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# Aphids, true hoppers, jumping plant-lice, scale insects, true bugs and whiteflies (Insecta: Hemiptera) from the Insect Limestone (latest Eocene) of the Isle of Wight, UK

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ABSTRACT: Representatives of the Hemiptera: Sternorrhyncha, Fulgoromorpha, Cicadomorpha and Heteroptera from the Late Eocene of the Isle of Wight, UK, are analysed and discussed. Psylloidea were reviewed and a key to the described taxa is given. Aphidoidea were studied, previously described taxa revised and new taxa described. New taxa of Aphidoidea are Hormaphididae: *Hormaphis? longistigma* Wegierek sp. nov.; Eriosomatidae: *Eriosoma gratshevi* Wegierek sp. nov. and *Colopha? incognita* Wegierek sp. nov.; Drepanosiphidae: *Panfossilis anglicus* Wegierek gen. et sp. nov. and *Betulaphis kozlovi* Wegierek sp. nov. Previously described Fulgoromorpha were revised and new taxa are described. The homonym *Hastites* Cockerell, 1922 (Cixiidae) preoccupied by *Hastites* Mayer-Eymar, 1883 is replaced by *Catulliastites* Szwedo nom. nov. for *Catulliastites muiri* (Cockerell) comb. nov. New taxa described are Cixiidae: *Klugga gnawa* Szwedo gen. et sp. nov., *Klugga regoa* Szwedo sp. nov., *Liwakka gelloa* Szwedo gen et sp. nov., *Delwa morikwa* Szwedo gen. et sp. nov., *Kommanosyne wrikkua* Szwedo gen. et sp. nov., *Kernastiridius nephlajeus* Szwedo gen. et sp. nov., *Margaxius angosus* Szwedo gen. et sp. nov., *Dweivera reikea* Szwedo gen. et sp. nov., *Samaliverus bikkanus* Szwedo gen. et sp. nov., *Komsitija tuberculata* Szwedo gen. et sp. nov., *Langsmaniko marous* Szwedo gen. et sp. nov., *Komnixta jarzembowskii* Szwedo gen. et sp. nov. and *Worodbera nimakka* gen. et sp. nov.; Tropiduchidae: *Reteotissus hooleyi* Szwedo gen. et sp. nov., *Phatanako* gen. nov. for *Phatanako wilmattae* (Cockerell) comb. nov., *Senogaetulia kwalea* Szwedo gen. et sp. nov., *Dakrutulia mikhailkozlovi* Szwedo gen. et sp. nov., *Keriophettus atibenus* Szwedo gen. et sp. nov. and *Sognotela emeljanovi* Szwedo gen. et sp. nov.; Issidae: *Krundia korba* Szwedo gen. et sp. nov., *Breukoscelis vadimgratshevi* Szwedo gen. et sp. nov., *Breukoscelis phrikkosus* Szwedo sp. nov. and *Uphodato garwoterus* Szwedo gen. et sp. nov.; Nogodinidae: Ambitaktoinae Szwedo subfam. nov., *Ambitaktoa stoumma* Szwedo gen. et sp. nov., *Phariberea gurdonika* Szwedo gen. et sp. nov., *Wixskimoa torxsea* Szwedo gen. et sp. nov., and Nadrimini trib. nov. with *Niadrima yulei* Szwedo gen. et sp. nov.; Lophopidae: *Ankomwarius brodiei* Szwedo gen. et sp. nov.; Ricaniidae: *Ankwlanno bluga* Szwedo gen. et sp. nov. Previously described Cicadomorpha were revised and new taxa are described: Cicadidae: *Kintusamo boulardi* Szwedo gen. et sp. nov; Aphrophoridae: *Blenniphora* Szwedo gen. nov. for *Blenniphora woodwardi* (Cockerell) comb. nov., *Blenniphora skaka* Szwedo sp. nov. and *Blenniphora bikkanoa* Szwedo sp. nov.; *Luisphantyelus briwus* Szwedo gen. et sp. nov., *Natajephora lijanka* Szwedo gen. et sp. nov.; Cercopidae: *Berro enissuextaensis* Szwedo gen. et sp. nov.; Cicadellidae: Mileewinae: *Teniwitta andrewrossi* Szwedo gen. et sp. nov. Formerly described true bugs (Heteroptera) are revised and several new taxa are described – Nepomorpha: Corixidae: *Diacorixites szwedoi* Popov gen. et sp. nov.; Cimicomorpha: Tingidae: *Parasinalda wappleri* Popov sp. nov., *Viktorgolubia* Popov gen. nov. for *Viktorgolubia seposita* (Cockerell) comb. nov.; Miridae: *Gurnardinia herczeki* Popov gen. et sp. nov.; Pentatomomorpha: Lygaeidae: Gurnardobayini Popov trib. nov., *Gurnardobaya rossi* Popov gen. et sp. nov.; Cydnidae: *Eocenocydnus lisi* Popov gen. et sp. nov.; Pentatomidae: *Podopinites coloratus* Popov gen. et sp. nov. and *Podopinites acourti* (Cockerell) comb. nov. An overview of the Late Eocene fauna of the Hemiptera is presented. Ecological and biogeographical patterns of the Hemiptera from the Isle of Wight deposits are discussed.

KEY WORDS: fossil bugs, homonymy, new combinations, new genera, new names, new species, new subfamily, new tribes.

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The Hemiptera Linnaeus, 1758 is one of the most successful lineages of insects, with over 300 families recognised during its geological history and high variability of morphology (Shcherbakov & Popov 2002; Szwedo *et al*. 2004; Grimaldi & Engel 2005; Szwedo 2018). The order is divided into six suborders: the extant Sternorrhyncha, Fulgoromorpha, Cicadomorpha, Coleorrhyncha and Heteroptera, and the extinct Paleorrhyncha. The last one currently comprises only one family, Archescytinidae, which needs re-study and reconsideration. The Hemiptera have been known since the Late Carboniferous (Nel *et al*. 2013) and they are likely to have been exclusively represented in the Palaeozoic by herbivorous taxa. Advanced plant sucking was the primary feeding adaptation in this lineage, which probably originated from ancestral Hypoperlida. The Permian Paleorrhyncha show some characters suggesting that both immatures and adults could have fed on gymnosperm ovules and/or immature seeds in cones, which is in accordance with the postulated plesiomorphic feeding on reproductive plant organs in general. Hemipterans evolved to shift from reproductive organs to photosynthetic tissues. Most of the Hemiptera since the Palaeozoic have been phloem feeders, whereas xylem feeding appeared in the Cicadomorpha in the Early Mesozoic. Mesophyll feeding probably also evolved during the Mesozoic. In the Hemiptera, predation is rare and occurs sporadically in modern Heteroptera; however, true bugs adopted zoophagy at the earliest stages of their evolution in the Triassic (Shcherbakov & Popov 2002; Zherikhin 2002; Shcherbakov 2008). Sap-feeding Hemiptera present one of the most extraordinary systems of close and mutual relationships containing obligate bacterial symbionts (Moran *et al*. 2005; Szwedo 2018).

The Palaeogene record of the Hemiptera is based on both compression fossils and amber inclusions throughout the world (e.g., EDNA 2018; PalaeoBioDB 2018 and references there).

Fossil assemblages from the Palaeocene are often dominated by the representatives of Fulgoroidea or Cercopoidea, while the other groups are not so abundant. Aphidomorpha are sometimes abundant, but Psyllodea are rather rare. Both Aleyrodomorpha and Coccomorpha are not very common in fossil assemblages. The most abundant water bugs are Nepomorpha (mainly Notonectidae and Corixidae), and the most abundant land bugs are Cimicomorpha (Miridae) and Pentatomomorpha (mainly Coreoidea and Pentatomoidea). Dominance of fulgoroids is usually related to warmer climatic conditions whereas a predominance of cercopoids represents a cooler climate. At the beginning of the Palaeogene a rapid evolution of the most specialised plant-sucking lineages of the Hemiptera continued, connected with the diversification of angiosperms and Cenophytic conifer lineages.

The early Cenozoic (Palaeogene) Bembridge Marls of the Isle of Wight is well known. Within it, the Insect Bed (Insect Limestone) occurs only in the northern half of the Isle of Wight. Most information dealing with the palaeontology, lithology and the age was summarised by Jarzembowski (1980) and more recently by Ross & Self (2014). There has been disagreement about the age of the Insect Bed and on the position of the Eocene/Oligocene boundary. It has been considered to be Late Eocene (late Priabonian) or Early Oligocene (early Rupelian) in age (Jarzembowski 1980; Collinson 1992; Hooker *et al*. 1995, 2004, 2007, 2009; Ross & Self 2014). Gale *et al*. (2006, 2007) investigated magnetostratigraphy, clay mineralogy, cyclostratigraphy and sequence stratigraphy postulating an Early Oligocene age for the Insect Bed. However, Hooker *et al*. (2007, 2009) disagreed. Hooker *et al*. (2009) indicated that the Bembridge Marls were deposited over about 300,000 years, which would date the Insect Bed at about 34.2 Ma ($\pm/\sim$100,000 years) and indicate that the Insect Bed was deposited over about 10,000–15,000 years, i.e., Late Eocene (Ross & Self 2014), which is followed here. The Bembridge Marls fauna, with regards to its family composition, differs from other European Eocene faunas: Baltic (including Bitterfeld and Ukrainian) amber, Oise amber and Messel. The Bembridge Marls age can be directly compared with that of the Florissant Formation in the USA, which is radiometrically dated at 34.07 million years old (Meyer 2003).

The Hemiptera from the Bembridge Marls, Isle of Wight, were studied by Cockerell (1915, 1921b, c, 1922, 1926, 1927) and Klimaszewski & Popov (1993), and resulted in the description of several taxa of psyllids and aphids (Sternorrhyncha), planthoppers (Fulgoromorpha), leafhoppers (Cicadomorpha) and true bugs (Heteroptera).

The Palaeogene and Neogene record of Psyllodea is poor (Becker-Migdisova 1985; Grimaldi & Engel 2005; Drohojowska 2011; Ouvrard *et al*. 2013). In addition to a few species from the Isle of Wight (Late Eocene), a few species are known from Eocene Baltic amber – *Palaeopsylloides oligocaenicus* (Enderlein, 1915), *Eogyropsylla eocenica* Klimaszewski, 1993b, *E. jantaria* Klimaszewski, 1993b, *Protoscena baltica* Klimaszewski, 1997b, *Eogyropsylla magna* Klimaszewski, 1997c, *E. parva* Klimaszewski, 1997c, *Parascenia weitschati* Klimaszewski, 1997c (Enderlein 1915; Klimaszewski 1993b, 1997b, c), *Eogyropsylla sedzimiri* Drohojowska, 2011 and *E. paveloctogenarius* Ouvrard *et al*., 2013 from the Middle Eocene Kishenehn Formation, Montana, USA, and a few from the terminal Eocene Florissant Formation in the USA (Scudder 1890). Representatives of the superfamily Psylloidea became more numerous in the fossil record from the Miocene, known from Dominican and Mexican ambers (Klimaszewski 1993a, 1996, 1997a; Drohojowska *et al*. 2016).

Aleyrodomorpha are recorded in several Palaeogene ambers: *'Aleurodes' aculeatus* Menge, 1856, *Paernis gregorius* Drohojowska & Szwedo, 2011b, *Rovnodicus wojciechowskii* Drohojowska & Szwedo, 2015 in Drohojowska *et al*. 2015 and *Snotra christelae* Szwedo & Drohojowska, 2016 from Baltic amber (Szwedo & Drohojowska 2016) and few additional specimens under survey; several taxa from the lowermost Eocene amber of Oise (Drohojowska & Szwedo 2013a) must be noted. Aleyrodomorpha as compression fossils from the Bembridge Marls were reported by Jarzembowski & Ross (1994). A few species were recorded from both compression fossils and amber from the Late Jurassic and Cretaceous (Schlee 1970; Shcherbakov 2000a; Drohojowska & Szwedo 2011a, 2013b, 2015), but this group remains poorly studied.

The scarcity of scale insect (Coccidomorpha) fossils is still a puzzle, but numbers of species representing both archeococcids and neococcids are known from fossil resins (Koteja 2000a, b, 2001, 2008; Koteja & Azar 2008; Vea & Grimaldi 2012, 2015; Simon & Żyła 2015; Wang *et al*. 2015). Compression fossils of scale insects are documented from the Lower Cretaceous of Transbaikalia (Koteja 1988, 1989) and England (Koteja 1999) – representing archeococcids (Matsucoccidae and Xylococcidae), Oligocene of North America (Scudder 1890), Miocene of Sicily (Pampaloni 1902, 1903; Koteja & Ben-Dov 2003), Eocene of Germany (Wappler & Ben-Dov 2008) and Miocene of Germany (Zeuner 1938; Koteja 2000b) – representing neococcids (Diaspididae) – and the Miocene of Darjeeling in India (Bera *et al*. 2006).

Cenozoic fossil aphids (Aphidomorpha) have been studied in varying degrees. So far the largest number of species has been described from Baltic amber (about 100 species; Heie & Wegierek 1998, 2011). Late Eocene/Oligocene aphids (24 species) are known from several deposits around the world. Most of the compression fossils were described in the 18th and 19th Centuries: from Aix-en-Provence, France (Hope 1847; Heer 1856; Théobald 1937); Florissant, Colorado, USA (Scudder 1890; Cockerell 1908b, 1909, 1913); Quesnel, British

Columbia, Canada (Scudder 1890, 1894) and the Isle of Wight, UK (Cockerell 1915, 1921b). Some were later revised by Heie (1967, 1970). Only specimens from East Siberia, Russia (Bolshaya Svetlovodnaya) and France (Céreste, Alpes de Haute Provence) were described much later (Heie 1989; Heie & Lutz 2002). Where present, aphids are also numerous in Miocene insect deposits (20 species; Heie 2005). Data on aphids from the more recent epochs (Pliocene and Pleistocene) are based on single species (Heie 1968, 1995).

The Fulgoromorpha is one of the most ancient lineages of the Hemiptera, and in the fossil record planthoppers have been known since the early Permian. The earliest Fulgoromorpha belong to the Permian superfamily Coleoscytoidea, the second taxon is the Permian–Triassic Surijokocixioidea; the Fulgoroidea have been known since the Jurassic. The Palaeogene record of Fulgoromorpha comprises both compression fossils and forms preserved in resins (ambers). These are present in the Palaeocene/Eocene Fur Formation of Denmark, Palaeocene/Eocene deposits of Menat in France, lowermost Eocene French amber, uppermost Palaeocene of Argentina, numerous specimens are known from Eocene Baltic amber, Eocene deposits of Germany, Eocene and Oligocene deposits of North America and China, and Miocene Dominican and Mexican ambers (Szwedo *et al*. 2004; Petrulevičius 2005; Szwedo 2005a, 2006a, b, 2007, 2008, 2011; Shcherbakov 2006; Szwedo *et al*. 2006; Szwedo & Wappler 2006; Stroiński & Szwedo 2008, 2011, 2012; Emeljanov & Shcherbakov 2009; Lin *et al*. 2010; Szwedo & Stroiński 2010, 2013, 2017; Szwedo *et al*. 2013, 2015). Several fossil Fulgoroidea have been reported so far from the Late Eocene Bembridge Marls of the Isle of Wight. The first descriptions were by Cockerell (1921b), who described *Poekilloptera melanospila* Cockerell, 1921b (transferred to Orthoptera by Nel *et al*. 2008; see Fulgoromorpha section). Later, more species were added under the names *Hastites muiri* Cockerell, 1922, *Hooleya indecisa* Cockerell, 1922 and *Myndus wilmattae* Cockerell, 1926. These taxa are discussed below.

The Cicadomorpha is the second suborder formerly placed together with Fulgoromorpha as 'Auchenorrhyncha', but not related directly to planthoppers (Bourgoin & Campbell 2002; Szwedo 2002; Szwedo *et al.* 2004). The Palaeogene record of Cicadomorpha is also rich and known throughout the world (Metcalf & Wade 1966; Lewis 1989; Szwedo 2005b), but many taxa require re-examination and revision (Gębicki & Szwedo 2006). Only a few species of Cicadidae and Tettigarctidae are known from the Palaeogene of France, Scotland and North America (Boulard & Nel 1990; Shcherbakov 2009; Moulds 2018); most of the known fossil cicadas are from the Miocene of Eurasia. Cercopoidea are quite common in Palaeogene deposits of North America, Greenland and Europe as well as in amber but most must be re-studied and their taxonomic status revised and/or confirmed. Membracoidea, Cicadellidae in particular, are frequently reported, but only a few species from the Palaeogene have been formally described (Szwedo 2002; Szwedo 2005b; Gębicki & Szwedo 2006; Szwedo & Gębicki 2008; Szwedo *et al*. 2010; Dietrich & Gonçalves 2014). Over 220 specimens from the Insect Limestone of the Isle of Wight, deposited in the Natural History Museum (NHM) in London, Maidstone Museum and Sedgwick Museum, Cambridge, representing Fulgoromorpha and Cicadomorpha were investigated.

The first true bugs from the Bembridge Marls were described by Cockerell (1921c, 1927). He referred them to the Tingidae (*Celantia*? *seposita* Cockerell, 1921c), Lygaeidae (*Lygaeites amabilis* Cockerell, 1921b) and Pentatomidae – *Pentatomites acourti* (Cockerell, 1921c). The last one was previously considered to be a lygaeid (Cockerell 1921c). A list of families of Hemiptera recorded from the Late Eocene Insect Limestone of the Isle of Wight is presented in Table 1.

The insects are preserved in concretions or tabular bands of very fine-grained micrite, known as Insect Limestone. The unit where these concretions/bands occur is known as the Insect Bed, which lies towards the base of the Bembridge Marls Member (Solent Group: Bouldnor Formation). The most extensive collection from the Insect Limestone are specimens preserved at the NHM. They belong to the collections of E.J. A'Court Smith (purchased 1877 and 1883), Reverend P. B. Brodie (purchased 1898) and R. W. Hooley (purchased 1924). They are labelled 'Gurnard Bay' or 'Gurnet Bay' (which is an old name for Gurnard Bay); however, A'Court Smith collected specimens all the way from West Cowes to Newtown River on the NW side of the Isle of Wight (Jarzembowski 1980; Ross & Self 2014). Most of the specimens probably came from Thorness Bay (Jarzembowski 1976). Brodie and Hooley acquired parts of Smith's collection, so parts and counterparts of individual insects have turned up in all three collections. The parts and counterparts often have different numbers because they were registered at different times. An additional collection was discovered at the Sedgwick Museum, Cambridge, by A. J. Ross. This collection has also yielded counterparts of specimens at the NHM, which indicates that this is another part of the Smith collection. A label with '1883' on it suggests that the Sedgwick Museum acquired this collection in 1883, the same year that the NHM purchased specimens from Smith.

The following collections have been examined and contained the Hemiptera in their care:

BMB – Booth Museum of Natural History, Brighton

CAMSM – Sedgwick Museum of Earth Sciences, University of Cambridge.

MIWG – Museum of Isle of Wight Geology.

NHMUK – Department of Earth Sciences, Natural History Museum, London.

USNM – Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

MNEMG – Maidstone Museum & Bentlif Art Gallery.

With the financial support of Project INTAS 03-51-4367, concerning the fauna and flora of the Isle of Wight, formerly described species were revised and additional material was examined resulting in new taxa that are described herein.

## 1. Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Jumping plant-lice (Hemiptera: Sternorrhyncha: Psylloidea)

by *Jowita Drohojowska*

The Eocene witnessed the emergence of the first representatives of the superfamily Psylloidea, commonly known as jumping plant-lice. The psyllid fauna of this epoch is known largely from Baltic amber (Enderlein 1915; Klimaszewski 1993a, 1997a, b; Drohojowska 2011; Ouvrard *et al*. 2013). Late Eocene fossils from the Bembridge Marls of the Isle of Wight were studied by Cockerell (1915, 1921b) and Klimaszewski in Klimaszewski & Popov (1993). The record was not exceptionally rich, with all the species of this age classified in one family, the Aphalaridae, and even in one subfamily, the Aphalarinae. No new taxa are described here; however, there have been some taxonomic changes since Klimaszewski & Popov (1993)

**Table 1** Families of the Hemiptera recorded from the Late Eocene Insect Limestone of the Isle of Wight.

| Suborder | Infraorder/Superfamily | Family | Number of genus level taxa | Number of species level taxa[1] |
|---|---|---|---|---|
| Sternorrhyncha | Psyllodea/Psylloidea | Aphalaridae | 5 | 19 |
| | Aleyrodomorpha/Aleyrodoidea | Aleyrodidae | | 1 |
| | Coccidomorpha | | | 1 |
| | Aphidomorpha | Drepanosiphidae | 3 | 3 |
| | | Elektraphididae | 1 | 1 |
| | | Eriosomatidae | 2 | 2 |
| | | Hormaphididae | 1 | 1 |
| Fulgoromorpha | Fulgoroidea | Achilidae | 1 | 1 |
| | | Cixiidae | 10 | 12 |
| | | Issidae | 3 | 4 |
| | | Lophopidae | 1 | 1 |
| | | Nogodinidae | 5 | 5 |
| | | Ricaniidae | 1 | 1 |
| | | Tropiduchidae | 4 | 4 |
| Cicadomorpha | Cicadoidea | Cicadidae | 2 | 2 |
| | Cercopoidea | Aphrophoridae | 6 | 9 |
| | | Cercopidae | 1 | 1 |
| | Membracoidea | Cicadellidae | 6 | 6 |
| Heteroptera | Nepomorpha | Belostomatidae | 1 | 1 |
| | | Corixidae | 1 | 1 |
| | Gerromorpha | Gerridae | 1 | 1 |
| | Cimicomorpha | Anthocoridae? | 1 | 1 |
| | | Miridae | 1 | 1 |
| | | Tingidae | 2 | 2 |
| | Pentatomomorpha | Alydidae | 1 | 1 |
| | | Coreidae | 1 | 1 |
| | | Cydnidae | 1 | 1 |
| | | Lygaeidae | 2 | 2 |
| | | Pentatomidae | 1 | 2 |

[1] Including specimens recognised as representing separate species, but not formally described.

was published so the fauna is summarised below. All the specimen numbers in Klimaszewski & Popov (1993) are incorrect – they used field numbers, not registration numbers. Paratypes are from the same locality as the holotype unless stated otherwise.

In Early Miocene Dominican amber (Klimaszewski 1996, 1997c), species appear that belong to several other families. Apart from the Aphalaridae, there are also species of Psyllidae, Carsidaridae and Triozidae (Becker-Migdisova 1964; Klimaszewski 1993a). In the Miocene Mexican amber the first fossil psyllid from family Liviidae was described (Drohojowska *et al.* 2016). In the Paleogene the family Aphalaridae dominated, then in the Neogene the family Psyllidae outnumbered other forms. This has continued to the present day, with the domination of Triozidae (over 1000 described species) and Psyllidae (nearly 1200 species) (Ouvrard 2019).

### Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843

### Infraorder Psyllodea Flor, 1861

### Superfamily Psylloidea Latreille, 1807

Key to the genera of jumping plant-lice from the Bembridge Marls

1. Cells $m_1$ and $cu_1$ large, vein $M_{1+2}$ on the forewing the same length or longer than vein M ....................... *Carsidarina*
   – Cells m1 and cu1 small, Vein $M_{1+2}$ on the forewing visibly shorter than vein M...................................... 2
2. Cell $cu_1$ relatively high, approximately as long as cell $m_1$................................................ *Lapidopsylla*
   – Cell $cu_1$ long and flat, distinctly longer than cell $m_1$............................................................... 3
3. Vein $Cu_{1a}$ very long and almost straight, cell $cu_1$ almost flat (much longer than high) ....................... *Paleopsylloides*
   – Vein $Cu_{1a}$ arcuate, cell $cu_1$ not flat (much longer than high).................................................. *Proeurotica*

### Family Aphalaridae Löw, 1879

### Subfamily Aphalarinae Löw, 1879

### Tribe Paleopsylloidini Becker-Migdisova, 1985

### Genus *Proeurotica* Becker-Migdisova, 1985

**Type species.** *Psylla exhumata* Cockerell, 1915; by original designation.

*Plesioaphalara* Klimaszewski in Klimaszewski & Popov, 1993

**Type species.** *Plesioaphalara arcana* Klimaszewski in Klimaszewski & Popov, 1993; by original designation.

**Diagnosis** (after Becker-Migdisova 1985 and Klimaszewski & Popov 1993). Length/width coefficient of forewing 2.3:1. Stem R + M short, slightly longer (1.1–1.2 times) than M + CuA and CuA. Rs long, straight, slightly curved at apex anteriad; stem R half of M + CuA stem length, 1.8 times shorter than stem CuA. Branches of M short, distinctly shorter than stem M. Cell $cu_1$ with length/width coefficient 3.1–4.5.

**Description.** Forewing elongated, with long, narrow cell $cu_1$. Stem R + M + CuA short, subequal to stem R. Cell m shorter than stem M.

**Remark.** The genus *Plesioaphalara* was synonymised under *Proeurotica* by Ouvrard *et al.* (2013). *Proeurotica exhumata* (type species) differs from all other species recently moved by Ouvrard *et al.* (2013) to the genus *Proeurotica* by the lack of a

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pterostigma. However, better preserved material is necessary to confirm or reject this situation.

*Proeurotica exhumata* (Cockerell, 1915)
(Pl. 1: 1; Fig. 1)

1915 *Psylla exhumata* Cockerell, p. 487, pl. 63, fig. 6.
1985 *Proeurotica eshumata* [sic]: Becker-Migdisova, p. 82.
1985 *Proeurotica exhumata*: Becker-Migdisova, p. 83, fig. 63.
1993b *Paleopsylloides exhumatus*: Klimaszewski, p. 10.
2013 *Proeurotica exhumata* Cockerell, 1915: Ouvrard *et al.*, p. 24.

**Holotype.** USNM No. 61427, Lacoe Collection 7619, Insect Limestone, NW Isle of Wight.
**Remarks.** Klimaszewski (1993b) transferred *Proeurotica exhumata* (Cockerell 1915) to the genus *Paleopsylloides* Becker-Migdisova, 1985 on the basis of misinterpreted characters.

*Proeurotica arcana* (Klimaszewski in Klimaszewski & Popov, 1993) comb. nov.
(Pl. 1: 2; Fig. 2)

1993 *Plesioaphalara arcana* Klimaszewski in Klimaszewski & Popov, pp. 19–20; fig. 2b; pl. 2, figs 1–3.
2013 *Plesioaphalara arcana* Klimaszewski, 1993: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018433 (BLS 1423); Insect Limestone, Thorness Bay, collected by A. A. Mitchell.
**Paratypes.** BMB 018434 (BLS 603), 018435 (BLS 1112), 018436 (BL 1319), 018437 (BL 131), 018438 (BL 145), all collected by A. A. Mitchell; 018439 (IL 61), collected by M. J. Warren.

*Proeurotica paulula* (Klimaszewski in Klimaszewski & Popov, 1993) comb. nov.
(Pl. 1: 3; Fig. 3)

1993 *Plesioaphalara paulula* Klimaszewski in Klimaszewski & Popov, pp. 20–21; fig. 3a; pl. 2, fig. 4.
2013 *Plesioaphalara paulula* Klimaszewski, 1993a: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018440 (BLS 723–32); Insect Limestone, Thorness Bay, collected by A. A. Mitchell.

*Proeurotica inanima* (Klimaszewski in Klimaszewski & Popov, 1993) comb. nov.
(Pl. 1: 4; Fig. 4)

1993 *Plesioaphalara inanima* Klimaszewski in Klimaszewski & Popov, p. 21; fig. 3b; pl. 2, figs. 5, 6.
2013 *Plesioaphalara inanima* Klimaszewski, 1993: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018441 (BLS 381); Insect Limestone, Thorness Bay, collected by A. A. Mitchell.
**Paratype.** BMB 018442 (BLS 978), Mitchell Collection

Key to the species of *Proeurotica* Becker-Migdisova

1. Costal margin of forewing straight, vein Rs subparallel to anterior margin of forewing.......................... *exhumata*
– Costal margin of forewing arcuate, vein Rs not subparallel to anterior margin of forewing....................... 2
2. Length of forewing up to 1 mm, width 0.45 mm, very short and high cell $m_1$ ..........................................*paulula*
– Length of forewing more than 1 mm, width more 0.5 mm, cell $m_1$ long......................................................... 3
3. Length of forewing more 2 mm, vein $Cu_1$ longer than vein $M + Cu_1$................................................. *inanima*
– Length of forewing up to 2 mm, vein $Cu_1$ always shorter than vein $M + Cu_1$....................................... *arcana*

Genus *Lapidopsylla* Klimaszewski in Klimaszewski & Popov, 1993

**Type species.** *Lapidopsylla thornessbaya* Klimaszewski in Klimaszewski & Popov, 1993; by original designation.

1993 *Lapidopsylla* Klimaszewski: Klimaszewski & Popov, p. 21.

*Lapidopsylla thornessbaya* Klimaszewski in Klimaszewski & Popov, 1993
(Pl. 1: 5; Fig. 5)

1993 *Lapidopsylla thornessbaya* Klimaszewski in Klimaszewski & Popov, 1993, p. 22; fig. 3c; pl. 2, fig. 7.
2013 *Lapidopsylla thornessbaya* Klimaszewski, 1993a, 1993b: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018443 (BLS 850-1); Insect Limestone, Thorness Bay, collected by A. A. Mitchell.

*Lapidopsylla memoranda* Klimaszewski in Klimaszewski & Popov, 1993
(Pl. 1: 6; Fig. 6)

1993 *Lapidopsylla memoranda* Klimaszewski in Klimaszewski & Popov, 1993, pp. 22–23; fig. 3d; pl. 2, fig. 8.
2013 *Lapidopsylla memoranda* Klimaszewski, 1993: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018444 (BLG 203); Insect Limestone, Thorness Bay, collected by A. A. Mitchell.

Key to the species of *Lapidopsylla* Klimaszewski

1. Length of forewing more than 2 mm, vein M long, about twice as long as vein $M_{1+2}$, vein $R_s$ visibly, arched towards forewing margin..................................... *memoranda*
– Length of forewing about 1.5 mm, vein M short, 1 5 times as long as vein $M_{1+2}$, vein $R_s$ almost straight............................................... *thornessbaya*

Genus *Carsidarina* Becker-Migdisova, 1985

**Type species.** *Livilla hooleyi* Cockerell, 1921c; by original designation.
**Remarks.** Ouvrard *et al.* (2013, p. 31) synonymised genus *Palaeoaphalara* Klimaszewski, 1993b with *Carsidarina* Becker-Migdisova, 1985, thus three species described by Klimaszewski (in Klimaszewski & Popov 1993) should be moved to *Carsidarina*. The genus *Carsidarina* Becker-Migdisova, 1985 was moved from Carsidaridae to the tribe Palaeopsylloidini Becker-Migdisova, 1985 of Aphalaridae: Aphalarinae (Ouvrard *et al.* 2013).

*Carsidarina hooleyi* (Cockerell, 1921)
(Pl. 1: 7; Fig. 7)

1921 *Livilla hooleyi* Cockerell, 1921c, p. 476, fig. 44.
1985 *Carsidarina hooleyi*: Becker-Migdisova, p. 86, fig. 66.
1992 *Livilla*: Carpenter, p. 253.
2013 *Carsidarina hooleyi* Cockerell, 1921 [sic]: Ouvrard *et al.*, p. 24.

