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Grasshoppers and crickets (Insecta: Orthoptera) from the Lower Cretaceous of southern England

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Abstract

This is a synoptic monograph of fossil Orthoptera from the English Lower Cretaceous (Purbeck and Wealden groups). The previously described taxa of these insects are revised on the basis of type specimens and examination of extensive new material. Eight new genera and 30 new species are proposed: *Probaisselcana cretacea* sp. nov., *Minelcana membranacea* gen. et sp. nov., *Panorpidium proximum* sp. nov., *P. bimaculatum* sp. nov., ?*P. parvum* sp. nov. (Elcanidae); ?*Cyrtophyllites cretaceus* sp. nov. (Haglidae); *Aenigmoilus minutus* gen. et sp. nov., *Pseudaboilus wealdensis* gen. et sp. nov., *P. purbeckensis* sp. nov., *Tettigoilus sonorus* gen. et sp. nov., ?*Agrionidium obscurum* sp. nov. (Prophalangopsidae); *Notocearagryllus britannicus* sp. nov., *N. grandispeculum* sp. nov., *N. cordispeculum* sp. nov., *Anglogryllus lyristes* gen. et sp. nov., *A. rotundispeculum* sp. nov., *Speculogryllus acutispeculum* gen. et sp. nov., *Sharategia davisi* sp. nov., *S. batchelorae* sp. nov., *S. baldocki* sp. nov. (Baissogryllidae); ?*Araripegryllus orientalis* sp. nov. (Gryllidae); *Deinovitimia occidentalis* sp. nov. (Ensifera: infraorder incertae sedis); *Cretoxya rasnitsyni* gen. et sp. nov. (Tridactylidae); *Locustopsis posterior* sp. nov., *Zeunerella prior* sp. nov., *Zessinia borealis* sp. nov., *Mesolocustopsis anglica* sp. nov., *M. angusta* sp. nov., *M. problematica* sp. nov., and *Britannacrida distincta* gen. et sp. nov (Locustopsidae). The subfamily Baisselcaninae is synonymized with Elcaninae, and a new subfamily (Archelcaninae subfam. nov.) is proposed for a segregate of Elcaninae. A preliminary comparison of the Purbeck/Wealden with other Early Cretaceous orthopteran faunas is given.

Keywords: Orthoptera; Lower Cretaceous; England; Revision; New taxa

1. Introduction

The Orthoptera is one of the oldest orders of insects, known from the Late Carboniferous to Recent. Throughout this long period, these insects have been relatively numerous and widely distributed. There are nearly 20,000 Recent species found on all continents except Antarctica. The classification of Orthoptera used here is as proposed by Gorochov (1995a,b, 2001a). The order is traditionally divided into two suborders: (1) paraphyletic Ensifera (long-horn grasshoppers, crickets) known from the Late Carboniferous–Recent and possibly ancestral to (2) holophyletic Caelifera (short-horn grasshoppers, locusts) known from the Early Triassic–Recent. They are both well represented in the Mesozoic and Cenozoic (including Recent) faunas. These suborders are divided into six infraorders: Ensifera into Oedischiidea (Late Carboniferous–Early Jurassic), Elcanidea (Early Permian–Early Cretaceous), Tettigoniidea and Gryllidea (Middle Triassic–Recent); Caelifera into Tridactylidea (Middle or Late Triassic–Recent) and Acrididea (Early Triassic–Recent). Five of these infraorders (perhaps all six) are present in the Lower Cretaceous of England, antedating both grasses and locusts, which are post-Cretaceous.

Several English Early Cretaceous Orthoptera with unclear subfamilial positions are discussed under their higher taxa. *Gryllidium oweni* Westwood, 1854, described as a "grasshopper" by Westwood (1854), *Blattidium nogaus* Westwood, 1854 (the counterpart specimen to the holotype of *B. symyrus*

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Westwood, 1854; A. Ross, pers. comm. 2004) included in Ensifera by Handlirsch (1906) and Zeuner (1939), and *Libellulium kaupii* Westwood, 1854, included in the list of Purbeck Orthoptera by Jarzembowski (1993), are probably not Orthoptera. The types of *G. oweni* and *L. kaupii* cannot be located in the collection of the Natural History Museum in London (A. Ross, pers. comm. 2004), and their true identities therefore cannot be verified. It is also possible that *Raphidium brephos* Westwood, 1854 (Lower Purbeck; Swanage, Dorset; holotype NHM I. 12509, coll. C. Willcox), regarded as neuropteran by Westwood (1854, pl. 17, fig. 16) and included in Phasmatoptera by Jarzembowski (1993, fig. 3), and an enigmatic wing (Upper Weald Clay; Smokejacks Brickworks, Surrey; NHM In. 64638 [S 39], coll. E. Jarzembowski), figured by Jarzembowski (1999, fig. 4) as an acridoid forewing, belong to Orthoptera, but the venation of these possible tegmina is very unusual, and does not permit more exact determination at present.

2. Systematic palaeontology

The studied material is deposited in the following collections: The Natural History Museum, London (NHM), Booth Museum of Natural History, Brighton (BMB), Maidstone Museum and Bentlif Art Gallery, Kent (MNEMG) and Sedgwick Museum, Cambridge. The wing venation nomenclature is based on that of Sharov (1968) and Gorochov (1995b).

Class: Insecta Linnaeus, 1758
Order: Orthoptera Olivier, 1789
Suborder: Ensifera Chopard, 1920
Infraorder: Elcanidea Handlirsch, 1906
Superfamily: Elcanoidea Handlirsch, 1906
Family: Elcanidae Handlirsch, 1906

Remarks. This family was divided into two subfamilies by Gorochov, 1986: Elcaninae (Early–Late Jurassic) and Baisselcaninae (Late Jurassic–Early Cretaceous). At present, the age of the Purbeck Limestone Group is considered most likely to be Early Cretaceous (Berriasian) and not Late Jurassic as stated by numerous previous authors, although the precise position of the Jurassic/Cretaceous boundary is still in dispute, and may in fact lie within the Purbeck (Allen and Wimbledon, 1991; Ensom, 2002). The revision of the holotype of *Panorpidium tesselatum* Westwood from these deposits has allowed us to synonymize the generic names *Panorpidium* Westwood, 1854 (=*Elcana* Giebel, 1856; both generic names are based on the same type species, *P. tesselatum*) and *Baisselcana* Sharov, 1968 (Jarzembowski, 1996). In this connection, the junior subfamily (Baisselcaninae) must be synonymized with Elcaninae, and Elcaninae sensu Gorochov renamed. For the latter subfamily, the new name Archelcaninae subfam. nov. is proposed here. This subfamily differs from Elcaninae in the more or less widened area between tegminal RA and RS, the free (rather than fused together) distal parts of tegminal CuA_2, CuP, and 1A (Fig. 1A), and probably the larger spines of the hind tibiae. Archelcaninae include four genera: Early Jurassic *Parelcana* Handlirsch, 1906 and *Synelcana* Zessin, 1988; Early and Middle Jurassic *Archelcana* Sharov, 1968 and Late Jurassic or Early Cretaceous *Sibelcana* Gorochov, 1990. The numerous species of Archelcaninae included in *Elcana* by earlier authors (Handlirsch, 1906; Sharov, 1968; Zessin, 1987) are in need of generic revision. Elcaninae are considered below. Two species of Elcanidae from the Lower Purbeck of Dorset have unclear subfamilial and generic positions: the holotype of ?*Elcana westwoodi* Handlirsch, 1906 (NHM I. 3974; Durlston Bay; coll. P. B. Brodie) is a small fragment of tegmen (Westwood 1854, pl. 18, fig. 37); the holotype of *Elcana beyrichi* Giebel, 1856 (NHM I. 12331; Swanage, Dorset; coll. C. Willcox), figured by Westwood (1854, pl. 17, fig. 12, *Panorpidium tesellatum* var.), is insufficiently preserved for more exact determination, although it is similar to *P. tesselatum* in size and number of Sc branches.

Subfamily: Elcaninae Handlirsch, 1906
[=Baisselcaninae Gorochov, 1986]

Remarks. This subfamily is characterized by the more or less narrowed area between tegminal RA and RS, the fused (with each other) distal parts of CuA_2, CuP, and 1A (Figs. 1C, 2–8) or only CuP and 1A (Fig. 1B), and possibly the rather small spines of the hind tibiae. Elcaninae include five genera: Late Jurassic and Early Cretaceous *Probaisselcana* Gorochov, 1989; Early Cretaceous *Panorpidium* Westwood, 1854 (=*Elcana* Giebel, 1856; =*Baisselcana* Sharov, 1968), *Eubaisselcana* Gorochov, 1986, *Cratoelcana* Martins-Neto, 1991, and *Minelcana* gen. nov.

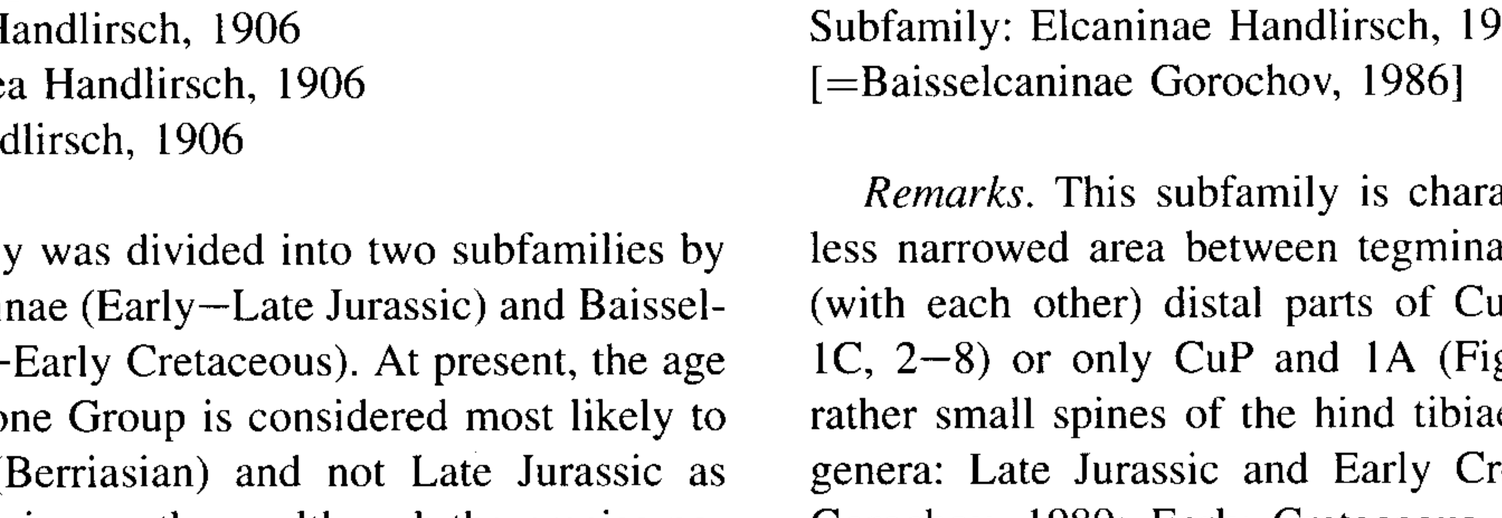


Fig. 1. Scheme of venation of proximal-medial parts of tegmina. A, *Archelcana liasina* (Giebel), Lower Jurassic, England. B, *Eubaisselcana sharovi* Gorochov, Lower Cretaceous, Mongolia. C, *Probaisselcana karatavica* (Sharov), Upper Jurassic, Kazakhstan.

Genus *Probaisselcana* Gorochov, 1989

Type species. *Elcana karatavica* Sharov, 1968, Upper Jurassic, Kazakhstan.

Diagnosis. Tegmina medium or large (not shorter than 15 mm), with relatively few branches of Sc, two longitudinal branches between basal part of RS and $MP + CuA_1$ (base of $1MA_1$ situated on basal part of RS), rather narrow and relatively short area between MA_2 and anal edge of tegmen divided by short transverse or irregular crossveins, and fusion of distal parts of CuA_2, CuP, and 1A with each other (Figs. 1C, 2).

Included species. Type species and *P. cretacea* sp. nov.

Probaisselcana cretacea sp. nov.
Fig. 2

Derivation of name. After the Cretaceous Period.

Holotype. MNEMG 2003.27 [Co 59] (part and counterpart); Lower Weald Clay; Cooden Beach, East Sussex (National Grid Reference TQ 710 065); Lower Hauterivian; collected by E.A. Jarzembowski.

Diagnosis. Tegmen distinguished from that of *P. karatavica* by longer distance between apices of two longitudinal branches of "C", shorter distance between proximal part of RS and distal part of $1MA_1$, longer distance between proximal part of RS and base of MA_2, and distinctly wider area between CuA_2 and CuP.

Description. Tegmen lacking small proximal-medial and very small apical parts. Length as preserved 15 mm; estimated total length of tegmen 15.5 mm.

Genus *Minelcana* gen. nov.

Derivation of name. Latin for small and old generic name.

Type species. *Minelcana membranacea* sp. nov.

Diagnosis. Tegmina small (not longer than 14 mm) with relatively few branches of Sc (unlike *Cratoelcana*), two longitudinal branches between basal part of RS and $MP + CuA_1$ (as in *Probaisselcana*), rather wide and very long area between MA_2 and anal edge of tegmen divided by comparatively long oblique and regular crossveins (the characteristic structure of this area clearly distinguishes *Minelcana* from all other genera of Elcaninae), and fusion of distal parts of CuA_2, CuP, and 1A with each other (Figs. 3, 4).

Included species. Type species, *Bittacus dubius* Giebel, 1856 (Lower Cretaceous, southern England) and possibly *Cratoelcana damianii* Martins-Neto, 1991 (Lower Cretaceous, Brazil).

Minelcana membranacea gen. et sp. nov.
Fig. 3

Derivation of name. Latin for membranous.

Holotype. MNEMG 2003.28 [DB175/ORTH 20] (part and counterpart); Clements' (1993) Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Paratype. MNEMG 2003.29 [DB175/ORTH 18] (part and counterpart); Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset (SZ 035 780); Upper Berriasian; collected by R.A. Coram.

Diagnosis. Tegmen distinguished from those of *M. dubia* and *Cratoelcana damianii* by distal half of subcostal area (region of RA branches) being distinctly wider than the area between RA and RS as well as by RS and MA having few branches (seven branches in total).

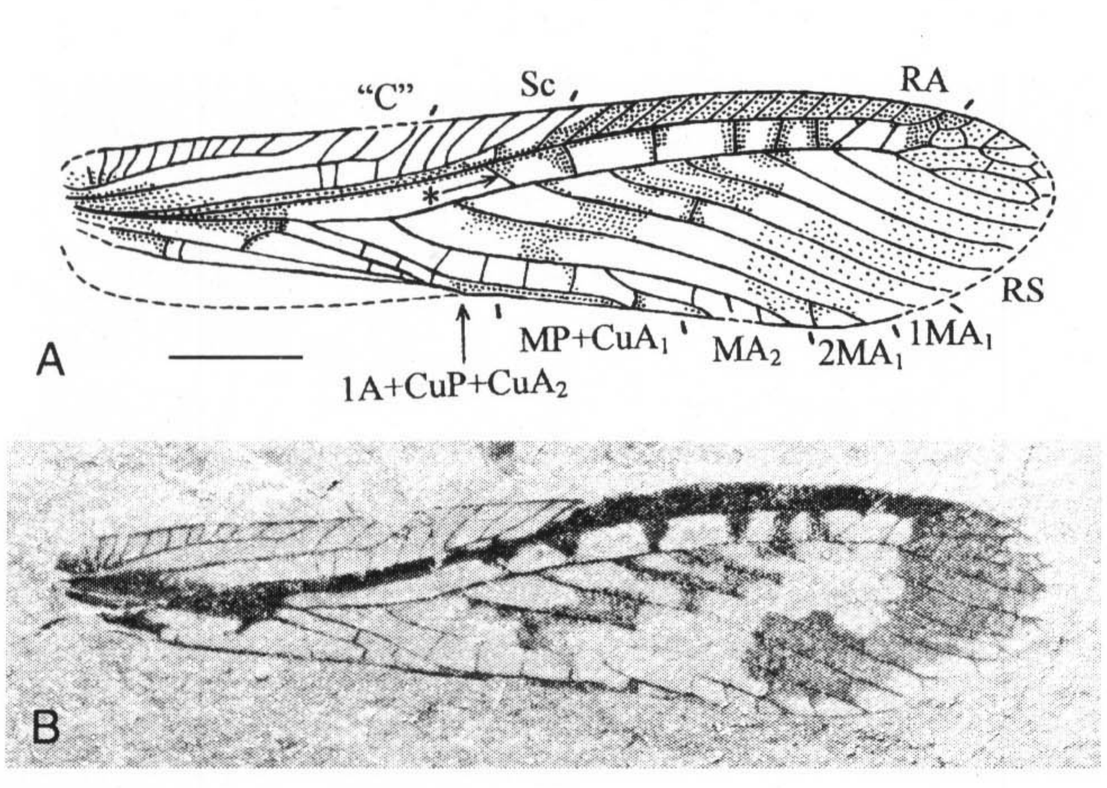


Fig. 2. A, B, *Probaisselcana cretacea* sp. nov., holotype MNEMG 2003.27; Cooden Beach, Lower Hauterivian; asterisk indicates position of basal part of RS. Scale bar represents 2 mm.

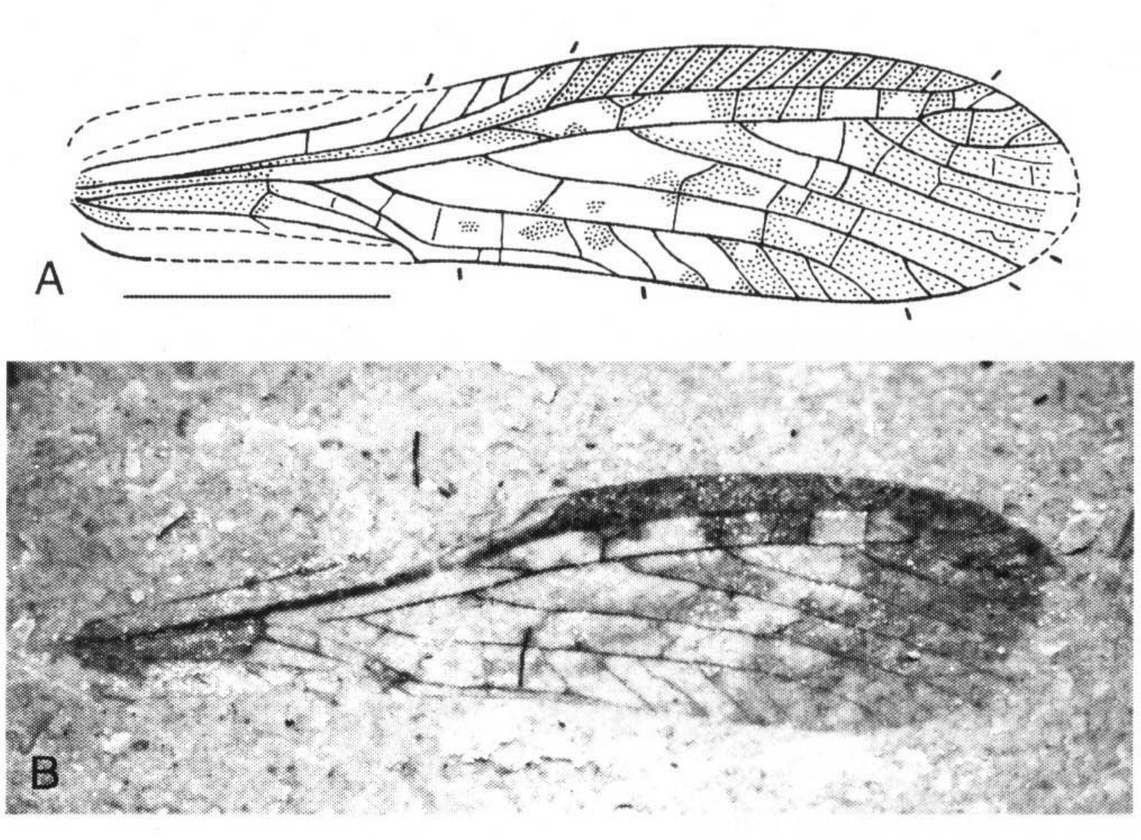


Fig. 3. A, B, *Minelcana membranacea* gen. et sp. nov., holotype MNEMG 2003.28; Durlston Bay, Upper Berriasian. Scale bar represents 2 mm.

