

Hölldobler, B. 1983. Territorial behaviour in the green tree ant (*Oecophylla smaragdina*). *Biotropica* 15: 241–250.

Hölldobler, B. and Wilson, E.O. 1977. Weaver Ants. *Scientific American* 237: 146–154.

Hölldobler, B. and Wilson, E.O. 1983. The evolution of communal nest-weaving in ants. *American Scientist* 71: 490–499.

Hölldobler, B. and Wilson, E.O. 1990. *The ants*. 732 pp. Springer Verlag, Berlin.

Hörnschemeyer, T. and Wedmann, S. 1994. Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 1. *Courier Forschungsinstitut Senckenberg* 170: 85–136.

Hoffeins, C. and Hoffeins, H.W. 2003. Untersuchungen über die Häufigkeit von Inklusen in Baltischem und Bitterfelder Bernstein (Tertiär, Eozän) aus unselektierten Aufsammlungen unter besonderer Berücksichtigung der Ordnung Diptera. *Studia Dipterologica* 10: 381–392.

Hooker, J.J., Collinson, M., Grimes, S., Sille, N., and Mattey, D. 2007. Discussion on the Eocene–Oligocene boundary in the UK. *Journal of the Geological Society* 164: 685–688.

Hong, Y.-C. 1984. Fossil insects in the diatoms of Shanwang. *Bulletin of the Tianjin Institute of Geology and Mineral Resources* 8: 1–15.

Johnson, R.N., Agapow, P.-M., and Crozier, R.H. 2003 A tree island approach to inferring phylogeny in the ant subfamily Formicinae, with especial reference to the evolution of weaving. *Molecular Phylogenetics and Evolution* 29: 317–330.

Knuth, G., Koch, T., Rappsilber, I., and Volland, L. 2002. Zum Bernstein im Bitterfelder Raum – Geologie und genetische Aspekte. *Hallesches Jahrbuch für Geowissenschaften B* 24: 35–46.

Latreille, P.A. 1802. Description d'une nouvelle espece de fourmi. *Bulletin des Sciences par la Societe Philomathique* 3: 65–66.

Latreille, P.A. 1809. *Genera crustaceorum et insectorum, secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata*. 399 pp. Amand Koenig, Paris.

Ledoux, A. 1949. Le cycle évolutif de la fourmi fileuse (*Oecophylla longinoda* Latr.). *Comptes rendus de l'Académie des Sciences* 229: 246–248.

Ledoux, A. 1950. Recherche sur la biologic de la fourmi fileuse (*Oecophylla longinoda* Latr.). *Annales des Sciences Naturelles (Zoologie)* 12: 313–461.

Lokkers, C. 1986. The distribution of the Weaver Ant, *Oecophylla smaragdina* (Fabricius) (Hymenoptera, Formicidae) in Northern Australia. *Australian Journal of Zoology* 34: 683–687.

Lutz, H. 1986. Eine neue Unterfamilie der Formicidae (Insecta: Hymenoptera) aus dem mittel-eozänen Ölschiefer der "Grube Messel" bei Darmstadt (Deutschland, S-Hessen). *Senckenbergiana lethaea* 67: 177–218.

Lutz, H. 1990. Systematische und palökologische Untersuchungen an Insekten aus dem Mittel-Eozän der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg* 124: 1–165.

Lutz, H. 1993. Zur Taphonomie der aquatischen und terrestrischen Fauna des "Eckfelder Maares" (Mittel-Eozän; Deutschland): Ergebnisse aus den Grabungen 1990–1992. *Mainzer Naturwissenschaftliches Archiv* 31: 85–113.

Lutz, H., Frankenhäuser, H., and Neuffer, F.O. 1998. *Fossilfundstätte Eckfelder Maar – Archiv eines mitteleozänen Lebensraumes in der Eifel*. 51 pp. Landessammlung für Naturkunde, Mainz.

Lutz, H. and Neuffer, F. O. 2000. The middle Eocene fossillagerstätte Eckfeld Maar. *Geologiska Föreningen* 122: 95–96.

Mayr, G. 1867. Vorläufige Studien über die Radoboj-Formiciden, in der Sammlung der k.k. geologischen Reichsanstalt. *Jahrbuch der k.k. Geologischen Reichsanstalt. Wien* 17: 47–62.

Mayr, G. 1868. Die Ameisen des baltischen Bernsteins. *Beiträge zur Naturkunde Preussens* 1: 1–102.

