



Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance

*Alexandr P. Rasnitsyn, †Edmund A. Jarzembowski
and ‡Andrew J. Ross

*Palaeontological Institute, Russian Academy of Sciences, Profsoyuznaya Str. 123, 117647, Moscow, Russia

†Maidstone Museum & Art Gallery, St. Faith's St., Maidstone, Kent, ME14 1LH; Postgraduate Research Institute for Sedimentology, University of Reading, PO Box 227, Whiteknights, Reading, RG6 2AB, UK

‡Department of Palaeontology, Natural History Museum, Cromwell Road, London, SW7 5BD; Earth and Environmental Science Research Unit, University of Brighton, BN2 4GJ, UK

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This is the first comprehensive study of the insectan order Vespida (Hymenoptera) in the English non-marine Lower Cretaceous (Purbeck and Wealden strata). The fauna includes diverse sawflies, parasitoid and aculeate wasps but with the exception of social groups. The stratigraphical occurrence and fossiliferous localities are reviewed by AJR. The wasps are revised, described, and keyed out by APR and EAJ who erect 10 new genera and 35 new species: *Undatoma stigmatica* sp. nov., *U. rudgwickensis* sp. nov., *U. bicolor* sp. nov. (Xyelotomidae); *Trematothorax clementsi* sp. nov., *T. valdensis* sp. nov. (Sepulcidae); *Eosyntexis tuffinae* sp. nov. (Anaxyelidae); *Turgonalus cooperi* sp. nov. (Trigonalidae); *Arossia joyceae* gen. et sp. nov. (Stephanoidea); *Manlaya oculatissima* sp. nov., *M. anglica* sp. nov., *M. ockleyensis* sp. nov., *M. capelensis* sp. nov. (Gasteruptiidae); *Tillywhimia spectra* gen. et sp. nov., *T. colorata* sp. nov. (?Gasteruptiidae); *Cretevania concordia* sp. nov. (Cretevaniidae); *Dintonia despectata* gen. et sp. nov., *Pallenites calcarius* gen. et sp. nov., *Peverella punctata* sp. nov. (Proctotrupidae); *Coramia minuta* gen. et sp. nov. (Diapriidae); *Amitchellia procera* gen. et sp. nov., *A. brevis* sp. nov. (Proctotrupoidea); *Purichneumon britannicus* gen. et sp. nov. (Eoichneumonidae); *Bethylonymellus feltoni* sp. nov. (Bethylonymidae); *Archisphex proximus* sp. nov., *A. curvus* sp. nov., *Angarosphex consensus* sp. nov., *A. bleachi* sp. nov., *Pompilopterus corpus* sp. nov., *P. wimbledonii* sp. nov., *P. keymerensis* sp. nov., ?*P. worssami* sp. nov., ?*P. leei* sp. nov., ?*P. difficilis* sp. nov., *Ivestia provecta* gen. et sp. nov. (Sphecidae); *Apocritites distinctus* gen. et sp. nov. (Apocrita). Taxonomic changes include *Prosyntexis gobiensis* (Rasnitsyn 1993) comb. nov. and *Prosyntexis okhotensis* (Rasnitsyn 1993) comb. nov. (Sepulcidae); *Angarosphex* Rasnitsyn 1975 = *Shandongodes* Zhang 1985 syn. nov. (Sphecidae); *Archisphex* Evans 1969 = *Cretosphex* Rasnitsyn 1975, = *Mateosphex* Zhang 1985, = *Palaeapis* Hong 1984 syn. nov. (Sphecidae). The Purbeck fauna is more diverse generically and contains a greater number of endemics than the Wealden fauna. The absence of xyelids from the Purbeck and Wealden is consistent with a warm climate. Late Mesozoic vespidan faunas are compared globally (especially with eastern Asia), and four Jurassic-Cretaceous assemblages are recognised: an ephialtitid-praeaulacine or aculeate-free Jurassic type; a Lower Cretaceous baissine type with earlier proctotrupid and later angarosphecine subtypes; an Upper Cretaceous armaniid type. The Purbeck-Wealden fauna is baissine with two Jurassic 'survivors' but lacks social groups; both assemblage subtypes are represented but the influx of aculeate wasps is accompanied by reduced endemism and generic diversity possibly indicative of ecological change in the hinterland.

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KEY WORDS: Vespida; Hymenoptera; wasps; Purbeck; Wealden; new genera and species; Cretaceous and Jurassic assemblages.

1. Introduction

The Vespida (Hymenoptera) are an abundant, ubiquitous, highly specialised and successful order of insects totalling some 130,000 living species. They include

familiar forms such as sawflies, wasps, bees and ants, although only the former two concern us here. They are traditionally divided into two suborders: Siricina (Symphyta) and Vespina (Apocrita), the latter comprising some 90% of all species. The Vespina is further divided into 'Parasitica' and Aculeata, the former division really comprising parasitoids, whereas the latter includes the most advanced vespids such as ants, bees, and social wasps.

Wasps and their relatives are uncommon insects in the Lower Cretaceous of southern England and only four species have been described previously, one from the Purbeck Limestone Group of Dorset (Westwood, 1854) and three from the Wealden Supergroup of the Weald (Evans, 1969; Jarzembowski, 1991b). Sustained collecting at the Clockhouse Rock Store, organized previously by AJR, and separately on the Dorset coast by Mr R. Coram, has resulted in the recovery of a diverse vespidan (hymenopteran) fauna from the Lower Weald Clay and Lulworth and Durlston formations respectively. In addition to this and other new material, some older finds discussed in Jarzembowski (1987) and from the Rev. P. B. Brodie's collection at the Natural History Museum, London, are included.

As a result, 35 new species and 10 new genera are established herein in at least 11 families belonging to both suborders. It may be noted that the Purbeck/Wealden vespidan fauna comprises sawflies and parasitoid and aculeate wasps, but no ants (Formicoidea) and bees (Apoidea s.s.). No doubt further new taxa await discovery.

Our increased knowledge of the English fauna allows useful comparison with other late Mesozoic faunas, especially in eastern Asia (see below). On a wider scale, the late Mesozoic faunal turnover enables us to define three global assemblage types, one of which is represented by its two subtypes in the Purbeck and Wealden respectively (*q.v.*). Furthermore, the ascendancy of the sphecids wasps in the Wealden may have coevolutionary implications for seed plants because it is broadly agreed that sphecids lie in the ancestry of bees.

2. Stratigraphy [AJR]

2.1. Lithostratigraphy

The Vespida were collected from the non-marine Purbeck Limestone Group and Wealden Supergroup of southern England. The Purbeck Limestone Group reaches a maximum thickness of approximately 120 m in the type area in Dorset. It consists of limestones, shales, clays and evaporites, and is subdivided into two formations, the Lulworth Formation below and the Durlston Formation above (Clements, 1992). Previously, it had also been split into three informal divisions (lower, middle and upper). The formations are further subdivided into 5 members and 15 groups of beds. The lithostratigraphy is shown in Figure 1 based on information from Clements (1992) and Westhead & Mather (1996).

The Wealden Supergroup reaches a maximum thickness of about 1200 m in the type area of the Weald. It is subdivided into two groups, the Hastings Beds and the overlying Weald Clay Group above. The Hastings Beds consist of sandstones, silts, shales and clays, and are subdivided into the Ashdown, Wadhurst Clay, Lower and Upper Tunbridge Wells Sand, and the Grinstead Clay formations. The Weald Clay Group consists of silty clays with minor sandstone and limestone beds, and is subdivided into lower and upper

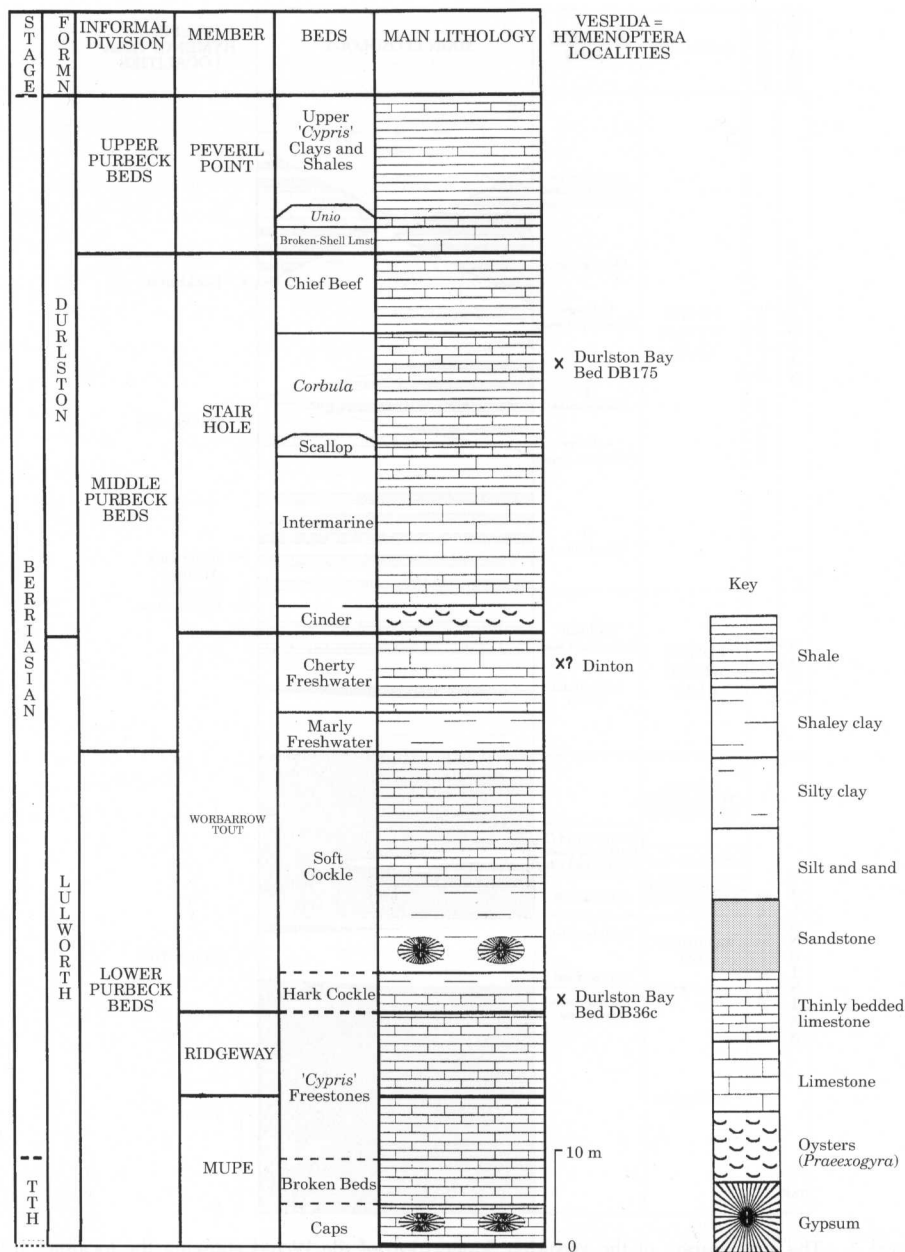


Figure 1. The stratigraphy of the Purbeck Limestone Group of Durlston Bay, Dorset, showing the localities and horizons where *Vespida* (Hymenoptera) have been found. Key also applies to Figure 2.

formations. Various sandstone and limestone beds within the sequence have been given names and/or numbers. The lithostratigraphy of this supergroup is shown in Figure 2 based on information from Gallois & Worssam (1993); Bristow & Bazley (1972); Thurrell *et al.* (1968) and calculations made from British Geological Survey (BGS) Sheet 301 (Haslemere).

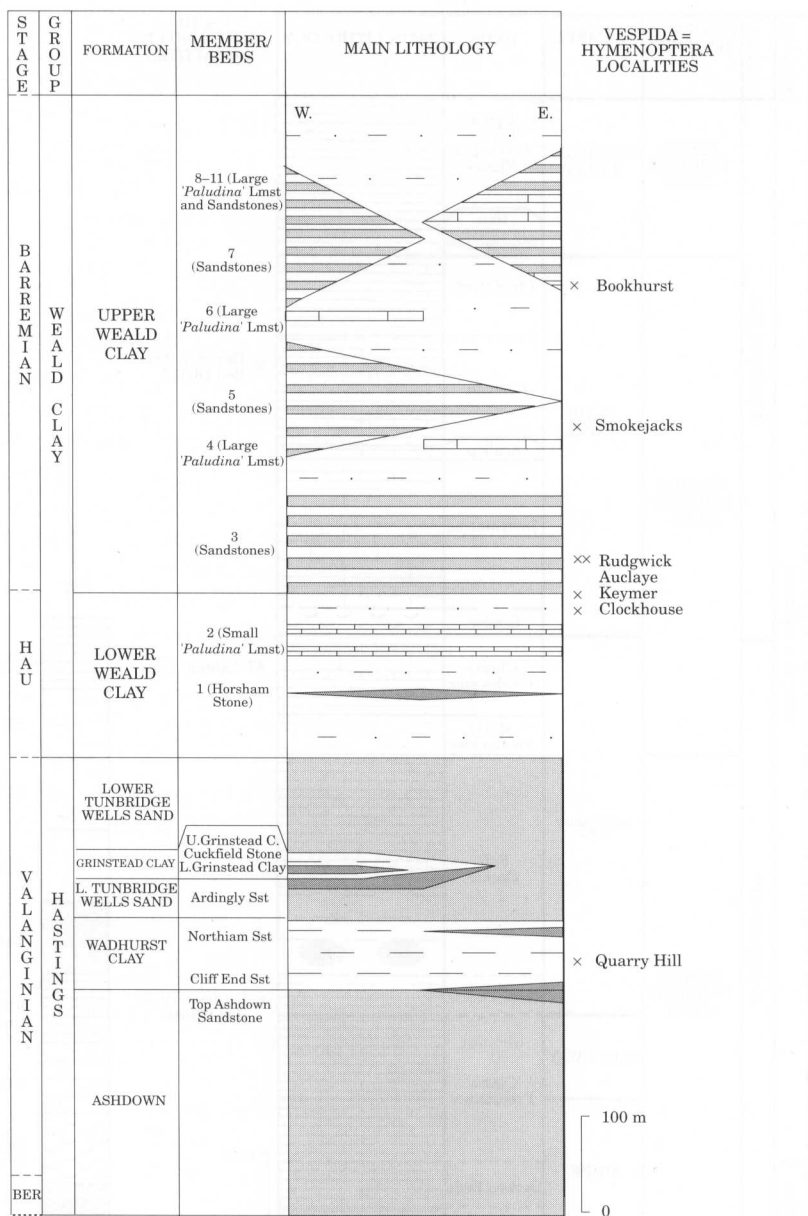


Figure 2. The stratigraphy of the Wealden Supergroup of the Weald showing the localities (pits) where *Vespida* have been found. Sst = Sandstone, Lmst = Limestone. For key, see Figure 1. BER = Berriasian; HAU = Hauterivian; C = clay; U., L. = Upper, Lower.

2.2. Biostratigraphy

The biostratigraphy of the Purbeck and Wealden is based on ostracods, consisting of zones, assemblages and faunicycles (Anderson, 1985, modified by Clements, 1992, and Horne, 1995). Unfortunately, Anderson (1985) only indicated exactly where these occur within four boreholes which are often difficult to correlate with the lithostratigraphy elsewhere.

The stratigraphy of the Weald Clay of Surrey is shown in more detail in Ross (1996). However, Anderson (in Thurrell *et al.*, 1968, p. 30) indicated that the

base of the *Cypridea valdensis* (ostracod) Zone occurs 4 m above a bed of Large 'Paludina' Limestone (BGS Bed 8a) at Bookhurst Tileworks, Surrey, and that the clays exposed at Northchapel, West Sussex lie within the *C. valdensis* Zone. BGS Beds 7c, 7e and 7f are exposed at Northchapel [BGS Sheet 301 (Haslemere), National Grid Reference TQ 95 29]; therefore it is likely that Bed 8a was deposited before Bed 7c! This means that figure 11 in Ross (1996), figure 2 in Ross & Cook (1995) and figure 2 in Thurrell *et al.* (1968) are incorrect. It seems probable that beds 8-11 are faulted sections of beds 6 and 7.

Chronostratigraphy

Recently there has been much discussion on the position of the Lower Cretaceous stage boundaries within the Purbeck and Wealden successions. This has come about due to various attempts to correlate these non-marine sequences with the marine Tethyan and Boreal realms. The Jurassic/Cretaceous (Tithonian/Berriasian) boundary was traditionally considered to lie at the base of the Cinder Member as this marked a marine transgression (Melville & Freshney, 1982). Later, on the basis of palynomorphs, it was suggested that it lay just above the base of the 'Cypris' Freestones (Hunt, 1987). This is supported by charophyte evidence which suggests that the boundary occurs near the base of this member (Feist *et al.*, 1995). Allen & Wimbledon (1991) indicated that the boundary lies right at the base of the Purbeck also using palynomorphs, whereas Ogg *et al.* (1994) suggested that it occurs between the lower 'Cypris' Freestones and the base of the Cinder Member based on magnetostratigraphy. Here we have followed Feist *et al.* (1995).

The Berriasian/Valanginian boundary was considered to lie at the very top of the Purbeck Limestone Group based on palynomorphs (Allen & Wimbledon, 1991). However Ogg *et al.* (1994) suggested that it occurs just below the top based on magnetostratigraphy. Here we have followed Allen & Wimbledon (1991). The top of the Purbeck Limestone Group of Dorset is also the top of the *Cypridea setina* Zone (Clements, 1992) which occurs at a depth of 184 m in the Fairlight borehole, East Sussex (Lake & Shephard-Thorn, 1987). This borehole passed through the Ashdown Formation from 7.52-219.15 m which means that the Berriasian/Valanginian boundary lies at about 35 m above the base of this formation.

The Valanginian/Hauterivian boundary was considered to lie at the boundary between the Upper Tunbridge Wells Sand and the Lower Weald Clay based on palynomorphs and ostracods (Worssam, 1978). This view is still accepted (Allen & Wimbledon, 1991).

The Hauterivian/Barremian boundary is considered to lie at a depth of about 432m in the Warlingham borehole based on palynomorphs (Hughes & McDougall, 1990). This is considered to correlate with the base of BGS Bed 3a in Surrey (Ross & Cook, 1995) and the top of a red clay in the Ripe borehole which lies just below BGS Bed 3c2 in East Sussex (Cook & Ross, 1996). The base of BGS Bed 3a marks the Lower/Upper Weald Clay boundary which had been incorrectly placed in the past owing to confusion over BGS and Topley (1875) bed numbers (Ross & Cook, 1995; Horne, 1995).

The Barremian/Aptian boundary was traditionally considered to lie at the top of the Upper Weald Clay (Worssam, 1978). Kerth & Hailwood (1988) suggested that it lay 20-25 m below the top of the Vectis Formation on the Isle of Wight using the base of the M0 magnetostratigraphy chron. The same ostracod species

occur in the Vectis Formation and at the top of the Upper Weald Clay (Anderson, 1985), but where they occur in the lithostratigraphy in relation to the base of the M0 chron is uncertain. Here we have followed Worssam (1978).

3. *Vespida* localities

3.1. *Durlston Bay, Swanage, Dorset [SZ 035 780]*

This long coastal exposure is the type section of the Purbeck Limestone Group (Clements, 1992). Fossil insects have been recovered from several horizons in the Hard and Soft Cockle beds (Lulworth Formation: Worbarrow Tout Member) and *Corbula* beds (Durlston Formation: Stair Hole Member); however *Vespida* have only been found *in situ* in beds DB36c (Hard Cockle beds) and DB175 (*Corbula* beds). The wasp specimens from this locality in the Natural History Museum (NHM) are preserved in a white fine-grained limestone which is the typical lithology of the insect-bearing horizons of the Soft Cockle beds. Therefore it is very likely that the specimens came from the Worbarrow Tout Member. The insect-bearing horizons in the *Corbula* beds are, by contrast, grey in colour. The Hard and Soft Cockle beds are considered to be early Berriasian in age and the *Corbula* beds are believed to be late Berriasian in age.

3.2. *Dinton, Vale of Wardour, Wiltshire [SU 015 315]*

A disused quarry near this village was where Brodie (1845) found most of the 'Wealden' insects that he figured in his book. Most of the insects came from a hard limestone which he called the Insect Limestone. Unfortunately the quarry was full of water when Brodie measured a section. However, he did refer to the Insect Limestone as lying below a thin bed containing oysters. An excavation has revealed that the Insect Limestone probably lies below the Cinder Member (Ross & Jarzembowski, 1996), and it is probable that the bed with oysters that Brodie recorded forms part of this member. The Insect Limestone probably correlates with part of the Cherty Freshwater beds (Lulworth Formation: Worbarrow Tout Member) and is considered Middle Berriasian in age.

3.3. *Quarry Hill Brickworks, Tonbridge, Kent [TQ 585 450]*

This quarry (now filled in and built on) was the site where Crowson found about a hundred insect fossils in the first half of this century (Crowson, 1946). The insects came from a fine-grained calcareous siltstone. The beds formerly exposed in the quarry belong to the middle of the Wadhurst Clay (Bristow & Bazley, 1972). The fossil insects from here are mid Valanginian in age.

3.4. *Keymer Tileworks, Burgess Hill, West Sussex [TQ 323 193]*

Several hundred insect fossils have been collected from this active quarry during the last few years (Cook & Ross, 1996). The insects came from sideritic and phosphatic mudstone and siltstone lenses and clay from the top of the Lower Weald Clay, just below BGS Bed 3a. They are late Hauterivian in age.