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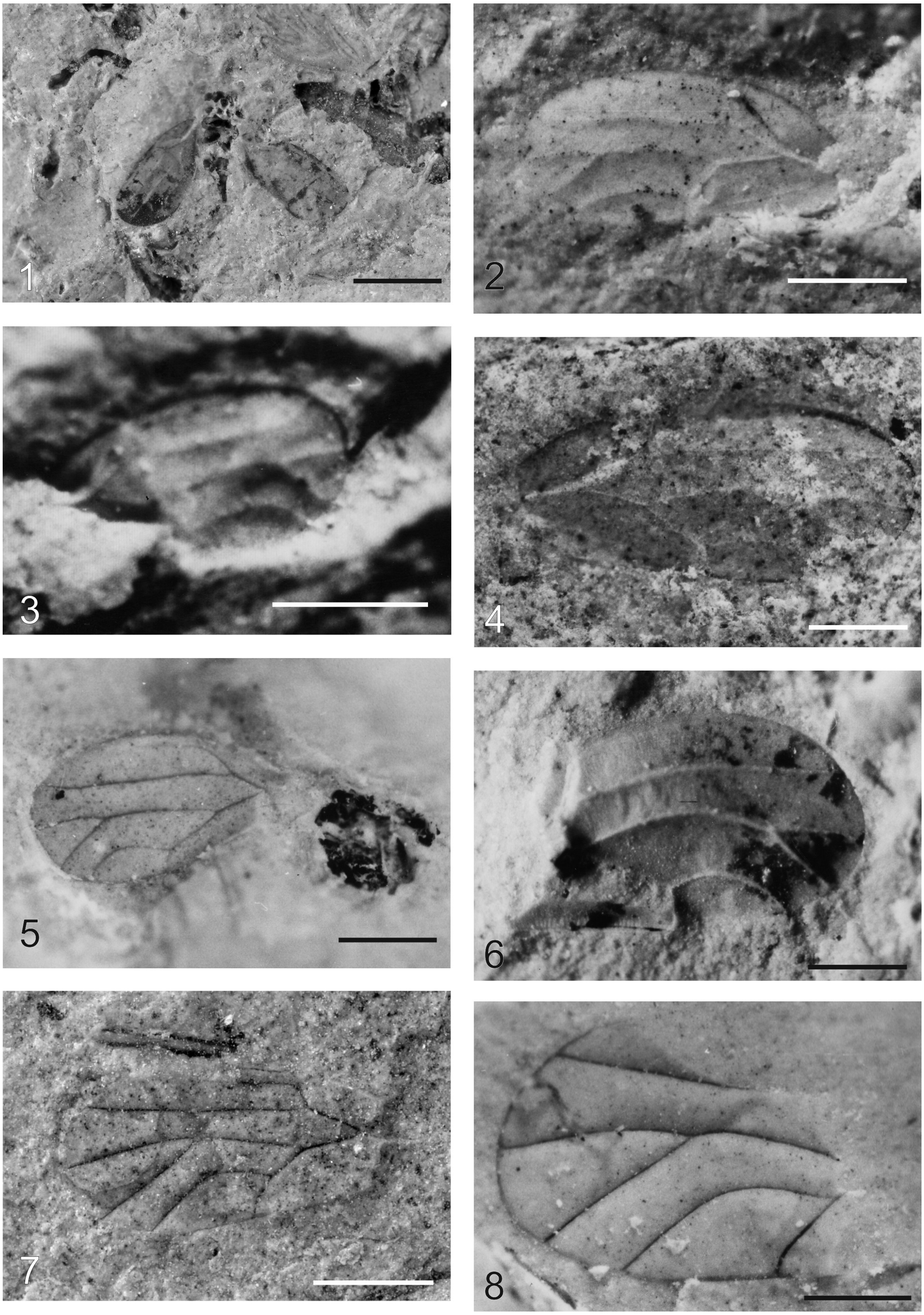
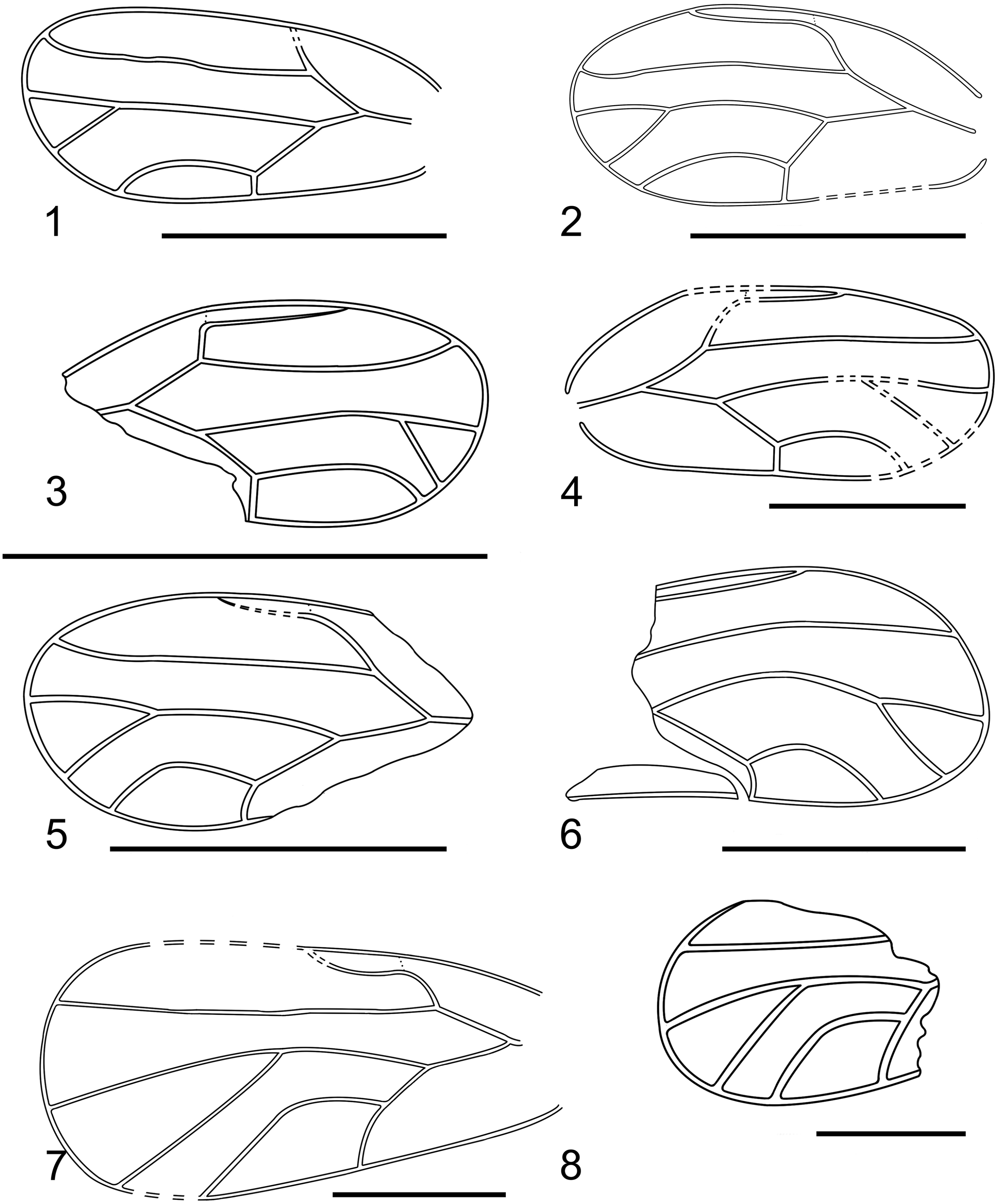


**Plate 1** (1) *Proeurotica exhumata* (Cockerell, 1915), holotype, USNM No. 61427. (2) *Proeurotica arcana* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018433, forewing. (3) *Proeurotica paulula* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018440, forewing. (4) *Proeurotica inanima* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018441, forewing. (5) *Lapidopsylla thornessbaya* Klimaszewski in Klimaszewski & Popov, 1993 holotype, BMB 018443, forewing. (6) *Lapidopsylla memoranda* Klimaszewski in Klimaszewski & Popov, 1993 holotype, BMB 018444, forewing. (7) *Carsidarina hooleyi* (Cockerell, 1921) holotype, NHMUK In. 24358a, part, forewing. (8) *Carsidarina jarzembowskii* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018424-5, part, forewing. Scale bar = 1 mm.




**Figures 1–8** Forewing. (1) *Proeurotica exhumata* (Cockerell, 1915), holotype, USNM No. 61427. (2) *Proeurotica arcana* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018433. (3) *Proeurotica paulula* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018440. (4) *Proeurotica inanima* Klimaszewski in Klimaszewski & Popov, 1993 holotype, BMB 018441. (5) *Lapidopsylla thornessbaya* Klimaszewski in Klimaszewski & Popov, 1993 holotype, BMB 018443. (6) *Lapidopsylla memoranda* Klimaszewski in Klimaszewski & Popov, 1993 holotype, BMB 018444. (7) *Carsidarina hooleyi* (Cockerell, 1921c) holotype, NHMUK In.24358a, part. (8) *Carsidarina jarzembowskii* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018424, part. Scale bar = 1 mm.

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**Holotype.** NHMUK In. 24358a, b (H. 430/H.445) (part and counterpart) Hooley Collection, Insect Limestone, NW Isle of Wight.

**Paratype.** NHMUK In. 24359 (H. 449). Hooley Collection.

*Carsidarina jarzembowskii* (Klimaszewski in Klimaszewski & Popov, 1993) comb. nov.
(Pl. 1: 8; Fig. 8)

1993 *Palaeoaphalara jarzembowskii* Klimaszewski in Klimaszewski & Popov, pp. 16–17; fig. 1a–c; pl. 1, figs 1–4.
1996 *Palaeoaphalara jarzembowski* [sic!]: Klimaszewski, p. 25.
2013 *Palaeoaphalara jarzembowskii* Klimaszewski, 1993: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018424-5 (IL 67 a, b) (part and counterpart); Insect Limestone, Thorness Bay, collected by A. J. Ross.

*Carsidarina ampla* (Klimaszewski in Klimaszewski & Popov, 1993) comb. nov.
(Pl. 2: 1; Fig. 9)

1993 *Palaeoaphalara ampla* Klimaszewski in Klimaszewski & Popov, pp. 17–18; fig. 2a; pl. 1, fig. 7.
2013 *Palaeoaphalara ampla* Klimaszewski, 1993: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018431 (BL 64); Insect Limestone, Thorness Bay, collected by A. A. Mitchell.

*Carsidarina media* (Klimaszewski in Klimaszewski & Popov, 1993) comb. nov.
(Pl. 2: 2; Fig. 10)

1993 *Palaeoaphalara media* Klimaszewski in Klimaszewski & Popov, 1993, p. 17; fig. 1d; pl. 1, figs. 5, 6.
2013 *Palaeoaphalara media* Klimaszewski, 1993: Ouvrard *et al.*, p. 24.

**Holotype.** BMB 018426-7 (IL 62a, b) (part and counterpart); Insect Limestone, Thorness Bay, collected by A. J. Ross.

**Paratypes.** BMB 018428-9 (IL 6), collected by T. B. E. Jarzembowski; BMB 018430 (BL 50), collected by A. A. Mitchell.

Key to the species of *Carsidarina* Becker-Migdisova

1. Vein Rs straight, vein M in distal portion concave ........ *hooleyi*
   – Vein Rs gently curved, vein M in distal portion not concave ........ 2
2. Cell $m_1$ is shorter than cell $cu_1$ ........ *jarzembowskii*
   – Cell $m_1$ longer or the same length as cell $cu_1$ ........ 3
3. Length of forewing more than 3 mm, width about 1.4 mm, vein $M + Cu_1$ 1.47 times as long as vein $Cu_1$ ........ *ampla*
   – Length of forewing no more than 2.7 mm, width no more than 1.15 mm, vein $M + Cu_1$ 1.8–2.0 times as long as vein $Cu_1$ ........ *media*

Subfamily Aphalarinae Löw, 1879

Tribe Aphalarini Löw, 1879

Genus *Paleopsylloides* Becker-Migdisova, 1985

**Type species.** *Strophingia oligocaenica* Enderlein, 1915; by original designation by Becker-Migdisova, 1985, p. 82.

*Paleopsylloides*? *anglica* (Cockerell, 1915)
(Pl. 2: 3; Fig. 11)

1915 *Necropsylla anglica* Cockerell, p. 487, pl. 63, fig. 5.
1985 *Camaratoscena? anglica*: Becker-Migdisova, p. 81, pl. 61.
1993b *Paleopsylloides? anglica*?: Klimaszewski, p. 11.
1993b *Necropsylla angelica* [sic]: Klimaszewski, p. 21.
2013 *Camaratoscena? anglica* (Cockerell, 1915): Ouvrard *et al.*, p. 24.

**Holotype.** USNM No. 61426, Lacoe Collection 7671. Next to the holotype ant (Formicidae) wing of *Emplastus hypolithus* (Cockerell 1915), USNM No. 61411. Insect Limestone, NW Isle of Wight.

**Remarks.** This species has been described on the basis of a fragment of a forewing. The preserved part comprises only veins $M_1$ and $Cu_1$, the distal part of veins $M + Cu_1$ and cells $M_1$ and $Cu_1$. Klimaszewski (Klimaszewski & Popov 1993) suggested that this species should be transferred to the monotypic genus *Paleopsylloides*, distinguished by Becker-Migdisova (1985). Despite the paucity of data offered by the forewing, this suggestion seems plausible. The use of a synonymous name – *Necropsylla angelica* [sic] – in Klimaszewski (1993b) seems to have been a mere oversight.

Whiteflies (Hemiptera: Sternorrhyncha: Aleyrodidae)

by *Jacek Szwedo and Jowita Drohojowska*

The oldest known whiteflies so far are of the Upper Jurassic of Kazakhstan (Shcherbakov 2000a); some others are recorded from the Early Cretaceous of England, Early Cretaceous Lebanese amber, Mid-Cretaceous Burmese amber Early Eocene Oise amber and Middle Eocene Baltic amber (Schlee 1970; Shcherbakov 2000a; Azar 2007; Drohojowska & Szwedo 2011a, b, 2013a, b, 2015; Drohojowska *et al.* 2015; Szwedo & Drohojowska 2016), Middle Eocene Geiseltal fossil Lagerstätte (Weigelt 1940). Whiteflies are also recorded in Miocene Mexican and Dominican ambers (Poinar 1992; Wu 1996), and Miocene Ethiopian amber (Schmidt *et al.* 2010) and Pliocene of Germany (Rietschel 1983).

Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843

Infraorder Aleyrodomorpha Chou, 1963

Superfamily Aleyrodoidea Westwood, 1840

Family Aleyrodidae Westwood, 1840

Aleyrodidae gen. and sp. indet.
(Pl. 2: 4–6)

1993 'aleyrodoid': Jarzembowski & Ross, p. 218, fig. 2.
2000a 'pupal case of Aleyrodoidea': Shcherbakov, p. 35.

**Material.** Specimen No. MNEMG IB, collected by A. A. Mitchell. Insect Limestone, NW Isle of Wight.

**Description.** Fossil of pupal case, dorsal view, 0.9 mm long, 0.65 mm wide. Margin smooth, thoracic tracheal pore not differentiaded from the margin. Submarginal area wide, with distinct submarginal lines. Cephalothoracic suture absent. Longitudinal moulting suture not reaching margin; transverse moulting suture not reaching margin of pupal case, slightly curved anteriad, but lateral portions not distinctly bent, but gently curved at wide angle. Abdomen with intersegmental sutures distinct, not extending into subdorsum. Abdominal rhachis absent. Lateral portions of abdominal segments with

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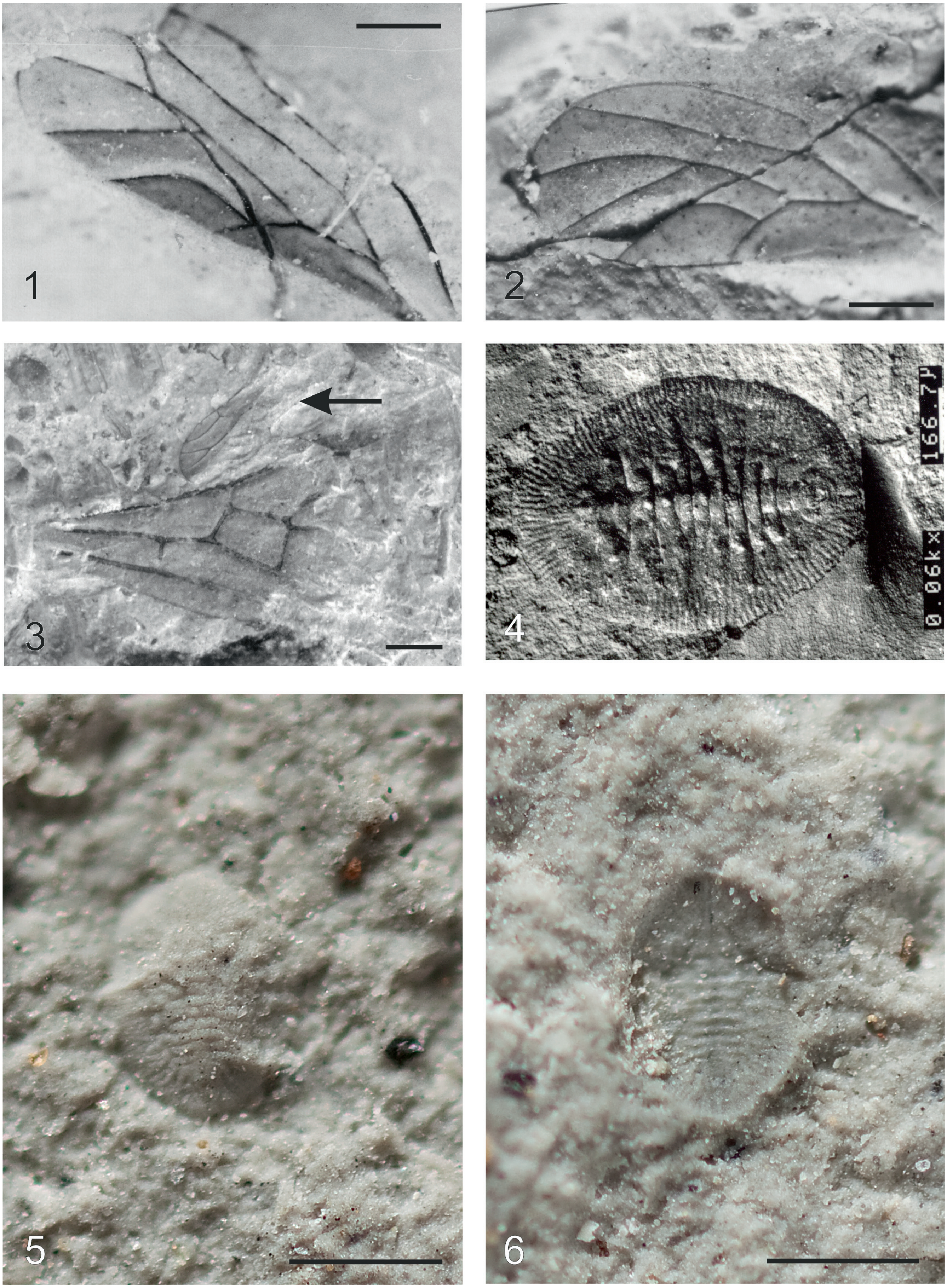


**Plate 2** (1) *Carsidarina ampla* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018431, forewing. (2) *Carsidarina media* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018426, forewing. (3) *Paleopsylloides*? *anglica* (Cockerell, 1915), holotype, USNM No. 61426, forewing (arrowed), with the holotype of the ant *Emplastus hypolithus* (Cockerell, 1915). (4) Aleyrodidae indet., MNEMG IB, SEM photo, puparium. (5–6) Aleyrodidae (?) indet., NHMUK II.2986a, b, puparium (?).

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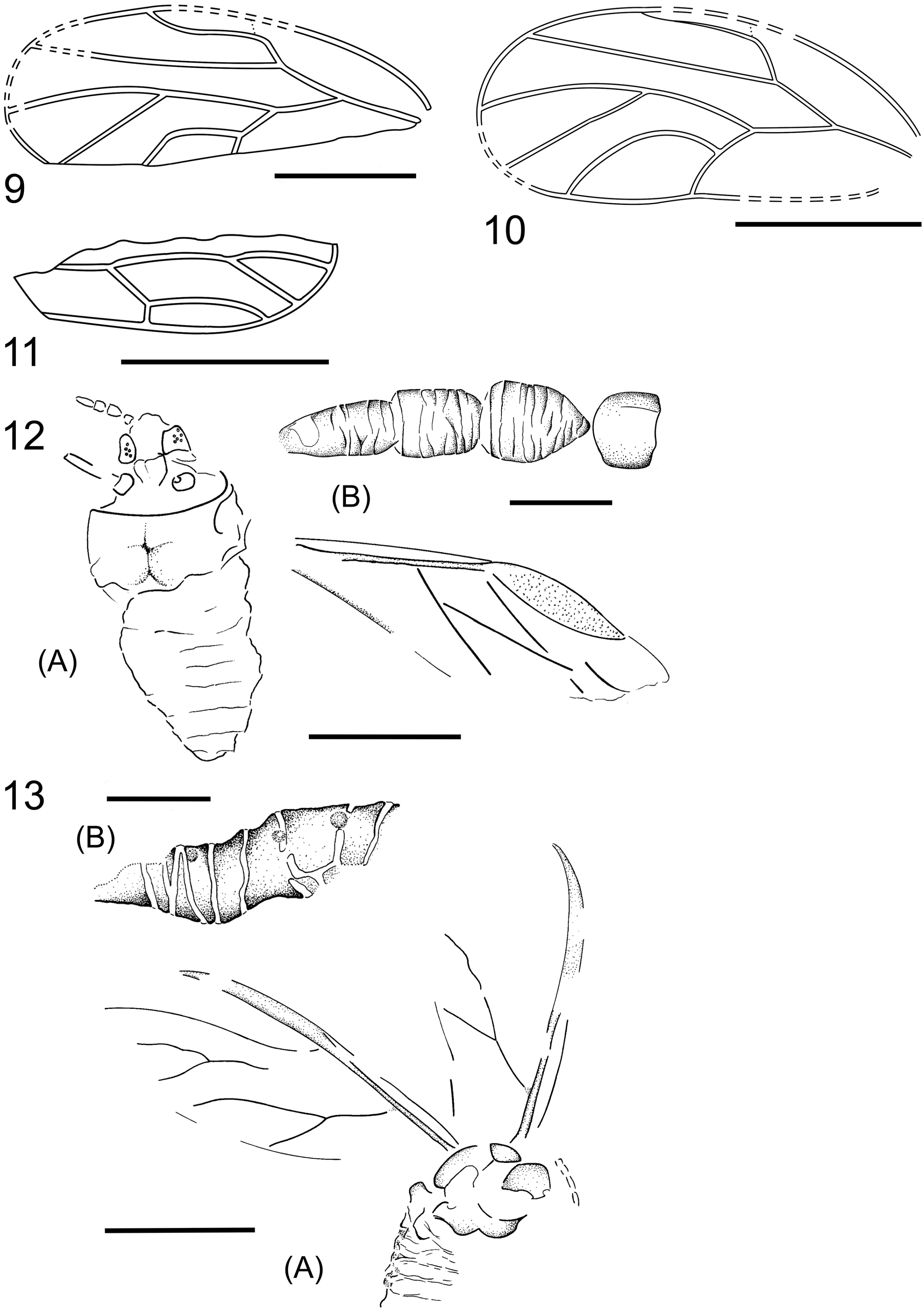


**Figures 9–13** (9–11) Forewing: (9) *Carsidarina ampla* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018431, forewing; (10) *Carsidarina media* (Klimaszewski in Klimaszewski & Popov, 1993) holotype, BMB 018426; (11) *Paleopsylloides*? *anglica* (Cockerell, 1915), holotype, USNM No.61426. Scale bar = 1 mm. (12) *Schizoneurites brevirostris* Cockerell, 1915, holotype, counterpart NHMUK I.9850: (A) general view; (B) right antenna. Scale bar = 0.05 mm. (13) *Hormaphis*? *longistigma* Wegierek sp. nov., holotype, NHMUK I.9595: (A) general view. Scale bar = 0.05 mm; (B) part of antennal segment. Scale bar = 0.02 mm.

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eminences (subdorsal pores?, wax pores?). Vasiform orifice triangular. Operculum rounded, lingula spatulate.

**Remarks.** A SEM (scanning electron microscope) photograph of this specimen was figured by Jarzembowski & Ross (1994, fig. 2). The subfamilial and tribal placement of the specimen needs further studies. A few additional specimens, with numbers, MNEMG 2018.6.719; MNEMG 2018.6.773; MNEMG 2018.6.1478; MNEMG 2018.6.2717; MNEMG 2018.6.3060 (field numbers 719, 773, 1478, 2717 and 3060 respectively, collected by Tony Mitchell) preliminarily identified as Aleyrodidae are stored in the Maidstone Museum. One specimen was found in the collection of the NHM, London, NHMUK II.2986a, b (Pl. 2: 5–6), but only provisionally ascribed to Aleyrodidae.

The Aleyrodomorpha is a group with great taxonomic difficulties. In the Aleyrodomorpha, the taxonomy of recent forms is based on the last pre-adult instar, the so called 'puparium', but that of the fossil forms, on winged adults (Gill 1990; Shcherbakov 2000a; Martin 2003). The Aleyrodidae comprises a single family including around 1550 currently valid species and subspecies names (Martin & Mound 2007; Ouvrard & Martin 2019). Relationships between Aleyrodidae and their host plants are still unclear, and this problem was addressed by Manzari & Quicke (2006) and Dubey & Ko (2006). Most studies on whitefly biology deal with plants of economic importance (Lenteren & Noldus 1990) and the lack of reliable behaviour and ecology data hampers the understanding of evolutionary patterns in this group. Few whitefly species are known as monophagous, most being oligo- or polyphagous. According to Mound & Halsey (1978) the majority of aleyrodids are recorded only from dicotyledonous angiosperms and a smaller, but significant, number feed on monocots, particularly grasses and palms. Few present-day whiteflies feed on non-angiosperm hosts, the record of a whitefly feeding on a gymnosperm, involving the highly polyphagous *Trialeurodes vaporariorum* is exceptional (Martin *et al.* 2000; Manzari & Quicke 2006). A few species habitually feed on ferns and other pteridophytes such as *Selaginella* (Mound *et al.* 1994); these are very much exceptions to the rule (Martin *et al.* 2000). Whiteflies appear to have evolved quite a long time ago, with the oldest known fossil remains from the Late Jurassic – the extinct Bernaeinae Shcherbakov 2000a surviving to the Mid-Cretaceous. The oldest Udamoselinae are recorded from Lower Cretaceous Lebanese amber (Hauterivian–Aptian), the first Aleurodicinae were found in Burmese amber (Cenomanian). No confirmed fossil record of Aleyrodinae is available at the moment (Shcherbakov 2000a). The present-day distribution of Aleyrodidae lineages shows that Aleurodicinae are distributed mainly in the Neotropical and Australasian regions, while Aleyrodinae are distributed worldwide (Mound & Halsey 1978; Martin & Mound 2007; Evans 2008). This distributional pattern and the availability of fossil data suggest a Palaeotropical origin of the whiteflies (Mound 1984; Bink-Moenen & Mound 1990; Manzari & Quicke 2006). The question of ancestral host plants of the Aleyrodidae is still open. It seems that the group evolved in relation to some Jurassic gymnosperms (or pro-angiosperms?); however, their accelerated diversification probably took place in concordance with the diversification of angiosperms and biotic reorganisation of the biosphere in the Mid-Cretaceous (Rasnitsyn 1988; Drohojowska & Szwedo 2015; Szwedo & Drohojowska 2016). Manzari & Quicke (2006) stated that the diversification pattern of Aleyrodidae with their host plants is obscured by widespread host switching. However, it could be said that the evolution of aleyrodid host plant affiliations appears not to be random as some groups have species feeding on related plants.

## Coccids (Hemiptera: Sternorrhyncha: Coccidomorpha)

by *Jacek Szwedo and Ewa Simon*

The scarcity of scale insects among Palaeogene fossils is still a puzzle, but the number of species representing both archeococcids (Orthezioidea) and neococcids (Coccoidea) are known from fossil resins (Koteja 2000a, b, 2001, 2004, 2008; Koteja & Azar 2008; Vea & Grimaldi 2012, 2015; Simon & Żyła 2015; Wang *et al*. 2015). The oldest neococcids are known from Lower Cretaceous Lebanese amber, and in the Palaeogene they represent a diverse group. It would be interesting to know on which host plants ancestral and fossil scale insects fed on in various periods of geological time, and with which types of vegetation and climatic conditions they were associated. Scale insects appeared as an abundant and diversified group in the Early Cretaceous, but their roots are unknown even if the supposed time of their origin is Triassic (Koteja 1985, 2001). It is believed that the most recent periods of scale insects diversification are related to the evolution of two other groups of organisms intimately associated with coccids: angiosperm plants and ants (Koteja 1985; Grimaldi & Engel 2005). To test the hypothesis about scale insect phylogeny and relationships, data on their biology, host–parasite relationships, origins of gall induction, biogeography, evolution of chromosome systems and molecular characteristics (Cook *et al*. 2002; Gullan & Cook 2007; Hodgson & Hardy 2013), as well as morphology-based palaeontological and neontological research and correlation of radiation events are necessary (Koteja 2000a, 2008; Koteja & Azar 2008; Vea & Grimaldi 2012, 2015; Wang *et al*. 2015).

### Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843

### Infraorder Coccidomorpha Heslop-Harrison, 1952

### Superfamily Coccoidea Fallén, 1814 indet.
(Pl. 3: 1)

**Material.** Specimen No. MNEMG HL1a, b, Jarzembowski Collection, Maidstone Museum. Insect Limestone, Hampstead Ledge.

**Description.** Imago, male, lanceolate forewing, 2.15 mm long, 1 mm wide. Subcostal ridge curved along forewing margin, slightly sigmoidal at base, not strongly curved in apical portion.

Compression fossil scale insects (Hemiptera: Sternorrhyncha: Coccomorpha) were documented from the Early Cretaceous of Transbaikalia (Koteja 1988, 1989) and England (Koteja 1999) – representing archeococcid males (Orthezioidea: Matsucoccidae and Xylococcidae). Only adult male scale insects have wings and we cannot glean anything about insect and plant interactions because the adult males do not feed. These records provide only morphological details. However, feeding stages of females and larvae preserved on fossil dicotyledonous leaves were documented from the Middle Eocene of Messel, Germany (Wappler & Ben-Dov 2008), Miocene deposits of Sicily (Pampaloni 1902; Koteja & Ben-Dov 2003), Germany (Zeuner 1938; Koteja 2000b), New Zealand (Harris *et al*. 2007) – representing neococcids (Coccoidea: Diaspididae) and unidentified scale insects (Schmidt *et al*. 2018) – and India (Bera *et al*. 2006).

