



Giant ants from the Paleogene of Denmark with a discussion of the fossil history and early evolution of ants (Hymenoptera: Formicidae)

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Received February 1997; accepted for publication October 1997

***Pachycondyla rebekkae* sp. nov.** (Formicidae, Ponerinae) is described from the Fur and Ølst Formations (transitional between Paleocene and Eocene, Denmark). About 95 complete or fragmentary gyne specimens and one almost complete male specimen were examined, revealing characters which permit classification and placement of the fossil species in the phylogenetic system of extant Formicidae. The palaeoecology and taphonomy of the insect fauna of the Fur and Ølst Formations are discussed. Finally, the significance of the new species is discussed in light of the fossil history and early evolution of ants.

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ADDITIONAL KEY WORDS:—fossil ants – Paleogene – Ølst/Fur Formation, Denmark – palaeoecology – taphonomy – fossil history – evolution.

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INTRODUCTION

The geological deposits of the Fur Formation (also known as 'mo-clay') and the basal part of the Ølst Formation of northwestern Denmark are the oldest known Tertiary sediments with a species-rich insect fauna in Europe (Larsson, 1975; Willmann, 1990; Andersen & Andersen, 1996). The geological age is estimated to be transitional between Paleocene and Eocene or 55 Myr (Heilmann-Clausen, 1996; Bonde, 1997). The sediments of the Fur Formation, 60 m thick, are composed of porous diatomites and about 180 volcanic ash layers (numbered from -39 to +140). In a few horizons fossiliferous calcareous cementstones appear, with insects as the most common fossils. These sediments crop out chiefly in the western Limfjord area of northwestern Jutland, Denmark, in particular on the islands of Fur and Mors (see map in Willmann, 1990: fig. 1). In the last decade, enormous amounts of new insect material have been gathered, mainly by private collectors. Today, we know of about 20 000 specimens housed in various collections.

So far, relatively few insect groups of the Fur Formation have been subject to scientific studies (see Kohring, 1994 for references), in recent years chiefly by Rainer Willmann, University of Göttingen, and his associates. Among these are hymenopterous insects belonging to the families Ichneumonidae, Braconidae and Proctotrupidae (Rust, 1990). Some of the most interesting and impressive fossil insects found during the last few years are giant ants, about 25 mm long. They were first discovered in 1990 by Henrik and Rebekka Madsen (Nykøbing Mors) and apart from three specimens, all material examined by us are collected by the Madsens. In the present paper we describe the morphology of the fossil ants and discuss their classification and placement in the phylogenetic system of ants. We also discuss the palaeoecology and taphonomy of the insect fauna of the Fur and Ølst Formations. Finally we discuss the significance of the new species in light of the fossil history and early evolution of ants.

MATERIAL AND METHODS

A complete list of the material examined is given in the Appendix. This material consists of 101 more or less complete specimens or isolated body parts. One almost complete and four isolated parts of male specimens are present. All the other material belongs to females (gynes, queens) except for one isolated head, which possibly belongs to a worker ant of unknown systematic position. The fossil insects of the Fur-Formation have in most cases been found in the calcareous cementstones and within these, only in a few horizons (Larsson, 1975; Willmann, 1990; Andersen & Andersen, 1996). In contrast, the ants described here are preserved as imprints in a grey, fine-grained and weakly hardened shale ('Stolle Klint Clay'; Heilmann-Clausen, 1996), which belongs to the basal part of the Ølst Formation. Most of the specimens were collected at the Stolleklint (on the island of Fur), only one has been found in a pit near Manhøj (Fur). The geological age is about 55 Myr, and the stratigraphic position is at the level of ash layer -33. Only a few specimens have been found in the level between ash layers -28 and -24 of the Fur Formation.

The fossil specimens are generally well preserved. Their colour is light to dark brown or black, according to the degree of their original sclerotization. In most cases the gaster is swollen as a result of early taphonomic processes. In order to

obtain a clear view, the specimens were covered with distilled water while they were examined, measured and photographed. Drawings were made with the use of a camera lucida. The following description is based on the characters of all specimens. In some cases particular specimens have been indicated with reference to the list of material in the Appendix. The following abbreviations have been used for depositories of material: CM, Collection H. and R. Madsen, Nykøbing Mors; FM, Fur Museum, Fur; GMUC, Geological Museum, University of Copenhagen; and MM, Moler-museet, Skarrehage, Mors (Collection B.S. Mikkelsen), all in Denmark.

TAXONOMY

Pachycondyla rebekkae sp. nov.

(Figs 1, 2, 3A, 4, 5A, 5B, 6)

Description of gyne

Size and shape. Maximum length 25 mm. Body fairly robust (Figs 1, 5A, 6).

Head (Fig. 2A–C). Head with weakly rounded, square outline, length 4.5 mm, width 4.5 mm. Vertexal margin nearly straight, with rounded vertexal corners. Eyes (Fig. 2B, EY) oval, fully developed; each eye located near middle of the lateral margin of head; maximum ocular diameter 1 mm (GMUC No. 1995 8B; specimen without wings, Fig. 2A, B). Mandibles (Fig. 2A, C, MN) very strong, broad, elongate-triangular. External margin of each mandible almost straight; masticatory margin armed with approximately 10 strong, blunt teeth. Clypeus short, fronto-clypeal suture apparently moderately curved. Frontal carinae weakly preserved, possibly vestigial. Antennae long, with at least 11 segments. Scape (Fig. 2B, SC) elongate, about 3.4 mm long, slightly widened distally. Funiculus (Fig. 2B, FU) filiform, about 4.7 mm long, only slightly widened distally. Antennae inserted close to the posterior clypeal margin. Three ocelli weakly preserved in the centre of the face of one isolated head (CM No. 16-A4345).

Mesosoma. Length about 7 mm, width about 4.5 mm (GMUC No. 1994 8). Mesosoma convex and domed, compact in lateral view, without sculpture. Structural organization of dorsal sclerites indistinct. Lateral organisation of mesosoma sclerites well preserved in one specimen (GMUC No. 1994 9; Fig. 2C). Pronotum short; mesonotum (MS) as long as one half the length of mesosoma, clearly curved; propodeum (PPD) truncated anteriorly due to taphonomic processes, not protruding dorsally. Propodeal spiracle is preserved as a small weak and arched structure (Fig. 2C, PS). The coxa of the hind leg (Fig. 2C, C3) is clearly preserved in the lower part of the alitrunk.