3.5. *Clockhouse Brickworks, Capel, Surrey [TQ 173 386]*

This active quarry and neighbouring disused pits have yielded thousands of insect remains during the last two decades (Jarzembowski, 1991a; Ross, 1996). They occur in siltstone and fine-grained sandstone lenses from near the top of the Lower Weald Clay between the Clockhouse Sandstone and the *Cassiope* Band

(see Worssam, 1978). The Clockhouse Sandstone (often referred to as BGS Bed 3) is a thin bed that lies below BGS Bed 3a. It is excluded from bed 3 in Figure 2 because it differs considerably in lithology from the other sandstones of Bed 3 (a-e) and should be regarded separately. Recently this site became a SSSI and rock was moved from the base of the disused pit to the top, prior to land-fill. The resulting rock pile is known as the Clockhouse Rock Store. The fossil insects from here are late Hauterivian in age.

3.6. *Auclaye Brickworks, Capel, Surrey [TQ 169 389]*

This disused quarry has yielded several hundred insect fossils, mainly collected during the 1980s (Jarzembowski, 1991a). They are preserved in phosphatic mudstone nodules from near the base of the Upper Weald Clay between BGS Beds 3a and 3c (3b does not occur in this area). The fossil insects from here are early Barremian in age.

3.7. *Rudgwick Brickworks, Rudgwick, West Sussex [TQ 083 343]*

Several hundred insect fossils have been collected from this active quarry during the last few years. They occur in phosphatic mudstone nodules and sideritic siltstone and mudstone lenses from near the base of the Upper Weald Clay between BGS Beds 3a and 3c (3b does not occur in this area). This site lies in a similar stratigraphical position to the previous one but there is uncertainty as to whether the insect-bearing phosphate horizons are at the same level or lie above or below those at Auclaye. The insects are early Barremian in age.

3.8. *Smokejacks Brickworks, Ockley, Surrey [TQ 113 373]*

This active quarry has yielded hundreds of insect fossils over the last two decades. They occur in sideritic siltstone and mudstone lenses below BGS Bed 5c (Ross & Cook, 1995) and are early Barremian in age.

3.9. *Bookhurst Tileworks, Cranleigh, Surrey [TQ 076 395]*

About 100 fossil insects have been collected from this small, active quarry during the last few years. They came from a buff siltstone (bed 10 of the section in Thurrell *et al.*, 1968, p. 56) that lies 3 m above a bed of Large 'Paludina' Limestone (BGS Bed 8a) (Ross, 1996). The fossil insects from here are late Barremian in age.

4. Systematic part [APR & EAJ]

The descriptions below follow the system used in the descriptive publications by APR. Morphological terms, including the vein and cell abbreviations (Figures 4, 13) are conventional. The specimen depositories are specified using the following abbreviations: NHM - Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD; BMB - Booth Museum of Natural History, 194 Dyke Road, Brighton BN1 5AA; MCZ - Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA. Reference is also made to PIN - Palaeontological Institute of the Russian Academy of Sciences.

Class Insecta Linné 1758

Order Vespida Laicharting 1781 (=Hymenoptera Linné 1758)

Suborder Siricina Billbergh 1820 (Latreille 1802) (=Symphyta Gerstaecker 1867)

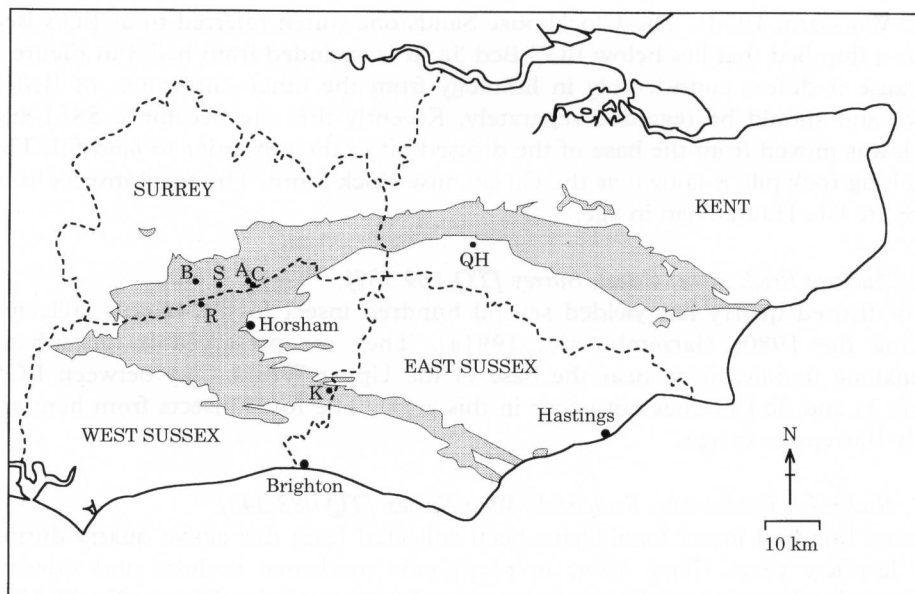


Figure 3. Map of south-east England showing the outcrop of the Weald Clay Group (stippled), county boundaries (dashed), towns and Vespida (Hymenoptera) localities (QH = Quarry Hill Brickworks, K = Keymer Tileworks, C = Clockhouse Brickworks, A = Auclaye Brickworks, R = Rudgwick Brickworks, S = Smokejacks Brickworks, B = Bookhurst Tileworks).

Superfamily Tenthredinoidea Latreille 1802

Family Xyelotomidae Rasnitsyn 1968

Genus *Undatoma* Rasnitsyn 1977

Type species. *Undatoma dahurica* Rasnitsyn 1977.

Diagnosis. This genus differs from others in the family in having cell 1mcu elongate postero-basally so that the 1st abscissa of M is subequal to or longer than the anterior (upper) side of the cell.

Included species. In addition to the type species from the Upper Jurassic/Lower Cretaceous of Transbaikalia and the species described below, there are undescribed species from the Upper Jurassic/Lower Cretaceous of River Kempendiay (Aldan Basin, Yakutia) and Khutel-Khara in east Mongolia, as well as from the Upper Jurassic of central Mongolia at Khoutiyn-Khotgor. Attributed tentatively to the genus are the poorly known *U. taksha* Rasnitsyn 1990 and *U. undurgensis* Rasnitsyn 1990 from the Lower Cretaceous of Transbaikalia. For descriptions of Asian species, see Rasnitsyn (1990a).

Undatoma rudgwickensis Rasnitsyn et Jarzembowski sp. nov.

Figure 4

Etymology. The species is named after its type locality.

Holotype. BMB 018502/-3 (part and counterpart); from between Beds 3a and 3c, Upper Weald Clay; Rudgwick Brickworks, Rudgwick, West Sussex; Lower Barremian; collected by Mr Morris Zdrzalek.

Diagnosis. Differs from all other species in reduced 1st abscissa of RS, short 1r, strong bend of M at 1m-cu, and, where known, light-coloured body; from described Asian species in well-developed SC, acute 3r, 2r-rs beyond pterostigmal

apex, short 3rm, and proximal position of cu-a; from species described below in oblique SC and black pterostigma.

Description. The unique type consists of an incomplete impression of the body lacking head, hindwings and abdominal tip. Forewing with C thin throughout; SC strong, oblique; pterostigma short; 1st abscissa of RS almost nonexistent (M joining RS at its very base); cell 1r short; 2r-rs, 3r and 3rm as in species below; RS + M extending to midlength of anterior side of 1mcu; M strongly angled at 1m-cu; 2m-cu meeting M near base of 3rm; cu-a meeting Cu near middle of 1mcu; body light, veins and pterostigma dark coloured.

Measurements. Preserved body length about 5 mm; forewing length 5.6 mm.

Undatoma stigmatica Rasnitsyn et Jarzembowski sp. nov.

Figure 5

Etymology. The name refers to distinct pigmentation of pterostigma.

Holotype. BMB 020499/-500 (part and counterpart); Clements' Bed DB175, Corbula beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Diagnosis. Differs from all other species in pterostigmal colour pattern; also from described Asian species in presence of well developed SC, acute 3r, 2r-rs beyond pterostigmal apex and in short 3rm; from Wealden species described here in subvertical SC.

Description. The unique type consists of the incomplete impression of a body, with the left pair of wings, antennal segment 3 and a hind(?) leg preserved. 3rd antennal segment long, ovoid, 0.8 as long as width of head. Head of normal width. Prescutum, scutellum and metanotum coarsely punctate with pits wider than interspaces. Hind(?) leg short, weak. Forewing with C thin throughout its length, SC forming a strong subvertical crossvein; pterostigma short; 1st abscissa of RS short but distinct, cell 1r elongate, 3r acute (as apical abscissa of RS is virtually straight) and about as long as 1r and 2rm combined; 2r-rs removed from apex of pterostigma by 0.6 of its length and is close to 2r-m; M is not angled by

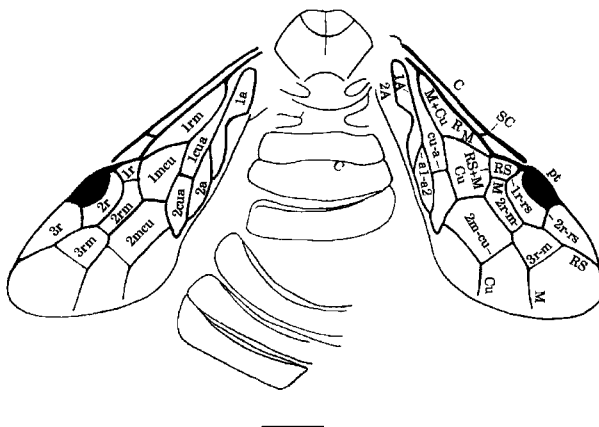


Figure 4. *Undatoma rudgwickensis* sp. nov., holotype BMB 018502/-3; Rudgwick Brickworks, Lower Barremian. Abbreviations here and elsewhere: C, SC, R, RS, M, Cu, A - longitudinal veins; 1r-rs, 2r-rs, 2r-m, 3r-m, 1m-cu, 2m-cu, cu-a, al-a2 - crossveins; 1r, 2r, 3r, 1rm, 2rm, 3rm, 1mcu, 2mcu, 1cua, 2cua, 1a, 2a - cells; pt - pterostigma. Scale bar here and elsewhere: 1 mm.

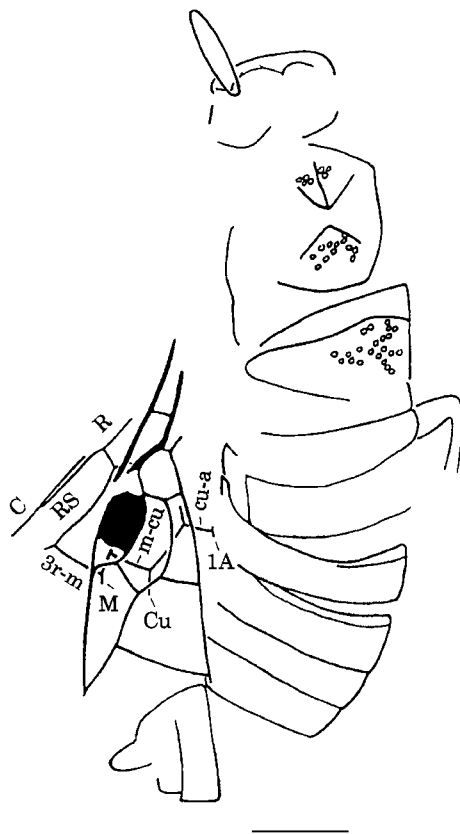


Figure 5. *Undatoma stigmatica* sp. nov., holotype BMB 020499/-500. Durlston Bay, Upper Berriasian.

1m-cu, cell 3rm with apical and posterior sides of equal length. Hindwing with 1st abscissa of RS long (possibly subequal to 1r-m); 2+3rm short (shorter than 3r in forewing), m-cu removed from 3r-m by about 0.5 of its length; cu-a removed from m-cu almost by twice its length. Abdominal terga lack coarse sculpture, shining weakly and probably coriaceous. Saw sheath short and narrow, slightly extending beyond the apex of the abdomen. The ground colour is dark, the preserved legs, pterostigmal base and apex appearing light.

Measurements. Body length *c.* 7.5 mm; forewing length about 5.0–5.5 mm.

Undatoma bicolor Rasnitsyn et Jarzembowski sp. nov.

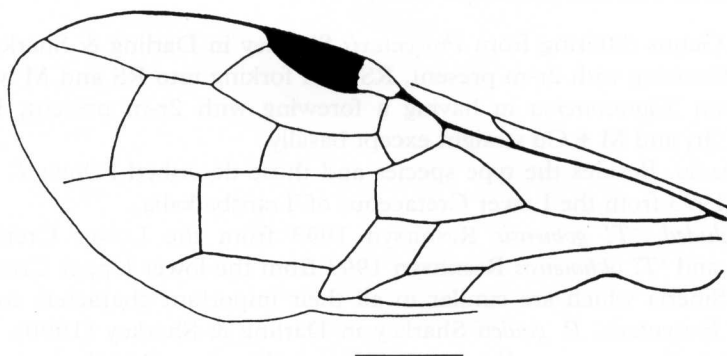
Figure 6

Etymology. The species epithet is Latin for ‘two-coloured’, referring to colour of pterostigma.

Holotype. BMB 018500/-1 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; Clockhouse Rock Store, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by Mr G. Bleach.

Diagnosis. Differs from all known species (except possibly *U. taksha*) in having a long pterostigma which is dark except basally. Similar to English but differing

A



B

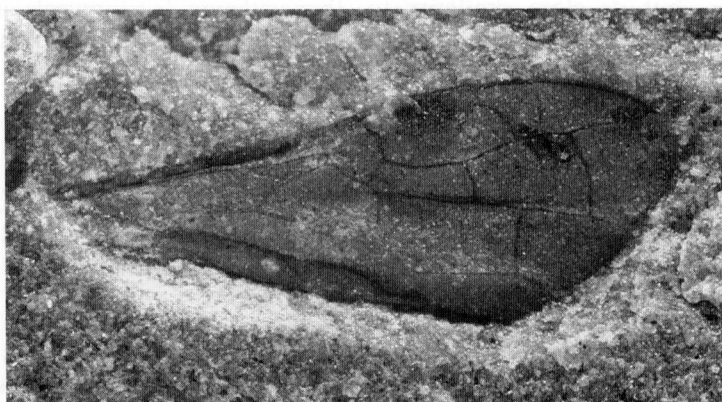


Figure 6. A, B. *Undatoma bicolor* sp. nov., holotype BMB 018500/-1, B, $\times 12$; Clockhouse Brickworks, Upper Hauterivian.

from Asian species in having SC well developed, and cu-a joining cell 1mcu submedially; differing from English species in having cells 3r and 3rm long, from *U. stigmatica* in possessing an oblique SC, and from *U. rudgwickensis* in having a longer cell 1r and RS + M and 2m-cu meeting 3rm submedially.

Description. The unique type consists of a forewing impression. Forewing with C thin throughout; SC strong, oblique, pterostigma long with 2r-rs separating almost apically; 1st abscissa of RS distinct; cell 1r about as long as wide; cell 3r subacute (RS somewhat sinuate subapically though distinctly less so than in *U. dahurica*) and much longer than 1r and 2rm combined, RS + M extending far beyond midlength of upper side of cell 1mcu; M not angled at 1 m-cu; 2r-m almost equidistant between 1r-rs and 2r-rs; cell 3rm long, receiving 2m-cu submedially; cu-a slightly beyond the midlength of cell 1mcu; pterostigma dark with light base.

Measurements. Forewing length 6.6 mm.

Superfamily Cephoidea Newman 1834

Family Sepulcidae Rasnitsyn 1968

Subfamily Trematothoracinae Rasnitsyn 1988

Genus *Trematothorax* Rasnitsyn 1988 (*sensu stricto*)

Type species. *T. baissensis* Rasnitsyn 1988.

Diagnosis. Genus differing from *Prosyntexis* Sharkey in Darling & Sharkey (1990) in having forewing with 2r-m present, RS + M forking into RS and M well before 1m-cu; from *Thoracotrema* in having a forewing with 2r-m present, R tubular within cell 3r, and M + Cu straight except basally.

Included species. Besides the type species and those described below: *T. ingodensis* Rasnitsyn 1993 from the Lower Cretaceous of Transbaikalia.

Species excluded. '*T. gobiensis* Rasnitsyn 1993 from the Lower Cretaceous of Mongolia, and '*T. okhotensis* Rasnitsyn 1993 from the lower Upper Cretaceous of northeast Siberia which are similar in all their important characters to the type species of *Prosyntexis*, *P. gouleti* Sharkey in Darling & Sharkey (1990). They are transferred to that genus as *Prosyntexis gobiensis* (Rasnitsyn 1993) comb. nov. and *Prosyntexis okhotensis* (Rasnitsyn 1993) comb. nov. *Prosyntexis* has been placed in Anaxyelidae, but its close similarity to *Trematothorax* (s.s.) reveals its correct position within Trematothoracinae (for the taxonomy of the subfamily, see Rasnitsyn, 1993a).

Trematothorax clements Rasnitsyn et Jarzembowski sp. nov.

Figure 7

Etymology. Species is named after Purbeck stratigrapher Dr R. Clements.

Holotype. BMB 020501/-2 (part and counterpart); Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Diagnosis. Species differing from all known species in a high 1mcu; differing from *T. baissensis* and *T. ingodensis* in medial position of 2r-rs at pterostigma, in intermediate position of 2r-m in relation to 2m-cu, and in C and R close to each other basally; differing from *T. baissensis* in simple basal bend of M + Cu and in rounded, wide apex of hindwing anal cell.

Description. The unique type consists of the incomplete impression of a head, thorax, forewing, fragment of hindwing and a hindleg. Antennal scape moderately short, slightly longer than wide. Body features difficult to interpret. Hind leg moderately small and weak. Forewing with C and R close to each other in their basal halves; 2r-rs at midlength of pterostigma; 2r-m distant from 2m-cu at half of its own length; pterostigmal apex nearly equidistant between 2r-rs and apex of cell 3r; M + Cu only bent (not sinuate) basally; cell 1mcu high with cu-a well before middle. Hindwing with anal cell broadly rounded apically. Colour (as preserved) light, head and thorax in part somewhat darkened.

Measurements. Forewing length 6.5 mm.

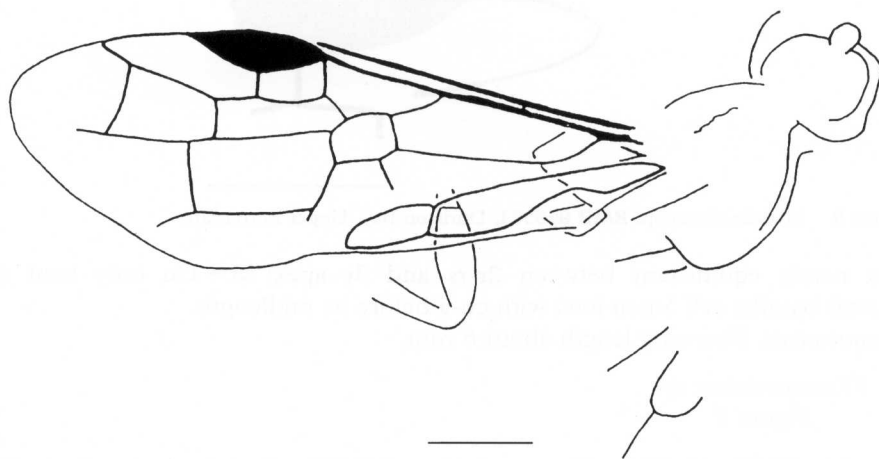
Trematothorax valdensis Rasnitsyn et Jarzembowski sp. nov.

Figure 8

Etymology. Species is named after the Weald.

Holotype. BMB 018531/018499 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; old pit, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. A. Jarzembowski.

A



B

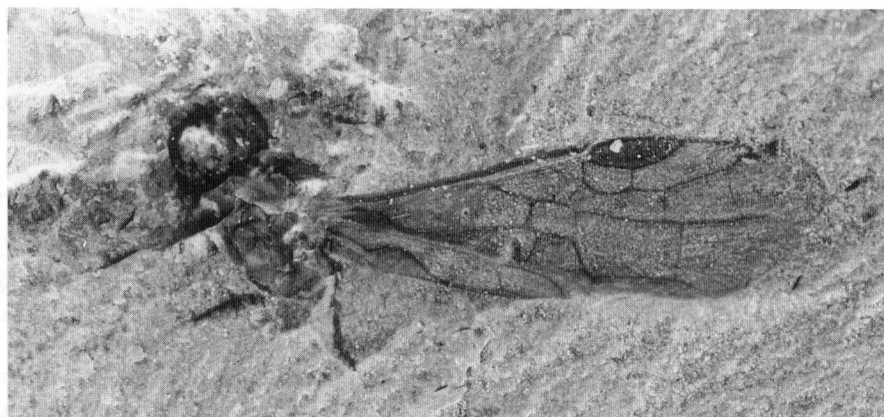


Figure 7. A, B. *Trematothorax clements* sp. nov., holotype BMB 020501/-2, B, $\times 12$; Durlston Bay, Upper Berriasian.

Diagnosis. Similar to above species except for low cell 1mcu and distant position of 2m-cu.

Description. The unique type consists of the impression of an incomplete forewing. Forewing with C and R close to each other in their basal halves; 2r-rs at pterostigmal midlength; 2r-m distant from 2m-cu by its own length; pterostigmal

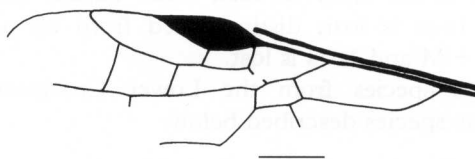


Figure 8. *Trematothorax valdensis* sp. nov., holotype BMB 018531; Clockhouse Brickworks, Upper Hauterivian.