## Aphids (Hemiptera: Sternorrhyncha: Aphidomorpha)

by *Piotr Wegierek*

The earliest published data on aphids from the Insect Limestone of the Isle of Wight concerned two species known from

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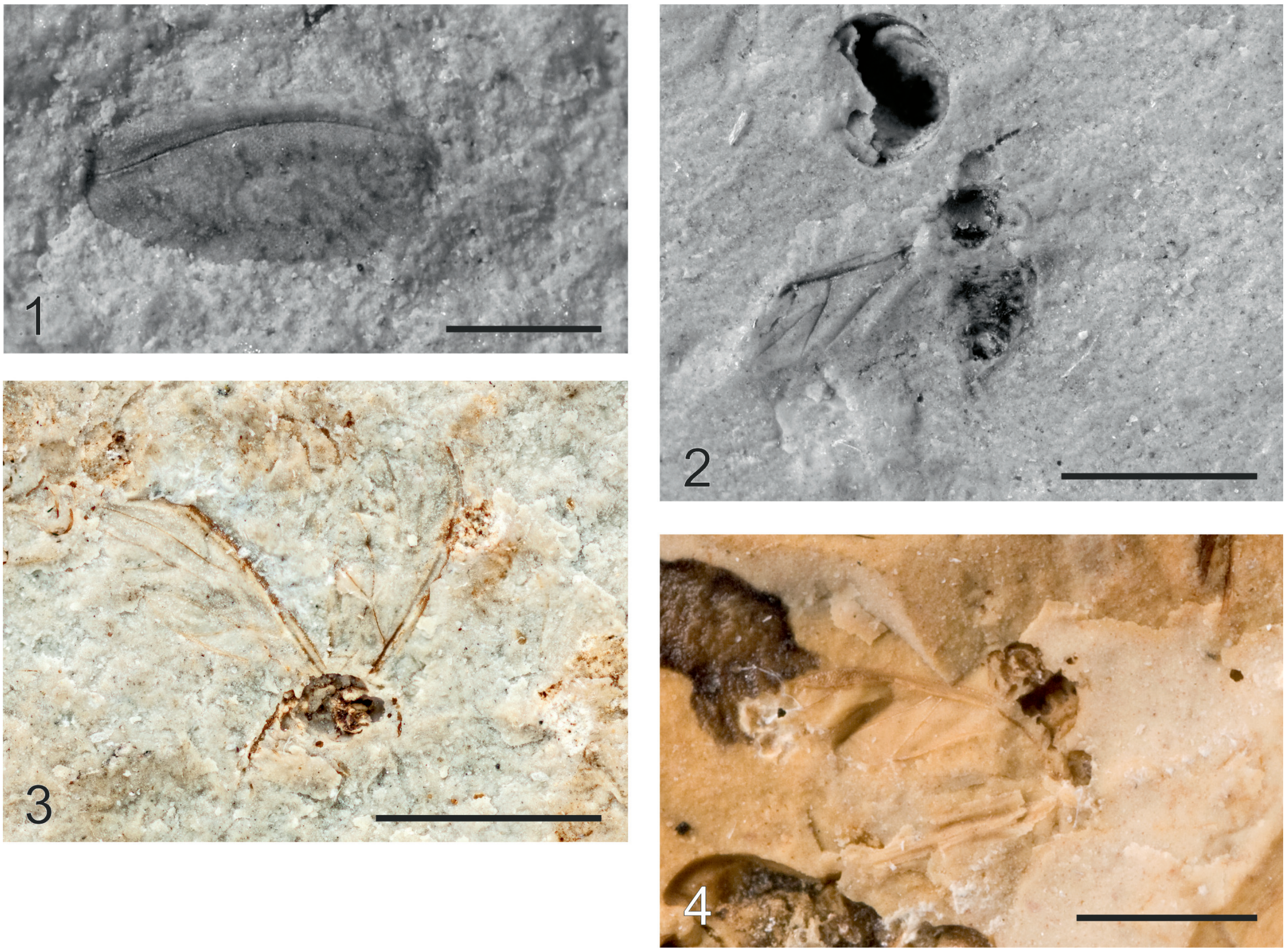


**Plate 3** (1) Coccoidea, MNEMG HL1b, male, forewing. (2) *Schizoneurites brevirostris* Cockerell, 1915, holotype, USNM 61428 part, dorsal part of body, without legs. (3) *Hormaphis*? *longistigma* Wegierek sp. nov., holotype, NHMUK I.9595. (4) *Eriosoma gratshevi* Wegierek sp. nov., holotype, NHMUK I.8585. Scale bar = 1 mm.

single specimens, which suggested that aphids were very rare in these strata and their taxonomic diversity was low. As a result of the present research, 25 fossils have been identified as Aphidoidea. The findings suggest a relatively high degree of taxonomic diversity (seven species representing one extinct and three extant families), comparable with Eocene/Oligocene deposits where aphids have been found (Scudder 1890; Heie 1989). In the present paper aphid species formerly described from the Isle of Wight, i.e., *Aphis gurnetensis* Cockerell, 1921a, b, c and *Schizoneurites brevirostris* Cockerell, 1915 are revised, and other fossils are described for the first time.

*Schizoneurites brevirostris* Cockerell, 1915 redescribed below, is the last known representative of the extinct family Elektraphididae. In contrast to the Baltic amber fauna, most of the described species are placed within recent genera. The condition of specimens prevents a more detailed comparative analysis.

Suborder Sternorrhyncha Amyot & Audinet-Serville, 1843

Infraorder Aphidomorpha Becker-Migdisova & Aizenberg, 1962

Superfamily Aphidoidea Geoffroy, 1762

Family Elektraphididae Steffan, 1968

Genus *Schizoneurites* Cockerell, 1915

**Type species.** *Schizoneurites brevirostris* Cockerell, 1915, Insect Limestone, NW Isle of Wight, UK; by original designation.

**Remarks.** This genus was redescribed by Heie (1970). He proposed that the genera *Antiquaphis* Heie, 1967 and *Elektraphis* Steffan, 1968 should be regarded as junior synonyms and belonged to the family *Elektraphididae* (Heie 1976). Steffan & Schlüter (1981) restored the formerly synonymised genera. However, the systematic position of the genus *Schizoneurites* was not specified. In the original description Cockerell (1915) emphasised its similarity to the genera *Schizoneura* Hartig, 1839 or *Eriosoma* Leach, 1818 of the family Eriosomatidae. The five-segmented antennae with transverse grooves, veins $CuA_1$ and $CuA_2$ connected basally suggest that this genus should be placed in the family Elektraphididae.

*Schizoneurites brevirostris* Cockerell, 1915
(Pl. 3: 2; Fig. 12A, B)

1915 *Schizoneurites brevirostris* Cockerell, p. 488.
1992 *Schizoneurites brevirostris*: Carpenter, p. 248.
1970 *Schizoneurites brevirostris*: Heie, p. 114.
1976 *Schizoneurites brevirostris*: Heie, p. 54.
1998 *Schizoneurites brevirostris*: Heie & Wegierek, p. 183.
2011 *Schizoneurites brevirostris*: Heie & Wegierek, p. 56.

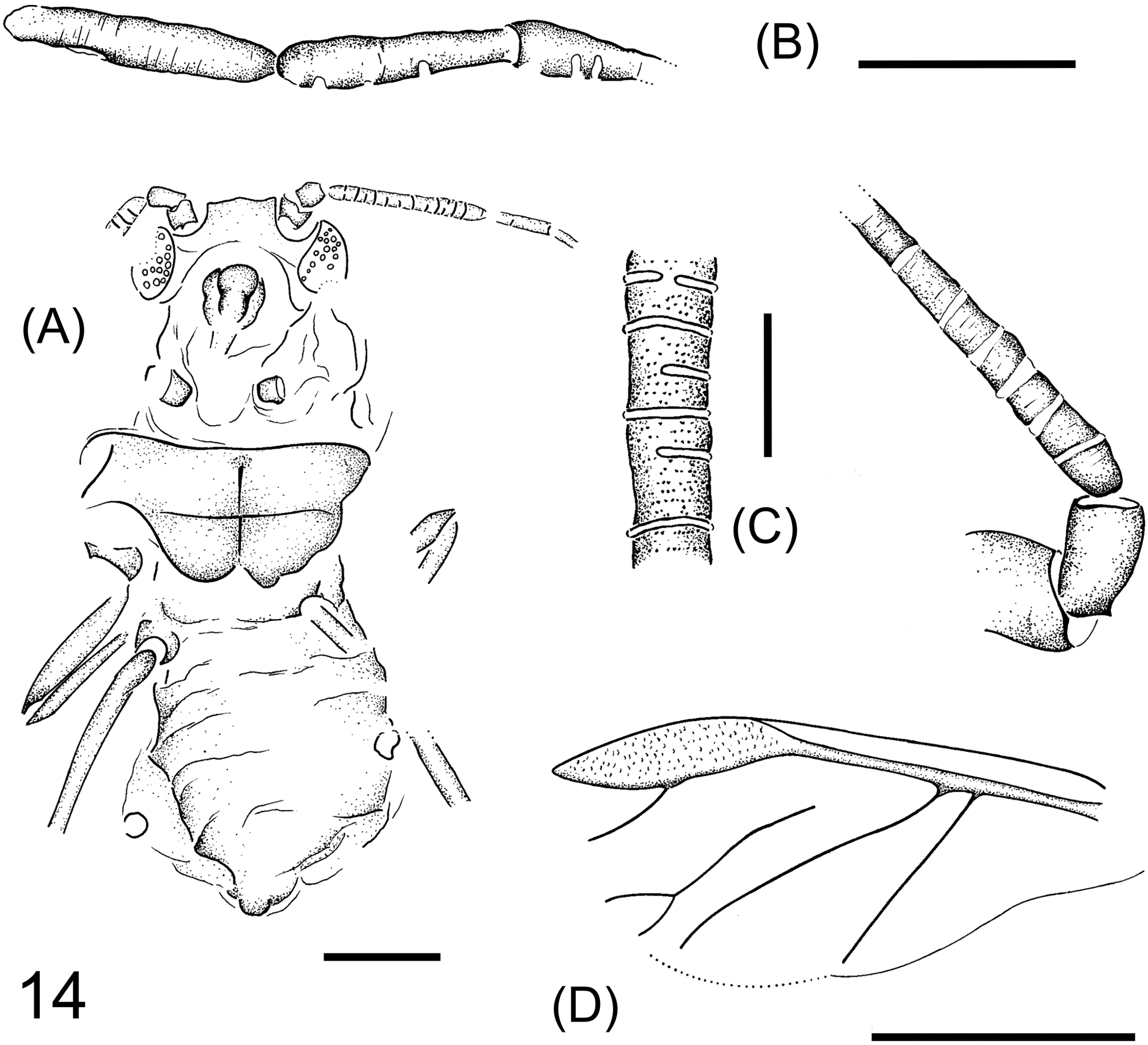


**Figure 14** *Eriosoma gratshevi* Wegierek sp. nov. (A) General view, paratype NHMUK I.8712. Scale bar = 0.02 mm. (B) Left antenna, paratype NHMUK I.8712. Scale bar = 0.05 mm. (C) Part of antennal segment, holotype NHMUK I.8585. Scale bar = 0.1 mm. (D) Left forewing, holotype NHMUK I.8585. Scale bar = 0.5 mm.

**Holotype part.** USNM 61428, Lacoe collection. Imprint of dorsal part of body, right antenna and fragments of legs preserved. Left fore- and hindwings visible, cubital veins on right wing distinct.

**Counterpart.** NHMUK I. 9850, Brodie Collection Imprint of ventral part of body, without legs. Right antenna and left forewing preserved. The counterpart was not seen for the original description.

**Diagnosis.** Veins $CuA_1$ and $CuA_2$ thick, with a common stem. Vein M undivided. Antennae five-segmented, with transverse grooves. Primary rhinaria invisible. In contrast to other representatives of this genus, the basal portion of vein M visible.

**Redescription.** Length of body 1.2 mm. Antennae five-segmented, segment III as long as IV (0.05 mm) and markedly shorter than longest segment V (about 0.06 mm). Basal part of segment III narrow, apical part wide. Segment IV approximately cylindrical, segment V tapering apically. All segments of flagellum with distinct transverse grooves.

Compound eyes extend to the ventral part of head. Front coxae contiguous with clypeus. Forewings 1.3 mm long. Pterostigma almost as long as the common stem of veins Sc + R + M, four times longer than wide. Cubital veins ($CuA_1$ and $CuA_2$) thicker than others, forming a short common stem ($CuA_{1+2}$), whose length equals the width of the pterostigma. Bases of cubital veins close to the pterostigma, distanced from it by two widths of the pterostigma. Vein M distinct in the basal part, branching off from the basal part of the pterostigma, basal part of Rs invisible.

Family Hormaphididae Mordvilko, 1908

Genus *Hormaphis* Osten-Sacken, 1861

**Type species.** *Hormaphis hamamelidis* Osten-Sacken, 1861, recent species, by original designation.

*Hormaphis*? *longistigma* Wegierek sp. nov.
(Pl. 3: 3; Fig. 13A, B)

**Etymology**. From 'longistigma', Latin – 'elongated pterostigma'.

**Holotype.** NHMUK I.9595, Brodie Collection; Insect Limestone, NW Isle of Wight. Part of head, thorax, abdomen, forewings and part of antenna.

**Diagnosis.** Veins $CuA_1$ and $CuA_2$ connected basally to form a common stem. Vein M with a single fork. Pterostigma long. Antennae with annular rhinaria.

**Description.** Body about 1.0 mm long and 0.4 mm wide across abdomen. Antennae five-segmented, about 0.2 mm long. Length of antennal segments in millimetres: II 0.04, III 0.06, IV 0.03-0.05, V 0.05–0.06. Last segment with annular rhinaria. Mesothoracic lobe not well developed. Forewings 1.3 mm long, 0.35–0.5 mm wide. Cubital veins $CuA_1$ and $CuA_2$ connected basally to form a common stem equal in length to vein $CuA_2$ or half the length of $CuA_1$. Vein M in the basal part invisible, in the apical part forked. Pterostigma thin and long, ten times longer than wide. Vein Rs s-shaped, branching off in the basal part of the pterostigma. Segment boundaries of abdomen well defined.

**Remarks.** Modern aphids rarely possess a common stem of $CuA_1$ and $CuA_2$. Such wing venation with annular secondary rhinaria is typical for Hormaphididae. Similar branching of CuA veins is to be found in the recent European species *Hormaphis betulae* Mordvilko. The newly described species, contrary to the recent one, has a forked vein M and elongated pterostigma.

Family Eriosomatidae Kirkaldy, 1905

Genus *Eriosoma* Leach, 1818

**Type species.** *Eriosoma lanigera* Hausmann, 1802 recent species.

*Eriosoma gratshevi* Wegierek sp. nov.
(Pl. 3: 4; Fig. 14A–D)

**Etymology.** In honour of Vadim G. Gratshev, the late Russian entomologist and good friend of the author.

**Holotype.** NHMUK I.8585, Brodie Collection, Insect Limestone, NW Isle of Wight. Ventral part of head, right antenna and mesosternum. Right forewing well visible.

**Paratype.** NHMUK I.8712, Brodie Collection. Ventral part of body, basal portions of legs and fragments of antennae.

**Diagnosis.** As in recent representatives of the genus *Eriosoma*, antennal segment III very long, with annular rhinaria. Segments IV and V with single rhinaria, last segment only with primary rhinarium. Vein M forked. Veins $CuA_1$ and $CuA_2$ branch off independently. Siphunculi porous.

**Description.** Length of body 1.3 mm. Compound eyes large, with distinct triommatidium, extending to the ventral side of head. Antennae six-segmented, 0.7 mm long. Length of antennal segments in mm: I 0.05, II 0.05–0.06, III 0.29, V 0.11, VIa 0.10, VIb 0.03. Antennal segment III with many annular rhinaria, segments IV and V with single semiannular rhinaria, the last segment only with primary rhinarium. Front coxae 0.04–0.05 mm long. Middle femora 0.28 mm long. Forewings about 1.2 mm long, 0.5 mm wide. Veins $CuA_1$ and $CuA_2$ branch off from the common stem independently, $CuA_1$ arcuate, $CuA_2$ straight. Vein M close to the base of $CuA_1$ but not reaching the common stem of $Sc + R + M$ because its basal part is not developed; in the apical part forked. Pterostigma lenticular, four times longer that wide. Rs branching off in the middle of pterostigma. Segment boundaries of abdomen clearly marked; siphunculi porous, 0.04 mm in diameter.

Genus *Colopha* Monell, 1877

**Type species.** *Byrsocrypta ulmicola* Fitch, 1859, recent species; by original designation.

*Colopha*? *incognita* Wegierek sp. nov.
(Pl. 4: 1; Fig. 15A, B)

**Etymology.** From '*incognitus*', Latin – 'unrecognisable.'

**Holotype.** NHMUK I.9203 (Fig. 15B), Brodie Collection, Insect Limestone, NW Isle of Wight. Ventral side of body without abdomen, right forewing preserved.

**Paratypes.** NHMUK I.8662, Brodie Collection – forewings and hindwing; In.17178, Smith Collection – forewings; In.17198, Smith Collection – head with parts of antenna and fragments of dorsal part of thorax; In.24837 (Fig. 15A), Hooley Collection – thorax and side of head, forewings and hindwing.

**Diagnosis.** Vein Rs branches off approximately in the middle of pterostigma, the fork shifted towards its base. M with a single fork, hindwings with a single vein.

**Description.** Forewing 1.7–2.0 mm long, 0.7–0.8 mm wide. Pterostigma 4.5–5.5 times longer than wide, in the apical part pointed, in the basal part broadening rapidly. Vein Rs branches off approximately in the middle of pterostigma, the fork shifted towards its basal part. Vein M separates from the common stem $Sc + R + M$ in the midpoint between the base of pterostigma and the base of vein $CuA_1$, with a single fork. The common stem of M as long as $M_{3+4}$. Veins $CuA_1$ and $CuA_2$ leave the common stem independently, almost parallel, $CuA_1$ slightly arcuate. Hindwings 1.1 mm long with a single vein.

**Remarks.** The preserved forewings resemble those in several genera of the subfamily Eriosomatinae (*sensu* Heie 1980). However, the set of characters – with vein M forked, the unique shape of the basal part of the pterostigma and hindwings with a single vein – seems closest to the genus *Colopha*.

Family Drepanosiphidae Herrich-Schäffer in Koch, 1857

Genus *Panfossilis* Wegierek gen. nov.

**Etymology.** The name of a recent genus *Panaphis* Kirkaldy, 1904, to which it bears resemblance, and Latin *fossilis*, 'fossil'.

**Type species.** *Panfossilis anglicus* sp. nov.; here designated.

**Diagnosis.** Circular rhinaria only on segment III, terminal process as long as the width of segment IVa at base. Pterostigma short, vein Rs short, bases of veins $CuA_1$ and $CuA_2$ wide apart.

**Description.** Antennae six-segmented; segment III with many circular secondary rhinaria along the whole segment. Other segments of flagellum without secondary rhinaria, with rows of small transverse depressions, which may be remnants of delicate spinules. Terminal process very short, blunt, as long as the width of segment VI at base. Pterostigma short and wide. Vein Rs short, arcuate, in the middle invisible. Veins $CuA_1$ and $CuA_2$ branch off independently, their bases wide apart.

*Panfossilis anglicus* Wegierek sp. nov.
(Pl. 4: 2; Fig. 16A–C)

**Etymology.** From 'Anglia' – the Polish name for England, part of Great Britain.

**Holotype.** NHMUK I.9033, Brodie Collection, Insect Limestone, NW Isle of Wight. Head with part of antenna, thorax in dorsal view, right forewing and base of left forewing.

**Paratype.** NHMUK I.8661, Brodie Collection Ventral side of body, whole left antenna preserved.

**Diagnosis.** As for genus as it is the only included species.

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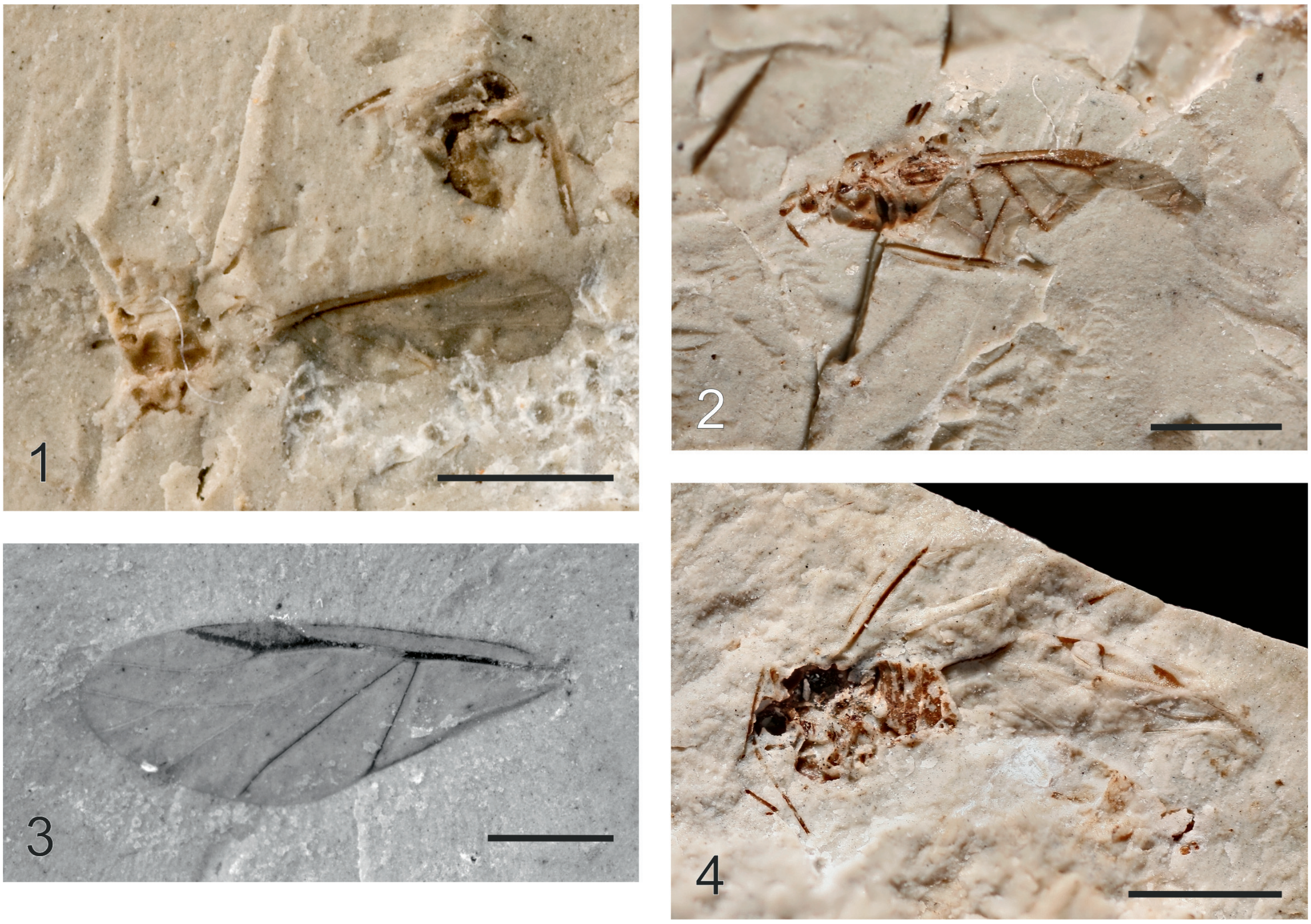


**Plate 4** (1) *Colopha*? *incognita* Wegierek sp. nov., holotype, NHMUK I.9203. (2) *Panfossilis anglicus* Wegierek gen. et sp. nov., holotype, NHMUK I.9033. (3) *Phyllaphis gurnetensis* (Cockerell, 1921b), holotype, NHMUK In.24357. (4) *Betulaphis kozlovi* Wegierek sp. nov., holotype, NHMUK I.9411.

**Description.** Length of body 1.4 mm. Compound eyes situated at sides of head. Antennal segment III shorter than the total length of other segments of flagellum. Length of antennal segments in millimetres: I 0.05–0.08, II 0.07, III 0.33, IV 0.15, V 0.15, VIa 0.13, VIb 0.02. Diameter of secondary rhinaria approximately as long as half the width of antennal segment III. Middle femora 0.32 mm long, hind coxae 0.09 mm long, hind femora 0.38 mm long. Pterostigma three times longer than wide. Base of vein Rs shifted beyond the midpoint of the pterostigma towards the apex.

Bases of veins $CuA_1$ and $CuA_2$ wide apart. The distance between the bases of veins M and $CuA_1$ equals the distance between the bases of cubital veins.

Genus *Phyllaphis* Koch, 1856

**Type species.** *Chermes fagi* Linnaeus, 1761, recent species; by original monotypy.

*Phyllaphis gurnetensis* (Cockerell, 1921b) comb. nov.
(Pl. 4: 3; Fig. 17A–D)

1921 *Aphis gurnetensis* Cockerell, 1921b, p. 476, fig. 43.
1962 *Aphis gurnetensis*: Becker-Migdisova & Aizenberg, p. 198, fig. 577.
1967 *Aphis gurnetensis*: Heie, p. 13.
1991 *Aphis gurnetensis*: Becker-Migdisova & Aizenberg, p. 273, fig. 577.
1998 *Aphis gurnetensis*: Heie & Wegierek, p. 164.

**Holotype.** NHMUK In.24357 (H 1124) (Fig. 17A), Hooley Collection, Insect Limestone, NW Isle of Wight. Forewing.

**Additional material.** NHMUK I.8512 (Fig. 17B, C), Brodie Collection – distorted body, poorly preserved antenna, creased forewings and hindwings; I.9098 (Fig. 17D), Brodie Collection – part of thorax and abdomen in dorsal view, right forewing and hindwing.

**Diagnosis.** Antennal segment III with circular secondary rhinaria arranged in a single row. Pterostigma lenticular, vein Rs arcuate, vein M with two forks, $M_1$ approximately as long as $M_{1+2}$. Cubital veins branch off independently, not far away from each other. Hindwings with two veins, their bases close together.

**Description.** Antennal segment III with circular secondary rhinaria located along the lower margin, their diameter as long as 1/3 of the segment width. Forewings 2.5–3.8 mm long and 1.0–1.5 mm wide. Pterostigma lenticular. Vein Rs arcuate, branching off in the middle of pterostigma. Vein M with two forks, the common stem of M approximately as long as $M_{3+4}$. $M_1$ as long as or only slightly shorter that $M_{1+2}$. Veins $CuA_1$ and $CuA_2$ branch off independently from the common stem, distance between their bases as long as or slightly shorter than the width of pterostigma. $CuA_2$ straight, $CuA_1$ slightly arcuate. Hindwings about 2.1 mm long, with two transverse

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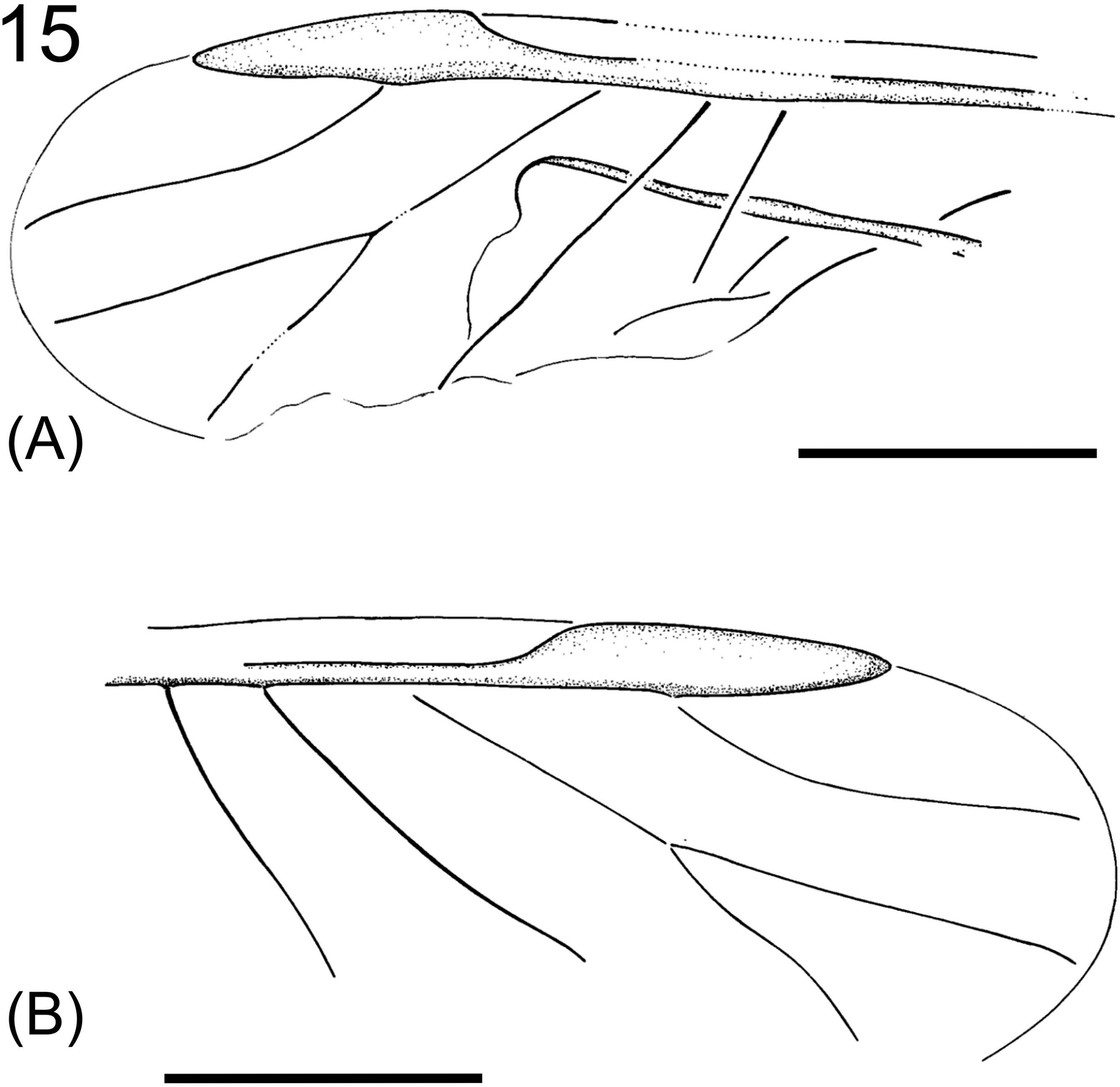


**Figure 15** *Colopha? incognita* Wegierek sp. nov. (A) Paratype, NHMUK In.24837, forewing and hindwing. (B) Holotype, NHMUK I.9203, right forewing. Scale bar = 0.5 mm.

veins located in the middle part of the wing, distance between their bases shorter than the width of pterostigma on forewing.

**Remark.** Becker-Migdisova & Aizenberg (1962, 1991) erroneously listed this species as originating from 'Oligocene, North America'. The species has been placed within the genus *Phyllaphis* on the basis of fore and hindwing structure and venation as well as on a highly characteristic shape of secondary rhinaria and their arrangement on antennal segment III.

Genus *Betulaphis* Glendenning, 1926

**Type species.** *Betulaphis occidentalis* Glendenning, 1926, recent species; by original designation.

*Betulaphis kozlovi* Wegierek sp. nov.
(Pl. 4: 4; Fig. 18A–C)

**Etymology.** In honour of the late Mikhail A. Kozlov, renowned Russian entomologist.

**Holotype.** NHMUK I.9411 (Fig. 18B, C), Brodie Collection, Insect Limestone, NW Isle of Wight. Head with part of antenna, dorsal side of thorax, fragment of front femur and tibia. Basal part of right forewing and creased left wing.

**Paratype.** NHMUK In.24499 (Fig. 18A). Forewing and hindwing.

**Diagnosis.** Antennal segment III with few semiannular rhinaria arranged in a single row. Pterostigma lenticular, vein Rs arcuate. Vein M with two forks, the common stem of M short, veins $M_1$ and $M_2$ very short. Veins $CuA_1$ and $CuA_2$ leave the common stem independently. Hindwings with two transverse veins.

