

The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the Insect Limestone (Late Eocene) of the Isle of Wight, UK

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ABSTRACT: The types and undescribed material of the hymenopteran fossils of the Insect Bed of the Bembridge Marls from the Isle of Wight (UK) are critically revised and studied. A total of 1460 fossils are recorded and attributed to 20 families: Gasteruptionidae s.l. (1); Proctotrupidae (3); Diapriidae (24); Cynipidae (7); Figitidae (6); Pteromalidae (1); Agaonidae (3); Scelionidae (12); Platygasteridae (2); Ichneumonidae (32); Braconidae (75); Bethyidae (3); Crabronidae (2); Sphecidae (1); Apidae (2); Scoliidae (1); Tiphiidae (2); Vespidae (4); and Formicidae (1220). Described as new are 51 species, 13 genera, two tribes and two subfamilies. Minimum number of species recorded (either as described species or representing higher taxa with no described species in the assemblage) is 118. The composition of the hymenopteran assemblage is most similar to that of Baltic amber and indicative of a well forested territory, as well as of a humid, equable (aseasonal but not very hot) climate, more typically equable than in the Baltic amber source area, judging from the absence of Aphidiinae and scarcity of aphids.

KEY WORDS: Bembridge Marls, Eocene, fossil insects, new combinations, new taxa

Material for the present study comprises the hymenopteran fossils preserved in concretions or tabular bands of very fine-grained micrite, known as Insect Limestone. The unit where these concretions/bands occur is known as the Insect Bed, which lies towards the base of the Bembridge Marls Member (Solent Group: Bouldnor Formation). The Bembridge Marls are dated as the latest Eocene (Hooker *et al.* 2009). The deposits outcrop in several sites along the north coast of the Isle of Wight near the south coast of Great Britain.

Most of the specimens studied are kept at the Natural History Museum (NHMUK). The majority of them belong to the collections of A'Court Smith (purchased 1877, 1883), P.B. Brodie (purchased 1898) and R.W. Hooley (purchased 1924). They are labelled 'Gurnard Bay' or 'Gurnet Bay' (which is an old name for Gurnard Bay). However, Smith collected specimens all the way from West Cowes to Newtown River on the northwest side of the Isle of Wight (Jarzembowski 1980). Most of the specimens probably came from Thorness Bay (Jarzembowski 1976). Brodie and Hooley acquired parts of Smith's collection, so parts and counterparts of individual insects have turned up in all three collections. The parts and counterparts often have different numbers, because they were registered

at different times. An additional collection was recently discovered at the Sedgwick Museum, Cambridge, by A.J. Ross. This collection has also yielded counterparts of specimens at the NHMUK which indicates that this is another part of the Smith collection. A label with '1883' on it suggests that the Sedgwick Museum acquired this collection in 1883, the same year in which the NHMUK purchased specimens from Smith.

A small collection of the fossils studied, referred to as USNM, is kept at the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. These are mostly the type material described by Cockerell (1915). They come from the same deposits.

Hymenopterans are the second most common insect order (after dipterans) in the Bembridge assemblage. Even if their high participation depends in part on the hyper-abundance of two species of a single ant genus (*Oecophylla* Smith, 1860 which is responsible for at least 40 per cent of the hymenopteran fossils), the order diversity is impressive, with its 20 families, over 100 genera and more than 120 species recorded conservatively after this non-exhaustive study of the available fossil material.



Table 1 Current taxonomic position of the previously described species of the Bembridge fossil hymenopterans

Taxa as described	Current taxonomic position
<i>Acourtia perplexa</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Townesitinae: <i>Acourtia perplexa</i> Cockerell, 1921
<i>Andricus vectensis</i> Cockerell, 1921, Cynipidae	not revised
<i>Aneurhynchus conservatus</i> Cockerell, 1915, Diapriidae	not studied
<i>Bathystomus peritus</i> Cockerell, 1921, Braconidae	Braconidae: Opiinae: <i>Biosteres peritus</i> (Cockerell, 1921)
<i>Calyptoides veterinus</i> Cockerell, 1921, Braconidae	Braconidae: Helconinae: <i>Calyptoides veterinus</i> Cockerell, 1921
<i>Camponotus (Colobopsis) brodiei</i> Donisthorpe, 1920, Formicidae	Formicidae incertae sedis: “ <i>Camponotus</i> ” <i>brodiei</i> Donisthorpe, 1920:
<i>Coleocentrus gurnetensis</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: subfam. indet.: “ <i>Coleocentrus</i> ” <i>gurnetensis</i> Cockerell, 1921
<i>Cremastus? arcuatus</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Orthocentrinae, Microleptini: <i>Eusterinx arcuatus</i> (Cockerell, 1921)
<i>Dacnusites reductus</i> Cockerell, 1921, Braconidae	Braconidae: Microgastrinae: <i>Dacnusites reductus</i> Cockerell, 1921
<i>Dacnusites sepultus</i> Cockerell, 1921, Braconidae	Braconidae: Microgastrinae: <i>Dacnusites sepultus</i> Cockerell, 1921
<i>Diospiloides hooleyi</i> Cockerell, 1921, Braconidae	Braconidae: Orgilinae: <i>Microtypus hooleyi</i> (Cockerell, 1921)
<i>Diospilus acourti</i> Cockerell, 1921, Braconidae	Braconidae: Helconinae: <i>Diospilus acourti</i> Cockerell, 1921
<i>Dolichoderus anglicus</i> Cockerell, 1915, Formicidae	Formicidae: Aneuretinae: <i>Britaneuretus anglicus</i> (Cockerell, 1915)
<i>Dolichoderus britannicus</i> Cockerell, 1915, Formicidae	Formicidae: Dolichoderinae: <i>Emplastus britannicus</i> (Cockerell, 1915)
<i>Dolichoderus gurnetensis</i> Donisthorpe, 1920, Formicidae	Formicidae: Dolichoderinae: <i>Emplastus gurnetensis</i> (Donisthorpe, 1920)
<i>Dolichoderus ovigerus</i> Cockerell, 1915, Formicidae	Formicidae: Dolichoderinae: <i>Emplastus britannicus</i> (Cockerell, 1915)
<i>Dolichoderus vectensis</i> Donisthorpe, 1920, Formicidae	Formicidae: Dolichoderinae: <i>Dolichoderus vectensis</i> Donisthorpe, 1920
<i>Emplastus emeryi</i> Donisthorpe, 1920, Formicidae	Formicidae: Dolichoderinae: <i>Emplastus britannicus</i> (Cockerell, 1915)
<i>Euponera crawleyi</i> Donisthorpe, 1920, Formicidae	Formicidae: Ponerinae: <i>Ponerites crawleyi</i> (Donisthorpe, 1920)
<i>Holomeristus? vectensis</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Orthocentrinae, Microleptini: <i>Eusterinx vectensis</i> (Cockerell, 1921)
<i>Ichneumon acourti</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Cryptinae: “ <i>Hemiteles</i> ” <i>acourti</i> (Cockerell, 1921)
<i>Iprobracon? micrarche</i> Cockerell, 1921, Braconidae	Braconidae: Braconinae: <i>Bracon micrarche</i> (Cockerell, 1921)
<i>Iprobracon? vectensis</i> Cockerell, 1921, Braconidae	Braconidae: Braconinae: <i>Cyanopterus vectensis</i> (Cockerell, 1921)
<i>Itoplectis saxosus</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Pimplinae: “ <i>Itoplectis</i> ” <i>saxosa</i> (Cockerell, 1921)
<i>Lampronota disrupta</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Townesitinae: <i>Marjorieta disrupta</i> (Cockerell, 1921)
<i>Leptothorax gurnetensis</i> Cockerell, 1915, Formicidae	Formicidae: Formicinae: <i>Leucotaphus gurnetensis</i> (Cockerell, 1915)
<i>Leucotaphus cockerelli</i> Donisthorpe, 1920, Formicidae	Formicidae: Formicinae: <i>Camponotus cockerelli</i> (Donisthorpe, 1920)
<i>Leucotaphus permanus</i> Cockerell, 1927, Formicidae	not studied (type lost)
<i>Lithapechtis fumosus</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: subfam. indet.: <i>Lithapechtis fumosus</i> Cockerell, 1921
<i>Lithobelyta reducta</i> Cockerell, 1921, Diapriidae	Chalcidoidea: <i>Lithobelyta reducta</i> Cockerell, 1921
<i>Macroteleia verna</i> Cockerell, 1921, Scelionidae	Scelionidae: Scelioninae: <i>Calliscelio veterinus</i> (Cockerell, 1921)
<i>Mesitius? reclinervis</i> Cockerell, 1921, Bethyloidea	not revised
<i>Miota? strigata</i> Cockerell, 1921, Diapriidae	not revised
<i>Oecophylla atavina</i> Cockerell 1915, Formicidae	Formicidae: Formicinae: <i>Oecophylla atavina</i> Cockerell 1915
<i>Oecophylla megarche</i> Cockerell, 1915, Formicidae	Formicidae: Formicinae: <i>Oecophylla megarche</i> Cockerell, 1915
<i>Oecophylla perdita</i> Cockerell, 1915, Formicidae	Formicidae: Formicinae: <i>Oecophylla atavina</i> Cockerell 1915
<i>Phanomeris? colenutti</i> Cockerell, 1921, Chalcidoidea	not revised
<i>Philoponites clarus</i> Cockerell, 1915, Sphecidae	Tiphidae: Tiphinae: <i>Philoponites clarus</i> Cockerell, 1915
<i>Polybia oblita</i> Cockerell, 1921, Vespidae	Vespidae: Polistinae: <i>Protopolistes oblita</i> (Cockerell, 1921)
<i>Polybia? anglica</i> Cockerell, 1921, Vespidae	Vespidae: Polistinae: <i>Palaeopolybia anglica</i> (Cockerell, 1921)
<i>Polychlistus anglicus</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Metopiinae: <i>Hypsicera anglica</i> (Cockerell, 1921)
<i>Polysphincta? atavina</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: subfam. & gen. indet.: “ <i>Polysphincta</i> ” <i>atavina</i> Cockerell, 1921
<i>Ponera hypolitha</i> Cockerell, 1915, Formicidae	Formicidae: Dolichoderinae: <i>Emplastus hypolithus</i> (Cockerell, 1915)
<i>Ponera minuta</i> Donisthorpe, 1920, Formicidae	Agaonidae: “ <i>Ponera</i> ” <i>minuta</i> Donisthorpe, 1920
<i>Pteromalus? vectensis</i> Cockerell, 1921, Pteromalidae	not revised
<i>Rhodites vetus</i> Cockerell, 1921, Cynipidae	not revised
<i>Sceliphron? brevior</i> Cockerell, 1921, Sphecidae	Sphecidae: Protosceliphriini: <i>Protosceliphron brevior</i> (Cockerell, 1921)
<i>Sigalphus cervicalis</i> Cockerell, 1921, Braconidae	Braconidae: Helconinae: <i>Taphaeus cervicalis</i> (Cockerell, 1921)
<i>Stilpnus oligocenus</i> Cockerell, 1921, Ichneumonidae	Ichneumonidae: Cryptinae: “ <i>Stilpnus</i> ” <i>oligocenus</i>
<i>Syntaphus wheeleri</i> Donisthorpe, 1920, Formicidae	Braconidae: Cheloninae: <i>Ascogaster (Syntaphus) wheeleri</i> (Donisthorpe, 1920)
<i>Vectevania vetula</i> Cockerell, 1922, (Evaniidae)	Gasteruptionidae: Aulacinae?: <i>Vectevania vetula</i> Cockerell, 1922
<i>Xenarcha? distracta</i> Cockerell, 1921 Braconidae	Braconidae: Doryctinae: <i>Ontsira distracta</i> (Cockerell, 1921)
<i>Zygota? filicornis</i> Cockerell, 1921, Diapriidae	not revised

The taxonomic history of the Bembridge hymenopteran fossils is short, in the sense that all descriptions predating the present project were made during a short interval of twelve years (Cockerell 1915–1927; Donisthorpe 1920) (Table 1).

In the framework of the present project, the following hymenopteran taxa recorded from the Bembridge Marls are thoroughly studied: aculeate wasps (except Chrysoidea) by

Dlussky and Prefilieva (ants) and Antropov (all others); Ichneumonoidea by Belokobylskij (Braconidae) and Khalaim (Ichneumonidae); Gasteruptionidae by Rasnitsyn; and Proctotrupidae by Kolyada. Diverse Proctotrupomorpha were being studied by the late Mikhail Kozlov, whose untimely death on 11 September 2006 has left this important group without thorough description (except for Proctotrupidae). For the groups

left unattended, there are preliminary identifications made by Kozlov and completed in part by Kolyada and Compton. Because of different styles in description, and particularly in morphological terminology, including symbols denoting various structures employed in different hymenopteran taxa, unification throughout has not been attempted.

The general compilation and editing of manuscripts by other participants, as well as this introduction, are by Rasnitsyn. The closing Discussion is written by Rasnitsyn, based on the results by other participants in the project.

1. Overview of the hymenopteran taxa found in the Bembridge Marls

Symphyta were not found. The absence of Tenthredinoidea is indicative of a warm climate (possibly warmer than in both Baltic amber and Florissant).

The only record of Evaniomorpha is *Vectevania vetula* Cockerell, 1922 (Gasteruptionidae: Aulacinae), a supposed parasite of xylophilous insect larvae, indicative of forested territory.

Proctotrupomorpha are moderately rich but unfortunately poorly studied. Proctotrupeoidea are known from Proctotrupidae (three fossils, described *Oxyserphus kozlovi* Kolyada, sp. nov. and *Mischoserphus* sp., both in the tribe Cryptoserphini, parasitising curculionoid beetles and dipteran larvae, respectively, mainly in mesic forests; see below) and Diapriidae (24 fossils). Earlier described Diapriidae are *Zygota? filicornis* Cockerell, 1921a and *Miota? strigata* Cockerell, 1921a; additional identifications (by Masner and Kolyada in 2006) are *Ambositrinae?* gen. sp., *Basalys* sp., *Belyta?* sp., *Lyteba* (?) sp., *Pantoclis* (?) sp., *Spilomicrini* gen. sp. and *Trichopria* sp. Diapriidae are parasites of dipteran larvae preferring mesic environments; *Ambositrinae* are mainly Gondwanan in their distribution (Australasian and Neotropical with one Afrotropical species known in southern Africa and Madagascar), with one species in North America, and known also in Baltic amber, with one Baltic species hardly distinguishable from an extant African one (Masner 1969).

Cynipoidea are known from 9–11 Cynipidae fossils, including *Andricus vectensis* Cockerell, 1921a and *Rhodites vetus* Cockerell, 1921a, and 6–8 Figitidae. Cockerell's generic identifications are not reliable enough to be used for further inferences.

Platygastridae are found with both living families Platygastridae (two fossils, including *Inostemma* sp., a genus of gall midge parasites, identified by both Kozlov and Masner) and Scelionidae. The latter comprise 12 fossils, including "*Macroteleia*" *veterna* Cockerell, 1921a = *Caloteleia*, a widespread genus of orthopteran parasites; an undescribed genus (determined by Kozlov) near *Apepus* Foerster, 1856, a Palaearctic and Oriental genus whose relatives parasitise tettigoniid eggs on trees; *Gryon* sp., a widespread genus attacking heteropteran eggs; *Scelionini* gen. sp., parasites on acridid eggs; *Baeinae* gen. sp. a group of spider egg parasites, and *Calliscelio* sp. (all determined by Masner). Scelionidae are a more xerophilous group than Diapriidae, and the modest participation of this family compared to the latter indicates generally mesic past environments.

Chalcidoidea fossils (15–16 specimens) remain poorly known. Three species are described, one originally as an ant *Ponera minuta* Donisthorpe, 1920, another as a diapriid *Lithobelyta reducta* Cockerell, 1921a, and only the third as a chalcidoid *Pteromalus? vectensis* Cockerell, 1921a. The latter might be a pteromalid, whilst the former, along with two other fossils, are redescribed below as representatives of the family of fig pollinators, Agaonidae (first identified by Kozlov). The family identity of *Lithobelyta reducta* needs clarification.

The superfamily Ichneumonoidea is particularly rich in the Bembridge Marls, yielding more than one hundred fossils (minimum 32 Ichneumonidae and 75 Braconidae) of more than 60 species (minimum 25 and 36, respectively). Detailed information about these insects is presented below.

Aculeate hymenopterans other than ants are not very diverse. This is particularly true for Chrysoidea, represented by only three fossils of the family Bethyloidea, which remain mostly unstudied. One described is *Mesitius? rectinervis* Cockerell, 1921a.

The higher wasps and bees (Aculeata s. str.) are fully revised here (see below). Except for ants, they are only moderately diverse. Apoid wasps and bees are known from two bees (one Apidae: Apinae, another unidentifiable Megachilidae) and three wasps (one Sphecidae and two Crabronidae, the latter indicative of a forested landscape). Vespoidea (s.l.) wasps are recorded from three families: Tiphidae (two fossils), Scolioidea (one) and Vespidae (four; one of these shows (sub)tropical affinities). See below for details.

Ants (Formicidae) are the most abundant and most indicative group in the Bembridge hymenopteran assemblage and the third most diverse one (some 1220 fossils, 20 species and ten genera). They comprise both thermophilous and temperate species, whose co-existence implies most convincingly the equable climate, and the high proportion of dendrobiotic or otherwise forest-dwelling ants infers a well forested source area. The ant assemblage is undoubtedly more related to the Baltic amber fauna than to Florissant, but this similarity might be geographically rather than geochronologically driven (for details see below).

Institutional repository abbreviations. CAMSM, Sedgwick Museum of Earth Sciences, University of Cambridge; IWCMS, Isle of Wight County Museum Service; NHMUK, Department of Palaeontology, Natural History Museum, London; USNM, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC.

2. Material and methods

The fossils were studied using the usual observation under a stereomicroscope, except that the application of any liquid was avoided because of salt crystals in the rock matrix, often within the fossil itself. Instead of liquid, polarising illumination was used to enhance visibility of the fossilised organic material when preserved. A.V. Antropov used Carl Zeiss Stemi SV 6 and Leica MZ 9.5 stereomicroscopes for study of the fossils, and Nikon Coolpix 885 / Nikon Coolpix 4500 digital cameras to make photographs, which were subsequently improved when necessary using Adobe Photoshop 7.0 software. The line drawings were prepared using CorelDRAW 7 software. All measurements were made with the help of an ocular-micrometer. G. M. Dlussky and K. S. Perfilieva used the Olympus C-4000 Zoom digital camera, and enlarged prints were hand-traced with a pen with the visual control of the specimen under a Leica S6E stereomicroscope. The resulting draft drawing was scanned with ScanExpress 6000 PS and improved finally using the program CorelDRAW 8. V.A. Kolyada used the Wuzhou XTL-3400E stereomicroscope and a Canon PowerShot S50 camera, with photographs automounted with Helicon Focus software and adjusted with Adobe Photoshop 6.0; line drawings were made with Adobe Illustrator 10 software. A. P. Rasnitsyn examined the fossils using LOMO MPS-2 and Leica MZ 9.5 microscopes and prepared photographs using a Nikon Coolpix4500 camera automounted with Helicon Focus software, and the line drawings were prepared using CorelDRAW 11 software.

of similar age: the Upper Eocene Baltic amber and the uppermost Eocene shales of Florissant (USA, Colorado) are of obvious interest.

Various xylobionts are common in Baltic amber. Species of the genera *Vespa*, *Palaeovespa* and *Polistes* (Vespidae) probably built their nests on or inside trees and prey directly in their crowns. Several genera of Apidae (*Electrobombus*, *Electrapis*, *Protobombus*, *Thaumastobombus*) were also discovered in Baltic amber and, though nothing is known about their nesting habits, they were probably forest inhabitants which could build underground nests as do extant species of Bombini. It is necessary to take into consideration that Vespidae and Apidae are not particular xylobionts, because their provisioning territories may spread far from the nest, and their chances of being fossilised in resin depend directly on the density of populations. Representatives of the families Ampulicidae (*Protodolichurus* Nemkov, 1988, *Dolichurus* Latreille, 1809) and Crabronidae (*Eopinoecus*, *Eoxyloecus*, *Passaloecus* Shuckard, 1837, *Pison* Jurine, 1808, *Tracheliodes* A. Morawitz, 1866 and, judging from the absence of foretarsal digging rakes, *Palanga* and *Eomimesa*) also hunt in the same biotopes. Species of Ampulicidae used available cracks of the tree trunks for concealing their prey, and species of Crabronidae, as well as comparatively small bees of the families Megachilidae (*Glyptapis* Cockerell, 1909, *Ctenoplectrella* Cockerell, 1909, *Glaesosmia* Engel, 2001), like their extant relatives, built their nests either in wood or inside old borings of various xylophagous insects. Obviously, these groups are closely linked to trees and had more chances to be fossilised in resin. The only exception to the rule is *Tiphia* (?) sp., which was mentioned by Brischke (1886) from the lost collection of Menge.

The more diverse fauna of the Florissant beds is somewhat different. Though Vespidae (*Palaeovespa*, *Polistes*) and even real xylobionts (Crabronidae, Pemphredoninae – *Passaloecus*) are present here, the prevailing groups are connecting with prey inhabiting soil (Tiphidae, Myziniinae – *Lithotiphia* Cockerell, 1906, *Geotiphia* Cockerell, 1906; Tiphinae – *Paratiphia*; Scoliididae, Archaeoscoliidinae – *Floriscolia* Rasnitsyn, 1993); with digging underground nests (Sphecidae, Ammophilinae – *Ammophila* Kirby, 1798; Crabronidae, Crabroninae – *Tracheliodes*, *Ectemnius* Dahlbom, 1845, Mellininae – *Mellinus* Fabricius, 1790, Bembicinae – *Gorytes* Latreille, 1805 (?*Psammaletes* Pate, 1936), *Psammaecius* Lepeletier, 1832, Philanthinae – *Philanthus* Fabricius, 1790, *Prophilantus* Cockerell, 1906); or so-called “mud-daubers”, who use moist clay from near water for building their nests (Sphecidae, Sceliphrinae – *Chalybion* Dahlbom, 1843, *Hoplisidia* Cockerell, 1906; Crabronidae, Crabroninae – *Pison*). Many other groups of Hymenoptera found in Florissant shales inhabited the shore territories of the fresh water lakes and also included ground-nesting or often weakly flying forms.

The composition of the aculeate wasp and bee fauna found in the Bembridge Marls, Isle of Wight, England, demonstrates wider generic diversity than is characteristic of the contemporary Palaeartic region. The studied fauna includes both xylobionts (*Palaeopolybia*, *Protopolistes*, *Sphaerancistrocerus*, *Tythopsen*, *Plisomena*, a megachilid bee and, probably, *Dryophia*) and ground-dwelling forms (*Philoponites*, *Palaeoscolia*, *Protosceliphron*, and *Oligobombus*). The most interesting fact is the high level of endemism; none of the discovered taxa were previously known from other formations. Another peculiarity is the presence of archaic forms, for instance the polistine wasp *Palaeopolybia*, which retains a vespine-like structure of its forewing submarginal area; *Protosceliphron* – the only known Sphecidae with a sessile metasoma lacking sternal petiole; and *Plisomena* – the only known Spilomenina with plesiomorphic (not enlarged) pterostigma. Presence of such

a generalised feature as a weak degree of costalisation of the anterior ends of recurrent veins in *Palaeopolybia*, *Tythopsen*, *Plisomena* and *Oligobombus* is also a very remarkable peculiarity of the studied fauna, because it is more archaic than those of the earlier resembling taxa. I think that it was a locally endemic fauna, probably isolated from the surrounding regions.

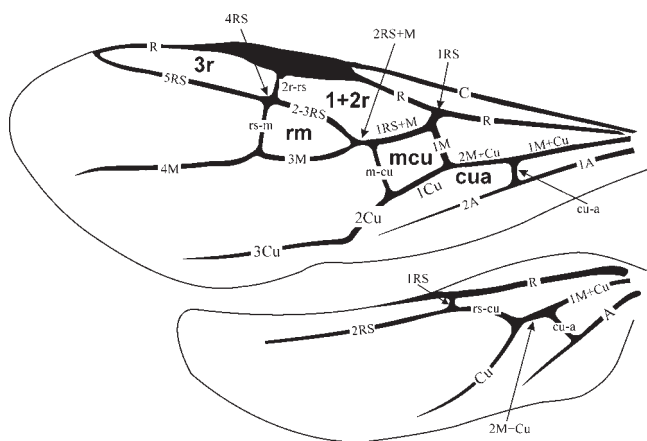
There are comparatively low numbers of Aculeata in Bembridge Marls (excluding winged ants, whose quantity is much more than of all other groups of Aculeata) and parasitic Hymenoptera. The first group perished in mass after swarming, while the second could easily be blown from the coast because of its comparatively weak flying abilities. However, this cannot explain the low quantity of Aculeates in the adjacent territories, because actively flying aculeate wasps and bees are not connected with a sea coast, where they can get neither prey nor building materials. That is why the probability of their fossilisation in such conditions was quite low. Nevertheless, the discovery of such taxa as Tiphidae, Scoliididae and Apidae indicates that large meadows with grasses and long-flowered herbs were present near the region of fossilisation. The occurrence of Spilomenina and small eumenine wasps occupying pre-existing borings in wood suggests the presence of broad-leaved trees. The comparatively weak degree of costalisation of the wing venation and significant sizes of the marginal cell in the discovered pemphredonines also testifies to their living in forest or forest–steppe regions. Furthermore, some taxa of apparently tropical affinities (*Palaeopolybia*) indicate a warm climate. I suggest that the region of fossilisation was a coastal plain with a warm climate, resembling the modern subtropical habitats of the Mediterranean region.

3.11. Superfamily Formicoidea Latreille, 1802

[By Gennady M. Dlussky and Ksenia S. Perfilieva.]

3.11.1. Family Formicidae Latreille, 1802. Ants are the most abundant group of insects in the Bembridge Marls. The first brief report on a finding of ants in the Bembridge Marls, with no description of species, appeared in the late 19th Century (Brodie 1875). A few years later Woodward (1879) referred to identifications by F. Smith and noted that ants from these deposits belong to genera *Myrmica* Latreille, 1804, *Formica* Linnaeus, 1758 and *Camponotus* Mayr, 1861. Donisthorpe (1915) reproduced this information. The same year, Cockerell (1915) finished the study of a small collection from the Bembridge Marls collected by Brodie (transferred to the United States National Museum as a part of the Laco collection) and published the first descriptions of species. His descriptions were based mainly on measurements of cells and veins of forewings of a few specimens. He described eight species and referred them to four subfamilies: *Ponera hypolitha* Cockerell, 1915 (Ponerinae); *Leptothorax gurnetensis* Cockerell, 1915 (Myrmicinae); *Dolichoderus britannicus* Cockerell, 1915, *D. anglicus* Cockerell, 1915, and *D. ovigerus* Cockerell, 1915 (Dolichoderinae); and *Oecophylla atavina* Cockerell, 1915, *O. perdita* Cockerell, 1915, and *O. megarche* Cockerell, 1915 (Formicinae).

Donisthorpe (1920) undertook revision of a large collection of fossils from the Bembridge Marls, collected by P. B. Brodie, E. J. A'Court Smith and R. W. Hooley and kept at the Natural History Museum, London. In this article, he demonstrated that the species described by Cockerell as *Leptothorax gurnetensis* actually belongs to the subfamily Formicinae, and placed it in a new genus *Leucotaphus* Donisthorpe, 1920. He also described seven new species: *Syntaphus wheeleri* Donisthorpe, 1920; *Euponera* (*Mesoponera*) *crawleyi* Donisthorpe, 1920; *Ponera minuta* Donisthorpe, 1920, *Emplastus emeryi* Donisthorpe, 1920 (Ponerinae); *Dolichoderus gurnetensis* Donisthorpe,



Text-figure 65 Wing venation of *Emplastus britannicus*, to show venational symbols used. Capitalised are longitudinal veins; dashed are cross-veins; neither of above are cells.