Figure 9. ?*Trematothorax* sp. BMB 020503; Durlston Bay, Upper Berriasian.

apex nearly equidistant between 2r-rs and 3r apex; M + Cu only bent (not sinuate) basally; cell 1mcu low, with cu-a before its midlength.

Measurements. Forewing length about 6 mm.

?*Trematothorax* sp.

Figure 9

Material. BMB 020503; Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Description. The unique specimen consists of the impression of an apical part of the forewing. Forewing with pterostigma issuing 2r-m subbasally and with apex much closer to 3r apex than to 2r-rs; 2r-m situated at level not beyond apical one third of pterostigma.

Measurements. Length of fragment, 2.0 mm; possible full forewing length *c.* 6 mm.

Remarks. The fragment is too small to be identified with certainty, but the general appearance especially the very short cell 3r and large pterostigma with basally located 2r-rs are suggestive of Trematothoracinae. Within the subfamily, the tubular R and well-developed 2r-m points to *Trematothorax*, whereas the very short 3r combined with the proximal position of both 2r-rs and 2r-m distinguish the fossil from all other known species, whilst coming closest to *T. ingodensis*.

Superfamily Siricoidea Billbergh 1820 (Latreille 1802)

Family Anaxyelidae Martynov 1925

Subfamily Syntexinae Benson 1935

Genus *Eosyntexis* Rasnitsyn 1990

Type species. *E. senilis* Rasnitsyn 1990.

Diagnosis. Differs from *Syntexis* Rohwer 1915, the only other genus in the subfamily, in C and R are close to each other basally (unknown in the new species below) and 1r-rs is lost; distinguished from all other Anaxyelidae in possessing a long RS + M and 1r-rs is lost.

Included species. Type species from the Lower Cretaceous (Neocomian) of Transbaikalia, and one species described below.

Eosyntexis tuffinae Rasnitsyn et Jarzembowski sp. nov.

Figure 10

Etymology. The species is named after the collector.

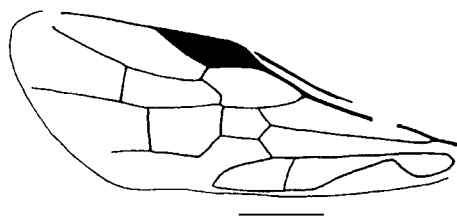


Figure 10. *Eosyntexis tuffinae* sp. nov., holotype BMB 020504; Durlston Bay, Lower Berriasian.

Holotype. BMB 020504; Bed DB36c, Hard Cockle beds, Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by Ms H. Tuffin.

Diagnosis. Species differing from the type species in possessing a large pterostigma, long 1st abscissa of RS, and basal position of 3r-m and 2m-cu.

Description. The unique type consists of the impression of a forewing. Pterostigma very large, joining 2r-rs submedially; 1st abscissa of RS more than twice as long as that of M; 3r-m closer to 2r-rs than to apex of cell 3r; cells 2 + 3rm and 2mcu short (2m-cu about level of pterostigmal apex).

Measurements. Forewing length 5.5 mm.

Family Siricidae Billbergh 1820 (Latreille 1802)

Subfamily Myrmiciinae Maa 1947 (Handlirsch 1906)

Genus *Myrmicium* Westwood 1854

Type species. *Myrmicium heerii* Westwood 1854.

Diagnosis. Genus differing from all other Siricidae and most probably from all other hymenopterans in possessing a corrugated wing membrane within the majority of the cells but similar to *Shurabisca* Rasnitsyn 1968 in that crossveins 2-3r-m and 2m-cu are lost. This was the only reason for assigning the two genera to Myrmiciinae (Rasnitsyn 1969) but that taxonomic decision is only provisional. Two more genera have been previously attributed to this subfamily (*loc. cit.*) from the Eocene: *Formicium* Westwood 1854 and *Megapterites* Cockerell 1920 which are now considered to be giant ants (Lutz, 1986).

Included species. Besides the type species from the English Purbeck, the dustbin species *Myrmicium schroeteri* (Germar 1839) *sensu* Maa (1947) is included from the Solnhofen Limestone (Tithonian of Bavaria), which probably comprises several species which are difficult to separate due to the poor preservation of most specimens. Some of the latter, particularly the holotype of *Belostomum elongatum* Germar 1839 (Oppenheim 1885, fig. 12), and specimen no. 5189 in the Carnegie Museum, New York (Carpenter, 1932, fig. 10) show crossvein r-m and weak or lost corrugation and can hardly be conspecific with *Myrmicium schroeteri*.

Myrmicium heerii Westwood 1854

Figure 11

1854 *Myrmicium heerii*: Westwood, p.396, pl. 18, fig. 21

1856 *Myrmica heerii*: Giebel, p. 178

1879 *Myrmica heerii*: Goss, p. 139

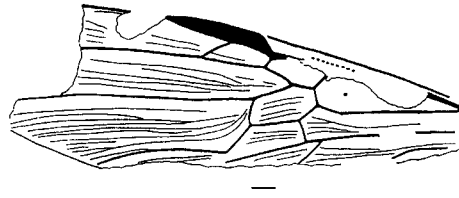


Figure 11. *Myrmicium heeri* Westwood, holotype NHM I. 3990; Durlston Bay, Lower Berriasian.

- 1885 *Myrmicium heeri*: Zittel, p. 815
 1886 *Myrmicium heeri*: Scudder, p. 97
 1891 *Myrmicium heeri*: Scudder, p. 231
 1895 *Myrmicium heeri*: Woodward, p. 390
 1906–08 *Pseudosirex heeri*: Handlirsch, p. 577, pl. 46, fig. 24
 1920 *Myrmicium heeri*: Donisthorpe, p. 81
 1939 *Pseudosirex heeri*: Handlirsch, p. 158
 1968 *Myrmicium heeri*: Rasnitsyn, p. 190
 1969 *Myrmicium heeri*: Rasnitsyn, p. 13, 17, 75, fig. 121
 1993 *Myrmicium heeri*: Jarzembowski, p. 179, fig. 6.

Holotype NHM I.3990; Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by the Rev. P. B. Brodie.

Diagnosis. Differs from *M. schroeteri* (judging from better preserved and more typical specimens of that species) in possessing a large pterostigma, 1st abscissa of RS long and angled with that of M which is directed anteroposteriorly rather than anterobasally; RS + M long, M + Cu bent further from fork; cu-a more distant from M + Cu fork; convexities along fore and inner sides of 1mcu absent (thus resembling respective parts of the cells in *M. schroeteri*, resulting in the false appearance of the cell as almost reaching RS base).

Description. The unique type consists of the incomplete impression of a forewing. Pterostigma large, wedge-shaped, issuing 2r-rs before its midlength; 1st abscissa of RS subequal to that of M and a little shorter than RS + M, not aligned with 1st abscissa of M which is directed obliquely anteroposteriorly; cells 1r and 2r of subequal length; RS + M occupying about 0.4 of 1mcu length; M + Cu angled before fork at distance subequal to that from fork to cu-a and to RS + M length; cell 1rm with nygma; no prominent longitudinal convexities connecting RS base with anterodistal and posterobasal corners of 1mcu.

Measurements. Length of impression, 20 mm; length of wing probably about 25 mm.

Suborder Vespina Laicharting 1781 (=Apocrita Gerstaecker 1867)
 Superfamily Stephanoidea Leach 1815
 Family Trigonalidae Cresson 1867
 Genus *Turgonalus* Rasnitsyn 1990

Type species. *Turgonalus minor* Rasnitsyn 1990.

Diagnosis. Genus differing from other Trigonalidae [except *Cretogonalys* Rasnitsyn 1977 from the lower Upper Cretaceous (Cenomanian) of Taimyr (North

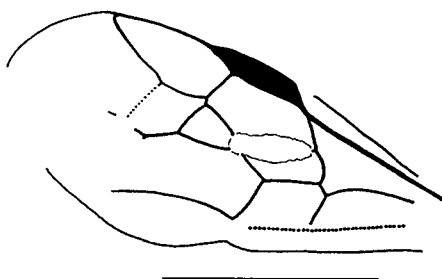


Figure 12. *Turgonalus cooperi* sp. nov., holotype BMB 016385/-6; Rudgwick Brickworks, Lower Barremian.

Siberia)] in its small size, 2m-cu (sometimes also 3r-m) not tubular and cu-a antefurcal.

Included species. Besides the type species, only the new one described below.

Turgonalus cooperi Rasnitsyn et Jarzembowski sp. nov.

Figure 12

Etymology. The species epithet is after Mr John A. Cooper, the Keeper of Geology & Keeper of the Booth Museum of Natural History, Brighton.

Holotype. BMB 016385/-6 (part and counterpart); from between Beds 3a and 3c, Upper Weald Clay; Rudgwick Brickworks, Rudgwick, West Sussex; Lower Barremian; collected by A. J. Ross.

Diagnosis. Species differs from the type species in having a large pterostigma, short cell 3r, more reduced venation, and smaller size.

Description. The unique type consists of the impression of a forewing. Pterostigma large, cell 3r short (hardly longer than pterostigma), cell 2rm distinctly petiolate, 3r-m and A not tubular, 2m-cu lost, M + Cu arching.

Measurements. Wing length 2.2mm.

Superfamily Stephanoidea

Family incertae sedis

Genus *Arossia* Rasnitsyn et Jarzembowski gen. nov.

Etymology. The genus is named after Mr Andrew J. Ross for organising productive fieldwork at Clockhouse Rock Store from 1991 to 1995.

Type species. *A. joyceae* sp. nov. described below.

Diagnosis. Genus similar to *Maimetsha* Rasnitsyn 1975 (Maimetshidae) from the Upper Cretaceous (Santonian) of Taimyr, and *Cretogonalys* Rasnitsyn 1977 (Trigonalidae) from the Upper Cretaceous (Cenomanian) of Taimyr, in that cell 1mcu is small, far removed from 2rm, 2m-cu is lost, and cu-a is antefurcal; differing from both genera in larger size, 1st abscissas of RS and M are practically aligned, 2r-rs is more oblique, and cell 3r is longer; also, from *Maimetsha* in the presence of two r-m crossveins, and from *Cretogonalys* in cell 2rm possessing a longer petiole, M + Cu arching, and A weak.

Remarks. Despite considerable venational similarity, Maimetshidae and Cretogoninae belong to clades distant enough (Rasnitsyn, 1988c) to make it impossible to combine them in a monophyletic group with *Arossia*. This genus

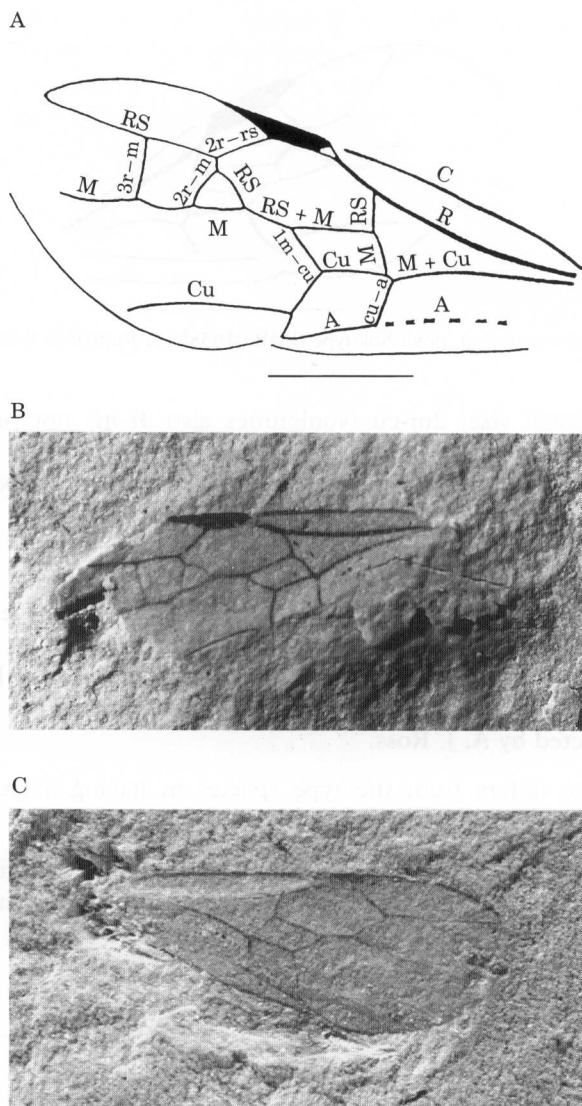


Figure 13. A, B, C. *Arossia joyceae* gen. et sp. nov., holotype BMB 018521/-2, B, C, $\times 12$; Auclaye Brickworks, Lower Barremian.

could form a monophyletic group with only one or none of them. The available venational characters are insufficient to make a decision at present.

Included species. One described below.

Arossia joyceae Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 13

Etymology. The species is named after the collector.

Holotype. BMB 018521/-2; from between Beds 3a and 3c, Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by Mrs Joyce Austen.

Description. The unique type consists of the impression of a forewing. Costal space very wide, R and M + Cu arching towards each other; pterostigma narrow; 1st abscissas of RS and M of subequal length; 2r-rs almost as long as cell 3rm; cell 2rm small with long petiole; 3r-m as long as distance to 2r-m, and almost half as long as distance to apex of cell 3r; 1m-cu originating only slightly beyond midlength of RS + M.

Measurements. Wing length 2.2mm.

Superfamily Evanioidea Latreille 1802

Family Gasteruptiidae Ashmead 1900 (Kirby 1837)

Subfamily Baissinae Rasnitsyn 1975

Genus *Manlaya* Rasnitsyn 1980

Type species. *Manlaya mongolica* Rasnitsyn 1980

Diagnosis. Genus differing from *Baissa* Rasnitsyn 1975 in having forewing A complete and 1st metasomal segment wide (not narrow conical).

Included species. 18 described species are included in the key (Table 1). Of these, *Aulocopsis laiyangensis* Hong & Wang 1990 and *Humiryssus leucus* Lin 1980 are included tentatively because the characters seen in published illustrations strongly suggest a close relationship to other species of *Manlaya* (which should be confirmed, however, by studies of the type material). As to the extra cell 'd' shown by Hong & Wang (1990, figs 163, 164), in the former species, it is most probably an error.

Additionally, there are numerous undescribed species from the Lower Cretaceous of Transbaikalia and Mongolia which also belong to *Manlaya*, whose total range includes the lower to mid Lower Cretaceous of southern England and eastern Central Asia (Transbaikalia, Mongolia and eastern China). The uppermost Upper Jurassic age of some Asian species cannot be ruled out at present.

Remarks. Species are difficult to identify and key out because of a rather uniform venation and incomplete preservation of many types which makes it difficult to use features of the body structure. As a result, the key (Table 1) is rather simplified and provisional.

Manlaya oculatissima Rasnitsyn et Jarzembowski sp. nov.

Figure 14

Etymology. The species epithet refers to the large eyes of the fossil.

Holotype. BMB 020505/-6 (part and counterpart); Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Diagnosis. Species differing from all others in the genus by its small size.

Description. The unique type consists of the incomplete impression of a body and one forewing. Head with large eyes and narrow temples. Mesonotum without distinct transverse sculpture. Mesopleura crenulate along hind margin laterally. Propodeum with coarse ridges. Coxae thin, moderately elongate; femora rather short, moderately thin. Forewing with pterostigma issuing 2r-rs submedially; cell 3r high (highest at 3r-m), short, with 2r-m rudimentary near 2r-rs; 3r-m rudimentary and almost equidistant between 2r-m and the cell apex; RS strongly bent at 3r-m; 1st abscissa of RS shorter than that of M; RS + M slightly

Table 1. Key for the identification of species of *Manlaya*, *Humirysus*, and *Aulocopsis* (Abbreviation: Fm, Formation).

1.	Forewing length 4.5 mm or less	2
	—Forewing length 5.5 mm or more, 3r long	16
2.	Forewing length 1.6 mm, pterostigma with 2r-rs near its midlength, 3r short, wide, with RS strongly angled at 3r-m, ovipositor sheath c. 0.5 of wing length <i>M. oculatissima</i> sp. nov., southern England, Middle Purbeck	
	—Forewing length 2 mm or more	3
3.	Pterostigma with 2r-rs near its midlength	4
	—Pterostigma with 2r-rs clearly beyond its midlength	13
4.	Sheath clearly more than half as long as forewing, forewing length 2.0–2.8 mm	5
	—Sheath less than half as long as forewing, forewing length 3.1–4.5 mm	9
5.	3r short, with RS strongly angled at 3r-m	6
	3r long, with RS weakly angled at 3r-m	7
6.	—Ground colour light, head and metasomal dorsum dark. Forewing length 2.0 mm, sheath length 1.3 mm <i>H. leucus</i> Lin 1980, East China, Zhejiang Province, Laocun, Laocun Fm —Ground colour dark. Forewing length 2.3 mm, sheath 1.4 mm <i>A. laiyangensis</i> Hong & Wang 1990, E. China, Shandong Prov., Tuanwang, Laiyang Fm	
7 (5).	Forewing length 2.2 mm <i>M. anglica</i> sp. nov., southern England, Lower Purbeck	
	Forewing length 2.5–2.8 mm	8
8.	Forewing length 2.5 mm, sheath length 2.0 mm <i>M. undurgensis</i> (Rasnitsyn 1975), Transbaikalia, Undurga, deposits corresponding possibly to Turga Fm —Forewing length 2.8 mm, sheath length 2.6 mm <i>M. caudata</i> Rasnitsyn 1986, West Mongolia, Gurvan-Ereney-Nuru, Gurvan-Eren Fm	
9 (4).	Forewing length 3.1 mm, sheath length 1.4 mm <i>M. pinguis</i> Rasnitsyn 1986, West Mongolia, Gurvan-Ereney-Nuru, Gurvan-Eren Fm —Forewing length 3.5–4.5 mm, sheath length 1.0–1.2 mm	10
10.	Forewing length 3.5 mm, sheath length 1.2 mm <i>M. obscura</i> Rasnitsyn 1986, West Mongolia, Gurvan-Ereney-Nuru, Gurvan-Eren Fm —Forewing length 4.0–4.5 mm	11
11.	Forewing length 4.5, sheath length 1.0 mm <i>M. pallida</i> Rasnitsyn 1986, West Mongolia, Gurvan-Ereney-Nuru, Gurvan-Eren Fm —Forewing length c. 4 mm	12
12.	Sheath length 1.2 mm, ground colour light <i>M. laevinota</i> Rasnitsyn 1986, West Mongolia, Miangat, Gurvan-Eren Fm —Sheath length 1.0 mm, head and mesonotum darkened <i>M. ventricosa</i> Rasnitsyn 1986, West Mongolia, Gurvan-Ereney-Nuru, Gurvan-Eren Fm	
13 (3).	Forewing length 2.5 mm	14
	—Forewing length 4.0–4.5 mm	15
14.	Sheath length 1.1 mm <i>M. ghidarina</i> Rasnitsyn 1990, Transbaikalia, Karabon, Ghidara Fm —Sheath length 0.7 mm <i>M. gurvanica</i> Rasnitsyn 1986, West Mongolia, Gurvan-Ereney-Nuru, Gurvan-Eren Fm	
15 (13).	Forewing length 4.0 mm, 3r highest at 2r-m, hardly angled at 3r-m <i>M. ockleyensis</i> sp. nov., southern England, Smokejacks Brickworks, lower Upper Weald Clay —Forewing length 4.5 mm, 3r highest at 3r-m, distinctly angled there, sheath broad, 1.9 mm long <i>M. pachyura</i> Rasnitsyn 1990, Transbaikalia, Turga, Turga Fm	
16 (1).	Pterostigma with 2r-rs near its midlength, forewing length 5.5 mm, sheath length 2.0 mm <i>M. mongolica</i> Rasnitsyn 1980, southeast Mongolia, Mogotuin Fm —Pterostigma with 2r-rs clearly beyond its midlength, forewing longer	17
17.	Forewing length about 5.8–6.0 mm, 3r-m very close to 2r-m, RS straight beyond 2r-m <i>M. capelensis</i> sp. nov., southern England, Auclaye Brickworks, lowermost Upper Weald Clay —Forewing longer than 7 mm <i>M. corrugata</i> Rasnitsyn 1986, West Mongolia, Gurvan-Ereney-Nuru, Gurvan-Eren Fm	



Figure 14. *Manlaya oculatissima* sp. nov., holotype BMB 020505/-6; Durlston Bay, Upper Berriasian.

surpassing 1m-cu apically. Metasoma short, ovoid, ovipositor sheath *ca.* 0.5 forewing length.

Measurements. Forewing length 1.6 mm; ovipositor sheath length 0.8 mm.

Manlaya anglica Rasnitsyn et Jarzembowski sp. nov.

Figure 15

Holotype. BMB 020507/-8 (part and counterpart); Bed DB36c, Hard Cockle beds, Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by Mr R. Coram.

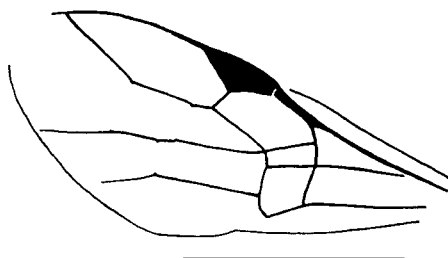


Figure 15. *Manlaya anglica* sp. nov., holotype BMB 020507/-8; Durlston Bay, Lower Berriasian.