**Description.** Compound eyes situated at sides of the head. Legs and antennae with rows of small transverse depressions, which may be remnants of delicate spinules. Antennal segment

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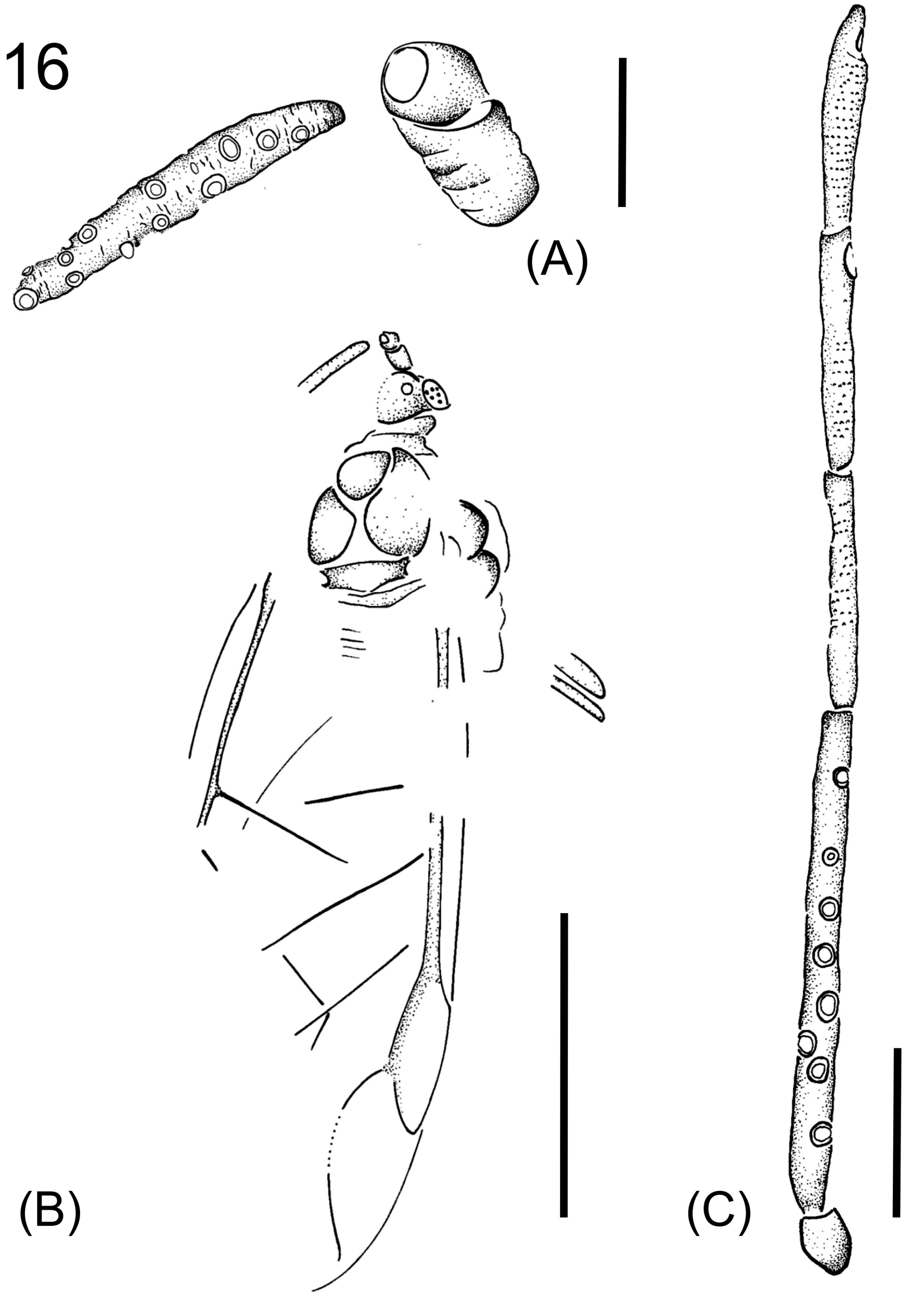


**Figure 16** *Panfossilis anglicus* gen. and sp. nov. (A) Holotype, NHMUK I.9033, part of antenna. Scale bar = 0.1 mm. (B) General view. Scale bar = 0.5 mm. (C) Paratype, NHMUK I. 8661, left antenna. Scale bar = 0.1 mm.

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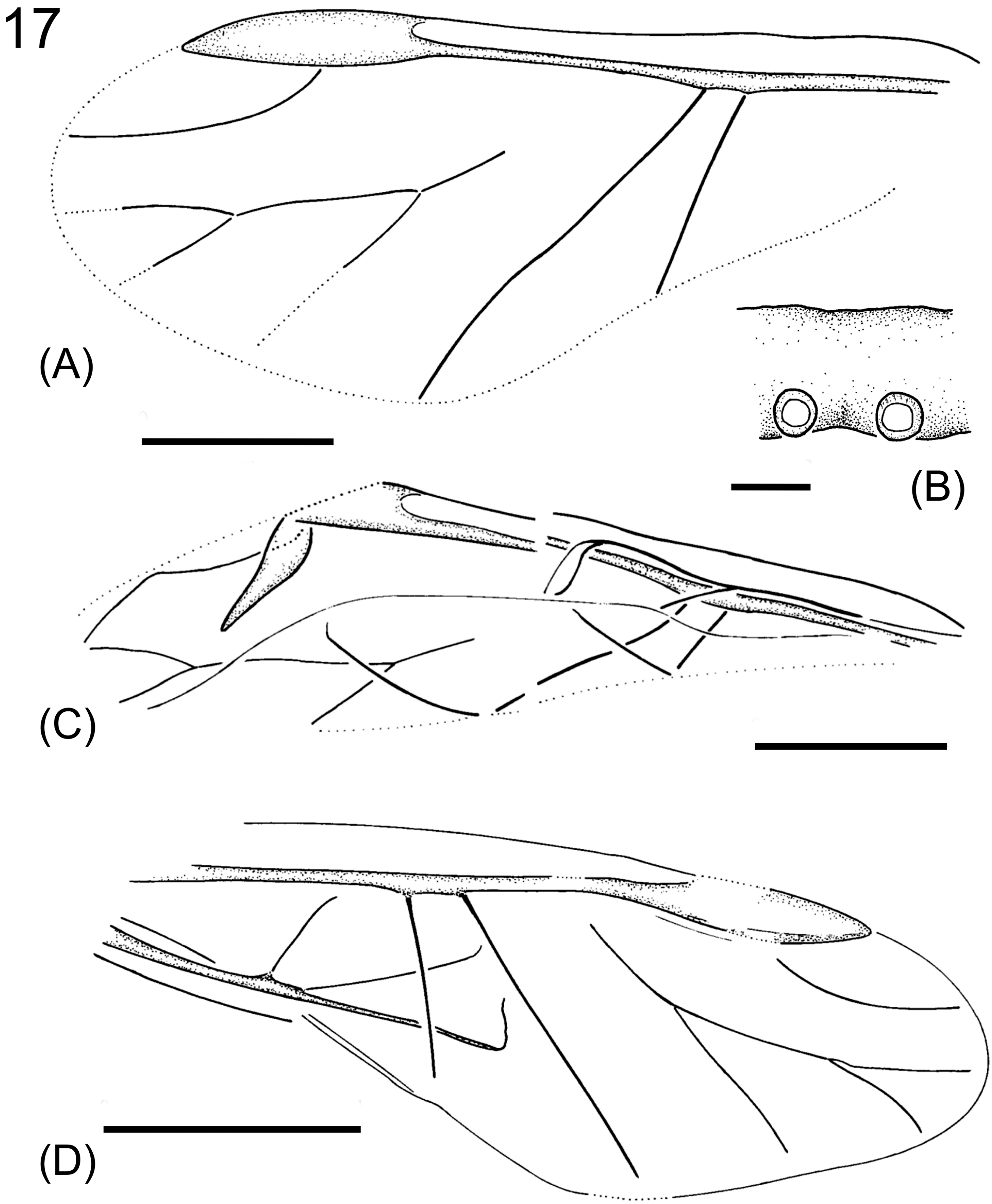


**Figure 17** *Phyllaphis gurnetensis* (Cockerell, 1921b). (A) Holotype NHMUK In. A 24357, forewing. Scale bar = 0.5 mm. (B) Part of antennal segment, NHMUK I.8512. Scale bar = 0.02 mm. (C) Forewing and hindwing, NHMUK I.8512. Scale bar = 0.5 mm. (D) NHMUK I.9098, forewing and hindwing. Scale bar = 1 mm.

III with semiannular rhinaria arranged ventrally in a single row at a distance of at least the width of the segment from each other. Forewings 3.4 mm long and 1.2 mm wide. Pterostigma thin, lance-shaped, pointed, four to five times longer than wide. Vein Rs arcuate, branching off in the middle of the pterostigma, with the base shifted towards its basal portion. Base of vein M in the middle of the distance between the bases of $CuA_1$ and Rs. Vein M with two forks. The common stem of $M_{1+2+3+4}$ short, half the length of $M_{3+4}$. Veins $M_1$ (shorter than half the length of $M_{1+2}$) and $M_2$ (shorter than 1/3 the length of $M_{1+2}$) very short. Veins $CuA_1$ and $CuA_2$ branch off from the common stem independently, their bases at the distance of the width of pterostigma from each other. Hindwings with two transverse veins.

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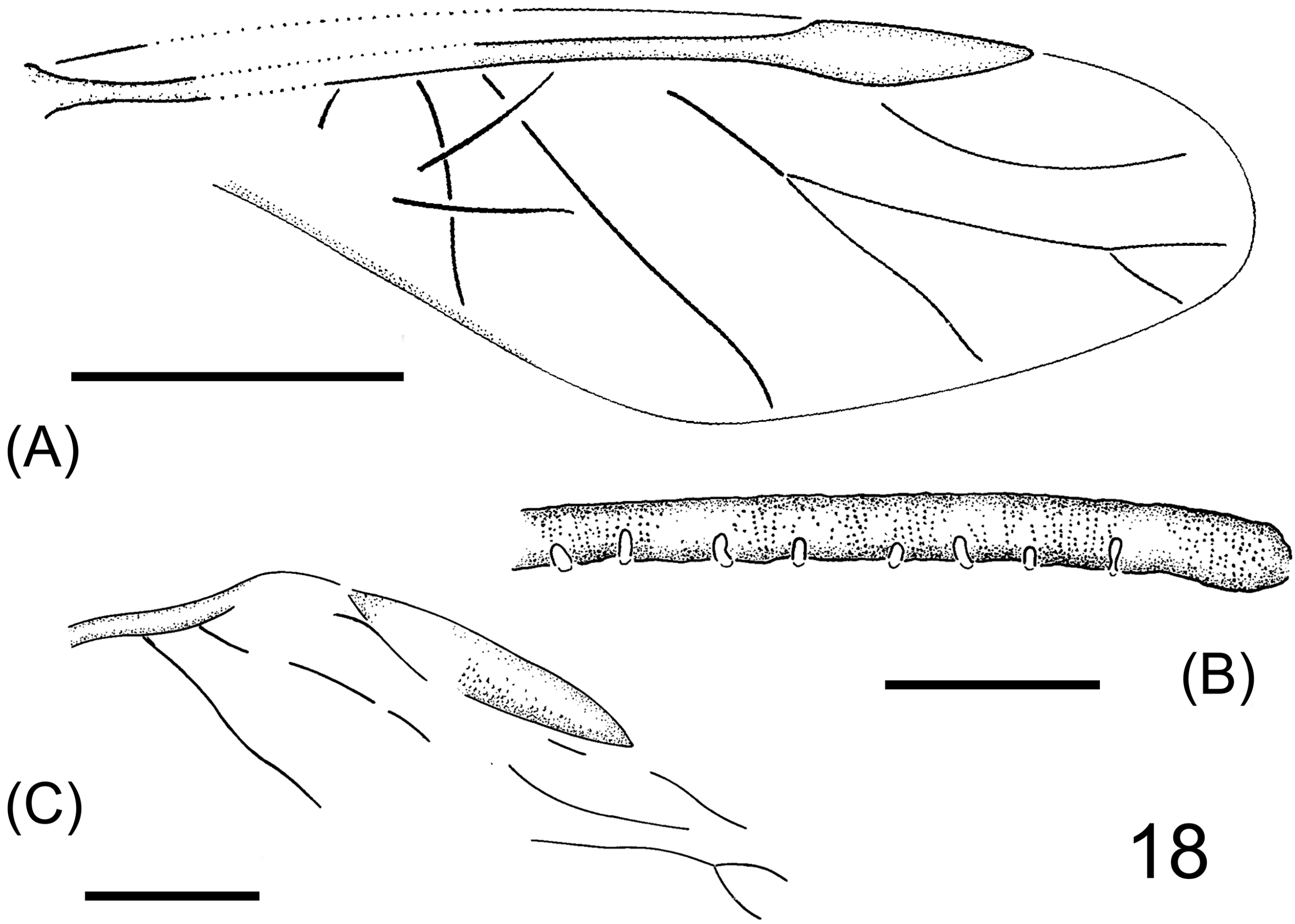


**Figure 18** *Betulaphis kozlovi* Wegierek sp. nov. (A) Forewing and hindwing, paratype, NHMUK In.24499. Scale bar = 1 mm. (B) Part of antennal segment, holotype, NHMUK I.9411. Scale bar = 0.1 mm. (C) Forewing, holotype, NHMUK I.9411. Scale bar = 0.5 mm.

Aphidoidea *incertae sedis*

**Material.** NHMUK I.9304, I.9596, I.9700, I.9943, I.10210, Brodie Collection; In.17198, In.17210 (2, 3) (with paratype of *Aeolothrips jarzembowskii* Shmakov, 2014), In.17214, A'Court Smith Collection; In.24625, Hooley Collection; II.2766a, b, II.2861, II.2862, II.3028 [det. J. Szwedo]. Insect Limestone, NW Isle of Wight.

**Discussion**. Most of the described aphid fauna was probably associated with arborescent angiosperm plants or angiosperm shrubs, mainly of the families Fagaceae, Betulaceae, Ulmaceae, Juglandaceae and Lauraceae. Representatives of the family Eriosomatidae might have migrated onto secondary hosts of Asteraceae (Compositae), Cyperaceae or Poaceae (Graminae). Today a group of species of the family Hormaphididae is also associated with Poaceae (especially Bambuseae) or Palmaceae. It is possible that Elektraphididae, like recent Adelgidae, were associated with Pinaceae.

Planthoppers, froghoppers, singing cicadas, leafhoppers (Hemiptera: Fulgoromorpha & Cicadomorpha)

by *Jacek Szwedo*

The Fulgoromorpha comprises one of the most ancient lineages of the Hemiptera, and in the fossil record planthoppers have been known since the Early Permian (Szwedo *et al*. 2004; Szwedo 2018). The earliest Fulgoromorpha are placed in the Permian superfamily Coleoscytoidea Martynov, 1935; the second group is the Permian–Triassic Surijokocixioidea Shcherbakov, 2000b and the Fulgoroidea have been known since the Jurassic.

Several fossil Fulgoroidea have been reported so far from the latest Eocene Bembridge Marls of the Isle of Wight. The first descriptions were by Cockerell (1921b), who described *Poekilloptera melanospila* Cockerell, 1921b (transferred to Orthoptera, see Nel *et al*. 2008). Later, more species were added under the names *Hastites muiri* Cockerell, 1922, *Hooleya indecisa* Cockerell, 1922 and *Myndus wilmattae* Cockerell, 1926. These taxa are discussed below.

Cicadomorpha is the second suborder formerly placed together with Fulgoromorpha as 'Auchenorrhyncha', but not related directly to planthoppers (Bourgoin & Campbell 2002; Szwedo 2002, 2018; Szwedo *et al.* 2004). Cicadomorpha comprises ancient lineages, some of them extinct (Dysmorphoptiloidea Handlirsch, 1906 (in 1906–8), Hylicelloidea Evans, 1956, Palaeontinoidea Handlirsch, 1906, Pereborioidea Zalessky, 1930, Prosboloidea Handlirsch, 1906 and Prosbolopseoidea Becker-Migdisova, 1946). The placement of the paraphyletic Scytinopteroidea Handlirsch, 1906 – forms ancestral to Coleorrhyncha Myers & China, 1929 and Heteroptera (Shcherbakov & Popov 2002) – remains unresolved, but close to Cicadomorpha (Shcherbakov & Popov 2002; Szwedo *et al.* 2004; Szwedo 2018). Only representatives of the superfamilies Cercopoidea, Cicadoidea and Cicadelloidea (together with the extinct Hylicelloidea Evans, 1956, extant Myerslopioidea Evans, 1957 and Membracoidea Rafinesque, 1815 forming the clade Clypeata Qadri, 1967) are reported here. Only a single

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representative of Cicadomorpha from the Bembridge Marls has been reported so far, named *Aphrophora woodwardi* Cockerell, 1922.

The venation interpretations of Fulgoromorpha follow Szwedo & Żyła (2009) and Bourgoin *et al*. (2015), and for Cicadomorpha follow interpretations of Emeljanov (1987), Wang *et al*. (2009) and Nel *et al*. (2013).

Suborder Fulgoromorpha Evans, 1946

Superfamily Fulgoroidea Latreille, 1807

Family Cixiidae Spinola, 1839

Subfamily Bothriocerinae Muir, 1923

Genus *Klugga* Szwedo gen. nov.

**Etymology.** Name is derived from Proto-Celtic word 'klugga' meaning 'stone'. Gender: feminine.

**Type species.** *Klugga gnawa* sp. nov., here designated.

**Diagnosis.** Tegmen with venation similar to *Bothriobaltia* Szwedo, 2002, but differs in having a larger stigma (stigma elongate and narrow in *Bothriobaltia*); wider basal cell (basal cell narrow and elongate in *Bothriobaltia*); shorter common stem ScP + R (common stem longer, reaching level of claval veins junction in *Bothriobaltia*); branching of vein ScP + $RA_1$ slightly basad of forking of vein CuA (forking of ScP + $RA_1$ slightly apicad of CuA forking in *Bothriobaltia*).

**Description.** Tegmen with costal margin slightly curved at base, striations on costal and apical margins distinct. Stigma distinct, about twice as long as wide, with corrugated texture. Basal cell about twice as long as wide. Stems of veins ScP + R, MP and CuA leaving basal cell independently; stem ScP + R leaving basal cell slightly basad of stem M; branch ScP + RA branched slightly basad of forking of stem CuA, terminal ScP + $RA_1$ distinctly curved anteriad, widened in apical portion; vein RP forked at same level as forking of anterior branch of vein MP, with three terminals; stem M forked at level of nodal line, anterior branch forked again at level of RP branching, and again at level of posterior branch of vein MP forking, vein MP with five terminals; stem CuA forked slightly posteriad of ScP + RA branching, posteriad of claval veins junction. Nodal line distinct, veinlet rp-mp oblique, veinlet mp-cua more or less oblique. Clavus short with apex reaching nearly half of tegmen length; claval veins Pcu and $A_1$ fused at about half of clavus length.

*Klugga gnawa* Szwedo sp. nov.
(Pl. 5: 1; Fig. 19)

**Etymology.** Specific epithet is derived from Proto-Celtic word 'gnawo' meaning 'clear'.

**Holotype.** NHMUK In.24513; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen with missing clavus and coloration partly preserved.

**Diagnosis.** Nodal veinlet m-cu not distinctly oblique; apical line of veinlets indistinct; cell C5 about as long as stigma; median portion of tegmen with darker, transverse, wide band.

**Description.** Length of tegmen 4.05 mm, width at widest point 2.05 mm. Basal and apical portion not coloured, median ⅓ of tegmen with darker transverse, wide band, with lighter portion mediad of stigma to anterior branch of vein M. Veins slightly darker.

*Klugga regoa* Szwedo sp. nov.
(Pl. 5: 2–3; Fig. 20)

**Etymology.** Specific epithet is derived from Proto-Celtic word 'rego' meaning 'band'.

**Holotype.** NHMUK In.24512; Hooley Collection, Insect Limestone, NW Isle of Wight. Impression of median portion of tegmen.

**Diagnosis.** Nodal veinlet m-cu distinctly oblique; apical line of veinlets distinct; apical veinlet m-cu oblique; cell C5 slightly longer than stigma; tegmen with slightly darker, narrow band at level of nodal line, passing to apex of clavus, darker band at level of apical veinlets.

**Description.** Length of preserved portion of tegmen 2.75 mm, width at widest point 1.9 mm. Tegmen with veins slightly darkened, two slightly darker transverse bands, first at level of nodal line and second at level of apical line of veinlets.

Genus *Liwakka* Szwedo gen. nov.

**Etymology.** Name is derived from Proto-Celtic word 'liwakk' meaning 'stone'. Gender: feminine.

**Type species.** *Liwakka gelloa* sp. nov.; here designated.

**Diagnosis.** Venation similar to *Klugga* gen. nov., but differs in branching of vein ScP + RA slightly posteriad of vein CuA forking (branching of vein ScP + RA slightly anteriad of CuA forking in *Klugga*); claval veins Pcu and $A_1$ fused at level of CuA forking (claval veins fused basad of CuA forking in *Klugga*); differs from *Bothriobaltia* Szwedo, 2002 by shorter stem ScP + R (stem ScP + R longer in *Bothriobaltia*); bigger stigma (stigma narrow and elongate in *Bothriobaltia*).

**Description.** Costal margin slightly curved at base, costal and apical margin with distinct striations. Stigma about twice as long as wide, with corrugated texture. Basal cell twice as long as wide. Stems of veins ScP + R, MP and CuA leaving basal cell independently; stem ScP + R leaving basal cell slightly basad of stem MP; branch ScP + $RA_1$ branched slightly apicad of forking of stem CuA, distinctly curved anteriad; vein RP forked at same level as forking of anterior branch of vein MP, with three terminals; stem MP forked at level of nodal line, anterior branch forked again at level of RP branching, and again at level of posterior branch of vein MP forking, vein MP with five terminals; stem CuA forked slightly basad of ScP + $RA_1$ branching, at level of claval veins junction. Nodal line distinct, veinlet rp-mp oblique, veinlet mp-cua short, straight, parallel to veinlet icu. Clavus short with apex reaching half of tegmen length; claval veins Pcu and $A_1$ fused apicad of half of clavus length.

*Liwakka gelloa* Szwedo sp. nov.
(Pl. 5: 4–7; Figs 21, 22)

**Etymology.** Specific epithet is derived from the Proto-Celtic word 'gello' meaning 'yellow, brown'; it refers to the coloration of the specimen.

**Holotype.** NHMUK In.26034 (Pl. 5: 4; Fig. 21); Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen, with part of clavus missing.

**Paratype.** NHMUK In.24547 (Plate 5: 5–7; Fig. 22); Hooley Collection. Tegmen with basal and claval portion not preserved.

**Diagnosis.** Nodal line very distinct, veinlets mp-cua and both veinlets icu straight, subparallel. Wide, transverse, brown band at level of nodal line, second wide, transverse, brown band in subapical portion of tegmen; clavus pigmented; veins darkened, brown.

**Description.** Length of tegmen 3.75 mm, width at widest point 1.9 mm. Wide, transverse, brown band at nodal line

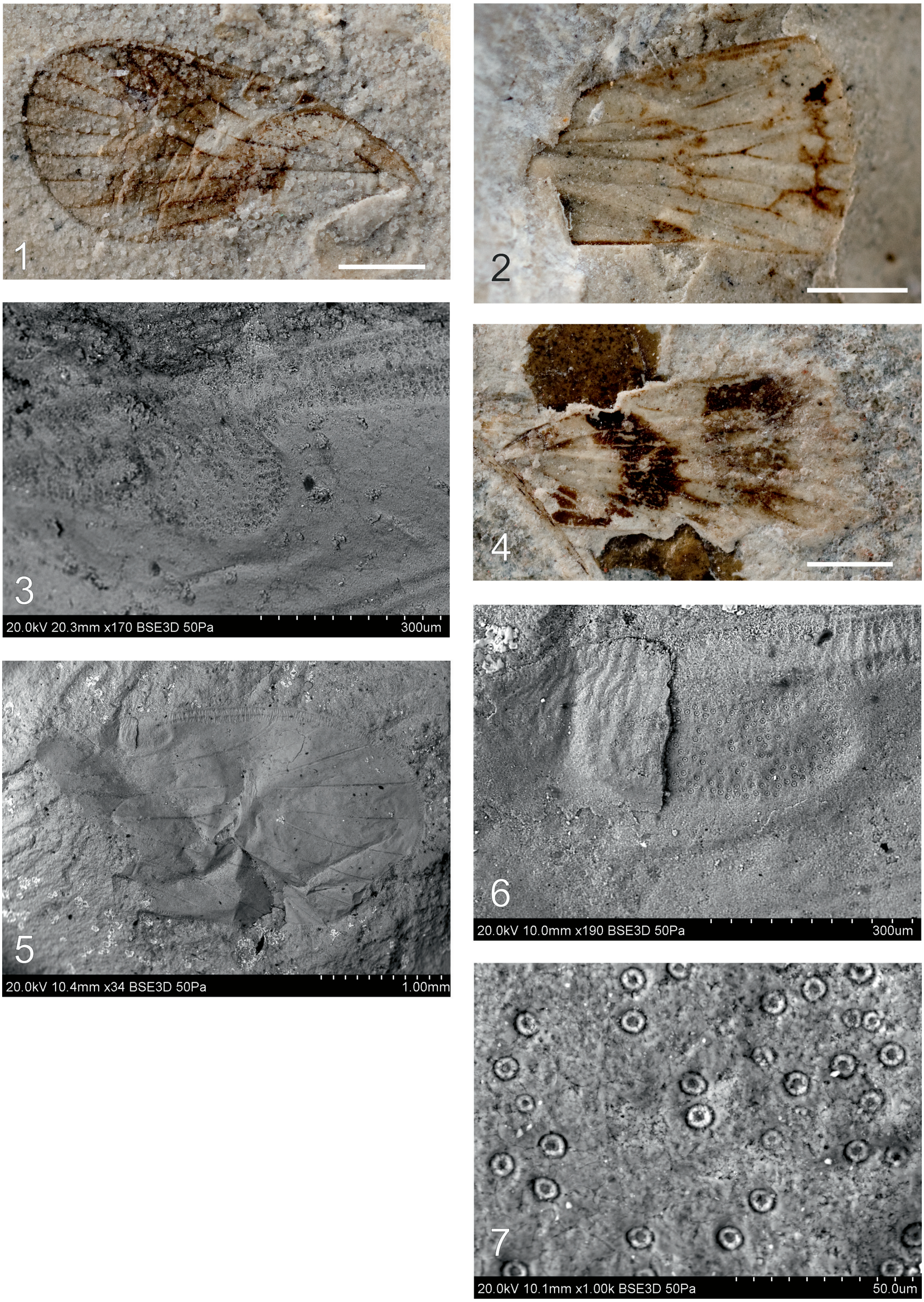


**Plate 5** (1) *Klugga gnawa* Szwedo gen. et sp. nov., holotype, NHMUK In.24513, tegmen. (2–3) *Klugga regoa* Szwedo gen. et sp. nov., holotype, NHMUK In.24512: (2) tegmen; (3) SEM photo of stigma area. (4–7) *Liwakka gelloa* Szwedo gen. et sp. nov.: (4) holotype, NHMUK In.26034, tegmen; (5) SEM photo of the paratype NHMUK In.25457, tegmen; (6) SEM photo of stigmal area; (7) SEM photo of stigmal area sensory pores. Scale bars = 1 mm for 1, 2 and 4.

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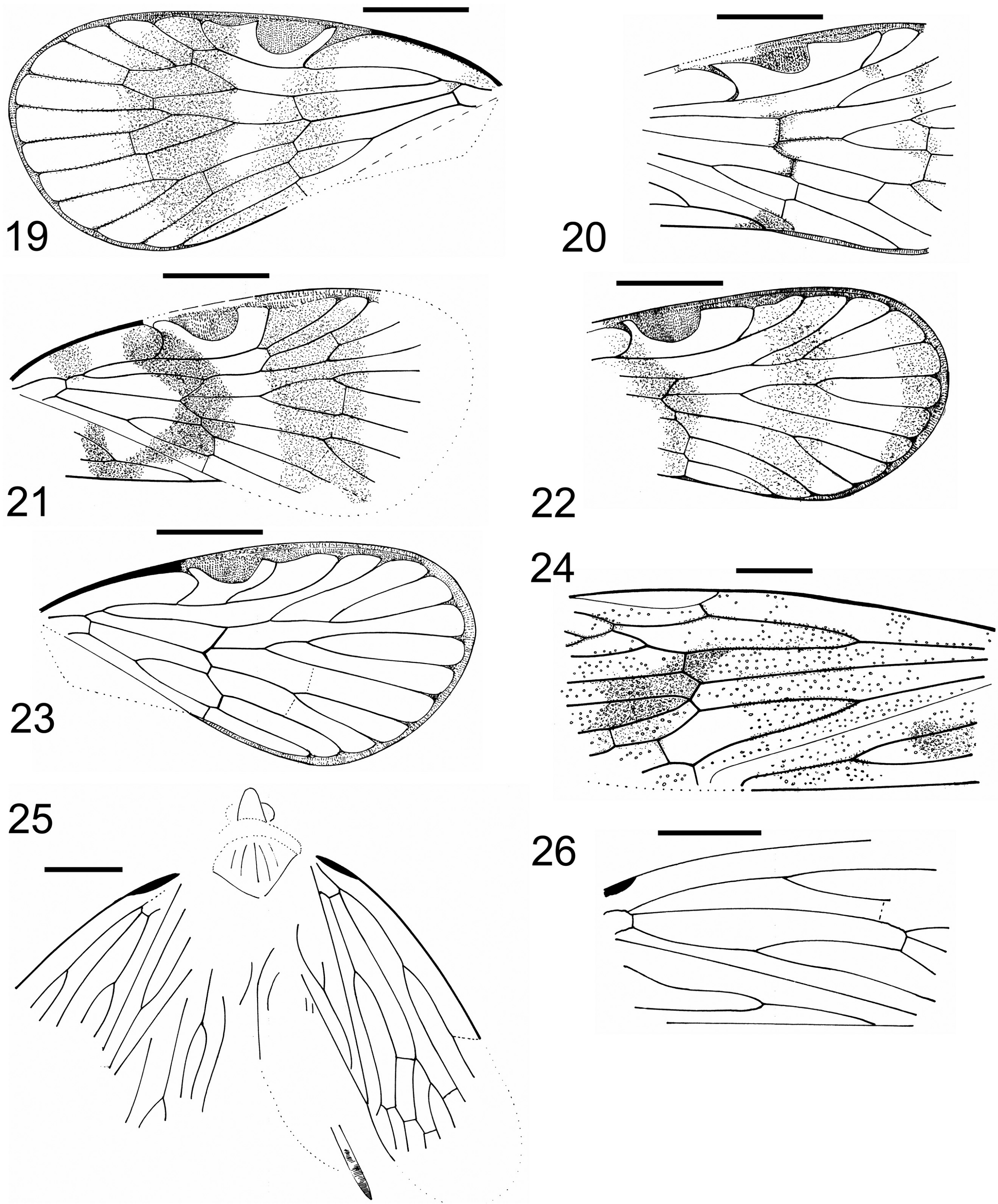


**Figures 19–26** (19–24) Tegmen: (19) *Klugga gnawa*, Szwedo gen. et sp. nov., holotype, NHMUK In.24513; (20) *Klugga regoa* Szwedo gen. et sp. nov., holotype NHMUK In.24512; (21) *Liwakka gelloa* Szwedo, gen et sp. nov., holotype NHMUK In.26034; (22) *Liwakka gelloa* Szwedo, gen et sp. nov., paratype NHMUK In.25457; (23) *Delwa morikwa* Szwedo gen. et sp. nov., holotype NHMUK I.8657; (24) *Kommanosyne wrikkua* Szwedo gen. et sp. nov., holotype NHMUK In.24521. (25) *Kernastirdius nephlajeus* Szwedo gen. et sp. nov., holotype NHMUK I.9023, anterior part of body, parts of tegmina and hindwing. (26) *Kernastirdius*? sp., NHMUK In.25480, tegmen. Scale bar = 1 mm.

arcuate apicad, wide, transverse, brown band in subapical portion not arcuate; clavus brown.