1920 (Dolichoderinae); *Leucotaphus cockerelli* Donisthorpe, 1920; and *Camponotus (Colobopsis) brodiei* Donisthorpe, 1920 (Formicinae). Later Cockerell (1927) described one more species, *Leucotaphus permaneus* Cockerell, 1927. There are no later publications about the ant fauna of the Bembridge Marls.

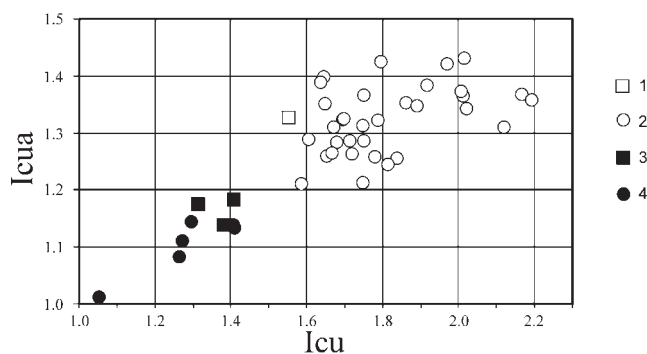
We studied 1136 specimens of fossil ants kept at the NHMUK including all of Donisthorpe's type specimens. We were able to study all of Cockerell's types, stored at the USNM (15 specimens) as well. It has only been possible to identify 105 of the specimens up to family level, due to insufficient preservation. The remaining 1031 specimens have been identified up to genus and 630 to species level. Digital photos have been prepared for 245 of the best preserved fossils, and some of them served as a base for line drawings.

Among the studied material, 234 specimens were earlier identified by Donisthorpe. Fifteen of them are not ants, and the references of 13 other fossils to ants seem doubtful. During the present revision, we found that Donisthorpe's article (1920) contains a number of mistakes, both in respect to definition of specimens and to taxonomic position of described species. There is an example, which can attest to the quality of this work: Donisthorpe described specimen NHMUK I.8675 as the holotype of *Euponera (Mesoponera) crawleyi* (Ponerinae) and identified its counterpart (I.8539) as *Leucotaphus gurnetensis*, hence referring it to another subfamily (Formicinae).

Some species described by Cockerell and Donisthorpe have been either synonymised or excluded from Formicidae, with only ten of 17 described species currently accepted, and the taxonomic status of six of them is changed. Additionally we describe ten new species below.

Preservation of the Bembridge fossils is unusual. In fact, they are not impressions but cavities. As a result, we see an insect from the inside, unlike other deposits where fossils are seen from the outside. This creates additional difficulties for interpretation. In particular, the fossils rarely split along the middle plane and as a result the insect contour looks deformed. It is rarely possible to combine part and counterpart. Also, measurements and their ratios are more variable than it is expected from intact ants.

In the line drawings, lines trace visible sclerite boundaries, dashed lines trace supposed sclerite boundaries, and dotted lines – visible margins of incomplete sclerites. Filled contours denote sclerites with the original matter preserved, even if chemically modified. Wing morphometrics were analysed using standard methods (cf. Bookstein 1991; Rohlf & Marcus 1993; Danforth 1989; Rust 1999). Measurements of larger structures



Text-figure 66 Differences of position of cross-vein cu-a in Aneuretinae, Dolichoderinae and Ponerinae from Bembridge Marls. Symbols: 1 = *Britaneuretus anglicus* (Aneuretinae); 2 = Dolichoderinae; 3 = *Taphopone petrosa* (Ponerinae); 4 = other Ponerinae.

(total body length, length of alitrunk, forewing, etc.) were made using an ocular micrometer. Smaller details (petiole length, height and width, maximum eye diameter, etc.) were measured from digital pictures.

Abbreviations of measurements taken: AL = alitrunk (mesosoma) length from junction with head to that with petiole; AW = maximum alitrunk width; BL = total body length; ED = maximum eye diameter; F1 = fore femur length; F3 = hind femur length; FWL = forewing length; FWW = forewing width measured between the pterostigmal base and indentation of wing hind margin next to junction of sections 2Cu and 3Cu (Text-fig. 65); HL = head length without mandibles; HW = maximum head width; n = number of specimens measured; PtL = petiole length; PtH = maximum petiole height; PtW = maximum petiole width; SL = scape length; ScL = scutum length; ScW = scutum width; SctL = scutellum length; SctW = scutellum width.

Nomenclature of the wing venation (Text-fig. 65) is as in our previous publications (Dlussky 1983; Perfilieva 2002; Dlussky & Perfilieva 2003). Two indices are used to help discriminate ant subfamilies: these concern relative position of cross-vein cu-a and are calculated as follows:

$$Icu = [1Cu + (2M + Cu)] / 1Cu,$$

$$Icu_a = [(1M + Cu) + (2M + Cu)] / (1M + Cu).$$

They are particularly helpful in the distinguishing of Ponerinae and Dolichoderinae (Text-fig. 66). The second index is more precise, because Icu depends not only on the position of cu-a but also on the size of cell m-cu. However, Icu is indispensable in the case of incomplete wings when Icu_a is not available for consideration.

Other terminology of ant morphology follows Bolton (1994). Statistics of the living and extinct genera and species are after Bolton (1995), corrected to consider overlooked and subsequent publications.

3.11.1.1. Subfamily Aneuretinae Emery, 1913

Taxa included. Subfamily Aneuretinae includes the unique extant species *Aneuretus semoni* Emery, 1893 that inhabits Sri Lanka (Wilson *et al.* 1956). Seven fossil species attributed to Aneuretinae were also described: *Cananeuretus occidentalis* Engel & Grimaldi, 2005 (Upper Cretaceous, Canadian amber); *Aneuretellus deformis* Dlussky, 1988 (Paleocene, Sakhalin amber); *Protaneuretus succineus* Wheeler, 1915, *Paraneuretus longicornis* Wheeler 1915 and *P. tornquisti* Wheeler, 1915 (Late Eocene, Baltic amber); *Mianeuretus mirabilis* Carpenter, 1930 (latest Eocene, Florissant); and *M. eocenicus* Dlussky & Rasnitsyn, 2002 (Middle Eocene, Green River). The incomplete

Burmomyrma rossi Dlussky, 1996 (mid-Cretaceous, Burmese amber) may also belong to this subfamily.

Genus *Britaneuretus* Dlussky & Perfilieva, gen. nov.

Etymology. After Britain and genus *Aneuretus*. Gender masculine.

Type species. *Dolichoderus anglicus* Cockerell, 1915.

Diagnosis. Female. Propodeum with a pair of short, obtuse teeth. Petiole elongate, without scale or distinct node. Forewing with cells 1+2r, rm, mcu and most likely 3r closed. 1RS and 2r-rs vertical to R. Cell mcu medium sized (visually about half area of cell 1+2r or little less), far distant of pterostigmal base level. Icu > 1.5, Icu_a > 1.2. Gaster oval, without constriction between first and second segments.

Remarks. Differs from *Cananeuretus* Engel & Grimaldi, 2005 from the Upper Cretaceous Canadian amber, *Protaneuretus* Wheeler, 1915 and *Paraneuretus* Wheeler, 1915 from the Late Eocene Baltic amber, *Mianeuretus* Carpenter, 1930 from the Middle and latest Eocene of North America, and from extant *Aneuretus* Emery, 1893 by absence of petiolar node. *Protaneuretus* and *Cananeuretus* have no propodeal teeth. *Aneuretellus* Dlussky, 1988 from the Palaeocene Sakhalin amber has no petiolar node but, unlike the new genus, has no propodeal teeth. The only known species *A. deiformis* is of very small size (body length about 3 mm, alitrunk length 0.88 mm).

Although no sting is visible in the fossil, a combination of petiole form and features of forewing venation indicate position of the new genus in Aneuretinae with sufficient confidence.

Britaneuretus anglicus (Cockerell, 1915), comb. nov.
Plate 18, fig. 1; Text-fig. 67.

1915 *Dolichoderus anglicus* Cockerell, p. 484, plate 65. fig. 8.
1978 *Dolichoderus anglicus* Cockerell; Burnham, p. 112.
1995 *Dolichoderus anglicus* Cockerell; Bolton, p. 172.

Holotype. USNM 61415, Laco Coll. Bembridge Marls, Isle of Wight, UK.

Description. Female. Propodeum angular in side view, with blunt teeth on boundary of propodeal dorsum and declivity; propodeal dorsum longer than propodeal declivity. Petiole 1.7 times as long as high and about half as long as propodeum. Anterior part of petiolar dorsum almost flat, posterior one feebly rounded in side view. Petiole with maximal height behind its midlength. Forewing: distance from 1RS to pterostigma more than 1.5 times as long as RS+M. 1M inclined and parallel to m-cu. RS+M nearly 0.65 as long as 2-3RS. Cell mcu trapezoid (RS+M and 1Cu noticeably longer than m-cu and 1M). Icu = 1.6, Icu_a = 1.3.

Measurements of holotype, mm: AL ~ 2.6; FWL ~ 8; PtL = 1.2; PtH = 0.7.

Remarks. Cockerell described *Dolichoderus anglicus* using only characters of forewing venation and ignored preserved body fragments. The wing venation is characteristic not only of *Dolichoderus*, but also of many other genera. At the same time, the form of the propodeum and petiole of the fossil is strictly unlike that of Dolichoderinae and particularly of *Dolichoderus*.

Cross-vein 2r-rs occurring distally in respect to rs-m appears to be an aberration in ant wings, being present often in only one wing of the pair. Therefore, we consider this feature as an aberration of the holotype and not as a diagnostic character of the taxon.

3.11.1.2. Subfamily Dolichoderinae Forel, 1878

Genus *Dolichoderus* Lund, 1831

Type species. *Formica attelaboides* Lund, 1831, by monotypy.

Other species. The genus *Dolichoderus* comprises 110 species in the modern fauna, the vast majority of which are distributed in the Neotropical (54) and Indo-Australian and Australian (41) regions. Only nine species are known from the Oriental region, four from the Nearctic region, two from the Palearctic region, and none were recorded from the Afrotropical region. The oldest species, *D. kohlsi* Dlussky & Rasnitsyn, 2002, is recorded in the Middle Eocene Formation Green River, USA. Sixteen species are described from the Late Eocene Baltic and Rovno ambers (Dlussky 2002; Dlussky & Perkovsky 2002) seven species from the near-boundary Eocene/Oligocene deposits: two from Florissant, USA (Carpenter 1930), five from the Isle of Wight, UK (Donisthorpe 1920), and six species from the Oligocene of continental Europe (Théobald 1937). Thirteen species are described from the Miocene of Central Europe (Radoboj, Croatia) and East Europe (Kerch, Ukraine), Eastern Asia (Shanwang, Shandong, China) and Central America (Dominican amber) (Mayr 1867; Dlussky 1981a; Wilson 1985; Zhang 1989; Zhang *et al.* 1994). However, after revision of the European fossil species, this number will undoubtedly change. As shown below, only one of five species described as *Dolichoderus* from the Bembridge Marls belongs there.

Diagnosis (for rock fossils of females and workers). Female. Head elliptical or oval, widest behind midlength of head sides; sometimes retort-shaped or subrectangular with rounded occipital corners, but never rectangular and longer than wide as in *Protazteca* Carpenter. Eyes of moderate size. Mandibles triangular, dentate. Propodeum bispinate, bidentate, or distinctly angular in side view, always with concave declivity. Petiole with scale proclined, or triangular in side view. Integument thick, often coarsely sculptured. Forewing with cells 1+2r, 3r, rm and mcu closed; rm usually triangular. 1RS vertical to R or slightly proclined. Cell 3r touching wing margin, crossveins 2r-rs and rs-m coincide on RS, or rs-m slightly distal. Cell mcu medium-sized, rhomboid or trapezoid (1Cu appreciably longer than RS+M). Gaster oval, without constriction between first and second segments. Integument thick, often coarsely sculptured.

Remarks. Almost all modern species of the genus are dendrobiotic, and there are no reasons to consider the present fossils as different.

Dolichoderus vectensis Donisthorpe, 1920
Plate 18, figs 2-3; Text-fig. 68A-C.

1920 *Dolichoderus vectensis* Donisthorpe, p. 88, plate V. fig. 6.
1978 *Dolichoderus vectensis* Donisthorpe; Burnham, p. 112.
1995 *Dolichoderus vectensis* Donisthorpe; Bolton, p. 177.

Holotype. NHMUK I.9198, ♀, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie (Plate 18, fig. 2; Text-fig. 68A).

Other material. Two females and four forewings in NHMUK collection, including well preserved lateral imprint of the female NHMUK In.24934 (Text-fig. 68B) and forewing NHMUK I.9373 (Plate 18, fig. 3; Text-fig. 68C). Bembridge Marls, NW Isle of Wight, UK, .

Diagnosis. Similar to extant and extinct species of *D. quadri-punctatus* group, particularly to *D. tertiarius* (Mayr 1868) from the Baltic amber and *D. poleusus* Dlussky, 2002 from the Rovno amber (Late Eocene), but differs from both in the rougher sculpture of the scutum and propodeum.

Description. Female. BL 4-4.5 mm. Head wide, with convex sides, rounded occipital corners and concave occipital

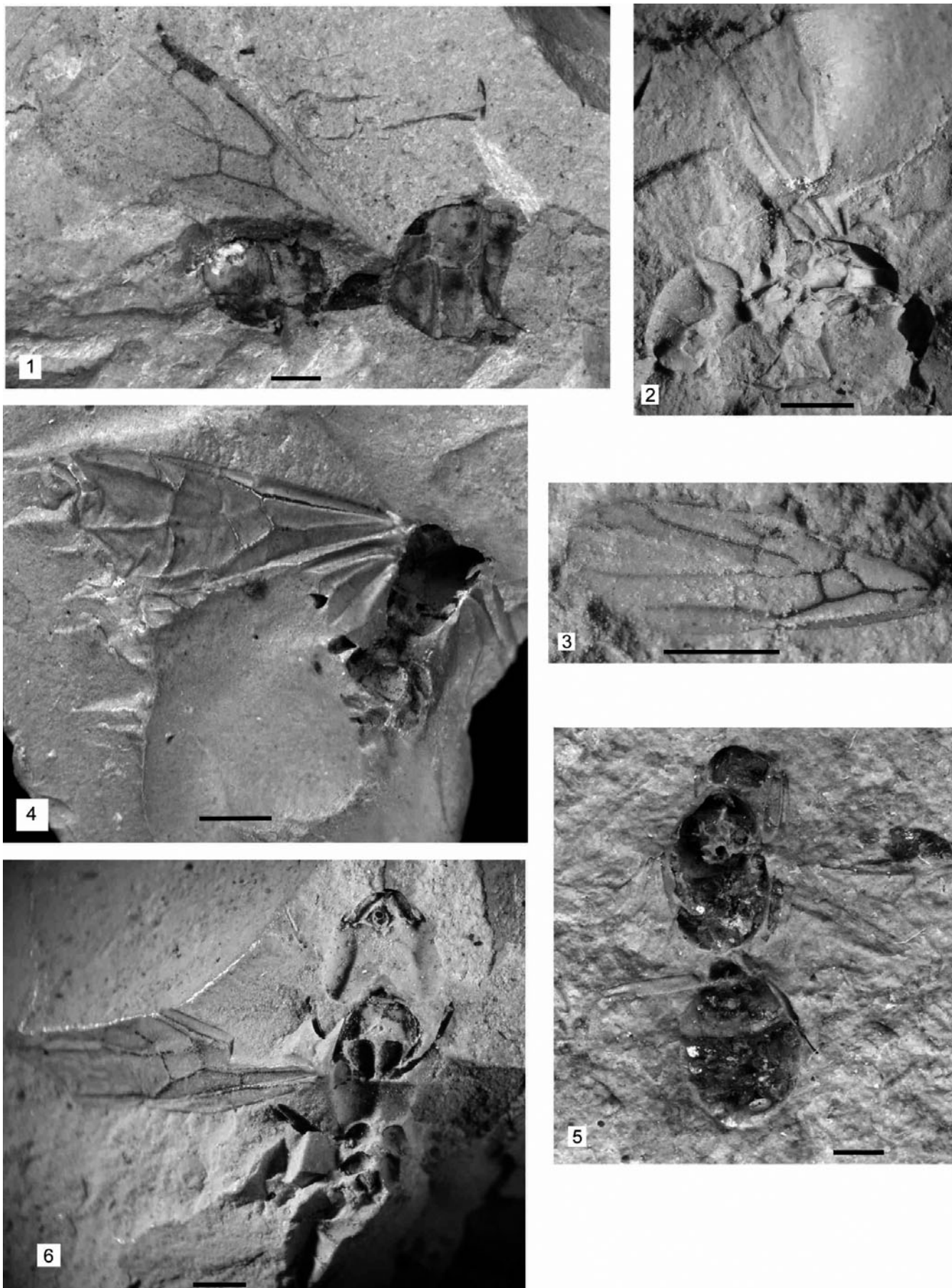
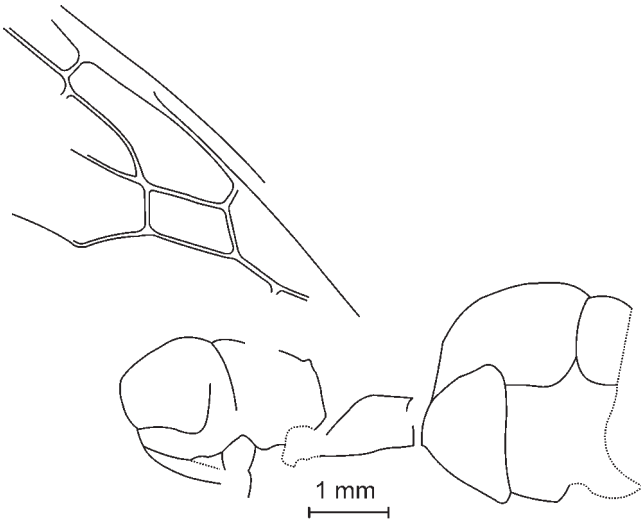
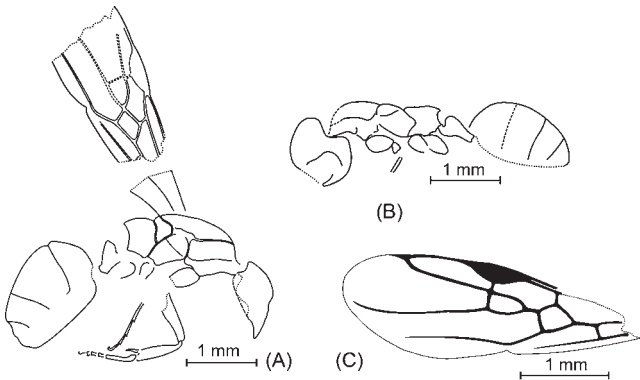


Plate 18 (1) *Britaneuretus anglicus* (Cockerell) comb. nov., holotype of *Dolichoderus anglicus* Cockerell, USNM 61415. (2–3) *Dolichoderus vectensis* Donisthorpe: (2) holotype, NHMUK I.9198; (3) forewing, NHMUK I.9373. (4–6) *Emplastus britannicus* (Cockerell), comb. nov.: (4) holotype of *Dolichoderus britannicus* Cockerell, USNM 61413; (5) holotype of *Dolichoderus ovigerus* Cockerell USNM 61416; (6) holotype of *Emplastus emeryi* Donisthorpe, NHMUK In.24367. Scale bars = 1 mm.



Text-figure 67 *Britaneuretus anglicus* (Cockerell), holotype of *Dolichoderus anglicus* Cockerell, USNM 6145.



Text-figure 68 *Dolichoderus vectensis* Donisthorpe: (A) ♀, holotype, NHMUK I.9198; (B) ♀, NHMUK In.24934; (C) forewing, NHMUK I.9373.

margin. Mandibles well developed, triangular. Scutum feebly convex, not overhanging pronotum. Mesopleurae with distinct longitudinal furrow. Propodeum angular, with distinct carina separating propodeal dorsum and declivity; propodeal dorsum convex, propodeal declivity concave in side view. Legs rather short and thick. Petiole with rounded node, 1.5–1.8 times as long as high. At least scutum and propodeal sides with rather rough sculpture consisting of large isolated foveolae. Mesopleurae with no noticeable sculpture. Forewing: FWL 3.3–4 mm. IRS and 2r–rs vertical to R. Cross-veins 2r–rs and rs–m coincide on RS, or rs–m shifted distally for about its width. Cell rm triangular, usually with distinct or (in holotype) short stem. Cell mcu of medium size. Icu = 1.55–2.0 mm; Icu = 1.4 mm.

Measurements in mm. NHMUK I.9198 (♀, holotype): BL = 4.4; AL = 1.6; HL ~ 0.8; FWL ~ 3.5. NHMUK In.24934 (♀): BL ~ 4; AL = 1.6; HL ~ 0.8; HW ~ 0.9; PtL = 0.52; PtH = 0.30. Other specimens (n = 3): FWL = 3.3–4.0; FWW = 0.8–1.1.

Remarks. Donisthorpe (1920) erroneously identified specimen I.9231 as *Leucotaphus gurnetensis*: all visible characters of this specimen including form of the propodeum are similar to the holotype of *D. vectensis*.

Morphogenus *Emplastus* Donisthorpe, 1920

1915 *Dolichoderus*; Cockerell, p. 483 (nec Lund, 1831).

1915 *Ponera*; Cockerell, p. 483 (nec Latreille, 1804).

1920 *Dolichoderus*; Donisthorpe, p. 87 (pars) (nec Lund, 1831).

1920 *Emplastus* Donisthorpe, p. 86.

Type species. *Emplastus emeryi* Donisthorpe, 1920 (= *Dolichoderus britannicus* Cockerell, 1915), by original designation.

Other species. *E. britannicus* (Cockerell, 1915), *E. hypolithus* (Cockerell, 1915), *E. gurnetensis* (Donisthorpe, 1920), and *E. kozlovi* sp. nov. Bembridge Marls, Isle of Wight, UK.

Diagnosis. Fossil ants not preserved well enough to fit orthotaxa, and with following combination of traits: size medium, head subrectangular with rounded occipital corners; mandibles triangular with denticulate masticatory margin; propodeum rounded in side view, petiole in side view with thick scale (females) or triangular (males). Forewing with cells 1+2r, 3r, rm and mcu closed; cell 3r with apex touching wing fore margin, IRS vertical to R or slightly proclined. Icu > 1.45 mm, Icu_a > 1.2 mm. Gaster without constriction between first and second segments.

Remarks. Donisthorpe (1920) placed this genus in the subfamily Ponerinae and considered it similar to the modern *Myopias* Roger, 1861. In his opinion *Emplastus*, as well as *Myopias*, has mandibles without teeth. In fact, the holotype has the masticatory margin of mandibles hidden. Specimen NHMUK In.24461, similar to *E. emeryi* in the body proportions and other visible characters, has masticatory margin of mandibles with blunt teeth. The position of cross-vein cu-a in the type species (Icu = 1.7) differs clearly from that of Ponerinae. In contrast, all characters visible on the holotype of *Emplastus emeryi* are identical to those of *Dolichoderus britannicus* Cockerell, and so justify synonymy of the former under the latter species name.

Cockerell (1915) and Donisthorpe (1920) described several species now included in *Emplastus*, based on the *Dolichoderus*-like forewing venation (characteristic of several other dolichoderine genera). However, this character is combined with the propodeum rounded in side view and not angular or bispinate with concave hind contour, as in all living and fossil *Dolichoderus*.

The morphogenus *Emplastus* may embrace representatives of various dolichoderine genera, particularly those earlier included into *Iridomyrmex* (*Anonichomyrma* Donisthorpe, 1947, *Ctenobethylus* Brues, 1939, and *Iridomyrmex* Mayr, 1862). *Emplastus* differs from *Liometopum* Mayr, 1861 (Late Eocene-present) in the apex of cell 3r of the forewing touching the wing margin (distant from it in *Liometopum*). As mentioned above, *Emplastus* differs from females of *Dolichoderus* in the form of the propodeum.

Emplastus britannicus (Cockerell, 1915), comb. nov.

Plate 18, figs 4–6; Text-figs 65, 69A–G, 88C

1915 *Dolichoderus britannicus* Cockerell, pp 483–484, plate 65, figs. 6–7.

1915 *Dolichoderus ovigerus* Cockerell, p. 484, plate 65, fig. 9; syn. nov.

1920 *Dolichoderus britannicus* Cockerell; Donisthorpe, pp 87–88.

1920 *Dolichoderus ovigerus* Cockerell; Donisthorpe, p. 88.

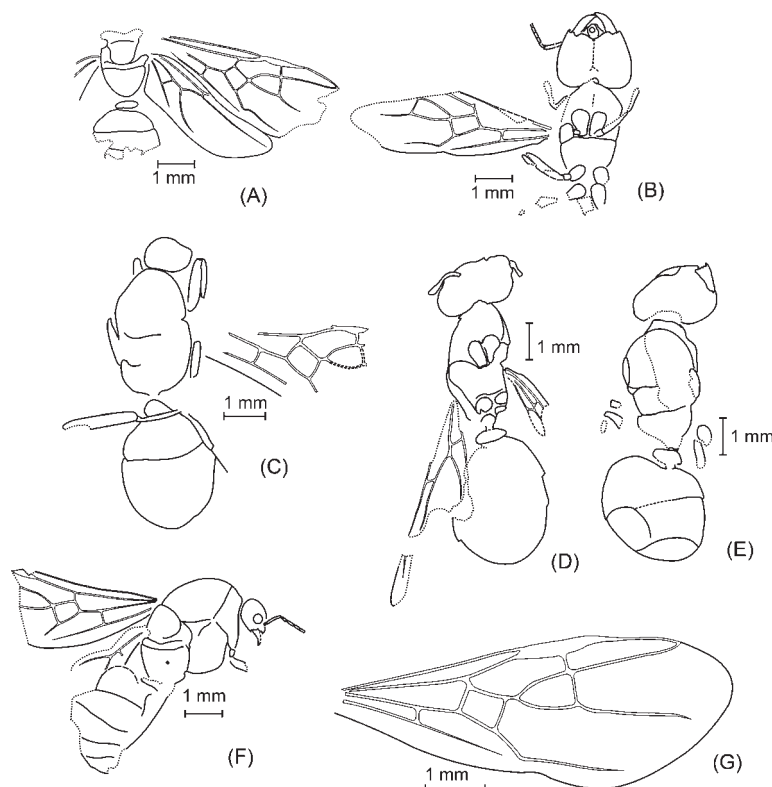
1920 *Emplastus emeryi* Donisthorpe, p. 86, plate V. fig. 5; syn. nov.

1978 *Dolichoderus britannicus* Cockerell; Burnham, p. 112.

1978 *Dolichoderus ovigerus* Cockerell; Burnham, p. 112.

1978 *Emplastus emeryi* Donisthorpe; Burnham, p. 109.

1992 *Emplastus emeryi* Donisthorpe; Carpenter, p. 492.



Text-figure 69 *Emplastus britannicus* (Cockerell): (A) ♀, USNM 61413 (holotype of *Dolichoderus britannicus* Cockerell); (B) ♀, NHMUK In.24367 (holotype of *Emplastus emeryi* Donisthorpe); (C) ♀, USNM 61416 (holotype of *Dolichoderus ovigerus* Cockerell); (D) ♀, NHMUK I.8922; (E) ♀, NHMUK In.2461; (F) ♂, NHMUK I.10142; (G) forewing, NHMUK In.25083.

1995 *Dolichoderus britannicus* Cockerell; Bolton, p. 173.

1995 *Dolichoderus ovigerus* Cockerell; Bolton, p. 175.

1995 *Emplastus emeryi* Donisthorpe; Bolton, p. 188.

Holotype. USNM 61413, part and counterpart, Bembridge Marls, NW Isle of Wight, UK; ♀ (Plate 18, fig. 4; Text-fig. 69A).

Paratype. USNM 61414, Bembridge Marls, NW Isle of Wight, UK, Lacoë coll., ♀.