Mertz, D.F. and Renne, P.R. 2005. A numerical age for the Messel fossil deposit (UNESCO World Heritage Site) derived from 40Ar/39Ar dating on a basaltic rock fragment. *Courier Forschungsinstitut Senckenberg* 255: 67–75.

Mertz, D.F., Harms, F.-J., Gabriel, G., and Felder, M. 2004. Arbeitstreffen in der Forschungsstation Grube Messel mit neuen Ergebnissen aus der Messel-Forschung. *Natur und Museum* 134: 289–290.

Mertz, D. F., Swisher, C.C., Franzen, J.L., Neuffer, F.O., and Lutz, H. 2000. Numerical dating of the Eckfeld maar fossil site, Eifel, Germany: A calibration mark for the Eocene time scale. *Naturwissenschaften* 87: 270–274.

Neuffer, F.O., Gruber, G., Lutz, H., and Frankenhäuser, H. 1996. *Das Eckfelder Maar – Zeuge tropischen Lebens in der Eifel*. 102 pp. Landessammlung für Naturkunde, Mainz.

Peeters, C. and Andersen, A.N. 1989. Cooperation between dealate queens during colony foundation in the Green tree ant, *Oecophylla smaragdina*. *Psyche* 96: 39–44.

Pirrung, M., Büchel, G., and Jacoby, W. 2001. The Tertiary volcanic basins of Eckfeld, Enspel and Messel (Germany). *Zeitschrift der Deutschen Geologischen Gesellschaft* 152: 27–59.

Richter, G. and Baszio, S. 2001. Traces of a limnic food web in the Eocene lake Messel—a preliminary report based on fish coprolite analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166: 345–368.

Riou, B. 1999. Descriptions de quelques insectes fossiles du Miocène supérieur de la Montagne d'Andance (Ardèche, France). *École Pratique des Hautes Études, Biologie et Evolution des Insectes* 11/12: 123–133.

Röschmann, F. and Mohrig, W. 1995. Die Trauermücken des Sächsischen Bernsteins aus dem Untermiozän von Bitterfeld/Deutschland (Diptera, Sciaridae). *Deutsche Entomologische Zeitschrift* 42: 17–54.

Schumann, H. and Wendt, H. 1989. Kenntnis der tierischen Inklusen des Sächsischen Bernsteins. *Deutsche Entomologische Zeitschrift* 36: 33–44.

Smith, F. 1860. Catalogue of hymenopterous insects collected by Mr. A. R. Wallace in the Islands of Bachian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea. *Journal of the Proceedings of the Linnean Society of London, Zoology* 5: 93–143.

Sudd, J.H. 1967. *An Introduction to the Behaviour of Ants*. 200 pp. Edward Arnold, London.

Théobald, N. 1937. *Les insectes fossiles des terrains oligocènes de France*. 473 pp. G. Thomas, Nancy.

Tröster, G. 1991. Eine neue Gattung der Elateridae (Insecta: Coleoptera) *Macropunctum* gen. n. aus der Messel-Formation des unteren Mittel-Eozän der Fundstätte Messel. *Courier Forschungsinstitut Senckenberg* 139: 99–117.

Tröster, G. 1993. Wasserkäfer und andere Raritäten – Neue Coleoptera-Funde aus den mitteleozänen Tonsteinen der Grube Messel bei Darmstadt. *Kaupia – Darmstädter Beiträge zur Naturgeschichte* 2: 145–154.

Tröster, G. 1994. Fossile Elateridae (Insecta: Coleoptera) aus dem Unteren Mitteleozän (Lutetium) der Grube Messel bei Darmstadt. *Courier Forschungsinstitut Senckenberg* 170: 11–64.

Tröster, G. 1999. An unusual new fossil click-beetle (Coleoptera: Elateridae) from the middle Eocene of the Grube Messel (Germany). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1999: 11–20.

Vanderplank, F.L. 1960. The bionomics and ecology of the red tree ant, *Oecophylla* sp. and its relationship to the coconut bug *Pseudotheraptus wayi* Brown (Coreidae). *The Journal of Animal Ecology* 29: 15–33.

Wappler, T. 2002. *Dicranoptycha* (Insecta: Nematocera: Limoniidae) aus der mitteleozänen Fossillagerstätte Eckfelder Maar bei Manderscheid / Eifel (Deutschland). *Mainzer Naturwissenschaftliches Archiv* 40: 129–134.