### Genus *Delwa* Szwedo gen. nov.

**Etymology.** Name from the Proto-Celtic word 'delwa' meaning 'form'. Gender: feminine.

**Type species.** *Delwa morikwa* sp. nov.; here designated.

**Diagnosis.** Similar to *Liwakka* gen. nov., but differs by more basad forking of anterior branch of MP; longer common stem of veins ScP + R, longer than arculus (in *Liwakka* and *Klugga* common stem ScP + R about as long as arculus).

**Description.** Costal margin merely curved, costal and apical margins with distinct striations. Stigma distinct, about twice as wide as long. Basal cell about 2.5 times as long as wide. Stems of veins ScP + R, MP and CuA leaving basal call independently; stem ScP + R leaving basal cell slightly basad of stem MP; common stem of vein ScP + R about three times as long as arculus; branch ScP + $RA_1$ branched slightly apicad of forking of stem CuA, distinctly curved anteriad; vein RP forked about at same level as forking of anterior branch of vein MP, with three terminals; stem MP forked at level of nodal line, anterior branch forked again at level of first RP branching, and again apicad of posterior branch of vein MP forking, vein MP with five terminals; stem CuA forked slightly basad of ScP + $RA_1$ branching. Nodal line distinct, veinlet rp-mp oblique, veinlet mp-cua straight, parallel to veinlet icu. Clavus short, with apex reaching half of tegmen length.

### *Delwa morikwa* Szwedo sp. nov.
(Pl. 6: 1–2; Fig. 23)

**Etymology.** Specific epithet is derived from Proto-Celtic word 'morikwa' meaning 'sea-shore'.

**Holotype.** NHMUK I.8657; Brodie Collection, Insect Limestone, NW Isle of Wight. Tegmen, with clavus missing.

**Diagnosis.** Tegmen twice as long as wide at widest point; cell C5 two times as long as stigma; nodal line distinct; stem MP thickened, branch $MP_{3+4}$ at nodal line thickened; apex of clavus reaching half of tegmen length.

**Description.** Length of tegmen 3.8 mm, width at widest point 1.9 mm. Other features as for the genus as it is the only included species.

**Remark.** Bothriocerinae is a group in need of revisionary studies. Recent species are unevenly distributed in the genera *Bothrioceretta* Caldwell, 1950 with four species and *Bothriocera* Burmeister, 1835 with 45 species present from south of the USA to Brazil and Bolivia, and the only known so far extinct genus *Bothriobaltia* Szwedo, 2001 with single species from Baltic amber (Bourgoin 2017).

## Subfamily Cixiinae Spinola, 1839

## Tribe Mnemosynini Emeljanov, 1992

### Genus *Kommanosyne* Szwedo gen. nov.

**Etymology.** Genus name is derived from Proto-Celtic word 'kommano' meaning 'memory', combined with generic name of cixiid planthopper *Mnemosyne* Stål, 1866. Gender: feminine.

**Type species.** *Kommanosyne wrikkua* sp. nov.; here designated.

**Diagnosis.** Tegmen venation similar to other genera of Mnemosynini, e.g., *Stalisyne* Szwedo *et al.*, 2006, *Mnaomaia* Szwedo *et al.*, 2006 and *Autrimpus* Szwedo, 2004. Differs from them by forking of common stem ScP + R at same level as stem CuA forking (stem ScP + R forked distinctly more basad in *Stalisyne*, *Mnaomaia* and *Autrimpus*); stigma very long, about eight times as long as wide (stigma shorter in *Stalisyne*, *Mnaomaia* and *Autrimpus*); cell C5 widened in apical portion (cell C5 not widened in apical portion in *Stalisyne*, *Mnaomaia* and *Autrimpus*).

**Description.** Tegmen with common stems of veins ScP + R and CuA forked at same level, at level of claval veins Pcu and $A_1$ junction. Stigma narrow and elongate, about eight times as long as wide. Cell C1 elongate, longer than cell C5, tapered in apical portion. Vein RA with single terminal; vein RP forked at level of half of length of stigma, anterior branch of RP forked again near apical end of stigma; anterior branch of vein MP, i.e., $MP_{1+2}$, not forked before apical end of stigma, posterior branch forked immediately after first MP forking at level of nodal line, i.e., veins $MP_3$ and $MP_4$ separated since the nodal line; stem CuA forked at level of claval veins junction; anterior margin shifted mediad, to the level of nodal line, then posteriad, posterior branch parallel to CuP; clavus long, distinctly exceeding half of tegmen length; claval veins Pcu and $A_1$ fused at level of stems ScP + R and CuA forkings. Veinlet ir between branches RA and RP very short; nodal veinlet rp-mp straight, perpendicular to branch $MP_{1+2}$; nodal veinlet mp-cua oblique, about as long as common stem $MP_{3+4}$; veinlet icu closing cell C5 merely oblique, at level of half of stigma length. Tegmen partly covered with setiferous tubercles.

### *Kommanosyne wrikkua* Szwedo sp. nov.
(Pl. 6: 3; Fig. 24)

**Etymology.** Specific epithet is derived from Proto-Celtic word 'wrikku' meaning 'bristle' and is referring to the presence of the setiferous tubercles on the tegmen.

**Holotype.** NHMUK In.24521; Hooley Collection, Insect Limestone, NW Isle of Wight. Part of tegmen, with basal and apical portions not preserved.

**Diagnosis.** Basal portion of cell C1, radial cell, medial cell, base of cell C5, cubital cell, claval cells with numerous setiferous tubercles; few setiferous tubercles in cell C2, C3a, C3b and C4; veins darkened, indistinct colour pattern: darker markings in basal portion of clavus, at level of nodal line, on cells C3a and C3b.

**Description.** Length of preserved part of tegmen 6.1 mm (estimated length of tegmen about 9 mm), width at widest point 2.74 mm. Other features as for the genus as it is the only included species.

## Tribe Pentastirini Emeljanov, 1971

### Genus *Kernastiridius* Szwedo gen. nov.

**Etymology.** Generic name is combination of the Proto-Celtic word 'kerna' meaning 'head', and *Pentastiridius* – generic name of pentastirine planthopper. Gender: masculine.

**Type species.** *Kernastiridius nephlajeus* sp. nov.; here designated.

**Diagnosis.** Tegmen venation similar to *Pentastiridius* Kirschbaum, 1868, but differs in more basal forking of stems ScP + R and CuA, at level of claval veins Pcu and $A_1$ junction (stems ScP + R and CuA forked apicad of claval veins junction in *Pentastiridius*); stem MP forked immediately apicad of nodal veinlet mp-cua (short stalk present before forking in *Pentastiridius*); first veinlet rp-mp apicad of nodal line, at level of claval apex (veinlet rp-mp basad of claval apex, basad of nodal veinlet mp-cua in *Pentastiridius*).

**Description.** Vertex slightly wider at base than long in mid line, anterior margin arcuately acute; head with compound

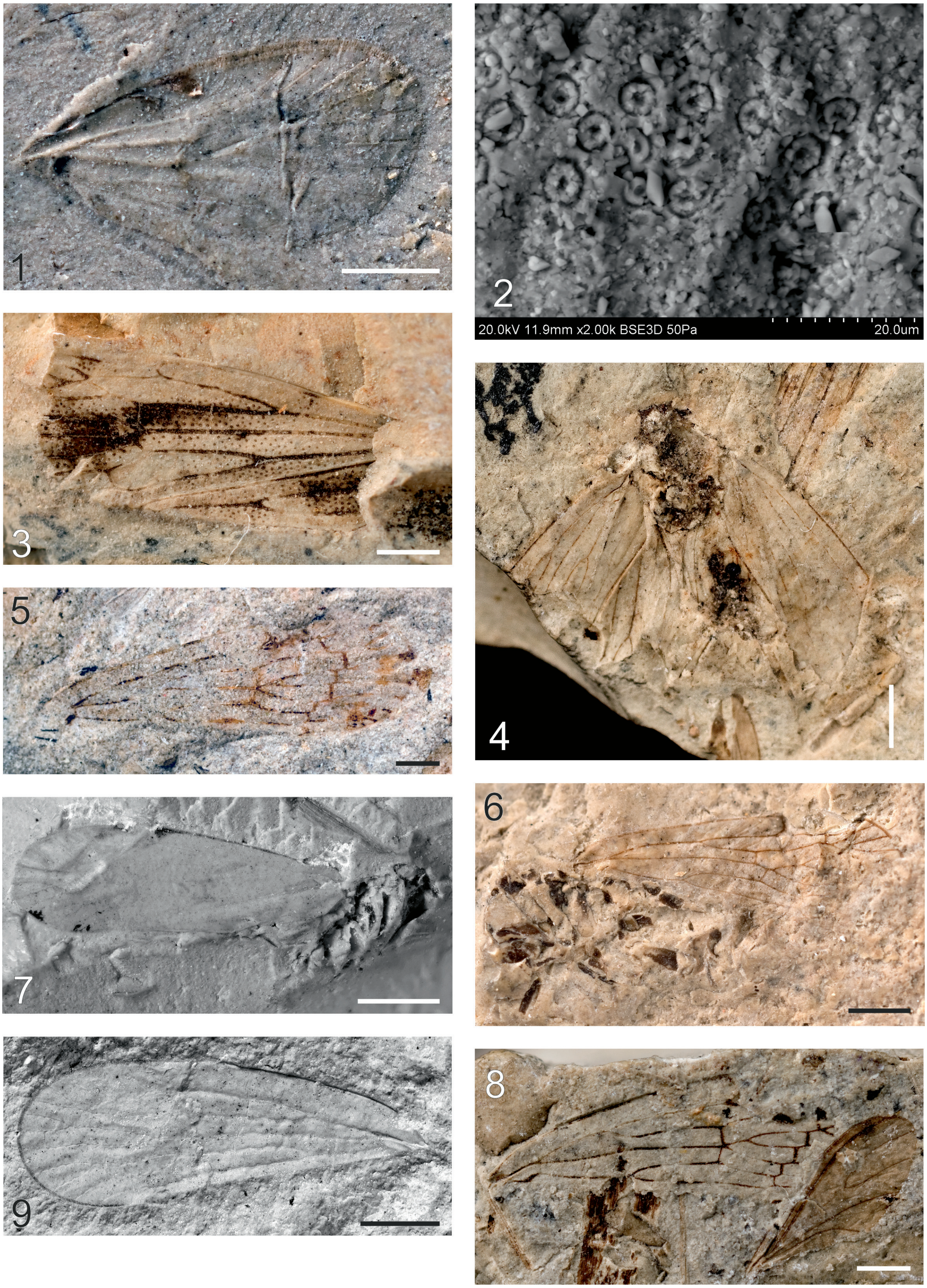


**Plate 6** (1–2) *Delwa morikwa* Szwedo gen. et sp. nov., holotype, NHMUK I.8657: (1) tegmen; (2) SEM photo of stigmal area sensory pores. (3) *Kommanosyne wrikkua* Szwedo gen. et sp. nov., holotype, NHMUK In.24521, tegmen. (4) *Kernastiridius nephlajeus* Szwedo sp. nov., holotype, NHMUK I.9023, anterior part of body, parts of tegmina and wings. (5) *Margaxius angosus* Szwedo sp. nov., holotype, NHMUK In.24620, tegmen with clavus missing. (6) *Dweivera reikea* Szwedo gen. et sp. nov., holotype, NHMUK I.10375, tegmen, counterpart. (7) *Samaliverus bikkanus* Szwedo gen. et sp. nov., holotype, NHMUK I.9199(2), tegmen. (8) *Langsmaniko marous* Szwedo gen. et sp. nov., holotype, NHMUK In. 25286(1), tegmen. (9) *Komsitija tuberculata* Szwedo gen. et sp. nov., holotype, NHMUK Pl II 2999, tegmen.

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eyes narrower than pronotum. Rostrum very long, exceeding length of body. Mesonotum about as long in mid line as wide, with five distinct carinae. Tegmen about 2.9 times as long as wide; costal margin more curved at base, then mildly curved, with slightly widened basicostal area; basal cell about three times as long as wide. Stems of veins ScP + R, MP and CuA leaving basal cell independently, stem ScP + R slightly anteriad of stem MP, but close to it; stem ScP + R forked slightly posteriad of CuA forking, posteriad of claval veins junction; stem MP forked basad of claval apex, merely apicad of nodal veinlet m-cu, anterior branch, i.e., branch $MP_{1+2}$ forked at level of claval apex; posterior branch, i.e., branch $MP_{3+4}$ forked apicad of claval apex; cell C5 more than twice as long as cell C4. Clavus long, with apex reaching 2/3 of length of tegmen, claval veins Pcu and $A_1$ fused at level of stem CuA forking, at half of clavus length.

### *Kernastiridius nephlajeus* Szwedo sp. nov.
(Pl. 6: 4; Figs 25)

**Etymology.** Specific epithet derived from the Proto-Celtic words 'ne' meaning 'not' and 'phlaje' meaning 'fold'.

**Material.** Holotype NHMUK I.9023; Brodie Collection, Insect Limestone, NW Isle of Wight. Compression of anterior part of body, parts of tegmina and wings.

**Diagnosis.** Tegmen with cell C5 widest at level of nodal veinlet mp-cua, then narrowing apicad; cell C4 about half of length of cell C5, subequal in length with cell C3b.

**Description.** Total length 5.9 mm, length of pronotum in mid-line *ca.*1 mm, length of preserved part of right tegmen 4.1 mm, estimated total length of tegmen *ca.*5 mm, width at widest point 1.7 mm. Other features as for the genus as it is the only included species.

**Remark**. Another specimen (Fig. 26) NHMUK In.25441/In.25480 (part and counterpart), Hooley Collection could belong to the genus *Kernastiridius* Szwedo. It is the median portion of a tegmen.

### Pentastirini gen. et sp. indet.
(Fig. 27)

**Material.** NHMUK I.10344; Brodie Collection, Insect Limestone, NW Isle of Wight. Mesonotum, parts of the body, portion of tegmen and (probably) part of hindwing.

**Description.** Length of mesonotum 1.2 mm. Length of tegmen 5.7 mm. Mesonotum with five distinct longitudinal carinae. Tegmen with base slightly curved at base, then only mildly curved, stigma elongate, about 3.6 times as long as broad. Stem ScP + R forked anteriad of stem CuA forking, branch RA with two terminals. Stem MP not forked before nodal veinlet rp-mp.

**Remark.** The specimen is not complete enough for the formal description of a new taxon. It differs in size and venation from *Kernastiridius* Szwedo, but could be placed in tribe Pentastirini.

## Tribe Cixiini Spinola, 1839

### Genus *Margaxius* Szwedo gen. nov.

**Etymology.** Genus name is combination of the Proto-Celtic word 'marga' meaning 'marl' and *Cixius* – generic name of cixiine planthopper. Gender: masculine.

**Type species.** *Margaxius angosus* sp. nov.; here designated.

**Diagnosis.** Tegmen venation resembles *Cixius* Latreille, 1804, but differs in barely curved basal portion of costal margin (more curved in *Cixius*); early branching of stems ScP + R and CuA, at about basal 1/4 of tegmen length (stems ScP + R and CuA forked at about 1/3 of tegmen length in *Cixius*); presence of veinlet rp-mp distinctly basad of nodal line (lack of basal veinlet rp-mp in *Cixius*).

**Description.** Tegmen narrow, elongate, three times as long as wide. Costal margin mildly curved since base, apical margin elongately rounded. Basal cell about twice as long as wide. Stems ScP + R, MP and CuA leaving basal cell independently, stem ScP + R slightly anteriad, but very close to stem MP. Stem ScP + R forked slightly apicad of CuA forking, at about basal 1/4 of tegmen length; branch ScP + RA forked slightly apicad of nodal veinlet rp-mp; RA with two terminals, RP forked slightly basad of veinlet rp-mp of apical line, with three terminals; stem MP forked merely basad of veinlets rp-mp and mp-cua of nodal line, anterior branch, i.e., branch $MP_{1+2}$ forked slightly apicad of nodal line, then forked apicad of veinlets of apical line, upper branch, i.e., branch $MP_{3+4}$ forked slightly basad of imp veinlet of apical line. Stem CuA forked slightly apicac of stem ScP + R forking, slightly basad of basal rp-mp veinlet. Clavus long, with apex reaching 2/3 of tegmen length. Apical line of veinlets rp-mp, imp, mp-cua and icu stepwise.

**Remark.** This genus is tentatively placed in the tribe Cixiini.

### *Margaxius angosus* Szwedo sp. nov.
(Pl. 6: 5; Fig. 28)

**Etymology.** Specific epithet derived from the Proto-Celtic word 'angos' meaning 'narrowness', referring to shape of the tegmen.

**Holotype.** NHMUK In.24620; Hooley Collection Insect Limestone, NW Isle of Wight. Tegmen with clavus missing.

**Diagnosis.** Apical line of veinlets stepwise; cell C1 longer than cell C5; cells C3a and C3b similar in length; apical cells elongate subequal in length to subapical ones; nodal veinlets r-m and m-cu and apical veinlets darkened.

**Description.** Length of tegmen 8.8 mm, width at widest point 2.9 mm. Other features as for the genus as it is the only included species.

**Remark.** Probably also specimen NHMUK In.17369, Smith Collection could be referred to the genus *Margaxius*.

### Genus *Dweivera* Szwedo gen. nov.

**Etymology.** Name derived from Proto-Celtic word 'dwei' meaning 'two' (feminine form) and generic name of cixiid planthopper – *Kuvera*. Gender: feminine.

**Type species.** *Dweivera reikea* sp. nov.; here designated.

**Diagnosis.** Tegmen venation similar to *Kuvera* Distant, 1906, but differs in short, but distinct common stem of veins ScP + R and MP leaving basal cell (stems ScP + R and MP leaving basal cell separately or with very short stem in *Kuvera*); nodal veinlet mp-cua slightly basad of stem MP forking (veinlet mp-cua distad of stem MP forking in *Kuvera*); cell C3a elongate (cell C3a short in *Kuvera*).

**Description.** Tegmen with costal margin distinctly curved at base, then mildly convex, apical margin elongately rounded. Basal cell about twice as long as wide. Stems ScP + R and MP leaving basal cell with a short common stem. Stem ScP + R forked slightly apicad of CuA forking, basad of half of tegmen length; branch ScP + RA forked apicad of nodal veinlets rp-mp and mp-cua; RA with single terminal, RP forked slightly apicad of apical line of veinlets, with three terminals. Stem MP forked distinctly apicad of nodal veinlet rp-mp and merely apicad of nodal veinlet mp-cua; branch $MP_{1+2}$ forked basad of branch $MP_{3+4}$ forking; branch $MP_{3+4}$

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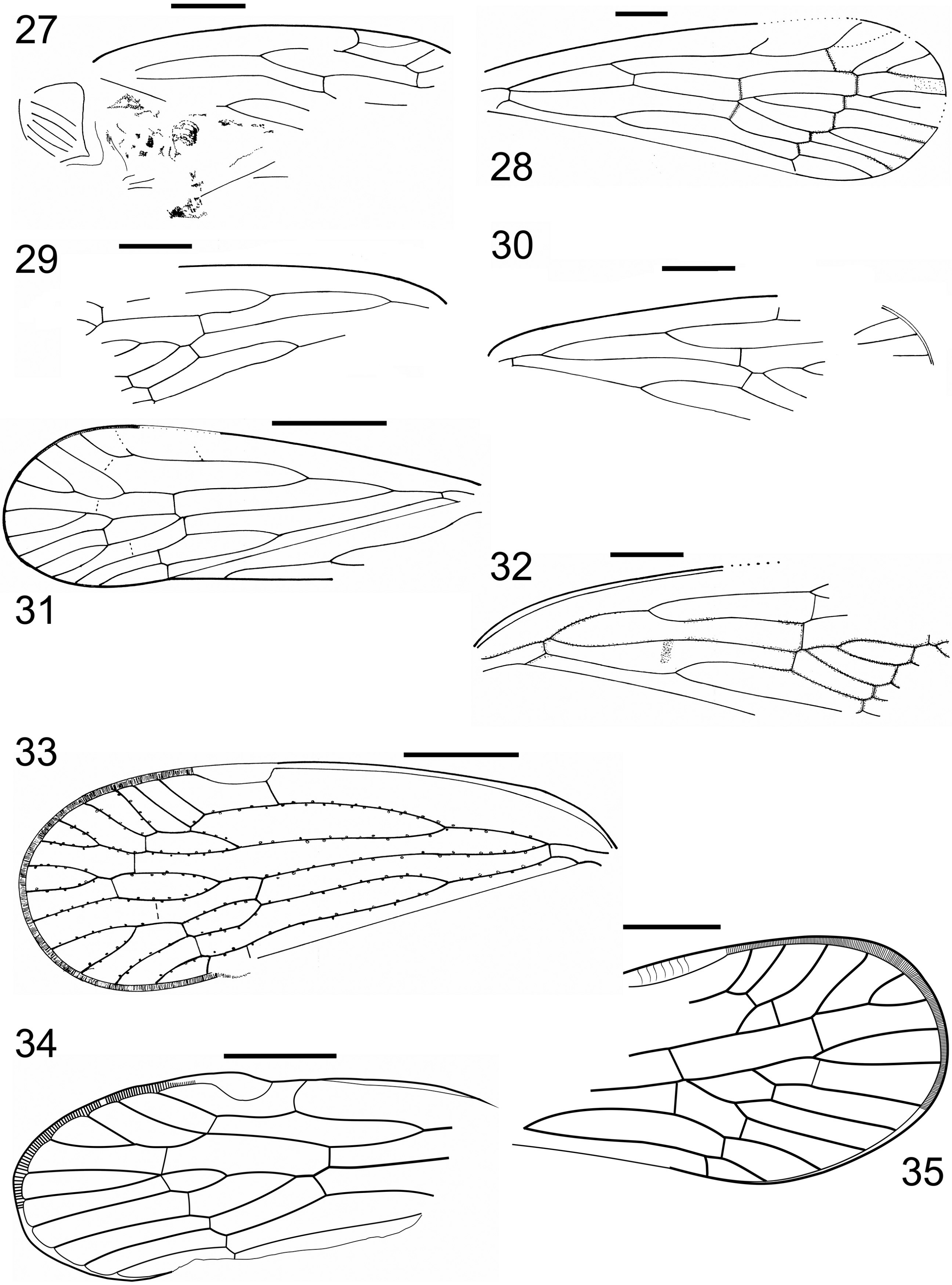


**Figures 27–35** (27) Cixiidae: Penatastirini, NHMUK I.10344, parts of the body, portion of tegmen and (probably) part of hindwing. (28) *Margaxius angosus* Szwedo gen. et sp. nov., holotype, NHMUK In.24620, tegmen. (29) *Dweivera reikea* Szwedo gen. et sp. nov., holotype, NHMUK I.9193, part. (30) *Dweivera reikea* Szwedo gen. et sp. nov., holotype NHMUK I.10375, counterpart. (31) *Samaliverus bikkanus* Szwedo gen. et sp. nov., holotype, NHMUK I.9199(2), tegmen. (32) *Langsmaniko marous* Szwedo gen. et sp. nov., holotype, NHMUK In. 25286(1), tegmen. (33) *Komsitija tuberculata* Szwedo gen. et sp. nov., holotype, NHMUK Pl II 2999, tegmen. (34) *Komnixta jarzembowskii* Szwedo sp. nov., holotype, MNEMG IL 87a, tegmen, part. (35) *Worodbera nimakka* Szwedo sp. nov., holotype, NHMUK In.43470, tegmen. Scale bar = 1 mm.

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forked apicad of apical line of veinlets. Stem CuA forked at about basal 1/3 of tegmen length, slightly basad of stem ScP + R forking. Veins with small tubercles. Clavus long, with apex reaching 2/3 of tegmen length.

**Remark.** This genus is tentatively placed in the tribe Cixiini.

*Dweivera reikea* Szwedo sp. nov.
(Pl. 6: 6; Figs 29, 30)

**Etymology.** Specific epithet is derived from Proto-Celtic word 'reike' meaning 'tear'.

**Holotype.** NHMUK I.9193/I.10375; Brodie Collection (part and counterpart), Insect Limestone, NW Isle of Wight. Tegmen with claval and apical portion not preserved (part); body and tegmen with claval and apical portion of tegmina not preserved (counterpart).

**Diagnosis.** Costal cell about as wide as cell C1; cell C4 subquadrate, cell C5 more than twice as long as cell C4; veinlet icu basad of veinlet mp-cua, close to veinlet icu connecting posterior branch of CuA with tegmen posterior margin; apex of clavus reaching 2/3 of tegmen length.

**Description.** Length of tegmen 5.5 mm, width at widest point 1.9 mm. Other features as for the genus as it is the only included species.

Genus *Samaliverus* Szwedo gen. nov.

**Etymology.** Generic name derived from the Proto-Celtic word 'samali' meaning 'similar', combined with masculine form of the generic name of cixiid planthopper *Dweivera*. Gender: masculine.

**Type species.** *Samaliverus bikkanus* sp. nov.; here designated.

**Diagnosis.** Tegmen shape and venation similar to *Dweivera* gen. nov., but differs in smaller size; stem ScP + R forked basad of stem CuA forking (stem ScP + R forked slightly apicad of stem CuA forking in *Dweivera*); nodal veinlet rp-mp slightly apicad of stem MP forking (nodal veinlet rp-mp distinctly basad of stem MP forking in *Dweivera*); nodal veinlet mp-cua merely apicad of stem MP forking (nodal veinlet mp-cua basad of stem MP forking in *Dweivera*).

**Description.** Costal margin barely curved, apical margin elongately rounded. Stigma about three times as long as wide. Basal cell narrow. Stem ScP + R and MP leaving basal cell with common stem; stem ScP + R+MP forked distinctly basad of claval veins junction. Stem ScP + R forked slightly apicad of claval veins junction, vein ScP + $RA_1$ forked at level of fusion of claval veins Pcu + $A_1$ with posterior margin, vein RA with two terminals, vein RP forked distinctly apicad of nodal line, with three terminals. Vein MP with branch $MP_{1+2}$ forked basad of apical line, branch $MP_{3+4}$ slightly apicad of apical line; vein MP with five terminals. Stem CuA forked apicad of stem ScP + R forking and apicad of claval veins junction. Clavus with apex at 2/3 of tegmen length, claval veins Pcu and $A_1$ fused at half of clavus length.

**Remark.** This genus is only tentatively placed in the tribe Cixiini.

*Samaliverus bikkanus* Szwedo sp. nov.
(Pl. 6: 7; Fig. 31)

**Etymology.** Specific epithet derived from the Proto-Celtic word 'bikkano' meaning 'small'.

**Holotype.** NHMUK I.9199(2), with holotype of the braconid wasp *Taphaeus cervicalis* (Cockerell 1921a); Brodie Collection, Insect Limestone, NW Isle of Wight. Tegmen with claval portion partly missing.

**Diagnosis.** Cell C1 very long, distinctly longer than cell C5; cell C3 shorter than cell C2, not divided into cells C3a and C3b basad of apical line of veinlets.

**Description.** Length of tegmen 4.06 mm, width at widest point 1.32 mm. Other features as for the genus as it is the only included species.

Genus *Langsmaniko* Szwedo gen, nov.

**Etymology.** Genus name from the Proto-Celtic word 'langsmaniko' meaning 'jumping'. Gender: neuter.

**Type species.** *Langsmaniko marous* sp. nov.; here designated.

**Diagnosis.** Tegmen with venation similar to *Samliverus* Szwedo, but differs in short common stalk ScP + R (distinctly longer in *Samaliverus*); branch RA forked slightly apicad of nodal veinlet *ir*; branch $MP_{1+2}$ forked slightly apicad of nodal veinlet r-m (branch $MP_{1+2}$ forked distinctly apicad of nodal veinlet rp-mp in *Samaliversus*).

**Description.** Tegmen with costal margin distinctly curved in basal portion, then nearly straight. Basal cell narrow, about 3.5 times as long as broad. Stalk ScP + R + MP, leaving basal cell very short. Stem ScP + R forked distinctly basad of stem CuA forking. Branch RA forked slightly basad of nodal veinlet ir. Stem MP not forked basad of nodal line veinlets; branch $MP_{1+2}$ forked slightly apicad of nodal veinlet rp-mp, forked again distinctly basad of apical veinlets, then anteriad branch forked again apicad of apical veinlets. Stem CuA forked apicad of stem ScP + R forking. Nodal veinlets ir, rp-mp and mp-cua close each other, stepwise; apical line of veinlets regular, stepwise.

*Langsmaniko marous* Szwedo sp. nov.
(Pl. 6: 8; Fig. 32)

**Etymology.** Specific epithet derived from the Proto-Celtic word 'maro' meaning 'remain'.

**Holotype.** NHMUK In.25286(1) (with Diptera: Sciaridae wing); Hooley Collection, Insect Limestone, NW Isle of Wight.

**Diagnosis.** Cell C1 shorter than cell C5. Cell C3a merely shorter than cell C3b; cell C3b of same length as cell C4.

**Description.** Estimated length of tegmen 7.4 mm. Indistinct narrow darker band apicad of Sc + R forking, longitudinal veins darker, veinlets of apical line distinctly darker.

Genus *Komsitija* Szwedo gen. nov.

**Etymology.** Genus name from the Proto-Celtic word 'komsitija' meaning 'equal length'. Gender feminine.

**Type species.** *Komsitija tuberculata* sp. nov.; here designated.

**Diagnosis.** Tegmen venation similar to *Macrocixius* Matsumura, 1914, but it differs in distinctly smaller length (about half of tegmen length of *Macrocixius*); forkings of stems ScP + R and CuA at same level (forking ScP + R slightly anteriad in *Macrocixius*); vein RA with two terminals (vein RA with single terminals in *Macrocixius*); nodal veinlet mp-cua very short, at level of $MP_{3+4}$ branch (nodal veinlet mp-cua long, apicad of branch $MP_{3+4}$ in *Macrocixius*); cells C3a and C3b subequal in length (cell C3b longer than cell C3a in *Macrocixius*).

**Description.** Costal margin curved at base, then gently curved, thickened. Stigma narrow, about 4.4 times as long as wide. Basal cell elongate, about 4 times as long as wide. Stems ScP + R and MP leaving basal cell at same point. Stem ScP + R forked at basal 1/3 of tegmen length, at same level as stem CuA forking; vein $ScRA_1$ forked basad of stem MP forking, branch RA forked at level of posterior margin of

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stigma, with two terminals; branch RP forked apicad of nodal line, at about half of length of stigma, then both branches forked again, i.e., RP with four terminals. Stem MP forked at level of claval apex, anterior branch, i.e., branch $MP_{1+2}$ forked again distinctly basad of apical line of veinlets, posterior branch, i.e., branch $MP_{3+4}$, forked apicad of apical line, vein MP with five terminals. Stem CuA forked at same level as stem ScP + R, at basal 1/3 of tegmen length, posterior branch forked at level of apical line, i.e., vein CuA with three terminals. Veinlet ir between RA and RP very short, nodal veinlet mp-cua very short; apical veinlets ir, rp-mp, im, icu forming distinct apical line.