Other material. Holotype of *Dolichoderus ovigerus*, USNM 61416, Bembridge Marls, NW Isle of Wight, UK, coll. Lacoë, ♀ (Plate 18, fig. 5; Text-fig. 69C). Holotype of *Emplastus emeryi*, NHMUK In.24367, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley, ♀ (Plate 18, fig. 6; Text-fig. 69B). Fifteen females, two males and 27 forewings in NHMUK collection and one forewing in CAMSM collection, including well preserved dorsal (NHMUK In.24461, Text-fig. 69E) and ventral (NHMUK I.8922, Text-fig. 69D) imprints of females, lateral imprint of male (NHMUK I.10142, Text-fig. 69F) and completely preserved imprint of forewing (NHMUK In.25083, Text-fig. 69G). Bembridge Marls, Isle of Wight, UK.

Description. Female. BL 6–8.5 mm, AL 2.5–3.5 mm, FWL 6–7 mm. Head wide (HW/HL = 1.2), as wide as alitrunk, broader behind than in front, with feebly convex sides, rounded occipital corners and concave occipital margin. Scape short, not reaching occipital margin. Mandibles massive, triangular, with few blunt teeth on masticatory margin. Alitrunk *c.* 1.8 times as long as wide. Scutum flat dorsally, rounded anteriorly, nearly as long as wide; not overhanging pronotum. Scutellum feebly convex, 1.7–1.9 times as wide as long. Propodeum evenly rounded in side view. Legs rather short and thick. Petiole with scale wide and thick, scale 2.5–3 times as

wide as thick. Gaster oval. Body integument matter preserved with chagrined surface.

Male. BL *c.* 6 mm, AL *c.* 3 mm, FWL 5.5–6 mm. Head small, clearly narrower than alitrunk. Eyes oval, situated slightly before midlength of head sides. Scape short, not reaching occipital margin, about as long as two or three flagellomeres. Mandibles well developed, triangular. Pronotum narrow, along midline less than 0.25 as long as scutum. Scutum and scutellum feebly convex, scutum half as long as alitrunk. Propodeum rounded in side view. Legs rather long and thin. Petiole triangular in side view, with rounded top, higher than long. As preserved, surface sculpture similar to, but finer than, in female.

Forewing IRS slightly proclined or, sometimes, vertical to R. Cross-veins 2r-rs and rs-m coincide on RS or, rarely, rs-m distal for cross-vein width. Cell rm triangular, not pedunculate or with very short stem, comparatively wide (1.6–2.1 times as long as wide). Cell mcu medium-sized, trapezoid or, rarely, rhomboid. Icu = 1.55–2.2, Icu_a = 1.2–1.4. Hindwing with two longitudinal veins RS and Cu and well developed IRS. Cross-vein rs-cu concave, longer than r-rs and 2Cu. Cross-vein cu-a more close to rs-cu than to wing base.

Measurements in mm. Types: USNM 61413 (♀, holotype of *Dolichoderus britannicus*): AW = 1.3; PtW = 0.66; FWL ~ 6. USNM 61414 (♀, paratype of *Dolichoderus britannicus*): BL = 5.7; AL = 2.7, FWL = 6.2. USNM 61416 (♀, holotype of *Dolichoderus ovigerus*): BL = 6.9; AL = 2.9, AW = 1.6. NHMUK In.24367 *Emplastus emeryi*): AL = 3.3; HL = 1.6; HW = 2.0. Other specimens: females: AL = 2.7–3.55 (n = 4); HW = 1.9–2.1 (n = 3); ScL = 1.4–1.5 (n = 3); SctW = 1.6–1.7 (n = 2); SctL = 0.65–0.7 (n = 3); PtW = 0.6–0.85; FWL = 6.0–7.05 (n = 3). Males: AL = 2.5–3.2 (n = 2); HL = 1.0 (n = 1); SL = 0.4 (n = 1); ED = 0.25 (n = 1);

FWL = 6.8 (n = 1); FWW = 1.9–2.1 (n = 2). Isolated forewings: FWL = 5.4–7.3 (n = 13); FWW = 1.6–2.1 (n = 11).

Remarks. Three specimens (NHMUK I.8922, NHMUK In.17067/NHMUK In.17074, NHMUK In.24461) were found in the NHMUK collection with the general appearance and available characters identical to those of the holotype of *Emplastus emeryi*. There are a significant number of incomplete fossils as well that form a complete transition between *Emplastus emeryi* Donisthorpe, *Dolichoderus britannicus* Cockerell and *D. ovigerus* Cockerell. Cockerell (1915) wrote that *D. ovigerus* had "Structure, including petiole, essentially as in *D. britannicus*, from which it may not be distinct" (Cockerell 1915, p. 484). The only indicated differences between these species are details in the forewing venation, particularly the pedunculate cell *rm* in *D. ovigerus*. However, this character is variable: for example, the specimen NHMUK In.25085 has cell *rm* long pedunculate in the right wing and with very short stem in the left one. This justifies synonymy of the three species resulting in the valid name *Emplastus britannicus* (Cockerell 1915).

There are ovoid bodies seen inside the abdomen of the holotype female of *D. ovigerus*. Cockerell described them as eggs. However, we observed similar structures inside the head and alitrunk of some other specimens, so we consider them to have a mineral origin.

Of the specimens listed by Donisthorpe (1920), we failed to find specimens NHMUK I.10257, NHMUK I.9347, NHMUK H.114, NHMUK H.262, NHMUK H.440, and NHMUK H.497, and found NHMUK I.9198 designated as the holotype of *Dolichoderus vectensis* Donisthorpe.

Donisthorpe (1920) erroneously identified specimen NHMUK I.8922 as *Oecophylla* sp. In fact, the specimen is very similar to the holotype of *Emplastus emeryi* and not to *Oecophylla*. He also identified a poorly preserved specimen NHMUK In.24410 (coll. R. W. Hooley) as *Oecophylla*, which probably belongs also to *E. britannicus*. Donisthorpe (1920, p. 84) cited W. M. Wheeler as having identified specimens NHMUK In.17074 and NHMUK In.24461 = NHMUK H.127 doubtfully as *Liometopum* queens.

Females of *Emplastus britannicus* have a general appearance similar to those of *Ctenobethylus* Brues, 1939 from Late Eocene ambers, and *Liometopum* Mayr, 1861 (Late Eocene–present). However, the key diagnostic characters of these genera (form of anterior margin of clypeus, presence or absence of ocelli, position of propodeal spiracles, etc.) are not visible on the studied specimens. Females of *E. britannicus* differ from *C. goepperti* in the wide petiole scale and from *Liometopum* in the wing venation (position of top of cell *rm*) and in the short antennal scape. Construction of the cranio-mandibular system of all of these females indicates that they built their nests most likely in rotten wood, similar to modern *Liometopum* and *Lasius* (subgenus *Dendrolasius* Ruzsky, 1912).

Emplastus hypolithus (Cockerell, 1915), comb. nov.
Plate 19, figs 1–2; Text-fig. 70A–C.

- 1915 *Ponera hypolitha* Cockerell, p. 483, plate 64, figs. 3–4.
1978 *Ponera hypolitha* Cockerell; Burnham, p. 109.
1964 *Poneropsis hypolitha* (Cockerell); Taylor, 139.
1995 *Poneropsis hypolitha* (Cockerell); Bolton, p. 363.

Holotype. USNM 61411, Bembridge Marls, NW Isle of Wight, UK, coll. Lacoë; forewing (Plate 19, fig. 1; Text-fig. 70A).

Other material. NHMUK In.17311, Bembridge Marls, NW Isle of Wight, UK, coll. E. J. A'Court Smith; male (Plate 19,

fig. 2; Text-fig. 70C) and 13 forewings (including NHMUK In.24368, Text-fig. 70B) in NHMUK collection. Bembridge Marls, Isle of Wight, UK.

Diagnosis. Differs from *E. britannicus*, the most common species of *Emplastus* in the Bembridge Marls, in form of the forewing cell *rm* and in position of 2r–rs.

Description. Male. BL 6.5 mm, AL 3 mm, FWL 5–6 mm. Head small, distinctively narrower than alitrunk. Eyes oval, situated slightly before midlength of head sides. Scape short, not reaching occipital margin, as long as three flagellomeres. Mandibles well developed, triangular. Pronotum comparatively wide, along midlength 0.33 times as long as scutum. Scutum feebly convex, half as long as alitrunk. Propodeum evenly rounded in side view. Legs rather long and thin. Petiole higher than long, in side view its anterior surface feebly concave, posterior surface straight, top rounded. Preserved remnants of body integuments chagrined.

Forewing. Cell *rm* triangular, not pedunculate, rarely quadrangular, comparatively narrow (2.5–2.8 times as long as wide). Cross-vein *rs–m* usually distal of 2r–rs, rarely coinciding. Cell *mcu* of medium size, trapezoid. *Icu* = 1.6–2.1, *Icu*_a = 1.3–1.4.

Measurements in mm. USNM 61412 (holotype of *Ponera hypolitha*): FWL ~ 6. NHMUK In.17311 (♂): BL = 6.5; AL = 3.0; HL ~ 1.1; F3L = 1.7; FWL ~ 6. Other specimens: FWL = 5.0–5.8 (n = 7); FWW = 1.2–1.5 (n = 4).

Remarks. Cockerell (1915) described this species as *Ponera hypolitha* based on a fragment of the forewing (holotype, USNM 61412) and a poorly preserved hind wing (paratype, USNM 61412). Position of cross-vein *cu–a* in the holotype (*Icu* = 1.6) clearly indicates the fossil belongs to Dolichoderinae. A complete male (NHMUK In.17311) apparently conspecific with the holotype permits the assignment of the species to the morphogenus *Emplastus*. Paratype hind wing has no visible venation: structures considered by Cockerell to be veins are in fact wing folds. There are no features justifying attribution of the paratype to either *Ponera* or *Emplastus*; it is therefore considered to be Formicidae *incertae sedis*.

Donisthorpe erroneously identified specimens NHMUK In.17311, NHMUK In.24368 and NHMUK In.24373 as *Dolichoderus britannicus*, and NHMUK In.9347 as *D. ovigerus*, in spite of their forewing venation and particularly position of 2r–rs and form of *rm* which show no similarity to *E. britannicus*.

Emplastus gurnetensis (Donisthorpe, 1920), comb. nov.
Plate 19, fig. 3; Text-fig. 71

- 1920 *Dolichoderus gurnetensis* Donisthorpe, p. 88, plate V, fig. 7.
1978 *Dolichoderus gurnetensis* Donisthorpe; Burnham, p. 112.
1995 *Dolichoderus gurnetensis* Donisthorpe; Bolton, p. 174.

Holotype. NHMUK: I.9755, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie; ♀ (Plate 19, fig. 3; Text-fig. 71A).

Other material: Female, two males (including I.9510; Text-fig. 71B) and four forewings in NHMUK collection. Bembridge Marls, Isle of Wight, UK.

Diagnosis. The species occupies an intermediate position between *E. britannicus* and *E. hypolithus*. Forewing venation is similar to *E. hypolithus*, and males are similar in general appearance to *E. britannicus*, but differing in smaller size. The female holotype differs from females of *E. britannicus* in head proportions and in form of petiole. Body fossils of female *E. hypolithus* are unknown, but male *E. hypolithus* is 1.5 times as long as female *E. gurnetensis* and therefore these two cannot be conspecific.

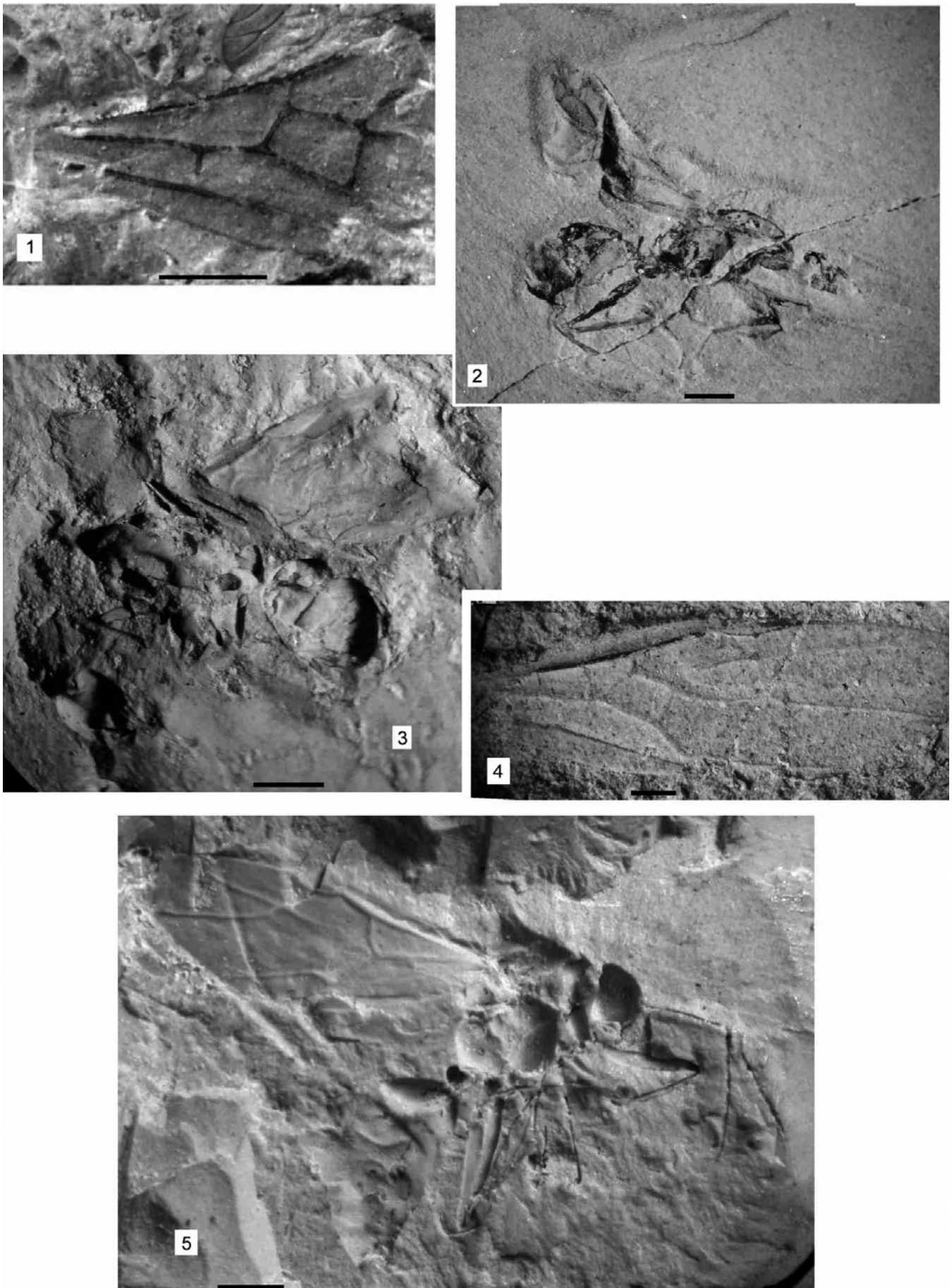
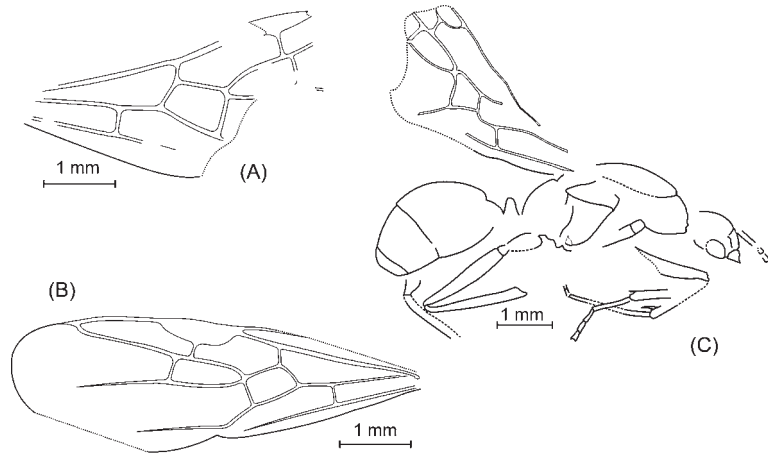
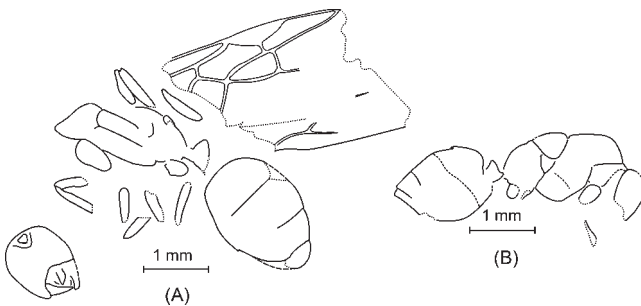


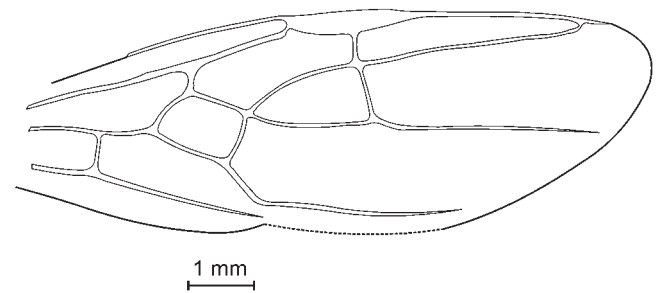
Plate 19 (1–2) *Emplastus hypolithus* (Cockerell) comb. nov.: (1) holotype of *Ponera hypolitha* Cockerell, USNM 61411; (2) ♂, NHMUK In.17311. (3) *Emplastus gurnetensis* (Donisthorpe), comb. nov., holotype of *Dolichoderus gurnetensis* Donisthorpe, NHMUK I.9755. (4) *Emplastus kozlovi* Perfilieva, sp. nov., holotype, NHMUK PI II.2784. (5) *Camponotus cockerelli* (Donisthorpe) comb. nov., holotype of *Leucotaphus cockerelli* Donisthorpe, NHMUK I.8517. Scale bars = 1 mm.



Text-figure 70 *Emplastus hypolithus* (Cockerell): (A) forewing, holotype of *Ponera hypolitha* Cockerell, USNM 61411; (B) forewing, NHMUK In.24368; (C) ♂, NHMUK In.17311.



Text-figure 71 *Emplastus gurnetensis* (Donisthorpe): (A) ♀, holotype of *Dolichoderus gurnetensis* Donisthorpe, NHMUK I.9755; (B) ♂, NHMUK I.9510.



Text-figure 72 *Emplastus kozlovi* Perfilieva, sp. nov., holotype, NHMUK PI II.2784.

Description. Female. BL *c.* 5.5 mm, AL *c.* 2 mm, FWL 5.5–6 mm. Head longer than wide (HL:HW = 1.07), about half as long as alitrunk, rectangular with slightly convex sides, rounded occipital corners and straight or feebly convex occipital margin. Mandibles massive, triangular. Propodeum evenly rounded in side view. Legs rather short and thick. Petiole with scale low, triangular in side view, about as long as high. Gaster oval. Body integument matter preserved with chagrined surface.

Male. BL *c.* 4 mm, AL 1.8–1.9 mm, FWL 3–4 mm. Head small. Alitrunk 2.5 times as long as head. Ocelli large (visible in NHMUK I.9082). Pronotum narrow, along midline less than 0.25 times as long as scutum. Scutum and scutellum convex in side view, scutum about half as long as alitrunk. Propodeum rounded in side view. Legs rather long and thin. Petiole in side view triangular, slightly higher than long. Body integument matter preserved with chagrined surface.

Forewing cell *rm* triangular, not pedunculate or with short stem 2.2–2.4 times as long as high. Cross-vein *rs–m* distal of 2*r–rs*. Cell *mcu* of medium size, rhomboid or trapezoid. *Icu* = 1.7–2.0, *Icu*_a = 1.24–1.38. Hind wing with three longitudinal veins (*RS*, *M*, *Cu*). 1*M* and *rs–m* of roughly same length. Cross-vein *cu–a* closer to *rs–cu* than to wing base.

Measurements in mm. NHMUK I.9755 (♀ holotype): BL ~ 5.5; AL = 2.1; HL = 1.01; HW = 0.94; FWL ~ 5.7. NHMUK I.8723: FWL = 6.1; FWW = 1.7. Males: AL = 1.8–1.9 (n = 2); HL = 0.75–0.8 (n = 2); ScL = 0.9 (n = 1); ScTL = 0.54 (n = 1). Forewings: FWL = 4.0–6.3 (n = 2); FWW = 2.1 (n = 1).

Remarks. Donisthorpe identified specimen NHMUK I.9082 as *Leucotaphus gurnetensis* (Cockerell), but it is larger and differs in body proportions. He also identified forewing NHMUK In.24373 as *Dolichoderus britannicus* in spite of its venational difference (in position of *r–rs* and in form of *rm*).

Emplastus kozlovi Dlussky & Perfilieva, sp. nov.
Plate 19 fig. 4; Text-fig. 72

Etymology. In memory of Mikhail Kozlov, who collected the holotype.

Holotype. NHMUK PI II.2784 a, b, Bembridge Marls, Burnt Wood, Isle of Wight, UK, collected by Belokobylsky, Khalaim, and Kozlov 24.05.2005; forewing, (Plate 19, fig. 4; Text-fig. 72).

Paratypes. NHMUK In. 24372, NHMUK In.24936, NHMUK In.25112, NHMUK In.25141, forewings, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley.

Diagnosis. Venationally similar to *E. britannicus*, but differs in larger size (7–9 mm in males and 11–12 mm in females; in contrast to, respectively, 5.5–6 mm and 6–7 mm in *E. britannicus*) and in relatively long cell *rm*.

Description. FWL 11–12 mm in females, 7.8–8.8 mm in males. 1*RS* and 2*r–rs* vertical to *R* and *RS*, respectively. Cell *rm* triangular, with no stem, rarely with very short stem, 2.2–2.5 times as long as wide. Cross-veins *rs–m* and 2*r–rs* coinciding. Cell *mcu* of medium size, trapezoid. *Icu* = 1.6–1.8, *Icu*_a = 1.3–1.5.

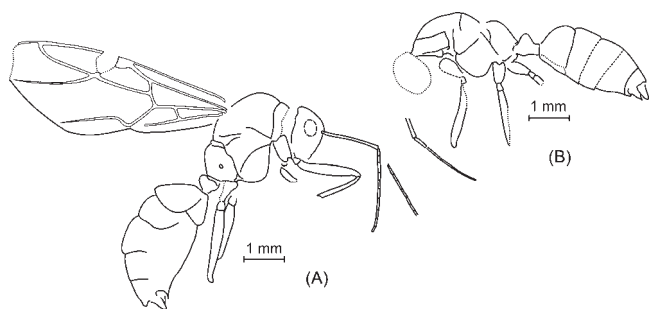
Measurements in mm. NHMUK: PI II.2784 (holotype): FWL = 11.3, FWW = 3.4; paratypes: FWL = 7.8–11.0, FWW = 1.8–3.0 (n = 4).

Remarks. Donisthorpe erroneously identified forewing NHMUK In.24372 as *E. britannicus*.

3.11.1.3. Subfamily Formicinae Latreille, 1809

Genus *Camponotus* Mayr, 1861

Type species. *Formica ligniperda* Latreille, 1802, by subsequent designation by Bingham (1903).



Text-figure 73 *Camponotus cockerelli* (Donisthorpe): (A) ♂, holotype of *Leucotaphus cockerelli* Donisthorpe, NHMUK I.8517; (B) ♂, NHMUK In.17280.

Other species. In the modern fauna *Camponotus* totals *c.* 950 species distributed on all continents from forest–tundra in the north of Eurasia and Boreal America to Tierra del Fuego in the south. The majority of species frequent humid arboreal ecosystems, but occur also in deserts and savannas, where they build underground nests.

Bolton (1995) listed 23 fossil species of *Camponotus*. He missed nine species described by Zhang (1989) from the Miocene deposits of China (Shanwang). Zhang further reported (apparently erroneously) three extant species there: *C. festinus* F. Smith, 1857; *C. luteus* F. Smith, 1858; and *C. mitis* F. Smith, 1858. There are also indications of findings of unidentified *Camponotus* in the Oligocene of Camoin-les Bains in France (Timon-David 1944), in the Miocene of the Dominican amber (Wilson 1985) and in the rock fossils of Bakhioti in Georgia and Chon-Tuz in Kirghizia (Dlussky 1981a). One more species is described below.

As a result, *c.* 40 species of fossil *Camponotus* are currently known. However, only a subset of them can be attributed to the genus with reasonable confidence. *C. mengei* Mayr, 1868, described from the Baltic amber, as well as those from the Miocene of Georgia and Kirghizia are undoubtedly *Camponotus*. *C. fuscipennis* Carpenter, 1930 (latest Eocene, Florissant, USA), ? *shanwangensis* Hong, 1984, *C. longus* Zhang, 1989, *C. plenus* Zhang, 1989 and *C. ambon* Zhang, 1989 (Miocene, Shanwang, China) also belong to this genus, based on their figures and descriptions. Preservation and/or quality of descriptions of other species leave some doubts about their identification. Until re-examination of the types, these species should be either attributed to morphogenus *Camponotites* Dlussky, 1981 (wings and winged fossils), or considered Formicidae *incertae sedis*.

Diagnosis (for rock fossils). Size medium to large, head sub-rectangular with rounded occipital corners; male and female antennae geniculate, scape attached at some distance from posterior clypeal margin; mandibles triangular with denticulate masticatory margin; petiole with scale thick (females) or triangular in side view (males). Forewing with cells 1+2r, 3r; closed rm and m-cu lost; RS usually convex downwards within cell 3r, 5RS and 4M join basally (rs–m lost). 1M and 1RS form smooth, almost straight, distinctly reclined vein. Cross-vein 2r–rs distinctly reclined in respect to RS. $Icu > 1.3$. Hindwing with two longitudinal veins RS and Cu. Gaster without constriction between first and second segments.

Camponotus cockerelli (Donisthorpe, 1920), comb. nov.
Plate 19, fig. 5; Text-fig. 73A, B

1920 *Leucotaphus cockerelli* Donisthorpe, pp 90–91, Plate V, fig. 10 (♂).

1978 *Leucotaphus cockerelli* Donisthorpe; Burnham, p. 111.

1995 *Leucotaphus cockerelli* Donisthorpe; Bolton, p. 246.

Holotype. NHMUK I.8517, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodi; ♂ (Plate 19, fig. 5; Text-fig. 73 A).

Other material. Four males (including well preserved lateral imprint) NHMUK In.17280; (Text-fig. 73B) and eight forewings in NHMUK collection, and two males in CAMSM collection. Bembridge Marls, Isle of Wight, UK.

Description. Male. BL 6–7.5 mm. Head about half as long as alitrunk. Eyes oval, situated above the midlength of head sides. Antennae geniculate, scape attached at some distance from clypeus; extending more than half its length beyond occipital margin. Scutum feebly convex in side view. Propodeum with dorsal surface short, convex, forming rounded blunt angle at junction with longer and almost straight declivous surface. Legs long and thin. Petiole triangular, a little longer than high in side view. Gaster cylindrical. Genital stipes short, narrow, rounded apically.

Forewing length of female 6.5–8 mm, male 5–6.5 mm. 2+3RS and 5RS both convex downward, not S-like. Distance between 1M and cu–a not longer than joint length 1M and 1RS. $Icu = 1.3–1.6$. Hindwing with two longitudinal veins RS and Cu. Section rs–cu about as long as 2M+Cu. Cross-vein cu–a near wing base.

Measurements in mm. Holotype ♂ NHMUK I.8517: BL = 7.5; AL = 2.6; HL ~ 1.3; SL = 1.4; ScL+ScLl = 1.9; FWL ~ 6; F3 = 1.8; NHMUK I.9225 (♂): AL = 1.9; NHMUK In.17280 (♂): BL = 7.5; AL = 2.7; ScL = 1.3; PtL = 0.6.