Legs. Femora robust, mesofemur measuring at least 3.2 mm; tibiae more slender than femora, mesotibia measuring 4.3 mm. Fore legs with single tibial spur, which is slender and elongate-triangular, measuring about 0.8 mm (GMUC No. 1995 8B; specimen without wings) and apparently pectinate (bearing a row of fine teeth). Mesotibiae with two different tibial spurs; shape of longest spur similar to that of fore legs; second spur more slender and shorter than the first, needle-like, measuring

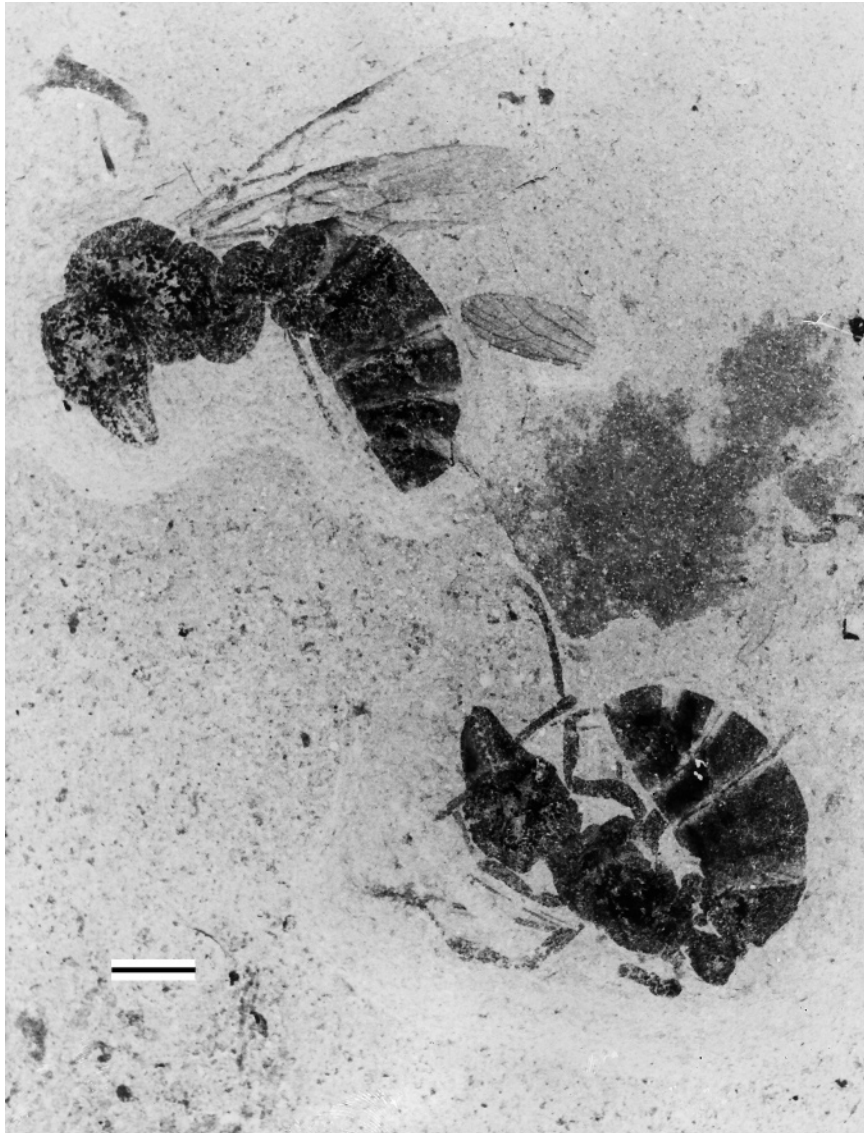


Figure 1. *Pachycondyla rebekkae* sp. nov. Winged gyne holotype (top) and dealate gyne paratype (bottom). Scale bar = 3 mm. Photograph by Gert Brovad, Zoological Museum, University of Copenhagen.

at least 0.3 mm. Shape of metatibial spur similar to that of fore legs, measuring about 1.2 mm (MM No. 13/6 95 '2'). Tarsi poorly preserved, measuring at least 4.5 mm; tarsal claws not preserved.

Forewing (terminology after Brown & Nutting, 1950; Lutz, 1990; Hölldobler & Wilson, 1990). The most complete although isolated forewing is specimen CM No. 16-A3417 (Fig. 3A, plate and counterplate). Other remains of forewings are preserved in the specimens GMUC No. 1995 8A and B (Fig. 1), GMUC No. 1995 9A, MM