Description. Tegmen unfortunately lacking proximal-medial part; colour pattern with relatively few (5–6) dark spots between RA and RS. Length of tegmen 7.5 mm.

Minelcana dubia (Giebel, 1856)
Fig. 4

Holotype. NHM I. 3496 (part and counterpart); *Archaeoniscus* Bed, Durlston Formation; Dinton, Wiltshire (SU 015 315); Upper Berriasian; collected by P.B. Brodie.

Other material. MNEMG 2003.30 [DB175/ORTH 38] (part and counterpart); Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Diagnosis. Tegmen differing from that of *M. membranacea* in that the width of the distal half of the subcostal area (region of RA branches) is subequal to the area between RA and RS; the branches of RA are slightly shorter and less oblique; RS and MA have more numerous branches (9–10), and more numerous (8–10) dark spots between RA and RS. The differences between *M. dubia* and *Cratoelcana damianii* are less clear (tegmina of *M. dubia* are generally slightly smaller: 8–10 mm in length).

Remarks. The holotype was previously figured by Ross and Jarzembowski (1996, fig. 3C).

Genus *Panorpidium* Westwood, 1854
[=*Elcana* Giebel, 1856, *Baisselcana* Sharov, 1968]

Type species. Of *Panorpidium* and *Elcana*: *Panorpidium tesselatum* Westwood, 1854, Lower Cretaceous, southern England; of *Baisselcana*: *Baisselcana sibirica* Sharov, 1968, Lower Cretaceous, Transbaikalia (Fig. 5C).

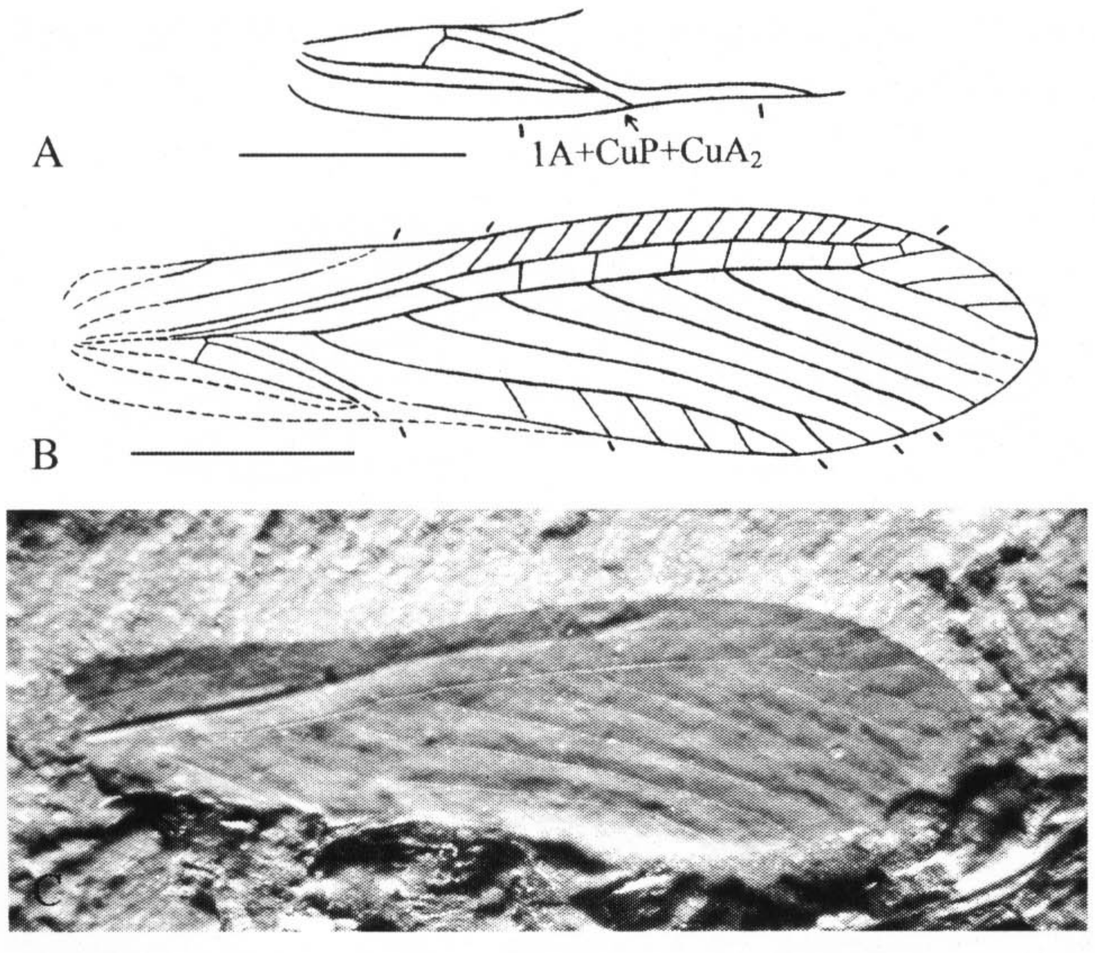


Fig. 4. *Minelcana dubia* (Giebel). A, holotype NHM I. 3496; Dinton, Upper Berriasian; venation of proximal-medial part of tegmen. B, C, MNEMG 2003.30; Durlston Bay, Upper Berriasian. Scale bars represent 2 mm.

Diagnosis. Tegmina usually medium or large (possibly sometimes small) with relatively few branches of Sc, 3 or 4 longitudinal branches between basal part of RS and MP + CuA_1 (this character distinguishes *Panorpidium* from *Probaisselcana* and *Minelcana*), narrow and relatively short area between MA_2 and anal edge of tegmen divided by short transverse or partly oblique crossveins (sometimes without crossveins), and fusion of distal parts of CuA_2, CuP and 1A with each other (in *Eubaisselcana* CuA_2 is free: Fig. 1B).

Included species. Two type species noted above as well as *P. proximum* sp. nov., *P. bimaculatum* sp. nov., and possibly *P. parvum* sp. nov.

Panorpidium tesselatum Westwood, 1854
Fig. 5A, B

Holotype. NHM I. 3982 and I. 12262 (part and counterpart); Middle Purbeck; Durlston Bay, Dorset; Upper Berriasian; collected by P.B. Brodie.

Remarks. The holotype was previously figured by Jarzembowski (1993, fig. 2).

Other material. MNEMG 2003.31 [DB175/ORTH 4] and 2003.32 [DB175/ORTH 7]; Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Remarks. This rather large species (length of tegmina 20–24 mm) is similar to *P. sibiricum* in the structure of the areas between tegminal CuP and 1A, and between 1A and the anal edge of the tegmen, both of which are slightly widened, and

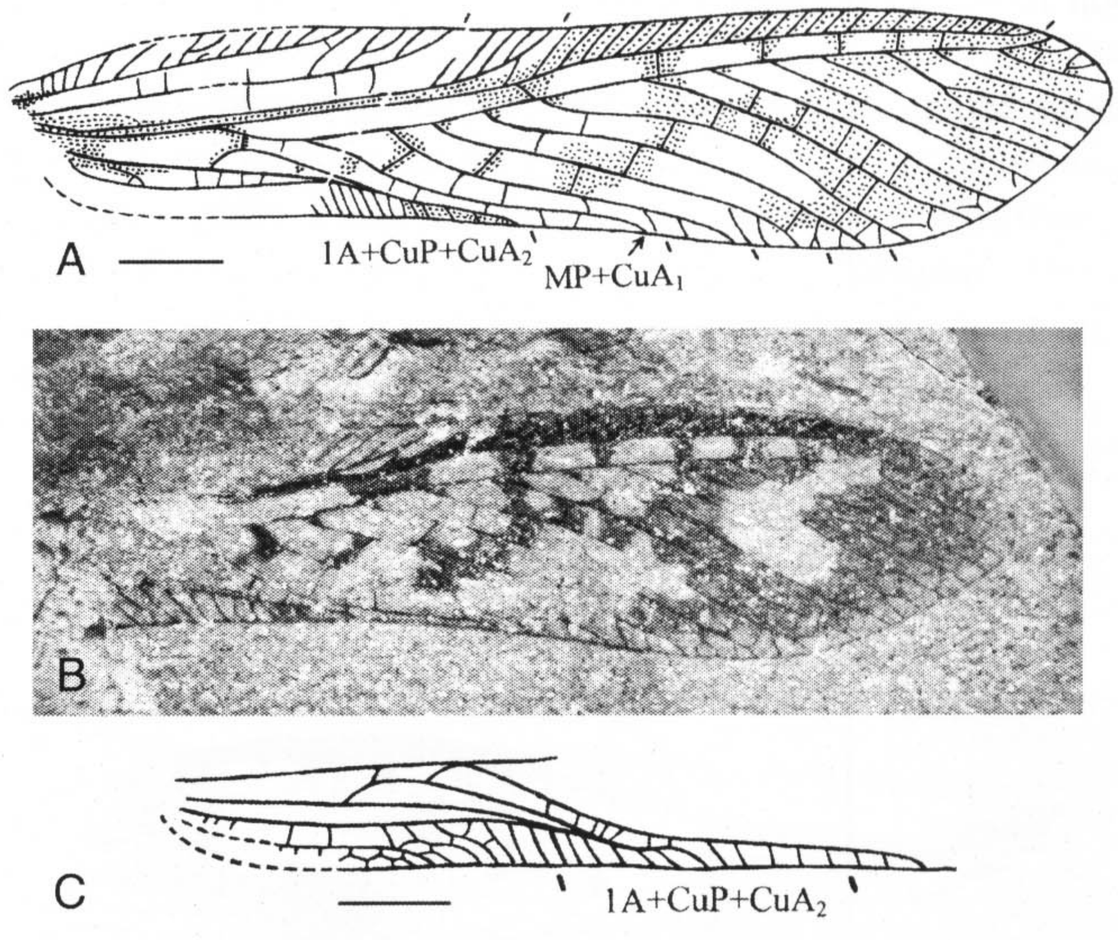


Fig. 5. *Panorpidium*, tegmina. A, B, *P. tesselatum* Westwood, MNEMG 2003.31 (with proximal addition to 5A from MNEMG 2003.32); Durlston Bay, Upper Berriasian. C, *P. sibiricum* (Sharov), holotype, Lower Cretaceous of Transbaikalia; venation of proximal-medial part of tegmen. Scale bars represent 2 mm.

with numerous dense subparallel crossveins in the distal half of the latter area (Fig. 5). *P. tesselatum* differs from *P. sibiricum* in the general shape of the tegmina and the colouration (*P. sibiricum* has one large round dark spot in the area of RS branches).

Panorpidium proximum sp. nov.
Fig. 6

Derivation of name. Latin for nearest.

Holotype. MNEMG 2003.33 [DB175/ORTH 1] (part and counterpart); Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Diagnosis. Tegmen distinguished from that of *P. tesselatum* and *P. sibiricum* by fewer branches of Sc distal to termination of C, narrower areas between CuP and 1A and between 1A and anal edge of tegmen, and less numerous, less regular, rather sparse crossveins in distal half of latter area (Figs. 5, 6). Additionally, *P. proximum* differs from *P. tesselatum* in the longer area between MP + CuA_1 and anal edge of tegmen.

Description. Tegmen unfortunately lacking a very small proximal–medial part. Length of tegmen 23 mm.

Panorpidium bimaculatum sp. nov.
Fig. 7

Derivation of name. Latin for two and spots.

Holotype. BMB 016391/-2 (part and counterpart); Upper Weald Clay; Rudgwick Brickworks, Rudgwick, West Sussex (TQ 083 343); Lower Barremian; collected by R. Strevens.

Paratypes. BMB 018602 [A 537], 018624 [A 332b], 018625 [A 4], 018632 [A 200], 018639 [A 320b]; Upper Weald Clay; Auclaye Brickworks, Capel, Surrey (TQ 169 389); Lower Barremian; collected by E. and B. Jarzembowski. BMB 025000/-2, five specimens on same bedding plane; Upper Weald Clay; Rudgwick Brickworks, Rudgwick, West

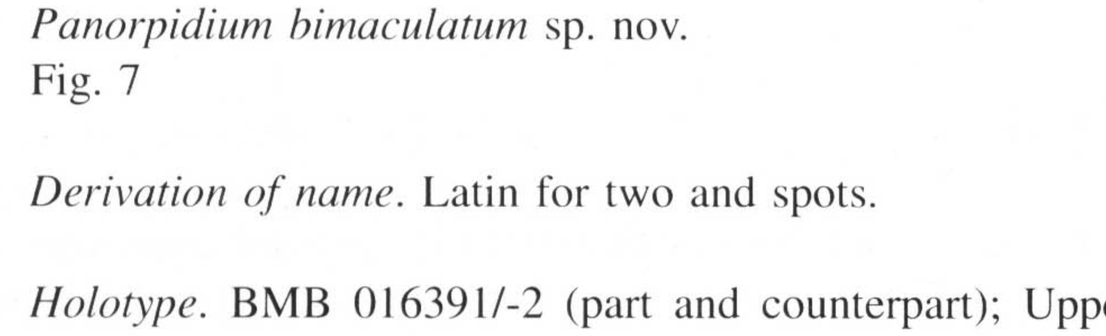


Fig. 6. *Panorpidium proximum* sp. nov., holotype MNEMG 2003.33; Durlston Bay, Upper Berriasian. Scale bar represents 2 mm.

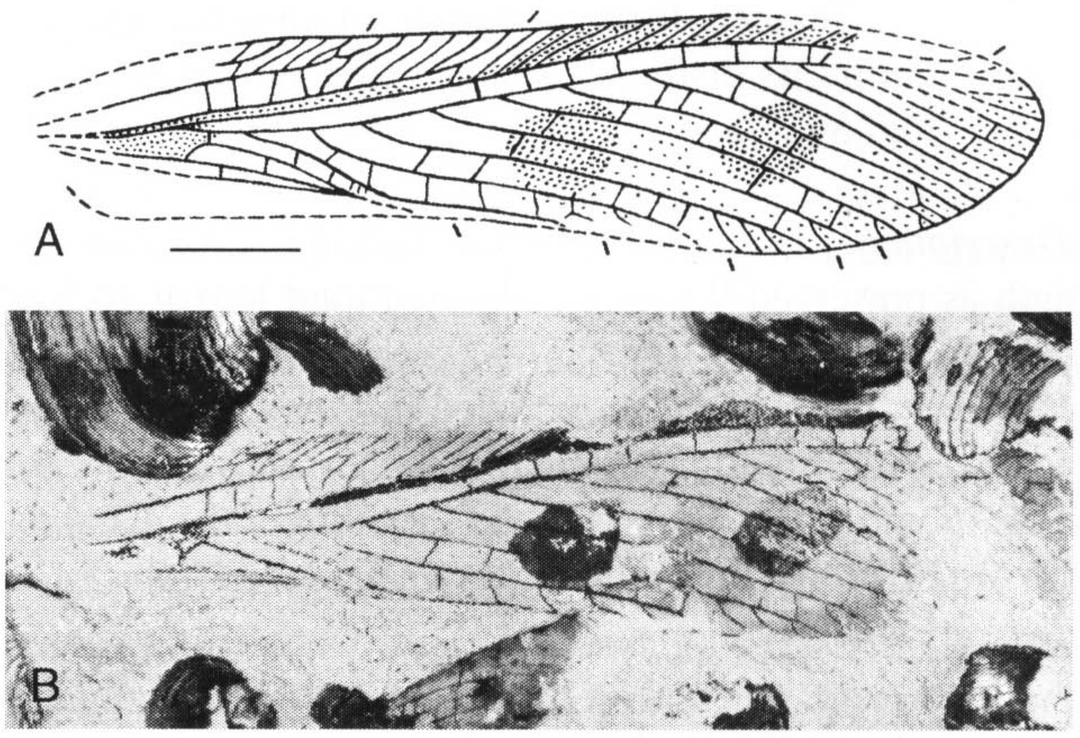


Fig. 7. *Panorpidium bimaculatum* sp. nov., holotype BMB 016391/-2; Rudgwick Brickworks, Lower Barremian. Scale bar represents 2 mm.

Sussex; Lower Barremian; collected by A. Ross. MNEMG 2003.34 [CH 698 xib], 2003.35 [CH 840h], 2003.36 [CH 864 xiv], 2003.37 [CH 868 xiiia, b]; Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey (TQ 173 386); Upper Hauterivian; collected by E. and B. Jarzembowski. MNEMG 2003.38 [S 526]; Upper Weald Clay, Smokejacks Brickworks, Ockley, Surrey (TQ 113 373); Lower Barremian; collected by E. and B. Jarzembowski. NHM II 2072; Upper Weald Clay, Smokejacks Brickworks, Surrey; Lower Barremian; collected by A. Ross.

Diagnosis. Tegmina distinctly smaller than those of *P. tesselatum*, *P. sibiricum*, and *P. proximum*; Sc with more numerous branches; area between MP + CuA_1 and anal edge of tegmen longer than in *P. tesselatum*; area between CuP and 1A wider than in *P. proximum*; characteristic tegminal colouration (with two large, round dark spots in region of RS and MA branches) clearly distinguishes *P. bimaculatum* from all other congeners (Fig. 7).

Description. Holotype tegmen lacking proximal-medial part. Length as preserved 15 mm; estimated total length 16.5 mm.

?*Panorpidium parvum* sp. nov.
Fig. 8

Derivation of name. Latin for little.

Holotype. MNEMG 2003.39 [Co 34] (part and counterpart); Lower Weald Clay; Cooden Beach, East Sussex; Lower Hauterivian; collected by R. Davis.

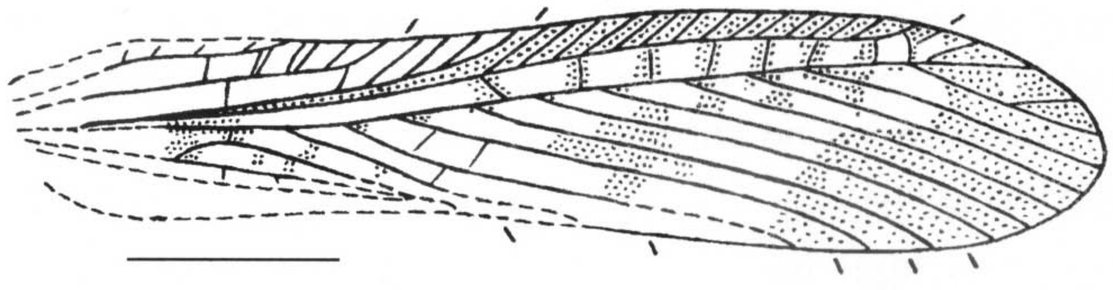


Fig. 8. ?*Panorpidium parvum* sp. nov., holotype, MNEMG 2003.39; Cooden Beach, Lower Hauterivian. Scale bar represents 2 mm.

Diagnosis. Tegmen distinguished from all other species of *Panorpidium* by its distinctly smaller size and details of colouration (Fig. 8).

Description. Holotype tegmen lacking proximal part. Length as preserved 9.5 mm; estimated total length 10.5 mm.