**Remark.** This genus is tentatively placed in the tribe Cixiini.

*Komsitija tuberculata* Szwedo sp. nov.
(Pl. 6: 9; Fig. 33)

**Etymology.** Specific epithet refers to the presence of distinct setiferous tubercles along the veins.

**Holotype.** NHMUK Pl II 2999; donated D. Azar, Insect Limestone, Thorness Bay. Tegmen with clavus missing.

**Diagnosis.** Costal cell wider than cell C1; cell C1 tapered in apical portion, cell C2 very long, delimited posteriorly by apical veinlet rp-mp; cells C1 and C5 subequal in length, cell C4 short, distinctly shorter than adjoining cell C3b.

**Description.** Length of tegmen 5.1 mm, width at widest point 1.77 mm. Other features as for the genus as it is the only included species.

Genus *Komnixta* Szwedo gen. nov.

**Etymology.** Genus name from the Proto-Celtic word 'komnixta' meaning 'first cousin (female)'. Gender: feminine.

**Type species.** *Komnixta jarzembowskii* sp. nov.; here designated.

**Diagnosis.** Tegmen venation similar to *Dweivera*, but differs in cell C5 longer than cell C1 (cell C5 shorter than C1 in *Dweivera*); cell C3b twice as long as cell C3a (cell C3b about 1.2 times as long as cell C3a in *Dweivera*); stem ScP + R forked apicad of stem CuA forking (stem Sc + R forked basad of stem CuA forking in *Dweivera*).

**Description.** Stem ScP + R forked apicad of CuA forking; branch ScP + RA forked slightly apicad of nodal veinlets r-m and m-cu; Stigma more than twice as long as wide; stem RA with single terminal, RP forked at level of ir veinlet, then forked apicad of line of apical veinlets; with three terminals. Stem MP forked distinctly apicad of nodal veinlet r-m and merely apicad of nodal veinlet mp-cua, at level of $ScP + RA_1$; branch $MP_{1+2}$ forked basad of branch $MP_{3+4}$ forking, then its anterior branch forked at level of apical veinlets; branch $MP_{3+4}$ not forked. Stem CuA forked basad of stem ScP + R forking. Cell C5 longer than cell C1, widest at level of nodal vein mp-cua. Veins with small tubercles.

**Remark.** This genus is tentatively placed in the tribe Cixiini.

*Komnixta jarzembowskii* Szwedo sp. nov.
(Pl. 7: 1–3; Fig. 34)

**Etymology.** Specific epithet is given in honour to Dr Edmund A. Jarzembowski, eminent palaeoentomologist.

**Holotype.** Part and counterpart. Labelled MNEMG IL 87a (part); MNEMG IL 87b (counterpart), Insect Limestone, NW Isle of Wight. Apical part of tegmen, basal portion and clavus missing.

**Diagnosis.** Costal cell slightly wider than cell C1; stigma *ca.*2.2 times as long as wide; cell C1 longer but narrower than cell C2; cell C4 of similar length as adjoining cell C3b; cell C3b more than twice as long as cell C3a; apical veinlets icu, mp-cua, im stepwise.

**Description.** Estimated length of tegmen *ca.*6–7 mm; width *ca.*2 mm; darker band at level of apical veinlets. Other features as for genus.

Tribe Pintalini Metcalf, 1938

Genus *Worodbera* Szwedo gen. nov.

**Type species.** *Worodbera nimakka* sp. nov.; here designated.

**Etymology.** Genus name is derived from the Proto-Celtic word '*wor-od-ber-o-' meaning 'additional work'. Gender: feminine.

**Diagnosis.** Venation of apical part of tegmen similar to some species of *Pintalia* Stål, 1862. Appendix wide up to claval apex (as in *Pintalia*), RA with two terminals, RP with four terminals, stem MP forked slightly apicad of transverse veinlets rp-mp and mp-cua, branch $MP_{1+2}$ forked basad of branch $MP_{3+4}$ fork, at level of forst RP fork; cell C5 nearly twice as long as cell C3; Apical line of veinlets regular.

**Description.** Tegmen with apical margin rounded, with widened appendix, stigma area (?) (thickened); stem ScP + R forked basad of stem MP fork, branch RA with two terminals reaching margin, branch RP with four terminals reaching margin, first fork, basad of ir veinlet, slightly apicad of RA fork, and slightly basad of terminal $MP_1$ fork, second fork slightly apicad of rp-mp veinlet, third fork before reaching margin; stem MP forked slightly apicad of nodal veinlets rp-mp and mp-cua, branch $MP_{1+2}$ forked slightly apicad of branch RP first fork, then terminal $MP_1$ forked more apicad before reaching the margin, branch $MP_{3+4}$ forked slightly basad of branch $MP_{1+2}$ fork; stem MP reaching apical margin with five terminals; stem CuA forked distinctly basad of stem M, reaching margin with two terminals. Cell C3 about 0.6 times as long as cell C2a.

*Worodbera nimakka* Szwedo sp. nov.
(Pl. 7: 4; Fig. 35)

**Etymology.** Specific epithet is derived from the Proto-Celtic words 'makko-' meaning 'surety' with a negative particle 'ni'.

**Holotype.** NHMUK In.43470; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen, costal portion weakly preserved.

**Diagnosis.** Cell C5 about 2.3 times as long as cell C3; cell C2a longer than cell C4a; cell C3a about 0.6 as long as cell C3; cell C3 narrowing toward apex; costal margin strengthened at level of nodal line, nodal line veinlet rp-mp oblique, slightly anteriad of straight nodal line mp-cua; apical line of veinlets regular.

**Description.** Preserved portion of tegmen 2.16 mm long. Costal margin strengthened at level of nodal line, appendix widened. Apical line of veinlets regular, composed of ir, rp-mp, im and icu veinlets.

Family Achilidae Stål, 1866

Subfamily Achilinae Stål, 1866

Tribe Achillini Emeljanov, 1991

Genus *Hooleya* Cockerell, 1922

**Type species.** *Hooleya indecisa* Cockerell, 1922, p. 160, by monotypy.

**Diagnosis.** Differs from *Achilla* Haglund, 1899 and *Maurisca* Emeljanov, 2005 by stem ScP + R leaving basal cell separately

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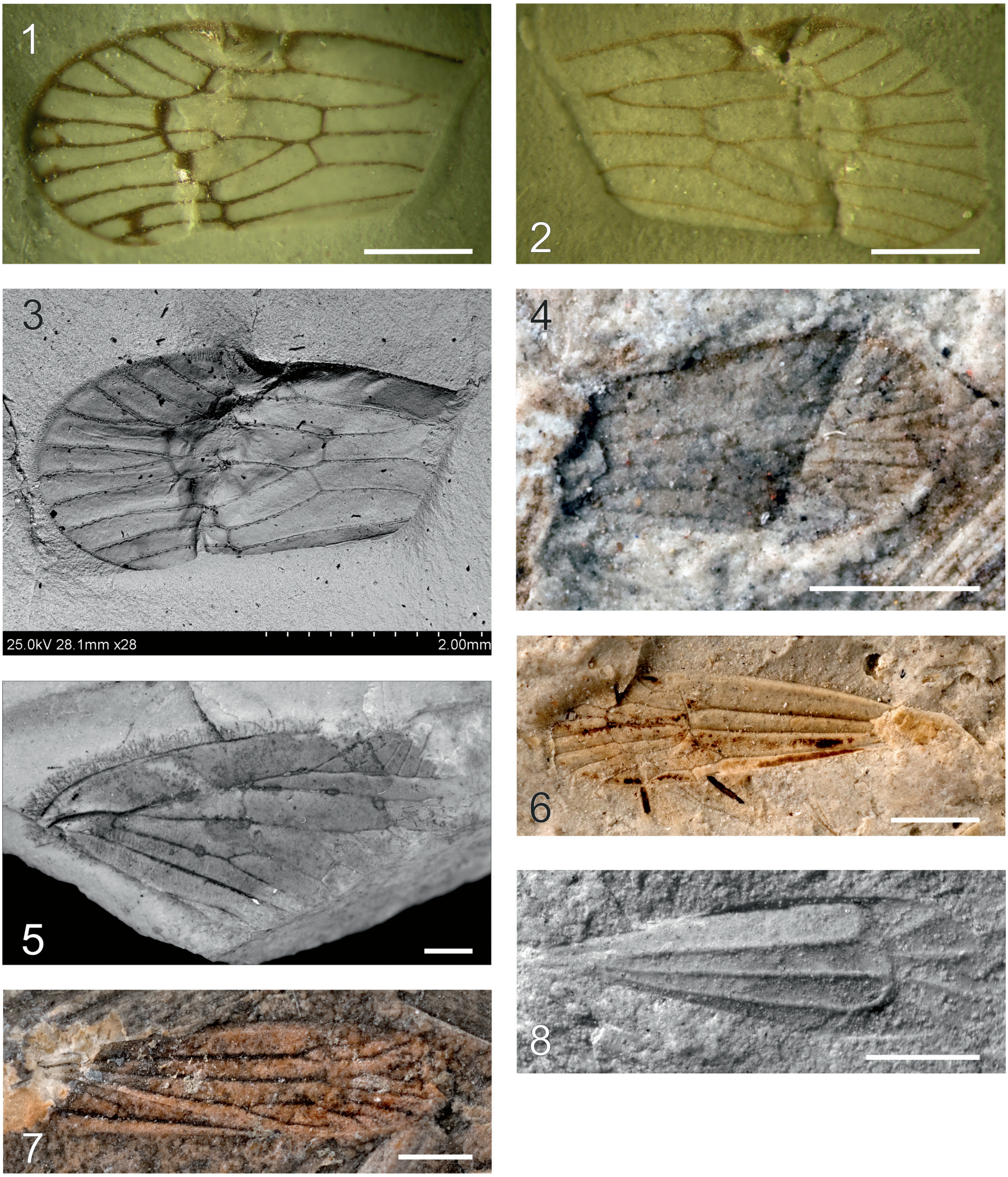


**Plate 7** (1–3) *Komnixta jarzembowskii* Szwedo gen. et sp. nov., holotype: (1) MNEMG IL 87a, part; (2) MNEMNG IL 87b, counterpart; (3) SEM image of MNEMG IL 87a, part. (4) *Worodbera nimakka* Szwedo gen. et sp. nov., holotype, NHMUK In.43470, tegmen. (5) *Hooleya indecisa* Cockerell, 1922, holotype, NHMUK In.24364, tegmen. (6) *Sognotela emeljanovi* Szwedo gen. et sp. nov., holotype, NHMUK In.25335, tegmen. (7) *Catulliastites muiri* (Cockerell, 1922) gen. nov., holotype, NHMUK In.24365, tegmen. (8) *Reteotissus hooleyi* Szwedo gen. et sp. nov., holotype, NHMUK In.24806, tegmen.

from stem of vein MP (short common stem ScP + R + MP in *Achilla* and *Maurisca*); branches of RA reaching costal margin obliquely, inclined apicad (branches of RA perpendicular or slightly inclined basad in *Achilla* and *Maurisca*); forkings of vein RP close each other (forkings of RP more widely spaced in *Achilla* and *Maurisca*), first veinlet r-m apicad of third forking of vein MP (apicad of first branching of MP in *Achilla* and *Maurisca*).

**Description.** Costal margin distinctly curved at base, then nearly straight; basicostal area distinct, comparatively wide at base and narrow in remainder portion, up to stigmal area. Costal margin at level of stigmal area slightly widened,

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striated. Basal cell relatively narrow, about three times as long as wide. Costal cell wide, slightly wider than cell C2, about twice as wide as cell C1. Stem ScP + R short, leaving basal cell separately from stem MP; vein RP separates from stem ScP + R at level of CuA forking; branch ScP + $RA_1$ strongly oblique, branches RA less oblique, five preserved terminals visible (probably seven or eight terminals); RP with three visible terminals, narrowly separated each other; vein MP forked at level of ScP + $RA_1$ forking, with four visible branches preserved (probably five terminals); vein CuA forked at level of stem ScP + R forking. Apex of clavus probably exceeding half of tegmen length. First veinlet rp-mp apicad of second MP forking, second veinlet rp-mp placed close to first, near third forking of RP; veinlet mp-cua perpendicular to lower branch of CuA, at level of ScP + $RA_1$ forking.

*Hooleya indecisa* Cockerell, 1922
(Pl. 7: 5; Figs 36, 37)

v*1922 *Hooleya indecisa* Cockerell, p. 160, fig. 2.
1992 *Hooleya indecisa*: Carpenter, p. 256.
1994 *Hooleya indecisa*: Emeljanov, p. 77: fig. 1a, pl. 7, fig. 1.
2004 *Hooleya indecisa*: Szwedo *et al.*, p. 42.
2006 *Hooleya indecisa*: Szwedo, 2006a, p. 167.

**Holotype.** NHMUK In.24364; Hooley Collection, Insect Limestone, NW Isle of Wight. Basal portion of tegmen, with part of claval portion preserved, apical portion of membrane missing.

**Diagnosis.** Tegmen with basicostal area elongate, widest at base. Branch ScP + $RA_1$ oblique, first terminal of vein RA subparallel to branch ScP + $RA_1$. Cell C1 half as wide as costal cell; cell C5 narrower than cell C2, about as wide as cell C1. First veinlet rp-mp oblique. First and second forkings of lower branch of vein MP at similar distance, about as width of cell C2.

**Description.** Length of preserved fragment of tegmen 8.8 mm, width 4.0 mm. Other features as for the genus as it is the only included species.

**Remark.** Originally placed in Derbidae, but transferred to Achilidae: Achillini by Emeljanov (1994). Emeljanov (1994) presented also a reconstruction of tegmen venation (Fig. 35). Carpenter (1992) listed it in 'Family uncertain' section.

Another, but very incomplete specimen, NHMUK In. 24822; Hooley Collection, could belong to the genus *Hooleya* Cockerell.

Family Tropiduchidae Stål, 1866

Subfamily Tropiduchinae Stål, 1866

Tribe Tambiniini Kirkaldy, 1907

Genus *Sognotela* Szwedo gen. nov.

**Etymology.** Combination of Proto-Celtic words 'sogno' meaning 'net' and extinct dictyopharid generic name *Netutela*, to which it is superficially similar. Gender: feminine.

**Type species.** *Sognotela emeljanovi* sp. nov.; here designated.

**Diagnosis.** Similar to some species of the genus *Tambinia* Stål, 1859, but tegmen more elongate, as in *Garumna* Melichar, 1914. It differs by shorter prenodal portion of cell C5 (more than twice as long as wide in *Tambinia*), less oblique nodal line, rounded postnodal line, postnodal cells about as long as apical cells (postnodal cells shorter than apical cells in *Garumna*); stem $MP_{3+4}$ forked merely apicad of nodal line level (stem $MP_{3+4}$ not forked or forked apicad of nodal line level in *Tambinia*).

**Description.** Tegmen elongate, narrow, costal margin slightly thickened, apical margin elongately rounded, clavus reaching 0.6 of tegmen length. Stem ScP + R long, forked slightly basad of apex of clavus, apicad of CuA forking; single terminal ScP + $RA_1$ and $RA_2$, RP with two terminals. Stem MP long, forked at level of nodal line, stem $MP_{1+2}$ forked at apical line, stem $MP_{3+4}$ forked merely apicad of nodal line, distinctly apicad of ScP + R and CuA forkings, lower branch forked at level of apical line of veinlets, with two terminals, upper branch forked merely apicad of nodal line, with two terminals. Stem CuA forked basad of ScP + R forking, basad of apex of clavus. Nodal line distinct, apical line of veinlets distinct, arcuate.

*Sognotela emeljanovi* Szwedo sp. nov.
(Pl. 7: 6; Fig. 38)

**Etymology.** Species is named in honour of Professor Alexander F. Emeljanov, an eminent specialist on planthoppers and leafhoppers.

**Holotype.** NHMUK In.25335; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen, with claval portion missing.

**Diagnosis.** Cell C1 short, subtriangular, cell C3a shorter than cell C3, with posterior margin arcuate. Single terminal of RA, two terminals of RP, four terminals of MP, veinlet *icu* apicad of nodal line present.

**Description**. Length of tegmen 3.9 mm, width at widest point 1.22 mm. Other features as for the genus as it is the only included species.

Tribe Catullini Melichar, 1914

Genus *Catulliastites* Szwedo nom. nov.

**Etymology.** Genus name is derived from the *Catullia* – generic name of tropiduchid planthopper combined with *Hastites* original, but homonymic name given to this fossil by Cockerell. Gender: masculine.

**Type species.** *Hastites muiri* Cockerell, 1922, p. 161; by monotypy.

*Hastites* Cockerell, 1922 (Insecta: Hemiptera: Cixiidae) nec *Hastites* Mayer-Eymar, 1883 (Mollusca: Cephalopoda: Belemnitida: Hastitidae)

1883 *Hastites* Mayer-Eymar, pp. 640, 642 (Mollusca); type species: *Belemnites clavatus* Schlotheim, 1820, p. 49.
1922 *Hastites* Cockerell, p. 161 (Insecta); type species: *Hastites muiri* Cockerell, 1922, p. 161.
1992 *Hastites* Cockerell; Carpenter, p. 256 (Insecta).
2004 *Hastites* Cockerell; Szwedo *et al.*, p. 93 (Insecta).

**Diagnosis.** Venation pattern similar to other genera of Catullini, but differs in more apicad line of transverse veinlets forming nodal line. It differs from *Catullia* Stål, 1870 by higher number of veinlets in basicostal area (only a few in *Catullia*); more apical forking of stem Sc + R, slightly apicad of apex of clavus (forking of stem ScP + R slightly basad of apex of clavus in *Catullia*).

**Description.** Tegmen with costal margin mildly curved. Basicostal area narrow, with few veinlets. Basal cell elongate, about three times as long as wide. Stem ScP + R leaving basal cell separately from stem MP; first forking of ScP + R slightly apical of apex of clavus; two terminals: ScP + $RA_1$ and $RA_2$; branch RP with single terminal. Stem MP very long, first forking more apicad than ScP + R forking, with four terminals. Stem CuA forked slightly basad of apex of clavus, with four

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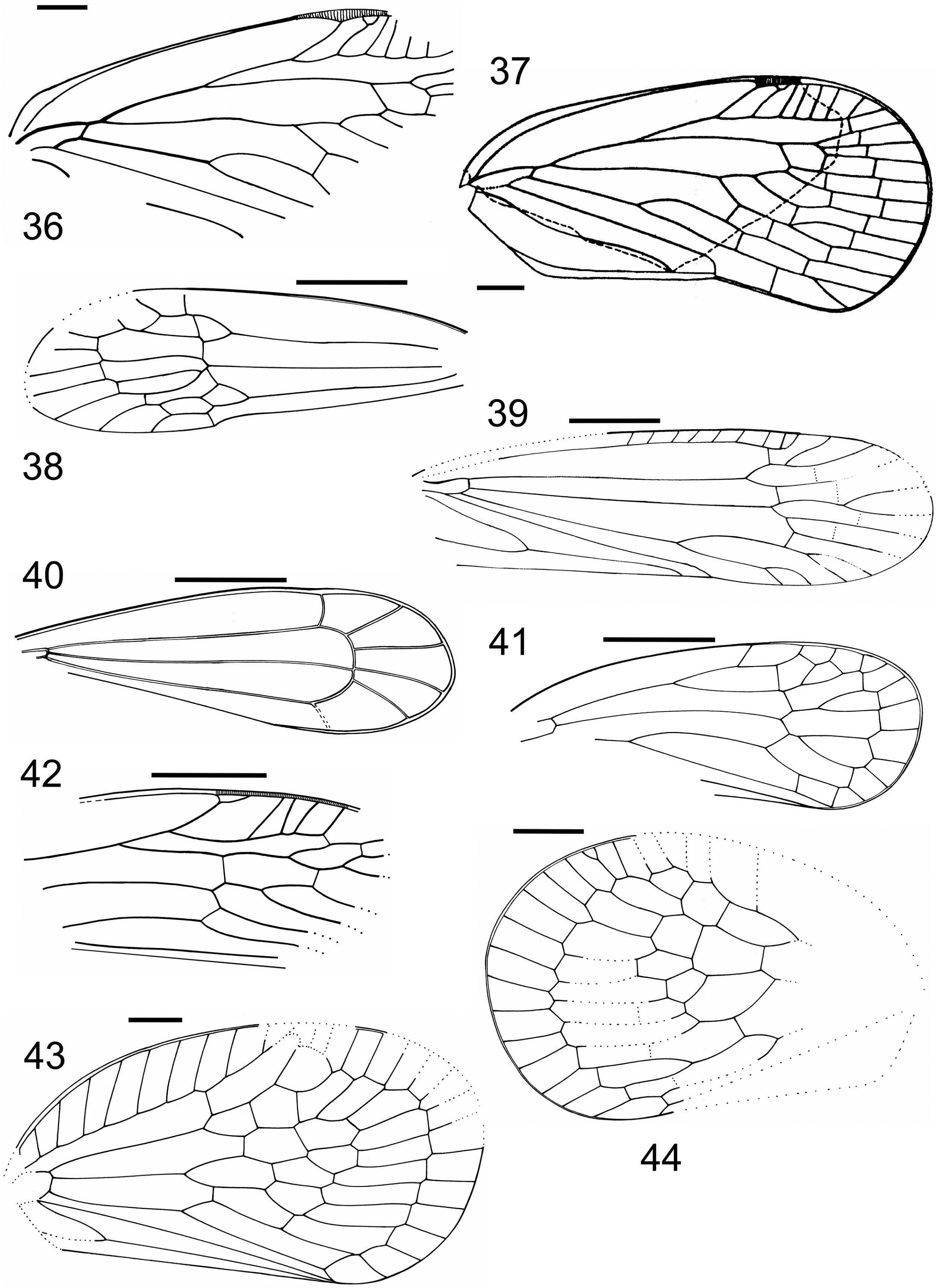


**Figures 36–44** (36) *Hooleya indecisa* Cockerell, 1921b, holotype, NHMUK In.24364, tegmen. (37) *Hooleya indecisa* Cockerell, 1921b, reconstruction of tegmen venation after Emeljanov (1994). (38–43) Tegmen: (38) *Sognotela emeljanovi* Szwedo gen. et sp. nov., holotype, NHMUK In.25335; (39) *Catulliastites muiri* (Cockerell, 1922) gen. nov., comb. nov., holotype, NHMUK In.24365; (40) *Reteotissus hooleyi* Szwedo gen. et sp. nov. holotype, NHMUK In.24806; (41) *Phatanako wilmattae* (Cockerell 1926) gen. nov., comb. nov., holotype, NHMUK In.26637; (42) *Keriophettus atibenus* Szwedo gen. et sp. nov., holotype, NHMUK In.24387; (43) *Senogaetulia kwalea* Szwedo gen. et sp. nov., holotype, IWCMS 2018.49. (44) *Dakrutulia mikhailkozlovi* Szwedo gen. et sp. nov., holotype, NHMUK In.24602, tegmen, part. Scale bar = 1 mm.

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terminals. Clavus long, with apex reaching 0.6 of tegmen length, claval veins Pcu and $A_1$ fused distinctly apicad of half of clavus length. Single veinlets between Pc + CP and ScP + R; RP and MP, and MP and CuA branches, apical row of veinlets rp-mp, im and mp-cua present.

**Remark.** According to Muir's opinion cited in Cockerell (1922), this genus could be placed in Dictyopharidae, relating it to the genera *Hasta* Melichar, 1914 and *Thanatodictya* Kirkaldy, 1906. It is not mentioned in Metcalf & Wade's (1966) catalogue. Carpenter (1992) listed it under 'Homoptera, Family uncertain'. The venation characters exclude it from Dictyopharidae and place it in the Tropiduchidae tribe Catullini.

*Catulliastites muiri* (Cockerell, 1922) comb. nov.
(Pl. 7: 7; Fig. 39)

v*1922 *Hastites muiri* Cockerell, 1922, p. 161, fig. 3.
1992 *Hastites muiri*; Carpenter, p. 256.
2004 *Hastites muiri*; Szwedo *et al.*, p. 93.

**Description.** Length of tegmen 5.6 mm, width at widest point 1.6 mm. Other features as for the genus as it is the only included species.

**Holotype**. NHMUK In.24365; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen, with some portion of basal portion not preserved.

**Diagnosis.** Tegmen elongate, length/width ratio about 3.46:1. Costal area present, long and narrow, exceeding apex of clavus, with few transverse veinlets. Nodal line of veinlets shifted apicad of apex of clavus, subapical line of a few veinlets. Cell C2 about as long as cell C3. Single terminals of $ScRA_1$, $RA_2$ and RP, vein M with four terminals, vein CuA with four terminals.

Tribe Trypetimorphini Melichar, 1914

Genus *Reteotissus* Szwedo gen. nov.

**Etymology.** Combination of the Celtic word 'reteo' meaning 'run' and tropiduchid generic name *Ommatissus*. Gender: masculine.

**Type species.** *Reteotissus hooleyi* sp. nov.; here designated.

**Diagnosis.** Differs from *Ommatissus* Fieber, 1875 by more simple venation, with veins not forked apicad of nodal line; stems ScP + R, MP and CuA leaving basal cell separately (common stem of M and CuA in *Ommatisus*). Common terminal of posterior branch of MP and anterior branch of CuA apical of nodal line reaching apical margin (terminals of MP and CuA reaching apical margin separately in *Ommatisus*).

**Description.** Costal margin gently curved, thickened, apical margin elongately rounded, veins thick, apex of clavus reaching 0.6 of tegmen length; basal cell elongate, narrow. Stems of veins ScP + R, MP and CuA leaving basal cell independently, but close each other. Stem ScP + R not forked before nodal line, single terminal ScP + RA, two terminals of RP; stem MP not forked before nodal line, posterior branch as common terminal with anterior branch of CuA; vein CuA forked at level of ScP + RA branching.

*Reteotissus hooleyi* Szwedo sp. nov.
(Pl. 7: 8; Fig. 40)

**Etymology.** Specific epithet is given after collector R. W. Hooley.

**Holotype.** NHMUK In.24806; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen with clavus missing.

**Diagnosis.** Venation reduced, costal margin thickened; five cells apicad of nodal line.

**Description.** Length of tegmen 4.2 mm, width of tegmen at widest point 1.3 mm. Other features as for the genus as it is the only included species.

Tribe Jantaritambini Szwedo, 2000

Genus *Phatanako* Szwedo gen. nov.

**Etymology.** The name is derived from Proto-Celtic word 'phatanako' meaning 'winged'. Gender: masculine.

**Type species.** *Myndus wilmattae* Cockerell, 1926; here designated.

**Diagnosis.** Venation similar to *Isporisa* Walker, 1857 (Isporisini) and *Jantaritambia* Szwedo, 2000 (Jantaritambini). From *Isporisa* it differs in tegmen widest at level of claval apex (tegmen widest near middle in *Isporisa*); apex of clavus exceeding 3/4 of tegmen length (clavus not extending beyond middle of clavus in *Isporisa*); apical margin shallowly rounded (deeply rounded in *Isporisa*); nodal line neither even nor oblique (nodal line apical cells distinctly shorter than half of subapical cells; apical cells longer than half of subapical cells in *Isporisa*). From *Jantaritambia* it differs by apex of clavus distinctly exceeding 3/4 of tegmen length (clavus reaching 3/4 of tegmen length in *Jantaritambia*); basal cell about twice as wide as long (three times as long as wide in *Jantaritambia*); apical cells less than half of length of subapical cells (apical cells more than half of length of subapical cells in *Jantaritambia*).

**Description.** Tegmen unpigmented, not coriaceous, widest slightly anteriad of apex of clavus, without basicostal area and transverse veinlets branching from Pc+CP. Nodal line nether oblique nor even, apical line not distinctly stepwise. Basal cell about twice as long as wide. Vein R forked once before nodal line, RA with single terminal, RP with three terminals; vein MP not united basally with vein CuA, not forked before nodal line, with five terminals; vein CuA forked once before nodal line, with two terminals. First veinlet *icu* nearly perpendicular to lower branch of CuA, lying at nodal line.

*Phatanako wilmattae* (Cockerell, 1926) comb. nov.
(Pl. 8: 1; Fig. 41)

v*1926 *Myndus wilmattae* Cockerell, p. 322, Fig. 12.
2004 *Myndus wilmattae*; Szwedo *et al.*, p. 97.

**Holotype.** NHMUK In.26637, Insect Limestone, NW Isle of Wight. Tegmen, with claval portion incomplete, basal portion not distinct.

**Diagnosis.** Tegmen with cell C1 slightly longer than cell C3, cell C3 slightly longer than cell C4, cell C5 the longest, nearly twice as long as cell C4. Tegmen with ten apical cells, distinctly shorter than subapical ones. Apical portion of tegmen widely rounded.

**Description.** Length of tegmen 5.2 mm, width at widest point 2.05 mm. Costal margin curved at base. Claval portion incomplete, other features as for the genus as it is the only included species.

**Remark.** Shcherbakov (2006) placed *Jantaritambia loculata* (Germar & Berendt 1856) and '*Cixius*' *succineus* Germar & Berendt, 1856 in the tribe Jantariambini, both from Eocene Baltic amber.

Genus *Keirophettus* Szwedo gen. nov.

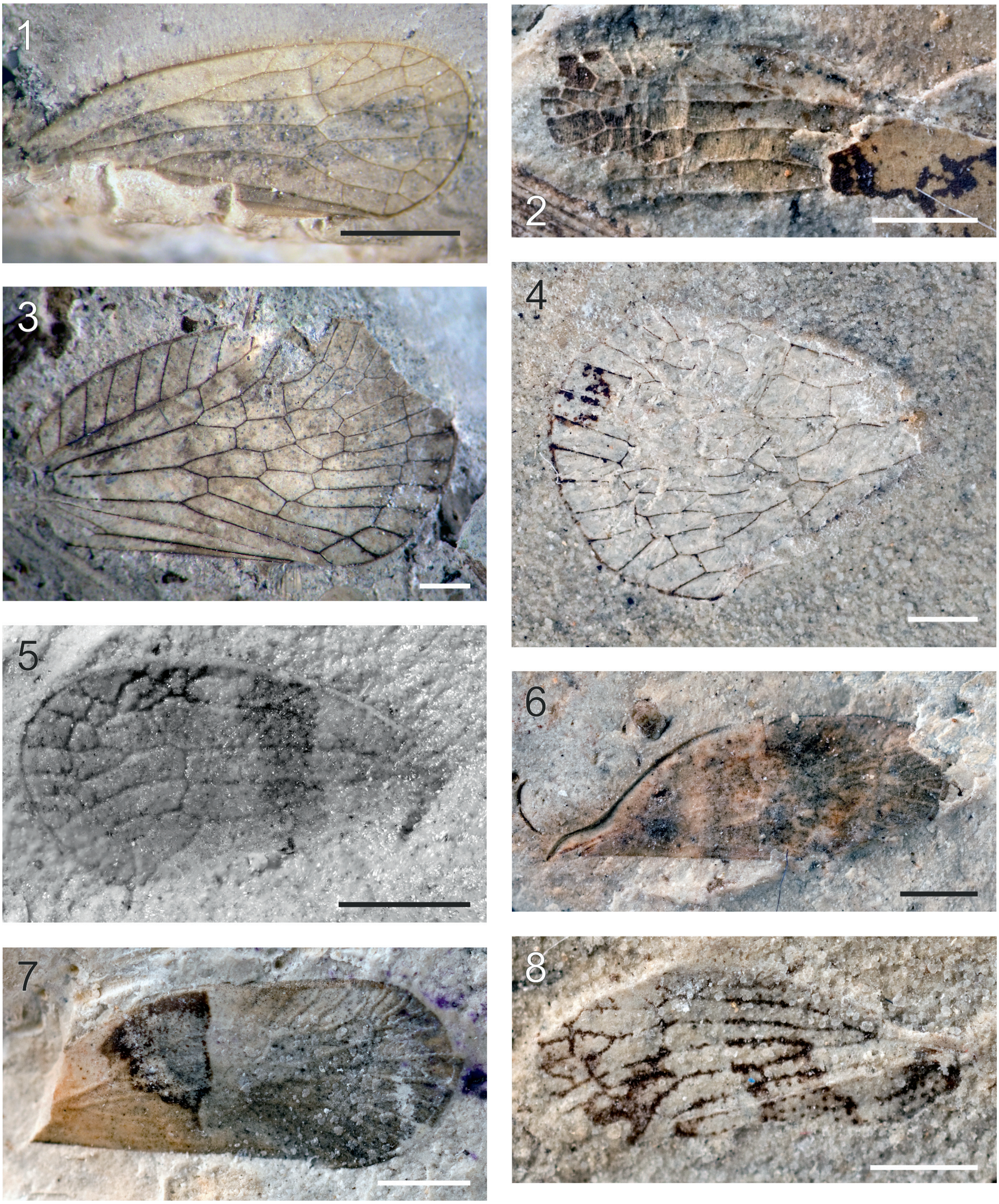


**Plate 8** (1) *Phatanako wilmattae* (Cockerell, 1926) gen. nov., comb. nov., holotype, NHMUK In.26637, tegmen. (2) *Keirophettus atibenus* Szwedo gen. et sp. nov., holotype, NHMUK In.24387, tegmen. (3) *Senogaetulia kwalea* Szwedo gen. et sp. nov., holotype, IWCMS 2018.49, tegmen. (4) *Dakrutulia mikhailkozlovi* Szwedo gen. et sp. nov., holotype, NHMUK In.24602, tegmen. (5) *Krundia korba* Szwedo gen. et sp. nov., holotype, NHMUK Pl II 2740a, tegmen, part. (6) *Breukoscelis vadimgratshevi* Szwedo gen. et sp. nov., holotype, NHMUK In.26043, tegmen. (7) *Breukoscelis phrikkosus* Szwedo gen. et sp. nov., holotype, NHMUK In.26035, tegmen. (8) *Uphodato garwoterus* Szwedo gen. et sp. nov., holotype, NHMUK In.24502, tegmen.