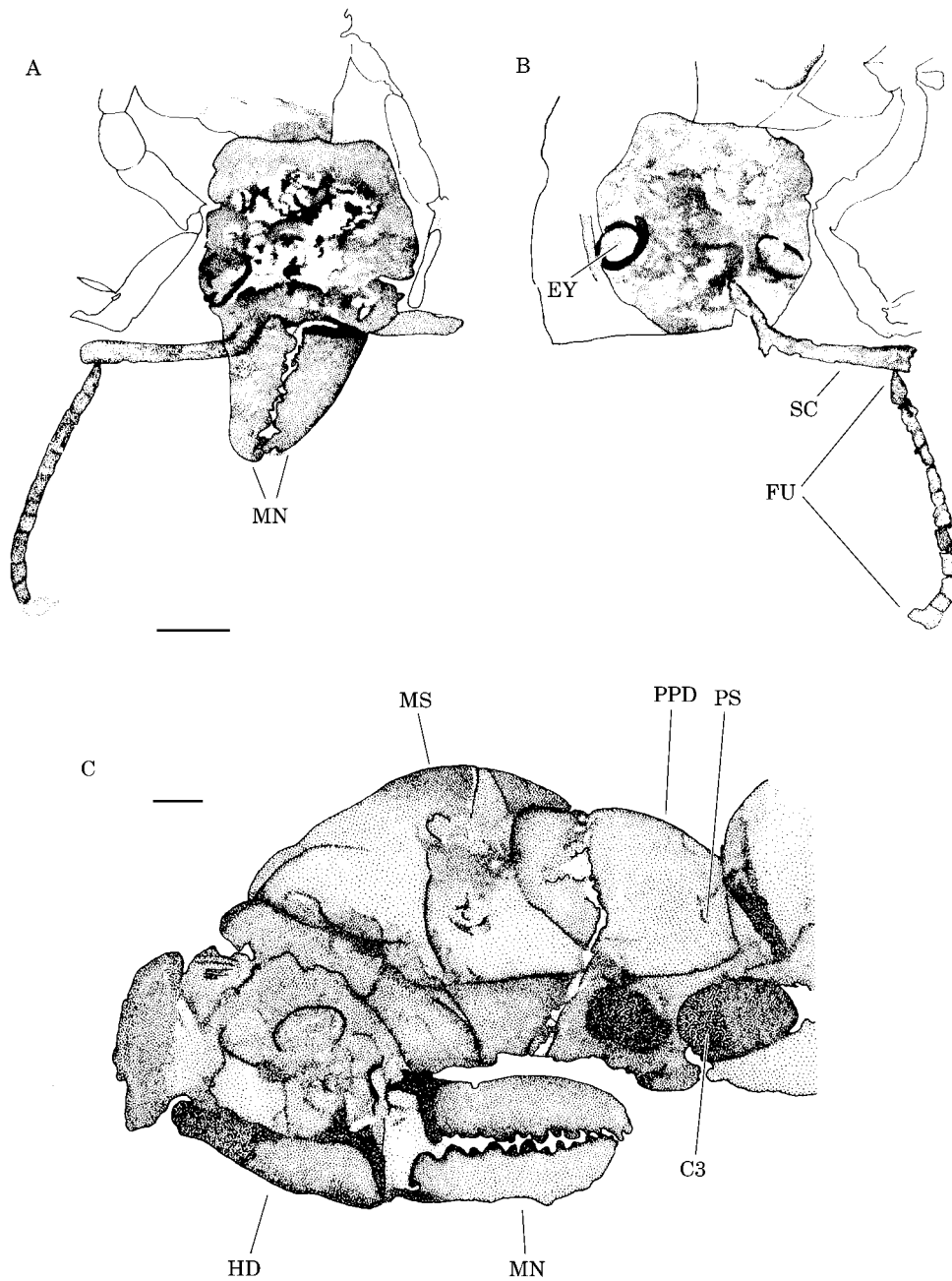


Figure 2. *Pachycondyla rebekkae* sp. nov. A & B, plate and counterplate of head showing strong mandibles, eyes and antennae (GMUC No. 1995 8B, wingless specimen). C, imprint of head and alitrunk in lateral view showing the organization of sclerites (GMUC No. 1994 9). Scale bars = 1 mm. Abbreviations explained in the text.

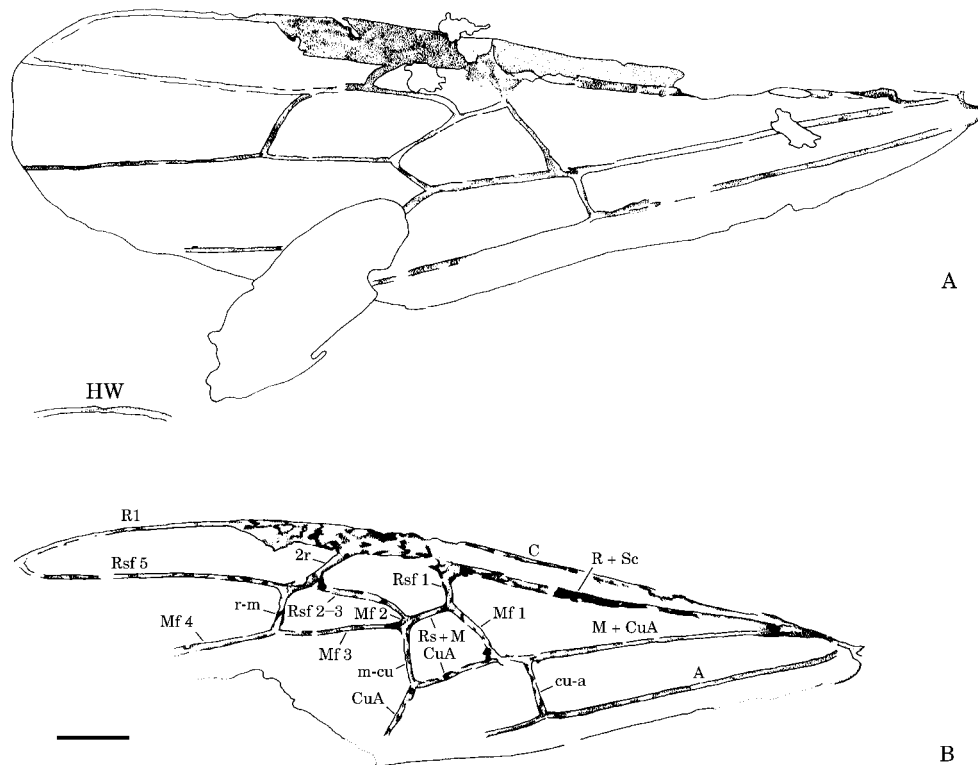


Figure 3. A, isolated fore wing of *Pachycondyla rebekkae* sp. nov. (CM No. 16-A3417). HW = isolated vein of the hind wing. B, isolated fore wing with different kind of venation (CM No. 16-B4520). Scale bar = 1 mm.

No. 13/6 95 '3', and CM No. 16-3079. Length of forewing about 14 mm (CM No. 16-A3417). Costal cell slender. Marginal cell long and slender, length about one half of forewing length. First submarginal cell without 1r. Second submarginal cell larger than first discoidal cell, positioned in the middle of the wing. Median vein branches off from cubital vein (CuA) near the junction of cubito-anal crossvein (cu-a). Anterior cubital vein (CuA1) branches off from cubital vein (CuA) after junction of anal vein (A). First submarginal and first discoidal cell located in the proximal section of the wing. Cuticle of stigma solid, dark brown. The whole wing surface is covered by tiny hairs.

Hindwing. Only small fragments of the hindwings are preserved. Proximal part of anterior hindwing section is visible in GMUC No. 1995 9A. A short section of the costal vein, shows branching parts of R1, Sc + R, and r-m, and a short part of Rs.

Petiole. Oval with laterally rounded shape (Fig. 4A, PT). Length about 1.5 mm; width about 2.3 mm (GMUC No. 1994 8). Dorsally arched, not turned up, without distinct sculpture. Subpetiolar process short, anteriorly prolonged. Attachment between petiole and gaster relatively broad.