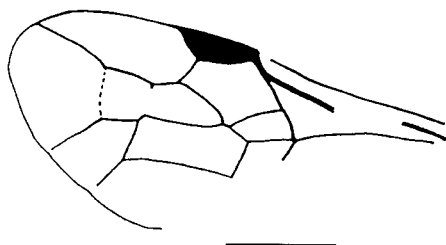


Figure 16. *Manlaya ockleyensis* sp. nov., holotype BMB 016405/-6 ; Smokejacks Brickworks, Lower Barremian.

Diagnosis. Species differing from other species of *Manlaya* in possessing a pterostigma with 2r-rs at its midlength in combination with a dark body, forewing nearly 2mm long, and long cell 3r.

Description. The unique type consists of the impression of a forewing. Pterostigma issuing 2r-rs submedially; cell 3r high (highest at 3r-m), long, with 2r-m rudimentary and distad of 2r-rs, almost as long as the latter; 3r-m rudimentary and almost equidistant between 2r-m and cell apex; RS slightly bent at 3r-m; 1st abscissa of RS shorter than that of M; RS + M slightly surpassing 1m-cu apically; 2m-cu beyond first quarter of 3m.

Measurements. Forewing length 2.2mm.

Manlaya ockleyensis Rasnitsyn et Jarzembowski sp. nov.

Figure 16

Etymology. The species is named after the village of Ockley near Smokejacks Brickworks.

Holotype. BMB 016405/-6 (part and counterpart); from below Bed 5c, Upper Weald Clay; Smokejacks Brickworks, Ockley, Surrey; Lower Barremian; collected by A. J. Ross.

Diagnosis. Species differing from other *Manlaya* species in possessing pterostigma with subapical position of 2r-rs; and in having forewing nearly 4 mm long with cell 3m highest apically.

Description. The unique type consists of the incomplete impression of a forewing. Pterostigma issuing 2r-rs far beyond middle; cell 3r high (highest at 2r-m), long, with 2r-m rudimentary and distad of 2r-rs almost equal to length of latter; 3r-m rudimentary and almost equidistant between 2r-m and cell apex; RS hardly bent at 3r-m; 1st abscissa of RS as long as that of M; RS + M slightly surpassing 1m-cu apically; 2m-cu near base of cell 3m.

Measurements. Forewing length 4.0 mm.

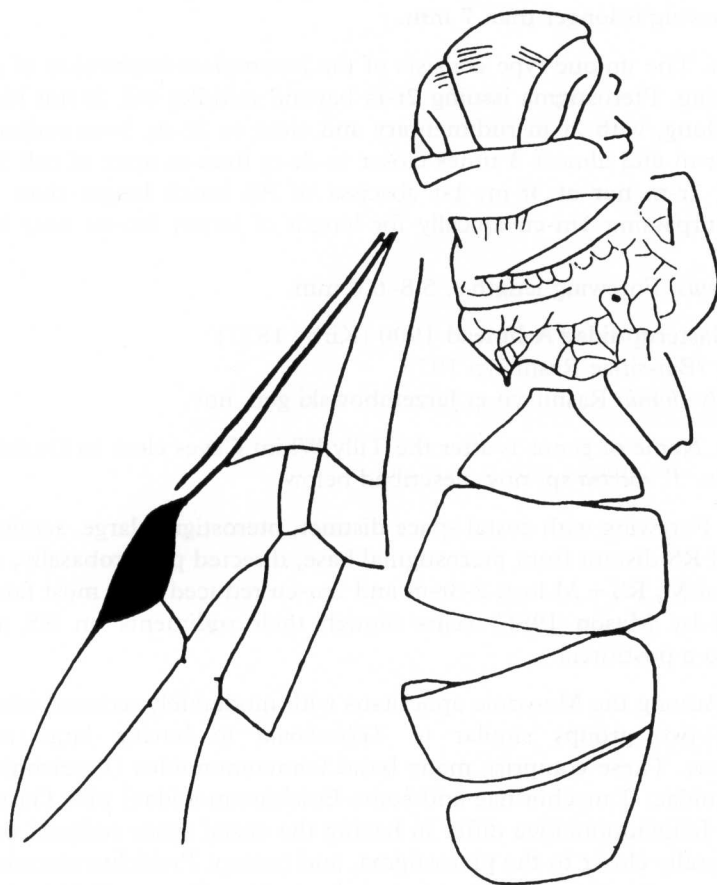
Manlaya capelensis Rasnitsyn et Jarzembowski sp. nov.

Figure 17

Etymology. The species is named after the village of Capel, near Auclaye Brickworks.

Holotype. BMB 018519/-20 (part and counterpart); from between Beds 3a and 3c, Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by E. A. Jarzembowski.

A



B

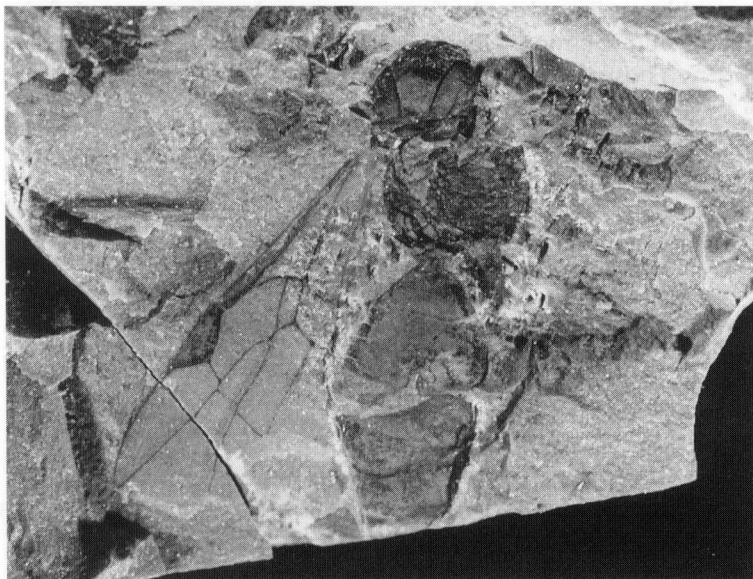


Figure 17. A, B. *Manlaya capelensis* sp. nov., holotype BMB 018519/-20, b, $\times 10$; Auclaye Brick-works. Lower Barremian.

Diagnosis. The second largest species in the genus; only smaller than *M. corrugata* whose forewing is longer than 7 mm.

Description. The unique type consists of the incomplete impression of a body and one forewing. Pterostigma issuing 2r-rs beyond middle; cell 3r not high (highest at 2r-m), long, with 2r-m rudimentary and close to 2r-rs; 3r-m rudimentary and close to 2r-m and almost 3 times closer to 2r-rs than to apex of cell 3r; RS bent neither at 2r-m nor at 3r-m; 1st abscissa of RS much longer than that of M; RS + M surpassing 1m-cu apically for length of latter; 2m-cu near base of cell 3rm.

Measurements. Forewing length *c.* 5.8–6.0 mm.

Family ?Gasteruptiidae Ashmead 1900 (Kirby 1837)

Subfamily ?Baissinae Rasnitsyn 1975

Genus *Tillywhimia* Rasnitsyn et Jarzembowski gen. nov.

Etymology. Name of genus is after the Tilly Whim Caves close to Durlston Bay.

Type species. *T. spectra* sp. nov. described below.

Diagnosis. Forewing with costal space distinct, pterostigma large, semicircular, 1st abscissa of RS distant from pterostigmal base, directed posterobasally, not aligned with that of M; RS + M lost; 2-3r-m and 2m-cu reduced to at most faint (spectral as termed by Mason 1986) veins though their rudiments on RS and M are distinct; cu-a postfurcal.

Remarks. Among the Mesozoic apocritans with moderately reduced wing venation there are two groups similar to *Tillywhimia* in having large semicircular pterostigmas. These comprise many basal Ichneumonoidea (Praeichneumonidae, Ichneumonidae: Tanychorinae and some Eoichneumonidae) plus Gasteruptiidae: Baissinae. Ichneumonoidea differ in having the costal space reduced or lost, base of RS generally closer to the pterostigma, and (except Praeichneumonidae) one of the r-m crossveins (possibly 2r-m) completely lost. Known Baissinae are unlike this genus in having cu-a interstitial or weakly postfurcal (in *Baissa*), and in a developed RS + M. These differences appear less important, and the general habitus of the wing suggests Baissinae rather than Ichneumonoidea. *Tillywhimia* is thus questionably attributed to the former group, though a more definite decision will only be possible if a more complete fossil comes to light.

Included species. Those described below.

Tillywhimia spectra Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 18

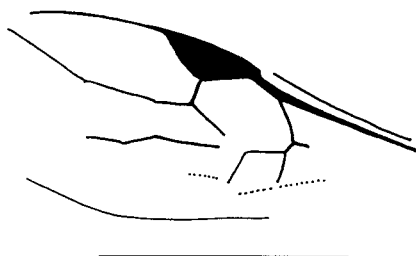


Figure 18. *Tillywhimia spectra* gen. et sp. nov., holotype BMB 020509/-10; Durlston Bay, Upper Berriasian.



Figure 19. *Tillywhimia colorata* gen. et sp. nov., holotype BMB 020511/020513; Durlston Bay, Lower Berriasian.

Etymology. The species name refers to the faint veins A and Cu.

Holotype. BMB 020509/-10 (part and counterpart); Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Description. The unique type consists of the incomplete impression of a forewing. Cell 3r high and long; RS weakly angled at 3r-m, straight between base and 2r-rs; 2r-rs near midlength of pterostigma, removed from 2r-m by more than its length; 3r-m probably nearly equidistant between 2r-rs and apex of cell 3r; 2m-cu not far from midlength of cell 3rm; cu-a *c.* 3 times closer to base of M than to Cu; A and a horizontal section of Cu within cell 2mcu appear faint (spectral).

Measurements. Forewing length *c.* 1.9–2.0 mm.

Tillywhimia colorata Rasnitsyn et Jarzembowski sp. nov.

Figure 19

Etymology. The species name refers to the coloured veins A and Cu.

Holotype. BMB 020511/020513; Bed DB36c, Hard Cockle beds, Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by Mr R. Coram.

Diagnosis. Differing from the type species in RS arches between RS + M and 2r-rs; in the proximal position of 2m-cu; and in the coloured A and distal part of Cu.

Description. The unique type consists of the incomplete impression of a forewing. Cell 3r high and long, RS gently curved at 3r-m, arching basad between RS + M and 2r-rs; 2r-rs near midlength of pterostigma, removed from 2r-m by almost twice its length; 3r-m nearly equidistant between 2r-rs and apex of cell 3r; 2m-cu near base of cell 3rm; cu-a greatly postfurcal; A and horizontal section of Cu coloured, tubular.

Measurements. Forewing length *c.* 1.9 mm.

Family Cretevaniidae Rasnitsyn 1975

Genus *Cretevania* Rasnitsyn 1975

Cretevania concordia Rasnitsyn et Jarzembowski sp. nov.

Figure 20

1984 *Cretevania* Jarzembowski, p. 90, fig. 52.

1987 *Cretevania* sp. nov. Jarzembowski, pp. 319, 320, figs 14.2, 14.6a,b.

Etymology. The species epithet is Latin for 'agreement'.

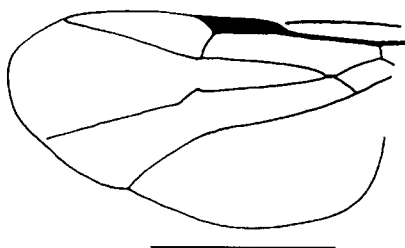


Figure 20. *Cretevania concordia* sp. nov., holotype BMB 018510/-1; Clockhouse Brickworks, Upper Hauterivian.

Holotype. BMB 018510/-1 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; old pit, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by E. A. Jarzembowski.

Diagnosis. The largest and least reduced species in the genus and most similar to another Lower Cretaceous species, *C. meridionalis* Rasnitsyn from Mongolia (see Rasnitsyn, 1991a); differing from Upper Cretaceous species from north Siberia, *C. minor* Rasnitsyn 1975, *C. major* Rasnitsyn 1975, *C. minuta* Rasnitsyn 1975 in possessing a short pterostigma and RS + M; differing from *C. meridionalis* as well as from all other species in the presence of a rudimentary 2m-cu and larger size.

Description. The unique type consists of the incomplete impression of a forewing. Pterostigma 0.65 as long as cell 3r; RS + M slightly surpassing 1m-cu apically, and before 1m-cu a little more than half as long as pterostigma; 2r-m scarcely distad of 2r-rs; the rudiment of 2m-cu is distinct, removed from 2r-m by almost the length of 2r-rs.

Measurements. Length of fossil, as preserved, 2.2mm; estimated length of forewing c. 3.0–3.2mm.

Superfamily Proctotrupeoidea Latreille 1802

Family Proctotrupidae Latreille 1802

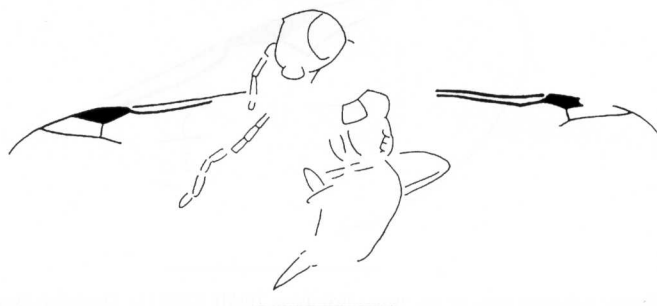
Genus *Dintonia* gen. nov.

Etymology. Genus name after locality of the type species.

Type species. *D. despectata* sp. nov. described below.

Diagnosis. Differs from all living proctotrupids (except *Heloriserphus* Masner) by a combination of long 3r and pterostigma not shortened apically (characteristic of *Vanhornia* Crawford and Acanthoserphinae), with reduced venation (veins lost except C, R, pterostigma, 2r-rs, and RS from before 2r-rs until apex of 3r) as in extant Proctotrupinae. Differing from *Heloriserphus* Masner and *Peradenia* Naumann & Masner (originally placed in Peradeniidae) (Naumann & Masner, 1985) and transferred to Heloridae by Rasnitsyn (1988c), but probably closer to Proctotrupidae despite long petiolate metasoma) by normal pterostigma and 2r-rs plus absence of sclerotization at junction of M + Cu fork with cu-a. In addition, differing from extant proctotrupids and *Peradenia*, but similar to some Mesozoic genera (e.g., *Gurvanotrupes* Rasnitsyn, *Oligoneuroides* Zhang) in R being bent at point of former divergence of base of RS. Among extinct genera, venationally similar to *Oligoneuroides* Zhang (Zhang, 1985) from the Laiyang Formation

A



B

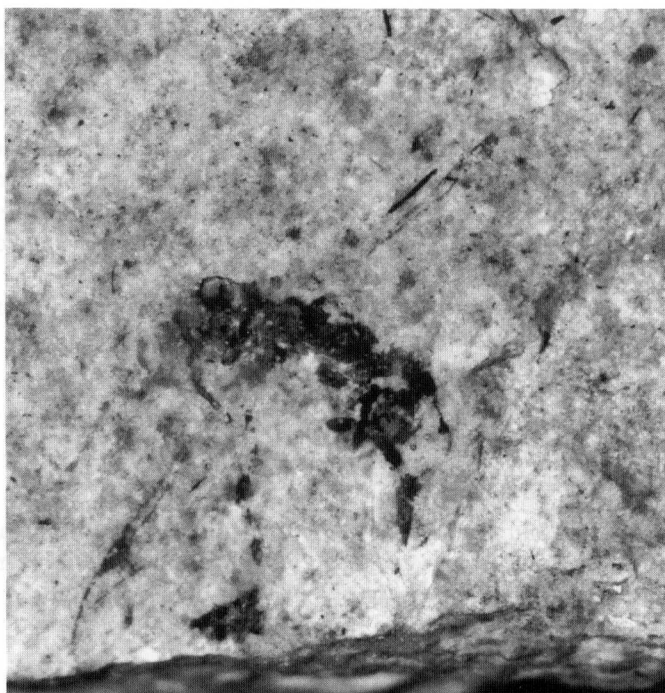


Figure 21. *Dintonia despectata* gen. et sp. nov., holotype NHM II. 778, B, $\times 20$; Dinton, Middle Berriasian.

(Upper Jurassic or, more likely, lower Lower Cretaceous of Shandong, China) but differing in smaller size, short stout metasoma, and short thick ovipositor.

Included species. Type species described below.

Dintonia despectata Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 21

Etymology. The species epithet is Latin for 'overlooked'.

Holotype. NHM II. 778; Insect Limestone, Worbarrow Tout Member, Lulworth Formation; Dinton, Vale of Wardour, Wiltshire; Middle Berriasian; collected by the Rev. P. B. Brodie.

Description. The unique type consists of the incomplete impression of a whole insect. Head rounded, with large rounded eyes, narrow temples, and somewhat

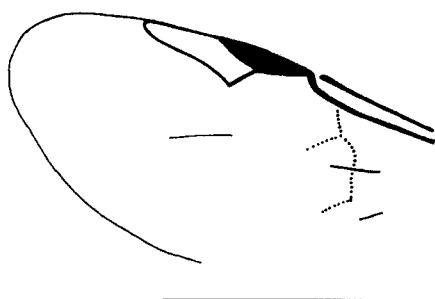


Figure 22. *Pallenites calcarius* gen. et sp. nov., holotype BMB 020511; Durlston Bay, Lower Berriasian.

protruding clypeus. Antenna 13-segmented (pedicel not seen), funicular segments elongate ranging from almost 3 times as long as wide (basal segment) to subquadrate (penultimate one). Forewing with R bent as far from pterostigmal base as 2r-rs; pterostigma about 3 times as long as high, issuing 2r-rs at its midlength; 2r-rs shorter than maximum height of pterostigma and considerably shorter than RS before it; cell 3r as long as pterostigma. Legs rather short. Metasoma short, rounded basally, shorter than thorax; segmentation not preserved. Ovipositor sheath shorter than pterostigma, wedge-shaped. Body and antenna dark, legs light.

Measurements. Body length without ovipositor, as preserved, 1.9 mm; forewing length about 1.9–2.0 mm; ovipositor sheath length 0.3 mm.

Genus *Pallenites* Rasnitsyn et Jarzembowski gen. nov.

Etymology. The genus name is after Prof. P. Allen FRS.

Type species. *P. calcarius* sp. nov. described below.

Diagnosis. Venationally similar to *Oligoneuroides* and *Dintonia*, differing from both in RS lost before 2r-rs and is sinuate beyond it; in rounded apex of 3r; in R being straight except just before the pterostigma; and in a partially coloured M and Cu.

Included species. Type species described below.

Pallenites calcarius Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 22

Etymology. The species name is from the Latin for 'calcareous'.

Holotype. BMB 020511; Bed DB36c, Hard Cockle beds, Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by Mr R. Coram.

Description. The unique type consists of the incomplete impression of a forewing. Pterostigma long, narrow and rounded below, issuing 2r-rs at its midlength; 2r-rs strongly oblique, subequal in length to pterostigmal height; cell 3r about 1.25 times as long as pterostigma; high cell 1mcu partly delimited by spectral (discoloured) veins; cu-a spectral, interstitial.

Measurements. Length of wing fragment, as preserved, 2.1 mm; estimated wing length c. 2.4 mm.

Genus *Peperella* Rasnitsyn et Jarzembowski gen. nov.

Etymology. Genus name after Peveril Point at north end of Durlston Bay.

Type species. *P. punctata* sp. nov. described below.

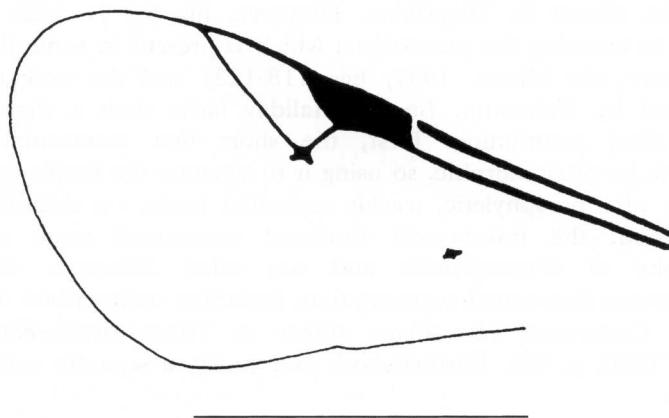
Diagnosis. Generally similar venation to *Oligoneuroides* and *Dintonia*. Differing from both in having a sclerotized spot at the junction of M + Cu fork with cu-a and short rudiment of 'RS₂'; also, R is straight and the pterostigma high - the latter issuing 2r-rs beyond its midlength. Similar to *Heloriserphus* and *Peradenia* in having a sclerotized spot at the junction of M + Cu fork with cu-a, differing from both in long 2r-rs, short RS before it, and in having short rudiment of 'RS₂'.

Included species. Type species described below.

Peverella punctata Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 23

A



B



Figure 23. A, B. *Peverella punctata* gen. et sp. nov., holotype BMB 020514/-5, Durlston Bay, B, c. $\times 50$; Upper Berriasian.

Etymology. Species epithet refers to a spot on the forewing.

Holotype. BMB 020514/-5 (part and counterpart); Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Description. The unique type consists of the incomplete impression of a forewing. Pterostigma moderately large, 3 times as long as high; 2r-rs shorter than pterostigmal height; cell 3r slightly longer than pterostigma; RS straight throughout.

Measurements. Length of fossil, as preserved, 2.0 mm; estimated wing length *c.* 2.1 mm.