Remarks. Donisthorpe described *Leucotaphus cockerelli* based on two specimens: holotype ♂ NHMUK I.8517 and paratype ♀ NHMUK I.9028. The holotype is described as having the forewing cell m-cu closed, but figured with cross-vein m–cu closing this cell and represented by a dotted line. The holotype examined shows no trace of m–cu and so with no closed cell m-cu, which is not a wing anomaly. In case of aberrative loss of m–cu in a species with cu–a normally present, the wing retains a trace of the formerly closed cell m-cu in form of a distinct angulation at the junction of 1RS and 1M: the holotype has this composite vein smooth. Additionally, Bembridge *Leucotaphus* exhibits a more proximal position of cu–a in comparison with the present specimen. However, the strongest evidence of the species belonging to *Camponotus* is the scape attached to the head distinctly above the clypeus.

The paratype NHMUK I.9028 is actually Diptera indet. Instead we have found the specimen NHMUK I.9731 labelled erroneously as the holotype of *Leucotaphus cockerelli* which fits the description of the paratype, including measurements (body length 5.5 mm), and apparently represents the female paratype. We identify it as *Leucotaphus gurnetensis* (Cockerell).

Thirteen more specimens fit the diagnosis of *Camponotus cockerelli* and are found in the NHMUK collection. Of them, specimens NHMUK I.8692, NHMUK I.9225 and NHMUK In.17280 are misidentified by Donisthorpe (1920) as *Oecophylla* sp., and NHMUK In.17066 as *Leucotaphus gurnetensis*. The petiole form of NHMUK I.8692 and NHMUK I.9225 is not characteristic for *Oecophylla*; the posterior margin of cell rm, formed by RS of wing impression NHMUK In.17066 is convex (concave in *Oecophylla*); cell m-cu is closed in NHMUK In.17066. Specimen NHMUK In.17280, a male body with poorly preserved wings, is almost identical to the holotype. Other specimens are forewings of Camponotini of a size similar to that of the holotype.

Forewing length of the studied fossils varies from 5 mm to 8 mm. The range is wide enough to suppose it covers more than a single species and sex. In living *Camponotus*, male wings are narrower than those of the female (Perfilieva 2005). The present material shows Iw (ratio of forewing length to width) range as 2.9–4.3, indicating the presence of both sexes.

Wing morphometrics were analysed using standard methods (see above). Two comparatively uniform groups have been identified, apparently representing males and females. Moreover, the results indicate the presence of two species, one including males NHMUK I.8517 (holotype, FWL = 5.6 mm; Iw = 2.9) and NHMUK In.24794 (FWL = 6.5 mm), and female NHMUK In.24931 (FWL = 8.0 mm; Iw = 4.3); and another with males NHMUK I.8692 (FWL = 5.0 mm; Iw = 3.0) and NHMUK I.9359 (FWL = 6.0 mm) and females NHMUK In.24842 (FWL = 6.5; Iw = 3.7), NHMUK In.24881 (FWL = 7.5 mm; Iw = 3.6) and NHMUK In.25175 (FWL = 7.7 mm). Unfortunately, the material is too limited to justify formal description of a new species.

Morphogenus *Leucotaphus* Donisthorpe, 1920

Type species. *Leptothorax gurnetensis* Cockerell, 1915, by original designation.

Other species. *Leucotaphus gurnetensis* (Cockerell, 1915), *L. peraneus* Cockerell, 1927, *L. donisthorpei* sp. nov., Bembridge Limestone, Isle of Wight, UK.

Diagnosis. Fossil ants not well enough preserved to fit orthotaxa, and with following combination of traits: mandibles triangular; male antennae geniculate; scape articulate to the posterior margin of clypeus; female and male scape protruding beyond the occipital margin of the head; propodeum rounded or angulate in side view; petiole with high scale (♀) or triangular (♂) in side view; gaster without constriction between the first and second gaster (III and IV abdominal) segments. Forewing with cells 1+2r, 3r and mcu and not rm closed. 2-3RS convex, rarely feebly arching, 5RS convex. Cell 3r with apex touching wing margin. Sections 5RS and 4M with joint start (rs-m lost). Cell mcu trapezoid (RS+M appreciably shorter than 1Cu), small (in terms of area, less than half cell 1+2r). Icu > 1.5, Icu a > 1.2. Hindwing with two longitudinal veins RS and Cu, 1RS lost (2RS and rs-cu join at R). Cross-vein cu-a near wing base.

Remarks. Many genera of formicine ants from the tribes Formicini and Lasiini (in particular, *Formica* Linnaeus, 1758 and *Lasius* Fabricius, 1804) fit the diagnosis of *Leucotaphus*. Undoubtedly many fossil species described as *Formica* and *Lasius* from poorly preserved impressions deserve transfer into this morphogenus. *Leucotaphus* would range at least from the Paleocene (undescribed wings from Tadushi Formation in the Russian Far East) up to the Miocene (*Lasius vetulus* Dlussky, 1981).

Leucotaphus gurnetensis (Cockerell, 1915)
Plate 20, figs 1-3; Text-figs 74A-E, 88B

- 1915 *Leptothorax gurnetensis* Cockerell, p. 485, plate 65, figs. 4, 5 (wing).
1920 *Leucotaphus gurnetensis* (Cockerell): Donisthorpe, p. 89, Plate V, fig. 8,9 (male).
1978 *Leptothorax gurnetensis* Cockerell: Burnham, p. 111.
1992 *Leptothorax gurnetensis* Cockerell: Carpenter, p. 492.
1995 *Leucotaphus gurnetensis* (Cockerell): Bolton, p. 246.

Holotype. USNM 61417, Bembridge Marls, NW Isle of Wight, UK, coll. Lacoë (holotype of *Leptothorax gurnetensis* Cockerell); ♂ (Plate 20, fig. 1; Text-fig. 74A).

Other material USNM 61418 (♂, Lacoë Coll., designated by Cockerell as *Leptothorax gurnetensis* var. a), 100 males, ten females, and 36 isolated forewings (32 ♂ and four ♀) in the NHMUK collection, and four ♂ forewings in the CAMSM collection, including: NHMUK I.9731 (♀, which is the para-

type of *Leucotaphus cockerelli* Donisthorpe, 1920); NHMUK I.9744 (♂, designated by Donisthorpe (1920) as ergatotype of *Leucotaphus gurnetensis*, Text-fig. 74E); NHMUK I.9756 (♂, designated by Donisthorpe (1920) as plesiotype of *Leucotaphus gurnetensis*); a well preserved dorsal imprint of female NHMUK I.8733 (Plate 20, fig. 2; Text-fig. 74B); and lateral imprints of males NHMUK I.10040 (Text-fig. 74C) and NHMUK I.9796 (Plate 20, fig. 3; Text-fig. 74D). Four males in CAMSM collection.

Description. Male. BL 2.2-3.8 mm, AL 1.0-1.7 mm, FWL 2.2-3.7 mm. Head subtrapezoid, narrower in front than behind, longer than wide, occipital corners rounded, occipital margin feebly convex. Eyes oval, situated slightly before mid-length of head sides; maximum eye diameter 2.6-3.1 times less than head length. Scape slightly protrudes beyond the occipital margin of the head; scape length a little less than head length. Mandibles well developed, triangular; mandibular teeth not visible in any specimen. Alitrunk 1.2-1.4 times as wide as head, twice as long as wide and 1.3-1.5 times as long as high. In side view scutum feebly convex, propodeum rounded or with the poorly expressed angle, in which case propodeal dorsum much shorter than declivity. Legs rather thin and long. Petiole in side view triangular, with rounded top, higher than long. Gaster oviform, narrowed behind. Genitals slightly exposed, with stipes short, narrow, rounded at the top.

Female. BL 5.0-6.5 mm, AL 2.2-3.2 mm, FWL 5-5.5 mm. Head narrower than alitrunk. Alitrunk 1.8-1.9 times as long as wide, 1.3-1.5 as long as high. In side view scutum rounded in front, flat behind. Propodeal dorsum and declivity forming rounded blunt angle at junction. Petiole 2.2-2.4 times as high as long, with scale high and wide, 2.5-3 times as wide as thick. Gaster oval.

Forewing length c. 5 mm (♀), 2.5-3.7 mm (♂). Icu 2.0-3.6 (mean 2.51 ± 0.09, n = 17), varying widely because of variable size of cell mcu which is always small (in terms of area far less than half cell 1+2r). Icu a = 1.2-2.2. Hind wing with cross-vein rs-cu almost straight, comparatively short (clearly shorter than 2M+Cu).

Measurements in mm. USNM 61417 (♂, holotype): BL = 3.05; AL = 1.2; FWL ~ 2.6. Other specimens: Males: BL = 2.2-3.8 (average = 2.92, std = 0.330, n = 40); AL = 1.0-1.7 (average = 1.35, std = 0.166, n = 40); HL = 0.44-0.69 (average = 0.54, std 0.09, n = 8); HW = 0.54 (n = 1); SL = 0.54 (n = 1); ED = 0.18-0.24 (n = 4); ScL = 0.57-0.87 (average = 0.67, std = 0.10, n = 7); SctL = 0.27-0.45 (n = 4); FWL = 2.2-3.7 (average = 3.05, std = 0.356, n = 55). Females: AL = 2.4-3.2 (average = 2.68, std = 0.34, n = 7); AW = 1.3-1.6 (n = 3); ScL = 1.1 (n = 1); ScW = 1.3 (n = 1); PtW = 0.58-0.65 (n = 5).

Remarks. When describing the holotype forewing (USNM 61417), Cockerell (1915) referred to the very small size of cell mcu as a key diagnostic character. The second studied specimen of this species (USNM 61418), with large mcu, he considered to be probably an individual variation. We found the holotype Icu = 3.1, Icu a = 1.7, and the specimen USNM 61418 Icu = 2.1, Icu a = 1.6. Cell mcu is really variable in size in *L. gurnetensis*: sometimes it is larger than even in var. α, sometimes it is less than in the holotype, and the majority of studied specimens it is of intermediate size.

Male *L. gurnetensis* is quite variable in size, with the forewing length distribution being bimodal: based on 55 measured wings, we found maximums at 2.8-2.9 mm and 3.2-3.3 mm. It can be excluded that the material represents a mixture of two different species. No discrete differences were revealed to discriminate the composing species. The current taxonomic concept of *L. gurnetensis* is best left until more knowledge is obtained.

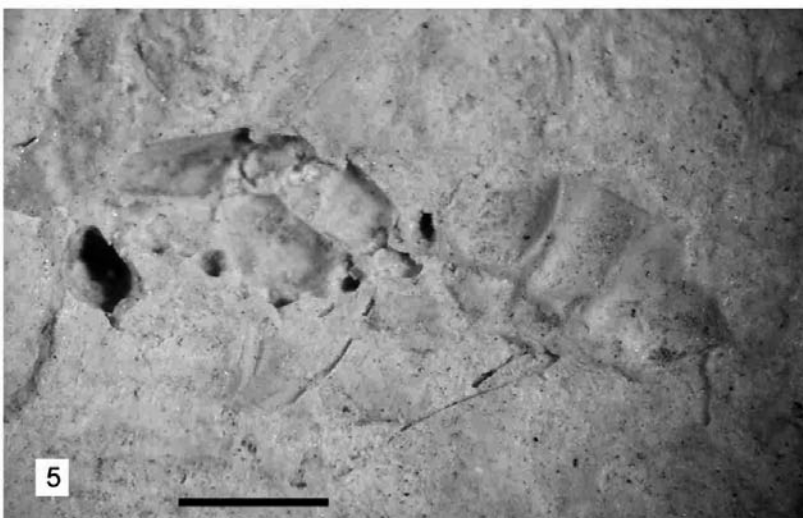
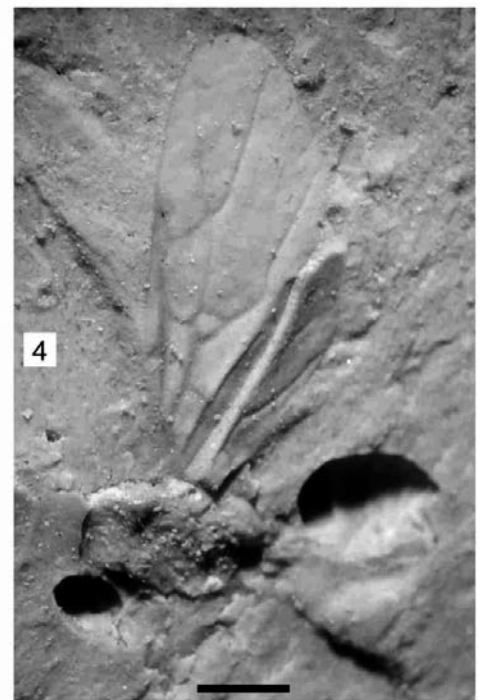
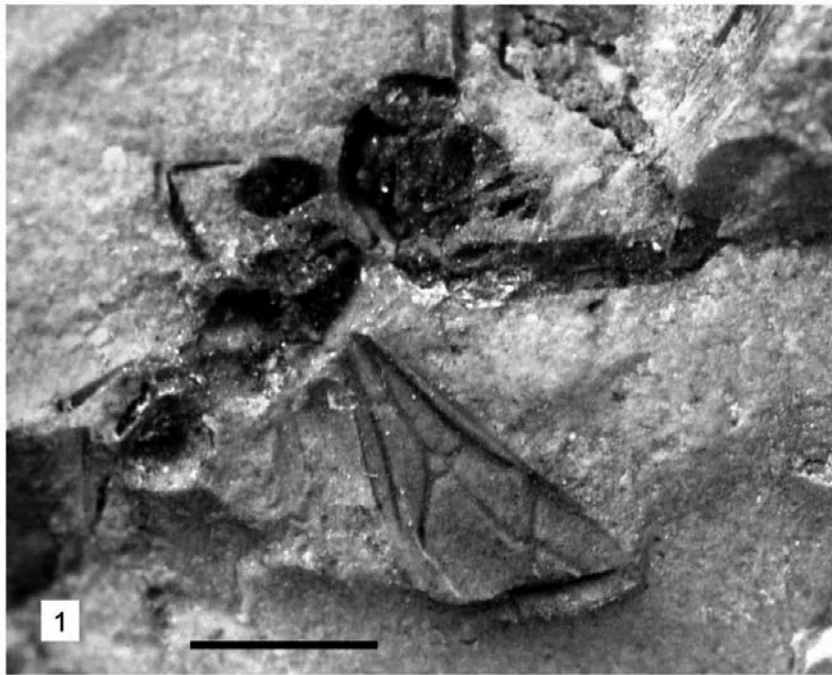
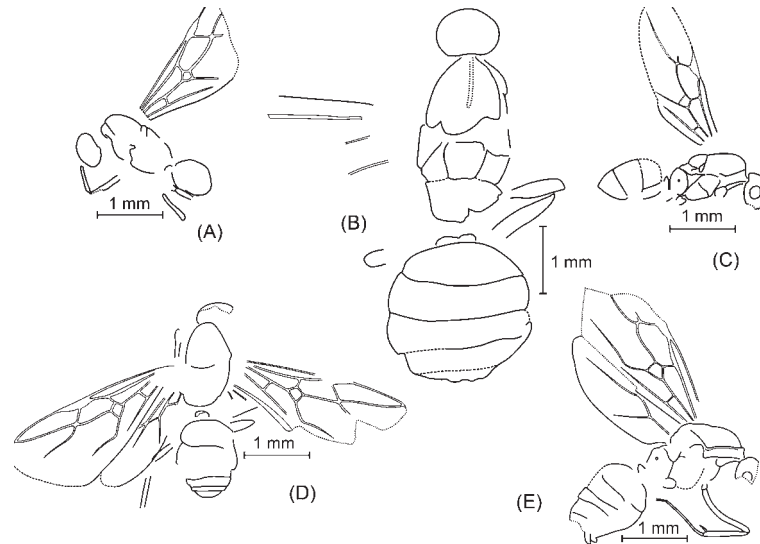


Plate 20 (1–3) *Leucotaphus gurnetensis* (Cockerell): (1) holotype of *Leptothorax gurnetensis* Cockerell, USNM 61417; (2) ♀, NHMUK I.8733; (3) ♂, NHMUK I.9796. (4–5) *Leucotaphus donisthorpei* Dlussky, sp. nov.: (4) holotype, NHMUK I.8765; (5) paratype, NHMUK I.10097. Scale bars = 1 mm.



Text-figure 74 *Leucotaphus gurnetensis* (Cockerell): (A) ♂, holotype of *Leptothorax gurnetensis* Cockerell, USNM 61417; (B) ♀, NHMUK I.8733; (C) ♂, NHMUK I.10040; (D) ♂, NHMUK I.9796; (E) ♂, NHMUK I.9744.

Donisthorpe (1920) listed 116 specimens identified as *Leucotaphus gurnetensis*. We have found two more specimens labelled and not listed (NHMUK I.9343, NHMUK I.9827), but have failed to locate 24 listed specimens: NHMUK I.7286, NHMUK I.8764, NHMUK I.8889, NHMUK I.8927, NHMUK I.9142, NHMUK I.9184, NHMUK I.9246, NHMUK I.9266, NHMUK I.9351, NHMUK I.9356, NHMUK I.9386, NHMUK I.9526, NHMUK I.9593, NHMUK I.9718, NHMUK I.9688, NHMUK I.10005, NHMUK I.10018, NHMUK I.10120, NHMUK I.1026, NHMUK In.17202, NHMUK In.17203, NHMUK In.17298, NHMUK In.19602 (= H.189). As a result, we were able to study 94 specimens identified by Donisthorpe. Most of them were really males of *Leucotaphus gurnetensis*, but some were found either to be of poor preservation, permitting only identification as Formicidae *incertae sedis* (NHMUK I.8994, NHMUK I.9281, NHMUK I.9677, NHMUK I.9958, NHMUK I.10265, NHMUK In.24376), or to be misidentified and belonging in fact to *Dolichoderus vectensis* (NHMUK I.9231), *Emplastus gurnetensis* sp. (NHMUK I.9082), *Camponotus cockerelli* (NHMUK In.17066), *Leucotaphus donisthorpei* (NHMUK I.8678, NHMUK I.8737, NHMUK I.8765, NHMUK I.10097), *Oecophylla atavina* (NHMUK In.17213), *Ponerites crawleyi* (NHMUK I.8539, NHMUK I.8684, NHMUK I.8759, NHMUK I.9406, NHMUK I.9774), *Ponerites hooleyi* (NHMUK I.9602, NHMUK I.9869), *Ponerites antropovi* (NHMUK I.9996), *Ponerites* sp. (NHMUK I.10123) and *Taphopone microptera* (NHMUK I.9763, NHMUK In.24378).

Wheeler identified specimen NHMUK In.24380 (=H.334) as a worker of *Camponotus* sp. (Donisthorpe 1920, p. 84). Actually, the constitution of its alitrunk, well developed and with scutum and scutellum separated, clearly specifies the fossil as a wingless female and not a worker. Specimen NHMUK I.8731 is designated by Donisthorpe as the paratype of *Leucotaphus cockerelli*. As shown above, the holotype of this species is actually a male of *Camponotus*. The specimen NHMUK I.8731 has the petiolar scale high and narrow, attesting it as a female, with size and body proportions fitting *Leucotaphus gurnetensis*.

Re-describing the male of *Leucotaphus gurnetensis*, Donisthorpe (1920, p. 90) noted that “there are several larger specimens, which may be the females of this species, this sex being, on that view, larger than the male, as in some of the subgenera

of *Acanthomyops*; some are dealated, others winged. One specimen (NHMUK I.10097) is very perfect, showing well the segments of the thorax and gaster.” Actually, this specimen has clearly visible male genitals. It is described below as a paratype of *Leucotaphus donisthorpei*.

Donisthorpe also described a cocoon and workers of *Leucotaphus gurnetensis*. Concerning workers he wrote (p. 89): “I have seen some eight workers, nearly all of them being on the same piece of rock as winged specimens. The head is small, the scale distinct, and some parts of the legs are present, but the general outline is not very clear. The length is 2–2.7 mm”. We have studied four of eight samples listed by him and found no workers. Sample NHMUK I.10248 includes poorly preserved impression of an insect other than an ant, samples NHMUK I.8722 and NHMUK I.9744 include only impressions of male *Leucotaphus gurnetensis*, and sample NHMUK In.17250 is poorly preserved fragments of *Oecophylla* sp. In general, ant workers and the more so their cocoons have very low chance of being preserved as rock fossils.

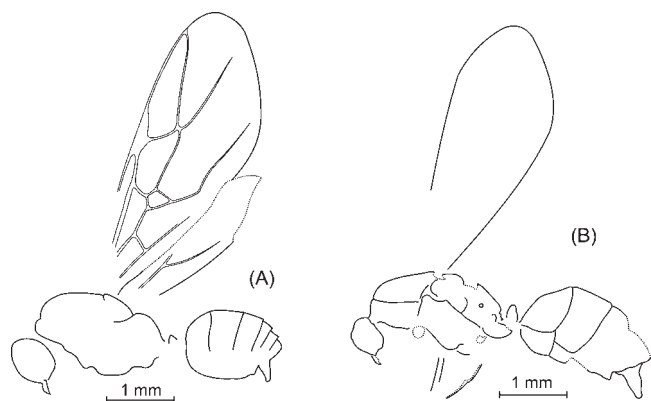
Leucotaphus gurnetensis is the third most abundant species (after two *Oecophylla* species) in the Bembridge Marls ant assemblage. It comprises 25% of all ant fossils identified to the species level. This ant is similar to the Recent *Lasius* Fabricius, 1804 in general appearance, and perhaps really belongs to this genus. However the level of preservation does not allow any sight of key characters that differ *Lasius* from other genera of Formicinae. It is also very similar to fossil ants described as *Lasius* from other deposits: *L. schiefferdeckeri* Mayr, 1868 (Late Eocene Baltic amber), *L. peritulus* (Cockerell, 1927) (latest Eocene, Florissant, USA), *L. epicentrus* Théobald, 1937 (Oligocene Aix-en-Provence, France), *L. redtenbacheri* (Heer, 1849) and others (Miocene, Radoboj, Croatia), *L. vetulus* Dlussky, 1981 (Vishnevaja Balka, Russia) and others. Like *L. gurnetensis* these ants are numerous in their taphocenoses (11% in Baltic amber, 25% in Florissant, 33% in Radoboj, 34% in Vishnevaja Balka).

Leucotaphus donisthorpei Dlussky & Perfilieva, sp. nov.

Plate 20, figs 4–5; Text-fig. 75A, B

Etymology. In honour of Horace St. J. K. Donisthorpe.

Holotype. NHMUK I.8765, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie, ♂ (Plate 20, fig. 4; Text-fig. 75 A).



Text-figure 75 *Leucotaphus donisthorpei* sp. nov.: (A) ♂, holotype, NHMUK I.8765; (B) ♂, paratype, NHMUK I.10097.

Paratypes. NHMUK: I.8678, I.8750, I.8948, I.10097, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie; ♂♂ (Plate 20, fig. 5; Text-fig. 75 B); NHMUK In 25124, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley; ♀ forewing.

Other material. Three males, three male forewings, and two female forewings in NHMUK collection. Bembridge Marls, Isle of Wight, UK.

Diagnosis. Differs from the type species in larger wing size.

Description. Male. BL 4.0–4.5 mm, AL 1.4–2.0 mm, FWL 3.8–4.5 mm. Head small, narrower than alitrunk. Scape longer than head, distinctly surpassing occipital margin. Mandibles well developed, triangular. Alitrunk 1.4–1.6 times as long as high. Scutum in side view rounded in front and flat behind. Propodeum in side view rounded. Petiole higher than long, with thick scale, narrowed upward, with rounded top. Gaster oviform. Genitals strongly exposed, with stipes long, triangular, rounded at apex.

Forewing length ♀ *c.* 7.5 mm, ♂ 3.8–4.5 mm, Icu = 1.9–2.3, Icu_a = 1.35–1.55. Fore and hind wing venation as in *L. gurnetensis*.

Measurements in mm. NHMUK I.8765 (♂, holotype): BL = 4.0; AL = 1.9; HL = 0.75; FWL = 4.5. Other specimens (♂♂); AL = 1.5–2.8 (n = 6); HL = 1.1 (n = 1); FWL = 3.8–4.3 (n = 4).

Remarks. There are two forewings (NHMUK In.24920 and NHMUK In.25124) with forewing venation characteristic for *Leucotaphus*, but larger than female forewings of *L. gurnetensis*. We assume that they belong to females of *L. donisthorpei*. Forewing fragment NHMUK I.9549 may also be a male of that species.

Donisthorpe erroneously identified specimens NHMUK I.8737, NHMUK I.8765, NHMUK I.8678, and NHMUK I.10097 as *Leucotaphus gurnetensis*, and NHMUK I.8673 as *Oecophylla* sp.

Genus *Oecophylla* F. Smith, 1860

Type species. *Formica virescens* Fabricius, 1775, a junior synonym of *Oecophylla smaragdina* (Fabricius, 1775), by subsequent designation of Bingham, 1903.

Other species. There are two extant species of this genus: *Oecophylla smaragdina* (Fabricius 1775) in the Oriental and Indo-Australian Regions, and *O. longinoda* (Latreille 1802) in the Afrotropical Region. Fifteen fossil species are described, the most ancient being the Middle Eocene: *O. longiceps* Dlussky in Dlussky *et al.*, 2008 from Grube Messel, Germany, and *O. eckfeldiana* Dlussky, in Dlussky *et al.* 2008 from Eckfeld,

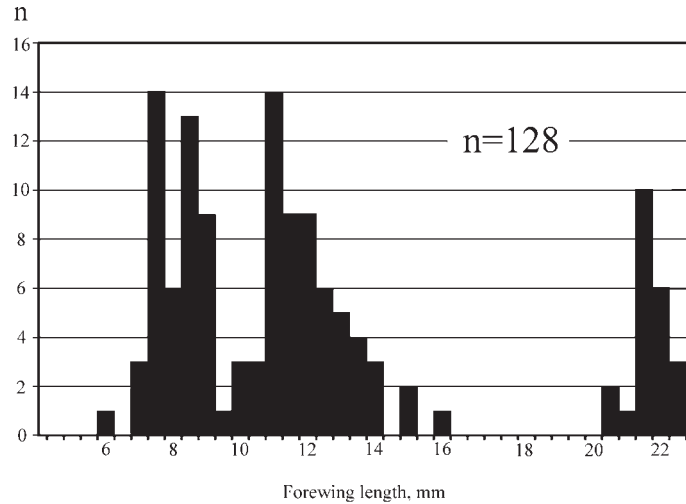
Germany (Dlussky *et al.*, 2008); and the Late Eocene: *O. brischkei* Mayr, 1868 and *O. crassinoda* Wheeler, 1922 (= *O. brevinodis* Wheeler, 1915) from the Baltic amber, *O. praeclara* Foerster (Brunstadt, Germany), *O. atavina* Cockerell, 1915, *O. perdita* Cockerell, 1915 and *O. megarche* Cockerell, 1915, from Bembridge, Isle of Wight, UK and *O. bartoniana* Cockerell, 1920b from the Eocene Bagshot Beds, Bournemouth, UK. Two species are described from European Oligocene deposits: *O. superba* Théobald, 1937 (Haut-Rhin, France) and *O. sicula* Emery, 1905 (Sicilian amber). Also, four species are known from Miocene deposits: *O. obesa* (Heer 1849), *O. radobojana* (Heer 1849) (Radoboj, Croatia), *O. leakeyi* Wilson & Taylor, 1964 (Victoria, Kenya) and *O. xiejiaheensis* (Hong, 1984) (Shanwang, China). However, the real number of fossil species is less. *O. xiejiaheensis* is transferred to the morphogenus *Campopotites* Dlussky, 1981 (Dlussky *et al.* 2008), and *O. perdita* is synonymised herein under *O. atavina*. *O. bartoniana* and *O. praeclara* were described from detached forewings, so they may be conspecific with other species known from complete fossils.