Remarks. This species is included in *Panorpidium* because its tegmen has three longitudinal branches between the basal part of RS and MP + CuA_1, but the structure of the distal parts of CuA_2, CuP, and 1A is unknown. Differences from *Eubaisselcana* are unclear.

Infraorder: Tettigoniidea Stol, 1788
Superfamily: Hagloidea Handlirsch, 1906
Family: Haglidae Handlirsch, 1906

Remarks. A unique fossil from the Purbeck of Dorset, which is attributed to this family, is characterized by strongly arched proximal "oblique veins" (crossveins) between CuA and CuP in the stridulatory apparatus of the male (Fig. 9). This structure is characteristic of two families of Hagloidea: Tuphellidae and Haglidae. Both families are known from the Triassic to Late Jurassic or Early Cretaceous, but in Tuphellidae, the above-mentioned crossveins are more strongly curved and the stridulatory vein (part of CuP) is distinctly less transverse. Late Mesozoic Haglidae are represented by the subfamily Cyrtophyllitinae only (all other subfamilies are known from the Triassic–Middle Jurassic) and the venation of the Purbeck fossil is consistent with this subfamily.

Subfamily: Cyrtophyllitinae Zeuner, 1935

Remarks. This subfamily is characterized by the appearance of a secondary tegminal C (an additional arched vein crossing mainly apical parts of Sc branches), the presence of a strong CuA_2 in male tegmina, and the development of a special "oblique vein" between the proximal parts of RS and $2MA_1$ from several crossveins partly fused together. Cyrtophyllitinae include four genera: *Archaboilus* Martynov, 1937 (Lower and Middle Jurassic); *Cyrtophyllites* Oppenheim, 1888 (Upper Jurassic); *Tasgorosailus* Gorochov, 1990 (Upper Jurassic or Lower Cretaceous); *Vitimoilus* Gorochov, 1996 (Lower Cretaceous). The fossil under consideration here differs from *Archaboilus* and *Tasgorosailus* in the disappearance of the medial (proximal) part of the "diagonal vein" (vein consisting of two parts: a single crossvein crossing some of the nearest crossveins between the base of the proximal branch of MP + CuA_1 and CuA_2, and several crossveins partly fused together between CuA_2 and CuP) in male tegmina, and from *Vitimoilus* in the distinctly shorter basal area of the male tegmen. The details of the stridulatory apparatus in *Cyrtophyllites* are insufficiently studied, but there are no current grounds for excluding the fossil from this genus.

?*Cyrtophyllites cretaceus* sp. nov.
Fig. 9

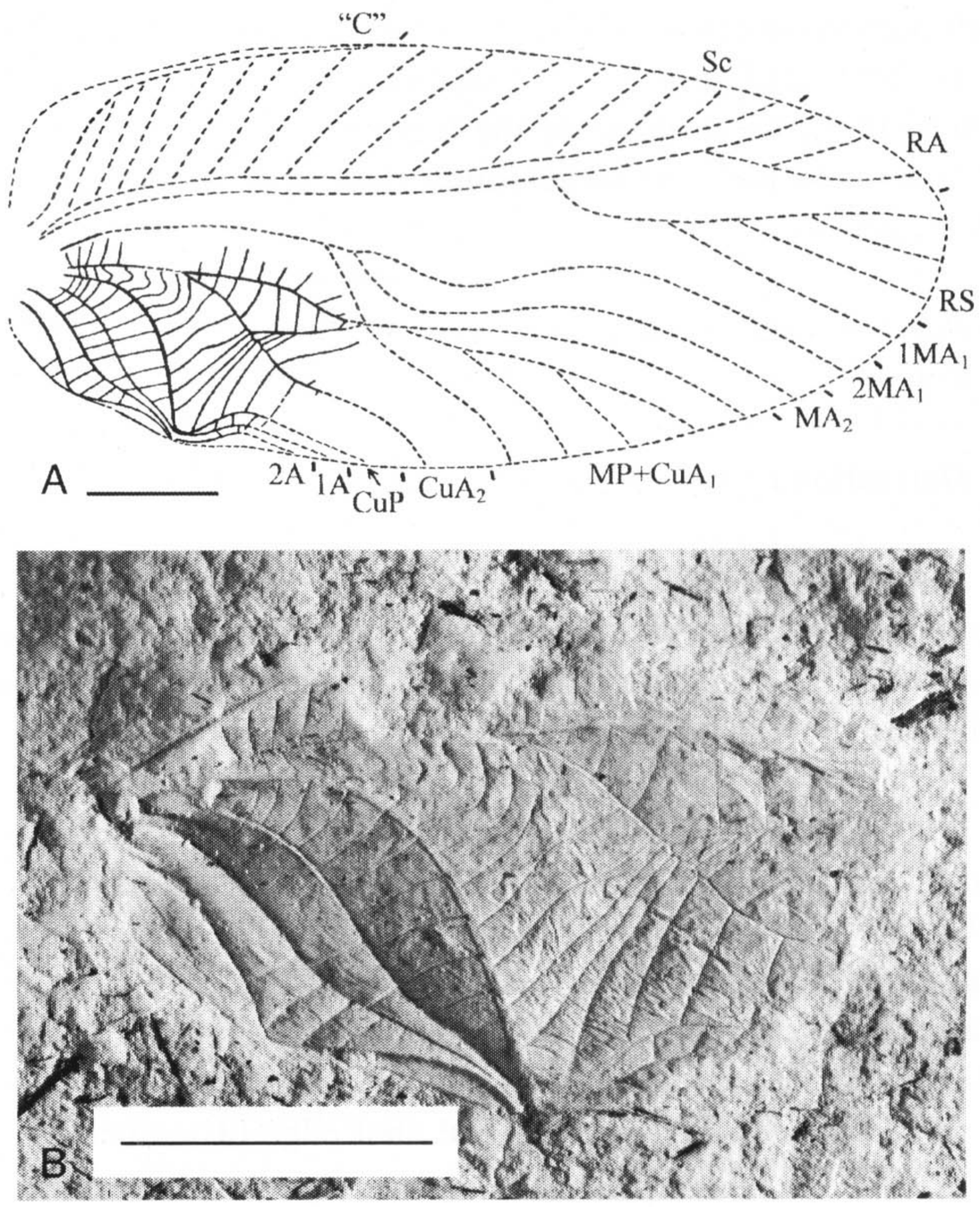


Fig. 9. ?*Cyrtophyllites cretaceus* sp. nov., male, holotype MNEMG 2003.40; Poxwell, Lower Berriasian. Scale bar represents 5 mm.

Derivation of name. After the Cretaceous Period.

Holotype. MNEMG 2003.40 [Pc 12] (part and counterpart); Lulworth Formation; Fisher's Lower Insect Bed; Poxwell, Dorset (SY 740 835); Lower Berriasian; collected by E. and B. Jarzembowski.

Diagnosis. Male tegmen with *Cyrtophyllites*-like venation and specialized stridulatory area with well-developed distal (lateral) portion of the "diagonal vein", long CuA_2, and a short basal area.

Description. Proximal-medial part of male tegmen with well-developed stridulatory apparatus; proximal part of CuA_2 rather long; "diagonal vein" with well-developed lateral half (between base of MP + CuA_1 and CuA_2) and without medial half (between CuA_2 and CuP); basal area (from base of tegmen to stridulatory vein) rather short. Length as preserved 13 mm; estimated total length of tegmen 40–50 mm.

Family: Prophalangopsidae Kirby, 1906

Remarks. This family is distinguished from Haglidae by the development of the other type of secondary tegminal C (less arched and crossing proximal and middle parts of Sc branches as well as their distal parts) and the straight or weakly arched proximal "oblique veins" (crossveins) between CuA and CuP in male tegmina. The secondary tegminal C sometimes

disappears (Chifengiinae), but the location of the base of MA_2 at the widest part of the area between R and MA in the stridulatory apparatus (a character present in all males of Prophalangopsidae) allows us to include such forms in Prophalangopsidae.

Subfamily: Aboilinae Martynov, 1925

Remarks. This subfamily differs from all other subfamilies of Prophalangopsidae in the well-developed secondary tegminal C, the straight or almost straight proximal "oblique veins" (crossveins) between CuA and CuP in male tegmina, the rather primitive male stridulatory apparatus (with all areas between base of R and CuP widened), and the location of the bases of RS and MA_2 close to each other (Fig. 10). Aboilinae include the following genera: *Sinoprophalangopsis* Hong, 1982 and *Bacharaboilus* Gorochov, 1988 (Middle Jurassic); *Aboilus* Martynov, 1925 (?=*Pamphagopsis* Martynov, 1925; ?=*Syndesmophyllum* Martynov, 1934) and the enigmatic *Karatailus* Gorochov, 1996 (Upper Jurassic); *Apsataboilus* Gorochov, 1990 (Upper Jurassic or Lower Cretaceous); *Prophalangopseides* Sharov, 1968 and *Tettaboilus* Gorochov, 1988 (Lower Cretaceous); *Utanaboilus* Gorochov, 1990 (Lower or Upper Cretaceous); possibly *Pycnophlebia* Deichmuller, 1886, *Pseudohagla* Sharov, 1962, *Brunneus* Hong, 1983, *Procyrtophyllites* Zeuner, 1935, *Nipponohagla* Fujiyama, 1978, and *Baissaboilus* Gorochov, 1996 (Lower Cretaceous) described from poor material or female tegmina.

Procyrtophyllites britannicus Zeuner, 1935
Fig. 10

Holotype. NHM I. 19064; Purbeck; Swanage, Dorset; Berriasian; collected by S.H. Beckles.

Remarks. The holotype is a small part of a very large tegmen (length as preserved 40 mm; estimated total length 90–100 mm) bearing several dark transverse bands. This tegmen is probably male as the area between R and MA is rather wide. Zeuner (1939) included this species in Cyrtophyllitinae, but the position of the secondary tegminal C is similar to that seen in Prophalangopsidae. The inclusion of this monotypic genus in Aboilinae is based on the location of the base of RS near to the base of MA_2, but the differences between *Procyrtophyllites* and some other genera of Aboilinae are unclear.

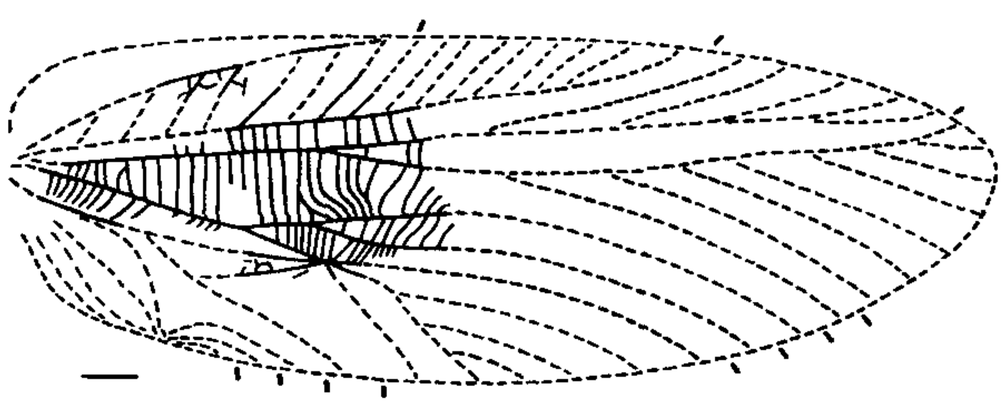


Fig. 10. *Procyrtophyllites britannicus* Zeuner, male, holotype NHM I. 19064; Swanage, Berriasian. Scale bar represents 5 mm.

Subfamily: Chifengiinae Hong, 1982

Remarks. This subfamily differs from all other Prophalangopsidae in the reduction and disappearance of the characteristic secondary tegminal C (one of the main characters of this family). This process can be traced by comparing primitive Jurassic representatives (in which the secondary Sc crosses a distal part of one Sc branch only) with derived Cretaceous ones (in which the secondary C does not cross any branches of Sc). The other tegminal characters of Chifengiinae are similar to those of Aboilinae (Fig. 11). Chifengiinae include the following genera: *Ashanga* Zherikhin, 1985 (Middle or Upper Jurassic); *Parahagla* Sharov, 1968 (=*Hebeihagla* Hong, 1982, syn. nov.; =*Habrohagla* Ren, Lu, Guo and Ji, 1995, syn. nov.; the synonymy is established because the tegmina of the type species of these genera are almost indistinguishable from each other); and *Chifengia* Hong, 1982 (Lower Cretaceous); and possibly *Aenigmoilus* gen. nov.

Genus *Aenigmoilus* gen. nov.

Derivation of name. Latin for enigma and *Aboilus*.

Type species. *Aenigmoilus minutus* sp. nov.

Diagnosis. Tegmina small (probably not longer than 30 mm), with rather long secondary C (which is distinctly longer than the nearest branches of Sc: in all other Chifengiinae, this vein is shorter or subequal in length to the nearest Sc branches), narrow area between R and MA in female, location of base of MA_2 near base of MP (but not near base of RS), and rather strongly curved CuP in female (Fig. 11).

Included species. Type species only.

Remarks. The characteristic structure of the secondary tegminal C, which does not cross any branches of Sc, may have arisen independently (convergently) in *Aenigmoilus* and in true Chifengiinae.

Aenigmoilus minutus sp. nov.
Fig. 11

Derivation of name. Latin for minute.

Holotype. MNEMG 2003.41 [CH 864 xlii] (part and counterpart); Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. and B. Jarzembowski.

Diagnosis. As for genus.

Description. Proximal half of female tegmen with rather dark colouration and numerous very small light spots (not shown on Fig. 11). Length as preserved 15 mm; estimated total length of tegmen 20–25 mm.

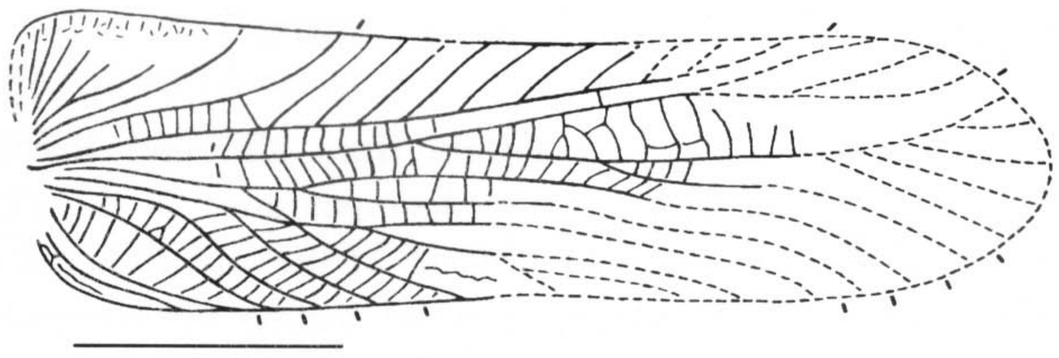


Fig. 11. *Aenigmoilus minutus* gen. et sp. nov, female, holotype MNEMG 2003.41; Clockhouse Brickworks, Upper Hauterivian. Scale bar represents 5 mm.

Subfamily: Termitidiinae Zeuner, 1939

Remarks. This subfamily is distinguished from all other subfamilies of Prophalangopsidae by the presence of a secondary tegminal C, the characteristic position of proximal "oblique veins" (crossveins) between CuA and CuP in male tegmina (the membranous area between the most proximal of these crossveins, lateral half of "diagonal vein", and basal parts of M and MP form a mirror-like cell analogous to the true mirror of Tettigonioidea; Fig. 12A, C, D), the narrow area between tegminal R and MA in the male, and the location of the bases of RS and MA_2 rather distant from each other (Figs. 12–17). Termitidiinae include five or six genera, which are considered below.

Genus *Pseudaboilus* gen. nov.

Derivation of name. From Greek for false and *Aboilus*.

Type species. *Pseudaboilus wealdensis* sp. nov.

Diagnosis. Tegmina large or medium size (length 38–80 mm), with long longitudinal branches of RA, narrow areas between these branches, characteristic S-shaped crossveins at base of mirror-like cell (between basal parts of M and CuA) in male, long CuA_2 and proximal branch of $MP + CuA_1$, partly reduced basal part of CuA_2 in male, comparatively oblique and short male stridulatory vein, and moderately long male chords (parts of CuP, 1A, and 2A situated distally of stridulatory vein) (Figs. 12, 13).

Included species. Type species and *P. purbeckensis* sp. nov.

Pseudaboilus wealdensis sp. nov.
Fig. 12

Derivation of name. After the Weald.

Holotype. BMB 014910 [A 400a] and 018644 (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by R. Batchelor.

Paratype. BMB 018617/-8 [A 412] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Surrey; Lower Barremian; collected by E. Jarzembowski.

Diagnosis. Large species of *Pseudaboilus*; male tegmen with dark mottling and expanded area bound by $MP + CuA_1$, "diagonal vein", and CuA_2.

Description. Holotype (male tegmina folded together; their apical parts isolated) and paratype (proximal part of male tegmen) belong to large insects (holotype length as preserved 60 mm; estimated total length of tegmen 70–80 mm); these tegmina have numerous dark spots and rather wide proximal part of area between $MP + CuA_1$, "diagonal vein", and CuA_2 (Fig. 12).

Remarks. A photograph of the holotype was previously published by Jarzembowski (1999, pl. 1, fig. 2).

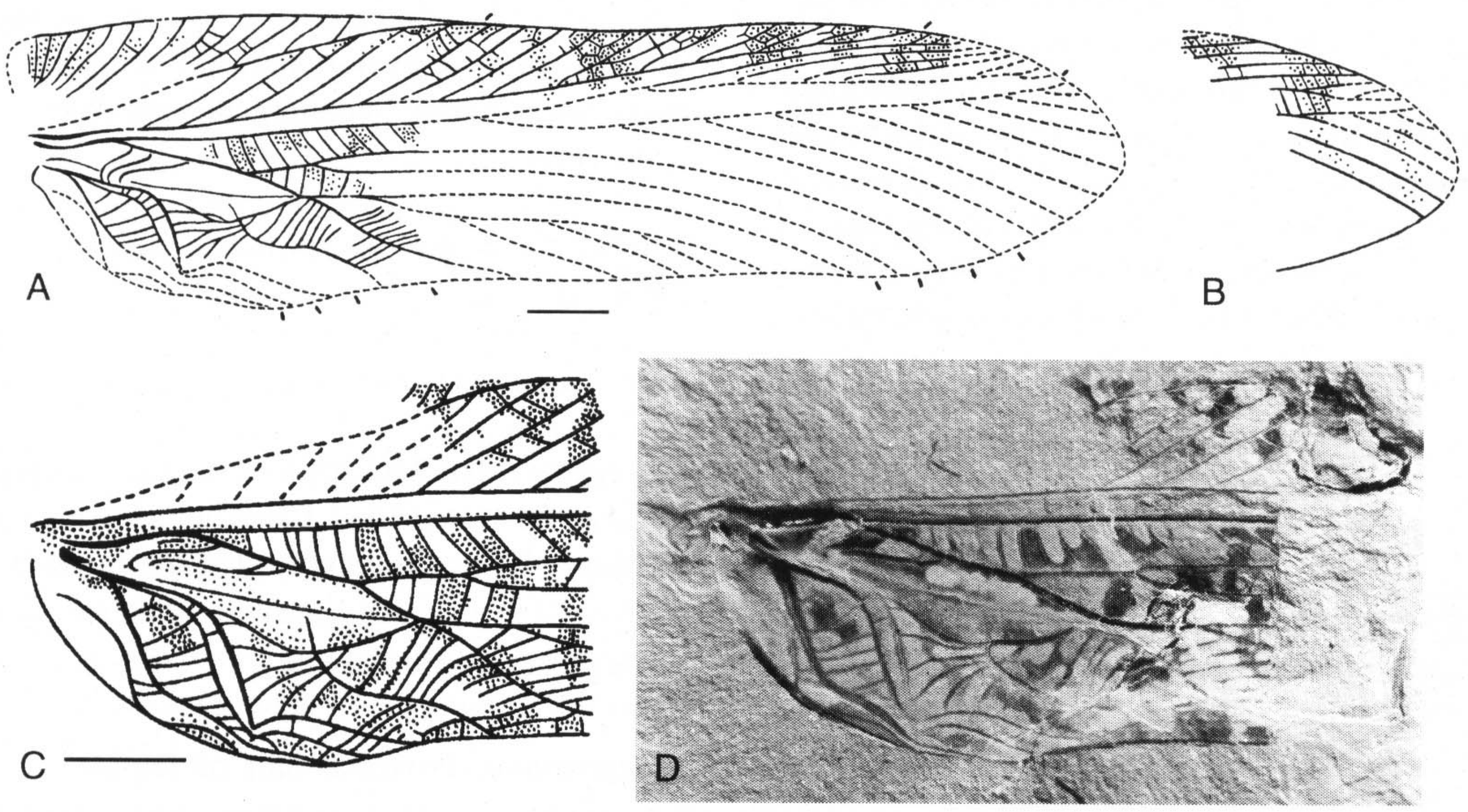


Fig. 12. *Pseudaboilus wealdensis* gen. et sp. nov., male tegmina; Auclaye Brickworks, Lower Barremian. A, holotype BMB 014910, without isolated apical part. B, its apical part; C, D, paratype, BMB 018617/-8. Scale bars represent 5 mm.