Gaster. Swollen in most specimens due to early taphonomic processes. In dorsal view egg-shaped, slightly elongate. Total length 12 mm, height 5 mm. Dorsal margin

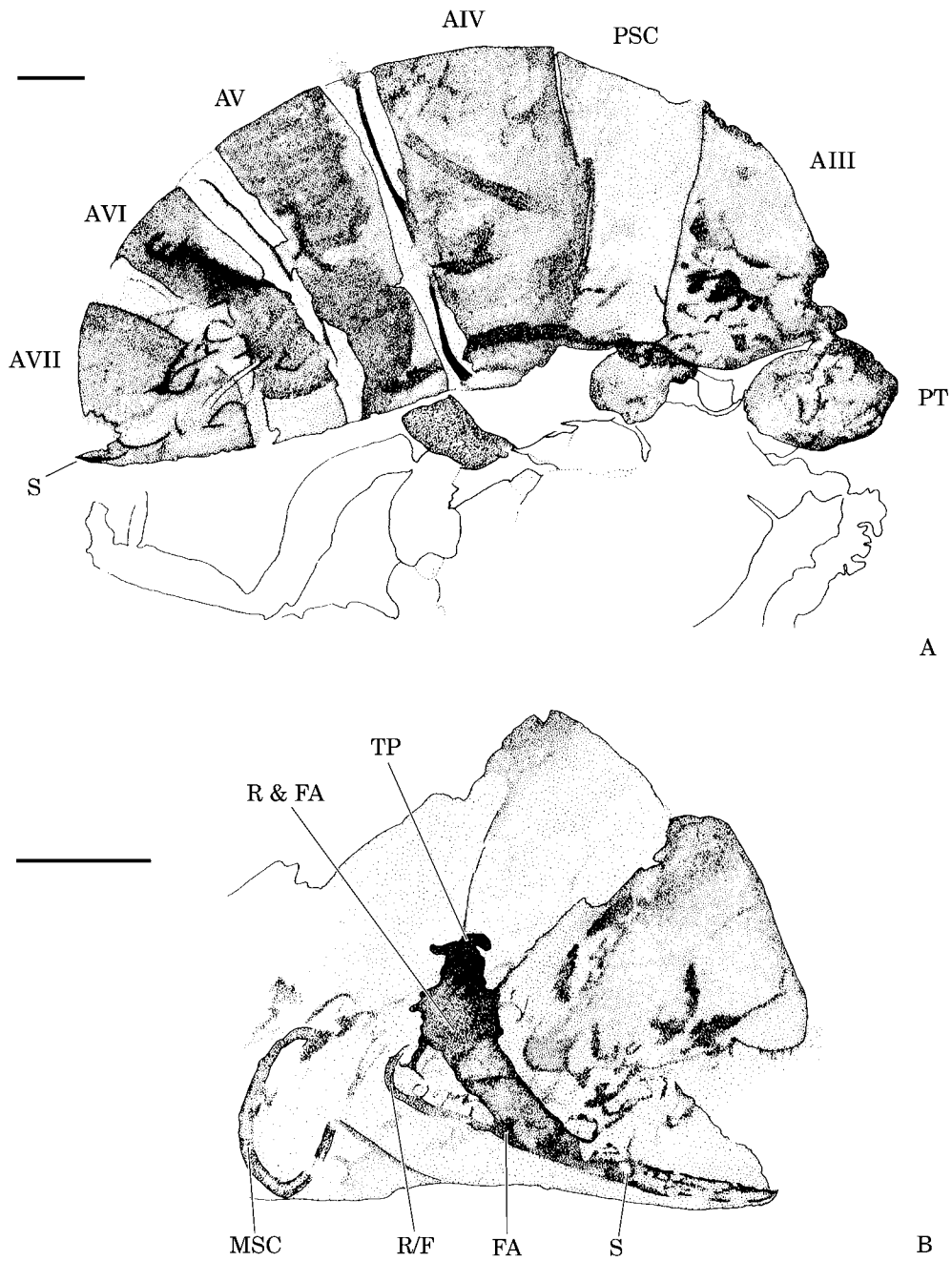


Figure 4. *Pachycondyla rebekkae* sp. nov. A, petiole and gaster in lateral view showing the organization of the abdominal segments and especially the long tubular presclerites of abdominal segment IV (GMUC No. 1995 B, wingless specimen). B, internal aspects of sting apparatus in lateral view (GMUC No. 1994 9). Scale bars = 1 mm. Abbreviations explained in the text.

strongly curved in lateral view (Fig. 4A); ventral margin only slightly curved. Weak but distinct constriction between abdominal segments III and IV. Abdominal segment III with two strong processes in the ventral part of the anterior boundary, establishing a connection with the petiole. Abdominal segment IV with long presclerite (Fig. 4A, PSC), which is at least 1.5 mm long (GMUC No. 1995 8B). Presclerite forming a tubular structure, darker than the intersegmental membranes between abdominal segments IV to VII. Abdominal segment IV measuring at least 2.5 mm without presclerite. No tergosternal suture preserved. Abdominal segment V measuring at least 1.5 mm, abdominal segment VI measuring 1.2 mm. Abdominal segment VII with a distinct sting chamber. Sting (Fig. 4A, S) short, only slightly protruding.

Sting apparatus. Specimen GMUC No. 1994 9 shows a greater part of the internal aspects of the sting apparatus in lateral or slightly ventrolateral view (Fig. 4B). The preservation of the structures requires careful interpretation and other explanations than the following are possible. As a result of taphonomic processes the sting apparatus, especially the solid parts, have been displaced. The main structures are heavily sclerotized and dark. A less sclerotized, slightly deformed oval structure in the anterior part may be the anterior margin of the sting chamber (MSC). A fork is present approximately in the middle of the heavily sclerotized structure, with a slender, anterodorsally directed branch, which is sharply curved distally. This may be remains of the ramus or furcula (R/F). A dark structure in the area of the fork may be the fulcral articulation (FA) between rami and sting (S). The dark, broad branch could be the remaining parts of the rami and fulcral arms (R & FA), one on top of the other. A short posteriorly directed process in the black dorsal part of the sting apparatus may be the remains of the triangular plate (TP). The less sclerotized structures, present in living ants, are not preserved or indistinguishable. Specimens GMUC No. 1994–9 and No. 1995–8B have very short and faint hairs in the dorsal wall of the entrance to the sting chamber (Fig. 4A, B), probably anal sensilla inserted on the posterior border of the anal plate.