Family Diapriidae Haliday 1933

Remarks. Following Rasnitsyn (1980, 1988c, Rasnitsyn in Darling & Sharkey, 1990, table 1), an enlarged concept of the family is employed here to include the Mesozoic species *Cretacoformica explicata* Jell & Duncan 1986 and the one described below. Naumann (1993) criticized this approach referring to a number of characters absent in Diapriidae. However, his list is open to criticism, particularly in omitting the pterostigma which is present in some diapriids (e.g., *Zygota* Förster; see Nixon, 1957, figs 118-122) and the antennal shelf. As acknowledged by Naumann, *Ismarus* Haliday lacks such a shelf. Two other characters need mentioning. First, the short first metasomal segment is considered to be plesiomorphic, so using it to separate the fossils would result in the creation of a paraphyletic, weakly separated taxon - a decision difficult to justify. Second, the transversely furrowed metasomal terga could be an autapomorphy of *Cretacoformica* and not other Mesozoic diapriids with subhomonomous metasomal segmentation, including undescribed diapriids from the Upper Cretaceous (Turonian) amber at Timmerdyakh-Khaya, Yakutia (Rasnitsyn, 1980, p. 92). Further work may justify a separate subfamily for all these fossils.

Genus *Coramia* Rasnitsyn et Jarzembowski gen. nov.

Etymology. Genus name after Mr Robert Coram, collector of numerous insect fossils in Purbeck Limestone Group in Durlston Bay.

Type species. *C. minuta* sp. nov. described below.

Diagnosis. Similar to *Cretacoformica* with well developed pterostigma and long but not closed cell 3r; differing in having a thin antenna which is expanded apically, forewing with a larger pterostigma, RS and M distinct from their point of divergence, cell 3r open widely apically, M directed basad towards base of RS rather than to base of M, and Cu distinct.

Included species. Type species described below.

Coramia minuta Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 24

Etymology. Species epithet refers to small size of fossil.



Figure 24. *Coramia minuta* gen. et sp. nov., holotype BMB 020512; Durlston Bay, Upper Berriasian.

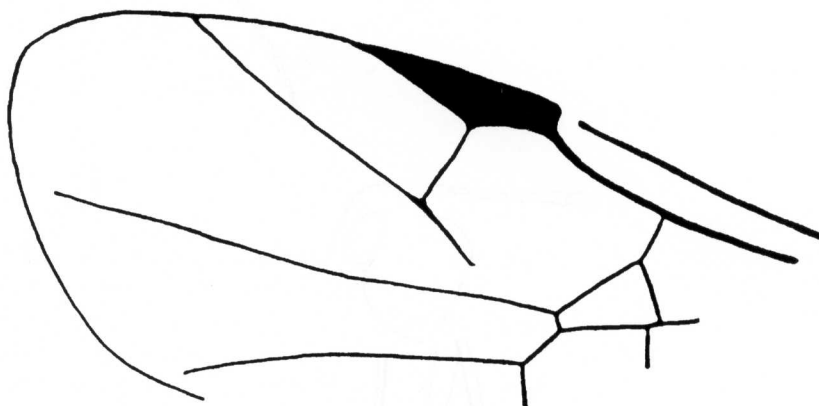
Holotype. BMB 020512; Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Description. The unique type consists of the impression of a head, antennae, part of thorax, and forewings. Head with eye large, elongate; temple narrow; lacking antennal shelf. Antenna with 10 flagellar segments clearly visible, basal and penultimate segments about 4 and 1.5 times as long as wide respectively. Ultimate segment almost 2 times as long as wide, and about 3 times as wide as 1st visible segment. Thorax wide, probably short. Forewing with pterostigma about 5 times as long as high, highest subbasally, issuing 2r-rs near its midlength; RS and M distinct, first, as a complete, smoothly arched basal vein and then distad of their point of divergence (that is, RS + M is missing); 2r-rs longer than pterostigmal height; cell 3r broadly open, estimated length more than that of pterostigma; Cu distinct from wing base until opposite the pterostigmal midlength.

Measurements. Length of fossil (without antenna), as preserved, 2.0 mm; length of antenna about 1.0–1.15 mm; wing length *c.* 1.35 mm.

Superfamily Proctotrupoidea
Family *incertae sedis*

A



B



Figure 25. A, B. *Amitchellia procera* gen. et sp. nov., holotype BMB 18506/-7, B, *c.* $\times 30$; Durlston Bay, Lower Berriasian.

Genus *Amitchellia* Rasnitsyn et Jarzembowski gen. nov.

Etymology. Genus name after Mr A. A. Mitchell, collector of the type species.

Type species. *A. procera* sp. nov. described below.

Diagnosis. Forewing strongly reminiscent both of Heloridae and Vanhorniinae in its wide costal space, well developed pterostigma, long triangular cell 3r with 2r-rs subvertical with respect to RS, 2-3r-m and 2m-cu absent, and subtriangular 1mcu with short 1m-cu. Differing from Heloridae in 1st abscissa of RS moderately long and meeting M at a distinct angle; from Vanhorniinae in pterostigma not inflated and 1m-cu distinct.

Remarks. The venation is more like *Vanhornia* Crawford than Heloridae, but it would be premature to attribute the fossil to Vanhorniinae. *Vanhornia*, the only

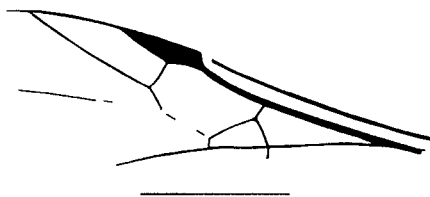


Figure 26. *Amitchellia brevis* gen. et sp. nov., holotype NHM I.12509; Durlston Bay, Lower Berriasian.

known and uncommon extant genus in the subfamily (excluding *Heloriserphus* Masner, following Masner in Townes & Townes, 1991) is too specialized in its body structure to include Mesozoic species based only on venational characters. It seems equally likely that the fossils represent a group of Mesozoic Heloridae (subfamily Mesohelorinae) with the 1st abscissa of RS modified in its position in convergence with *Vanhornia*. Within Mesohelorinae, most taxa have a rather standard wing venation, so natural classification is often only possible when bodies are known. The detached wings with unspecialised venation are assigned to 'formal' genera dependent on size: *Protohelorus* Kozlov 1968 (large wings) or *Gurvanhelorus* Rasnitsyn 1986 (small wings) (Rasnitsyn, 1990a). *Amitchellia* differs from both genera, as well as from numerous undescribed ones at PIN, in that the 1st abscissa of RS is moderately long and meets M at a distinct angle; also, it differs from all Mesohelorinae (except *Mesohelorus*) in having 1mcu high (half or more of length). *Included species.* Described below.

Amitchellia procera Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 25

Etymology. Species epithet is Latin for 'tall' referring to tall cell 1mcu.

Holotype. BMB 018506/-7 (part and counterpart); Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by Mr A. A. Mitchell.

Description. The unique type consists of the incomplete impression of a forewing. Cell 3r comparatively high; 2r-rs almost twice as long as pterostigma is high; M (including RS + M) straight beyond 1m-cu, estimated point of forking of RS + M much closer to 1m-cu than to 2r-rs; Cu angled at 1m-cu and at end of cell 2cua; cu-a slightly postfurcal.

Measurements. Fossil length, as preserved, 3.5 mm; estimated wing length c. 4 mm.

Amitchellia brevis Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 26

Etymology. Species epithet is Latin for 'low', referring to low cell 1mcu.

Holotype. NHM I.12509; Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by the Rev. P. B. Brodie.

Diagnosis. Differs from *A. procera* in lower cell 3r, angled M, straight Cu, interstitial cu-a and smaller size.

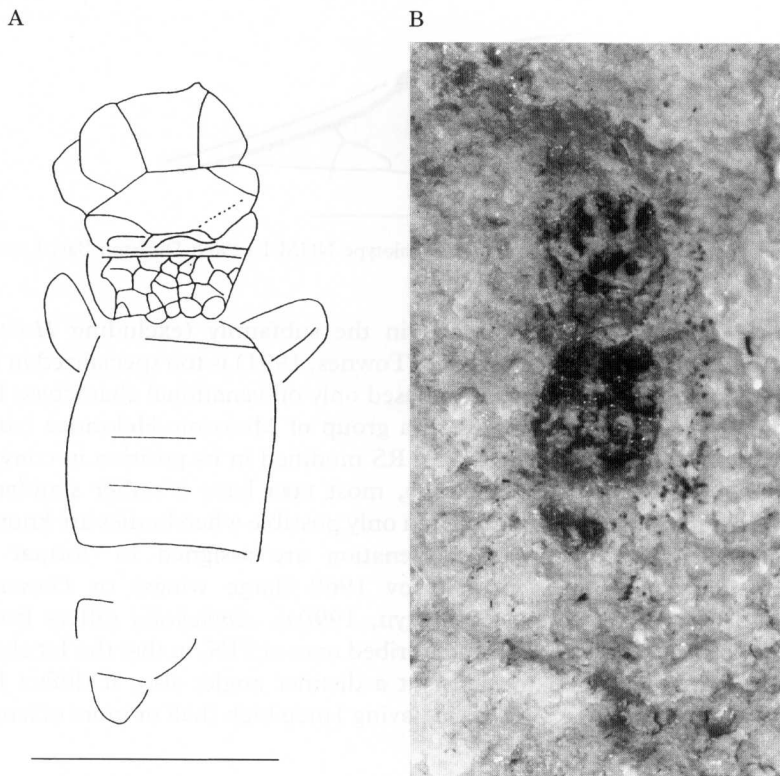


Figure 27. A, B. *Proctotrumpomorpha* gen. et sp. indet., NHM I.12648, B, $\times 20$; Dinton, Middle Berriasian.

Description. The unique type consists of the incomplete impression of a forewing. Cell 3r only moderately high: 2r-rs slightly longer than pterostigma is high; M bent at RS + M fork which is further to 1m-cu than to 2r-rs; Cu straight throughout; cu-a interstitial.

Measurements. Forewing length 3.3 mm.

Infraorder Proctotrumpomorpha
Superfamily and family *incertae sedis*

Gen. et sp. indet.

Figure 27

Material. NHM I.12648; Insect Limestone, Worbarrow Tout Member, Lulworth Formation; Dinton, Vale of Wardour, Wiltshire; Middle Berriasian; collected by the Rev. P. B. Brodie.

Description. The unique specimen consists of an incomplete impression of body without head, wings and most of legs. Body small, stout. Thorax lacking coarse sculpture except on propodeum, with distinct notauli which are percurrent, slightly diverging forward and distant at scutellum; scutellum large; transcutal line straight; axillae small, not reaching notauli; metanotum and metapostnotum distinct, narrow; propodeum reticulate, with lower metasomal articulation. Hind legs short, stout. Metasoma long and wide, broad basally; 6 terga discernible, the 2nd being longest (unless it is a pair of terga with the boundary between them not

preserved); 2nd to 4th terga of subequal width, the remainder narrower. Body dark, legs somewhat lighter.

Measurements. Body length, as preserved, 2.7 mm.

Remarks. The entire and comparatively long propodeum, separated from the metasoma by a constriction, place this specimen definitely in the suborder Vespina (Apocrita). Within the latter, the absence of the medial scutal sulcus and the adlateral lines, combined with the low position of the propodeo-metasomal articulation, exclude it from Evaniomorpha. The absence of the adlateral lines also points against a vespomorph relationship. Cretaceous Ichneumonomorpha are generally less stout with the 1st metasomal tergum longer, even in Praeichneumonidae, than in the Purbeck fossil. This leaves Proctotrupomorpha as the only possibility. In that group, Cynipoidea and the majority of the Proctotrupeoidea *s.l.* (i.e., including Diaprioidea and Scelionoidea) can be ruled out because of their distinct tubular 1st metasomal segment. However, it could belong to Mesoserphidae (cf. *Auliserphus cretaceus* Rasnitsyn 1990), Scelionidae and various Chalcidoidea - or even an unknown group.

Superfamily Ichneumonoidea Latreille 1802

Family Eoichneumonidae Jell & Duncan 1986.

Genus *Purichneumon* Rasnitsyn et Jarzembowski gen. nov.

Etymology. Genus name is a combination based on Purbeck Limestone Group and living genus *Ichneumon*.

Type species. *P. britannicus* sp. nov. described below.

Diagnosis. Unlike other Eoichneumonidae, RS + M is lost; cell 3r is short, subtriangular, with RS practically straight between 2r-rs and cell apex; 2 + 3rm very short, with 3r-m placed far basad of 2m-cu. Also, differs from most other eoichneumonids in that the basal vein arches smoothly and cu-a is greatly postfurcal.

Included species. Type species described below.

Purichneumon britannicus Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 28

Holotype. BMB 020516; Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Description. The unique type consists of the impression of a forewing. Pterostigma subtriangular, very wide (2.3 times as long as high); basal vein smoothly arched, reaching base of pterostigma; RS + M lost; 3r less than twice as long as pterostigma, far from wing apex; RS practically straight between 2r-rs and cell 3r apex; 2r-rs as long as pterostigma is high, subequal to distance from it to point of divergence of RS and M, and longer than distance to 3r-m; 2m-cu distad of 3r-m; cu-a separated from base of M by about half its length.

Measurements. Forewing length 3.2mm.

Superfamily Bethyлонymoidea Rasnitsyn 1975

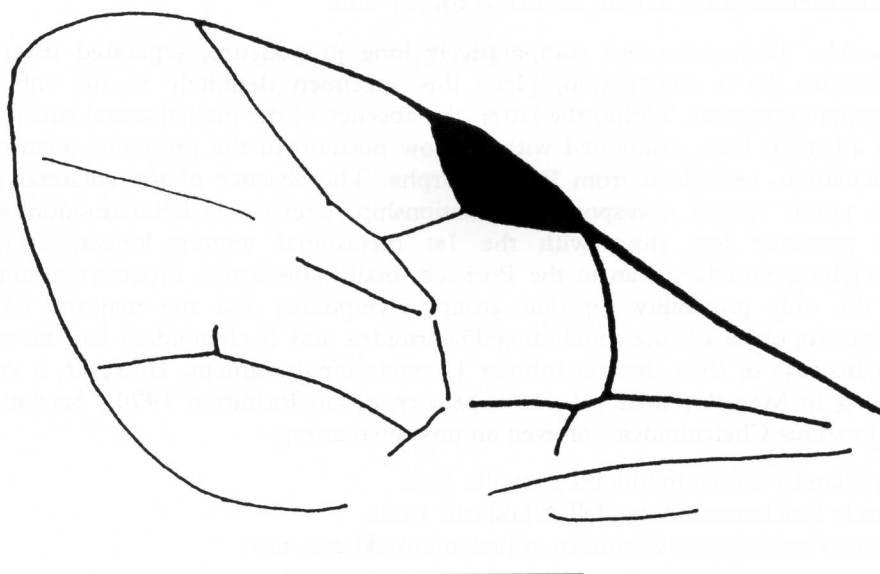
Family Bethyлонymidae Rasnitsyn 1975

Genus *Bethyлонymellus* Rasnitsyn 1975

Bethyлонymellus feltoni Rasnitsyn et Jarzembowski sp. nov.

Figure 29

A



B



Figure 28. A, B. *Purichneumon britannicus* gen. et sp. nov., holotype BMB 020516, B, $\times 33$; Durlston Bay, Upper Berriasian.

Etymology. The species epithet is after Mr. J. C. Felton, the late hymenopterist.

Holotype BMB 020518; Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Diagnosis. Similar to *B. bethyloides* Rasnitsyn 1975 in possessing a pterostigma which is widest at 2r-rs, RS + M which forks well before 1m-cu and interstitial

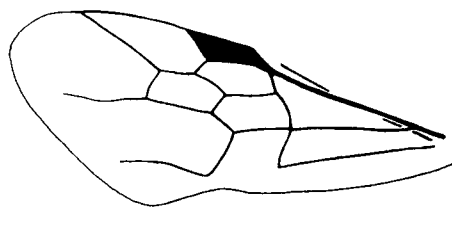
Bethylonymellus feltoni

Figure 29. *Bethylonymellus feltoni* sp. nov., holotype BMB 020518; Durlston Bay, Upper Berriasian. cu-a; but differs in smaller size, straight apical section of RS and lost apical section of A.

Description. The unique type consists of the impression of a forewing. Pterostigma large and subtriangular, widest at 2r-rs; 2r-rs considerably shorter than pterostigma wide; fork of RS + M away from 1m-cu by half of latter's length; RS straight beyond 2r-m; no trace of 3r-m on either RS or M; trace of 2m-cu present as a bend of M; cu-a interstitial; A undeveloped beyond cu-a.

Measurements. Forewing length 1.75 mm.

Superfamily Apoidea Latreille 1802 (=Sphecoidea Latreille 1802)

Family Sphecidae Latreille 1802

Table 2. Key for the identification of species of *Archisphex*.

1.	Base of RS removed from pterostigmal base by about a pterostigmal length; 3r-m removed from 3r apex by at most half its length; wing length about 8 mm or more	2
	— Base of RS closer to pterostigmal base; 3r-m removed from 3r apex by about its length or more; wing length less than 8 mm	3
2.	2r-m removed from 2m-cu by almost half its length, wing length 7.9–9.4 mm	
	<i>A. boothi</i> Jarzembowski 1991, lowermost Upper to uppermost Lower Weald Clay of southern England	
	— 2r-m close to 2m-cu, wing length 12.5 mm	
	<i>A. proximus</i> sp. nov.; uppermost Lower Weald Clay of southern England	
3(1).	2r-m removed from 2m-cu by more than 0.3 of its length, 1r-rs rudiment present, cell 2rm very short on RS, cu-a nearly interstitial, wing length 7.6 mm	
	<i>A. catalunicus</i> (Ansorge 1993); Lower Barremian of northeast Spain	
	— 2r-m close to 2m-cu	4
4.	cu-a interstitial, M + Cu less than twice as long as distance from its apex to 1m-cu, 2cua much longer on Cu than on A, wing length 7.4 mm	
	<i>A. beiboziensis</i> (Hong 1984) comb. nov.; Laiyang Fm, Shandong, China (Upper Jurassic or, rather, lower Lower Cretaceous)	
	— cu-a antefurcal, M + Cu more than twice as long as distance from its apex to 1m-cu, 2cua of subequal length on Cu and A	5
5.	1r-rs rudiment absent, 2r-rs shorter than pterostigma beyond it, 2r-m straight or nearly so, 3r-m weakly bent or sinuate	6
	— 1r-rs rudiment present, 2r-rs longer than pterostigma beyond it, 2r-m curved, 3r-m strongly sinuate	7
6.	M within 2rm shorter than within 3rm, 3rm longer on M than on RS, wing length 5 mm	
	<i>A. crowsoni</i> Evans 1969; Wadhurst Clay (Valanginian) of southern England	
	— M within cell 2rm longer than within 3rm, 3rm of subequal length on RS and M, wing length 4.2 mm	
	<i>A. venulosus</i> (Zhang 1985) comb. nov.; same deposits and region as <i>A. beiboziensis</i>	
7 (5).	Cell 3rm scarcely longer on M than on RS, wing length 4.5 mm	
	<i>A. incertus</i> (Rasnitsyn 1975) comb. nov.; Transbaikalia, Zaza Fm	
	— Cell 3rm more than twice as long on M as on RS, wing length 5.6 mm, lowermost Upper Weald Clay of southern England	
	<i>A. curvus</i> sp. nov.	

Genus *Archisphex* Evans 1969

=*Cretosphex* Rasnitsyn 1975 syn. nov. (Type species, *C. incertus* Rasnitsyn 1975).

=*Mateosphex* Zhang 1985 syn. nov. (Type species, *M. venulosus* Zhang 1985).

=*Palaeapis* Hong 1984 syn. nov. (Type species, *P. beiboziensis* Hong 1984).

Type species. *Archisphex crowsoni* Evans 1969; Lower Cretaceous of southern England.

Diagnosis. *Archisphex* belongs to a group of Lower Cretaceous apoid wasps with cells 2rm and 1mcu touching each other for a short distance (if at all) instead of overlapping each other for a long distance as in the vast majority of other Apoidea (which are almost all of Upper Cretaceous or Cenozoic age). Within its group, *Archisphex* differs from other genera except *Trichobaissodes* Rasnitsyn in that cell 2rm receives 2m-cu, from *Trichobaissodes* in the apex of cell 3r being acuminate and situated on the wing margin.

Included species. See Table 2; their range extends from the pre-Aptian Lower Cretaceous deposits of Spain to East China. There are also many undescribed fossils at PIN from the supposed Aptian of central Mongolia.

Remarks. The reason for the above synonymization is that *Cretosphex incertus* and *Mateosphex venulosus* have no important venational differences from *Archisphex crowsoni*. *Palaeapis beiboziensis* differs from the latter in possessing elongate cells 1mcu and 2cua, but *Archisphex boothi* provides intermediates. *Cretosphex magnus*

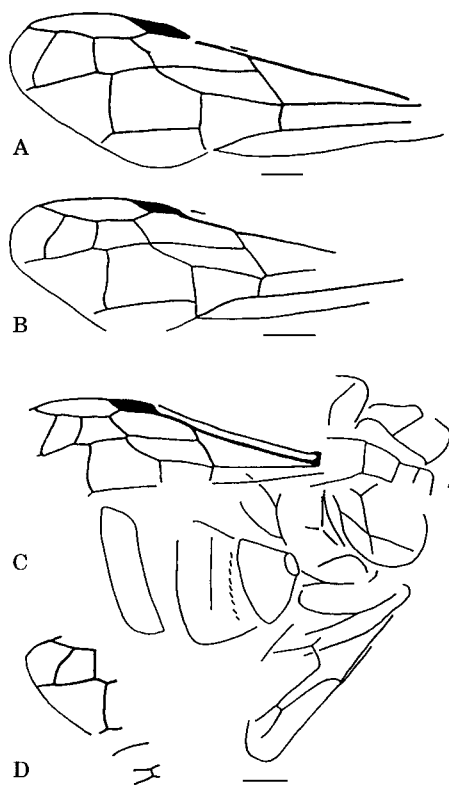


Figure 30. A–D. *Archisphex boothi* Jarzembowski 1991 A, BMB 014895/-6; B, 018514; C, 018527/-8; D, 018529.