Diagnosis (for rock fossils). Size large, head subrectangular with rounded occipital corners; antennae geniculate in both sexes; scape attached at some distance from clypeus; mandibles large, triangular, with sharp teeth on the masticatory margin; petiole elongate, without scale, or nodiform (only at females); gaster without constriction between first and second gastral (III and IV abdominal) segments; forewing with closed cells 1+2r, 3r, with no closed rm and mcu; posterior margin of cell 3r (formed by RS) always concave.

Remarks. Both modern species of the genus (“weaver ants”) live in the crown of trees of tropical forests and construct nests from leaves, fastened by silk secreted by the larvae. Morphology of *Oecophylla* agrees with their mode of life. Long legs and antennae allow them to step or jump in the crown from one leaf to another. The original petiole construction is connected with their ability to lift the gaster upwards, providing large maneuverability during leaps (Dlussky 1981b). Large flat mandibles with sharp teeth are adapted to cutting leaves for construction of the nest. The morphological resemblance of extinct and extant species allows confidence to assert that their modes of life also were similar. It proves to be true also from the fossilised nest of *O. leakeyi* in the Miocene deposits of Kenya (Wilson & Taylor 1964). However, their tropical preference should not be considered as strict, because of their discovery in the European Miocene which had a subtropical to warm temperate rather than a tropical climate.

Oecophylla are the most numerous ants in Bembridge Marls assemblage comprising 69.8% of all ant fossils identified to the generic level. However, this proportion is obviously overestimated. Firstly, large fossils such as *Oecophylla*, the largest ant in the assemblage, are better preserved and easier to collect. Secondly, the original shape and structure of these ants, jointly with their large size, helps identification, even from small fragments that are usually not noticed in the case of other ants. When comparing only more complete fossils identifiable to the species level, the proportion of *Oecophylla* falls to 51.8%, and yet remains higher than that of any other ant (*Leucotaphus gurnetensis* 24.9%; *Emplastus britannicus* 10%).

Cockerell (1915) described three *Oecophylla* species from the Bembridge Marls: *O. atavina*, *O. perdita* and *O. megarche*. He distinguished them by using small details of forewing venation, which lie well within the range of intraspecific variability. Donisthorpe (1920) distinguished only *O. megarche* based on the very large size, and wrote about other species: “They are all smaller than specimens of *O. megarche*. A chart of the measurements allows that they vary in every possible



Text-figure 76 Frequency distributions of forewing length classes among *Oecophylla*.

way – in size, size of wings, and all other measurements. Nor does it appear to me that any good purpose would be served by creating a number of new species, which would probably embrace or overlap Cockerell's *O. atavina* and *O. perdita*" (p. 92).

Initially we supposed that all *Oecophylla* fossils belong to one species. However, when we made a diagram of frequency distribution of forewing size, we found it three-modal (Text-fig. 76). All specimens can be divided into three distinct clusters: the small ones, with FWL 6.0–9.4 mm, mode 7.5 mm; the medium ones (FWL 9.5–16 mm, mode 11 mm); and the large ones (FW 21–23 mm). The ranges of variation are, respectively, 3.5 mm (47% of modal wing length), 6.5 mm (59%), and 2.0 mm (9%). The studied samples of living Formicidae (Perfilieva 2005) show variation ranges of forewing length as some 17% and not above 40% (in case of polymorphic females). This indicates that the present middle and, less certainly, smaller clusters are probably of a mixed nature.

Small specimens with bodies preserved are mostly males, including ♂ holotype of *O. atavina*, FWL = 7.6 mm and ♂ paratype of *O. perdita*, FWL = 6.8 mm; except the only female NHMUK In.24400 with FWL = 8.5 mm. Large fossils, including the holotype of *O. megarche* with FWL = 23 mm, are mainly represented by isolated wings; except the paratype of *O. megarche* USNM 61425, which shows additionally a head and a fragment of alitrunk. However there is no doubt that all of them belong to females. In contrast, specimens of the medium group with bodies preserved represent both males and females. Holotype (♀, FWL = 12.7 mm) and one paratype (♀ FWL = 11.8 mm) of *O. perdita* belong to this group. Standard morphometric analysis (see above) of wings 9–17 mm long for characters discriminating male and female ant wings (Perfilieva 2005) reveals two distinct clusters. This makes it possible to appreciate two species of *Oecophylla* present in the Bembridge Marls ant assemblage, with the small species (AL 2.0–2.8 mm; FWL 6.0–9.5 mm; ♀ AL 3.5–4.5 mm; FWL 8.5–13.7 mm) being *Oecophylla atavina* Cockerell, 1915 (= *O. perdita* Cockerell, 1915), and the large species (♂ AL 4.5–5.5 mm; FWL 10–15.9 mm; ♀ FWL 20.7–23.0 mm) *Oecophylla megarche* Cockerell, 1915.

We have identified 195 specimens as *O. atavina*, and 122 specimens as *O. megarche*. 366 incomplete fossils (fragments of bodies and wings) in the NHMUK collection and 37 in the CAMSM collection are left identified as *Oecophylla* sp.

Oecophylla atavina Cockerell, 1915
Plate 21, figs 1–5; Text-figs 77, 88A

- 1915 *Oecophylla atavina* Cockerell, p. 485, plate 64, fig. 7 (♂).
1915 *Oecophylla perdita* Cockerell, pp 485–486, plate 64, figs. 5–6 (♀♀) syn. nov.
1920 *Oecophylla megarche* Cockerell; Donisthorpe, pp 91–92, (partim, *quoad* Plate V, fig. 12).
1978 *Oecophylla atavina* Cockerell; Burnham, p. 114.
1978 *Oecophylla perdita* Cockerell; Burnham, p. 114.
1995 *Oecophylla atavina* Cockerell; Bolton, p. 298.
1995 *Oecophylla perdita* Cockerell; Bolton, p. 298.
2008 *Oecophylla atavina* Cockerell; Dlussky *et al.*, p. 616

Holotype. USNM 61419, Bembridge Marls, NW Isle of Wight, UK; ♂ (Plate 21, figs 1, 2; Text-fig. 77A).

Other material. USNM 61420, ♀, forewing, holotype of *Oecophylla perdita* Cockerell (Plate 21, fig. 5; Text-fig. 77B); USNM 61421, ♀, paratype of *Oecophylla perdita* Cockerell; USNM 61422 ♂, forewing, paratype of *Oecophylla perdita* Cockerell, coll. Lacoë (Plate 21, fig. 5); 156 males and 29 females in the NHMUK collection and six males in the CAMSM collection, including NHMUK I.8702, ♀, designated by Donisthorpe (1920) as the plesiotype of *O. megarche* Cockerell (Text-fig. 77D), NHMUK I.8711 (♀, identified by Donisthorpe as *O. megarche* Cockerell, Plate 21, fig. 4; Text-fig. 77C), NHMUK I.8768 (Text-fig. 77E), NHMUK I.9143 (Plate 21, fig. 3; Text-fig. 77G) and NHMUK I.9345 (♂) (Text-fig. 77F). All from Bembridge Marls, Isle of Wight, UK.

Diagnosis. Smaller species: ♂AL 2.0–2.8 mm; FWL 6.0–9.5 mm; ♀ AL 3.5–4.5 mm; FWL 8.5–13.7 mm.

Description. Female. BL 8–12 mm, AL 3.5–4.5 mm, FWL 8.5–13.7 mm. Head subtrapezoidal, narrower in front than behind, about as long as wide. Occipital corners rounded, occipital margin feebly convex. Anterior margin of clypeus rounded. Eyes comparative small, oval, situated slightly behind midlength of head sides; maximum eye diameter about 0.3 head length. Mandibles large, triangular with large sharp teeth. Scape protrudes far beyond the occipital margin of the head, about twice as long as head. Alitrunk massive, a little wider than head. Scutum wider than long (in NHMUK I.8527, ScW/ScL = 1.2), flat above, rounded anteriorly, overhanging pronotum in dorsal view. Propodeum feebly convex in

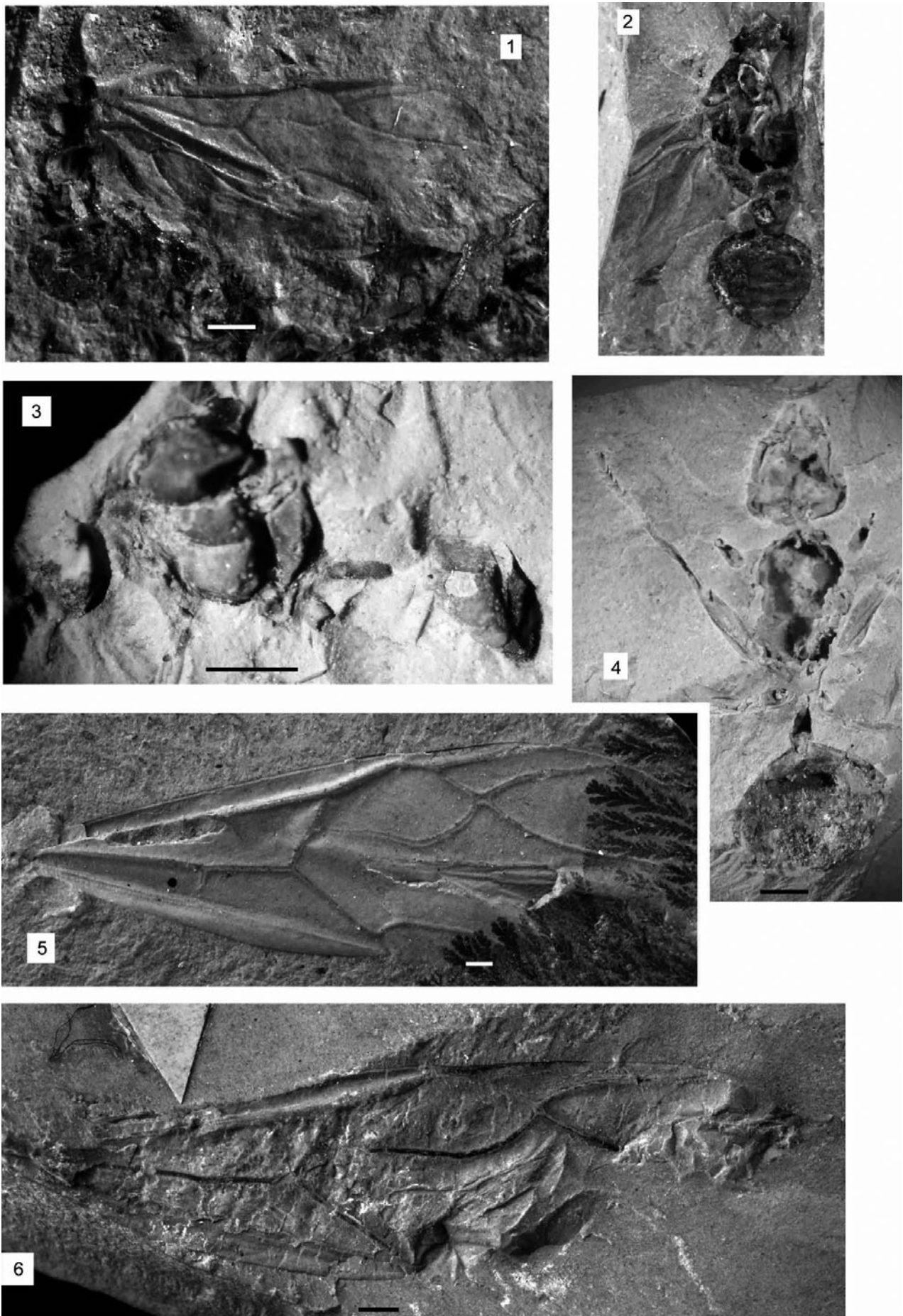
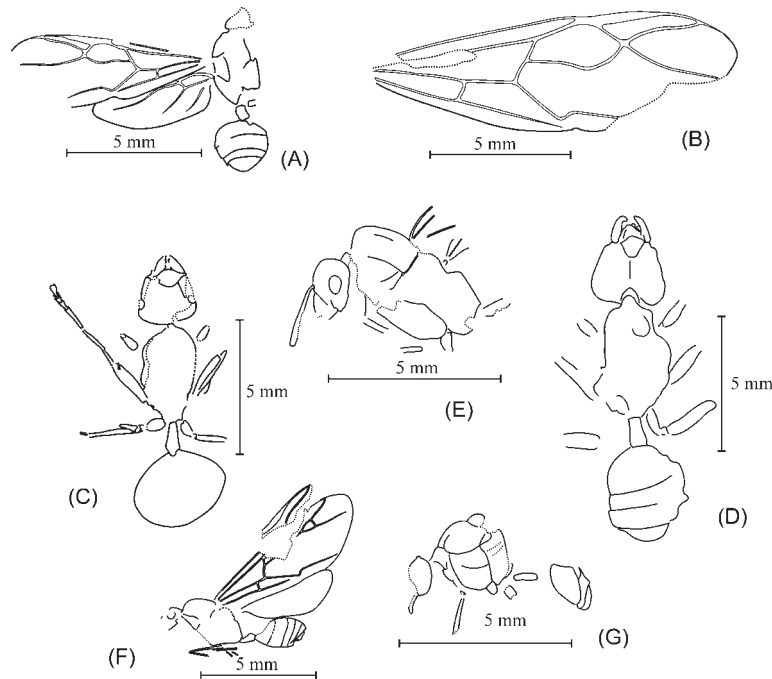


Plate 21 (1–5) *Oecophylla atavina* Cockerell: (1–2) holotype, USNM 61419 (part and counterpart); (3) ♂, NHMUK I.9143; (4) ♀, NHMUK I.8711; (5) holotype of *Oecophylla perdita* Cockerell, USNM 61420. (6) *Oecophylla megarche* Cockerell, holotype, USNM 61423. Scale bars = 1 mm.



Text-figure 77 *Oecophylla atavina* Cockerell: (A) ♂, holotype, USNM 61419; (B) forewing, holotype of *Oecophylla perdita* Cockerell, USNM 61420; (C) ♀, NHMUK I.8711; (D) ♀, NHMUK I.8702; (E) ♀, NHMUK I.8968; (F) ♂, NHMUK I.9345; (G) ♂, NHMUK I.9143.

side view. Legs rather short and thick; hind femur shorter than alitrunk. Petiole without scale or node, narrowed anteriorly, twice as long as wide and high. Gaster oval.

Male. BL 5–6.3 mm, AL 2.0–2.8 mm, FWL 6–9.5 mm. Head comparatively small, considerably narrower than alitrunk. Eyes convex. Alitrunk short and high (in NHMUK I.9143, 1.2 times as long as high). Scutum convex, a little longer than wide. Propodeum feebly convex or straight in side view. Legs rather long and thin. Petiole without scale or node, narrowed anteriorly, 2.5–3 times as long as wide and high. Gaster oviform, narrowed behind. Posterior margin of subgenital plate uniformly concave. Genitals small, poorly exposed from gaster. Genital stipes with rounded apex, about 1.5 times as long as wide.

Forewing IRS proclined, forming acute angle with R, 2r–rs proclined. Cell 3r comparatively narrow, 5RS bent into 3r. Section 2–3RS (delimiting cell 1+2r from below) bent. 3Cu convex. Hind wing with two longitudinal veins RS and Cu. 1RS distinct, short. Section rs–cu concave, much longer than 2M+Cu. Cross-vein cu–a about as long as rs–cu, placed near it.

Measurements in mm. USNM 61419 (♂, holotype): BL = 5.9; AL = 2.7; FWL = 7.6. USNM 61420 (♀, holotype of *O. perdita*): FWL = 12.7. USNM 61421 (♀, paratype of *O. perdita*): FWL = 11.8. USNM 61422 (♂, paratype of *O. perdita*): HW = 0.90. SL = 0.94. FWL = 6.8. Other specimens: Males: BL = 5.0–6.3 (average = 5.61, std = 0.46, n = 16). AL = 2.0–2.8 (average = 2.44, std = 0.35, n = 11). PtL = 0.6–0.75 (n = 3). FWL = 6.0–9.4 (average = 7.66, std = 0.723, n = 81). Females: BL = 8.2–12.1 (n = 20). AL = 2.6–4.6 (average = 4.0, std = 0.69, n = 8). HL = 1.5–2.8 (n = 5). HW = 2.8 (n = 1). SL = 1.9 (n = 1). ED = 0.4–0.5 (n = 2). PtL = 0.9–1.1 (n = 4). FWL = 10.0–15.9 (average = 11.72, std = 1.408, n = 22).

Remarks. Donisthorpe (1920) identified the wingless females NHMUK I.8702 and NHMUK I.8711 as *O. megarche*, and even designated the former a plesiotype and represented it on Pl.V. fig. 12. However, their size (AL 4.6 and 3.7 mm, respectively) indicates their FWL is not above 13 mm, well below the range of *O. megarche*.

Oecophylla megarche Cockerell, 1915
Plate 21, fig. 6; Text-fig. 78A–E

1915 *Oecophylla megarche* Cockerell, p. 486, plate 65, figs. 1–3.

1920 *Oecophylla megarche* Cockerell; Donisthorpe, pp 91–92 (part., *quoad* fig. 11).

1978 *Oecophylla megarche* Cockerell; Burnham, p. 114.

1995 *Oecophylla megarche* Cockerell; Bolton, p. 298.

Holotype. USNM 61423, Bembridge Marls, NW Isle of Wight, UK, coll. Lacoë; ♀ forewing (Plate 21, fig. 6; Text-fig. 78A).

Paratypes. USNM 61424, Bembridge Marls, NW Isle of Wight, UK; hind wing of ♀; USNM 61425, Bembridge Marls, NW Isle of Wight, UK, coll. Lacoë; ♀ (Text-fig. 78B).

Other material. 46 males and 68 females in the NHMUK collection and on male and four females in the CAMSM collection, including: NHMUK I.8729 (Text-fig. 78D); NHMUK In.24391 (Text-fig. 78C); NHMUK In.24909 (Text-fig. 78E). All from Bembridge Marls, Isle of Wight, UK.

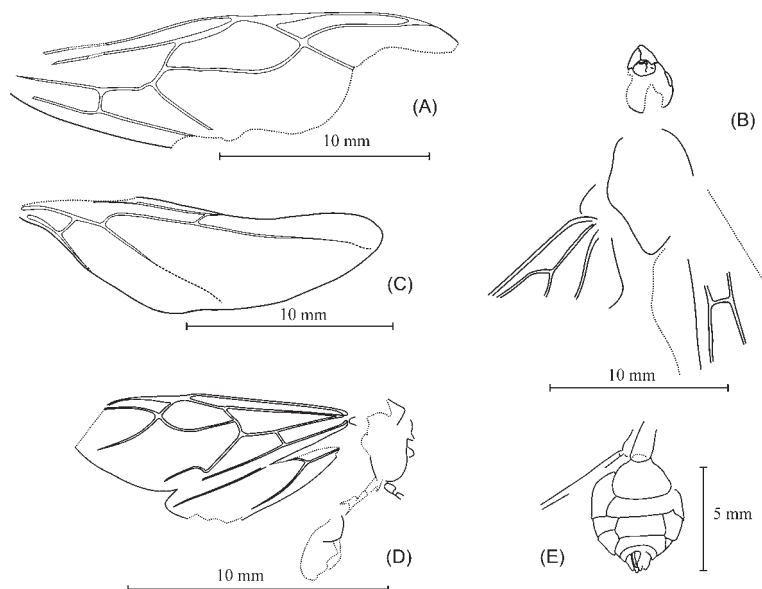
Diagnosis. Bigger species: ♂ AL 4–5.5 mm, FWL 10–15.9 mm, ♀ FWL 20.7–23.0 mm.

Description. Male. AL 4–5.5 mm, FWL 10–16 mm. Similar to *O. atavina*, except for larger size, shorter petiole and longer genital stipes. Scutum a little longer than wide (1.1 times as long as wide in NHMUK I.8670). Petiole 1.8–2.1 times longer than wide. Genital stipes twice as long as wide.

Female. FWL 20–24 mm. Based on proportions of *O. atavina* and living *O. smaragdina*, apparently AL *c.* 6 mm, BL > 15 mm. The only known head about as long as wide and *c.* 3.5 times as long as maximum eye diameter (paratype USNM 61425, Text-fig. 37).

Wing venation of fore and hind wings as in *O. atavina*.

Measurements in mm. USNM 61423 (♀, holotype): FWL = 20.7. USNM 61424 (♀, paratype): hind wing 16.8. USNM 61425 (♀, paratype): HW = 3.2. NHMUK I.8703 (♂): AL = 4.0; FWL = 11.4. NHMUK I.10086 (♂): PtL = 1.3. Other specimens: ♂♂: FWL = 10.0–15.9 (average = 11.74, std = 1.408, n = 40). ♀♀: FWL = 20.7–23.0 (average = 21.94, std = 0.767, n = 25).



Text-figure 78 *Oecophylla megarche* Cockerell: (A) ♀ forewing, holotype, USNM 61423; (B) ♀, paratype, USNM 61425; (C) hind wing of ♀, NHMUK In.24391; (D) ♂, NHMUK I.8729; (E) gaster of ♂ from above, NHMUK In.24909.

3.11.1.4. Subfamily Ponerinae Lepeletier, 1836

Morphogenus *Ponerites* Dlussky & Rasnitsyn, 2002

Type species. *Ponerites eocenicus* Dlussky & Rasnitsyn, 2002, by original designation.

Other species. *P. coloradensis* Dlussky & Rasnitsyn, 2002 and *P. hypoponeroides* Dlussky & Rasnitsyn, 2002 from the Green River Formation, Middle Eocene of USA (Dlussky & Rasnitsyn 2002), *P. umbrus* (Popov 1932) from the Middle Miocene of North Caucasus, and *P. crawleyi* (Donisthorpe, 1920) and two new species from the Bembridge Marls described below. Some European Miocene and Oligocene ants described as *Ponera* also apparently deserve placement here.

Diagnosis. Fossil ants not well enough preserved to fit orthotaxa, and with following combination of traits: size small to medium, head subrectangular with rounded occipital corners; eyes comparatively small, situated before midlength of head sides; mandibles triangular with denticulate masticatory margin; promesonotal and mesopropodeal sutures present in workers; sculpture conspicuous, head, alitrunk and waist with no denticles or spines; petiole with thick scale; gaster with constriction between first and second segments of gaster (III and IV abdominal segments); second gastral tergite and sternite subequal, apex of the gaster not directed downwards; sting well developed. Forewing with closed cells 1+2r, 3r, rm and mcu; cross-vein cu—a sutured near mcu, so usually $Icu < 1.45$ and $Icu < 1.2$.

Remarks. Key traits used to distinguish extant genera of the tribe Ponerini (shape of ventral petiolar lobe, dentition of mandibular masticatory margin, number of spurs of middle and hind tibiae) are not visible in most rock fossils of small, nonspecialised Ponerinae. Taylor (1964) designated these fossils as “*Ponera* (?)”, and the informal name “*Ponerites*” was later coined for them (Dlussky 1981a). Later Dlussky & Rasnitsyn (2002) proposed to use the latter name as valid for a morphogenus with the above diagnosis.

The extant genera *Ponera* Latreille, 1804, *Hypoponera* Santachi, 1938 and, partially, *Pachycondyla* F. Smith, 1858 and perhaps some other ponerine genera agree with the diagnosis of *Ponerites*.

Ponerites crawleyi (Donisthorpe, 1920), comb. nov.
Plate 22, fig. 1; Text-fig. 79A–E

1920 *Euponera* (*Mesoponera*) *crawleyi* Donisthorpe, p. 85, plate V. fig. 3.

1978 *Euponera* (*Mesoponera*) *crawleyi* Donisthorpe: Burnham, p. 109.

1995 *Pachycondyla crawleyi* (Donisthorpe): Bolton, p. 304.

Holotype. NHMUK I.8675/I.8539 print and conterprint, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie; ♀ (Plate 22, fig. 1, Text-fig. 79A, B).

Other material. Three females and three males in the NHMUK collection, including NHMUK I.8759 (♀) (Text-fig. 79C), NHMUK I.9406 (♂) (Text-fig. 79E) and NHMUK I.9774, coll. P. B. Brodie; ♂ (Text-fig. 79D); all from Bembridge Marls, Isle of Wight, UK.

Description. Female. BL *c.* 4 mm, AL *c.* 1.5 mm. Head elongate, longer than wide, with parallel sides, rounded occipital corners, and feebly concave occipital margin. Eyes oval, strongly displaced forward, length of cheek less than scape diameter. Scape reaching occipital margin or perhaps slightly protruding beyond it. Mandibles well developed, triangular, with numerous small teeth on masticatory margin. Scutum feebly convex, not overhanging pronotum anteriorly. Scutum and scutellum separated with distinct impression in side view. Mesopleural suture well developed. Propodeum angulated in side view with dorsum somewhat shorter than declivity. Petiole 1.6–1.7 times as high as long, with high scale, in side view, with almost parallel anterior and posterior surfaces and smoothly rounded top. Rear part of petiole with ventral rounded lobe. No spurs preserved with fragments of middle and hind tibiae as preserved in holotype. Tubular articulation between first and second gastral segments well developed (preserved in specimens NHMUK I.8539 and NHMUK I.8759). First gastral segment higher than long. Sting short and sharp. Preserved organic integument of alitrunk and gaster with very fine shagreened sculpture.