Description of male

There is only one complete male specimen (Fig. 5B) with only a very small part of a fore wing (MM No. I 396, plate and counterplate). Body shorter and more slender than in gyne, length 18 mm. Head small, length 2 mm, height 1.2 mm, with large, fully developed eyes. Mandibles short. Antennae not preserved. Mesosoma smaller than in female, length about 6 mm, width about 3.5 mm. Counterplate shows a little but distinct opening in the area of the metapleural gland; opening surrounded by a small dark wall like structure. Petiole more differentiated than in female, articulation between propodeum and petiole and between petiole and gaster short. Only fragments of legs preserved. Gaster smaller and more elongate than in gynes; length 8 mm, height 3.5 mm. Genital structures not preserved. The extent of the morphological differences between female and male resembles that of extant ponerine ants.

Type material

Holotype. Winged female (Fig. 1, top), GMUC No. 1995 8B (plate) and 1995 8A (counterplate), Stolleklint, Fur, Denmark, September 1994, leg. Rebekka Madsen (CM No. 16-A4218), deposited in the Geological Museum, University of Copenhagen, Denmark.

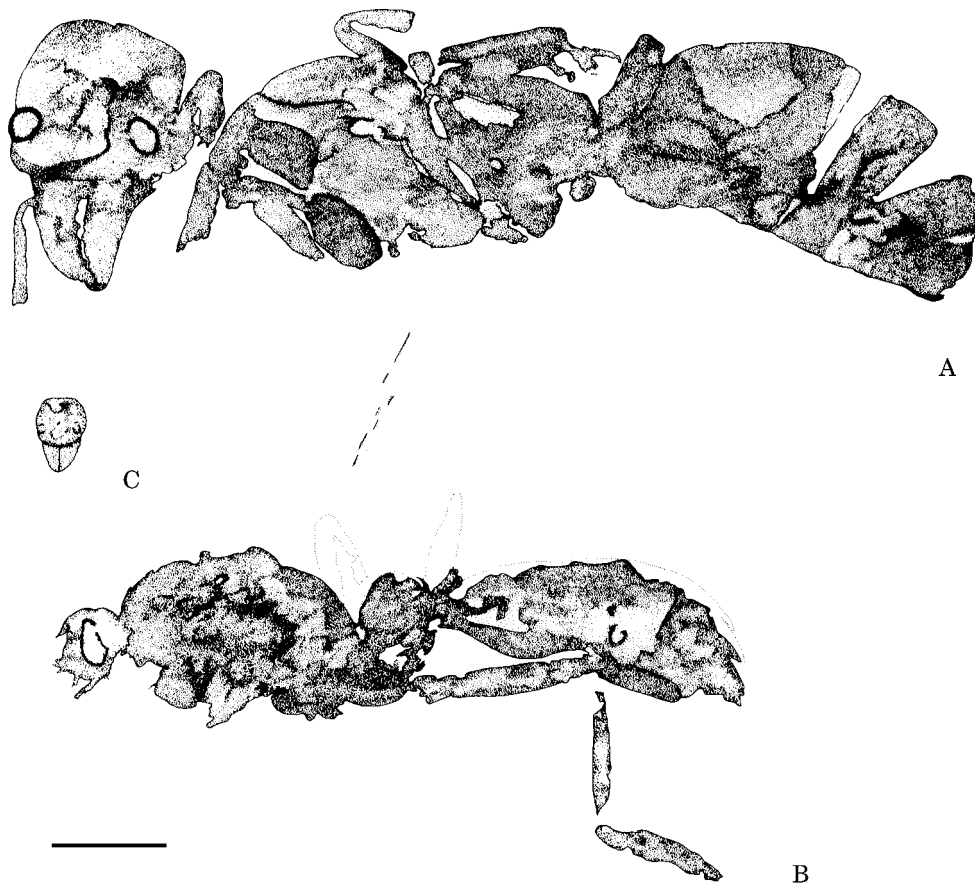


Figure 5. *Pachycondyla rebekkae* sp. nov. A, dealate gyne in lateral view (CM No. 16-B2205). B, male with weak remains of a fore wing above the body in lateral view (MM No. I 396). Additional remains from counterplate outlined (dotted line). C, small isolated head, presumably of a worker ant. Systematic position unknown (CM No. 16-B4997). Scale bar = 3 mm.

Paratypes. Dealate gyne (Fig. 1, bottom) in same plate and counterplate as holotype (GMUC). Other specimens listed in the Appendix are also designated paratypes.

Etymology. The new species is named in honour of Mrs Rebekka Madsen who found the holotype.

Other specimens

One isolated head (CM No. 16-B4997; Fig. 5C) probably belongs to a worker ant. The general habitus resembles that of the gyne of *Pachycondyla rebekkae*. Head length 2 mm. Mandibles shorter but strong. Eyes well developed. Weak carinae in the vertexal section. The systematic position of this specimen is doubtful until more complete specimens become available.

An isolated fore wing (CM No. 16-B4520, plate and counterplate; Fig. 3B) shows a different kind of venation than described above. Length of fore wing about 12 mm. Second submarginal cell and first discoidal cell smaller, Mf2 much smaller. Median