Pseudaboilus purbeckensis sp. nov.
Fig. 13

Derivation of name. After Purbeck region.

Holotype. MNEMG 2003.42 [DB175/ORTH 33]; Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Diagnosis. Small species of *Pseudaboilus*; male tegmen with more distinct transverse dark colour bands and narrow area bound by $MP + CuA_1$, "diagonal vein" and CuA_2.

Description. This male tegmen lacking the basal part belongs to a species that is distinctly smaller than *P. wealdensis* (length of tegmen as preserved 35 mm; estimated total length 38–40 mm); this tegmen has dark transverse bands and narrower (than in *P. wealdensis*) proximal part of area between $MP + CuA_1$, "diagonal vein", and CuA_2 (Fig. 13).

Genus *Tettigoilus* gen. nov.

Derivation of name. From *Tettigonia* and *Aboilus*.

Type species. *Tettigoilus sonorus* sp. nov.

Diagnosis. Tegmen small (length approximately 20 mm), lacking basal part of CuA_2 and without crossveins at base of mirror-like cell (between basal parts of M and CuA) in male, with very short CuA_2 and proximal branch of $MP + CuA_1$, transverse and very long male stridulatory vein, and short male chords (Fig. 14).

Included species. Type species only.

Remarks. This genus has partial convergent similarity to Tettigoniidae in the structure of the male stridulatory apparatus: the stridulatory areas are situated at the bases of the tegmina only and one of these areas is widened and membranous; however, in Tettigoniidae it is the true mirror between $MP + CuA_1$, "diagonal vein", and CuA_2, and in *Tettigoilus* it is the mirror-like area between M, "diagonal vein", and proximal crossvein connecting CuA_2 with CuP (Fig. 14).

Tettigoilus sonorus sp. nov.
Fig. 14

Derivation of name. Latin for loud.

Holotype. MNEMG 2003.43 [A 171] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by E. and B. Jarzembowski.

Diagnosis. As for genus.

Description. Proximal-medial part of male tegmen with stridulatory apparatus; basal part (situated proximal to stridulatory vein) very short; area between second branch of $MP + CuA_1$ and anal edge of tegmen very narrow; colouration unknown. Length as preserved 5.8 mm; estimated total length 20 mm.

Genus *Termitidium* Westwood, 1854

Type species. *Termitidium ignotum* Westwood, 1854; Lower Cretaceous, southern England.

Diagnosis. Tegmina medium size (length about 40 mm), with branches of RA similar to those of *Pseudaboilus*, structure of basal part of CuA_2 and crossveins at base of mirror-like cell (between CuA and basal part of M) in male similar to *Tettigoilus*. Intermediate between *Pseudaboilus* and *Tettigoilus* are length of CuA_2, proximal branch of $MP + CuA_1$, and male chords, as well as length and position of male stridulatory vein (Fig. 15).

Included species. Type species only.

Termitidium ignotum Westwood, 1854
Fig. 15

Holotype. NHM I. 11955 (part and counterpart); Middle Purbeck; Durlston Bay, Dorset; mid-Berriasian; collected by P.B. Brodie.

Remarks. The holotype is a male tegmen lacking small proximal-lateral and apical parts (length as preserved 37 mm; estimated total length 40 mm). Study of the holotype

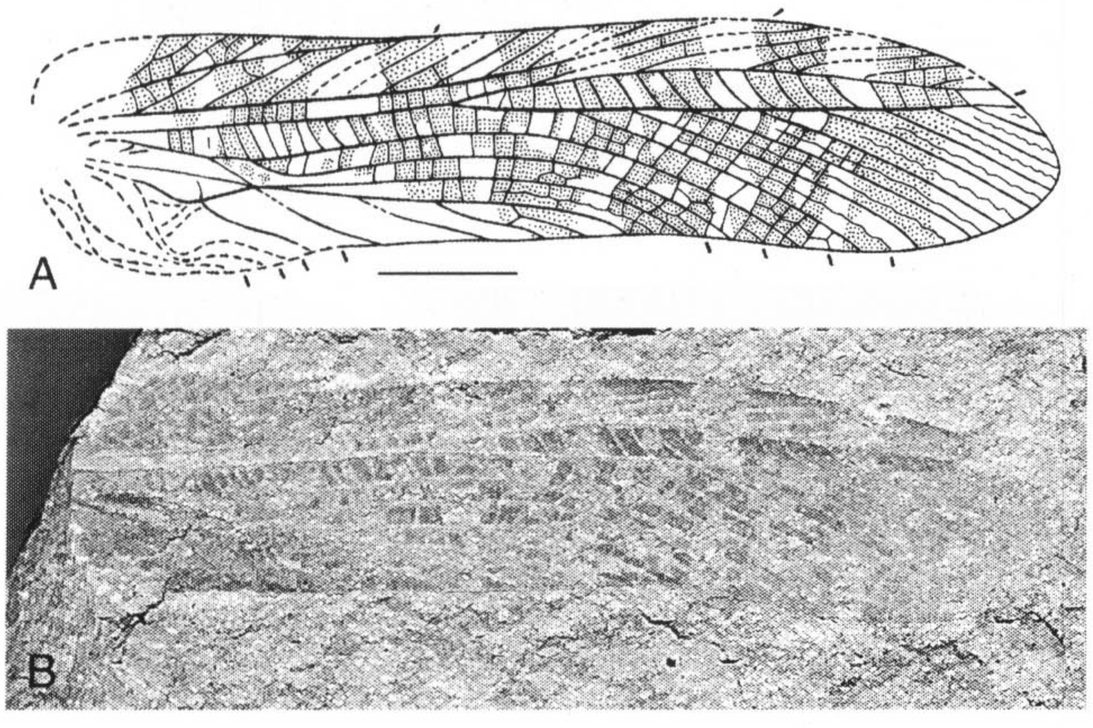


Fig. 13. *Pseudaboilus purbeckensis* gen. et sp. nov., male, holotype, MNEMG 2003.42; Durlston Bay, Upper Berriasian. Scale bar represents 5 mm.

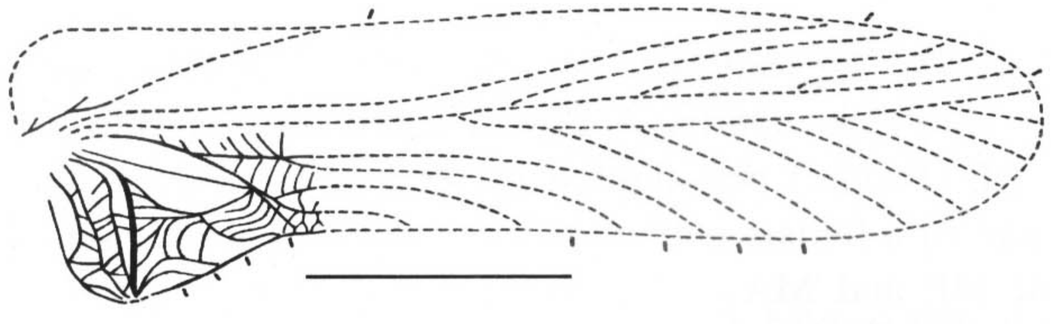


Fig. 14. *Tettigoilus sonorus* gen. et sp. nov., male, holotype MNEMG 2003.43; Auclaye Brickworks, Lower Barremian. Scale bar represents 5 mm.

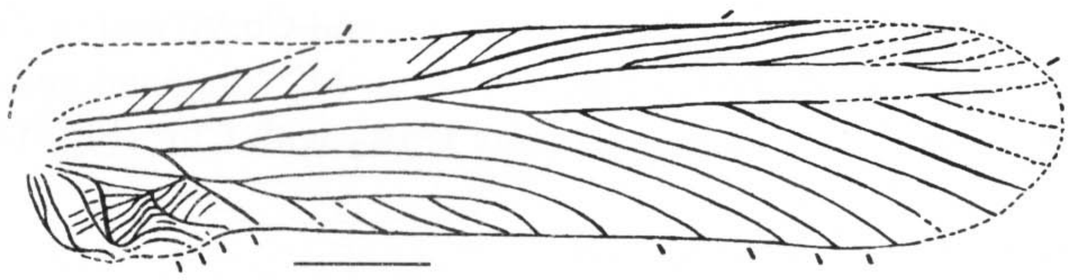


Fig. 15. *Termitidium ignotum* Westwood, male, holotype NHM I. 11955; Durlston Bay, Upper Berriasian. Scale bar represents 5 mm.

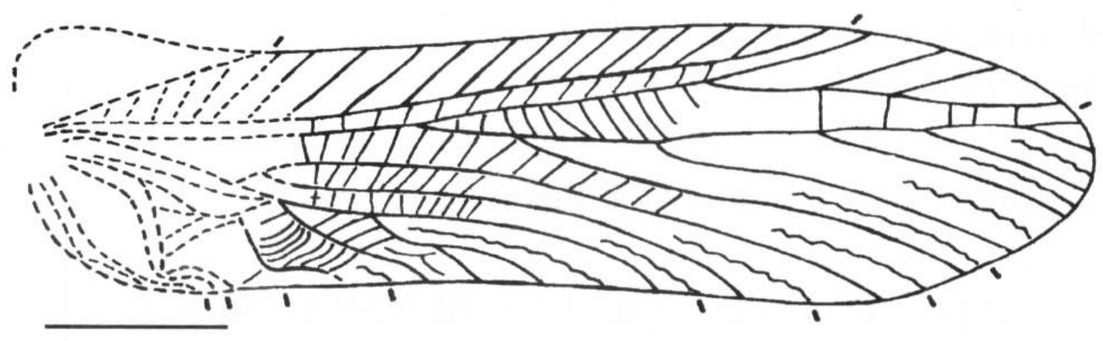


Fig. 16. *Zalmona brodiei* Giebel, male, holotype NHM I. 3533; Dinton, mid-Berriasian. Scale bar represents 5 mm.

shows that Sc is shorter and RA branches are more numerous than in Zeuner's and Sharov's figures (Zeuner 1939, fig. 43, 3; Sharov 1968, fig. 23), and that the stridulatory apparatus is as in Fig. 15.

Genus *Zalmona* Giebel, 1856

Type species. *Zalmona brodiei* Giebel, 1856; Lower Cretaceous, southern England.

Diagnosis. Tegmina rather small (length about 30 mm) and distinguished from those of other genera of Termitidiinae by the rather short oblique branches of RA, rather wide areas between these branches, long CuA_2 and proximal branch of $MP + CuA_1$ (as in *Pseudaboilus*), and widened middle part of area between proximal branch of $MP + CuA_1$ and CuA_2 in male (in males of other Termitidiinae, this area is widened more proximally) (Fig. 16).

Included species. Type species only.

Zalmona brodiei Giebel, 1856
Fig. 16

Holotype. NHM I. 3533; Middle Purbeck; Dinton, Wiltshire; mid-Berriasian; collected by P.B. Brodie.

Remarks. The holotype is a male tegmen lacking proximal part (length as preserved 23 mm; estimated total length 30 mm). Zeuner (1939, fig. 27, 1) included in this species the proximal part of another male tegmen from the Lower Purbeck of Durlston Bay (NHM I. 1276; coll. P.B. Brodie), but study of this specimen suggests that it may belong to another subfamily as its CuA_2 has a long proximal part similar to that of males of Aboilinae and Chifengiinae (in males of Termitidiinae this part is short and reduced, or absent).

Mesogryllus achelous (Westwood, 1854)
[=*Blattidium achelous* Westwood, 1854]

Remarks. The holotype of this species (NHM I. 12302; Lower Purbeck; Durlston Bay, Dorset; Lower Berriasian; coll. P.B. Brodie) was figured by Zeuner (1939, fig. 37, 1). It is part of a female tegmen with a large gap between the bases of MP and MA_2. The distinctions between this species (based on a female tegmen) and the previous taxa of Termitidiinae (based on male tegmina) are unclear.

?*Agrionidium obscurum* sp. nov.
Fig. 17

Derivation of name. Latin for obscure.

Holotype. MNEMG 2003.44 [DB175/ORTH 32] (part and counterpart); Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Diagnosis. Tegmen differing from those of all other Termitidiinae by very wide area between MA_2 and $MP + CuA_1$.

Description. Large female tegmen lacking edges and apical part, having dark colouration with small light spots, structure of RA branches similar to that of *Pseudaboilus* and *Termitidium*, very long distance between bases of RS and MA_2 (this is the basis for preliminary inclusion of this species in Termitidiinae), widened area between R and base of MP, and rather weakly curved CuP. Length as preserved 47 mm; estimated total length 50–60 mm.

Agrionidium aetna Westwood, 1854

Holotype. NHM I. 3958; Lower Purbeck; Durlston Bay, Dorset; Lower Berriasian; collected by P.B. Brodie.

Remarks. This fossil, figured by Westwood (1854, pl. 18, fig. 39), resembles a small part of the tegmen (at the region of branches of RA and RS) of ?*A. obscurum* in its large

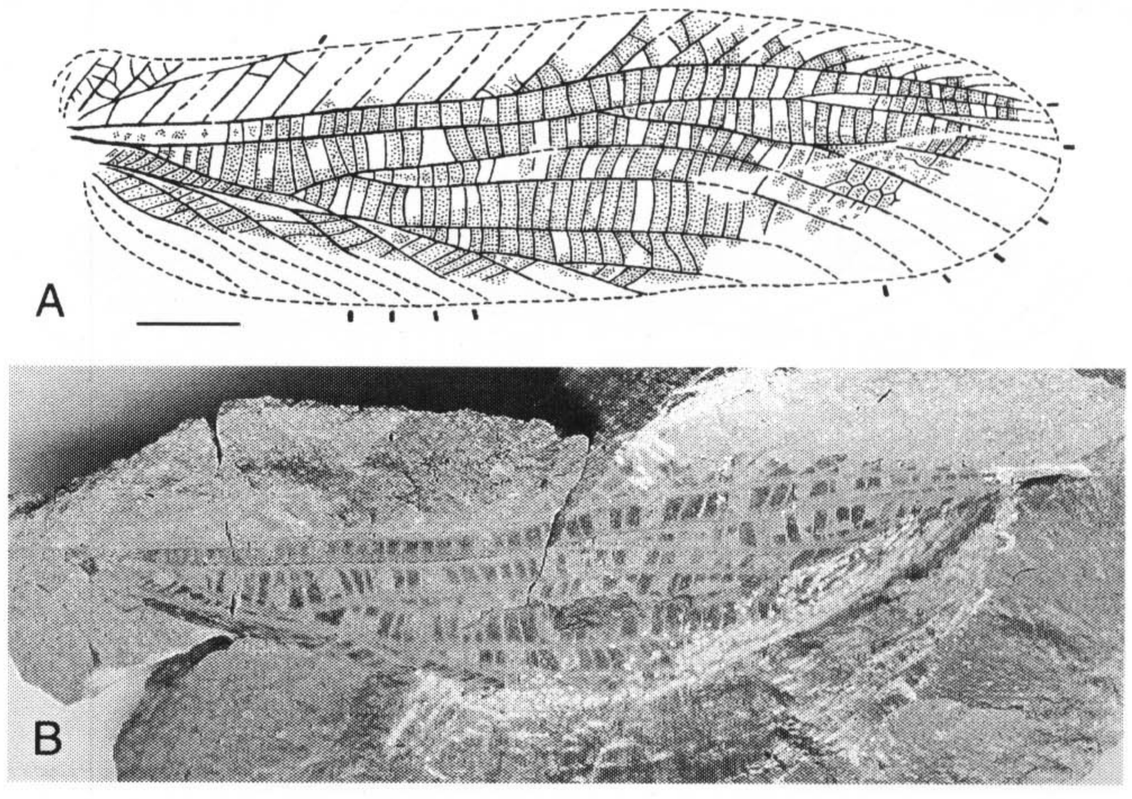


Fig. 17. ?*Agrionidium obscurum* sp. nov., female, holotype MNEMG 2003.44; Durlston Bay, Upper Berriasian. Scale bar represents 5 mm.

size, dark colouration, and details of venation, but it is distinguished by the absence of light spots. There is some doubt regarding inclusion of this species and the monobasic genus *Agrionidium* Westwood, 1854 in Termitidiinae as well as the inclusion of ?*A. obscurum* in this genus.

Infraorder: Gryllidea Laicharting, 1781
Superfamily: Grylloidea Laicharting, 1781
Family: Baissogryllidae Gorochov, 1985

Remarks. This family is known from the Early Cretaceous and possibly Late Jurassic. It differs from Protogryllidae (Jurassic and possibly Late Triassic) and Gryllotalpidae (Cretaceous and Cenozoic) in the development of a true mirror in the male tegminal stridulatory apparatus as a result of the appearance of the characteristic S-shaped curve of the proximal branch of $MP + CuA_1$ and distinct widening of the area between CuA_2, lateral part of "diagonal vein", and proximal part of the above-mentioned branch of $MP + CuA_1$ (Figs. 18–26). It differs from Gryllidae (Cretaceous and Cenozoic) and Mogoplistidae (Cenozoic) in the primitive position of the "dividing veins" (crossveins) of the mirror (which are obliquely longitudinal, more or less parallel to the true "oblique veins"; for comparison see Figs. 18–26 and 27A, B), and from Myrmecophilidae (Recent) in the presence of wings. The differences between the females of Baissogryllidae and those of Protogryllidae and Gryllidae are unclear. In this connection, the holotype of *Acheta sedgwicki* Brodie, 1845 (NHM I. 11990 and I. 3525, part and counterpart; Purbeck beds, Dinton, Wiltshire; mid-Berriasian; coll. P.B. Brodie; figured by Ross and Jarzembowski, 1996, fig. 3D), represented by a female with indistinct venation, and a female tegmen, determined by Zeuner (1939) as *Protogryllus minor* (Bode, 1905) (NHM I. 12315 and I. 12532; Lower Purbeck, Durlston Bay, Dorset; Lower Berriasian; coll. P.B. Brodie), may be included in Baissogryllidae or equally well in Gryllidae or Protogryllidae; these species are Grylloidea incertae sedis that cannot be compared with taxa in families based on males only. Baissogryllidae consist of three subfamilies, considered below.