Male. BL 3–3.5 mm. Eyes of moderate size, oval, displaced a little forward. Antenna filiform, long, deflexed back reaching

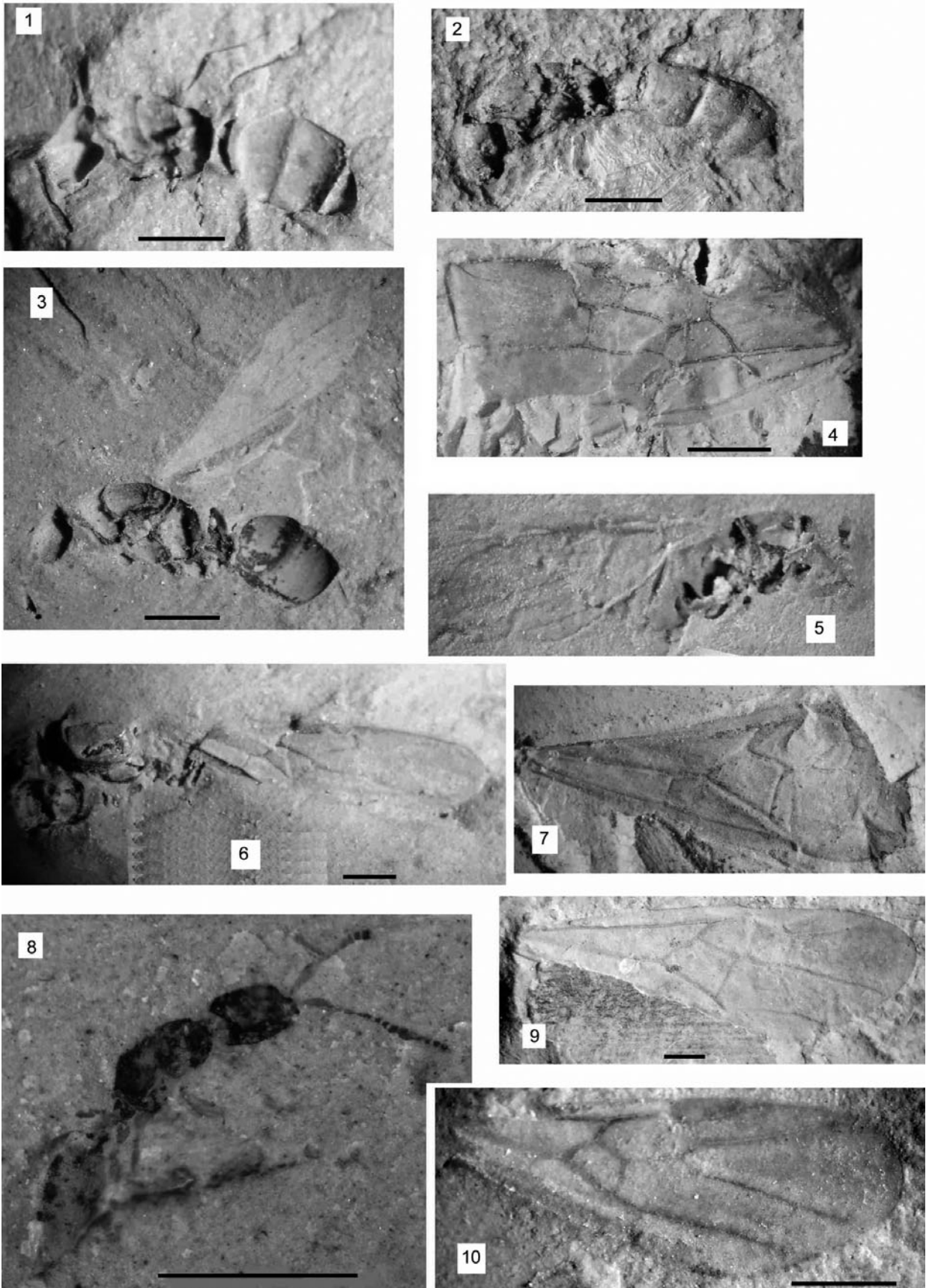
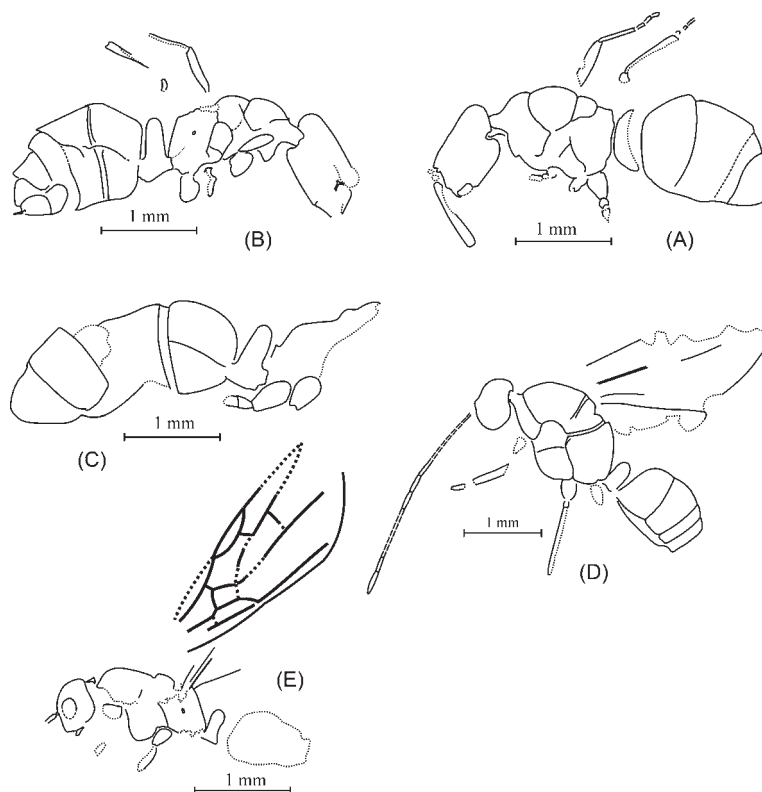


Plate 22 (1) *Ponerites crawleyi* (Donisthorpe), comb. nov., holotype (*Euponera crawleyi* Donisthorpe), NHMUK I.8675. (2) *Ponerites antropovi* Dlussky, sp. nov., holotype, NHMUK I.9996. (3) *Ponerites hooleyi* Dlussky & Perfilieva sp. nov., holotype, NHMUK In.24971. (4–5) *Taphopone macroptera* Perfilieva, 1 sp. nov.: (4) holotype, NHMUK I.9494; (5) paratype, NHMUK In.24378. (6) *Taphopone petrosa* Perfilieva, sp. nov., holotype, NHMUK In.24369. (7) *Taphopone aberrans* Perfilieva, sp. nov., paratype, NHMUK In.24910. (8) *Solenopsites rossi* Dlussky, sp. nov., holotype, NHMUK I.9968. (9) *Taphopone aberrans* Perfilieva, sp. nov., holotype, NHMUK In.24917. (10) *Paraphaenogaster hooleyana* Perfilieva, sp. nov., holotype, NHMUK In.24963. Scale bars = 1 mm.



Text-figure 79 *Ponerites crawleyi* (Donisthorpe): (A) ♀, holotype of *Euponera crawleyi* Donisthorpe, NHMUK I.8675; (B) counterprint of the same specimen, identified by Donisthorpe as *Leucotaphus gurnetensis* (Cockerell); (C) ♀, NHMUK I.8759; (D) ♂, NHMUK I.9774; (E) ♂ NHMUK I.9406.

middle of gaster. Scape very short, flagellomeres elongate, four times as long as thick in middle of flagellum. In side view, scutum uniformly convex, propodeum gradually rounded. Propodeal spiracles small, oval. Legs rather long and thin. Petiole with high scale, in side view, with almost parallel anterior and posterior surfaces and smoothly round top. Constriction between first and second gastral segments poorly expressed.

Forewing (known only for males) with closed cells 1+2r, rm , mcu (specimen NHMUK I.9406), and supposedly 3r. 1RS perpendicular to R. 1M more than twice as long as 1RS. Cross-vein 2r-rs slightly proclined, rs-m more distal than 2r-rs, a little distal comparing level of pterostigmal apex. Cell rm triangular, not pedunculate. Cell mcu of medium size, rhomboid, reaching level of pterostigmal base. Cross-vein $cu-a$ joining 1M+Cu near mcu . $Icu = 1.25-1.3$, $Icu_a = 1.1$.

Measurements in mm. NHMUK I.8675 (♀, holotype): BL = 3.6; AL = 1.5; HL = 0.9; SL = 0.75; ScL = 0.5; SctL = 0.23; PtL = 0.31; PtH = 0.60. NHMUK I.8759 (♀): PtL = 0.39; PtH = 0.69. NHMUK I.9774 (♂): AL = 1.6; ScL = 0.7; AntL = 2.7; PtH = 0.4. NHMUK I.9406 (♂): AL = 1.3; HL = 0.55; FWL = 2.9; PtH = 0.34.

Remarks. Donisthorpe (1920) misidentified specimens NHMUK I.8539, NHMUK I.8684, NHMUK I.8759, NHMUK I.9406 and NHMUK I.9774 as *Leucotaphus gurnetensis*. Constriction between first and second gastral segments, the key character of Ponerinae, is clearly visible on specimens NHMUK I.8539, NHMUK I.8759 and NHMUK I.9774. Furthermore, NHMUK I.8539 represents a counterpart of NHMUK I.8675, the holotype of *Euponera crawleyi*. Forewings of NHMUK I.9406 show cross-vein $cu-a$ near cell mcu ($Icu = 1.3$; $Icu_a = 1.1$), which is equally a key character of Ponerinae. Male NHMUK I.9774 has filiform antennae unlike males of *Leucotaphus*, which have geniculate antennae.

Unfortunately there is no diagnostic character discriminating *Ponera*, *Hypoponera* or *Pachycondyla* (= *Euponera*) (tibial

spur formula, ventral lobe of petiole, dentation of mandibles etc.) preserved in the material available, thus forcing us to refer this species to the morphogenus *Ponerites*.

Ponerites antropovi Dlussky & Perfilieva, sp. nov.

Plate 22, fig. 2; Text-fig. 80

Etymology. After Alexander V. Antropov who was the first to identify this ant as Ponerinae.

Holotype. NHMUK I.9996, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie; ♀ (Plate 19, fig. 22; Text-fig. 80).

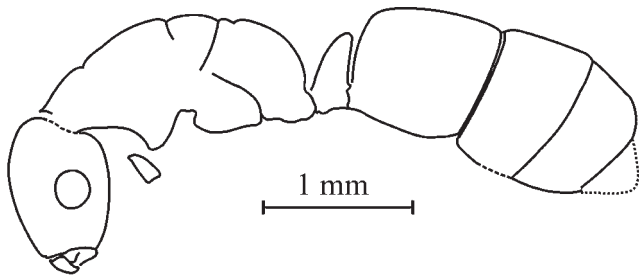
Diagnosis. Differs from *P. crawleyi* and *P. hooleyi* in position of eyes near the middle of head sides, propodeum rounded in side view, scale with fore-surface feebly convex, and in elongated first gastral segment.

Description. Female. BL 4.5 mm. Eyes round, situated near the middle of head sides. Scutum feebly convex, not overhanging pronotum anteriorly. Scutellum feebly convex. Propodeum rounded in side view. Petiole with high scale, fore-surface of scale feebly convex, back surface feebly concave, top rounded. Gaster with distinct constriction between first and second segments showing well preserved tubular rings, first gastral segment a little longer than high.

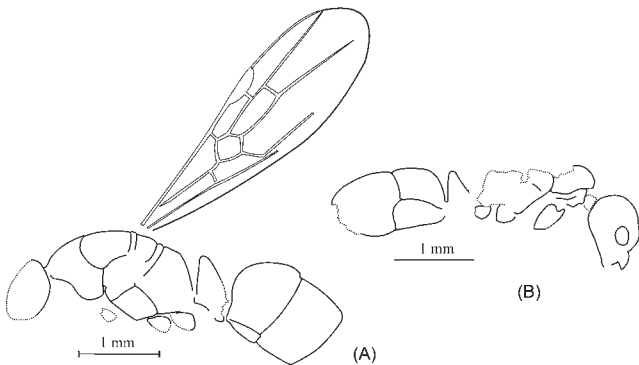
Male unknown.

Measurements of holotype in mm. AL = 1.65; HL = 1.0; ED = 0.25.

Remarks. Donisthorpe misidentified the holotype as *Leucotaphus gurnetensis*. During preliminary study of the material, Dr Alexander Antropov correctly identified it as Ponerinae. The new species is attributed to the morphogenus *Ponerites* because the diagnostic characters of the genera *Ponera*, *Hypoponera* or *Pachycondyla* (= *Euponera*) (tibial spur formula, ventral lobe of petiole, dentation of mandibles etc.) cannot be seen in the current material.



Text-figure 80 *Ponerites antropovi* Dlussky, sp. nov., ♀, holotype, NHMUK I.9996.



Text-figure 81 *Ponerites hooleyi* Dlussky et Perfilieva, sp. nov.: (A) ♀, holotype, NHMUK In.24971; (B) ♀, paratype, NHMUK I.9869.

Ponerites hooleyi Dlussky & Perfilieva sp. nov.
Plate 22, fig. 3; Text-fig. 81A, B.

Etymology. In honour of R. W. Hooley, collector of the type specimen.

Holotype. NHMUK In.24971, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley; ♀ (Plate 22, fig. 3; Text-fig. 81A).

Paratypes. NHMUK I.9602 (♂), NHMUK I.9869 (♀) (Text-fig. 81B); both from Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie.

Diagnosis. Differs from *P. crawleyi* by high scale, in side view, clearly narrowed upwards with a narrowly round top; in propodeum angulate, in side view, eyes displaced forward; differs from *P. antropovi* by the above position of eyes and short first segment of the gaster.

Description. Female. BL about 4–5 mm. Eyes oval, displaced forward; length of cheek similar to maximal diameter of eye. Scutum rather small, feebly convex, not over-hanging pronotum anteriorly. Scutellum feebly convex. Mesopleural suture well developed. Propodeum in side view angulated; propodeal dorsum much shorter than propodeal declivity. Petiole more high than long, with high scale, in side view clearly narrowed upwards with the narrowly round top. Gaster with distinct constriction between first and second segments. First segment of the gaster higher than long.

Male. BL about 3 mm. Head absent in both paratypes. Scutum and scutellum are feebly convex. Propodeum rounded in side view. Petiole in side view triangulate, with rounded top. Gaster with weak constriction between first and second segments.

Forewing. 1RS and 2r–rs perpendicular to R. Cell 3r comparatively long, more than four times as long as wide, its apex touching wing margin. Cell rm quadrangular. Cross-vein rs–m far distal in respect of 2r–rs, but not distal of level of pterostigmal apex. Cell mcu pentagonal, in terms of area more than

half as large as 1+2r. 2M and RS+M of subequal length. Cell mcu not reaching level of pterostigmal base. 1M more than twice as long as 1RS. Cross-vein cu–a meeting 1M+Cu near mcu. Icu = 1.4, Icu_a = 1.13.

Measurements in mm. NHMUK In.24971 (♀, holotype): AL = 1.9; FWL = 3.75. NHMUK I.9859 (♀, paratype): AL = 1.5; HL = 0.9; ED = 0.23. NHMUK I.9602 (♂, paratype): BL = 3.1, AL = 1.25. NHMUK In.24378 (♂, paratype): AL = 1.5, FWL = 3.0.

Remarks. Donisthorpe (1920) identified specimens NHMUK I.9602, NHMUK I.9869, and NHMUK In.24378 as *Leucotaphus gurnetensis*. However, the presence of a constriction between the first and second segments of NHMUK I.9602 and NHMUK I.9869 and the presence of closed cell rm and position of cross-vein cu–a on forewing of NHMUK In.24378 indicate these ants belong to subfamily Ponerinae.

As no diagnostic characters separating the genera *Ponera*, *Hypoponera* or *Pachycondyla* (tibial spur formula, ventral lobe of petiole, dentation of mandibles etc.) can be seen on impressions, we include this species in the morphogenus *Ponerites*.

Morphogenus *Taphopone* Dlussky & Perfilieva, gen. nov.

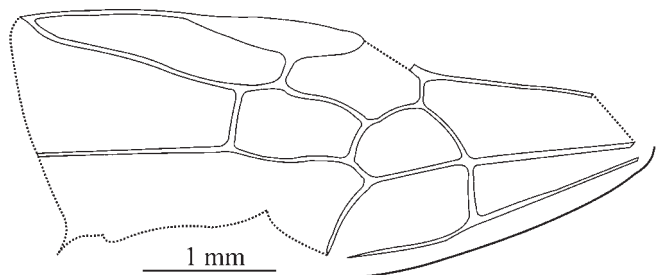
Etymology. From Greek *taphos* for grave and genus *Ponera*. Gender feminine.

Types species. “*Ponerites*” *karaganensis* Dlussky, 1981, Miocene, Vishnevaya Balka, Stauropol reg., Russia.

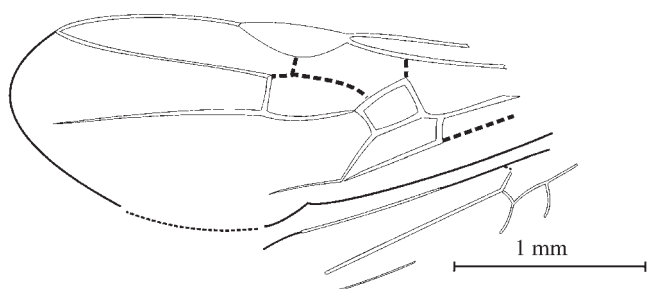
Other species. Attributed with confidence to this morphogenus are *Taphopone karaganensis* (Dlussky, 1981), comb. nov. (= “*Ponerites*” *karaganensis*) and *Taphopone stauropolitana* (Dlussky, 1981), comb. nov. (= “*Ponerites*” *stauropolitanus*) from the Miocene of Stavropol region (Russia) and four species described below. Most likely, some other species from other Miocene deposits of Europe, described in genera *Ponera* Latreille, 1804 and *Poneropsis* Heer, 1867 and included in the morphogenus *Poneropsis* Heer, 1867 by Taylor (1964), may also deserve transfer to this genus.

Diagnosis. Isolated ant forewings with closed cells 1+2r, 3r, rm and mcu, and with distal position of cross-vein cu–a (usually with Icu < 1.4). Cross-vein 1r–rs (subdividing cell 1+2r on two separated cells), or its rudiment, lost (unlike some Armaniidae and Sphecomyrminae). Cells 3r, rm and mcu are not grouped in the central part of the wing (unlike *Formicium* Westwood, 1854, subfamily Formiciinae).

Remarks. While revising the genus *Ponera* Latreille, 1804, Taylor (1964) placed 19 species described previously from forewing fossils from the Miocene of Europe as *Ponera* Latreille and *Poneropsis* Heer, as well as *Ponera hypolitha* Cockerell from the Bembridge Marls, in the morphogenus *Poneropsis*. Taylor’s re-definition of *Poneropsis* resulted in its much wider application for all detached ant wings with complete venation. This is because Taylor overlooked some important traits, particularly the position of cross-vein cu–a, which can be used to distinguish forewings of Ponerinae and several other primitive ant subfamilies (Armaniinae, Sphecomyrminae, Myrmeciinae, Amblyoponinae, Ectatomminae, Cerapachyinae, Ectoninae) from the venationally advanced subfamilies Myrmicinae, Aneuretinae, Dolichoderinae and Formiciinae. As a result, *Poneropsis* sensu Taylor can accommodate the majority of the ant wing fossils. The name *Poneropsis* further causes confusion. Mayr (1867) re-examined three specimens identified as *Ponera fuliginosa* (type species of genus *Poneropsis*) by Heer and found that they had a two-segmented waist and might be females of *Aphaenogaster* Mayr, 1853, a genus of Myrmicinae. Therefore we propose a new morphogenus for impressions of ant forewings with closed cells 1+2r, 3r, rm and mcu, and



Text-figure 82 *Taphopone macroptera* Perfilieva, sp. nov., forewing, holotype, NHMUK I.9494.



Text-figure 83 *Taphopone microptera* Perfilieva, sp. nov., forewing, holotype, NHMUK In.9763.

with a distal position to cross-vein cu-a ($Icu < 1.4$), which certainly belong to Ponerinae or other venationally-primitive ant subfamilies. We also include some additional characters in the diagnosis which exclude the most archaic (Armaniidae, Sphecomyrminae) and aberrant ants (Formiciinae).

The new species are diagnosed in the key below (section 3.11.3).

Taphopone macroptera Dlussky & Perfilieva, sp. nov.
Plate 22, fig. 4; Text-fig. 82

Etymology. *Macroptera* is Latin for "large wings".

Holotype. NHMUK I.9494, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie; forewing (Plate 22, fig. 4; Text-fig. 82).

Paratype. NHMUK I.10172, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie; forewing (Plate 22, fig. 5).

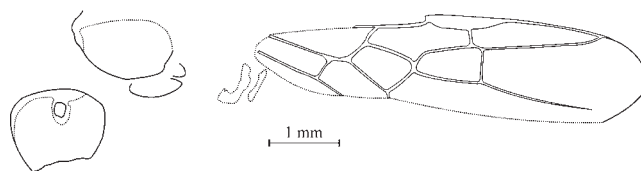
Description. FWL $c. 5.5$ – 6 mm. 1RS slightly reclined, not strictly perpendicular to R. Cell 3r comparatively short (less than four times as long as wide), its apex touching wing margin. Cell rm quadrangular, rs-m distal in respect to 2r-rs, but not in respect of pterostigmal apex. 2r-rs somewhat proclined. Cell mcu large (more than half cell 1+2r in terms of area), pentagonal, 2M shorter than RS+M. Cross-vein m-cu surpassing level of pterostigmal base. 1M more than twice as long as 1RS. Cell cua well developed. Crossvein cu-a almost reaching mcu (2M+Cu practically lost). $Icu = 1.05$, $Icua = 1.01$ (holotype; paratype $Icu = 1.09$).

Remarks. The holotype is labelled as *Pachycondyla* sp., however Donisthorpe did not mention this specimen in his paper. This might well be correct, but cannot be reasonably confirmed because of the absence of diagnostic characters (cf. above). That is why the new species is included in the morpho-genus *Taphopone*.

T. macroptera is venationally similar to *Ponerites hooleyi*, but differs in having a larger wing (3–4 mm in the latter).

Taphopone microptera Dlussky & Perfilieva, sp. nov.
Text-fig. 83

Etymology. *Microptera* is Latin for "small wings".



Text-figure 84 *Taphopone petrosa* Perfilieva, sp. nov., holotype, NHMUK In.24369.

Holotype. NHMUK I.9763, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie; forewing (Text-fig. 83).

Paratype. NHMUK In.24378 Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley; forewing.

Description. FWL $c. 3$ mm. Cell 3r comparatively long (four times as long as wide), touching wing margin. Cell rm quadrangular. Cross-vein rs-m far distal in relation to 2r-rs but not distal of pterostigmal apex. Cell mcu pentagonal, reaching level of pterostigmal base. Cross-vein m-cu and 1M shorter than 1Cu. Cell cua well developed. Cross-vein cu-a almost reaching mcu (2M+Cu practically lost). $Icu = 1.1$ – 1.3 , $Icua = 1.1$ (holotype).

Hindwing (holotype) with three longitudinal veins RS, M, and Cu. 1RS and rs-m of near equal length, m-cu longitudinal, longer than rs-m.

Measurements in mm (holotype): AL = 1.55; FWL = 3.1; FWW = 0.9.

Remarks. Donisthorpe misidentified both forewings of this species as *Leucotaphus gurnetensis*, even though they have cell rm closed and forewing cross-vein cu-a takes distal position.

Taphopone petrosa Dlussky & Perfilieva, sp. nov.
Plate 22, fig. 6; Text-fig. 84

Etymology. *petrosa* is Latin for stony.

Holotype NHMUK In.24369, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley; ♀ (Plate 22, fig. 6, Text-fig. 84).

Paratypes. NHMUK In.24927; NHMUK In.24949 (forewings); NHMUK In.25006 (two forewings), coll. R. W. Hooley; CAMSM X.50140.21 (TN 71) (forewing). All from Bembridge Marls, Isle of Wight, UK,

Description. Female. FWL 6–7.5 mm. Head subrectangular, wider than long, with convex sides and rounded occipital corners.

Forewing. 1RS reclined. Apex of cell 3r touching wing margin. Cell rm triangular with short stem or not pedunculate, 2.2–2.4 times as long as wide. Cross-vein rs-m level with 2r-rs, or more distal than that but not more than for vein width. Cell mcu trapezoid, of medium size, 1M shorter than m-cu. M+Cu distinctly bent at junction with cu-a. Cross-vein cu-a near cell mcu. $Icu 1.3$ – 1.4 , $Icua 1.14$ – 1.18 .

Measurements in mm. Holotype: HW = 1.45; FWL = 6.1. Paratype NHMUK In.24927: FWL = 6.1; FWW = 2.1. Paratype NHMUK In.24949: FWL = 7.2; FWW = 1.9.

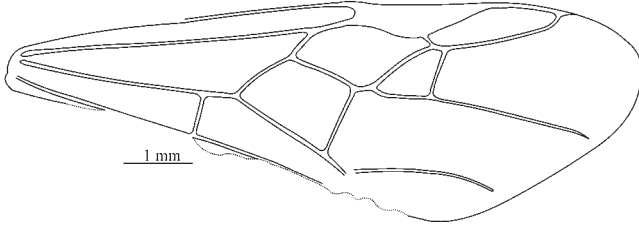
Remarks. Donisthorpe (1920) misidentified the holotype as *Dolichoderus britannicus*, even though the distal position of cross-vein cu-a indicates clearly that it belongs to Ponerinae.

Taphopone aberrans Dlussky & Perfilieva, sp. nov.
Plate 22, figs 7, 9; Text-fig. 85

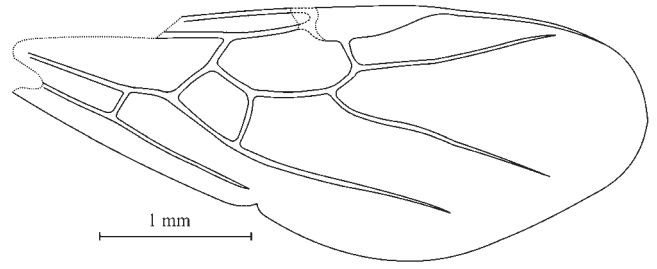
Etymology. *Aberrans* is Latin for aberrant.

Holotype. NHMUK In.24917, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley; forewing (Plate 22, fig. 9; Text-fig. 85).

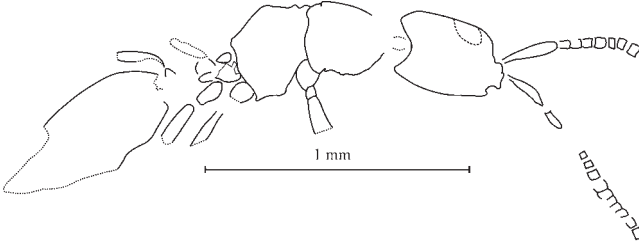
Paratypes. Forewings. NHMUK I.8574, coll. P. B. Brodie; NHMUK In.24847; NHMUK In.24910 (Plate 22, fig. 7);



Text-figure 85 *Taphopone aberrans* Perfilieva, sp. nov., forewing, holotype, NHMUK In.24917.



Text-figure 87 *Paraphaenogaster hooleyana* Perfilieva, sp. nov., forewing, holotype, NHMUK In.24963.



Text-figure 86 *Solenopsites rossi* Dlussky, sp. nov., ♀, holotype, NHMUK I.9968.

NHMUK In.24917; NHMUK In.24960, coll. R. W. Hooley; CAMSM: X.50140.117 (TN.173). All from Bembridge Marls, Isle of Wight, UK.

Description. Forewing. FWL *c.* 9 mm. 1RS distinctly reclined. Cell 3r short, less than three times as long as wide, its apex touching wing margin. Cell rm rather small, triangular, usually with long stem. Cross-vein 2r-rs reclined, cross-vein rs-m somewhat distal in respect to 2r-rs, but not beyond pterostigmal apex, often meeting M more proximal than RS. Cell mcu large, subequal to 1+2r in terms of area, trapezoid (RS+M and 1M shorter than m-cu and 1Cu, respectively). 1M more than twice as long as 1RS. Cross-vein m-cu placed distal of level of pterostigmal base. Cross-vein cu-a meeting 1M+Cu near cell mcu. Icu = 1.3–1.45, Icu_a = 1.13–1.14.

Measurements in mm. FWL = 9.1 (holotype).

Remarks. The distal position of cu-a indicates the wing belongs to a representative of Ponerinae but differs from other Bembridge Ponerinae in the form of cell rm.

3.11.1.5. Subfamily Myrmicinae Lepeletier de Saint-Fargeau, 1836

Morphogenus *Solenopsites* Dlussky & Rasnitsyn, 2002

Type species. *Solenopsites minutus* Dlussky & Rasnitsyn, 2002, by original designation.

Other species. *S. minutus* (Middle Eocene, Green River Formation, USA) and *S. rossi* sp. nov. (Bembridge Marls, Isle of Wight, UK).

Diagnosis. Ant rock fossils with waist two-segmented and long (more than half as long as gaster and nearly half as long as the alitrunk), with propodeum unarmed, petiole pedunculate and postpetiole narrowly attached to gaster, which cannot be identified more precisely.

Remarks. This morphogenus can include all poorly preserved impressions of small Myrmicinae without propodeal spines or teeth and with a pedunculate petiole, but really belong to many different orthotaxa.

Solenopsites rossi Dlussky & Perfilieva, sp. nov.
Plate 22, fig. 8; Text-fig. 86

Etymology. In honour of Dr Andrew Ross, appreciating his help in preparing this work.

Holotype NHMUK I.9968, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie, ♀ (Plate 22, fig. 8; Text-fig. 86).

Description. Wingless female. BL about 2 mm. Head sub-rectangular, longer than wide, with feebly convex sides, rounded occipital corners and concave occipital margin. Eyes oval, strongly displaced forward. Antennae geniculate, scape thick and short, not reaching the occipital margin, middle flagellomeres thicker than long. Propodeum angulate in side view, without spines or teeth. Legs short and thick.