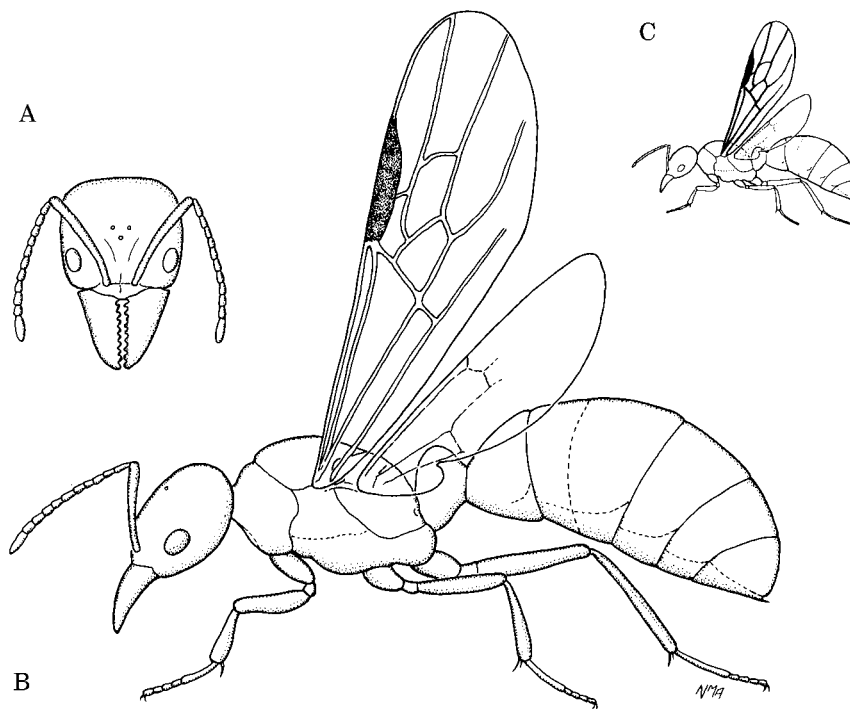


Figure 6. *Pachycondyla rebekkae* sp. nov. Reconstruction of gyne. A, head in frontal view. B, complete specimen in lateral view. C, same, natural size.

vein (Mf1) branches off from cubital proximal (CuA) after the junction of the cubito-anal cross vein (cu-a). The wing possibly belongs to the male of *Pachycondyla rebekkae*, but this assignment is doubtful until more complete specimens become available.

Distribution and geological horizon

Holotype and most paratypes originate from Stolleklint on the island of Fur, northwestern Jutland, Denmark. The fossils are imprinted in a greyish laminated and shale-like clay. This deposit belongs to the Ølst Formation with a geological age of about 55 Myr (Upper Paleocene/Lower Eocene).

DISCUSSION

Classification and phylogeny

Figure 6 shows a reconstruction of a female *Pachycondyla rebekkae* sp. nov. based upon the characters given in the description (see above). The classification and phylogenetic assignment of fossil ants is hampered by several factors. First, important apomorphic characters used in the analysis of the phylogeny of living ants are rarely preserved. Second, the time of first appearance and sequence of evolution is unknown for most apomorphic characters. This may cause difficulties in the classification of

geological old species sharing mainly plesiomorphic characters. Third and finally, many phylogenetic studies of ants completely neglect the fossil record.

In the most recent and exhaustive work on the phylogeny of ants, Baroni Urbani *et al.* (1992) listed 68 characters used in their phylogenetic (cladistic) analyses. The following character states are discernible in *Pachycondyla rebekkae*, sp. nov. (numbers refer to the list of characters in Baroni Urbani *et al.*, 1992: 304–314):

- (1) Head prognathous.
- (7) Malar area visible in dorsal view.
- (9) Antennae with scape elongated.
- (25) Abdominal segment IV with differentiated presternite and pretergite.
- (27) Presclerites of abdominal segment IV longer than one half of A III and with the sides running parallel. In the fossil material the sides of abdominal segment IV are to a great extent parallel.
- (28) Presternite of abdominal segment IV, subequal to or longer than the pretergite. The presternite of the holotype (GMUC No. 1995 8B; Fig. 4A) is subequal in length to the pretergite for about two thirds of its visible height. The dorsal part of the pretergite has been stretched due to a supposed postmortal curvature of the gaster.

In our opinion, these character states clearly suggest that *Pachycondyla rebekkae* belongs to the ant subfamily Ponerinae. According to Baroni Urbani *et al.* (1992), the relatively long presclerite of abdominal segment IV (character 27) is present only among Myrmeciinae, Ponerinae, and Cerapachyinae. In general, *Pachycondyla rebekkae* shares characters known among members of the Ponerinae and differs from all known species of Cerapachyinae and Myrmeciinae. In particular, the fossil species does not share the special mandibular dentition of the Myrmeciinae and the spinose pygidium of Cerapachyinae, apomorphies which should be visible in fossils. Thus, in our opinion, the character states listed above justify the classification of *Pachycondyla rebekkae* in the ant subfamily Ponerinae. The general morphology of the female and male of the fossil ant indicates close affinity with large species of the extant genus *Pachycondyla* (e.g. Kempf, 1961). In particular, the head structure of *Pachycondyla rebekkae* (e.g. strong mandibles, position of eyes and antennae) is similar to that of extant species of *Pachycondyla* from tropical forests (e.g. Wheeler, 1922). Despite the absence of information on the structure of the worker caste, we prefer to classify the fossil species in this genus.

Palaeoecology and taphonomy

General accounts of the palaeoecology of the biota of the Fur formation have been given by Larsson (1975) Bonde, (1987), Willmann (1990) and Andersen & Andersen (1996). The diatomite of this formation is deposited in a marine environment and Bonde (1973, 1979, 1997) assumed a distance of about 100 km from the nearest coast and water depths from 50 to 500 m. The composition of the fish fauna indicates a tropical or subtropical climate. No animal bottom feeders, coastal marine, or freshwater fishes have been recorded. According to Larsson (1975), the composition of the insect fauna indicates a source area of land dominated by meadows with bushes and isolated trees, but without true forests. Water striders (Gerridae, Hydrometridae; Andersen, 1982), aquatic bugs (Belostomatidae; Larsson,

1975; Rust & Ansorge, 1996), and several insect groups with aquatic larvae (e.g. damselflies, caddisflies, and mosquitoes; Larsson, 1975; Cylindrotomidae; Freiwald, 1991), show that freshwater habitats must have been abundant in the source area.

According to Larsson (1975), Willmann, (1990) and Andersen & Andersen (1996) the lack of wingless insects and insect larvae in the Ølst and Fur Formations suggests that the insects have been transported by air and not by water currents. However, it is important to distinguish between passive transport of insects by strong air currents and active migration (e.g. Johnson, 1969; Bowden & Johnson, 1976). In some aspects, e.g. only about 8% Coleoptera (Larsson, 1975), the composition of the insect fauna of the Ølst and Fur Formation resembles that of living insects trapped over the sea ('aerial plankton'). Ansorge (1993) showed that the female dominance among the Ichneumonidae of the Fur formation can be explained as a result of the migration of the females after mating. As Horstmann (1970) pointed out, 80% of the Ichneumonidae trapped on light ships on the northwestern coast of Germany were females, while in the breeding areas the males dominate (only 25% females).