Darling 1990 and *C. parvus* Darling 1990 do not belong to *Archisphex* because of the distal position of 2r-m.

Archisphex crowsoni Evans 1969

1969 *Archisphex crowsoni* Evans, p. 254, fig. 1.

Holotype. MCZ 6312; middle Wadhurst Clay; Quarry Hill Brickworks, Tonbridge, Kent; mid Valanginian. The unique type consists of the impression of an incomplete forewing (not examined).

Archisphex boothi Jarzembowski 1991

Figure 30

1987 *Archisphex* n. sp. Jarzembowski, p. 330, figs 14, 15, 17.

1991b *Archisphex boothi* Jarzembowski, p. 104, fig. 16.

Holotype. BMB 014895/-6 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; old pit, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by E. A. Jarzembowski; impression of incomplete forewing.

Paratype. NHM In. 64650/64656 (part and counterpart); from below Bed 5c, Upper Weald Clay; Smokejacks Brickworks, Ockley, Surrey; Lower Barremian; collected by E. A. Jarzembowski.

Additional material. BMB 018514, from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; old pit, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by E. A. Jarzembowski; impression of incomplete forewing 8.4 mm long. BMB 018527/-8 (part and counterpart) from between Beds 3a and 3c, Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by A. J. Ross; incomplete body without head and most of legs, with forewing length 7.9 mm. Possibly BMB 018529, from between Beds 3a and 3c, Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by E. A. Jarzembowski; small fragment of apices of fore- and hindwings.

Remarks. The new material does not add much to our knowledge of the species morphology. The size variation is modest (7.9–9.4 mm for the forewing length). Body structures are difficult to interpret, except for the moderately long and thick legs, light ground colour of the body, and hindwing with cu-a placed somewhere before the M + Cu fork.

Archisphex proximus Rasnitsyn et Jarzembowski sp. nov.

Figure 31

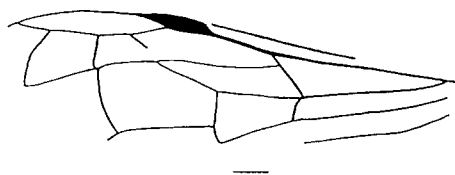


Figure 31. *Archisphex proximus* sp. nov., holotype BMB 018530; Clockhouse Brickworks, Upper Hauterivian.

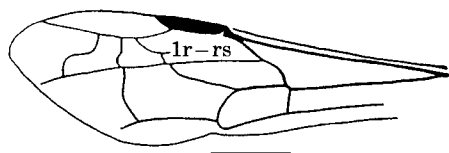


Figure 32. *Archisphex curvus* sp. nov., holotype BMB 018504; Auclaye Brickworks, Lower Barremian.

Etymology. The species epithet is Latin for 'close' and refers to position of the crossvein 2r-m in respect to 2m-cu.

Holotype. BMB 018530; from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; old pit, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by Mr A. A. Mitchell.

Diagnosis. The largest species in the genus; similar to *A. boothi* in having base of RS removed from pterostigma but differing in 2r-m which is close to 2m-cu.

Description. The unique type consists of the incomplete impression of a forewing. Pterostigma issuing 2r-rs near its apex (at a point less than the length of 2r-rs); base of RS removed from pterostigmal base for about a pterostigmal length; RS between 2r-rs and 2r-m of same length as 2r-rs; 1r-rs rudiment absent; cell 2rm twice as long as high, probably slightly overlapping with 1mcu; cell 3rm longer than 2rm; 2r-m almost straight; 3r-m slightly bent, distant from 3r apex by half its length; cu-a scarcely postfurcal; cell 2cua of subequal length on Cu and A.

Measurements. Forewing length 12.5 mm.

Archisphex curvus Rasnitsyn et Jarzembowski sp. nov.

Figure 32

Etymology. The species epithet refers to the very curved crossvein 3r-m.

Holotype. BMB 018504; from between Beds 3a and 3c, Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by Mr A. A. Mitchell.

Diagnosis. Differs from other species in markedly sinuate 3r-m.

Description. The unique type consists of the impression of a forewing. Pterostigma issuing 2r-rs near its apex (at a point less than the length of 2r-rs); base of RS close to pterostigmal base; RS between 2r-rs and 2r-m much shorter than 2r-rs; 1r-rs rudiment well developed; cell 2rm far from 1mcu with length and height subequal; 2-3r-m sinuate; 3r-m removed from apex of cell 3r by about its length; cell 3rm more than twice as long on M as on RS; cu-a antefurcal; cell 2cua longer on Cu than on A.

Measurements. Forewing length 5.6 mm.

Genus *Angarosphex* Rasnitsyn 1975

=*Shandongodes* Zhang 1985 syn. nov. (Type species, *S. lithodes* Zhang 1985).

Type species. *Angarosphex myrmicopterus* Rasnitsyn 1975, Lower Cretaceous of Transbaikalia.

Diagnosis. Like *Archisphex*, *Angarosphex* belongs to a group of Lower Cretaceous apoid wasps with cells 2rm and 1mcu touching each other for a short distance or

Table 3. Key for identification of species of *Angarosphex*.

1.	2r-rs distinctly shorter than pterostigmal height	2
	— 2r-rs not shorter than pterostigmal height	6
2.	1r-rs rudiment long, RS between 2r-rs and 2r-m shorter than pterostigmal height. Forewing length 7.9 mm <i>A. goldringi</i> Jarzembowski 1991, Weald Clay of southern England	
	— 1r-rs rudiment short or absent, RS between 2r-rs and 2r-m not shorter than pterostigmal height	3
3.	3r-m strongly oblique, sinuate. Forewing length 5.8 mm <i>A. consensus</i> sp. nov., Weald Clay of southern England	
	— 3r-m subvertical, not sinuate	4
4.	Pterostigma issuing 2r-rs before its midlength, cells 2rm and 3rm of equal length, upper and lower sides of cell 1mcu of equal length; forewing length about 6 mm <i>A. myrmicopterus</i> Rasnitsyn 1975, Lower Cretaceous of Transbaikalia	
	— Pterostigma issuing 2r-rs beyond its midlength, cell 3rm much longer than 2rm, upper side of cell 1mcu much longer than its lower side	5
5.	Pterostigma subtriangular, issuing 2r-rs near apical 1/3 of its length; 3r-m away from apex of cell 3r by about its length; forewing length c. 5 mm <i>A. pallidus</i> Rasnitsyn 1986, Lower Cretaceous of West Mongolia	
	— Pterostigma parallel-sided, issuing 2r-rs near its apical 1/4, 3r-m closer to apex of cell 3r; forewing length 10 mm <i>A. bleachi</i> sp. nov., Weald Clay of southern England	
6(1).	RS between RS + M and 2r-rs subvertical. Aptian of Brazil	7
	— RS between RS + M and 2r-rs strongly oblique. Pre-Aptian of Eurasia	8
7.	Forewing length c. 6.5 mm <i>A. parvus</i> (Darling 1990)	
	— Forewing length 9–10 mm <i>A. magnus</i> (Darling 1990)	
8(6).	RS base near pterostigmal base, pterostigma issuing 2r-rs near its midlength. Forewing length about 5–6 mm <i>A. niger</i> Rasnitsyn 1990, Lower Cretaceous of Transbaikalia	
	— RS base far from pterostigmal base, pterostigma issuing 2r-rs well beyond its midlength. Forewing length 5.6 mm <i>A. lithodes</i> (Zhang 1985), Laiyang Fm (Upper Jurassic or, rather, lower Lower Cretaceous), Shandong, China	

not at all. Within this group, *Angarosphex* differs from *Archisphex* Evans and *Trichobaissodes* Rasnitsyn in 3rm receiving 2m-cu, and from the other described genera in the antefurcal cu-a; additionally it differs from *Baissodes* Rasnitsyn in a comparatively short 2rm, and from *Vitimobaissodes* Rasnitsyn and *Oryctobaissodes* Rasnitsyn in the acuminate apex of 3r which is situated on the wing margin or very close to it.

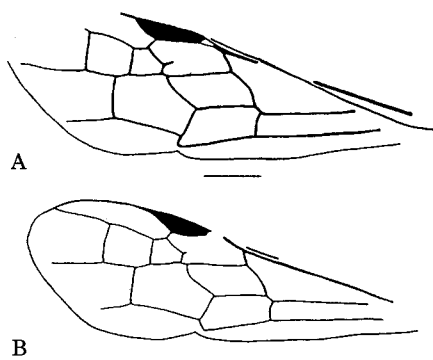


Figure 33. *Angarosphex goldringi* Jarzembowski: A, holotype BMB 014893/-4, Auclaye Brickworks, Lower Barremian; B, BMB 016403/-4, Upper Weald Clay, Bookhurst Tileworks, Upper Barremian.

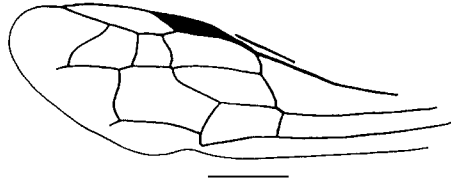


Figure 34. *Angarosphex consensus* sp. nov., holotype BMB 018532/-3; Clockhouse Brickworks, Upper Hauterivian.

Included species. These are keyed out in Table 3, their range extending from the pre-Aptian Lower Cretaceous deposits of England to east China plus the Aptian of Brazil. An undescribed fossil is also known from the Lower Barremian of northeast Spain (Gómez Pallerola, 1986, fig. 2, photograph 35); additional material is in PIN, including from the supposed Aptian of central Mongolia.

Remarks. *Shandongodes necrodes* Zhang 1985 belongs neither to Sphecidae nor to other aculeate wasps, judging from its external ovipositor.

Angarosphex goldringi Jarzembowski 1991b

Figure 33

1991b *Angarosphex goldringi* Jarzembowski, p. 105, fig. 17.

Holotype. BMB 014893/-4 (part and counterpart); from between Beds 3a and 3c, Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by E. A. Jarzembowski; impression of incomplete forewing.

Additional material. BMB 016403/-4 (part and counterpart), from above Bed 8a, Upper Weald Clay; Bookhurst Tileworks, Cranleigh, Surrey; Upper Barremian; collected by A. J. Ross; impression of forewing virtually identical to holotype.

Angarosphex consensus Rasnitsyn et Jarzembowski sp. nov.

Figure 34

Etymology. Species epithet is from Latin for 'agreement'.

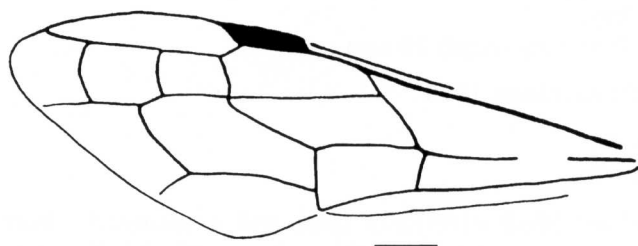
Holotype. BMB 018532/-3 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; old pit, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by E. A. Jarzembowski.

Diagnosis. The species differs from other congeners with their short 2r-rs by sinuate 3r-m.

Description. The unique type consists of the impression of an incomplete forewing. Pterostigma issuing 2r-rs beyond its midlength and somewhat widened towards that point; RS base removed from pterostigma base by less than the pterostigmal length; RS (between 2r-rs and 1m-cu) sinuate, subperpendicular, lacking 1r-rs rudiment and longer than between 2r-rs and 2r-m; length of 2r-rs about half pterostigmal height; 2r-m almost straight; 3r-m subperpendicular, oblique, sinuate, closer to 2r-m than to 3r apex though removed from the latter by less than its length; upper side of 1m-cu much longer than its lower side; 2m-cu in basal quarter of 3r-m.

Measurements. Forewing length 5.8 mm.

A



B

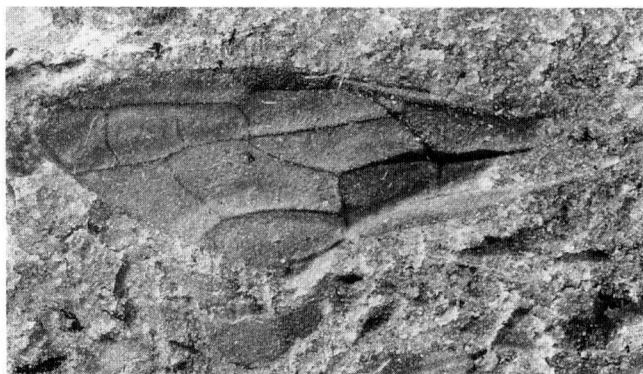


Figure 35. A, B. *Angarosphex bleachi* sp. nov., holotype BMB 018515/-6, B, $\times 8$; Clockhouse Brickworks, Upper Hauterivian.

Angarosphex bleachi Rasnitsyn et Jarzembowski sp. nov.

Figure 35

Etymology. Species named after collector, Mr G. Bleach.

Holotype BMB 018515/-6 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; Clockhouse Rock Store, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by Mr G. Bleach.

Diagnosis. New species similar to *A. magnus* in large size but differs in short 2r-rs.

Description. The unique type consists of the impression of a forewing. Forewing with pterostigma parallel-sided, issuing 2r-rs subapically; RS base distant from pterostigmal base by almost pterostigmal length; RS between 2r-rs and 1m-cu almost straight, subvertical, lacking 1r-rs rudiment, shorter than between 2r-rs and 2r-m; 2r-rs about as long as pterostigma high; 2-3r-m subvertical, slightly

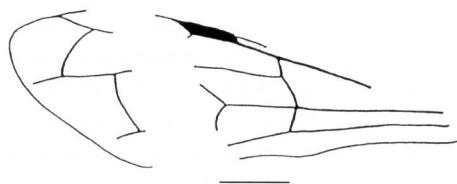


Figure 36. ?*Baissodes* sp., BMB 18512/-3; Clockhouse Brickworks, Upper Hauterivian.

arching; 3r-m removed from 3r apex for 0.7 of its length, from 2r-m for more than its length; upper side of 1mcu much longer than its lower side; 2m-cu in basal third of 3rm.

Measurements. Forewing length 10 mm.

Genus *Baissodes* Rasnitsyn 1975

?*Baissodes* sp.

Figure 36

Material examined. BMB 018512/-3 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; Clockhouse Rock Store, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by Mr W. Gordon.

Description. The unique specimen consists of the impression of an incomplete forewing. Pterostigma parallel-sided, issuing 2r-rs subapically; base of RS removed from pterostigmal base by almost the pterostigmal length; cell 3r acuminate at wing margin; 3r-m oblique, slightly arching, removed from 3r apex by about half its length; upper side of cell 1mcu much longer than its lower side, probably slightly or not at all overlapping 2rm; 2m-cu well beyond 2r-m; cu-a interstitial.

Measurements. Forewing length 6.6 mm.

Remarks. The size and general appearance of the wing conform well with the Lower Cretaceous sphecids in which the forewing cell 1mcu overlaps slightly or not at all with cell 2rm (Sphecidae + Angarosphecidae + Baissodidae *sensu* Rasnitsyn, 1975). Within that group, the only known genus combining an acuminate cell 3r with an interstitial cu-a is *Baissodes* Rasnitsyn 1975. However, the Wealden form differs from all known species (*B. robustus* Rasnitsyn 1975, *B. magnus* Rasnitsyn 1975, *B. longus* Rasnitsyn 1986) in that 3r-m is more oblique and less distant from the apex of cell 3r, and also by a smaller wing size.

Genus *Pompilopterus* Rasnitsyn 1975

Type species. *Pompilopterus ciliatus* Rasnitsyn 1975, Lower Cretaceous of Transbaikalia.

Diagnosis. Differs from other Lower Cretaceous sphecids in having cells 1mcu and 2rm extensively overlapping. Unique venational differences from all other Sphecidae are unknown, but at least the extant subfamilies represented in the Cretaceous (Ampulicinae and Pemphredoninae) rarely possess the above character.

Included species. These are keyed out in Table 4, being known from the pre-Aptian Lower Cretaceous of England and Transbaikalia. Undescribed fossils from the supposed Aptian of Central Mongolia are in PIN.

Remarks. *Pompilopterus ciliatus* has been described (Rasnitsyn, 1975: 106) as a member of Pompilidae based on general appearance, despite the narrow 3r cell not being at all characteristic of that family. Now the discovery of body material (*Pompilopterus corpus* sp. nov. below) shows reliable diagnostic features of Apoidea, viz. pronotal spiracular lobes strongly elongate backwards and the presence of a propodeal enclosure. As to the position of the genus within apoidea, this problem needs consideration in the light of all available material of Lower

Table 4. Key for identification of species of *Pompilopterus*.

1.	M weakly angled at fork with RS and at 1m-cu; pterostigma parallel-sided or weakly expanded below, usually issuing 2r-rs beyond its midlength; RS not arching forward between 2r-m and 3r-m; 1m-cu in 2nd third of cell 2rm — M strongly angled at fork with RS and at 1m-cu; pterostigma issuing 2r-rs at its midlength; cell 2rm longer than 3rm; 1m-cu at 1st third of 2rm (questionable <i>Pompilopterus</i>)	2 5
2.	cu-a antefurcal; RS between RS + M and 2r-rs longer than between 2r-rs and 2r-m — cu-a postfurcal; RS between RS + M and 2r-rs shorter than between 2r-rs and 2r-m (but unknown for <i>P. ciliatus</i>)	3 4
3.	cell 2rm much shorter than cell 1mcu; pterostigma issuing 2r-rs far beyond its midlength; forewing length 7.2 mm <i>P. corpus</i> sp. nov. — 2rm longer than 1mcu; pterostigma issuing 2r-rs near its midlength; forewing length 6.5 mm <i>P. wimbledoni</i> sp. nov.	
4(2).	RS between RS + M and 2r-rs straight, about 2 times as long as 2r-rs; forewing length about 8.0–8.5 mm <i>P. ciliatus</i> Rasnitsyn 1975 — RS between RS + M and 2r-rs bent, about 3 times as long as 2r-rs; forewing length about 5.0–5.5 mm <i>P. keymerensis</i> sp. nov.	
5(1).	pterostigma low triangular, RS long and bent between RS + M and 2r-rs, arching forward between 2r-m and 3r-m; 2r-m subvertical — pterostigma parallel-sided; RS short and almost straight between RS + M and 2r-rs, 2r-m very oblique ? <i>P. difficilis</i> sp. nov.	6
6.	RS between RS + M and 2r-rs sinuate; cell 3rm elongate; forewing length 7.5 mm ? <i>P. worssami</i> sp. nov. — RS between RS + M and 2r-rs gently arching; cell 3rm higher than long; forewing length 4.6 mm ? <i>P. leei</i> sp. nov.	

Cretaceous putative Apoidea and lies much beyond the scope of the present paper. However, what is evident is that the long pronotum and long, percurrent notauli in *Pompilopterus* are symplesiomorphic with Ampulicinae and the above grouping of Cretaceous Sphecidae (i.e., *Archisphex*, *Angarosphex*, *Baissodes*) which lacks ampulicine apomorphies as outlined by Alexander (1992), viz. a pitted basal sulcus of the scutellum (as in *Pompilopterus*; Figure 37) and reduced number of male metasomal segments. This means that the fossils most probably represent one or more extinct, possibly paraphyletic subfamilies of Sphecidae.

Pompilopterus corpus Rasnitsyn et Jarzembowski sp. nov.

Figure 37

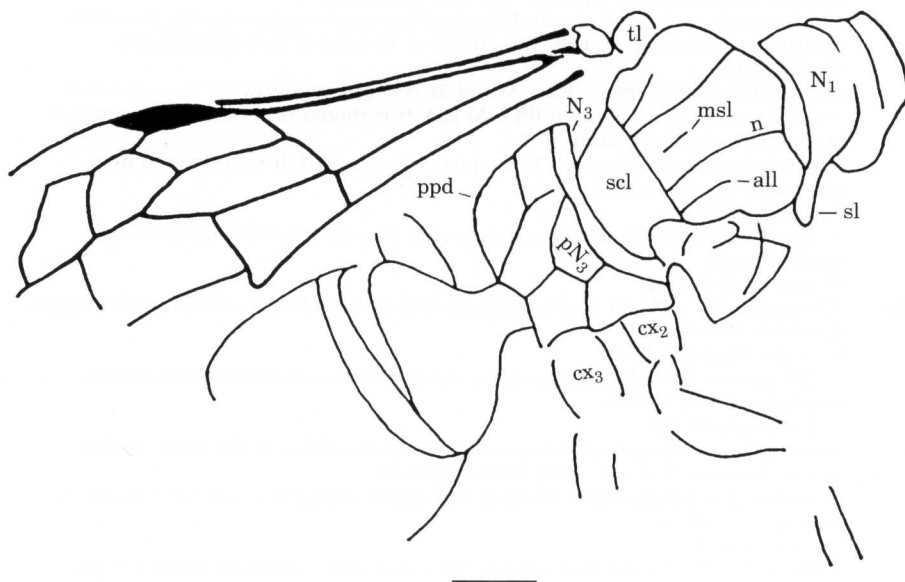
Etymology. Species epithet is Latin for 'body' referring to the first known body remains of this genus.

Holotype. BMB 018523/-4 (part and counterpart); from between Beds 3a and 3c, Upper Weald Clay; Rudgwick Brickworks, Rudgwick, West Sussex; Lower Barremian; collected by A. J. Ross.

Diagnosis. Differs from other congeners in its very short cell 2rm.