Subfamily: Bontzaganiinae Gorochov, 1985

Remarks. Bontzaganiinae are characterized by the rather large lancet-like area, virtually devoid of crossveins, between R and proximal part of MA in male tegmina; the relatively numerous and almost longitudinal "dividing veins" (crossveins) of the mirror; and the location of the largest mirror cells at the lateral part of the mirror (Figs. 18–22). This subfamily includes the following Early Cretaceous genera: *Bontzagania* Gorochov, 1985; *Santanagryllus* Martins-Neto, 1991; *Notocearagryllus* Martins-Neto, 1998; *Anglogryllus* gen. nov.; and possibly *Cearagryllus* Martins-Neto, 1991. The type species of *Cearagryllus* has a rather small (unusual for this subfamily) lateral cell of the mirror (although the venation of the holotype is poorly preserved), but some other species included in this genus (e.g., *C. gorochovi* Martins-Neto) are more similar to the type species of *Santanagryllus* and *Notocearagryllus* (Martins-Neto 1991, 1999).

Genus *Notocearagryllus* Martins-Neto, 1998

Type species. *Notocearagryllus dutrae* Martins-Neto, 1998, Lower Cretaceous, Brazil.

Diagnosis. Differences between this genus and *Santanagryllus* are unclear (holotype of *N. dutrae* studied by AVG). *Notocearagryllus* differs from *Bontzagania* in having less numerous "dividing veins" (crossveins) in the male mirror and the acute proximal angle of the mirror. It is distinguished from *Anglogryllus* gen. nov. by the normal (primitive) position of the "oblique veins" in male tegmina (these crossveins are almost parallel to the "diagonal vein", and almost not crossed by the latter vein and the basal part of CuA_2) (Figs. 18–20).

Included species. Type species and three species described below.

Notocearagryllus britannicus sp. nov.
Fig. 18

Derivation of name. Latin for British.

Holotype. BMB 018615/-6 [A 225] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by E. and B. Jarzembowski.

Paratype. MNEMG 2003.45 [CH 879 xxxiv] (part and counterpart); Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. and B. Jarzembowski.

Diagnosis. Male tegmen distinguished from that of *N. dutrae* by distinctly less S-shaped proximal branch of $MP + CuA_1$ and distal "oblique vein" (crossvein) not fused with basal part of CuA_2. It differs from other similar species

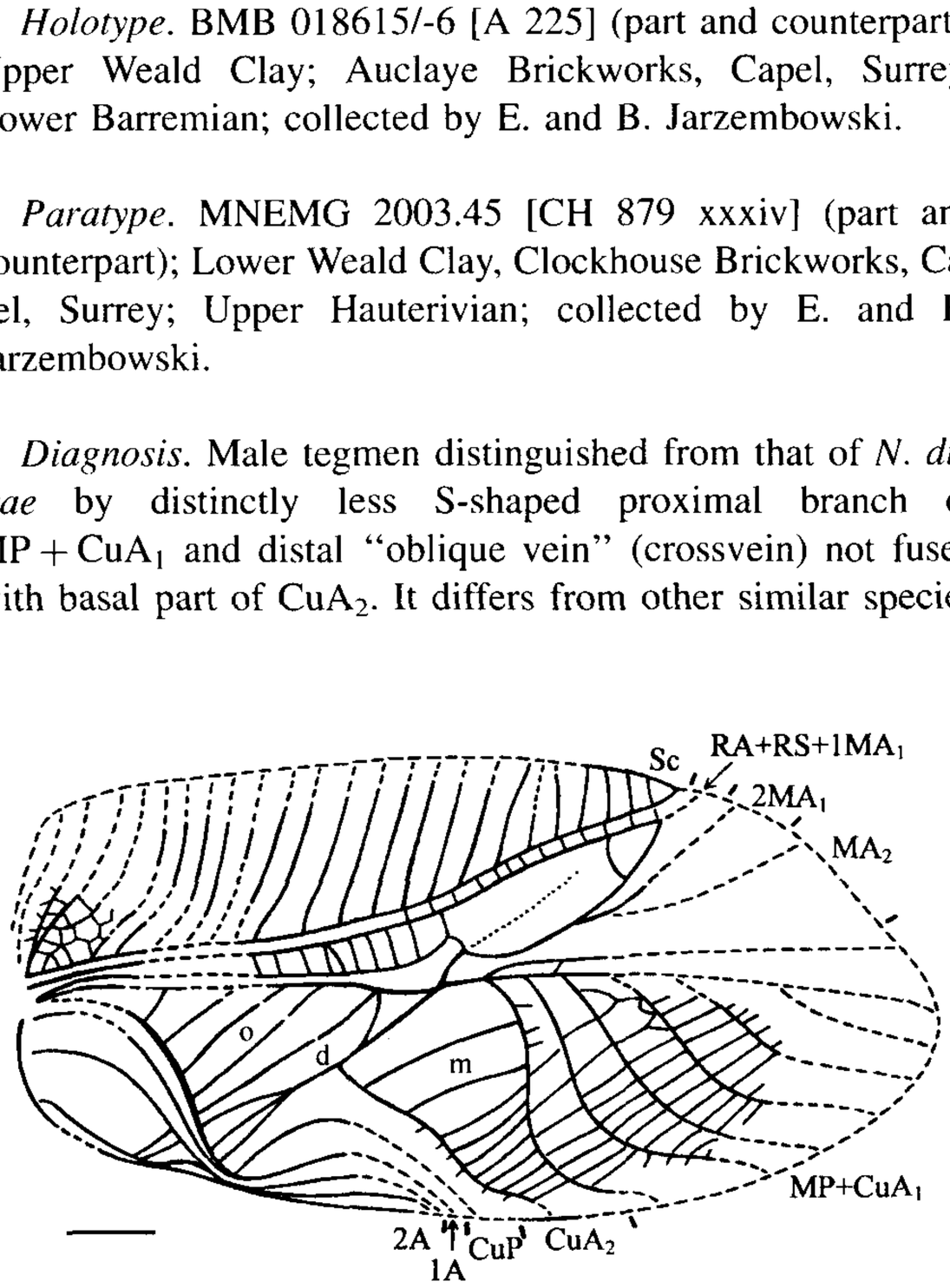


Fig. 18. *Notocearagryllus britannicus* sp. nov., male, holotype BMB 014910; Auclaye Brickworks, Lower Barremian. Abbreviations: o, "oblique veins"; d, "diagonal vein"; m, mirror. Scale bar represents 2 mm.

(including species described in the genera *Santanagryllus* and *Cearagryllus*) in the characteristic shape of the mirror and its lateral cell: the mirror is not very large, with a comparatively wide proximal part of its lateral cell and two free "dividing veins" (the distal ends of which are not fused with the nearest crossvein).

Description. Male tegmen unfortunately lacking apical and some lateral areas. Length as preserved 17 mm; estimated total length 20 mm.

Notocearagryllus grandispeculum sp. nov.
Fig. 19

Derivation of name. Latin for grand and mirror.

Holotype. BMB 025003/-4 [Ross 7/5/93] (part and counterpart); Upper Weald Clay; Rudgwick Brickworks, Rudgwick, West Sussex; Lower Barremian; collected by A. Ross.

Diagnosis. Male tegmen differs from that of *N. britannicus* in its larger mirror with narrow proximal part of its lateral cell and three "dividing veins" (distal of which is fused with nearest crossvein); distinctly shorter basal part of CuA_2; and more numerous "oblique veins". From *N. dutrae*, it is distinguished as in *N. britannicus* and by a relatively short basal part of CuA_2. This new species differs from all other similar species in the number or structure of the "dividing veins" of the mirror.

Description. Male tegmen lacking basal, lateral, and distal parts; length as preserved 10 mm; estimated total length 16–17 mm.

Notocearagryllus cordispeculum sp. nov.
Fig. 20

Derivation of name. Latin for heart and mirror.

Holotype. BMB 018621/-2 [A 552] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by A. Ross.

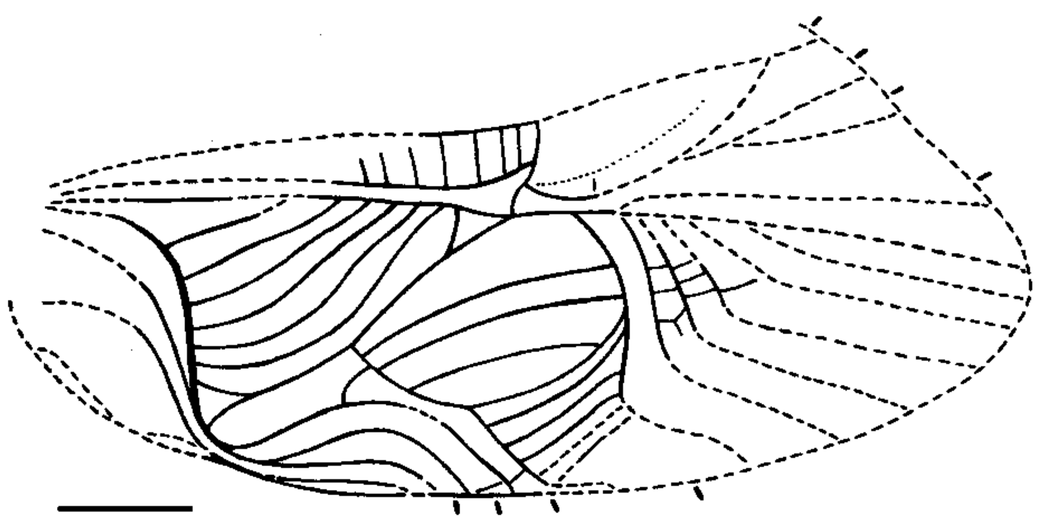


Fig. 19. *Notocearagryllus grandispeculum* sp. nov., male, holotype BMB 025003/-4; Rudgwick Brickworks, Lower Barremian. Scale bar represents 2 mm.

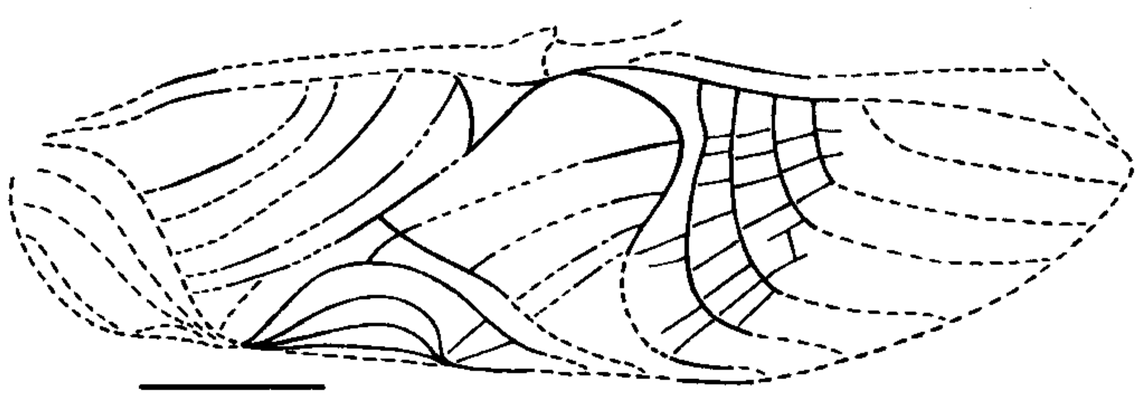


Fig. 20. *Notocearagryllus cordispeculum* sp. nov., male, holotype BMB 018621/-2; Auclaye Brickworks, Lower Barremian. Scale bar represents 2 mm.

Diagnosis. Male tegmen differs from *N. britannicus* and *N. grandispeculum* in its strongly S-shaped proximal branch of $MP + CuA_1$; in addition, from *N. britannicus* in the short basal part of CuA_2 and from *N. grandispeculum* in the presence of two free "dividing veins" in the mirror. This new species is distinguished from *N. dutrae* in the shorter basal part of CuA_2 as well as the presence of two "dividing veins" in the mirror; and from all other similar species in the shape of the proximal branch of $MP + CuA_1$ and the basal part of CuA_2.

Description. Central-medial part of male tegmen; length as preserved 7.5 mm; estimated total length 12–13 mm.

Genus *Anglogryllus* gen. nov.

Derivation of name. Latin for England and *Gryllus*.

Type species. *Anglogryllus lyristes* sp. nov.

Diagnosis. This genus is clearly distinguished from all other genera of Bontzaganiinae by the migration of lateral parts of several "oblique veins" (in male tegmina) on the "diagonal vein" and basal part of CuA_2 (Figs. 21, 22).

Included species. Type species and *A. rotundispeculum* sp. nov.

Anglogryllus lyristes sp. nov.
Fig. 21

Derivation of name. Latin for lyrist.

Holotype. MNEMG 2003.46 [A 225] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by E. and B. Jarzembowski.

Diagnosis. Male tegmen distinguished from that of *A. rotundispeculum* gen. et sp. nov. by the more angled (proximally) mirror; narrow lateral cell; larger basal part of CuA_2; comparatively simple "diagonal vein"; and weakly arched chords.

Description. Male tegmen with somewhat deformed distal part and lacking the lateral part; proximal branch of $MP + CuA_1$ weakly S-shaped; mirror with two free "dividing

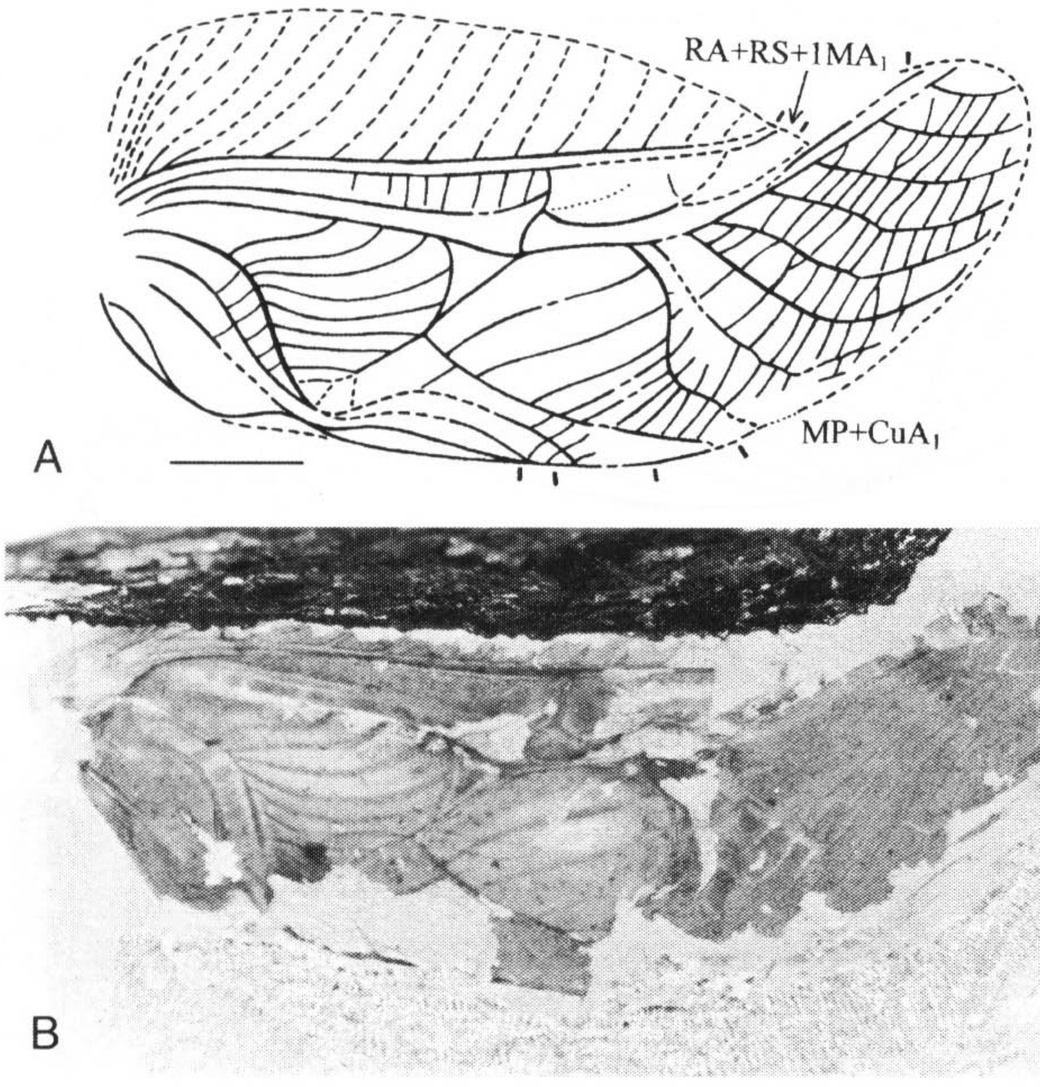


Fig. 21. *Anglogryllus lyristes* gen. et sp. nov., male, holotype MNEMG 2003.46; Auclaye Brickworks, Lower Barremian. Scale bar represents 2 mm.

veins", comparatively narrow lateral cell, and rather acute proximal angle of mirror; basal part of CuA_2 long; "diagonal vein" rather simple; chords weakly arched. Length as preserved 14.5 mm; estimated total length 16 mm.

Remarks. A figure of the holotype and a photograph of its stridulatory file were previously published by Jarzembowski (1984, figs. 21, 22; 1999, pl. 2, fig. 3).

Anglogryllus rotundispeculum sp. nov.
Fig. 22

Derivation of name. Latin for round and mirror.

Holotype. BMB 018633/-4 [A 214] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by E. and B. Jarzembowski.

Diagnosis. Male tegmen distinguished from that of *A. lyristes* by almost round mirror with comparatively wide lateral

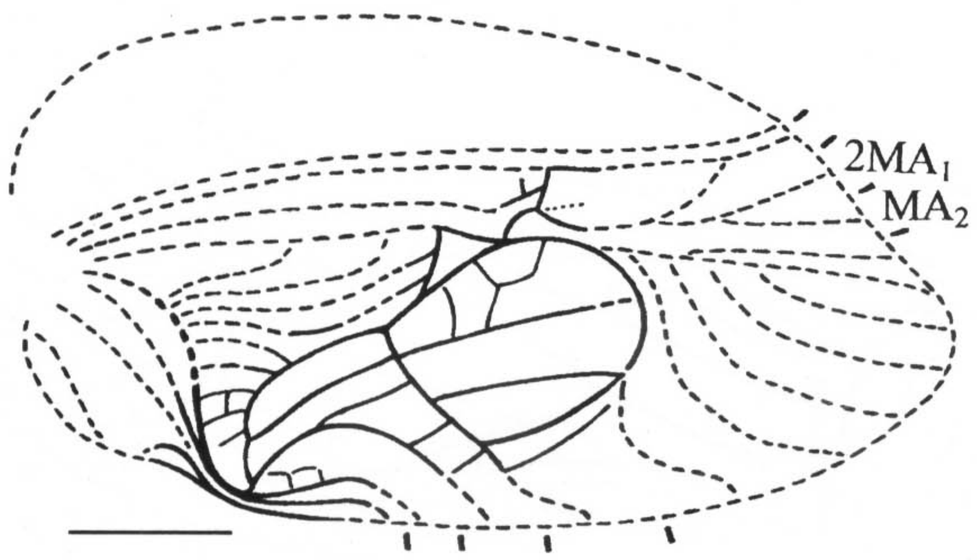


Fig. 22. *Anglogryllus rotundispeculum* gen. et sp. nov., male, holotype BMB 018633/-4; Auclaye Brickworks, Lower Barremian. Scale bar represents 2 mm.

cell; shorter basal part of CuA_2; "diagonal vein" partly fused with nearest (distal) crossvein between CuA_2 and CuP; and strongly arched chords.

Description. Central-medial part of male tegmen. Length as preserved 6.3 mm; estimated total length 12 mm.