Active migration, associated with mating and/or colony founding swarms dominated by females, can also be expected for ants like *Pachycondyla rebekkae*. This interpretation is supported by the occurrence of all individuals except one at the same locality, seemingly only in a few sediment layers. Due to their large size, it can be assumed that the females were poor flyers, like some extant large ants such as *Lasius niger* and *Camponotus herculeanus* (Hölldobler & Maschwitz, 1965). Thus, it is possible that the female ants have been pressed down on the sea surface by the lack of upward air currents or due to exhaustion. Observations by Lutz (1990) show that insects often cling to each other after arriving on the water surface, when they try to reach any kind of solid substrate and that they stay in this position after death. The subsequent quick growth of bacteria and fungi provides an additional fixation, even when the specimens sink to the bottom. This phenomenon is described for a group of three ants from the Eocene Messel Lake formation (Lutz, 1990), and may also explain why two specimens of *Pachycondyla rebekkae* ended up close together in the same horizon (Fig. 1).

The strong mandibles of the queen of *Pachycondyla rebekkae* may have been effective tools for excavating nest chambers in soil or wood during the founding of a new colony. Owing to their large size and great abundance, the giant ants have probably been important as food for birds and other insectivorous animals of the Palaeogene fauna of southern Scandinavia.

Fossil history and early evolution of ants

A complete checklist of fossil ant taxa is given by Bolton (1995). The presumed oldest fossil ant cited in recent literature (Bolton, 1994; Hölldobler & Wilson, 1995, Crozier *et al.*, 1997) is *Cariridris bipetiolata* described by Brandão *et al.* (1989) from the early Cretaceous (Aptian) of the Santana-Formation of Brazil. Rasnitsyn (1994) was the first to disargue, classifying *C. bipetiolata* as a member of the Ampulicinae (Sphecidae). An intensive re-examination of old and new material by Verhaagh (1996) clearly shows that the specimens belong to the Sphecidae. Crozier *et al.* (1997) failed to notice this fact when they dated the origin of ants back to early Jurassic by taking the age of *C. bipetiolata* for time calibration of a molecular clock of

mitochondrial DNA sequences. A statement by Hennig (1969: 366) on a fossil ant from the Lower Cretaceous Lebanese amber has been overlooked by all authors except Königsmann, (1978: 392). In a personal communication (to J.R.), Dr D. Schlee (Staatliches Museum für Naturkunde, Stuttgart) recently pointed out that Dr C. Baroni Urbani has re-examined the Lebanese amber specimen, concluding that it is not an ant. The occurrence of a fossil ant in the Lower Cretaceous of Australia (Jell & Duncan, 1986) was questioned by Naumann (1993), and additional material is needed to verify this record. In 1995 a photograph of a well preserved presumed ant from a new amber site in Spain (Alava) was published by Gorospe. The amber deposit is of Lower Cretaceous age (Albium) and if confirmed, this may be the oldest record of a fossil ant. The photograph however, shows a probably female hymenopteron with very short antennal scapes and lacking in this way one of the most important ant synapomorphies.

Numerous true or presumed ants or ant-related taxa have been reported from the Late Cretaceous of the U.S.S.R., U.S.A., and Canada (e.g. Dlussky, 1983, 1987; Dlussky & Fedoseeva, 1988; Wilson, 1985, 1987; Wilson *et al.*, 1967); but there are conflicting opinions about their systematic position (see below). Most recently, Dlussky (1996) described ants from Burmese amber of Late Cretaceous age.

Lower Tertiary ants of supposed Paleocene age have been reported from Sakhalin amber by Dlussky (1988). The species belong to the extant subfamilies Ponerinae, Aneuretinae, Dolichoderinae, and Formicinae. Mitchell & Wighton (1979) reported two fragments of Formicidae from the Paleocene Paskapoo Formation of Alberta (Canada). *Eomyrmex guchengziensis* (Hong *et al.*, 1974) was described from the early Eocene of Fushun, China, and placed in the subfamily Myrmicinae. Other Eocene ants have been described from U.S.A. (e.g. Carpenter, 1930; Wilson, 1985), Canada (Rice, 1947), Germany (Lutz, 1988, 1990), and from Baltic amber (e.g. Wheeler, 1914; Rasnitsyn & Kulicka, 1990). The extinct subfamily Formiciinae (Lutz, 1986) from the Middle Eocene of Germany was included in the phylogenetic analysis by Baroni Urbani *et al.* (1992).

Our knowledge of the phylogeny and early evolution of ants is severely impeded by the different opinions on the systematic position of the Cretaceous ants. Dlussky (1987) and Dlussky & Fedoseeva (1988) argued that the Cretaceous taxa belong to families of their own, the Sphecomyrmidae and Armaniidae, which are not true ants (see also Baroni Urbani, 1989). In their opinion, the true ants (Formicidae) first appear in the early Tertiary (Paleocene). In contrast to this view, Wilson (1987) and Hölldobler & Wilson (1990) emphasized that all Cretaceous formicoids belong to only two genera, *Sphecomyrma* and *Cretomyrma*, and a single subfamily, the Sphecomyrminae, which can be classified in the Formicidae. Furthermore, Wilson (1987) proposed a differentiation of Cretaceous ants into the queen and worker castes, meaning that a social organisation already had been established by that time.

Pachycondyla rebekkae sp. nov. is among the oldest known ants which can be assigned to an extant subfamily (Ponerinae) and to an extant genus. Furthermore it is one of the earliest records of true ants. According to Bolton (1995) the fossil record of *Pachycondyla* includes six species all from Oligocene deposits in Europe (England, France, Baltic amber). Today the taxon contains more than 200 species in all zoogeographical regions.

Although the phylogenetic (cladistic) analyses of Baroni Urbani *et al.* (1992) are somewhat ambiguous, the results consistently supported a basal division of the Formicidae into a 'formicoid' and a 'poneroid' clade. Paleocene records of species

belonging to both these clades are therefore significant. According to Baroni Urbani *et al.* (1992: 321), ponerines are not particularly plesiomorphic, but intermediate in 'specialization' (degree of divergence from presumptive ancestral conditions) among the ant subfamilies. In our opinion, early Tertiary records of true ants like *Pachycondyla* support the hypothesis of a pre-Tertiary origin of the ant lineage (and of caste differentiation and social organisation of populations) and a relatively rapid diversification of extant subfamilies during the early Tertiary.