**Etymology.** Generic name is derived from Proto-Celtic words: 'keiro' meaning dark brown and 'phett' wing. Gender: masculine.

**Type species.** *Keirophettus atibenus* sp. nov.

**Diagnosis.** Differs from *Phatanako* by very oblique stem portion of ScP + RA prolonged by ScP + $RA_1$, reaching costal margin (ScP + $RA_1$ less oblique in *Phatanako*, more arcuate in *Jantaritambia*); branch RA reaching margin with four terminals (single terminal in *Phatanako*, two terminals in *Jantaritambia*); branch $MP_{3+4}$ single (as in *Jantaritambia*, forked in *Phatanako*); cell C1 narrow, without veinlet (cell C1 about as wide as cell C2, with nodal line veinlet *ir* in *Phatanako* and *Jantaritambia*).

**Description.** Costal margin strengthened, appendix with transverse wrinkles visible. Stem ScP + R forked slightly apicad of stem CuA fork, distinctly basad of stem MP forking; branch ScP + RA basad of ScP + $RA_1$ terminal about as long as terminal ScP + $RA_1$, branch RA after ScP + $RA_1$ leaving slightly arcuate, reaching margin with four terminals; branch RP forked in apical portion of membrane, reaching margin with three terminals; stem MP forked at nodal line level, slightly anteriad of nodal veinlets rp-mp and mp-cua; branch $MP_{1+2}$ forked again on membrane, basad of RP forking; branch $MP_{3+4}$ single; stem CuA forked basad of stem ScP + R forking. Nodal line not fully developed, composed of nodal veinlet rp-mp, perpendicular to branch RP, basal portions of $MP_{1+2}$ and $MP_{3+4}$ branches and oblique veinlet mp-cua. Membrane with subapical veinlet ir and rp-mp, and apical veinlet ir (other veinlets not preserved). Stigmal area with indistinct sigmoid veinlet. Cell C1 narrow, about 7 times as long as wide, closed apically by subapical veinlet ir; Cell C2a about 2.5 times as long as wide; cell C5 long, lanceolate.

*Keirophettus atibenus* Szwedo sp. nov.
(Pl. 8: 2; Fig. 42)

**Etymology.** Specific epithet derived from Proto-Celtic 'atibena' meaning cut.

**Holotype.** NHMUK In.24387 (H102), Hooley Collection, Insect Limestone, NW Isle of Wight. Part of tegmen, with basal and apical portions deteriorated; traces of coloration preserved.

**Diagnosis.** Cell C1 about 2.2 times as long as cell C2a; terminal ScP + $RA_1$ forked near connection to costal margin; forking of branch RP more apical than forking of branch $MP_{1+2}$; branch $RP_2$ forked again apically; cells formed between terminals of RA, narrow, longer than wide.

**Description.** Length of preserved portion of tegmen 3.1 mm, width 1.33 mm. Basal and apical portion not preserved, clavus missing. Apical half darkened, with several patchy lighter spots; basal portion light, with a few indistinct darker patches. Other features as for the genus as it is the only included species.

Subfamily Elicinae Melichar, 1915

Tribe Elicini Melichar, 1915

Genus *Senogaetulia* Szwedo gen. nov.

**Etymology.** Combination of Proto-Celtic 'seno' meaning 'old' and generic name *Gaetulia* Stål, 1864. Gender: feminine.

**Type species.** *Senogaetulia kwalea* sp. nov.; here designated.

**Diagnosis.** Tegmen with venation pattern similar to *Indogaetulia* Schmidt, 1919. It differs by tegmen with basicostal area wider than costal cell (basicostal area about as wide as costal cell in *Indogaetulia*), cell C5 long, not separated by veinlet (cell C5 short, delimited by transverse veinlet in *Indogaetulia*); cell C3 about 3 times as long as wide (twice as long as wide in *Indogaetulia*); first forkings of stem MP and CuA at same level (stem CuA forked slightly anteriad of stem MP forking in *Indogaetulia*).

**Description.** Tegmen with costal margin distinctly curved at base, anterior angle angulate, apical margin arcuate, posterior angle angulate. Clavus long, apex of clavus reaching 2/3 of tegmen length. Basicostal area wider than costal cell, with few veinlets. Basal cell wide, stems ScP + R, MP and CuA leaving basal cell independently; stem ScP + R forked.

*Senogaetulia kwalea* Szwedo sp. nov.
(Pl. 8: 3; Fig. 43)

**Etymology.** Specific epithet from Proto-Celtic word 'kwale' meaning 'dig'.

**Holotype.** IWCMS 2018.49, Insect Limestone, NW Isle of Wight. Tegmen, with apical portion partly not preserved.

**Diagnosis.** Cell C3 about as long as cell C4; posteroapical margin of tegmen angulately rounded; four darker spots near the apical margin of tegmen.

**Description.** Length of tegmen 7.5 mm, width at widest point 4.2 mm. Other features as for the genus, as it is the only included species.

Genus *Dakrutulia* Szwedo gen. nov.

**Etymology.** Generic name is combination of the Proto-Celtic word 'dakru' meaning 'tear' with nogodinid planthopper genus name *Gaetulia* Stål, 1864. Gender: feminine.

**Type species.** *Dakrutulia mikhailkozlovi* sp. nov., here designated.

**Diagnosis.** Tegmen with pattern of venation similar to *Indogaetulia* Schmidt, 1919. It differs by short and more rounded shape of tegmen (tegmen elongate), about twice as long as wide in *Indogaetulia*; cell C1 longer than cell C3 (cells C1 and C3 subequal in length in *Indogaetulia*); cell C3 with three cell adjoining cells apicad (two adjoining cells apicad in *Indogaetulia*); cell C5 elongate, without preapical icu veinlet (preapical veinlet *icu* present in *Indogaetulia*).

**Description.** Tegmen short, rounded; apical margin roundly arcuate. Stem ScP + R forked slightly basad of stem MP forking. Branch ScP + RA with a few terminals, branch RP with four terminals. Stem MP with branch $MP_{1+2}$ with five terminals, branch $MP_{3+4}$ with three terminals, i.e., MP with eight terminals; stem CuA forked at level of stem MP forking, then at level of branch $MP_{3+4}$ forking, with three terminals. Subapical line of veinlets strongly stepwise; apical line distinct, regular. Cells apically adjoining cells C1, C2 and C3, shorter of them.

**Remark**. The fossil tegmen consists of strongly torn remnants, but the pattern of venation could be reconstructed. It matches the venation pattern found in the representatives of the tribe Gaetulini.

*Dakrutulia mikhailkozlovi* Szwedo sp. nov.
(Pl. 8: 4; Fig. 44)

**Etymology.** Specific epithet is given in honour of the late Mikhail A. Kozlov, specialist on Hymenoptera: Proctotrupoidea.

**Holotype.** part NHMUK In.24602, Hooley Collection; counterpart CAMSM X.50140.33 (TN 83), Smith Collection, Insect Limestone, NW Isle of Wight. Tegmen, torn, with clavus, basal and costal portions missing.

**Diagnosis.** Both cells adjoining cell C2 apicad distinctly shorter of it; basal veinlet r-m basad of veinlet m-cu; apical cells slightly shorter than subapical cells.

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**Description.** Preserved length of tegmen 5.1 mm, width 4.2 mm. Other features as for the genus as it is the only included species.

Family Issidae Spinola, 1839

Subfamily Issinae Spinola, 1839

Tribe Issini Spinola, 1839

Genus *Krundia* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word 'krundi' meaning 'round'. Gender: feminine.

**Type species.** *Krundia korba* sp. nov.; here designated.

**Diagnosis.** In shape of tegmen and pattern of venation resembling some genera formerly placed in the tribe Thioniini Melichar, 1906 (Gnezdilov 2013). In respect to strong convexity of tegmen it resembles representatives of Issidae: Hemisphaeriini Melichar, 1906. It could be characterised by the following combination of characters: tegmen curved at costal margin, widely rounded at apical margin; common stalk ScP + R relatively long, stem ScP + R forked slightly apicad of stem MP forking; stem CuA single, nodal line of veinlets basad of apex of clavus, apical line of veinlets regular, distinct; apical cells shorter than subapical cells.

**Description.** Tegmen about 1.8 times as long as wide. Costal margin slightly curved, apical margin widely rounded. Basal cell about twice as long as wide; very short stem ScP + R + MP leaving basal cell; stem ScP + R shorter than stem MP. Stem ScP + R forked at 1/4 of tegmen length, slightly basad of stem MP forking; vein ScP + $RA_1$ forked at level of nodal line, branch RA forked apicad of nodal line; branch RP forked basad of apical line of veinlets. Stem MP forked slightly apicad of stem ScP + R forking, anterior branch forked apicad of apical line of veinlets; posterior branch forked slightly basad of nodal line, then mediad branch forked again basad of apical line. Stem CuA single. Apex of clavus exceeding half of tegmen length.

**Remark**. The genus is tentatively placed in the subfamily Issinae, tribe Issini. In shape of tegmen and pattern of venation it resembles some of Issidae: Issinae: Thioniini. In respect to strong convexity of tegmen it resembles representatives of Issidae: Hemisphaeriini. Strongly convex tegmina are also present in the genus *Breukoscelis* Szwedo gen. nov. from the same deposit (see below in the same section).

*Krundia korba* Szwedo sp. nov.
(Pl. 8: 5; Fig. 45)

**Etymology.** Specific epithet derived from the Proto-Celtic word 'korb' meaning 'stain' and refers to colour pattern of the tegmen.

**Holotype.** NHMUK Pl II 2740a, b (part and counterpart); collected by C. Buckley, Insect Limestone, Thorness Bay. Tegmen with clavus missing.

**Diagnosis.** Costal cell about as wide as cell C1; nodal veinlet ir distinctly oblique, nodal veinlets rp-mp, and im arranged in row; apical veinlets arranged in row; anterocubital cell, between stems CuA and CuP, about half of width of cell C4 at widest point.

**Description.** Length of tegmen 3.2 mm, width at widest point 1.76 mm. Darker wide, transverse band apicad of half of tegmen length; darker spot at level of ScP + $RA_1$ branch. Other features as for the genus as it is the only included species.

**Remark.** Another specimen, NHMUK Pl II 2714, collected by the 'Polish Team' 23 May 2005, N. end Thorness Bay, is probably also related to *Krundia*.

Genus *Breukoscelis* Szwedo gen. nov.

**Etymology.** Combination of the Proto-Celtic word 'breuko' of not recognised meaning and generic name of the planthopper – *Caliscelis* Laporte, 1833. Gender: masculine.

**Type species.** *Breukoscelis vadimgratshevi* sp. nov., here designated.

**Diagnosis.** General shape of tegmen and venation similar to various genera of Issidae. It can be recognised by the following combination of characters: tegmen elongate, strongly convex; basicostal area very distinct, thickened, elongate; short common stem ScP + R + MP; stem MP forked basad of stem ScP + R forking; stem RP forked at level of stem $MP_{1+2}$ forking, with several terminals; stem $MP_{1+2}$ with several terminals, stem $MP_{3+4}$ with a few terminals; stem CuA single.

**Description.** Tegmen about 2.5 times as long as wide, base of costal margin strongly curved, with distinct and thickened, elongate basicostal area, median portion of costal margin merely curved, posterior margin widely arcuate. Common stem ScP + R and MP short; stem ScP + R forked apicad of stem MP forking; branch ScP + RA relatively short, reaching costal margin with terminals ScP + $RA_1$ and $RA_2$; branch RP forked at level of $RA_2$ branching, anterior branch of RP with four terminals reaching costal margin and anterior angle; posterior branch of RP reaching apical margin with a few terminals. Stem MP forked shortly after separation of stem ScP + R, basad of stem ScP + R forking; branch $MP_{1+2}$ forked at level of branch RP forking, then forked at level of apical line of veinlets. Stem CuA single. Veinlet mp-cua placed distinctly basad of subapical veinlets *ir* and im; subapical veinlets ir and im not forming distinct line; apical row of veinlets regular.

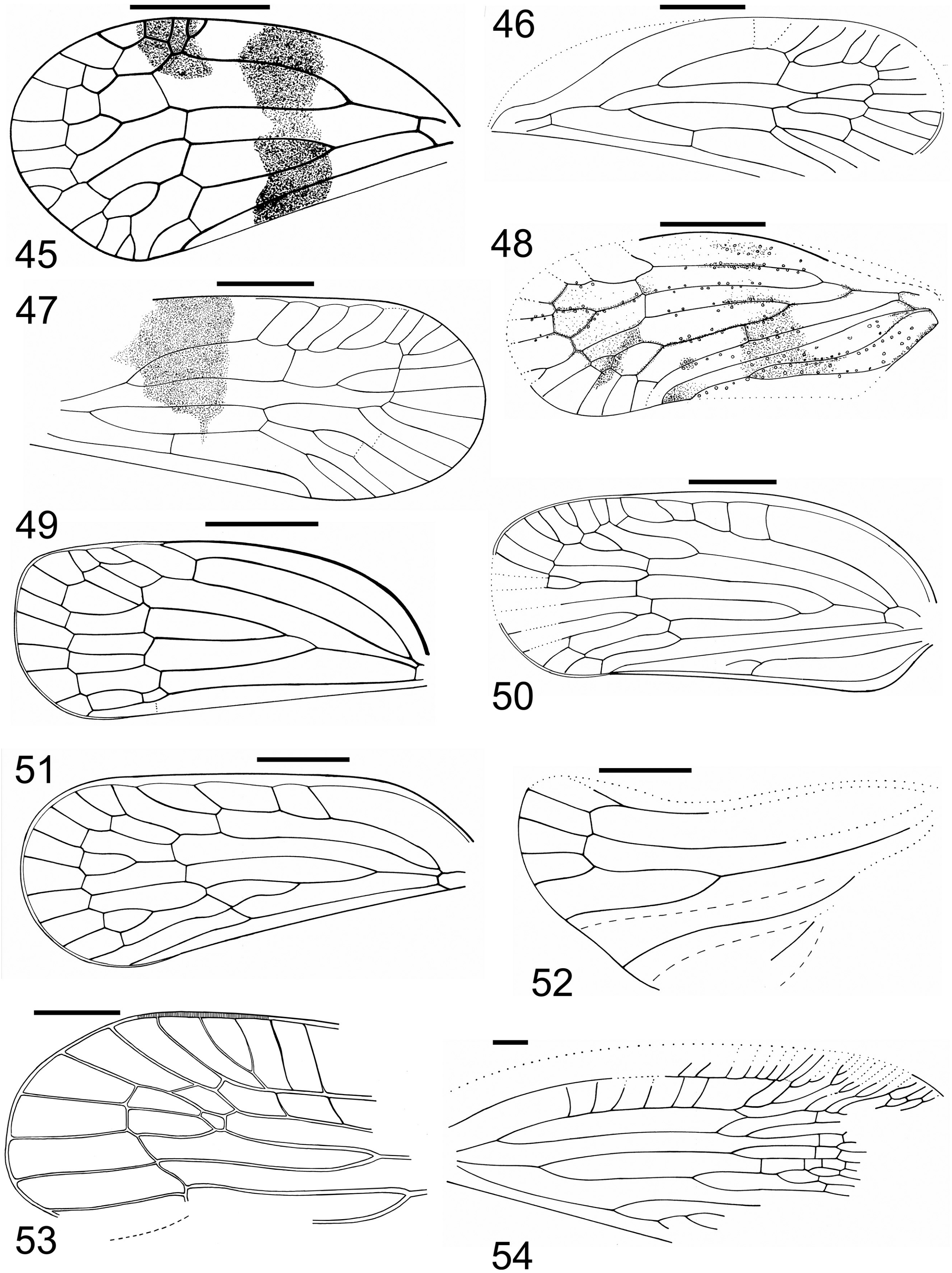
**Remark.** The genus described above presents a very peculiar set of characters. In some respect its venation could resemble patterns found in macropterous forms of Caliscelidae Amyot & Audinet-Serville, 1843. However Issidae: Issinae and Acanaloniidae also present high variability in venation patterns, and some similarities can be found. Forms with strongly convex tegmina are present in all of these families. In Emeljanov's (1999) opinion Issidae are distinguished by pterygomonomorphism with slightly diminished, peculiar, case-shaped or steeply tectiform tegmina. Caliscelidae are distinguished by the pterygonodimorphism with prevalence of strongly brachypterous forms. Acanaloniidae are characteristic of tegmina without costal area. Based only on the tegminal characters it is not possible to resolve the taxonomic placement of the genus. However, it is tentatively placed in the subfamily Issinae, but given its very particular pattern of venation it could represent separate taxon of tribal or subfamilial level.

*Breukoscelis vadimgratshevi* Szwedo sp. nov.
(Pl. 8: 6; Fig. 46)

**Etymology.** Specific epithet is given in the honour of the late Vadim G. Gratshev, specialist on curculionid beetles.

**Holotype.** NHMUK In.26043; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen with basal portion and clavus missing.

**Diagnosis.** Branch RP forked at level of forking of branch $MP_{1+2}$, anteriad branch with four terminals, mediad branch forked at level of apical line, with two terminals; branch




**Figures 45–54** (45) *Krundia korba* Szwedo gen. et sp. nov., holotype In. Pl II 2740a, tegmen, part. (46–51) Tegmen: (46) *Breukoscelis vadimgratshevi* Szwedo gen. et sp. nov., holotype, NHMUK In.26043; (47) *Breukoscelis phrikkosus* Szwedo gen. et sp. nov., holotype, NHMUK In.26035; (48) *Uphodato garwoterus* Szwedo gen. et sp. nov., holotype, NHMUK In.24502; (49) *Ambitaktoa stoumma* Szwedo gen. et sp. nov., holotype, NHMUK In.17282; (50) *Phariberea gurdonika* Szwedo gen. et sp. nov., holotype, NHMUK I.17096; (51) *Wixskimoa torxsea* Szwedo gen. et sp. nov., holotype, MIWG 3609. (52) *Wixskimoa torxsea* Szwedo gen. et sp. nov., holotype, MIWG 3609, visible portion of hindwing. (53, 54) Tegmen: (53) *Niadrima yulei* Szwedo gen. et sp. nov., holotype, NHMUK II.3046; (54) *Ankwomwarius brodiei* Szwedo gen. et sp. nov., holotype, NHMUK I. 8803. Scale bar = 1 mm.

$MP_{1+2}$ forked at level of branch RP forking, with seven terminals; branch $MP_{3+4}$ with single terminal; short veinlet rp-mp apicad of subapical veinlets ir and im; cell C1 less than 1.5 times as long as adjoining subapical cell; cell C2 not extending to apical row of veinlets, delimited apically by short veinlet rp-mp.

**Description.** Length of tegmen 5.3 mm, width at widest point 1.9 mm.

*Breukoscelis phrikkosus* Szwedo sp. nov.
(Pl. 8: 7; Fig. 47)

**Etymology.** Specific epithet is derived from the Proto-Celtic word 'phrikko' meaning 'furrow'.

**Holotype**. NHMUK In.26035; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen with basal portion and clavus missing.

**Diagnosis.** Tegmen smaller than in *Breukoscelis vadimgratshevi* sp. nov.; branch RP with eight terminals (six terminals in *B. vadimgrachevi*), branch $MP_1$ with three terminals, branch $MP_2$ with two terminals, branch $MP_{3+4}$ with two terminals respectively (five, two and one terminals respectively in *B. vadimgrachevi*); cell C1 about 1.5 times as long as adjoining subapical cell; cell C2 narrow and elongate, delimited apically by veinlet rp-mp of apical row.

**Description.** Length of tegmen 4.7 mm, width at widest point *ca.*2 mm; dark, triangular spot in median portion of tegmen.

Genus *Uphodato* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word 'uphodato' meaning 'sediment'. Gender: neuter.

**Type species.** *Uphodato garwoterus* sp. nov.; here designated.

**Diagnosis.** Tegmen with venation superficially resembling *Breukoscelis* Szwedo, but distinctly smaller. Tegmen tuberculate along veins. Common stalk ScP + R+MP elongate (similarly to *Breukoscelis*); stem ScP + R forked distinctly more basad than stem M forking (stem ScP + R forked apicad of stem MP forking in *Breukoscelis*); stem CuA forked apicad of nodal line (stem CuA not forked in *Breukoscelis*); subapical line of veinlets apicad of apex of clavus (subapical veinlets basad of apex of clavus in *Breukoscelis*).

**Description.** Tegmen with widened basicostal area, about 2.5 times as long as wide, with rounded apical portion; with apex reaching 2/3 of tegmen length. Basal cell elongate, about twice as long as broad. Common stalk ScP + R + MP elongate, longer than basal cell. Stem MP forked basad of 1/4 of tegmen length; stem ScP + R forked well basad of stem MP first forking. Branch ScP + RA forked slightly basad of subapical line of veinlets; vein RA with two terminals; vein RP forked basad of apical line of veinlets, reaching margin with three terminals. Branch $MP_{1+2}$ not forked basad of apical line of veinlets; branch $MP_{3+4}$ forked at level of claval apex, basad of subapical veinlets rp-mp and im, reaching apical margin with three terminals. Stem CuA forked at level of apex of clavus. Clavus elongate, claval veins Pcu and $A_1$ fused basad of half of tegmen length, at level of subapical veinlet m-cu. Apical veinlets ir, rp-mp, im and mp-cua forming nearly regular line.

**Remark.** Placement of this genus in Issidae: Issinae is only tentative. Similar forms with tubercular tegmina are known among recent Nogodinidae Melichar, 1898 – *Andrewsiella* Izzard, 1936 and *Distiana* Metcalf, 1958. Venation pattern, placement of tubercles between veins and very long clavus reaching near the apex of tegmen differs them easily from *Uphodato* Szwedo. The two above-mentioned recent genera were placed in the family Acanaloniidae Amyot & Audinet-Serville, 1843, which was recently redefined (Gnezdilov 2012a) and the genera were moved to Nogodinidae. Also the generic content of the family Issidae was revised recently (Gnezdilov 2013), with a new tribal classification proposed.

*Uphodato garwoterus* Szwedo sp. nov.
(Pl. 8: 8; Fig. 48)

**Etymology.** Specific epithet is derived from the Proto-Celtic word 'garwotero' meaning 'roughness'.

**Holotype.** NHMUK In.24502; Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen with basicostal portion and part of clavus missing.

**Diagnosis.** Tegmen with subapical cells adjoining to cells C1 and C2 of same length; cell C4 shorter than cell C3; apical cells shorter than subapical ones; basal portion of tegmen darkened; wide, darker band basad of half of tegmen length; apical portion with indistinct dark pattern.

**Description.** Length of tegmen 4.1 mm, width of tegmen 1.56 mm. Other features as for the genus as it is the only included species.

Family Nogodinidae Melichar, 1898

Subfamily Ambitaktoinae Szwedo subfam. nov.

**Type genus.** *Ambitaktoa* gen. nov.; here designated.

**Diagnosis.** Differs from all other subfamilies of Nogodinidae by the following combination of characters: tegmen with stems ScP + RA and RP separated since base or with a short common stalk; stem MP forked very basad, about 1/4 of tegmen length, then forked again; two rows of veinlets: subapical and apical, relatively regular; stem CuA single; clavus very long, reaching nearly to the posterior angle of tegmen.

**Remark.** The subfamily Ambitaktoinae subfam. nov. is tentatively placed within the Nogodinidae. The content of the family needs to be reconsidered. Emeljanov (1999) suggested that Nogodinidae *sensu stricto* comprises forms with tegmen with costal area ('precostal' in his nomenclature) present and with veinlets; hind tibiae with lateral spines, and postclypeus with lateral keels. He also redefined the Acanaloniidae Amyot & Audinet-Serville, 1843 in his key to Issidae-like families distinguishing characters of these families are compared in couplets of the key opposing them to Nogodinidae. Shcherbakov (2006) discussed several extinct taxa and their placement in Nogodinidae *sensu lato*. The content and definitions of subfamilies and tribes placed in Nogodinidae were recently discussed by Gnezdilov (2017). Representatives of Ambitaktoini resemble some taxa placed in the Tonginae (group placed in Issidae, later Acanaloniidae, then Nogodinidae – Gnezdilov, 2007, recently redefined and partly supressed under Nogodinidae – Gnezdilov, 2017), but tegminal characters which are available are not enough for definite conclusion of placement of Ambitaktoinae.

The suprageneric classification and phylogeny of the family Nogodinidae is not understood. Fennah (1978, 1984, 1987) divided it into two subfamilies: Nogodininae Melichar, 1898 with seven tribes (Nogodinini Melichar, 1898, Bladinini Kirkaldy, 1907, Mithymnini Fennah, 1967, Pisachini Fennah, 1978, Varciini Fennah, 1978, Epacriini Fennah, 1978, Lipocalliini Fennah, 1984), and the monotypical Gastriniinae Fennah, 1987. Later, Gnezdilov (2007) supplemented Nogodininae with the tribe Tongini Kirkaldy, 1907 (moved and downgraded from the family Issidae), but excluded the subtribe Gaetuliina Fennah, 1978 from the tribe Bladinini Kirkaldy, and transferred it to the family Tropiduchidae (Gnezdilov 2007, 2013). In addition, Gnezdilov (2012b) changed the status and position of Colpopterini Gnezdilov, 2003 (formerly placed in Issidae) as subfamily Colpopterinae in Nogodinidae. Recent, molecular investigations (Sun *et al*. 2015) supported separation of Tonginae from Issinae *sensu stricto*, but placement within Issidae is postulated by these authors. Gnezdilov (2017) divided Nogodinidae into four subfamilies with 11 recent tribes: Bladininae Kirkaldy, 1907 with Bladinini, Colpopterinae Gnezdilov, 2003 with Colpopterini Gnezdilov 2003, Gastriniinae with Gastriniini Fennah, 1987, Nogodininae with tribes Lipocalliini, Nogodinini, Bilbiliini Gnezdilov, 2017, Mithymini, Pisachini, Varciini, Tongini and Epacriini. Extinct Celinapterixini Petrulevičius, 2005 are to be placed in Nogodininae (Bourgoin 2017).

Genus *Ambitaktoa* Szwedo gen. nov.

**Etymology.** Generic name is derived from the Proto-Celtic word 'ambitakto' meaning 'wander'. Gender: feminine.

**Type species.** *Ambitaktoa stoumma* sp. nov.; here designated.

**Diagnosis.** Characterised by the following combination of features: costal margin strongly curved at base, then gently curved, thickened; short common stem ScP + R leaving basal cell short, forked very basally; branch ScP + RA curved, subparallel to costal margin, branch RP nearly straight; stem MP forked at about 1/4 of tegmen length, anterior branch forked again; costal cell narrower than cell C1.

**Description.** Tegmen with costal margin thickened, strongly curved at basal portion than gently curved; anterior apical angle angulately rounded, posterior angle rounded. Stems ScP + R, MP and CuA leaving basal cell independently. Common stem ScP + R very short; branch ScP + RA curved, subparallel to costal margin, without additional branches, branch RP forked at level of basal line of veinlets, with three terminals. Stem MP forked at 1/4 of tegmen length, anterior branch forked again, mediad branch forked at level of basal veinlets, anteriad branch forked slightly apicad of basal line of veinlets; posterior branch forked at level of basal line of veinlets, i.e., vein MP with six terminals. Stem CuA not forked, reaching to posterior angle near apex of clavus. First veinlet ir basad of basal line of veinlets; basal line veinlets rp-mp, im and mp-cua almost in one line. Apical line of veinlets subparallel to apical margin.

*Ambitaktoa stoumma* Szwedo sp. nov.
(Pl. 9: 1; Fig. 49)

**Etymology.** Specific epithet is derived from the Proto-Celtic word 'stoumma' meaning 'bend'.

**Holotype.** NHMUK In.17282, Smith Collection. Tegmen with clavus missing.

**Diagnosis.** Cell C3a less than two times than adjoining subapical cell; cell C3b more than two times as long as adjoining subapical cells; apical line veinlet ir very short; three veinlets uniting posterior branch of vein MP and stem CuA in apical portion of tegmen.

**Description.** Length of tegmen 3.59 mm, width at widest point 1.5 mm. Other features as for the genus as it is the only included species.

Genus *Phariberea* Szwedo gen. nov.

**Etymology.** Generic name derived from the Proto-Celtic word 'pharibere' meaning 'enjoy'. Gender feminine.

**Type species.** *Phariberea gurdonika* sp. nov.; here designated.

**Diagnosis.** Larger than *Ambitaktoa* gen. nov.; costal margin strongly thickened (not so strongly thickened in *Ambitaktoa*); branch RA forked, with a few terminals (branch RA not forked in *Ambitakoa*); branch RP forked basad of first veinlet ir (branch RP not forked basad of ir in *Ambitakoa*); posteriad branch of MP forked (anteriad branch of stem MP forked in *Ambitaktoa*); costal cell wider than cell C1 (costal cell narrower than cell C1 in *Ambitaktoa*).

**Description.** Tegmen with costal margin strongly thickened, distinctly curved at base then gently curved; apical margin angulately rounded. Costal cell widest near base of tegmen, then narrowing, with a few branches of ScP + RA stem, reaching margin. Basal cell about twice as long as broad. Stems ScP + RA, RP, MP and CuA leaving basal cell separately. Stems ScP + RA and RP separated at base; stem RP forked distad of half of tegmen length, with six terminals. Stalk MP short, forked at 1/4 of tegmen length, then posterior branch forked again, i.e., three prenodal branches, branches of MP forked at level of preapical veinlets and apicad of preapical veinlets, probably eight terminals. Stem CuA forked slightly basad of nodal line. Clavus long, with apex exceeding 2/3 of tegmen length; claval veins Pcu and $A_1$ fused at half of clavus length. Preapical line of veinlets rp-mp, im, and mp-cua distinct, regular.