Description. The unique type consists of the impression of a forewing and an incomplete body without head and much of legs and metasoma. Pronotum long, narrow, with two transverse sulci and elongate spiracular lobes directed posterolaterally although form of lower corners is unknown. Mesonotum with notauli percurrent, adlateral lines well developed, medial scutal line rudimentary,

A



B



Figure 37. *Pompilopterus corpus* sp. nov., holotype BMB 018523/-4, B, $\times 8$; Rudgwick Brickworks, Lower Barremian. Abbreviations: all - adlateral line, cx_2 - mid coxa, cx_3 - hind coxa, msl - mid-scutal line, N_1 - pronotum, N_3 - metanotum, n - notaulus, pN_3 - metapostnotum, ppd - propodeum, scl - scutellum, sl - spiracular lobe, tl - tegula.

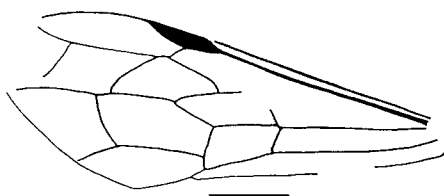


Figure 38. *Pompilopterus wimbledoni* sp. nov., holotype NHM In. 59217; Durlston Bay, Lower Berriasian.

and no transcutal suture independent of straight scuto-scutellar one. Metanotum narrow and ribbon-like; metapostnotum (propodeal enclosure) triangular and followed by a midpropodeal line; propodeum with lateral longitudinal and transverse lines. Mid and hind coxae elongate, midlegs moderately thick, femora thickest subbasally. Forewing with base of RS close to pterostigmal base, pterostigma nearly parallel-sided and issuing 2r-rs far beyond its midlength; 2r-rs shorter than pterostigmal height; RS between RS + M and 2r-rs almost straight, the same section plus two following ones of RS becoming progressively shorter, not arching forward between 2r-m and 3r-m; cell 2rm shorter than 1 + 2r and with 1m-cu near its midlength; 2- and 3r-m both oblique, 3r-m sinuate; M not distinctly bent where leaving RS + M and at 1m-cu; 2m-cu meeting cell 3rm in its basal third; cu-a slightly antefurcal. 1st metasomal segment wide and short, appearing short petiolate.

Measurements. Length of body, as preserved, 9.0 mm; length of forewing, 7.2mm.

Pompilopterus wimbledoni Rasnitsyn et Jarzembowski sp. nov.

Figure 38

Etymology. Species named after Dr W. A. Wimbledon, Jurassic and Cretaceous stratigrapher.

Holotype. NHM In. 59217; Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collector unknown.

Diagnosis. Differs from other congeners in extraordinarily long cell 2rm.

Description. The unique type consists of the impression of a forewing. Pterostigma slightly arched below, issuing 2r-rs at its midlength; 2r-rs shorter than pterostigmal height; RS between RS + M and 2r-rs very long, bent subbasally but between 2r-rs and 2r-m very short (shorter than 2r-rs) and between 2r-m and 3r-m very long, not arching forward; 2r-m very oblique, 3r-m considerably so; cell 2rm longer than cells 1 + 2r, 3rm, 1m-cu, with 1m-cu reaching near its

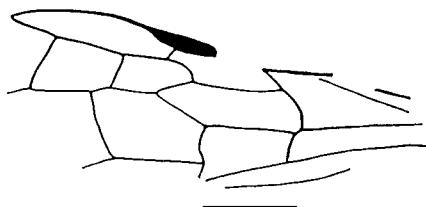


Figure 39. *Pompilopterus keymerensis* sp. nov., holotype BMB 018517/-8; Keymer Tileworks, Upper Hauterivian.

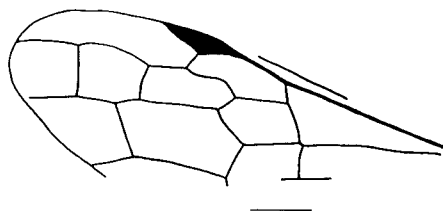


Figure 40. ?*Pompilopterus worssami* sp. nov., holotype BMB 018508/-9; Clockhouse Brickworks, Upper Hauterivian.

midlength; M not distinctly bent where leaving RS + M and at 1m-cu; 2m-cu meeting cell 3rm near its base; cu-a slightly antefurcal.

Measurements. Length of forewing, 6.5 mm.

Pompilopterus keymerensis Rasnitsyn et Jarzembowski sp. nov.

Figure 39

Etymology. Species named after type locality.

Holotype. BMB 018517/-8 (part and counterpart); from below Bed 3a, Lower Weald Clay; Keymer Tileworks, Burgess Hill, West Sussex; Upper Hauterivian; collected by A. J. Ross.

Diagnosis. Similar to *P. ciliatus* in postfurcal cu-a but differing in smaller size and sinuate RS between M and 2r-rs.

Description. The unique type consists of the impression of an incomplete, damaged forewing. RS base well before pterostigmal base, pterostigma almost parallel-sided, issuing 2r-rs somewhat beyond its midlength; 2r-rs shorter than pterostigmal height; RS between RS + M and 2r-rs moderately bent, shorter than between 2r-rs and 2r-m and much shorter than between 2r-m and 3r-m; RS between 2r-m and 3r-m not arching forward; 2r-m and 3r-m slightly oblique; cell 2rm shorter than cells 1 + 2r, 3rm, 1mcu with 1m-cu near its midlength; M not distinctly bent where leaving RS + M and at 1m-cu; 2m-cu meeting 3rm near its 1st quarter; cu-a postfurcal.

Measurements. Length of forewing, *c.* 5.0–5.5 mm.

?*Pompilopterus worssami* Rasnitsyn et Jarzembowski sp. nov.

Figure 40

Etymology. Species named after Mr B. Worssam, Wealden surveyor.

Holotype. BMB 018508/-9 (part and counterpart); from between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; new pit, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by E. A. Jarzembowski.

Diagnosis. Differs from other *Pompilopterus* in RS sinuate between RS + M and 2r-rs; from ?*P. leei* in larger size and in longer cells 2- and 3r-m.

Description. The unique type consists of the impression of a forewing. RS removed from pterostigmal base by a pterostigmal length; pterostigma low triangular issuing 2r-rs at its midlength; 2r-rs shorter than pterostigmal height; RS between RS + M and 2r-rs sinuate, longer than between 2r-rs and 2r-m, longer than RS + M, arching forward between 2r-m and 3r-m; 2r-m and 3r-m subvertical, almost straight; cell 2rm longer than cells 3rm and 1mcu; 3rm longer than

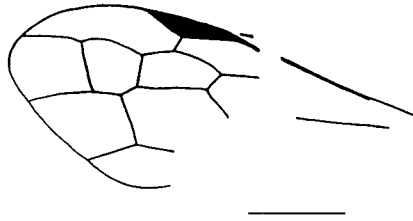


Figure 41. ?*Pompilopterus leei* sp. nov., holotype BMB 018525/-6; Clockhouse Brickworks, Upper Hauterivian.

high; M distinctly bent where leaving RS + M and at 1m-cu; 1m-cu near 1st quarter of cell 2rm; 2m-cu meeting cell 3rm slightly before its midlength; cu-a antefurcal.

Measurements. Length of forewing, 7.5 mm.

Remarks. This and the following species differ from other *Pompilopterus* and Cretaceous Sphecidae in general in their short and pentagonal cell 1m-cu, and conspicuously bent RS between RS + M and 2r-rs. No other close relatives are recognized at present. That is why the species *worssami* and *leei* are questionably assigned to *Pompilopterus*.

?*Pompilopterus leei* Rasnitsyn et Jarzembowski sp. nov.

Figure 41

Etymology. Species named after Mr A. Lee, regular Rock Store collector.

Holotype BMB 018525/-6 (part and counterpart); between the Clockhouse Sandstone and *Cassiope* Band, Lower Weald Clay; Clockhouse Rock Store, Clockhouse Brickworks, Capel, Surrey, Upper Hauterivian; collected by A. J. Ross. The unique type consists of the impression of an incomplete forewing.

Diagnosis. Very similar to previous species, but differing in smaller size, RS between RS + M and 2r-rs gently arching instead of sinuate; 2- and 3rm shorter.

Measurements. Length of forewing, 4.6 mm.

?*Pompilopterus difficilis* Rasnitsyn et Jarzembowski sp. nov.

Figure 42

Etymology. Species epithet is Latin for 'difficult', referring to its obscure taxonomic position.

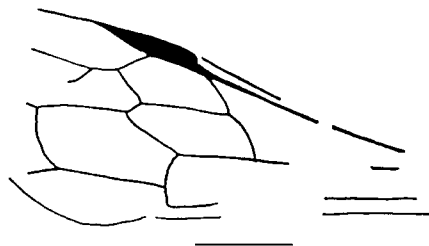


Figure 42. ?*Pompilopterus difficilis* sp. nov., holotype NHM In. 59222; Durlston Bay, Lower Berriasian.

Holotype. NHM In. 59222; Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by the Rev. O. Fisher. The unique type consists of the impression of an incomplete forewing.

Diagnosis. Differs from other congeners in its very oblique 2r-m.

Description. RS close to pterostigmal base; pterostigma parallel-sided, issuing 2r-rs slightly beyond its midlength; 2r-rs longer than pterostigmal height; RS between RS + M and 2r-rs straight, longer than between 2r-rs and 2r-m, slightly longer than 2r-rs, not arching forward beyond 2r-m; 2r-m very oblique (possibly sinuate); M distinctly bent where leaving RS + M and at 1m-cu, short between these points; cu-a interstitial.

Measurements. Length of forewing, 5.4–5.7 mm.

Remarks. The incomplete fossil is somewhat reminiscent of some *Pompilopterus* wings but differs in the relatively distal position of the base of RS, and the proximal position of 1m-cu. As in the two previous species, no other close relative is recognized at present. The new species is referred questionably to *Pompilopterus*.

Genus *Ivestia* Rasnitsyn et Jarzembowski gen. nov.

Etymology. Genus named after Dr I. West, Purbeck sedimentologist.

Type species. *I. provecta* sp. nov. described below.

Diagnosis. Forewing similar to that found in Sphecidae: Pemphredonina (*sensu* Bohart & Menke, 1976) characterised by 3r acuminate at wing margin; cells 1 + 2r and 2rm fused (with corresponding loss of RS connection); 3r-m and 1- and 2m-cu present; 1m-cu meeting M near former point of divergence of RS and M (judging from position of spectral vein rudiment of RS), 2m-cu meeting 3rm. Differing from the subtribe Pemphredonina in the base of RS being separated from the pterostigma by almost a pterostigmal length (close to pterostigma in Pemphredonina); in cu-a meeting Cu almost at right angles (clearly not an obtuse angle) and in RS between cells 1 + 2r and 2rm being not completely lost but preserved as a faint (spectral in terms of Mason, 1986) vein (indicated by dots in fig. 43).

Included species. Type species described below.

Remarks. The forewing is unique among Upper Cretaceous and Jurassic apocritans in having lost RS between RS + M and 2r-rs; otherwise the venation is virtually complete. Pemphredonina are known from the Upper Cretaceous (*Pittoecus* Evans 1973 and probably *Cretoecus* Budrys; Budrys 1993) so that this

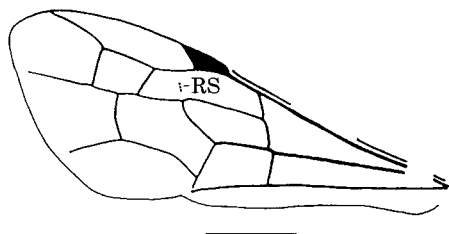


Figure 43. *Ivestia provecta* gen. et sp. nov., holotype BMB 018505/021008; Durlston Bay, Lower Berriasian.



Figure 44. ?sphecid gen. et sp. indet., NHM I.12612; Dinton, Middle Berriasian.

fossil could represent an early member or lie close to the ancestry of this subtribe. However, it could equally well be a descendant of a stem sphecid which has lost RS between RS + M and 2r-rs convergently with Pemphredonina.

Iwestia provecta Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 43

Etymology. Species epithet is Latin for 'advanced' referring to advanced venation.

Holotype. BMB 018505/021008; Worbarrow Tout Member, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by Mr A. A. Mitchell. The unique type consists of the impression of a forewing.

Description. Pterostigma short, triangular, moderately large, issuing 2r-rs slightly beyond its midlength; 2r-m slightly oblique, removed from pterostigma by more than its length; 3r-m vertical, away from 2r-m by slightly more than its length and from apex of cell 3r by about 1.5 times its length; cell 1mcu with upper side 1.5 times longer than lower side; 2m-cu meeting cell 3rm at about 0.4 of its length; Cu bent nearly at 1st one third of 2mcu and then running subparallel to M; cu-a antefurcal.

Measurements. Length of forewing, 5.4 mm.

?sphecid gen. et sp. indet.

Figure 44

Material examined: NHM I.12612; Worbarrow Tout Member, Insect Limestone, Lulworth Formation; Dinton, Vale of Wardour, Wiltshire; Middle Berriasian; collected by the Rev. P. B. Brodie.

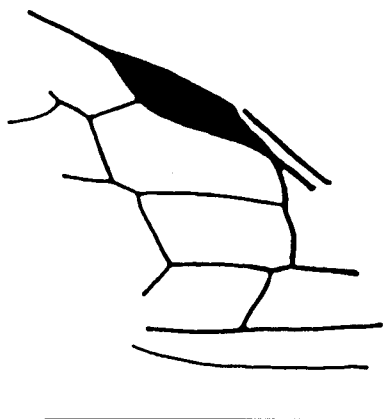


Figure 45. *Apocritites distinctus* gen. et sp. nov., holotype BMB 020517; Durlston Bay, Upper Berriasian.

Description. The unique specimen consists of the incomplete impression of a body without a head and most of the wings. Body moderately robust, of wasp-like general appearance but with few details clearly visible. Ground colour light, no coarse sculpture discernible. Legs moderately short, thick, hind tibia with spur thin, slightly curved. Forewing with cu-a long, oblique, antefurcal.

Measurements. Length of body without head, 10.6 mm, length of forewing from base to base of M, 3 mm.

Remarks. The general habitus and size are suggestive of Sphecidae and the observable characters are consistent with this interpretation. *Ivestia provecta* and *Pompilopterus wimbledoni* are similar in possessing an antefurcal cu-a but differ in size (forewing sections 3 mm long and 2 mm long respectively). However, *Angarosphex* and many species of *Archisphex* also have an antefurcal cu-a. Even a tentative generic assignment is therefore impossible and more material is needed.

Suborder Vespina

Superfamily *incertae sedis*

Genus *Apocritites* Rasnitsyn et Jarzembowski gen. nov.

Etymology. Genus name is derived from Apocrita, the name of higher hymenopterans; gender: masculine.

Type species. *A. distinctus* sp. nov. described below.

Diagnosis. The wing fragment under consideration is too small to permit a reliable comparison with all main groups of apocritans. However, it cannot belong to Karatavitidae and Ephialtitidae because of its small size, to Ichneumonomorpha because of a distinct costal space, and to Proctotrupomorpha because of 2r-m which leaves RS much distad of 2r-rs. Thus the new genus could belong either to Evaniomorpha, or to Vespomorpha. In neither of these two infraorders, and particularly in none of their Mesozoic members are we aware of the presence of an unusual combination of characters, viz. very long and wide pterostigma, distal position of the RS + M fork, strongly proclined 2r-m, and postfurcal cu-a.

Apocritites distinctus Rasnitsyn et Jarzembowski gen. et sp. nov.

Figure 45

Table 5. List of Vespida by family from the Purbeck (P) and Wealden (W) of southern England († extinct family), and number of specimens recovered.

1.	†Xyelotomidae (xyelotomid sawflies)	<i>Undatoma stigmatica</i> sp. nov.	1 P
2.		<i>Undatoma rudgwickensis</i> sp. nov.	1 W
3.		<i>Undatoma bicolor</i> sp. nov.	1 W
4.	†Sepulcidae (sepulcid sawflies)	<i>Trematothorax clementsi</i> sp. nov.	1 P
5.		<i>Trematothorax valdensis</i> sp. nov.	1 W
6.		? <i>Trematothorax</i> sp.	1 P
7.	Anaxyelidae (anaxyelid wood wasps)	<i>Eosyntexis tuffinae</i> sp. nov.	1 P
8.	Siricidae (wood wasps/horntails)	<i>Myrmicium heeri</i> Westwood	1 P
9.	Trigonalidae (trigonalid wasps)	<i>Turgonalus cooperi</i> sp. nov.	1 W
10.	Stephanoidea <i>incertae sedis</i> (stephanoid wasps)	<i>Arossia joyceae</i> gen. et sp. nov.	1 W
11.	Gasteruptiidae (gasteruptiid wasps)	<i>Manlaya oculatissima</i> sp. nov.	1 P
12.		<i>Manlaya anglica</i> sp. nov.	1 P
13.		<i>Manlaya ockleyensis</i> sp. nov.	1 W
14.		<i>Manlaya capelensis</i> sp. nov.	1 W
15.	?Gasteruptiidae	<i>Tillywhimia spectra</i> gen. et sp. nov.	1 P
16.		<i>Tillywhimia colorata</i> gen. et sp. nov.	1 P
17.	†Cretevaniidae (Cretaceous ensign wasps)	<i>Cretevania concordia</i> sp. nov.	1 W
18.	Proctotrupidae (proctotrupid wasps)	<i>Dintonia despectata</i> gen. et sp. nov.	1 P
19.		<i>Pallenites calcarius</i> gen. et sp. nov.	1 P
20.		<i>Peverella punctata</i> gen. et sp. nov.	1 P
21.	Diapriidae (diapriid wasps)	<i>Coramia minuta</i> gen. et sp. nov.	1 P
22.	Proctotrupoidea <i>incertae sedis</i> (proctotrupoid wasps)	<i>Amitchellia procera</i> gen. et sp. nov.	1 P
23.		<i>Amitchellia brevis</i> gen. et sp. nov.	1 P
24.	Proctotrupomorpha <i>incertae sedis</i> (proctotrupomorph wasps)	Gen. et sp. indet.	1 P
25.	†Eoichneumonidae (dawn ichneumon flies)	<i>Purichneumon britannicus</i> gen. et sp. nov.	1 P
26.	†Bethylonymidae (bethylonymid wasps)	<i>Bethylonymellus feltoni</i> sp. nov.	1 P
27.	Sphecidae (digger wasps)	<i>Archisphex croxsoni</i> Evans	1 W
28.		<i>Archisphex boothi</i> Jarzembowski	4 W
29.		<i>Archisphex ?boothi</i> Jarzembowski	1 W
30.		<i>Archisphex proximus</i> sp. nov.	1 W
31.		<i>Archisphex curvus</i> sp. nov.	1 W
32.		<i>Angarosphex goldringi</i> Jarzembowski	2 W
33.		<i>Angarosphex consensus</i> sp. nov.	1 W
34.		<i>Angarosphex bleachi</i> sp. nov.	1 W
35.		? <i>Baissodes</i> sp.	1 W
36.		<i>Pompilopterus corpus</i> sp. nov.	1 W
37.		<i>Pompilopterus wimbledoni</i> sp. nov.	1 P
38.		<i>Pompilopterus keymerensis</i> sp. nov.	1 W
39.		? <i>Pompilopterus worssami</i> sp. nov.	1 W
40.		? <i>Pompilopterus leei</i> sp. nov.	1 W
41.		? <i>Pompilopterus difficilis</i> sp. nov.	1 P
42.		<i>Iwestia provecta</i> gen. et sp. nov.	1 P
43.	?Sphecidae (?digger wasps)	Gen. et sp. indet.	1 P
44.	Apocrita <i>incertae sedis</i> (wasps)	<i>Apocritites distinctus</i> gen. et sp. nov.	1 P

Total 48 specimens (23 P, 25 W)

Holotype. BMB 020517; Clements' Bed DB175, *Corbula* beds, Stair Hole Member, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by Mr R. Coram.

Description. The unique specimen consists of an incomplete forewing (without base and apex). Costal space distinct but not wide; base of RS close to pterostigma, directed posterobasally, slightly angled with M at junction; pterostigma high and long, broadening subapically near 2r-rs; RS + M forking well beyond 1m-cu; RS section between RS + M and 2r-rs of subequal length with 2r-rs and maximum height of pterostigma, and almost twice as long as RS between 2r-rs

Table 6. Material examined: origin and relations. The three columns are Wealden/Purbeck species (left), nearest relative(s) (middle), and assemblage type or range (right). Abbreviations: L, l., lower; Cret., Cretaceous; s/type, subtype; U, u, upper.