Measurements in mm. AL = 0.65; HL = 0.39, HW = 0.29; SL = 0.23.

Remarks. Despite the waist being only partially preserved, position of the alitrunk, gaster and preserved fragments of the waist indicate two-segmented waist. The new species differs from all other ants in the Bembridge assemblage in its small size, and from *S. minutus* in the form of head.

Morphogenus *Paraphaenogaster* Dlussky, 1981

Type species. *Paraphaenogaster microphthalmus* Dlussky, 1981, by original designation.

Other species. *P. hooleyana* sp. nov. *Aphaenogaster shanwangensis* (Hong, 1984), *A. lapidescens* Zhang, and *A. paludosa* Zhang from the Middle Miocene of Shanwang (Shandong, China) are similar venationally (Zhang, 1989) and might belong there as well.

Diagnosis. Isolated ant wings with cells 1+2r and mcu, cell 3r open at apex, and r-m present, apical sections of RS and M leaving cell 1+2r+rm separately.

Remarks. Similar venation is characteristic of some Myrmicinae: Pheidolini (a part of *Aphaenogaster* Mayr) and Solenopsidini (*Solenopsis* Westwood, *Oligomyrmex* Mayr).

Paraphaenogaster hooleyana Dlussky & Perfilieva, sp. nov.
Plate 22, fig. 10; Text-fig. 87

Etymology. After Mr. R. W. Hooley.

Holotype. NHMUK In.24963, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley; forewing (Plate 22, fig. 10).

Paratype NHMUK In.25082, Bembridge Marls, NW Isle of Wight, UK, coll. R. W. Hooley; forewing.

Description. Forewing. Cell mcu trapezoid (1Cu appreciably longer than 1M and RS+M), of medium size (not more than half of cell 1+2r in terms of area), not reaching level of pterostigmal base. 4M leaving RS+M basal of 2r-rs and at level of pterostigmal base in holotype (slightly more distal in paratype). 1RS reclined. Cross-vein cu-a well distant from mcu. Icu = 1.5–1.7, Icu_a ~ 1.2.

Remarks. Holotype and paratype wings differ in size significantly, restored values being 4.6 mm and 3.8 mm, respectively. Position of base of apical section of M on cell rm, relative length of 1M and 1RS, and inclination of 2r-rs differ as

well. Nevertheless they may be the same species, supposing the holotype is a female and paratype a male.

There is also a poorly preserved wing NHMUK In.25081 of apparently similar venation, but differing in still smaller size (FWL ~ 3 mm).

3.11.2. Species doubtfully and erroneously described as Formicidae

Camponotus brodiei Donisthorpe, 1920

1920 *Camponotus brodiei* Donisthorpe, p. 93, plate V. fig. 13.

1995 *Camponotus brodiei* Donisthorpe, Bolton, p. 89.

Holotype NHMUK I.9551, Bembridge Marls, NW Isle of Wight, UK, coll. P. B. Brodie.

Remarks. The holotype is possibly an ant but so poorly preserved that it does not permit attribution to a subfamily. We refer it to as Formicidae *incertae sedis*.

Leucotaphus permaneus Cockerell, 1927

1927 *Leucotaphus permaneus* Cockerell, p. 165 (footnote).

The original description is short and of little help, and the holotype is lost from the USNM collection. We propose to consider this species as *nomen dubium*.

Ponera minuta Donisthorpe, 1920

Remarks. Belongs to Agaonidae (see Donisthorpe 1920, p. 17).

Syntaphus wheeleri Donisthorpe, 1920

Remarks. Belongs to Braconidae (see Donisthorpe 1920, p. 69).

3.11.3. Keys for the identification of ant fossils from the Bembridge Marls. Preservation of ant fossils in Bembridge Marls is variable: forewings are unknown for some species (*Solenopsis rossi*, *Ponerites antropovi*) and are the only known parts of some others (*Emplastus kozlovi*, *Paraphaenogaster hooleyana* and all *Taphopone* species). This meant that separate keys had to be constructed for bodies and for forewings.

3.11.3.1. Key to bodies with or without wings

- 1 – Waist with one segment (petiole); forewing with closed cell 3r.go to 2.
 - Waist with two segments (petiole and postpetiole); forewing often with opened cell 3r (Myrmicinae). The only myrmicine species with a preserved body is *Solenopsis rossi* sp. nov. BL ~ 2 mm. Head longer than width, subrectangular, with slightly convex sides and concave occipital margin. Wing venation unknown.
- 2 – Gaster with constriction between first and second segments; male antennae filiform, with very short scape; forewing with closed cells 1+2r, 3r, rm and mcu; cross-vein cu—a close to cell mcu, so usually Icu < 1.45 and Icu < 1.2 (Ponerinae).go to 3.
 - Gaster without constriction between first and second segments; cross-vein cu—a displaced proximally, so usually Icu > 1.5 and Icu > 1.2.go to 5.
- 3 – Petiole with high scale, in side view with almost parallel anterior and posterior surfaces and smoothly round top; forewing with triangular cell rm; BL 3–3.5 mm. ♀: eyes oval; strongly displaced forward, so length of cheek less than scape diameter; propodeum in side view angular, with dorsum somewhat shorter than declivity. ♂: eyes of moderate size, oval, less displaced forward; propodeum evenly rounded in side view. = *Ponerites crawleyi* (Donisthorpe).
 - Petiole with high scale, in side view clearly narrowed upwards with narrowly rounded top; cheek about as long as eye diameter or longer. BL 4–4.5 mm.go to 4.

- 4 – First gastral tergite longer than high; eyes oval, slightly displaced forward; ♀ cheek about as long as maximum eye diameter; wing venation unknown = *Ponerites antropovi* sp. nov.
 - First gastral tergite shorter than high; eyes rounded, situated near the middle of head sides; ♀ cheek longer than eye diameter; forewing with cell rm quadrangular = *Ponerites hooleyi* sp. nov.
- 5 – Propodeum angular, with distinct carina separating propodeal dorsum and declivity, with dorsum convex and declivity concave in side view.; petiole with rounded node, 1.5–1.8 times as long as high; forewing with closed cells 1+2r, 3r, rm and mcu; BL 3–3.5 mm; FWL 3.5–4 mm. (Dolichoderinae) = ♀ *Dolichoderus vectensis* Donisthorpe.
 - Propodeum gradually rounded or angular in side view, with straight or feebly convex propodeal declivity; petiole of other form.go to 6.
- 6 – Petiole elongate, longer than wide, without node or scale.go to 7.
 - Petiole with scale (♀) or triangular in side view (♂).go to 11.
- 7 – Propodeum angular in side view, with blunt teeth on the border of propodeal dorsum and declivity, with dorsum longer than declivity; petiole 1.7 times as long as high and about half as long as propodeum; anterior part of petiolar dorsum almost straight, and posterior feebly rounded in side view; maximum petiole height is behind its midlength; forewing with closed cells 1+2r, rm, mcu and apparently 3r; FWL about 8 mm. (Aneuretinae) = *Britaneuretus anglicus* (Cockerell).
 - Propodeum feebly convex or straight in side view; petiole narrowed anteriorly, 1.8–3 times as long as wide and high. scape extending far beyond occipital margin; ♀ mandibles large, triangular, with large sharp teeth; forewings with closed cells 1+2r and 3r and not rm and mcu; 5RS and 4M leaving the same point (no cross-vein rs–m). (Formicinae, *Oecophylla*).go to 9.
- 8 – BL 5–6.3 mm; AL 2–3 mm; FWL 6–9.5 mm; petiole 2.5–3 times as long as wide and high; scutum a little longer than wide = ♂ *Oecophylla atavina* Cockerell.
 - AL > 3.5 mm; FWL usually > 9.5 mm; petiole about twice as long as wide.go to 9.
- 9 – FWL 19–25 mm, restored BL more than 16 mm = ♀ *Oecophylla megarche* Cockerell.
 - FWL 10–16 mm; BL < 10 mm.go to 10.
- 10 – Scutum a little longer than wide; alitrunk short and high, a little longer than high; gaster with six segments and exposed genitals; AL 3.5–4.5 mm; FWL 8.3–16 mm = ♂ *Oecophylla megarche* Cockerell.
 - Scutum a little wider than long; alitrunk longer, nearly twice as long as high; gaster with five segments; AL 4–5.55 mm; FWL 8.5–13.7 mm = ♀ *Oecophylla atavina* Cockerell.
- 11 – Forewing with closed cells 1+2r, 3r, rm and mcu; male antennae filiform with very short scape. (Dolichoderinae).go to 12.
 - Forewing without closed cell rm; 5RS and 4M starting from the same point (cross-vein rs–m lost). Antennae geniculate in both sexes, scape always extending beyond occipital margin. (Formicinae).go to 16.
- 12 – Head about as wide as alitrunk or a little narrower; antennae geniculate; gaster with five segments (♀♀)go to 13.

- Head distinctly narrower than alitrunk; antennae filiform, with very short scape; petiole triangular in side view; gaster with six segments (♂♂). go to 14.
 - 13 – Head wider than long; scape short, not reaching occipital margin; petiole with scale 2.5–3 times as wide as thick; cell rm comparatively wide (1.6–2.1 times as long as wide); cross-veins 2r–rs and rs–m aligned at RS (4RS absent), or rs–m slightly distal, leaving 4RS as long as about vein thickness; BL 6–8.5 mm; AL 2.5–3.5 mm; FWL 6–7 mm = ♀ *Emplastus britannicus* (Cockerell).
 - Head longer than wide; petiole with low scale (about as long as high), triangular in side view; cell rm 2.2–2.4 times as long as wide; cross-veins rs–m noticeable distal on RS than 2r–rs, 4RS much longer than vein thickness; BL 5–6.5 mm; AL 2.2–3.2 mm; FWL 5–5.5 mm = ♀ *Emplastus gurnetensis* (Donisthorpe).
 - 14 – Cell rm 1.6–2.1 times as long as wide; cross-veins 2r–rs and rs–m aligned at RS, 4RS lost, or rs–m a little more distal, leaving 4RS about as long as vein thickness; BL ~ 6 mm; AL ~ 3 mm; FWL 5–5.6 mm = ♂ *Emplastus britannicus* (Cockerell).
 - Cell rm 2.2–2.8 times as long as wide; cross-vein rs–m noticeably distal on RS in respect of 2r–rs, 4RS distinctly longer than vein thickness. go to 15.
 - 15 – Cell rm 2.5–2.8 times as long as wide; BL 6.5 mm; AL 3 mm; FWL 5–6 mm = ♂ *Emplastus hypolithus* (Cockerell).
 - Cell rm 2.2–2.4 times as long as wide; BL ~ 4 mm; AL sim; 2 mm; FWL 4 mm. = ♂ *Emplastus gurnetensis* (Donisthorpe).
 - 16 – Scape attached distant from posterior margin of clypeus; forewing lacking closed cell mcu = *Camponotus cockerelli* (Donisthorpe).
 - Scape attached at the posterior clypeal margin. Cell mcu present. go to 17.
 - 17 – ♂: BL 2.2–3.8 mm; AL 1.0–1.7 mm; FWL 2.2–3.7 mm; petiole triangular in side view; genitals poorly exposed, with stipes short, narrow, rounded at top. ♀: BL 5.0–5.7 mm; AL 2.2–3.2 mm; FWL 5–5.5 mm; petiole with scale high and wide, 2.2–2.4 times as high as long and 2.5–3 times as wide as thick = *Leucotaphus gurnetensis* (Cockerell).
 - ♂: BL 4.0–4.5 mm; AL 1.4–2.0 mm; FWL 3.8–4.5 mm; petiole triangular in side view; genitals well exposed, with stipes long, triangular, rounded at top. ♀: FWL 7.4–7.5 mm = *Leucotaphus donisthorpei* sp. nov.
- 3.11.3.2. Key to wings**
- 1 – Forewings with cells 1+2r, 3r, rm and mcu closed. go to 2.
 - Closed cell rm absent. go to 13.
 - 2 – Cross-vein cu–a near cell mcu, so usually Icu < 1.45 and Icu a < 1.2 (Ponerinae). . . go to 3.
 - Cross-vein cu–a displaced proximal, so usually Icu > 1.5 and Icu a > 1.2. go to 8.
 - 3 – Cell rm triangular. go to 4.
 - Cell rm quadrangular. go to 6.
 - 4 – Cell rm small, pedunculate, with long stem; FWL c. 9 mm; Icu = 1.3–1.45; Icu a = 1.13–1.14 = *Taphopone aberrans* sp. nov.
 - Cell rm with no or very short stem. go to 5.
 - 5 – Cross-vein 2r–rs clearly proximal of rs–m; FWL c. 3 mm; Icu 1.25–1.3; Icu a 1.1 = *Ponerites crawleyi* (Donisthorpe).
 - Cross-veins 2r–rs and rs–m coinciding on RS (4RS is absent) or rs–m a little distal leaving 4RS about as long as vein thickness; FWL c. 7 mm; Icu 1.3–1.4; Icu a 1.14–1.18 = *Taphopone petrosa* sp. nov.
 - 6 – Cell cua lost; cross-vein cu–a distant from cell mcu, so as 2M+Cu well developed and Icu ≥ 1.4; Icu a ≥ 1.13; FWL 3–4 mm = *Ponerites hooleyi* sp. nov.
 - 2Cu leaving cell mcu at clear angle forming distinct cell cua; cross-vein cu–a close to mcu, resulting in Icu ≤ 1.3; Icu a ≤ 1.1. go to 7.
 - 7 – Cell 3r comparatively short, four times as long as wide; FWL 5.5–6 mm; Icu = 1.05; Icu a = 1.01 (holotype) = *Taphopone macroptera* sp. nov.
 - Cell 3r more than four times as long as wide; FWL c. 3 mm; Icu = 1.1–1.3; Icu a = 1.08–1.10; Hind wing with three longitudinal veins (RS, M and Cu) = *Taphopone microptera* sp. nov.
 - 8 – Cross-vein 2r–rs distal of rs–m (possibly an aberration, for normally it is rs–m which can be more distal); FWL c. 8 mm; Icu = 1.6; Icu a = 1.3 = *Britaneuretus anglicus* (Cockerell) (Aneuretinae).
 - Cross-vein 2r–rs either proximal of, or coinciding with, rs–m. (Dolichoderinae). go to 9.
 - 9 – FWL 3–3.5 mm. Cell rm triangular, pedunculate (rarely with stem very short). Cross-vein 2r–rs coinciding with rs–m or a little distal of it = *Dolichoderus vectensis* Donisthorpe.
 - FWL > 4.5 mm. go to 10.
 - 10 – Cell rm 1.5–2.1 times as long as wide; cell rm triangular with very short or no stem; cross-veins 2r–rs and rs–m coinciding on RS (4RS absent), or rs–m distal a little (4RS about as long as vein thickness); FWL 5.5–7 mm; Icu 1.55–2.2; Icu a 1.2–1.4; hindwing with two longitudinal vein (RS and Cu) = *Emplastus britannicus* (Cockerell).
 - Cell rm 2.2–2.8 times as long as wide. go to 11.
 - 11 – Cell rm 2.5–2.8 times as long as wide; cell rm quadrangular or triangular, not pedunculate; cross-vein rs–m noticeably distal on RS compared to 2r–rs; 4RS distinctly longer than vein thickness, rarely rs–m and 2r–rs coinciding on RS; FWL 5–6 mm; Icu 1.6–2.1; Icu a 1.3–1.4 = *Emplastus hypolithus* (Cockerell).
 - Cell rm 2.2–2.5 times as long as wide. Cell rm triangular without stem. go to 12.
 - 12 – Cross-vein rs–m distinctly distal on RS compared to 2r–rs, 4RS distinctly longer than vein thickness; FWL 4–6 mm; Icu = 1.8; Icu a = 1.25; hindwing with three longitudinal veins (RS, M and Cu) = *Emplastus gurnetensis* (Donisthorpe).
 - Cross-veins 2r–rs and rs–m coinciding on RS; FWL 7.8–12 mm; Icu 1.6–1.8; Icu a 1.3–1.5 = *Emplastus kozlovi* sp. nov.
 - 13 – Cell mcu closed. go to 14.
 - Cell mcu absent (Formicinae). go to 18.
 - 14 – 4M leaving cell 1+2r long before 2r–rs and 5RS; cell 3r open apically, even if sometimes very narrowly and inconspicuously; FWL 3.5–4.5 mm; Icu 1.5–1.7; Icu a c. 1.2 = *Paraphaenogaster hooleyana* sp. nov. (Myrmicinae).
 - 5RS and 4M with joint origin (no rs–m); cell 3r always closed; Icu 2.0–3.6; Icu a 1.2–2.2 (*Leucotaphus*, Formicinae). go to 15.
 - 15 – FWL 2.2–3.7 mm = ♂ *L. gurnetensis* (Cockerell).
 - FWL > 3.7 mm. go to 16.
 - 16 – FWL 3.8–4.5 mm = ♂ *L. donisthorpei* sp. nov.
 - FWL > 4.5 mm. go to 17.
 - 17 – FWL 5–5.5 mm = ♀ *L. gurnetensis* (Cockerell).
 - FWL c. 7.5 mm = ♂ *L. donisthorpei* sp. nov.
 - 18 – 5RS always convex (cell 3r bent outward); FWL 5–8 mm; hindwing with cross-vein rs–cu subequal to 2M+Cu, cross-vein cu–a near to wing base compared to rs–cu = *Camponotus cockerelli* (Donisthorpe).

Table 2 Taxonomic composition (numbers and % of total) of ants in the Bembridge Marls.

Taxa	All fossils		Identified up to species level	
	n	%	n	%
Aneuretinae				
<i>Britaneuretus anglicus</i> (Cockerell)	1	0.1	1	0.2
Dolichoderinae				
<i>Dolichoderus vectensis</i> Donisthorpe	7	0.6	6	1.1
<i>Emplastus britannicus</i> (Cockerell)	52	4.6	52	8.3
<i>Emplastus hypolithus</i> (Cockerell)	15	1.3	15	2.4
<i>Emplastus gurnetensis</i> (Donisthorpe)	8	0.7	8	1.3
<i>Emplastus kozlovi</i> Perfilieva, sp. nov.	5	0.4	5	0.8
<i>Emplastus</i> sp.	1	0.1		
Formicinae				
<i>Camponotus cockerelli</i> (Donisthorpe)	15	1.3	15	2.4
<i>Camponotus</i> sp.	1	0.1		
<i>Leucotaphus gurnetensis</i> (Cockerell)	158	13.9	158	25.1
<i>Leucotaphus donisthorpei</i> Dlussky, sp. nov.	16	1.4	16	2.5
<i>Leucotaphus</i> sp.	1	0.1		
<i>Oecophylla atavina</i> Cockerell	199	17.5	199	31.6
<i>Oecophylla megarche</i> Cockerell	124	10.9	124	19.7
<i>Oecophylla</i> sp.	397	34.9		
Ponerinae				
<i>Ponerites crawleyi</i> (Donisthorpe)	7	0.6	7	1.1
<i>Ponerites hooleyi</i> Dlussky et Perfilieva, sp. nov.	3	0.3	4	0.5
<i>Ponerites antropovi</i> Dlussky, sp. nov.	1	0.1	1	0.2
<i>Ponerites</i> sp.	1	0.1		
<i>Taphopone macroptera</i> Perfilieva, sp. nov.	2	0.2	2	0.3
<i>Taphopone microptera</i> Perfilieva, sp. nov.	2	0.2	2	0.3
<i>Taphopone petrosa</i> Perfilieva, sp. nov.	6	0.5	6	1.0
<i>Taphopone aberrans</i> Perfilieva, sp. nov.	6	0.5	6	1.0
<i>Taphopone</i> sp.	1	0.1	1	0.2
Myrmicinae				
<i>Solenopsites rossi</i> Dlussky, sp. nov.	1	0.1	1	0.2
<i>Paraphaenogaster hooleyana</i> Perfilieva, sp. nov.	2	0.2	2	0.3
<i>Paraphaenogaster</i> sp.	1	0.1		
Formicidae indet.	105	9.2		
TOTAL	1136	100.1	630	100.5

– 5RS always concave (bent into cell 3r); hindwing with rs-cu much longer than 2M+Cu and with cu-a more close to rs-cu than to wing base.go to 19.

19 – FWL 6–9.5 mm = ♂ *Oecophylla atavina* Cockerell.

– FWL > 9.5 mm.go to 20.

20 – FWL 20–23 mm = ♀ *Oecophylla megarche* Cockerell.

– FWL 10–16 mm.go to 21.

21 – Apical corner of cell 1+2r obtuse, rarely *c.* 90°; FWL 10–16 mm = ♂ *Oecophylla megarche* Cockerell

– Apical corner of cell 1+2 more acute; FWL 8.5–13.7 mm. = ♀ *Oecophylla atavina* Cockerell.

3.11.4. Discussion. The Bembridge Marls Insect Bed has yielded 20 ant species belonging to ten genera and five sub-families (Table 2). The most striking feature of the assemblage is the hyperabundance of *Oecophylla*, not recorded in any other circumstance in the past. *Oecophylla* fossils represent 63.4% of all the ants collected and 69.8% of those identified up to genus level. There is no question that the figures are exaggerated, because these ants are generally of larger size and rather striking general appearance, which make them easier to be collected and identified, even from small fragments. The collecting bias is not easy to account for; unlike the identification bias, which can be partially taken into account due to considering only the better preserved fossils which permit species level identification. This approach excludes 403 fossils identified as *Oeco-*

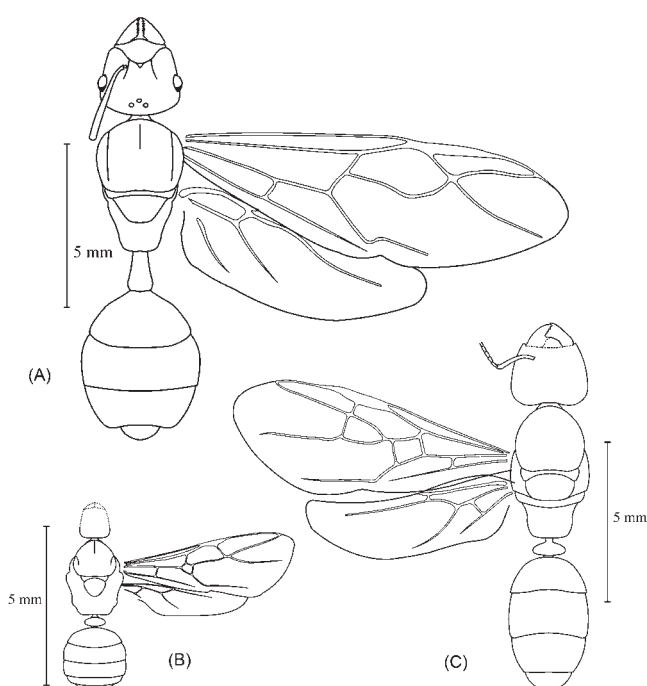
phylla sp. and 111 as Formicidae indet. The resulting figures are a bit lower, with *Oecophylla* making up 51.3% of ants (31.6% – *O. atavina* and 19.7% – *O. megarche*) while the second most abundant species, *Leucotaphus gurnetensis*, comprises 25.1%, and the fourth, *Emplastus britannicus* is 8.3%. The general appearance of females of the most abundant ant species are reconstructed in Text-figure 88. All remaining species identified in the assemblage are much rarer, each with its share being under 3% of the ant fauna.

The above data make it possible to draw some inference on the environments near the target water body of the Bembridge Marls insect burial. No doubt the landscape was rich in forest, as the abundance of dendrobiotic ants suggests. These dendro-bions form the most common three species (both species of *Oecophylla* and *Emplastus britannicus*) whose joint share is 59.5% of all ants. Their morphology discussed above, as well as the biology of their living relatives or analogues, indicates their dendrobiotic habits with considerable confidence. Judging from habits of extant relatives, *Dolichoderus vectensis* and *Camponotus cockerelli* were dendrobiotic as well: they are responsible for 3.5% of the ant assemblage.

Bembridge Ponerinae, which make up 4.3% of the assemblage, were most probably forest floor dwellers, judging from both their morphology (forward position of female eyes) and analogy with Ponerinae in the Baltic amber and other late

Table 3 Composition (% of total) of ant subfamilies in better known fossil assemblages

Subfamily	Late Cretaceous (all data)	Eocene				Oligocene	Miocene	
		Green River	Baltic amber	Bembridge Marls	Florissant	Sicilian amber	Radoboj	Visnevaja balka
Aneuretinae	1.9	3.1	0.3	0.2	0.02	0	0	0
Dolichoderinae	1.9	75.0	64.1	13.8	62.6	7.7	13.1	3.9
Formicinae	1.9	3.1	32.8	81.3	32.5	35.9	64.2	52.6
Ponerinae	1.9	10.4	0.7	4.3	0.04	5.1	0.7	2.6
Cerapachyinae	0	0	0.1	0	0	0	0	0
Myrmeciinae	0	6.3	0.1	0	0	0	0	0
Pseudomyrmecinae	0	0	0.2	0	0.04	0	0	0
Myrmicinae	1.9	2.1	1.7	0.5	4.8	51.3	21.9	40.8
Armaniidae	36.9	0	0	0	0	0	0	0
Sphecomyrminae	47.2	0	0	0	0	0	0	0
Brownimeciinae	3.8	0	0	0	0	0	0	0
Specimens studied	53	96	10919	630	5592	39	137	76



Text-figure 88 Restored general appearance of female ants most common in the Bembridge Marls: (A) *Oecophylla atavina* Cockerell; (B) *Leucotaphus gurnetensis* (Cockerell); (C) *Emplastus britannicus* (Cockerell).

Eocene European ambers, which certainly formed in forested areas. Of all Ponerinae found (except for *Bradoponera meieri* Mayr, 1867), 94% are winged sexual forms, which implies that their workers do not normally visit tree trunks and kept to the forest floor, unlike sexual forms which probably started their nuptial flight from trees and other high points.

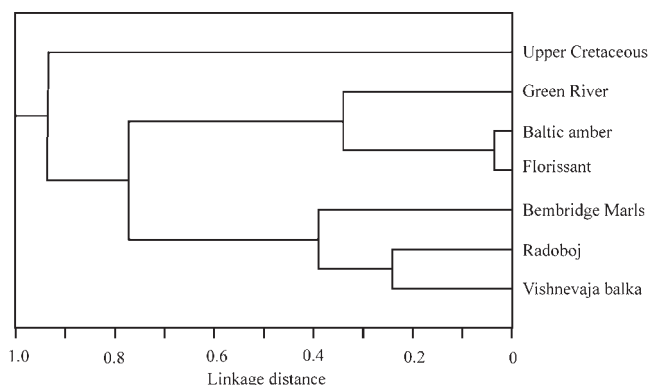
Hence, at least two thirds of the Bembridge ant assemblage consists of forest ants. Of the remaining species, the second most abundant, *Leucotaphus gurnetensis*, most probably resembles *Lasius*, which is a eurybiotic ant genus commonly found in forests, meadows and steppe. In the late Eocene European ambers, *Lasius schiefferdeckeri* Mayr, 1867, is the second most abundant ant species (after *Ctenobethylus goepperti* (Mayr, 1867)).

The Bembridge ants indicate a warm climate. Extant *Oecophylla* is characteristic of tropics and southern subtropics. One

of the authors (GMD) had a chance to observe *O. smaragdina* introduced from China to North Caucasus (Lazarevskoye Insectarium, All-Union Institute of Plant Protection). After a successful winter (1963/64) spent in a greenhouse, the ants did well during the summer in the open air in a garden, including raising larvae, but they became inactive when the temperature dropped below 18°C. Unfortunately, they were not returned to the greenhouse in time, so they died out when the temperature dropped below zero. Since *Oecophylla* makes its nest only from living leaves, they can only populate forests with evergreen angiosperm trees. We have no reason to hypothesise different habits in the past, except that the ants could have existed in a somewhat less hot climate than now: they are found in the late Miocene of Oeningen in Germany, where the climate is reconstructed as warm temperate rather than subtropical (Mai 1995).