Subfamily: Baissogryllinae Gorochov, 1985

Remarks. Baissogryllinae are characterized by the smaller lancet-like area between R and the proximal part of MA which bears several crossveins (in male tegmina); the relatively numerous and distinctly oblique "dividing veins" of the mirror; and the proximal cell of the mirror being smaller than the neighbouring one (Fig. 23). This subfamily includes the following Early Cretaceous genera: *Baissogryllus* Sharov, 1968; *Eubaissogryllus* Gorochov, 1985; *Storozhenkoana* Gorochov, 1992; and possibly *Ponomarenkoana* Gorochov, 1992, *Castilogryllus* Martins-Neto, 1995, and *Speculogryllus* gen. nov.

Genus *Speculogryllus* gen. nov.

Derivation of name. Latin for mirror and *Gryllus*.

Type species. *Speculogryllus acutispeculum* sp. nov.

Diagnosis. This genus differs from *Castilogryllus* in having far fewer "dividing veins" in the mirror (in male tegmina) and from all other genera of Baissogryllinae in the very acute proximal angle of the mirror and short medial part of the "diagonal vein" (between the mirror and CuP) (Fig. 23).

Included species. Type species only.

Speculogryllus acutispeculum sp. nov.
Fig. 23

Derivation of name. Latin for sharp and mirror.

Holotype. MNEMG 2003.47 [S 1454]; Upper Weald Clay; Smokejacks Brickworks, Ockley, Surrey; Lower Barremian; collected by E. and B. Jarzembowski.

Diagnosis. As for genus.

Description. Proximal half of male tegmen lacking basal and lateral parts; mirror with at least three "dividing veins"; "diagonal vein" simple; lateral parts of "oblique veins" connected with each other by additional crossveins; chords probably long (Fig. 23). Length as preserved 6 mm; estimated total length of tegmen 13–14 mm.

Subfamily: Sharategiinae Gorochov, 1990

Remarks. This subfamily is distinguished from the two other subfamilies by the distinctly smaller lancet-like area between R and the proximal part of MA (in male tegmina), the

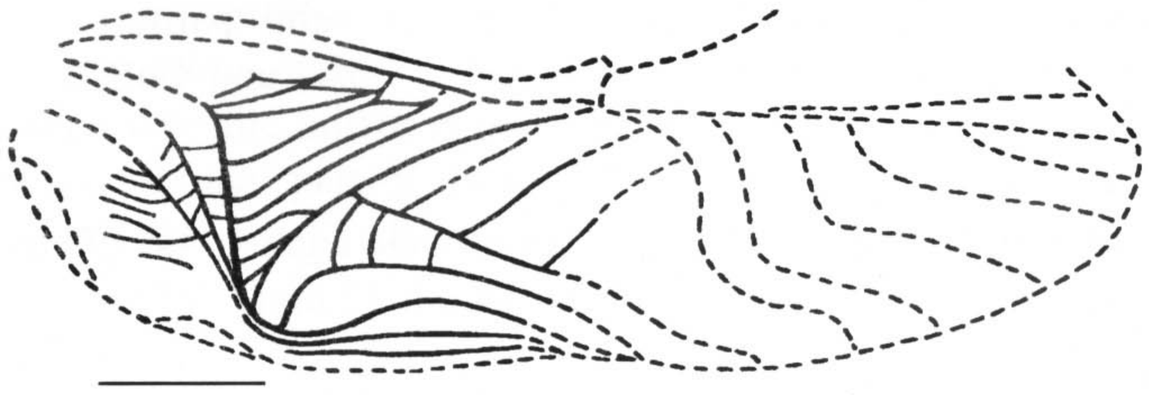


Fig. 23. *Speculogryllus acutispeculum* gen. et sp. nov., male, holotype MNEMG 2003.47; Smokejacks Brickworks, Lower Barremian. Scale bar represents 2 mm.

absence of a narrow "neck" separating this cell from its base, and a single "dividing vein" in the mirror. Sharategiinae include the following genera: Early Cretaceous *Mongologryllus* Gorochov, 1985, *Caririgryllus* Martins-Neto, 1991, and *Neosharategia* Gorochov, 1992; and Early Cretaceous and possibly Upper Jurassic *Sharategia* Gorochov, 1990.

Genus *Sharategia* Gorochov, 1990

Type species. *Sharategia rasnitsyni* Gorochov, 1990, Lower Cretaceous, Mongolia.

Diagnosis. *Sharategia* differs from *Mongologryllus* and *Caririgryllus* in having a distinctly narrower cell between the "diagonal vein" and distal "oblique vein" in male tegmina. Additionally, it differs from *Mongologryllus* in having a well-developed lancet-like area (lacking crossveins) between R and the proximal part of MA in males, and from *Caririgryllus* by the clearly longer medial part of the "diagonal vein" between CuA_2 and CuP in male tegmina. It differs from *Neosharategia* in the oblique (as opposed to almost transverse) position of the "dividing vein" of the mirror and narrow areas between the branches of MP + CuA_1 in male tegmina (Figs. 24–26).

Included species. Type species and three species described below.

Sharategia davisi sp. nov.
Fig. 24

Derivation of name. After Richard Davis of Gillingham, Kent, museum volunteer.

Holotype. MNEMG 2003.48 [DB175/ORTH 70] (part and counterpart); Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Diagnosis. Tegmen distinguished from that of *S. rasnitsyni* by almost oval mirror with a rather narrow medial part of the proximal cell, more numerous "oblique veins" between CuA and CuP, and a longer crossvein between the mirror and the chords (near the medial part of the "diagonal vein").

Description. Dorsal part of male tegmen; length 8.0 mm.

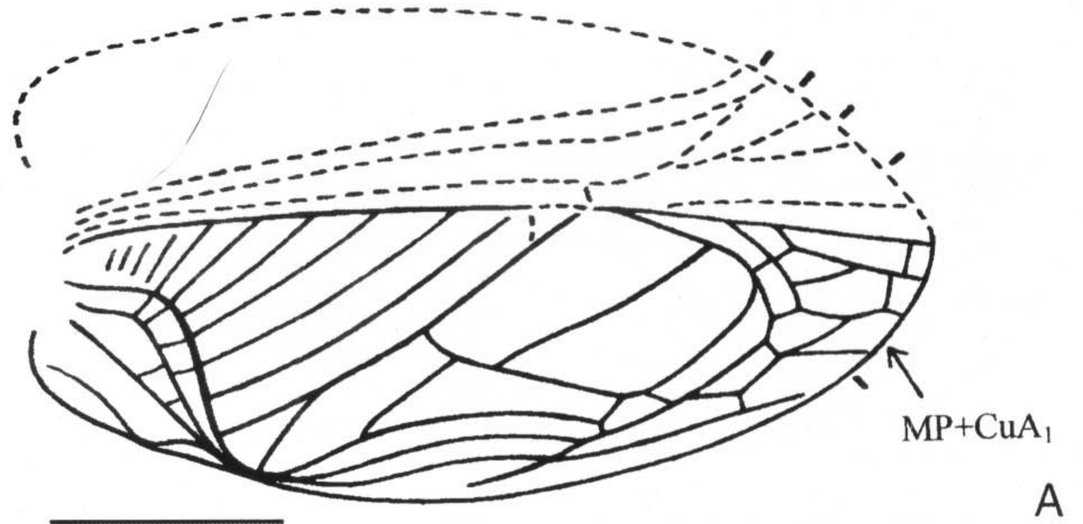


Fig. 24. *Sharategia davisi* sp. nov., male, holotype MNEMG 2003.48; Durlston Bay, Upper Berriasian. Scale bar represents 2 mm.

Additional material. NHM I. 12235 (part and counterpart); Middle Purbeck; Durlston Bay, Dorset; mid-Berriasian; coll. P.B. Brodie. This basal half of a male tegmen was determined by Zeuner (1939) as *Protogryllus dobbertinensis* (Geinitz) and described from the Early Jurassic as belonging to the Protogryllidae, but it is in fact very similar to the holotype of *S. davisi*.

Sharategia batchelorae sp. nov.
Fig. 25

Derivation of name. After Rita Batchelor of Redhill, fossil collector.

Holotype. MNEMG 2003.49 [CH 1038 and CH 879 xxvi] (part and counterpart); Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. and B. Jarzembowski.

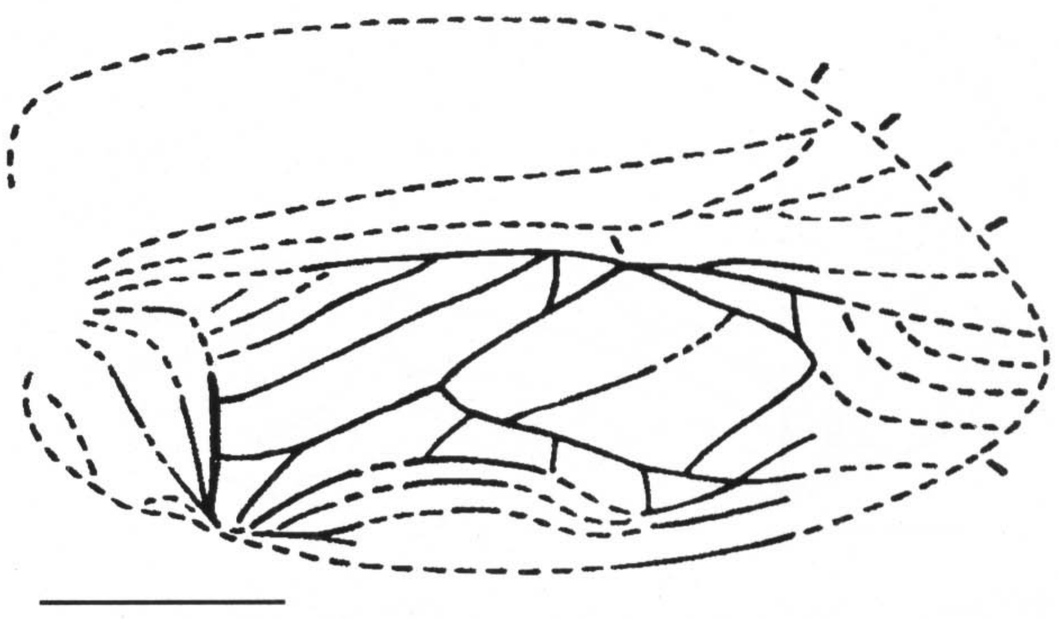


Fig. 25. *Sharategia batchelorae* sp. nov., male, holotype MNEMG 2003.49; Clockhouse Brickworks, Upper Hauterivian. Scale bar represents 2 mm.

Diagnosis. Tegmen similar to that of *S. davisi*, but with a more transverse stridulatory vein, less numerous "oblique veins", and much shorter crossvein between the mirror and the chords near the "diagonal vein". *S. batchelorae* differs from *S. rasnitsyni* in mirror details, like *S. davisi*.

Description. Dorsal part of male tegmen lacking basal and apical areas. Length as preserved 6.2 mm; estimated total length of tegmen 8–9 mm.

Sharategia baldocki sp. nov.
Fig. 26

Derivation of name. After David Baldock of Milford, Orthoptera recorder.

Holotype. MNEMG 2003.50 [CH 81e]; Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. and B. Jarzembowski.

Diagnosis. Tegmen distinguished from those of all other congeners by an oval mirror with a wide medial part of the proximal cell and a longer crossvein between the mirror and the chords near the "diagonal vein".

Description. Dorsal part of tegmen lacking apex. Length as preserved 9 mm; estimated total length of tegmen 10–12 mm.

Additional material. MNEMG 2005.48 [CH 1039], a small fragment of male tegmen; Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. and B. Jarzembowski.

Family: Gryllidae Laicharting, 1781

Remarks. This extant family (true crickets) is known from fossils dating back to the Early Cretaceous (Gorochov 1985, 1995b). It differs from Protogryllidae and Gryllotalpidae in the development of a true mirror in the male tegminal stridulatory apparatus. It is distinguished from Baissogryllidae, which also have a true mirror and may be ancestral to Gryllidae, by the characteristic position of the "dividing veins" in the mirror: these crossveins are transverse or strongly curved as a result of the migration of the medial (proximal) part(s) from CuA_2 towards the crossvein limiting the mirror distally (Fig. 27A, B). The differences between Gryllidae, Myrmecophilidae and Mogoplistidae are clear for Recent forms only. Gryllidae comprises numerous Recent and two fossil subfamilies.

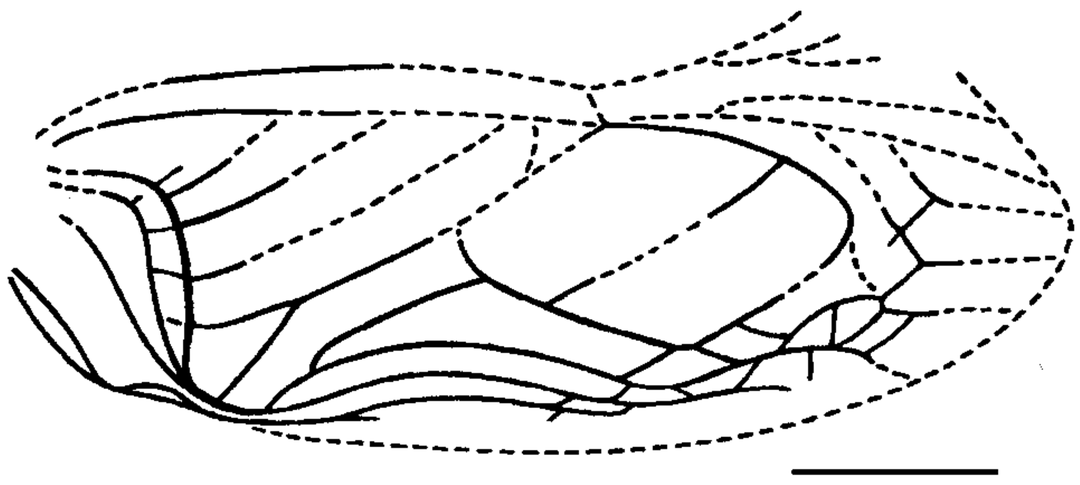


Fig. 26. *Sharategia baldocki* sp. nov., male, holotype MNEMG 2003.50; Clockhouse Brickworks, Upper Hauterivian. Scale bar represents 2 mm.

Subfamily: Gryllospeculinae Gorochov, 1985

Remarks. Early Cretaceous Gryllospeculinae and Olindagryllinae Martins-Neto, 1998 differ from all Recent subfamilies and from Mogoplistidae in the absence of the characteristic additional fusion of the proximal parts of 1A and nearest 2A branch near the plectrum: these veins form a more or less distinct loop in Mogoplistidae and Late Cretaceous and Cenozoic Gryllidae (Fig. 27C). This absence of fusion is primitive and seen also in Baissogryllidae (the additional fusion of these veins in the basal area of the holotype of *Notocearagryllus dutrae* is probably an individual aberration), Protogryllidae, Gryllotalpidae, Gryllavoidea and Hagloidea. In this connection, Mogoplistidae must be considered the descendants of Gryllidae possibly younger than Early Cretaceous. The differences between Gryllospeculinae and Olindagryllinae are less distinct: the former has two (or one) strongly curved "dividing vein(s)" in the mirror and now includes only three genera (*Gryllospeculum* Gorochov, 1985; *Mongolospeculum* Gorochov, 1985; and *Araripegryllus* Martins-Neto, 1991); the latter subfamily has three straight or almost straight "dividing veins" in the mirror and now includes one or two genera (*Olindagryllus* Martins-Neto, 1998 and possibly *Brontogryllus* Martins-Neto, 1991). The subfamily position of *Cratogryllus* Martins-Neto, 1991 is currently unclear as it has one straight "dividing vein" in the mirror.

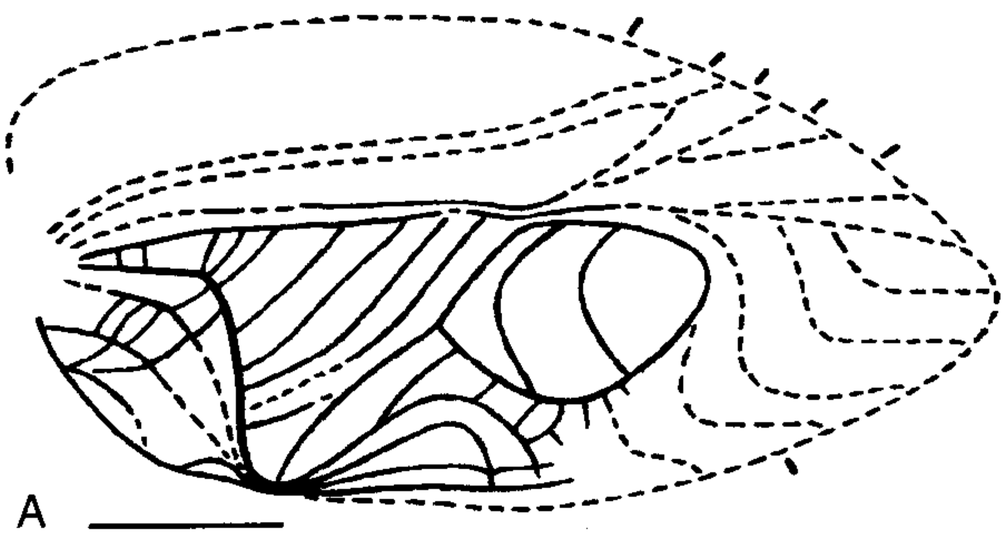
?*Araripegryllus orientalis* sp. nov.
Fig. 27A

Derivation of name. Latin for oriental.

Holotype. MNEMG 2003.51 [CH 1064] (part and counterpart); Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. and B. Jarzembowski.

Diagnosis. Tegmen distinguished from that of other male congeners by a wider cell between the "dividing veins" of the mirror, narrower proximal cell of the mirror and narrower area between the "diagonal vein" and distal "oblique vein". The structure of the area distal to the mirror is unknown; therefore, the inclusion of this species in the Brazilian genus *Araripegryllus* is tentative, as in true *Araripegryllus* this area has a characteristic long cell around the distal half of the mirror (Fig. 27B: c, m, respectively).

Description. Dorsal part of male tegmen lacking the apical area. Length as preserved 7.2 mm; estimated total length 10–12 mm.



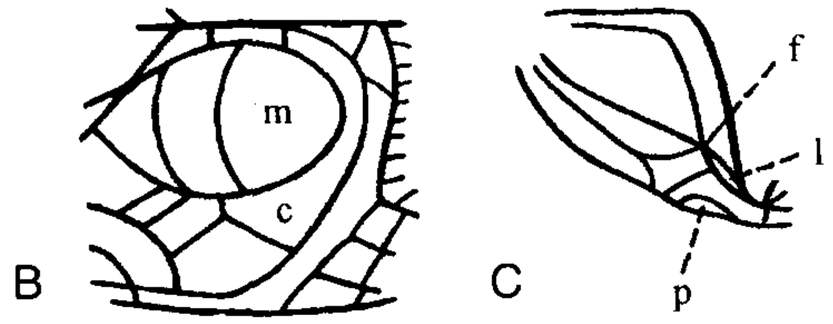


Fig. 27. A, ?*Araripegryllus orientalis* sp. nov., male, holotype, MNEMG 2003.51; Clockhouse Brickworks, Upper Hauterivian. B, *Araripegryllus camposae* Martins-Neto (1991, fig. 6), central-medial part of male tegmen, Lower Cretaceous, Brazil. C, *Acheta domesticus* L., basal part of male tegmen (Recent Gryllidae). Abbreviations: c, long cell around distal half of mirror; f, additional fusion of 1A and nearest branch of 2A near plectrum; l, loop between proximal parts of these veins; m, mirror; p, plectrum. Scale bar represents 2 mm.

Infraorder: incertae sedis
Family: Vitimiidae Sharov, 1968

Remarks. This Early Cretaceous family has tegmina with a secondary C crossing the apical parts of the proximal Sc branches. This peculiarity is characteristic of primitive members of the superfamily Oedishioidea (infraorder Oedischiidea), but not of primitive Hagloidea (infraorder Tettigoniidea). In Vitimiidae, a tegminal stridulatory apparatus with a true stridulatory vein on CuP is unknown (Fig. 28). If this apparatus was originally absent, Vitimiidae must be included in Oedischioidea, but if it was present in their ancestor, then this family may be included in Hagloidea. Vitimiidae contain two genera: *Vitimia* Sharov, 1968 and *Deinovitimia* Gorochov, 1989.