WEALD CLAY GROUP		
Upper Weald Clay Formation, Barremian		
UPPER BARREMIAN (from above Bed 8a, Bookhurst Tileworks, Surrey);		
<i>Angarosphex goldringi</i>	<i>Angarosphex</i> spp.	L. Cret. type (E.Asia) & Aptian (Brazil)
LOWER BARREMIAN		
from below Bed 5c (Smokejacks Brickworks, Surrey)		
<i>Manlaya ockleyensis</i>	<i>Manlaya</i> spp.	L. Cret. type (E.Asia)
<i>Archisphex boothi</i>	<i>Archisphex</i> spp.	L. Cret. type (E.Asia) & L. Barremian (Spain)
from between Beds 3a and 3c		
Rudgwick Brickworks, West Sussex		
<i>Undatoma rudgwickensis</i>	<i>Undatoma</i> spp.	Jur. type & l. L. Cret. s/type (E.Asia)
<i>Turgonalus cooperi</i>	<i>Turgonalus minor</i> Rasn.	l. L. Cret. s/type (Transbaikalia)
<i>Pompilopterus corpus</i>	<i>Pompilopterus</i> spp.	L. Cret. type (E.Asia)
Aucley Brickworks, Surrey		
<i>Arossia joyceae</i>	?	?
<i>Manlaya capelensis</i>	<i>Manlaya</i> spp.	L. Cret. type (E.Asia)
<i>Archisphex boothi</i>	<i>Archisphex</i> spp.	L. Cret. type (E.Asia) & L. Barremian (Spain)
? <i>Archisphex boothi</i>	as above	as above
<i>Archisphex curvus</i>	as above	as above
<i>Angarosphex goldringi</i>	<i>Angarosphex</i> spp.	L. Cret. type (E.Asia) & Aptian (Brazil)
Lower Weald Clay Formation, Hauterivian		
UPPER HAUTERIVIAN from below Bed 3a (Keymer Tileworks, West Sussex)		
<i>Pompilopterus keymerensis</i>	<i>Pompilopterus</i> spp.	L. Cret. type (E.Asia)
from between the Clockhouse Sandstone and <i>Cassiope</i> Band (Clockhouse Brickworks, Surrey)		
<i>Undatoma bicolor</i>	<i>Undatoma</i> spp.	Jurassic type & l. L. Cret. s/type (E.Asia)
<i>Trematothorax valdensis</i>	<i>Trematothorax</i> spp.	L. Cret. type (Transbaikalia)
<i>Cretevania concordia</i>	<i>C. meridionalis</i> Rasn.	u. L. Cret. type (Mongolia)
<i>Archisphex boothi</i>	<i>Archisphex</i> spp.	L. Cret. type (E.Asia) & L. Barremian (Spain)
<i>Archisphex proximus</i>	as above	as above
<i>Angarosphex consensus</i>	<i>Angarosphex</i> spp.	L. Cret. type (E.Asia) & Aptian (Brazil)
<i>Angarosphex bleachi</i>	as above	as above
? <i>Baissodes</i> sp.	<i>Baissodes</i> spp.	l. L. Cret. s/type (E. Asia)
? <i>Pompilopterus worssami</i>	<i>Pompilopterus</i> spp.	L. Cret. type (E.Asia)
? <i>Pompilopterus leei</i>	as above	as above
HASTINGS GROUP		
Wadhurst Clay Formation, Middle Valanginian		
Quarry Hill Brickworks, Kent		
<i>Archisphex crowsoni</i>		
Evans	<i>Archisphex</i> spp.	L. Cret. type (E.Asia) & L. Barremian (Spain)
PURBECK LIMESTONE GROUP		
Durlston Formation, Upper & Middle Berriasian		
UPPER BERRIASIAN (Bed DB175, Durlston Bay, Dorset)		
<i>Undatoma stigmatica</i>	<i>Undatoma</i> spp.	Jur. type & l. L. Cret. s/type (E.Asia)
<i>Trematothorax clementsi</i>	<i>Trematothorax</i> spp.	l & ?u. L. Cret. s/types (Transbaikalia)
? <i>Trematothorax</i> sp.	as above	as above
<i>Manlaya oculatissima</i>	<i>Manlaya</i> spp.	L. Cret. type (E.Asia)
<i>Tillywhimia spectra</i>	Baissinae	as above
<i>Peperella punctata</i>	<i>Oligoneuroides</i> Zhang	l. L. Cret. s/type (China)
<i>Coramia minuta</i>	<i>Cretacoformica</i> Jell & Duncan	Aptian (Australia)
<i>Purichneumon britannicus</i>	Eoichneumonidae	l. L. Cret. s/type (E. Asia) & Aptian (Australia)
<i>Bethylonymellus feltoni</i>	<i>Bethylonymellus</i> spp.	l. U. Jurassic (S. Kazakhstan)
<i>Apocritites distinctus</i>	?	?
Lulworth Formation, Middle & Lower Berriasian		
MIDDLE BERRIASIAN (Insect Limestone, Dinton, Wiltshire)		
<i>Dintonia despectata</i>	Proctotrupidae	l. L. Cret. - Recent widespread
<i>Proctotrupomorpha indet.</i>	?	?

?Sphecidae gen. sp. indet.	Sphecidae	1. L. Cret. - Recent widespread
LOWER BERRIASIAN		
(Bed DB36c, Durlston Bay, Dorset)		
<i>Eosyntexis tuffinae</i>	<i>Eosyntexis semilis</i> Rasn.	1. L. Cret. s/type (Transbaikalia)
<i>Manlaya anglica</i>	<i>Manlaya</i> spp.	L. Cret. type (E.Asia)
<i>Tillywhimia colorata</i>	Baissinae	L. Cret. type (E.Asia)
<i>Pallenites calcarius</i>	<i>Oligoneuroides</i> Zhang	L. Cret. type (China)
<i>Amitchellia brevis</i>	Proctotrupoidea	L. Cret. - Recent widespread
(Worbarrow Tout Member, Durlston Bay, Dorset)		
<i>Myrmicium heeri</i>	<i>Myrmicium schroeteri</i> Germ.	Tithonian (Bavaria)
<i>Amitchellia procera</i>	Proctotrupoidea	L. Cret. - Recent widespread
<i>Pompilopterus</i> <i>wimbletoni</i>	<i>Pompilopterus</i> spp.	L. Cret. type (E.Asia)
? <i>Pompilopterus difficilis</i>	<i>Pompilopterus</i> spp.	L. Cret. type (E.Asia)
<i>Iwestia provecta</i>	?Pemphredonina	U. Cret. - Recent widespread

and 2r-m; 2r-m very strongly oblique; cell 1mcu with upper and lower sides of almost equal length; cu-a postfurcal, oblique.

Measurements. Length of fragment, 1.4 mm; possible length of forewing c. 2mm.

5. Discussion [APR & EAJ]

The total number of hymenopterans found in the Purbeck and Wealden has now reached 48 specimens representing at least 42 species, 22 genera and 12 families (Table 5). The list of taxa is long enough to allow some discussion considering the factors responsible for the composition of the assemblages studied.

5.1. Climate

Upper Mesozoic hymenopteran assemblages are known to be indicative of past environments and particularly of climatic conditions. Fossil assemblages rich in thermophilous insects and plants have a low content of Xyelidae (now a relict group characteristic of temperate areas); conversely, those rich in Xyelidae are poor in animals and plants indicative of a warm climate (Rasnitsyn, 1969, 1980). The present study has not revealed a single member of Xyelidae, which is consistent with a warm climate in Purbeck and Wealden times.

5.2. Diversity

The Purbeck and Wealden have yielded nearly equal numbers of hymenopteran fossils, 23 and 25 specimens respectively. The two assemblages are both from non-arenaceous formations considered to represent similar environments of deposition (lowland muddy wetland: Allen, 1976). These two factors permit rather straightforward comparison of the two assemblages. However, despite their numerical parity and depositional similarity, the diversity of the assemblages is markedly different at generic level (Tables 6, 7). Thus the Wealden material represents 10 genera and 19 species, whereas there are probably 18 genera and 23 species in the Purbeck, the minimum number being 16 genera depending on a rather unlikely possibility that the fossils identified as Proctotrupomorpha fam., gen. et sp. indet. and ?Sphecidae gen. et sp. indet. turn out to be congeneric and conspecific with better preserved taxa. Evidently, the Purbeck source fauna was significantly more diverse.

The low diversity of the Wealden assemblage could be due to either environmental or evolutionary factors. We could postulate ecological monotony in

Table 7. Number of specimens referred to the genera in the assemblages studied.

Upper Weald Clay Formation - 12:		<i>Coramia</i>	1
<i>Undatoma</i>	1	<i>Purichneumon</i>	1
<i>Turgonalus</i>	1	<i>Bethylonymellus</i>	1
<i>Arossia</i>	1	<i>Apocritites</i>	1
<i>Manlaya</i>	2	Lulworth Formation - 13:	
<i>ArchispheX</i>	4	<i>Eosyntexis</i>	1
<i>AngarospheX</i>	2	<i>Myrmicium</i>	1
<i>Pompilopterus</i>	1	<i>Manlaya</i>	1
Lower Weald Clay Formation - 12:		<i>Tillywhimia</i>	1
<i>Undatoma</i>	1	<i>Pallenites</i>	1
<i>Trematothorax</i>	1	<i>Dintonia</i>	1
<i>Cretevania</i>	1	<i>Amitchellia</i>	2
<i>ArchispheX</i>	3	Proctotrupomorpha fam., gen. et sp. indet.	1
<i>AngarospheX</i>	2	<i>Pompilopterus</i>	2
? <i>Baissodes</i>	1	<i>Iwestia</i>	1
<i>Pompilopterus</i>	3	?Sphecidae gen. et sp. indet.	1
Wadhurst Clay Formation - 1:		Purbeck total - 23:	
Hastings Group total - 1:		<i>Undatoma</i>	1
<i>ArchispheX</i>	1	<i>Trematothorax</i>	2
Wealden Supergroup total - 25:		<i>Eosyntexis</i>	1
<i>Undatoma</i>	2	<i>Myrmicium</i>	1
<i>Trematothorax</i>	1	<i>Manlaya</i>	2
<i>Turgonalus</i>	1	<i>Tillywhimia</i>	2
<i>Arossia</i>	1	<i>Pepperella</i>	1
<i>Manlaya</i>	2	<i>Pallenites</i>	1
<i>Cretevania</i>	1	<i>Dintonia</i>	1
<i>ArchispheX</i>	8	<i>Coramia</i>	1
<i>AngarospheX</i>	4	<i>Amitchellia</i>	2
<i>Pompilopterus</i>	4	Proctotrupomorpha fam., gen. et sp. indet.	1
? <i>Baissodes</i>	1	<i>Purichneumon</i>	1
Durlston Formation - 10:		<i>Bethylonymellus</i>	1
<i>Undatoma</i>	1	<i>Pompilopterus</i>	2
<i>Trematothorax</i>	2	<i>Iwestia</i>	1
<i>Manlaya</i>	1	?Sphecidae gen. et sp. indet.	1
<i>Tillywhimia</i>	1	<i>Apocritites</i>	1
<i>Pepperella</i>	1		

southern England during the Wealden compared with Purbeck times; alternatively, we might consider that a significant extinction event affected the Wealden fauna. Taking the latter first, 10 out of 11 genera found in the Purbeck and not in the Weald are also unknown elsewhere from the Cretaceous (excluding imprecisely identified fossils). In contrast, 1 out of 6 genera found in the Weald but not in the Purbeck are unknown elsewhere from the Cretaceous. This could indicate a significant pre-Wealden extinction, though caution is needed. Of 10 endemic genera in the Purbeck, 5 belong to Proctotrupoidea which is a well represented superfamily that has not yet been studied in detail in extensive collections from East Asia. Future work may well extend the range of what are now considered Purbeck endemics. As to the hypothesis of environmental monotony for the source fauna of the Wealden assemblage, it should be tested using wider palaeontological and palaeoenvironmental information. This goal lies well beyond the scope of the present study, but it may be noted that the arrival of angiosperms in the Wealden could have begun to displace older ecological associations (cf. Zherikhin, 1978, 1993; Jarzembowski, 1995), although angiosperms are likely to have been only a minor component of the Wealden vegetation (Prof. D. J. Batten, written comm.).

5.3. *Stratigraphy*

To consider the stratigraphical implications of the Wealden and Purbeck hymenopterans, we need to correlate with other reference points in the general Late Mesozoic faunal turnover. For the latter, we selected the richest and best known (though not always most exhaustively described) East Asian assemblages from Karatau (S Kazakhstan), Baissa (Transbaikalia), Bon-Tsagan (central Mongolia), and Obeshchayushchiy (NE Siberia). Unfortunately, only the Karatau assemblage has been studied in detail taxonomically, while at Bon-Tsagan and Obeshchayushchiy only a fraction of the fossils are formally described, the rest of the material being identified only to family, subfamily and (less commonly) genus level. The Baissa assemblage is slightly better known. Earlier information on these assemblages is summarized by Rasnitsyn (1980); for later additions see Rasnitsyn (1983, 1986, 1988a, b, 1990a–c, 1991a, b, 1993a, b), Carpenter & Rasnitsyn (1990), Rasnitsyn & Kovalev (1988), Rasnitsyn & Sharkey (1988) and Dlussky (1983).

The stratigraphy of the East Asian non-marine deposits is in a state of continuing discussion, and the above-mentioned assemblages are dated far less precisely than we would like. However, few workers doubt that the Karatau assemblage belongs to the pre-Tithonian Upper or uppermost Middle Jurassic. Baissa is probably pre-Aptian Cretaceous, though an Upper Jurassic age has been claimed; Bon-Tsagan is possibly of Barremian or Aptian age, and Obeshchayushchiy is almost certainly Cenomanian (see Doludenko, Sakulina & Ponomarenko, 1990; Neustrueva, 1990; Ponomarenko, 1990; Rasnitsyn, 1990b, and Scoblo & Liamina, 1990).

On the basis of the above reference assemblages, it is possible to identify successive changes in late Mesozoic hymenopteran faunas (Rasnitsyn, 1990b). The taxonomic composition of other less rich assemblages was also taken into consideration, as well as sub-assemblages from particular beds within the reference assemblages. As a result, several assemblages and sub-assemblages have been recognised (*op. cit.*). They were named originally after their supposed stratigraphical intervals, but this became inappropriate because of considerable differences between the typology and stratigraphical position of some assemblages. The types and subtypes are now given taxonomically rather than stratigraphically based names. The following classification is based mostly on the presence and abundance of apocritans (Suborder Vespina) because the more common Late Mesozoic symphytan hymenopterans (Suborder Siricina) are generally less affected by the general faunal change.

The former 'Jurassic type' assemblages are identified as dominated by Ephialtitidae, Cleistogastrinae (Megalyridae), Praeaulacinae (Praeaulacidae), Mesoserphidae and Protochelorinae (Heloridae), with lack of Gasteruptiidae *s.l.*, Proctotrupidae, Ichneumonoidea and Aculeata. We now call these the 'ephiialtitid-praeaulacine' or 'aculeate-free type' of assemblages. A few local assemblages from Karatau and several other East Asian ones conform to this definition, evidently because of the general scarcity of rich Jurassic hymenopteran assemblages.

The former 'Lower Cretaceous type' is dominated by Baissinae (Gasteruptiidae), Proctotrupidae, Ichneumonoidea, and/or archaic Sphecidae (including Baissodidae). Ephialtitidae, Cleistogastrinae, Mesoserphidae, and Protochelorinae are rare; Praeaulacinae are lacking, as well as primitive ants. This type of assemblage is here renamed the 'baissine type'.

There are two distinct sub-assemblages in the baissine type which most probably reflect succeeding stages in the development of the source fauna. Initially, they were separated on the abundance of Manlayinae (*recte* Baissinae), Proctotrupidae and Eoichneumonidae in a subtype originally called 'Neocomian', while Tenthredinidae, Sepulcidae and Ichneumonidae are common in another subtype formerly referred to the Aptian. Subsequent work has shown that the frequency of archaic aculeate wasps is a more reliable criterion to distinguish the two subtypes. Thus the one with low representation of these wasps is renamed here as the 'proctotrupid subtype', while the other one is called the 'angarosphecine subtype'.

The proctotrupid subtype is exemplified by the Baissa assemblage; similar assemblages are numerous in East Siberia, Mongolia and China: they are often associated with a giant mayfly *Ephemeropsis* Eichwald. The Australian Koonwarra assemblage also agrees with the definition of this subtype despite its younger (Aptian) age. There are three possible explanations: (i) stratigraphical error in either the Koonwarra or east Asian assemblages; (ii) the Australian hymenopteran fauna was relict in the Aptian; (iii) the Koonwarra assemblage represents a palaeoenvironmental reversal, e.g., linked to the cool climate of the region (cf. Jarzembowski, 1995). More work is needed here.

The angarosphecine subtype is exemplified by the Bon-Tsagan assemblage and also includes several similar (though less diverse) assemblages in Mongolia and possibly in Transbaikalia; they never occur with *Ephemeropsis*. Additionally, the Ceará (Brazil; Darling & Sharkey, 1990), and Montsech (Spain; Ansorge, 1993; Martínez-Delclòs & Nel, 1995) assemblages belong to this subtype. They are usually dated as Aptian or Barremian, and can be considered younger than those of the proctotrupid subtype (except possibly the Koonwarra assemblage).

The Upper Cretaceous is the last and youngest type of assemblage considered here. It is characterized by the presence of archaic ants of the family Armaniidae and will now be referred to as the 'armaniid type'. Additionally, Ichneumonidae are abundant, while Ephialtitidae, Cleistogastrinae, Praeaulacidae and Baissinae are absent. The typical assemblage of this type is that from Obeshchayushchiy, two others being the Turonian Kzyl-Zhar assemblage of Kazakhstan, and the uppermost Lower Cretaceous (mid-Albian) Emanra assemblage from near the coast of the Okhotsk Sea.

The transition between the aculeate-free and baissine types lies somewhere below the Jurassic/Cretaceous boundary (see below). It is likely that the transition between assemblages of the baissine and armaniid types lies somewhat below the Lower/Upper Cretaceous boundary because the Emanra assemblage is a typical but impoverished example of the armaniid type despite its mid-Albian age (Gromov & Dmitriev, 1993).

To facilitate the stratigraphical discussion on the Purbeck and Wealden assemblages, Table 8 shows key taxa and assemblages. Comparison of Tables 6 and 8 shows that with only two exceptions, both Purbeck and Wealden assemblages consist either of new taxa or of those represented in assemblages of the Cretaceous baissine type. The exceptions are *Myrmicium heeri* and *Bethylonymellus feltoni*, whose nearest relatives are Jurassic. However, one of these, *M. schroeteri*, whilst undisputably uppermost Jurassic in age, does not belong to the aculeate-free assemblage type. Indeed, the Bavarian Tithonian deposits have yielded not a single hymenopteran fossil characteristic of this type. In contrast, there is a reason to believe that an aculeate wasp has been found at

Table 8. Abundance of important taxa in late Mesozoic vespidan assemblages; (absent) = the taxon has been found only in Late Cretaceous amber.

Taxon	type:	aculeate-free	Abundance		armaniid
	subtype:		proctotrupid	baissine angarosphecine	
<i>Undatoma</i> (Xyelotomidae)		rare	locally common	absent	absent
Thoracotrematinae					
(Sepulcidae)		absent	common	common	uncommon
Anaxyelinae (Anaxyelidae)		common	absent	absent	absent
Syntexinae (Anaxyelidae)		absent	rare	absent	absent
Ephialtitidae		common	rare	rare	absent
Cleistogastrinae (Megalyridae)		common	rare	rare	absent
Cretogonulinae (Trigonulidae)		absent	rare	absent	(absent)
Baissinae (Gasteruptiidae)		absent	common	common	absent
Cretevaniidae		absent	absent	rare	(absent)
Mesoserphidae, Heloridae		common	uncommon	uncommon	rare
other Proctotrupomorpha		absent except for rare Roproniidae	common	common	common
Bethylonymidae		locally common	absent	absent	absent
Diapriidae		absent	rare	rare	(absent)
Ichneumonomorpha		absent	common	common	common
Sphecidae		absent	uncommon	common	common
Armaniidae		absent	absent	absent	common

Solnhofen: a poorly preserved fossil of undoubted aculeate habit is in the Natural History Museum, Vienna (Dr A. G. Ponomarenko, pers. comm.).

It is also useful to examine the Wealden assemblage more closely. We do not separate the Wadhurst Clay from this discussion because it has yielded only one hymenopteran, *Archisphex crowsoni*, which is congeneric with species in the Lower Weald Clay Formation but not in the Durlston Formation. The differences between the Lower and Upper Weald Clay are probably fortuitous because there are 4 genera shared by both assemblages in a total of 10 genera and every genus represented by more than 2 specimens is represented in both assemblages. This diversity test, though less reliable because of the small sample size, is based on 17 out of 24 specimens found in the Upper and Lower Weald Clay. In conclusion the Wealden hymenopterans are considered to be a single assemblage.

The number of specimens and genera in the Durlston and Lulworth Formations is almost the same and close to that for the Wealden formations, viz. 10 specimens and 9 genera recorded from the Durlston Formation, and 11 specimens and 9 genera in the Lulworth Formation (unidentified forms excepted). However, in the Purbeck total of 16 genera, only 2 are found in both formations, and only 3 are represented by more than one (by two) specimens in any formation. Evidently, it is a matter of chance whether a particular genus is found or not in any of these assemblages. Like the Wealden, we have considered all the Purbeck hymenopterans to form a single assemblage, until a distinction becomes apparent. Even within these limitations, a comparison of the Purbeck and Wealden hymenopterans, against a background of the general pattern of Late Mesozoic faunal turnover, provides some interesting results. The assemblages correspond well to the baissine type due to the presence of Baissinae, Proctotrupidae, aculeate wasps and some other taxa. Also, the Purbeck assemblage shows features of the older proctotrupid subtype (low sphecoid content), and two forms with clear Jurassic affinities [*Bethylonymellus*, a genus characteristic of assemblages of the ephialtitid-praeaulacine (aculeate-free) type;

and *Myrmicium*, which is otherwise only known from the uppermost Jurassic (Tithonian) limestones of Bavaria (Table 8)]. In contrast, the Wealden assemblage is a typical representative of the angarosphecine subtype as implied by the abundance of aculeate wasps (16 out of the 24 specimens examined) and the presence of *Cretevania*, a genus known otherwise in the Bon-Tsagan assemblage of the angarosphecine subtype, and in undoubtedly Upper Cretaceous Taimyr amber, northern Siberia (Rasnitsyn, 1980).

Our knowledge of Purbeck/Wealden hymenopterans has increased considerably since Westwood (1854). However, this important living order is uncommon as fossils and more fieldwork is needed.

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