Wappler, T. 2003a. Die Insekten aus dem Mittel-Eozän des Eckfelder Maares, Vulkaneifel. *Mainzer Naturwissenschaftliches Archiv Beiheft* 27: 1–234.

Wappler, T. 2003b. New fossil lace bugs (Heteroptera: Tingidae) from the Middle Eocene of the Grube Messel (Germany), with a catalog of fossil lace bugs. *Zootaxa* 374: 1–26.

Wappler, T. 2006. *Lutetiacader*, a puzzling new genus of cantacaderid lace bugs (Heteroptera: Tingidae) from the Middle Eocene Messel Maar, Germany. *Palaeontology* 49: 435–444.

Wappler, T. and Andersen, N.M. 2004. Fossil water striders from the Middle Eocene fossil sites of Eckfeld and Messel, Germany (Hemiptera, Gerromorpha). *Paläontologische Zeitschrift* 78: 41–52.

Wappler, T. and Engel, M.S. 2003. The middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea). *Journal of Paleontology* 77: 908–921.

Wappler, T. and Engel, M.S. 2006. A new record of *Mastotermes* from the Eocene of Germany (Isoptera: Mastotermitidae). *Journal of Paleontology* 80: 380–385.

Wappler, T., Smith, V. S., and Dalgleish, R.C. 2004. Scratching an ancient itch: an Eocene bird louse fossil. *Proceedings of the Royal Society of London B* 271 (Supplement to No. 5): 255–258.

Way, M.J. 1954. Studies on the life history and ecology of the ant *Oecophylla longinoda* Latreille. *Bulletin of Entomological Research* 45: 93–112.

Way, M. and Kahoo K. 1992. Role of ants in pest management. *Annual Review of Entom*ology 37: 479–503.

Weber, N.A. 1949. The functional significance of dimorphism in African ant, *Oecophylla*. *Ecology* 30: 397–400.

Wedmann, S. 2005. Annotated taxon-list of the invertebrate animals from the Eocene fossil site Grube Messel near Darmstadt, Germany. *Courier Forschungsinstitut Senckenberg* 255: 103–110.

Wedmann, S. 2007. A nemestrinid fly (Insecta: Diptera: Nemestrinidae: cf. *Hirmoneura*) from the Eocene Messel Pit (Germany). *Journal of Paleontology* 81: 1114–1117.

Wedmann, S. and Hörnschemeyer, T. 1994. Fossile Prachtkäfer (Coleoptera: Buprestidae: Buprestinae und Agrilinae) aus dem Mitteleozän der Grube Messel bei Darmstadt, Teil 2. *Courier Forschungsinstitut Senckenberg* 170: 137–187.

Wedmann, S. and Makarkin, V. 2007. A new genus of Mantispidae (Insecta: Neuroptera) from the Eocene of Germany, with a review of the fossil record and palaeobiogeography of the family. *Zoological Journal of the Linnean Society* 149: 701–716.

Wedmann, S. and Richter, G. 2007. The ecological role of immature phantom midges (Diptera: Chaoboridae) in the Eocene Lake Messel, Germany. *African Invertebrates* 48: 59–70.

Wedmann, S. and Yeates, D. 2008. Eocene records of bee flies (Insecta, Diptera, Bombyliidae, *Comptosia*): Their paleobiogeographic implications and remarks on the evolutionary history of bombyliids. *Palaeontology* 51: 231–240.

Wedmann, S., Bradler, S., and Rust, J. 2007. The first fossil leaf insect: 47 million years of specialized cryptic morphology and behaviour. *Proceedings of the National Academy of Sciences* 104: 565–569.

Weitschat, W. 1997. Bitterfelder Bernstein – Ein eozäner Bernstein auf miozäner Lägerstätte. *Metalla* 66: 71–84.

Wheeler, W.M. 1915. The ants of the Baltic Amber. *Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg* 55 (for 1914): 1–142.

Wheeler, W.M. 1922. Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. II. The ants collected by the American Museum Congo Expedition. *Bulletin of the American Museum of Natural History* 45: 39–269.

Wilde, V. and Frankenhäuser, H. 1998. The Middle Eocene plant taphocoenosis from Eckfeld (Eifel, Germany). *Review of Palaeobotany and Palynology* 101: 7–28.

Wilson, E.O. and Taylor, R.W. 1964. A fossil ant colony: new evidence of social antiquity. *Psyche* 71: 93–103.

Zhang, J. 1989. *Fossil Insects from Shanwang, Shandong, China*. 459 pp. Shandong Science and Technology Publishing House, Jinan.