ACKNOWLEDGEMENTS

The authors are grateful to Henrik and Rebekka Madsen, Nykøbing Mors, and Bent Søe Mikkelsen, Molermuseet, Mors, for the loan of fossil ant material collected by them. This work would not have been possible without their immense engagement in collecting fossils of the Fur and Ølst Formations. We also thank Søren Floris, Geological Museum, University of Copenhagen, and Georg Stenstrop, Fur Museum, Fur, for the permission to study material under their care, Stig Andersen and Rainer Willmann for useful comments on an earlier draft of the manuscript, and Gert Brovad for taking the photograph. This study was supported in part by a German Science Foundation grant (to J.R.) and by a grant from the Danish Natural Science Research Council (to N.M.A.).

NOTE ADDED IN PROOF

Since this paper was submitted, two relevant articles have appeared, by Agosti *et al.* (1997) and Grimaldi *et al.* (1997). The authors describe seven specimens of the so far oldest known ants from Cretaceous (Turonian, 92 Myr) amber from New Jersey and review all Cretaceous records of ants.

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APPENDIX

List of material examined with collection numbers, state of preservation (a, plate, b, counterplate), and characterization of material. Gyne specimens except as noticed. List arranged according to depositories.

Fur Museum, Fur, Denmark

13/6 95 '2'	a	specimen with small part of wing in dorsal view
13/6 95 '3'	a + b(?)	incomplete specimen with part of wing

Geological Museum, University of Copenhagen, Denmark

1995 8A&B	a + b	two complete specimens, winged holotype and wingless paratype (also labelled 16-A4218)
1995 9A	a + b	specimen with incomplete wings (also labelled 16-3573)
1994 8	a	wingless specimen in dorsal view (also labelled 16-3964)
1994 9	a + b	wingless specimen in lateral view (also labelled Stolle Klint 8/8 92)

Collection Henrik and Rebekka Madsen, Nykøbing Mors, Denmark

Stolle 22/6-93	a + b	part of head (with mandibles)
16-3079	a + b	wing fragment, normal type
16-3324	a + b	head
16-3384	a + b	part of mesosoma, petiole, gaster and legs
16-3521	a + b	head, mesosoma, petiole and part of legs
16-3524	a + b	mesosoma and part of petiole
16-3851	a + b	small part of mesosoma, ant?
16-3980	a + b	part of mesosoma and legs
16-3991	a + b	body fragment, legs
16-4317	a + b	mesosoma, petiole, gaster and part of legs
16-4368	a + b	part of mesosoma, gaster and legs
16-4499	a + b	part of mesosoma, petiole, gaster and legs
16-4512	a + b	gaster and part of mesosoma
16-4688	a + b	head
16-4748	a + b	body fragment
16-4752	a	part of head, mesosoma, petiole and gaster(?)
16-4770	a + b	fragment (ant?)
16-4891	a + b	complete, without wings, well preserved
16-4985	a + b	part of head
16-6026	a + b	part of head, mesosoma, petiole and gaster
16-A2420	a + b	fragment
16-A2426	a	gaster and petiole
16-A2560	a + b	mesosoma, petiole and gaster
16-A2561	a + b	head and body fragments
16-A2641	a + b	isolated head (small, male?), fragment of gaster
16-A2649	a + b	part of mesosoma and petiole
16-A2777	a + b	gaster
16-A2782	a + b	head
16-A3098	a	fragment of ant?
16-A3110	a + b	part of mesosoma and petiole
16-A3123	a + b	part of mesosoma and petiole
16-A3139	a + b	part of gaster
16-A3154	a + b	head?
16-A3320	a + b	mesosoma, petiole and gaster
16-A3386	a + b	mesosoma, petiole and gaster
16-A3395	a + b	part of mesosoma and petiole
16-A3417	a + b	complete fore wing, isolated, well preserved
16-A3563	a + b	part of mesosoma and petiole
16-A3617	a + b	part of mesosoma and petiole
16-A4215	a + b	head
16-A4217	a + b	gaster
16-A4224	a + b	head
16-A4231	a + b	gaster
16-A4236	a + b	small mesosoma (dorsal view?), possibly male
16-A4238	a + b	part of head
16-A4345	a + b	head, with ocelli?
16-A4388	a + b	part of head
16-A4389	a + b	part of head
16-A4392	a + b	part of mesosoma and petiole
16-A4397	a + b	mesosoma and petiole
16-A4429	a + b	part of mesosoma, petiole and legs
16-A4431	a + b	fragment of gaster
16-A4516	a + b	part of mesosoma and petiole
16-A4615	a + b	head, part of mesosoma and gaster
16-A4618	a + b	mesosoma, petiole and gaster, head on alitrunk
16-A4620	a + b	part of mesosoma and petiole

16-A4690	a + b	mesosoma and part of legs
16-A4700	a + b	gaster
16-A4766	a + b	head
16-A4767	a + b	mesosoma
16-A4772	a	gaster?
16-A4804	a + b	gaster
16-A4807	a + b	fragment of mesosoma and petiole
16-A4808	a + b	gaster
16-A4812	a + b	mesosoma, petiole and gaster
16-A4826	a + b	gaster
16-A4948	a + b	fragment of mesosoma, petiole and gaster
16-A4963	a + b	gaster
16-B2024	a + b	head, part of mesosoma, gaster and legs
16-B2034	a	mesosoma and petiole
16-B2038	a + b	fragments of mesosoma and petiole
16-B2042	a + b	head
16-B2048	a	gaster
16-B2060	a + b	part of mesosoma and petiole
16-B2068	a + b	part of mesosoma and legs
16-B2080	a	part of gaster
16-B2205	a + b	complete, without wings, well preserved
16-B2208	a + b	fragment of body and legs
16-B2213	a + b	head and very small part of mesosoma
16-B2222	a + b	head
16-B2234	a + b	head
16-B2274	a + b	fragment of gaster
23X-B2867	a + b	part of mesosoma, petiole, gaster and legs
16-B3175	a + b	gaster
16-B3181	a + b	fragment
16-B3187	a + b	gaster, part of petiole
16-B3193	a + b	head
16-B3525	a + b	complete, without wings
16-B3618	a	gaster, part of petiole and legs
16-B4520	a + b	wing of different type (see description of forewings)
16-B4544	a + b	gaster and petiole
16-B4976	a + b	gaster
16-B4997	a	isolated head of a worker, very small, with small eyes and strong mandibles (as in female)

Molermuseet, Skarrehage, Mors, Denmark (coll. B.S. Mikkelsen)

1396	a + b	complete specimen without wings, male
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