The above results enable a possible comparison of the Bembridge assemblage with some other past ant assemblages. In this comparison, we rely on the following sources: for Late Cretaceous – Dlussky (1975, 1983, 1987, 1996, 1999a,b), Dlussky *et al.* (2004), Grimaldi *et al.* (1997), Grimaldi & Agosti (2000), Engel & Grimaldi (2005); for Green River (Middle Eocene of western North America) – Dlussky & Rasnitsyn (2002), for Baltic amber (Russia and Poland, Late Eocene) – Wheeler (1915) and our unpublished observations; for Florissant (latest Eocene, Colorado, USA) – Carpenter (1930); for Sicilian amber (Upper Oligocene of Italy) – Emery (1891); for Radoboj (Lower Miocene of Croatia) – Mayr (1867) with our additions; for Vishnevaja Balka (Middle Miocene of Stavropol, Russia) – Dlussky (1981a).

The comparison traditionally refers to composition of past assemblages at the subfamily level (Table 3). It has been shown (Dlussky 1983, 1987; Dlussky & Rasnitsyn 2002) that the Late Cretaceous assemblages were dominated by extinct Armaniidae and Sphecomyrminae, with extant subfamilies Aneuretinae, Dolichoderinae, Formicinae, Ponerinae and Myrmicinae known from rare (usually unique) plesiomorphic fossils. Since the end of the Late Cretaceous, Armaniidae and Sphecomyrminae are no longer found in the fossil record; which starts containing only extant subfamilies, with the sole exception of the short-living (Early and Middle Eocene only) monotypical giant Formicinae, and subfamilies became the highest-level changes in composition of the ant assemblages. The Palaeocene (Sakhalin amber), Eocene (Green River and European ambers) and possibly in Oligocene (except the zoogeographically different – Afrotropical – Sicilian amber, and



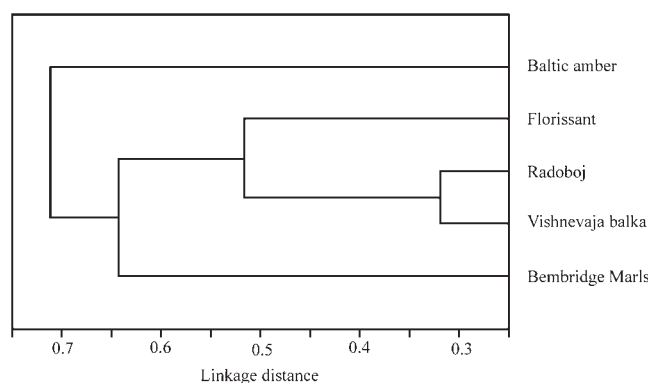
Text-figure 89 Dendrogram of similarity of the subfamily level composition of the best known ant rock fossil assemblages in the unweighted pair-group average.

supposing the Florissant assemblage to be of Oligocene rather than uppermost Eocene in age) are characterised by dominating Dolichoderinae and rare Myrmicinae. It is only in the Miocene (or in the Late Oligocene, if Sicilian amber is taken into consideration) when the subfamily level composition of the ant assemblages approached the contemporary pattern, with dominating Formicinae and Myrmicinae and far subordinated Dolichoderinae.

Table 3 shows that the Bembridge assemblage differs somewhat from the above sequence in that it is strictly dominated by Formicinae (81.3%, the highest percentage ever observed throughout the known ant history), Dolichoderinae far subordinate (13.8%), and Myrmicinae (0.5%) being the rarest. The dendrogram based on cluster analysis shows this pattern particularly clearly (Text-fig. 89). Cretaceous assemblages are naturally the most distinct, and the Cenozoic ones form two clusters; one composed of the Baltic amber and Florissant, and a little more distant Green River, and the other cluster embracing the Bembridge and Miocene assemblages. The particular similarity of the Baltic amber and Florissant is based on their virtually identical shares of Formicinae and Dolichoderinae; that of the second cluster is the result their high share of Formicinae, and the still higher similarity of Vishnevaya and Radoboj depends on the high participation of Myrmicinae. Hence, the geochronologically similar Bembridge and Florissant faunas reveal quite different relationships – the former closer to Miocene, and the latter to Eocene assemblages.

However, the pattern does not seem convincing, particularly when considering the generic level composition of the assemblages. Indeed, Florissant is dominated by *Protazteca* (28.2%) which has no analogue in Baltic amber, and *Liometopum* (30.4%) known in Baltic assemblage from two specimens of the same species. Unlike Florissant, the Baltic assemblage is dominated by *Ctenobethylus* (47.0%) unknown at Florissant. This makes it important to make a wider generic level comparison; which is difficult, however, because the Bembridge assemblage is rich in morphogenera not directly comparable to genera in other assemblages.

The problem might be resolved to some extent by relying partly on intuition, comparing the similarity of morphogenera to particular ant orthogenera. In particular, we associate *Emplastus* with *Iridomyrmex* s.l. (*Iridomyrmex* + *Anonychomyrma* + *Ctenobethylus*), *Leucotaphus gurnetensis* with *Lasius*, *Leucotaphus donisthorpei* with *Prenolepis*, and *Ponerites* + *Taphopone* with *Ponera* + *Hypoconera* + small-sized *Pachycondyla*. The Cretaceous and Green River assemblages are excluded from consideration because these genera are absent there, and Green River is dominated by the morphogenus



Text-figure 90 Dendrogram of similarity of the genus level composition of the best known ant rock fossil assemblages in the unweighted pair-group average.

Eoformica, which is impossible at present to associate with orthogenera because of poor preservation.

The resulting dendrogram (Text-fig. 90) shows the Baltic amber assemblage to be isolated while Florissant is closer to the Miocene assemblages than Bembridge is; apparently because of a higher share of *Lasius* (25.0% in Florissant, 33.3% in Radoboj and 34.2% in Vishnevaya, as opposed to 13.9% of *Leucotaphus gurnetensis* in Bembridge).

The isolated position of the Baltic amber assemblage is apparently taphonomically based (Dlussky & Rasnitsyn 2002). The ants trapped in resin are mostly workers running about on tree trunks, with those of smaller size having more chance to be trapped there. As a result, larger ants and soil and litter dwellers have less chance to become amber inclusions. Unlike them, to become impression fossils, an ant has to be buried in the bottom sediments of an ancient lake. The allochthonous insects (those living outside the target lake) find their way to future burial mostly from the air (Zherikhin 1980). That is why the chance to become an impression fossil is higher for winged ants, and particularly for those in aerial swarms (mating flight with copulation starting in air, as opposed to the ground swarm where males and females copulate only after the dispersal flight is over (Kannowski 1963)). Aerial swarms often involve numerous ant sexual forms, travelling far from their start area (swarms can be found tens of kilometres beyond the ants' northern limits as recorded in tundra (Dlussky 1967)). In contrast, ground swarming female ants (for example, *Formica* L.) execute a comparatively short flight, while males are flying low over the ground to seek females by their pheromones. Thus their potential to become impression fossils is lower.

Hypothesising the burial of ants inhabiting the source environments of the late Eocene European ambers (Baltic and others) in water bodies whose deposits would become fossiliferous rocks, we would expect the resulting ant assemblages to be much different than those in the ambers. Firstly, they would probably have a higher proportion of *Oecophylla*. Baltic amber has yielded two species of the genus, jointly producing less than 1% of the assemblage. This is not surprising, as these ants are large and long-legged, and more likely to escape resin traps compared to other ants. Still more importantly, they are tightly connected with angiosperm trees and their workers would have had little reason to visit the amber source trees, which were conifers. Secondly, the proportion of *Ctenobethylus* would be much lower. Alates of this genus are noticeably rare in amber – 0.3% (n = 5685; figures in this paragraph summarise those by Mayr 1868, Wheeler 1915, and our unpublished observations). Other ants, both supposed dendrobiotic and herpeto-biotic (forager on the surface of soil), show a higher share of

their sexual forms: herpetobiotic *Lasius schiefferdeckeri* Mayr – 3.7% (n = 1719), *Formica* spp. 9.9% (n = 1448), *Prenolepis henschei* Mayr – 10.3% (n = 715); herpetobiotic or dendrobiotic *Iridomyrmex geinitzi* (Mayr) – 2.6% (n = 1260); specialised dendrobiotic *Tetraponera* spp. – 3.3% (n = 61); and *Dolichoderus* spp. – 4.6% (n = 653). As to geo- and stratiobiotic ants (foraging within soil and leaf litter respectively), their amber inclusions are almost invariably alates: *Paratrechina pygmaea* (Mayr) – 98% (n = 107), *Hypoconerina atavia* (Mayr) – 94% (n = 52). This is quite natural, because their workers rarely leave the soil and leaf litter, unlike sexual forms that climb use trees to start their nuptial flight.

The exceedingly high proportion of worker inclusions in the case of *Ctenobethylus* has only one explanation: this ant nested in old conifer trees, had huge families and made very active trails towards colonies of symbiotic aphids. This inference is confirmed by the common syninclusions of these ants with *Germaraphis* aphids (Perkovsky 2006) and the high proportion of multiple inclusions of *Ctenobethylus* in a piece of amber. Our observations produced a figure of 9.2% (56 out of 608), with more than one worker per piece (up to 11); and Wheeler (1915) noticed numerous such cases, including seven pieces with more than ten workers each (up to 50). As already mentioned, *Ctenobethylus* is apparently a close analogue (the closest relative) of *Emplastus britannicus*, the fourth most common ant in the Bembridge assemblage, with a share of 10.1%.

The third most likely feature of the fossil ant assemblage expected in rocks resulting from an ant community populating the amber forest is a lower proportion of *Formica*. This inference can be deduced from the observation that these ants do not form nuptial swarms and thus have a comparatively low chance of being buried in a target water body. *Formica* is absent from the Vishnevays Balka, although there is little doubt that these ants lived near the water body of burial. The Bembridge Marls apparently lack ant fossils referable to that genus (there are no large *Leucotaphus* there comparable to the *Formica* sexual forms). In contrast, 10% of the Baltic assemblage are *Formica* ants, mainly *Formica flori* Mayr, 1868 and *Formica gustawi* Dlussky, 1967.

Thus, the expected rock fossil assemblage of ants from the Late Eocene amber forest would show considerable similarity to the Bembridge assemblage. This would then only highlight differences between the European (Baltic and Bembridge) and American (Florissant) assemblages, as follows:

1. *Protazteca* is the most abundant ant group in Florissant (28.3%), but neither the genus nor its analogues are known in the present and past in Europe.
2. In contrast, *Oecophylla* is common in the European Eocene, Oligocene and Miocene, as well as in the contemporary tropics of the Old World, but has never been recorded in the past and present Americas.
3. The Florissant assemblage lacks small Ponerinae dwelling within the leaf litter (*Ponera*, *Hypoconerina*, *Ponerites*), which are well represented in the Cenozoic assemblages of Europe.

In contrast, the Bembridge ant assemblage shows significant similarity to those in the European Miocene. As already mentioned, the second most abundant Bembridge species, *Leucotaphus gurnetensis*, is probably similar to *Lasius*; the Vishnevaya Balka assemblage has *Lasius vetulus* Dlussky, 1981, equally the second most common ant there, which probably deserves to be transferred to *Leucotaphus*. The Bembridge Marls contain ant wings attributable to *Paraphaenogaster*, which were previously known only from the Miocene of Europe (described from Vishnevays and also identified by GMD in the collections from Oeningan and Parschlung kept at the NHMUK) and China. *Aphaenogaster sommerfeldti*

Mayr, 1868 from Baltic amber and *A. mayri* Carpenter, 1930 from Florissant are not attributable to *Paraphaenogaster* because they have cell rm closed. It is quite possible that the wing described as *Camponotites macropterus* Dlussky, 1981 in fact represents *Oecophylla*, otherwise known in the European Miocene of Radoboj and Oeningen (*O. obesa* (Heer), Mayr, 1867). *Dolichoderus vectensis* of the Bembridge Marls belongs to the *D. quadripunctatus* group equally known in Baltic amber (Dlussky 2002) and the European Miocene (*D. haueri* (Mayr, 1867) from Radoboj, *D. tauricus* Dlussky, 1981 from Kerch, Ukraine) and not in the present and past Americas.

The above pattern indicates that the widely traceable generic level similarity of the Cenozoic (late Eocene through to Miocene) ant faunas shows its geographic orientation as more distinct than the temporal one. Within the above time interval, the Old World ant faunas are more similar to each other than to the synchronous American assemblages. For insects at least, this is a rather uncommon example of a geographically constrained evolution which inherits features of taxonomic composition of regional faunas for a long time, despite their intense evolution. There are further examples of this sort; e.g., the Myrmicinae ants whose evolution was apparently mostly confined to Africa (Dlussky *et al.* 2004), or honey bees which are confined to the Old World throughout all their rather long history (Engel 2006). This may indicate that evolution of highly social insects might be particularly geographically constrained compared to other insects. However, more detailed testing of this hypothesis lies far beyond the scope of the present project.

4. General discussion

4.1. Composition of the Bembridge Marls hymenopteran assemblage

1460 fossils were studied, which yielded a minimum of 118 species, counting those identified to any level, but only those that are evidently different from others identified to the same level. These 118 species represent 20 families and at least 78 genera.

In Ichneumonidae, 32 fossils were studied, including the types of 11 species described by Cockerell (1921a). One new genus and eight new species are described: *Exeristes gurnetor* Khalaim, sp. nov.; *Scambus fossilis* Khalaim, sp. nov.; *Eusterinx humalai* Khalaim, sp. nov.; *Hemiteles dirus* Khalaim, sp. nov.; *Hemiteles protervus* Khalaim, sp. nov., *Paxylobembra kozlovi* Khalaim, gen. et sp. nov.; *Marjorieta gigantea* Khalaim, sp. nov.; and *Lithapechtis salmacidus* Khalaim, sp. nov. The genus *Acourtia* Cockerell, 1921 is transferred to the subfamily Townesitinae. The following new combinations are established: *Eusterinx arcuatus* (Cockerell, 1921); *Hemiteles acurti* (Cockerell, 1921); and *Marjorieta disrupta* (Cockerell, 1921). The most abundant subfamilies are Cryptinae (five specimens), Pimplinae (five specimens), Townesitinae (three specimens) and Orthocentrinae (three specimens), and the genus *Lithapechtis* Cockerell, 1921 (three specimens) of uncertain subfamily assignment. The subfamilies Metopiinae and Paxylommatinae are known from a single specimen each. Fossil Townesitinae and Paxylommatinae are known from the Bembridge Marls and from Baltic amber only. Townesitinae are quite numerous and are very similar morphologically in both deposits. The ichneumonid fauna of the Bembridge Marls is close to that of the Baltic amber, and these two are apparently older than that of Florissant.

The Braconidae are represented by 13 subfamilies (Agathidinae, Brachistinae, Braconinae, Cheloninae, Doryctinae, Euphorinae, Exothecinae, Helconinae, Homolobinae, Microgasterinae, Opiinae, Orgilinae and Rhyssalinae) and 23 genera and 36 species are recorded. Two new genera and 26 new

species are described: *Bassus magnareola* Belokobylskij, sp. nov.; *Eubazus* ? *brodiei* Belokobylskij, sp. nov.; *E. flavistigma* Belokobylskij, sp. nov.; *E. ? grandareola* Belokobylskij, sp. nov.; *E. ? hooleyi* Belokobylskij, sp. nov.; *E. nanus* Belokobylskij, sp. nov.; *Bembracon acourtsmithi* Belokobylskij, gen. sp. nov.; *B. medialis* Belokobylskij, sp. nov.; *Bracon* ? *antefurcalis* Belokobylskij, sp. nov.; *B. brodiei* Belokobylskij, sp. nov.; *Ascogaster* (*Ascogaster*) *brodiei* Belokobylskij, sp. nov.; *A. (A.) yulei* Belokobylskij, sp. nov.; *A. (A.) pygmaea* Belokobylskij, sp. nov.; *Ontsira cenozoica* Belokobylskij, sp. nov.; *Meteorius applanatus* Belokobylskij, sp. nov.; *M. crassitergum* Belokobylskij, sp. nov.; *Chremylus infuscatus* Belokobylskij, sp. nov.; *Aspicolpus temporalis* Belokobylskij, sp. nov.; *Diospilus curtithorax* Belokobylskij, sp. nov.; *Hellenius* ? *kozlovi* Belokobylskij, sp. nov.; *Homolobus rasnitsyni* Belokobylskij, sp. nov.; *Palaeomicrogaster oculatus* Belokobylskij, gen. sp. nov.; *Semionis wightensis* Belokobylskij, sp. nov.; *Dolopsidea* ? *intermedia* Belokobylskij, sp. nov.; *Oncophanes andrewrossi* Belokobylskij, sp. nov.; and *Rhyssalus bruesi* Belokobylskij, sp. nov. The taxonomic status of *Syntaphus* Donisthorpe, 1920 is reduced to subgeneric level into *Ascogaster* Wesmäl, 1835 (syn. nov.). The genus *Diospiloides* Cockerell, 1921 is a junior synonym of *Microtypus* Ratzeburg, 1848 (syn. nov.). The following new combinations are suggested: *Bassus quadrangularis* (Brues, 1933), *Bracon micrarche* (Cockerell, 1921), *Cyanopterus vectensis* (Cockerell, 1921), *Ascogaster wheeleri* (Donisthorpe, 1920), *Ontsira coleutti* (Cockerell, 1921), *O. distracta* (Cockerell, 1921), *Taphaeus cervicalis* (Cockerell, 1921), *Biosteres peritus* (Cockerell, 1921), and *Microtypus hooleyi* (Cockerell, 1921). The genus *Calypitoides* Cockerell is transferred to the subfamily Helconinae and the genus *Dacnuses* Cockerell to Microgastrinae. A discussion about contents, validity, generic and species combinations in the aforementioned subfamilies is provided.

In Aculeata s.str., other than ants, two new monotypic genera *Palaeopolybia* Antropov, gen. nov. for *P. anglica* (Cockerell, 1921), and *Protopolistes* Antropov, gen. nov. for *O. oblitus* (Cockerell, 1921) are established in Polistinae, and *Sphaerancistrocerus petiolatus* Antropov, gen. sp. nov. is described in Eumeninae (Vespidae). Also described are *Dryophia oculata* Antropov, gen. et sp. nov. (Dryophiinae, Tiphidae) and *Palaeoscolia relicta* Antropov, gen. sp. nov. (Palaeoscolinae Antropov, subfam. nov., Scoliidae), and *Oligobombus cuspidatus* Antropov, gen. et sp. nov. is described in Apinae (Apidae). Protosceliphriini Antropov, trib. nov. and *Protosceliphron* Antropov, gen. nov. are described for *Sceliphron brevior* Cockerell, 1921 in the family Sphecidae. *Tytthopsen nanus* Antropov, gen. et sp. nov. and *Plisomena gigantea* Antropov, gen. et sp. nov. are described in Pemphredoninae (Crabronidae).

The ant (Formicidae) assemblage studied includes 20 species, ten genera, and five subfamilies, of which nine species and two genera are described as new: *Emplastus kozlovi* Dlussky & Perfilieva, sp. nov.; *Leucotaphus donisthorpei* Dlussky & Perfilieva, sp. nov.; *Ponerites hooleyi* Dlussky & Perfilieva, sp. nov.; *P. antropovi* Dlussky & Perfilieva, sp. nov.; *Taphopone macroptera* Dlussky & Perfilieva, sp. nov.; *T. microptera* Dlussky & Perfilieva, sp. nov.; *T. petrosa* Dlussky & Perfilieva, sp. nov.; *T. aberrans* Dlussky & Perfilieva, sp. nov.; *Paraphaenogaster hooleyana* Dlussky & Perfilieva, sp. nov.; *Britaneuretus* Dlussky & Perfilieva, gen. nov.; and *Taphopone* Dlussky & Perfilieva, gen. nov. Nine new combinations are proposed: *Britaneuretus anglicus* (Cockerell, 1915); *Emplastus britannicus* (Cockerell, 1915); *E. hypolithus* (Cockerell, 1915); *E. gurnetensis* (Donisthorpe, 1920); *Campnotus cockerelli* (Donisthorpe, 1920); *Leucotaphus gurnetensis* (Cockerell, 1915); *Ponerites crawleyi* (Donisthorpe, 1920); *Taphopone karaganensis* (Dlussky, 1981); and *Taphopone stauropolitana* (Dlussky, 1981). Ants are the most common hyme-

nopteran family in the Bembridge Marls, differing from other fossil ant assemblages because of the overwhelming dominance of *Oecophylla* weaver ants. Composition of the ant assemblage indicates a warm climate, with temperature permanently above 0°C, and a forested landscape with abundant broad-leaved trees. At a generic level, past ant assemblages have more in common geographically than geochronologically. Also described is *Oxyserphus kozlovi* Kolyada, sp. nov. (Proctotrupidae).

Thus, the assemblage appears to be one of the richest among the rock fossil hymenopteran assemblages, even if it is second to the Florissant assemblage, which has always attracted much more attention, comprising 291 species, 161 genera and 37 families described but largely not yet revised (Meyer 2003). Out of 52 orthotaxonomical genera named in the Bembridge assemblage 18 are extinct (35%). Also extinct are all species, two tribes and three subfamilies. All species but one, two tribes and two subfamilies are endemic to the Bembridge Marls hymenopteran fauna, with one species and one tribe endemic jointly to the Bembridge Marls and the Baltic amber. Aculeate wasps and bees are highly endemic, with all genera and several higher taxa known from no other fossil site, nor from any contemporary fauna. Other groups are less specific in distribution. The assemblage is overwhelmingly dominated by winged ants (84%), an ordinary feature for the Cenozoic since the Eocene (Dlussky & Rasnitsyn 2002). These are followed by Braconidae (5.1%), Ichneumonidae (2.3%), Diapriidae (1.6%) and Scelionidae (0.8%), with the remaining families less than 0.5% each. The braconid dominance over Ichneumonidae is unusual: this is characteristic of assemblages of amber inclusions, primarily because of the generally smaller size of braconids that are more likely to be stuck in resin traps, as compared with the water surface trap that produces rock fossils. In the Cenozoic rock fossil assemblages, ichneumonid wasps are normally either much more common than the braconid ones (in the Paleocene of Tadushi and in the Eocene/Oligocene of Biarno, the Asian analogue of Florissant, both in the Russian far east; and in the Miocene of Stavropol in Ciscaucasian, personal observation by APR), or of roughly similar proportion (in the Eocene of Green River, western N. America, personal observation by APR; and near the the Oligocene/Miocene boundary of Rott in Germany; Statz 1936).

4.2. Palaeoenvironmental inferences

4.2.1. Climate.

Palaeoclimatic inferences from hymenopteran fossils are somewhat contradictory, a usual case for the Paleogene (Archibald & Farrell 2003). Undoubtedly, the climate was warmer than it is now in southern England, as the absence of sawflies suggests, amongst many other indications. However, when looking at the details, we found some fossils of both tropical and warm subtropical affinities (Agaonidae fig pollinators, *Oecophylla* ants, Polybiini wasps), and those implying temperate conditions (at most a warm temperate climate), particularly the majority of Braconidae and several abundant ant taxa (noticeably *Leucotaphus gurnetensis*, which is similar to the genus *Lasius*). This contradiction can be resolved by employing the concept of an equable climate; that is, weakly seasonal even if not very warm, and so suiting both high and low thermophilous taxa (Archibald & Farrell 2003). This reveals another problem, however: the paradigmatic example of equable climate is that exemplified by the Baltic amber biota, which nevertheless includes an appreciable share of animals depending on a seasonable climate, particularly the aphids. The Bembridge Marls biota shows few aphids and not their specific parasites (Aphidiidae) and so better fits the concept of equability.

4.2.2. Landscape. Landscape signals from the Bembridge hymenopterans are also contradictory. The contradiction arises from the observation that some groups indicate a heavily forested territory, and the others imply extensive open meadows (A.J. Ross pers. comm., 2010). The former are primarily ants which are dendrobiotic, forming 60% of the fossil specimens, including those nesting in tree crowns and in tree trunks. 5% live in the forest floor leaf litter, with the remaining ants being mainly eurytopic. Additionally, fig-pollinating Agaonidae indicate the presence of fig trees, and there are several xylobiotic parasitic and aculeate wasps found there (Gasteruptionidae, some Braconidae and Crabronidae). Ichneumonidae recorded are predominantly forest dwellers, and Orthocentrinae are particularly indicative of humid forests. Diapriidae being more abundant than Scelionidae also suggest a forested environment. In contrast, the majority of Braconidae indicate dominance of open meadows, and about a half of aculeate wasps and bees are ground- and not wood-nesting.

4.2.3. Biotic indication. As already mentioned, Agaonidae wasps infer the presence of fig trees. *Oecophylla* ants are closely connected to broadleaf trees, and some Braconidae indicate this type of vegetation. Braconid and, to a lesser extent, ichneumonid wasps imply an abundance of moths, both macro- and particularly microlepidopterans, including leaf miners. This confirms the hypothesis that the rarity of the lepidopterans in the Cenozoic rock fossil assemblages is taphonomically caused, and does not necessarily imply their rarity in the source biocenoses. However, Jarzembowski (1980) described 21 moth taxa from the Bembridge Marls. Parasitic wasps infer the presence of various other insect hosts. Noteworthy is the comparative rarity of xylobiotic hosts and an absence of the aphidiid parasites of aphids, and of Alysiinae, the specialised parasites of higher (calyptrate) flies.

4.2.4. Geography. The majority of the fossils are either non-indicative in respect of large-scale biogeography, or otherwise fit the hypothesis of the predominantly Eurasian (Palaeartic + Oriental) character of the past fauna. This holds particularly true of ants that share more taxa with the Eurasian assemblages of different age (e.g. Miocene ones) than with the Florissant assemblage of similar age in N. America. Alternative indications are uncommon, including Ambositrinae (Diapriidae) which are mainly Australasian and Neotropical now, with one species Nearctic, one Afrotropical and three recorded in the Baltic amber, one being very close to the Afrotropical one. *Oxyserphys* (Proctotrupidae) is also mainly Australian, but known in the Oriental region up to Japan and in Central America as well. *Semionis* (Braconidae) is now restricted to S. Africa. As in many other cases, the “Gondwanan” distribution of the above taxa results most probably from contraction of the wider past distribution (Eskov 2002). As to the unexpectedly high level of endemism of aculeate wasps and bees in the Bembridge assemblage, which concerns all their genera and a few tribes and subfamilies, this effect shows no parallel in other hymenopteran taxa and so should be considered as characteristic of these aculeates themselves, rather than an indication of the isolated position of the source territory. Indeed, there are many genera there in common with the Baltic amber and Florissant, and one species (*Bassus quadrangularis*, Braconidae) and one subfamily (Townesitinae, Ichneumonidae) only occur in the Bembridge and Baltic assemblages.

4.2.5. Geochronology. Hymenopteran evolution is comparatively slow during the Cenozoic, with few higher rank taxa going extinct in that interval, and well dated cases of first appearances are uncommon. That is why the geological time correlation signals from the Cenozoic hymenopterans are rarely conclusive. Yet we have some signals of that sort; first of all, the presence of Townesitinae and the absence of Ichneu-

moninae (Ichneumonidae) from the Bembridge assemblage. Townesitinae is an extinct subfamily characteristic of Baltic amber and the Bembridge fauna and not recorded in younger strata, including the Florissant beds. Alternatively, Ichneumoninae are recorded neither in the Bembridge Marls, nor in the Baltic amber or in any older fossil sites, but they are common in the Florissant beds and also recorded from the Miocene. The same might also hold true of Alysiinae (Braconidae): this group is recorded in number from the Florissant and Miocene deposits, unlike the Bembridge fauna, the Baltic amber and all the older insect sites. However, all records of Alysiinae badly need revision and so should be used carefully. Also, the higher (calyptrate) Diptera, the alysiine hosts, have a generally similar time range. Taken altogether, these observations suggest that the Bembridge Marls might be older than the Florissant.

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