Genus *Deinovitimia* Gorochov, 1989

Type species. *Deinovitimia insolita* Gorochov, 1989, Lower Cretaceous, Transbaikalia and Mongolia.

Diagnosis. This genus differs from the typical genus *Vitimia* in having more numerous, longer, and more or less transverse branches of tegminal Sc; very narrow areas between tegminal Sc and R and between proximal halves of R and M; and very numerous crossveins between R and $MP + CuA_1$ (Fig. 28).

Included species. Type species and a new species described below.

Deinovitimia occidentalis sp. nov.
Fig. 28

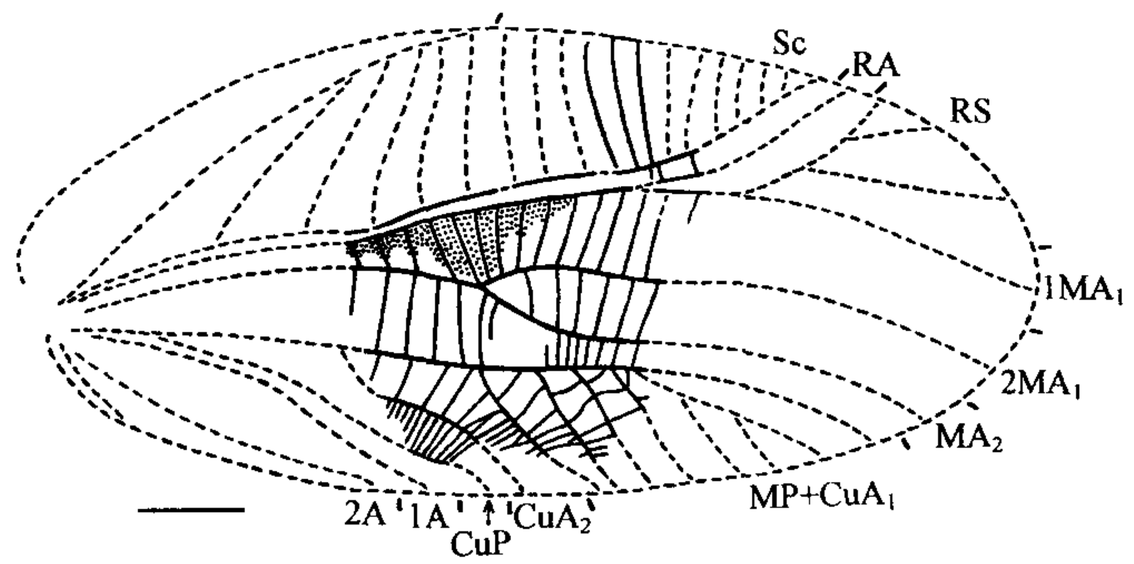


Fig. 28. *Deinovitimia occidentalis* sp. nov., holotype BMB 018628/-9; Auclaye Brickworks, Lower Barremian. Scale bar represents 2 mm.

Derivation of name. Latin for occidental.

Holotype. BMB 018628/-9 [A 368/-9; A 359/-60] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by A.A. Mitchell.

Diagnosis. Tegmen distinguished from that of *D. insolita* by location of bases of RS and MA_2 near to each other, distinctly narrower area between MA_2 and $MP + CuA_1$, and almost transverse (not oblique) crossveins between MA (proximal to base of MA_2) and CuA_1 (proximal to branching of $MP + CuA_1$).

Description. Central-medial part of tegmen lacking posterior medial edge. Length as preserved 7 mm; estimated total length 19–20 mm.

Suborder: Caelifera Ander, 1936
Infraorder: Tridactylidea Brullé, 1835
Superfamily: Tridactyloidea Brullé, 1835
Family: Tridactylidae Brullé, 1835

Remarks. This Recent family (pygmy mole crickets) is known from the Early Cretaceous onwards. It differs from the Early Jurassic Regiatidae in the partial reduction of primitive tegminal venation (this reduction may be strong or comparatively weak, comprising the shortening of RS, reduction or disappearance of $MP + CuA_1$ and CuA_2, and development of secondary or additional veins along the anal edge of the tegmen; Fig. 29); and from Recent Cylindrachetidae in the rather short body, hind legs adapted for jumping, and presence of wings. Tridactylidae include three subfamilies: two Recent (Tridactylinae and Rhipipteriginae) and one Early Cretaceous (Mongoloxyinae).

Subfamily: Mongoloxyinae Gorochov, 1992

Remarks. This Early Cretaceous subfamily is distinguished from both Recent ones by the rather rich venation of the tegmina (Fig. 29). In the Recent subfamilies, the venation comprises 2–4 relatively weak longitudinal veins only. Mongoloxyinae include *Monodactylus* Sharov, 1968; *Monodactyloides* Sharov, 1968; *Mongoloxya* Gorochov, 1992;

Cretoxya gen. nov.; and possibly *Cratodactylus* Martins-Neto, 1990.

Genus *Cretoxya* gen. nov.

Derivation of name. Latin for Cretaceous and *Mongoloxya*.

Type species. *Cretoxya rasnitsyni* sp. nov.

Diagnosis. Tegmen distinguished from that of *Mongoloxya* by partly reduced venation of Sc and R, disappearance of $2MA_1$, $MP + CuA_1$ and CuA_2; shorter CuP; narrower "proximal area" (between the proximal part of CuP and long, parallel veins along the anal edge of the tegmen) divided by two comparatively short longitudinal veins (one of them, nearest to CuP, is possibly 1A; in *Mongoloxya*, this area is divided by four similar veins). *Cretoxya* differs from *Monodactylus* in its distinctly longer Sc, much wider area between R and M, and absence of $2MA_1$ in tegmina; from *Monodactyloides* in the different shape of tegminal R and absence of tegminal $2MA_1$. Differences between *Cretoxya* and *Cratodactylus* are unclear since the tegminal venation of the latter genus is obscure.

Included species. Type species only.

Cretoxya rasnitsyni sp. nov.
Fig. 29

Derivation of name. After Prof. A.P. Rasnitsyn of the Palaeontological Institute, Russian Academy of Sciences, Moscow.

Holotype. MNEMG 2003.52 [DB64-8/WING 24] (part and counterpart); Soft Cockle beds (probably Clements' Bed DB66), Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by R.A. Coram.

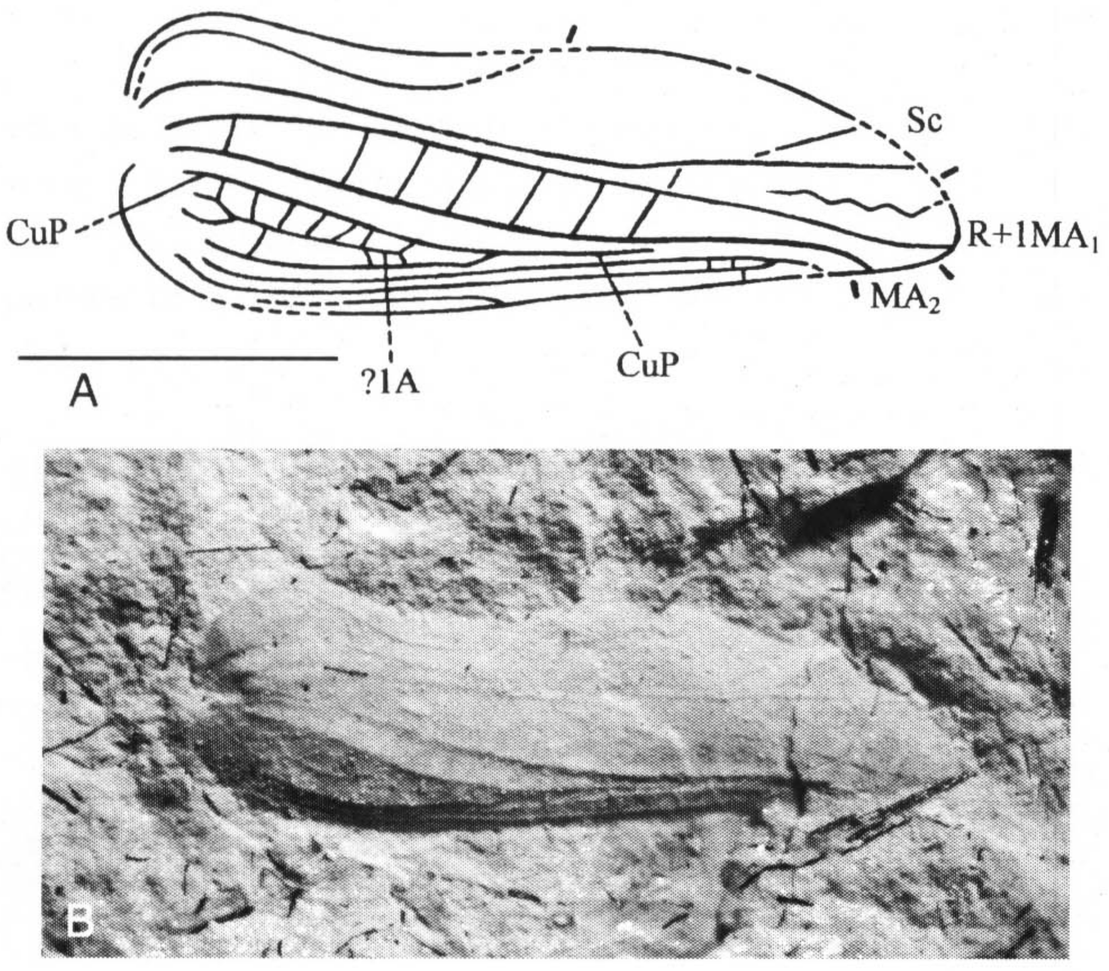


Fig. 29. *Cretoxya rasnitsyni* gen. et sp. nov., holotype MNEMG 2003.52; Durlston Bay, Lower Berriasian. Scale bar represents 2 mm.

Diagnosis. As for genus.

Description. Tegmen with rather distinct venation, narrow apical part, S-shaped costal (lateral) edge, almost straight anal (medial) edge, wide R-M area divided by rather sparse and slightly oblique crossveins, and characteristic venation of medial part of tegmen (Fig. 29). Length of tegmen 5.3 mm.

Infraorder: Acrididea MacLeay, 1821
Superfamily: Locustopsoidea Handlirsch, 1906
Family: Locustopsidae Handlirsch, 1906

Remarks. This family is known from the Early Triassic–Late Cretaceous. It differs from the more primitive Triassic Locustavidae in the modified tegminal venation: the base of CuA_2 is displaced from the basal part of the tegmen and $MP + CuA_1$ has relatively few (one to three) branches. (In Locustavidae, CuA_2 is located almost at the base of the tegmen, and $MP + CuA_1$ has five branches.) The differences between Locustopsidae and Recent Locustopsoidea in the family Tanaoceridae are unclear, as the latter family is apterous and fossil bodies of Locustopsidae are insufficiently known. Locustopsidae comprise two (or three) subfamilies, one known from the Late Triassic or Early Jurassic to Late Cretaceous (Locustopsinae, see below), and a second is present in the Early Cretaceous only (Araripelocustinae). The genus *Locustrix* Martins-Neto, 2003 (Lower Cretaceous, Brazil) is possibly a member of a third (undescribed) subfamily characterized by a short tegminal Sc. *Cratolocustopsis contumax* Martins-Neto, 2003 may be a representative of the superfamily Eumastacoidea rather than a locustopsid.

Subfamily: Locustopsinae Handlirsch, 1906

Remarks. This subfamily is rather primitive and the tegmina are characterized by a long Sc and two or three distinct branches of MA (Figs. 30–35). Locustopsinae contain 10 or 11 essentially form genera (characterized by several details of venation that may be the results of convergence): *Schwinzia* Zessin, 1983, *Orichalcum* Whalley, 1985, and *Plesioschwinzia* Zessin, 1988 (Lower Jurassic); *Locustopsis* Handlirsch, 1906 and *Mesolocustopsis* Hong and Wang, 1990 (Lower Jurassic–Lower Cretaceous); *Zeunerella* Sharov, 1968 (Lower Jurassic–Upper Cretaceous); *Parapleurites* Brauer, Redtenbacher and Ganglbauer, 1889 (Lower or Middle Jurassic); *Zessinia* Martins-Neto, 1990, *Cratozeunerella* Martins-Neto, 1998 and *Cratolocustopsis* Martins-Neto, 2003 (Lower Cretaceous); and possibly *Conocephalella* Strand, 1928 (Upper Jurassic).

Genus *Locustopsis* Handlirsch, 1906

Type species. *Locustopsis elegans* Handlirsch, 1906, Lower Jurassic, Germany.

Diagnosis. This form genus is characterized by three branches of MA (with a primitive position of $2MA_1$) and two branches of $MP + CuA_1$ (*Parapleurites* has two branches

of MA; *Schwinzia* has three branches of MP + CuA_1; *Orichalcum* and *Plesioschwinzia* are possibly aberrant *Locustopsis*; diagnostic characters of other genera, except for the insufficiently known *Conocephalella*, are considered below).

Remarks. *Locustopsis* includes numerous species from various Jurassic localities in Eurasia that are in need of revision, a single species from possible Upper Triassic of England, *Cratozeunerella nervosa* Martins-Neto, 2003, *C. godoii* Martins-Neto, 2003, *C. titanella* Martins-Neto, 2003 (Lower Cretaceous, Brazil), a new species described below, and possibly *Cratozeunerella soaresi* Martins-Neto, 2003 (Lower Cretaceous, Brazil).

Locustopsis posterior sp. nov.
Fig. 30

Derivation of name. Latin for posterior.

Holotype. Sedgwick Museum no. 36; Lower Purbeck; Ridgeway, Dorset (SY 672 853); Lower Berriasian; collected by O. Fisher.

Diagnosis. Tegmen distinguished from that of all other congeners by the fusion of apical parts of branches of MP + CuA_1 (Fig. 30).

Description. Tegmen lacking apical and some proximal parts. Length as preserved 13.5 mm; estimated total length 15–17 mm.

Remarks. This tegmen was previously figured by Jarzembowski and Coram (1997, fig. 12).

Genus *Zeunerella* Sharov, 1968

Type species. *Zeunerella arborea* Sharov, 1968, Upper Cretaceous, Kazakhstan.

Diagnosis. This form genus is similar to *Locustopsis* (differences between *Zeunerella* and other genera of Locustopsinae are as in *Locustopsis*) but its tegminal MA is modified in that the base of $2MA_1$ is situated on MA_2 rather than on $1MA_1$ (Fig. 31). Differences between *Zeunerella* and *Cratozeunerella neotropica* Martins-Neto, 1998 (the type species of *Cratozeunerella*) are unclear as the holotype of the latter has insufficiently preserved MP + CuA_1 branches (this vein may have two branches as in *Locustopsis* and *Zeunerella*, or three as in *Schwinzia*). The significance of other possible differences between these genera (such as the number of branches of tegminal RS, and presence of crossveins in the tegminal subcostal area) will become more apparent after study of new material deposited in the Palaeontological Institute of the Russian Academy of Sciences.

Included species. Type species, *Locustopsis reticulata* Handlirsch, 1939 and *L. mecklenburgica* Zessin, 1983 (Lower Jurassic, Germany), a new species described below, *Cratozeunerella amedegnatoi* Martins-Neto, 1998 and possibly *C. neotropica* Martins-Neto, 1998 (Lower Cretaceous, Brazil).

Zeunerella prior sp. nov.
Fig. 31

Derivation of name. Latin for prior.

Holotype. MNEMG 2003.53 [CH 504]; Lower Weald Clay, Clockhouse Brickworks, Capel, Surrey; Upper Hauterivian; collected by E. and B. Jarzembowski.

Diagnosis. Tegmen differs from that of *Z. arborea*, *C. neotropica* and *C. amedegnatoi* in the arched RA and general structure of RS. This new species is distinguished from Lower Jurassic species by the normal (long) tegminal MA_2, arched branches of R, and rather wide area between M and the proximal part of CuA_1.

Description. Patterned tegmen lacking apex and some parts of the tegminal edges, with several transverse dark bands and rather large spots. Length as preserved 13.5 mm; estimated total length 18 mm.

Genus *Zessinia* Martins-Neto, 1990

Type species. *Zessinia pulcherrima* Martins-Neto, 1990, Lower Cretaceous, Brazil.

Diagnosis. This form genus is distinguished from all other genera of Locustopsinae by the single branch of MP + CuA_1 and the presence of three branches of MA modified as in *Zeunerella* (with the base of $2MA_1$ situated on MA_2) in tegmina (Fig. 32).

Included species. Type species, species described below and possibly *Zessinia reticulata* Martins-Neto, 1990 (Lower Cretaceous, Brazil).

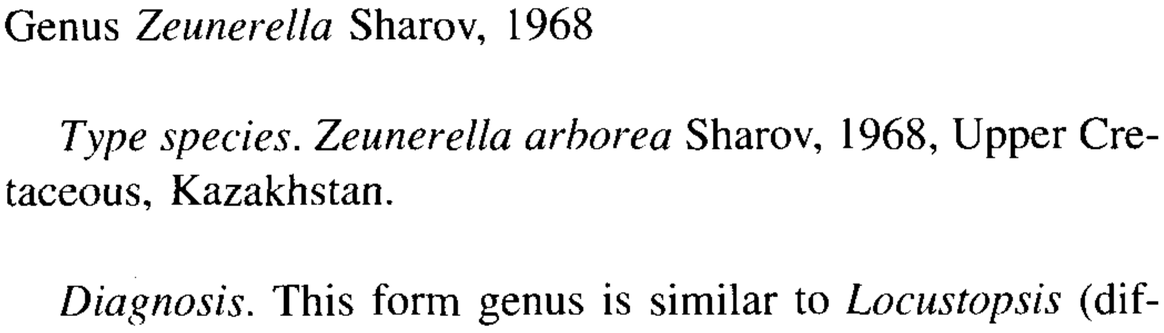


Fig. 30. *Locustopsis posterior* sp. nov., holotype Sedgwick Museum no. 36; Ridgeway, Dorset, Lower Berriasian. Scale bar represents 2 mm.

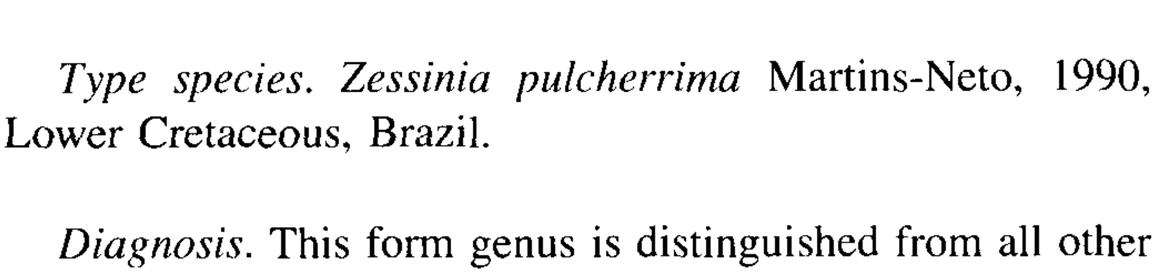


Fig. 31. *Zeunerella prior* sp. nov., holotype MNEMG 2003.53; Clockhouse Brickworks, Upper Hauterivian. Scale bar represents 2 mm.

Zessinia borealis sp. nov.
Fig. 32

Derivation of name. Latin for boreal.

Holotype. MNEMG 2003.54 [DB36c/WING 16] (part and counterpart); Clements' Bed DB36c, Hard Cockle beds, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by R.A. Coram.

Diagnosis. Tegmen distinguished from that of other congeners by the distinctly wider area between RS and MA, position of the base of RS proximal to base of $1MA_1$, and narrower area between CuA_1 ($MP + CuA_1$) and CuA_2 (this area is also narrower than the area between M and CuA_1: in both of the other species of *Zessinia* it is much wider than the latter area) (Fig. 32).

Description. Tegmen lacking apical, proximal-medial, and basal-lateral parts. Length as preserved 7 mm; estimated total length 9–11 mm.

Genus *Mesolocustopsis* Hong and Wang, 1990

Type species. *Mesolocustopsis sinica* Hong and Wang, 1990, Lower Cretaceous, China.

Diagnosis. This form genus is similar to *Zessinia* in having a single branch of tegminal $MP + CuA_1$, but its MA (with three branches) is normal (primitive) as in *Locustopsis* (Figs. 33–35). Differences between this genus and *Cratolocustopsis* were not stated in the original diagnosis of the latter genus (Martins-Neto, 2003) and so remain unclear.

Included species. Type species, five species from the Lower Cretaceous of Brazil (*Zessinia caririensis* Martins-Neto, 1990, *Z. petruleviciusi* Martins-Neto, 2003, *Z. vikingi* Martins-Neto, 2003, *Cratolocustopsis cretacea* Martins-Neto, 2003, *C. araripensis* Martins-Neto, 2003), three new species described below, and possibly *Locustopsis dobbertinensis* Handlirsch, 1906 and *L. magnifica* Handlirsch, 1939 (Lower Jurassic, Germany).

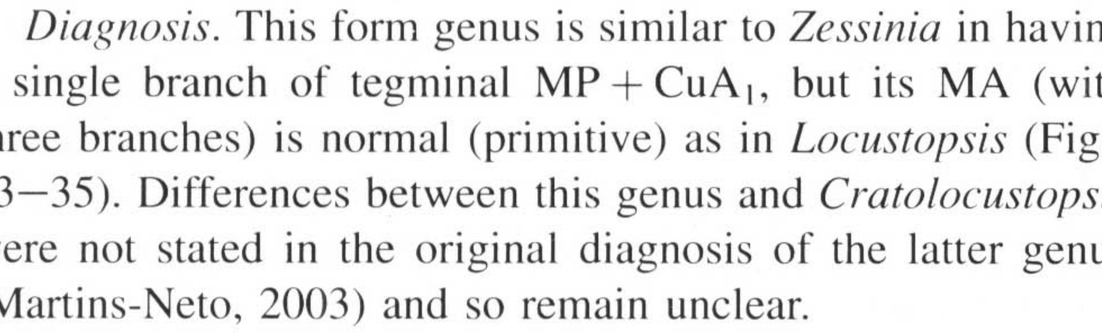


Fig. 32. *Zessinia borealis* sp. nov., holotype MNEMG 2003.54; Durlston Bay, Lower Berriasian. Scale bars represent 2 mm.

Mesolocustopsis anglica sp. nov.
Fig. 33

Derivation of name. Latin for English.

Holotype. MNEMG 2003.55 [DB175/ORTH 59] (part and counterpart); Clements' Bed DB175, Corbula beds, Durlston Formation; Durlston Bay, Swanage, Dorset; Upper Berriasian; collected by R.A. Coram.

Diagnosis. Tegmen distinguished from that of other congeners by the position of the base of RS proximally to the base of MA_2 and a narrow area between CuA_1 ($MP + CuA_1$) and CuA_2 (this area is marginally narrower than the area between M and CuA_1).

Description. Middle and apical parts of tegmen preserved. Length of longest half (distal part of tegmen) 5.5 mm; estimated total length of tegmen 13–15 mm.

Mesolocustopsis angusta sp. nov.
Fig. 34

Derivation of name. Latin for narrow.

Holotype. BMB 018604/-5 [A 572] (part and counterpart); Upper Weald Clay; Auclaye Brickworks, Capel, Surrey; Lower Barremian; collected by A. Ross.

Diagnosis. Tegmen distinguished by the base of RS being situated much more distally of the base of MA_2, the very narrow area between RS and $1MA_1$, the rather narrow area between CuA_1 ($MP + CuA_1$) and CuA_2 (this area being distinctly narrower than the area between $MP + CuA_1$ and the base of MA_2), and the long and weakly curved $MP + CuA_1$.

Description. Tegmen lacking basal, proximal-medial, and some apical parts. Length as preserved 16 mm; estimated total length 17 mm.

Mesolocustopsis problematica sp. nov.
Fig. 35

Derivation of name. From Greek for problematical.

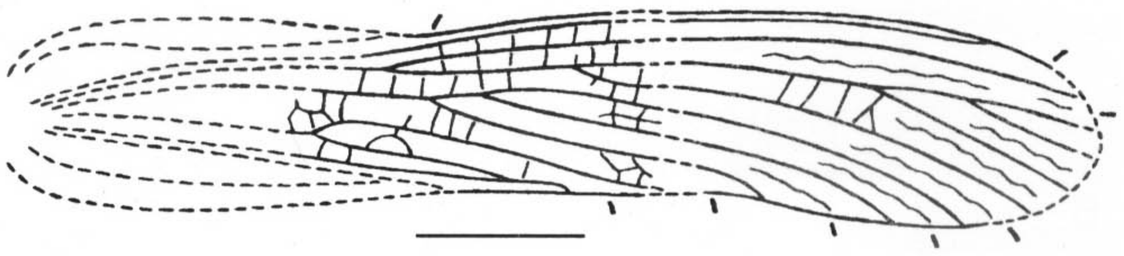


Fig. 33. *Mesolocustopsis anglica* sp. nov., holotype MNEMG 2003.55; Durlston Bay, Upper Berriasian. Scale bar represents 2 mm.

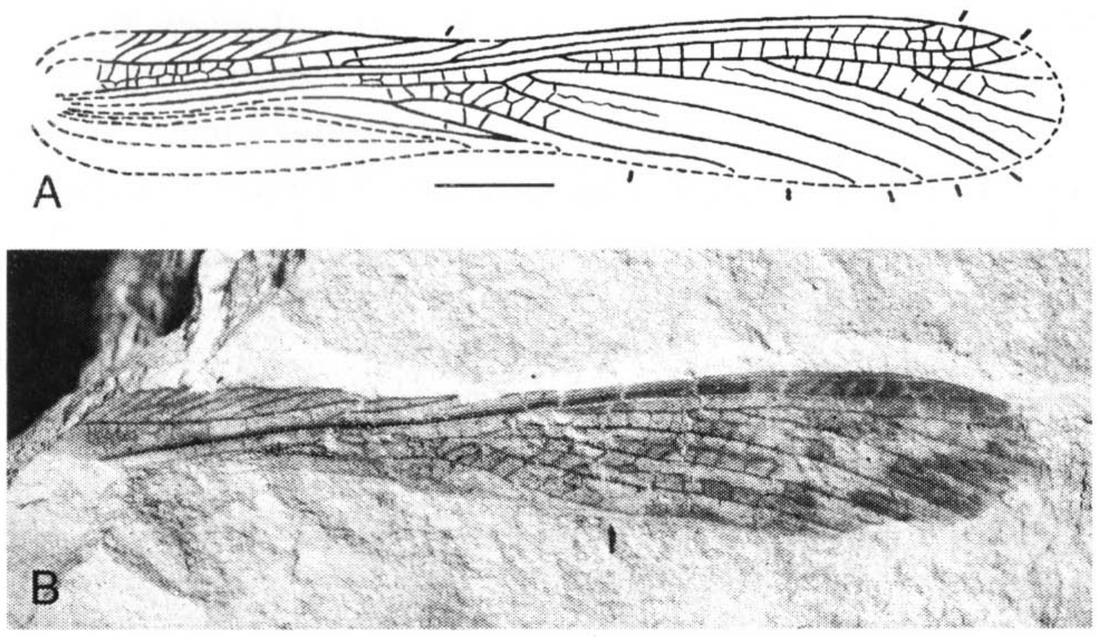


Fig. 34. *Mesolocustopsis angusta* sp. nov., holotype BMB 018604/-5; Auclaye Brickworks, Lower Barremian. Scale bar represents 2 mm.

Holotype. MNEMG 1996.304 [S 716] (part and counterpart); Upper Weald Clay, Smokejacks Brickworks, Ockley, Surrey; Lower Barremian; collected by B. Jarzembowski.

Diagnosis. Tegmen differs from that of other congeners by the base of RS being proximal to the base of MA_2, a narrow area between RS and MA branches, a very wide area between M and the base of CuA_1, a rather narrow area between $MP + CuA_1$ and the base of MA_2, a medium-wide area between CuA_1 ($MP + CuA_1$) and CuA_2, and a distinct fusion of the proximal parts of CuA and CuP.

Description. Tegmen lacking proximal-medial and some basal-lateral and apical parts. Length as preserved 16.5 mm; estimated total length 18–19 mm.

Remarks. A photograph of this wing showing colour mottling was previously published by Jarzembowski and Coram (1997: fig. 13).

Subfamily: Araripelocustinae Martins-Neto, 1995

Remarks. This subfamily was described by Martins-Neto (1995) as a family but its autopomorphies (development of rather long hind lobe of the pronotum and presence of a single branch of tegminal MA) seem insufficient for separation as a family. Araripelocustinae include two Lower Cretaceous genera: *Araripelocusta* Martins-Neto, 1995 and *Britannacrida* gen. nov. below.

Genus *Britannacrida* gen. nov.

Derivation of name. Latin for Britain and *Acrida*.

Type species. *Britannacrida distincta* sp. nov.

Diagnosis. Tegmen distinguished from that of *Araripelocusta* by shorter and wider area between RA and RS, presence of two branches of $MP + CuA_1$ (in *Araripelocusta* this vein is single), and much longer CuA_2 (Fig. 36).

Included species. Type species only.

Britannacrida distincta sp. nov.
Fig. 36

Derivation of name. Latin for distinct.

Holotype. MNEMG 2003.56 [DB36c/ORTH 2] (part and counterpart); Clements' Bed DB36c, Hard Cockle beds, Lulworth Formation; Durlston Bay, Swanage, Dorset; Lower Berriasian; collected by R.A. Coram.

Diagnosis. As for genus.

Description. Tegmen lacking small basal-lateral, proximal-medial, and apical parts. Sc fairly short; RS with four branches and rather wide areas between them; branches of $MP + CuA_1$ rather short. Length as preserved 13 mm; estimated total length of tegmen 13.5–14 mm.

3. Discussion

This is the first comprehensive treatment of the British Cretaceous Orthoptera. The fauna, treated as a whole, is rather similar to Early Cretaceous (and partly Late Jurassic) faunas from Siberia–Mongolia and Brazil (six/seven subfamilies in

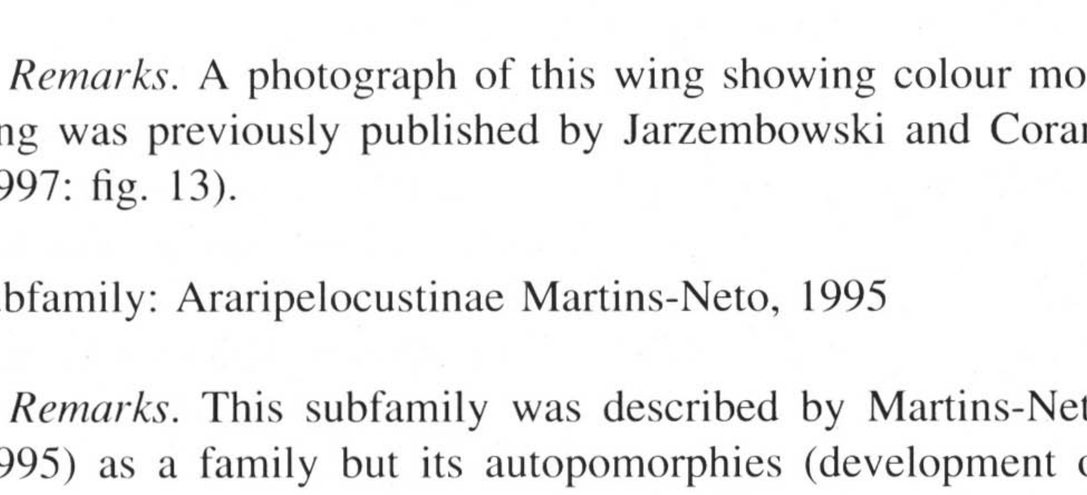


Fig. 35. *Mesolocustopsis problematica* sp. nov., holotype MNEMG 1996.304; Smokejacks Brickworks, Lower Barremian. Scale bar represents 2 mm.

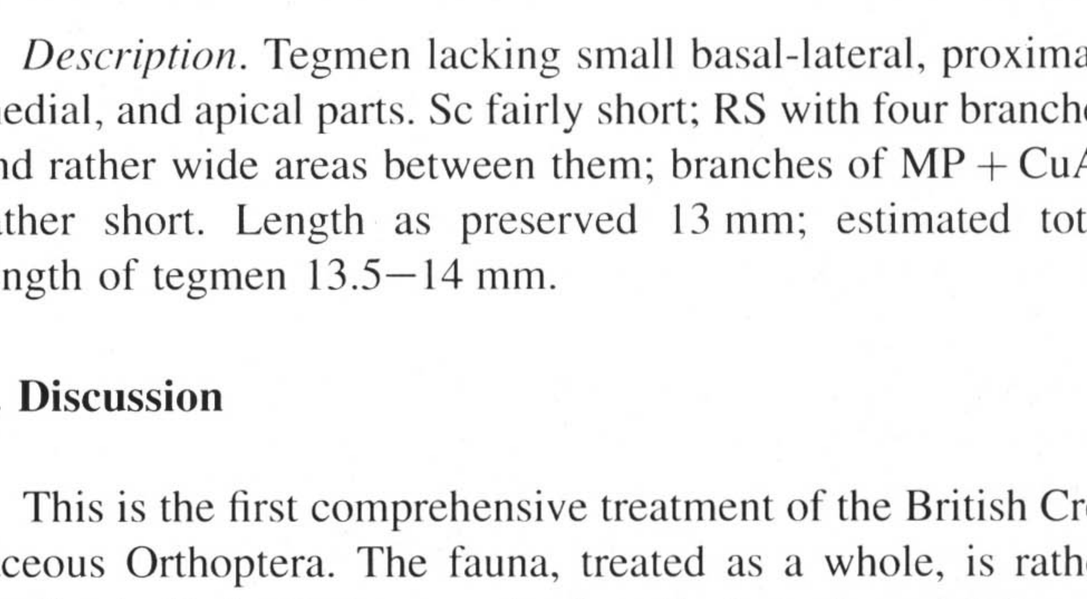


Fig. 36. *Britannacrida distincta* gen. et sp. nov., holotype MNEMG 2003.56; Durlston Bay, Lower Berriasian. Scale bar represents 2 mm.

common, but with no definite cosmopolitan genera or species). This observation was first noted for Ensifera by Gorochov (2001b) and the material described herein allows us to augment that paper and to correct some of its conclusions.

The extinct superfamily Elcanoidea is represented in the Lower Cretaceous of Eurasia and South America by the same subfamily (Elcaninae) of the family Elcanidae; this subfamily includes one genus possibly found in both England and Brazil (*Minelcana*), two genera common to England and Asia (*Probaisselcana* and *Panorpidium*), one Mongolian (*Eubaisselcana*) and one Brazilian (*Cratoelcana*) genus.

The superfamily Hagloidea (now relict) includes one possible genus of the family Haglidae from the Lower Cretaceous of England (*Cyrtophyllites*): this genus is also present in the Late Jurassic of Europe and is the typical representative of the Cyrtophyllitinae, which is probably the only subfamily of Haglidae represented in the Lower Cretaceous of Asia (by the genera *Tasgorosailus* and *Vitimoilus*). The other family of Hagloidea (Prophalangopsidae) is represented in the Lower Cretaceous of England, Asia, and South America probably by endemic genera only; in South America, these genera are enigmatic and uncommon (*Kevania* and *Cratohaglopsis*); in the Old World, the family is represented by two possible English genera (*Mesogryllus* and *Procyrtophyllites*) and probably five Asian genera (*Apsataboilus*, *Prophalangopseides*, *Tettaboilus*, *Utanaboilus*, *Nipponohagla*) of the subfamily Aboilinae; one possible English genus (*Aenigmoilus*) and two Asian genera (*Parahagla* and *Chifengia*) of the subfamily Chifengiinae; and four or five genera of the endemic English subfamily Termitidiinae (*Pseudaboilus*, *Tettigoilus*, *Termitidium*, *Zalmona* and possibly *Agrionidium*).

The superfamily Grylloidea is represented in the English Lower Cretaceous mainly by genera of the family Baissogryllidae: *Notocearagryllus*, also known from Brazil, and endemic *Anglogryllus* (Bontzaganiinae: this subfamily also includes *Bontzagania* from Mongolia, *Santanagryllus* and possibly *Cearagryllus* from Brazil), endemic *Speculogryllus* (Baissogryllinae, which also includes four probable genera from Asia and possibly *Castilogryllus* from South America), and *Sharategia*, known also from Mongolia (Sharategiinae, including two other Asian genera and one Brazilian genus). The other family of Grylloidea (Gryllidae) is less numerous in the English deposits; it is represented only by the subfamily Gryllospeculinae, which includes one genus known possibly from England and Brazil (*Araripegryllus*), one probable South American genus (*Cratogryllus*), and two Mongolian genera. In Brazil, there is another Early Cretaceous gryllid subfamily, Olindagryllinae, with two genera.

The occurrence of the same genus of the family Vitimiidae (*Deinovitimia*) in the Lower Cretaceous of England and Siberia may indicate a link between their entomofaunas and a degree of isolation from South America. The absence of this family from South America and the presence of Gryllotalpidae (Grylloidea) in the Brazilian Lower Cretaceous only, as well as the presence of Protogryllidae (Grylloidea) and possibly Tuphellidae (Hagloidea) in Asian deposits only, are not, however, taken into consideration in this analysis because these rather rare higher taxa may be discovered in all these deposits in future.

Tridactyloidea are represented in the English, Siberian-Mongolian, and Brazilian Lower Cretaceous by probable endemic genera in a single subfamily (Mongoloxyinae) of the family Tridactylidae. These genera are English *Cretoxya*, Asian *Monodactylus*, *Monodactyloides* and *Mongoloxya*, and possibly Brazilian *Cratodactylus*.

All English Early Cretaceous genera of the subfamily Locustopsinae (Locustopsoidea: Locustopsidae) are widely distributed, but they are formal and unsuitable for biogeographic analysis; another subfamily of the Locustopsidae (Araripelocustinae) is represented in England and Brazil by only two endemic genera (English *Britannacrida* and Brazilian *Araripelocusta*).

This study suggests a more or less "intermediate" position for the English Early Cretaceous orthopteran fauna between the Siberian–Mongolian and South American ones. Three/four genera and one subfamily are shared between England and Brazil, three subfamilies and three/four genera are shared between England and Siberia–Mongolia, and no subfamilies/genera are definitely shared between Brazil and Siberia–Mongolia. The English fauna is, however, more similar to the Asian fauna than to the South American one in relation to the number of common subfamilies. There could be some ecological similarity between the English and North Asian Early Cretaceous faunas: they are both much richer in Hagloidea than the Brazilian fauna, but Grylloidea are somewhat less numerous and diverse than in Brazil. These differences may be a result of the burgeoning South American isolation and/or some Cretaceous climatic differences reflecting the tropical climate in Brazil and a more temperate one in northern Eurasia. Differences between the English and North Asian Early Cretaceous faunas are also evident: there are more numerous and diverse Aboilinae in Siberia–Mongolia and endemic Termitidiinae with four or five genera in England. Further collecting and study are needed to test these geographic peculiarities.

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