*Phariberea gurdonika* Szwedo sp. nov.
(Pl. 9: 2; Fig. 50)

**Etymology**. Specific epithet derived from the Proto-Celtic word 'gurdoniko' meaning 'rough'.

**Holotype.** NHMUK In.17096, Smith Collection, Insect Limestone, NW Isle of Wight. Tegmen, with some parts of membrane missing.

**Diagnosis.** Single prenodal veinlet rp-mp at level of nodal mp-cua veinlet; cell C3a elongate, cell C3b, about 3/4 of cell C3a length; additional veinlets rp-mp, ir and mp-cua apicad of preapical line of veinlets.

**Description.** Length of tegmen 4.8 mm, width at widest point *ca*.2 mm. Other features as for the genus as it is the only included species.

Genus *Wixskimoa* Szwedo gen. nov.

**Etymology**. Generic name derived from the Proto-Celtic word 'wixskimo' meaning 'turbulent'. Gender: feminine.

**Type species.** *Wixskimoa torxsea* sp. nov.; here designated.

**Diagnosis.** Tegmen smaller in size, with venation pattern similar to *Phariberea* gen. nov.; costal margin of tegmen more thickened than in *Phariberea*; branch RP forked distinctly apicad of first veinlet ir (branch RP forked basad of first ir in *Phariberea*); stem ScP + RA forked anteriad of branch $MP_{3+4}$ forking (ScP + RA forked posteriad of branch $MP_{3+4}$ forking in *Phariberea*); posterior branch of stem MP and anterior branch of stem CuA fused at point (distinct veinlet mp-cua present in *Phariberea*). Hindwing with single terminals of veins ScP + RA, RP and MP, CuA with three terminals.

**Description.** Tegmen with costal margin strongly thickened, distinctly curved at base, then nearly straight, apical margin rounded. Costal cell widest at base of tegmen then narrowing, transected by ScP + RA stem branches. Basal cell about twice as long as broad. Stems ScP + RA + RP, MP and CuA leaving basal cell separately. ScP + RA + RP with a very short common stem, ScP + RA forked anteriad of branch $MP_{3+4}$ forking, vein RA with three terminals reaching margin. Stem RP forked at level of preapical veinlet im, with three terminals. Stem MP forked at basal 1/4 of tegmen length, then posterior branch forked again at level of first RA terminal; two branches of MP forked basad of apical line of veinlets, five terminals reaching margin. Stem CuA forked slightly basad of veinlet ir.

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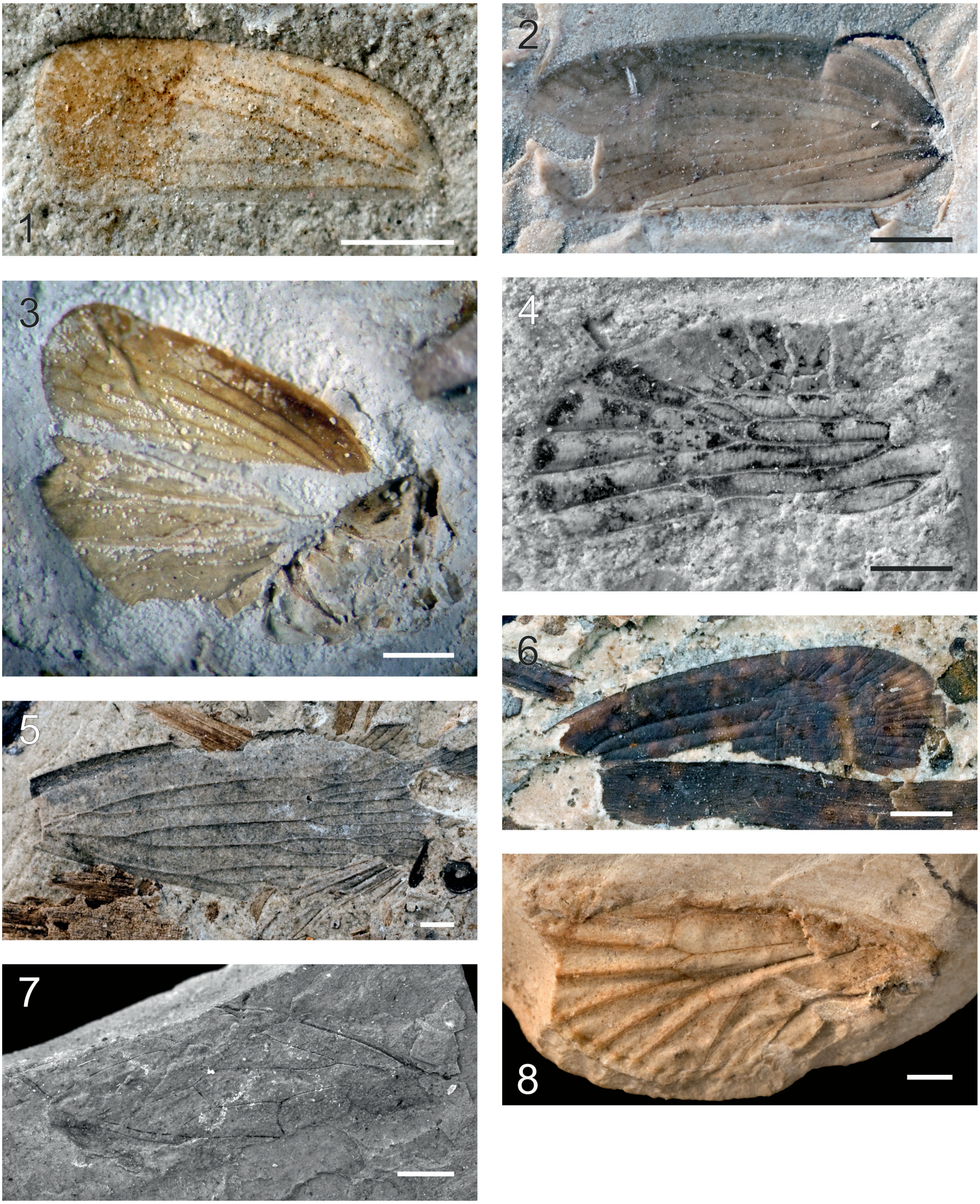


**Plate 9** (1) *Ambitaktoa stoumma* Szwedo gen. et sp. nov., holotype, NHMUK In.17282, tegmen. (2) *Phariberea gurdonika* Szwedo gen. et sp. nov., holotype, NHMUK In.17096, tegmen. (3) *Wixskimoa torxsea* Szwedo gen. et sp. nov., holotype, MIWG 3609, tegmen, part of wing and part of body. (4) *Niadrima yulei* Szwedo gen. et sp. nov., holotype, NHMUK II.3046, tegmen. (5) *Ankomwarius brodiei* Szwedo gen. et sp. nov., holotype, NHMUK I.8803, tegmen. (6) *Ankwlanno bluga* Szwedo gen. et sp. nov., holotype, NHMUK In.26069(1)b, tegmen, counterpart. (7) *Kintusamo boulardi* Szwedo gen. et sp. nov., holotype, NHMUK In.25267, tegmen. (8) Cicadidae, NHMUK In.25244, hindwing.

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Clavus long with apex exceeding 2/3 of tegmen length. Preapical veinlet ir slightly apicad of stem CuA branching; preapical veinlets rp-mp and im stepwise. Apical line of veinlets regular. Hindwing wide. Stem ScP + R with terminals ScRA and RP. Stem M single. Stem CuA forked distinctly basad of veinlets rp-mp and mp-cua, anterior branch forked again basad of veinlet mp-cua. Stem CuP single shifted from CuA. Intercubital fold distinct.

*Wixskimoa torxsea* Szwedo sp. nov.
(Pl. 9: 3; Figs 51, 52)

**Etymology**. Specific epithet from Proto-Celtic work 'torxse' meaning 'break'.

**Holotype**. MIWG 3609 (part and counterpart), Insect Limestone, NW Isle of Wight. Tegmen, part of wing and part of body.

**Diagnosis.** Cell C3a twice as long as cell C3b; cell C3b about 3/4 of length of adjoining subapical cell; subapical cells about 1.5 times as long as apical cells.

**Description.** Length of tegmen 4.35 mm, width of tegmen at widest point 1.6 mm. Other features as for the genus as it is the only included species.

**Remark.** It is the only specimen with a hindwing partly preserved. Visible portion of venation matches the hindwing venation of Nogodinidae as defined by Shcherbakov (1982).

Subfamily Colpopterinae Gnezdilov, 2003

Tribe Niadrimini Szwedo trib. nov.

**Type genus.** *Niadrima* Szwedo gen. nov.; here designated.

**Diagnosis.** Differs from Colpopterini by tegmina not so elongated, without apical narrowing, membrane with row of apical veinlets (numerous, often irregular veinlets in Colpopterini); stem ScP + R forked basad, stem MP forked apicad of stem CuA forking (similarly to Colpopterini, sometimes stem CuA single in Colpopterini); ScP + RA with two (three) terminals (as in Colpopterini), branches of M not forking on membrane (branches of MP forking on membrane in Colpopterini); branch $CuA_1$ single ($CuA_1$ sometimes branching or amalgamated with branches of MP in Colpopterini).

Genus *Niadrima* Szwedo gen. nov.

**Etymology.** Generic name is derived from the Proto-Celtic name '*ad-rīmā' meaning number with negative particle 'ni'. Gender: feminine.

**Type species.** *Niadrima yulei* sp. nov.; here designated.

**Diagnosis.** Tegmen with costal margin thickened, postcostal cell very wide, with prenodal veinlets; RP with two terminals reaching margin; stem MP forked apicad of stem CuA fork, branch $MP_{1+2}$ forked basad of apical line of veinlets; branch $MP_{3+4}$ single; branches $CuA_1$ and $CuA_2$ reaching margin as single terminals. Cell C3 about as long as cell C5. Radial cell with veinlets in apical portion.

**Description.** Tegmen with postcostal cell wide, intersected by prenodal veinlets. Stem ScP + R forked basad, branch ScP + RA reaching margin at anteroapical angle; branch RP forked at level of nodal area, with two terminals reaching margin at anteroapical angle. Stem MP forked slightly apicad of stem CuA forking, branch $MP_{1+2}$ forked slightly apicad of nodal line, reaching margin with single terminals $MP_1$ and $MP_2$, branch $MP_{3+4}$ not forked on membrane reaching margin as single terminal. Stem CuA forked in basal portion, terminals $CuA_1$ and $CuA_2$ single. Radial cell with a few transverse veinlets; nodal area with veinlets ir, and two veinlets rp-mp; apical line of veinlets composed of thick rp-mp, im, mp-cua and icua.

*Niadrima yulei* Szwedo sp. nov.
(Pl. 9: 4; Fig. 53)

**Etymology.** Specific epithet is given in honour to the collector of the specimen, Mr Andy Yule.

**Holotype.** NHMUK II.3046; Yule Collection, Insect Limestone, NW Isle of Wight. Apical portion of tegmen, with clavus missing.

**Diagnosis.** Branch RP forked at level of nodal area; terminal $ScRA_1$ forked; prenodal veinlets sigmoid; veinlets of radial cell oblique; apical veinlets im and mp-cua oblique. Cell C3a about 1/3 as long as cell C3. Apical cells longer than preapical cells C3a and C2c.

**Description.** Preserved portion of tegmen about 4.77 mm long. Venation distinct, veins thick. Anteroapical angle widely rounded. Costal cell about three times as wide as radial cell; radial cell with transverse veinlets in apical portion, basad of nodal area. apical margin with traces of darker coloration, apical cells intersected with narrow, darker band, anteroapical angle and apical line of veinlets with traces of darker coloration, nodal area with darker spot, traces of coloration along longitudinal veinlets on corium. Other characters as for genus.

Family Lophopidae Stål, 1866
Genus *Ankomwarius* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word 'ankomwari' meaning 'disarranged'. Gender: masculine.

**Type species.** *Ankomwarius brodiei* sp. nov.; here designated.

**Diagnosis.** Regarding tegmen venation similar to extant genera *Serida* Walker, 1857 and *Sarebasa* Distant, 1909, but differs in more branches of posteriad branch of vein CuA (mediad branch of CuA more branched in *Serida* and *Sarebasa*); stems $MP_{1+2}$ and $M_{3+4}$ branched apicad of half of tegmen length (stems $MP_{1+2}$ and $MP_{3+4}$ branched basad of half of tegmen length in *Serida* and *Sarebasa*); stem $MP_{1+2}$ branched more anteriad of stem $MP_{3+4}$ branching (stems $MP_{1+2}$ and $MP_{3+4}$ branched at same level in *Sarebasa*); stem RP forked posteriad of stem $MP_{3+4}$ branching (RP forked at same level in *Serida*, RP forked anteriad of stem $MP_{3+4}$ forking in *Sarebasa*); costal cell wider than basicostal field, with a few veinlets (costal cell without veinlets in *Serida* and *Sarebasa*, as wide as basicostal field in *Serida*, narrower than basicostal field in *Sarebasa*).

**Description.** Tegmen about 2.5 times as long as wide, with anterior margin gently curved. Basicostal field narrower than costal cell, with transverse veinlets. Stem ScP + R with a short common stalk. Stem ScP + RA forked slightly posteriad of stem RP forking. Stem RP forked basad of stem $MP_{1+2}$ forking, then mediad branch of RP forked basad of anteriad branch of RP. Stem MP forked apicad of stem ScP + R forking, basad of stem CuA forking. Branch $MP_{1+2}$ forked apicad of branch $MP_{3+4}$ forking. Stem CuA forked distinctly basad of stem $MP_{3+4}$ forking, then posteriad branch forked again, basad of stem $MP_{3+4}$ forking.

*Ankomwarius brodiei* Szwedo sp. nov.
(Pl. 9: 5; Fig. 54)

**Etymology.** Specific epithet is given in honour of eminent British palaeoentomologist and collector Rev. P. B. Brodie.

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**Holotype**. NHMUK I.8803, Brodie Collection, Insect Limestone, NW Isle of Wight. Part of tegmen.

**Diagnosis.** Cell C1 longer than cell C3; veinlet ir oblique, placed basad of branch ScP + RA forking; veinlet im slightly apicad of ir.

**Description.** Length of tegmen *ca.*14 mm width at widest point 5.5 mm. Other features as for the genus as it is the only included species.

**Remark.** The state of preservation is too incomplete for definite placement of the genus. Observable characters place it in the Sarebasa$^+$ group as defined by Soulier-Perkins (1998, 2000). It comprises a group of 11 extant genera, four of which are widely distributed on Oriental and Australian regions, and two present in Afrotropical, Oriental and Australian regions. Some of these genera have members which show a great ability to disperse. Biogeographic hypothesis for the group infers their common ancestor originated in Southeast Asia (Soulier-Perkins 2000). *Baninus thuringiorum* Szwedo & Wappler, 2006, representing another group of Lophopidae – the Bisma$^+$ group – is recorded from the Middle Eocene of Messel Maar in Germany (Szwedo & Wappler 2006). The oldest fossil Lophopidae comes from the Palaeocene of Tibet (Szwedo *et al.* 2015). The species described above also proves the presence of Lophopidae in Europe during the Palaeogene. The tropic relationships of Lophopidae need further attention, as the full host plant range is not entirely known (Soulier-Perkins 1998, 2000; Soulier-Perkins *et al.* 2007). The ancestor of the family Lophopidae was postulated as feeding on Arecaceae, with two later changes to Poaceae and Musaceae (Soulier-Perkins *et al.* 2007). The Sarebasa$^+$ group is the lineage which shifted to feed on Poaceae (Soulier-Perkins *et al.* 2007).

It could be postulated that *Ankomwarius* Szwedo had been inhabiting rather open areas in which monocotyledon host plants, maybe Poaceae, have been present. Massive diversification and expansion in Poaceae took place in the Palaeogene (Jones *et al.* 2014; Magallón *et al.* 2015). The success of some extant Lophopidae, particularly in African savannahs, could be related to expansion of grassy habitats during the Miocene (Soulier-Perkins 2000).

## Family Ricaniidae Amyot & Audinet-Serville, 1843

### Genus *Ankwlanno* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word ‘ankwlanno’ meaning ‘having no clan’. Gender: neuter.

**Type species.** *Ankwlanno bluga* sp. nov.; here designated.

**Diagnosis.** Tegmen with common stem ScP + R very short (longer common stalk present in *Hammapteryx anglica* Cockerell, 1920); common stem of M long. From *Hammapteryx anglica*, described from the Middle Eocene Bagshot Beds, Bournemouth, by distinctly narrower costal cell (distinctly wider than costal cell in *H. anglica*); stem RP not forked distinctly basad of subapical line (stem RP forked distinctly basad of subapical line in *H. anglica*).

**Description.** Tegmen about 2.5 times as long as wide, costal margin distinctly curved at base, then gently curved, anterior apical angle widely rounded. Costal cell narrower than costal cell. Stem ScP + R leaving basal cell with a very short common stalk, stem ScP + RA forked slightly basad of preapical line of veinlets. Stem RP forked slightly basad of preapical line of veinlets. Stem MP forked at about basal 1/3 of tegmen length, stem $MP_{1+2}$ forked at level of preapical veinlets, stem $MP_{3+4}$ forked distinctly more basad. Preapical line of veinlets almost straight and regular; apical line of veinlets arcuately stepwise, regular. Anteapical cells longer than apical cells.

**Remark.** Placement of particular species ascribed to the genus *Hammapteryx* remains unclear. Szwedo *et al.* (2004) placed the genus in the family Ricaniidae. Petrulevičius (2005) transferred *Hammapteryx paucistriata* Henriksen, 1922 to the newly erected genus *Henriksenopteryx* Petrulevičius, 2005. Shcherbakov (2006) moved the whole genus *Hammapteryx* to Nogodinidae *sensu lato*, discussing some of its venational characters, and placing generic status of *Hammapteryx* in doubt, but with no further discussion of this opinion. Placement of these fossils was not discussed by Gnezdilov (2007, 2017), and the features of Nogodinidae and Ricaniidae need much more attention as most of the venational characters used to distinguish these families need to be re-examined and re-interpreted.

### *Ankwlanno bluga* Szwedo sp. Nov.
(Pl. 9: 6; Fig. 55)

**Etymology.** Specific epithet from Proto-Celtic word ‘bluga’ meaning ‘piece’.

**Holotype.** NHMUK In.26069(1) a, b (part and counterpart, with a psychodid fly figured by Krzeminski *et al.* 2019), Hooley Collection, Insect Limestone, NW Isle of Wight. Incomplete tegmen.

**Diagnosis.** Tegmen with costal field equally wide near to the apical portion, when tapered; vein RP with six terminals; anteapical cells about 1.5 times as long as adjoining apical cells.

**Description.** Length of tegmen 6.8 mm, width at widest point 2.75 mm. Other features as for the genus as it is the only included species.

**Remark.** Placement of the genus *Ankwlanno* Szwedo described above in Ricaniidae is only tentative. It possesses some venation features close to the Afrotropical genera *Privesa* Stål, 1862a and *Acroprivesa* Schmidt, 1912. It also resembles *Henriksenopterix* Petrulevičius, 2005 (created for *Hammapteryx paucistriata* based on tegmen), which was placed in Nogodinidae *sensu lato* (Petrulevičius 2005; Shcherbakov 2006). This genus and *Celinapterix bellisima* Petrulevičius, 2005 were placed in Nogodinidae *sensu lato* on account of bidentate second and long first metatarsomeres discovered in *Celinapterix* and also RA not reaching tegminal apex, tornus remote from claval apex and one or two RA-RP branches sigmoidal (Petrulevičius 2005; Shcherbakov 2006). A monobasic tribe Celinapterixini is described from the Late Paleocene of Argentina (Petrulevičius 2005). The correct name of this tribe should be Celinapterygini, but according to Article 29.4 of the ICZN the spelling ‘Celinapterixini’ is to be maintained. However, the characters mentioned above are also found in some Ricaniidae, e.g., in the primitive genus *Cotrades* Walker, 1858 (Fennah 1949, 1968, fig. 3), that also lack a precostal lobe in the hindwings, characteristic of Ricaniidae (Shcherbakov 1982, 2006). In the genus *Ankwlanno* Szwedo vein RA seems not to reach apex, and branches of RA-RP are more or less sigmoidal, so its placement in Nogodinidae *sensu lato* or in Ricaniidae cannot be resolved. Placement of the species included in the genus *Hammapteryx* Scudder, 1890 requires further research. In particular, *Hammapteryx anglica* Cockerell from the Middle Eocene of the UK and some other Old World fossil species ascribed to this genus need revising. Some of them seem to represent Ricaniidae, while some others could be members of Nogodinidae *sensu lato*. Placement of some extinct taxa ascribed formerly to Ricaniidae, Nogodinidae and Flatidae was recently discussed by Shcherbakov (2006), who transferred some of them to Nogodinidae *sensu lato*.

## Suborder Cicadomorpha Evans, 1946

## Superfamily Cicadoidea Latreille, 1802

## Family Cicadidae Latreille, 1802

### Genus *Kintusamo* Szwedo gen. nov.

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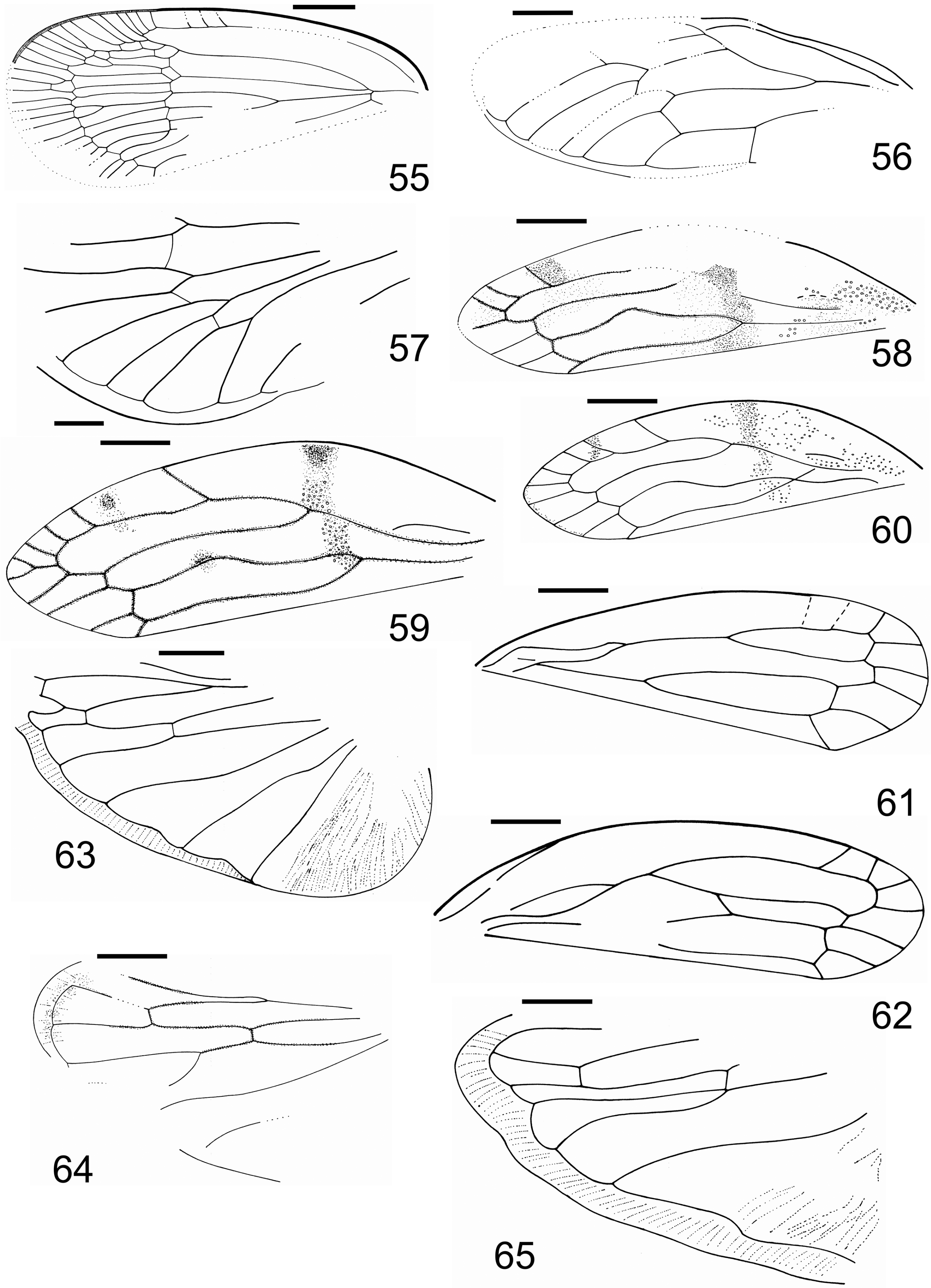


**Figures 55–65** (55) *Ankwlanno bluga* Szwedo gen. et sp. nov., holotype, NHMUK In. 26069(1)a, tegmen, part. (56) *Kintusamo boulardi* Szwedo gen. et sp. nov., holotype, NHMUK In.25267, tegmen. (57) Cicadidae, NHMUK In.25244, hindwing. (58) *Blenniphora woodwardi* (Cockerell, 1922), holotype, NHMUK In. 24363, tegmen, counterpart. (59–61) Tegmen: (59) *Blenniphora skaka* Szwedo gen. et sp. nov., holotype, CAMSM X.50140.90; (60) *Blenniphora bikkanoa* Szwedo gen. et sp. nov., holotype, NHMUK In.24503; (61) *Luisphantyelus briwus* Szwedo gen. et sp. nov., holotype, NHMUK In. 24533. (62) *Natajephora lijanka* Szwedo gen. et sp. nov., holotype NHMUK I.8874, tegmen, part. (63–65) Hindwing: (63) Aphrophoridae gen. et sp. indet. 1, NHMUK In.24496; (64) Aphrophoridae gen. et sp. indet. 2, NHMUK In.24501; (65) Aphrophoridae gen. et sp. indet. 3, NHMUK In.24560. Scale bar = 1 mm.

**Etymology.** Genus name derived from the Proto-Celtic word 'kintusamo' meaning 'first'. Gender: neuter.

**Type species.** *Kintusamo boulardi* sp. nov.; here designated.

**Diagnosis.** Similar in size to *Paracicadetta* Boulard & Nel, 1990 but differs by unfused and separated stems MP and CuA at basal cell (stems MP and CuA meeting at basal cell in *Paracicadetta*); forking of $CuA_1$–$CuA_2$ forming an acute angle (forking of $CuA_1$–$CuA_2$ forming an obtuse angle in *Paracicadetta*); apical cell a8 elongately rhomboidal, about twice as long as broad (cell a8 trapezoidal, about three times as long as broad in *Paracicadetta*).

**Description.** Tegmen about three times as long as broad. Pterostigma present, weak. Stem ScP + R close to costal margin. Branch $MP_{1+2}$ in basal part slightly concave. Veinlet r-mp in line prolonging basal portion of $MP_{1+2}$. Apical cell a8 trapezoid, about three times as long as broad; apical cells a6 and a5 of similar length.

*Kintusamo boulardi* Szwedo sp. nov.
(Pl. 9: 7; Fig. 56)

**Etymology.** Specific epithet is given in honour of eminent specialist on Cicadoidea – Michel Boulard.

**Holotype**. NHMUK In.25267, Insect Limestone, NW Isle of Wight. Tegmen with apical portion and clavus indistinct.

**Diagnosis.** Apical cell a8 elongately rhomboidal; subapical veinlets mp-cua and im placed slightly apicad of stem $MP_{1+2}$ and $MP_{3+4}$ forkings.

**Description.** Preserved length of tegmen 15 mm, width at widest point 5.3 mm.

**Remark.** Few fossil Cicadidae have been described from Cenozoic deposits (Cooper 1941; Metcalf & Wade 1966; Wagner 1967; Fujiyama 1969, 1979, 1982; Kinugasa & Miyatake 1976; Kinugasa & Yorio 1979; Boulard & Riou 1988, 1999; Boulard & Nel 1990; Carpenter 1992; Riou 1995; Prokop & Boulard 2000; Moulds 2018). The higher classification of Cicadoidea was recently presented by Moulds (2005), and alternative views are presented by Sanborn (2014). Unfortunately the venation of the tegmen is of limited use for taxonomic purposes. The specimen of *Kintusamo* Szwedo is only part of tegmen and it is very difficult to make a formal placement for it in one of the recently recognised subfamilies and tribes. According to Moulds (2005, 2018) separation of the stems MP and CuA at basal cell excludes it from Cicadettini Buckton, 1890. Presence of pterostigma relates it to Cryptotympanini Handlirsch, 1925, the tribe to which some Early Oligocene taxa from Europe and North America are placed, and with fossil East Asian Leptopsaltriini Moulton, 1923 (Moulds 2018), to which it is also similar in structure of basal part of $MP_{1+2}$ branch and prolonging r-mp veinlet.

Gen. et sp. indet.
(Pl. 9: 8; Fig. 57)

**Material.** NHMUK In.24511/In.25244 (part and counterpart) Hooley Collection, Insect Limestone, NW Isle of Wight. Hindwing with anal and apical portions missing.

**Description.** Preserved portion of hindwing length 8.33 mm.

**Remark.** The venation of the hindwing is of limited use for taxonomic purposes. The specimen is only partly preserved and it is impossible to make a formal placement for it. As the appendix is relatively wide, it seems more likely to belong to the Cicadidae than the Tettigarctidae; however, Tettigarctidae were present in Europe during the Palaeogene (Zeuner 1944).

## Superfamily Cercopoidea Leach, 1815

## Family Aphrophoridae Amyot & Audinet-Serville, 1843

### Genus *Blenniphora* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word 'blenni' meaning 'spittle'. Gender: masculine.

**Type species.** *Aphrophora woodwardi* Cockerell, 1922; here designated.

**Diagnosis.** Tegmen shape and venation similar to *Aphrophora* Germar, 1821, but differs in stem MP distinctly curved mediad apicad of half of tegmen length (stem MP nearly straight in *Aphrophora*); terminal branches of RP not forked before apex (terminal branches of RP usually forked just before apex in *Aphrophora*).

**Description.** Tegmen about three times as long as wide, costal margin distinctly curved, apical portion acutely rounded, clavus long, surface punctate. Stem Sc + R forked basad of half of tegmen length, but apicad of stem MP + CuA forking. Vein $ScRA_1$ distinctly oblique, RA with three terminals. Vein RP forked apicad of r-m veinlet, with three terminals. Stem M + CuA forked distinctly basad of half of tegmen length; vein M distinctly curved mediad apical of half of tegmen length. Vein CuA sigmoidal.

*Blenniphora woodwardi* (Cockerell, 1922) comb. nov.
(Pl. 10: 1; Fig. 58)

v*1922 *Aphrophora woodwardi* Cockerell, p. 159, fig. 1.
1992 *Aphrophora* Cockerell, 1922; Carpenter, p. 231.

**Holotype.** NHMUK In. 24363/In.64098 (part and counterpart), Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen with clavus and median part of costal portion missing.

**Diagnosis.** Tegmen about three times as long as wide, costal margin distinctly arcuate, apical portion acutely rounded. Narrow darker band at basal 1/3 of tegmen length. Veins thick, darker. Surface covered with minute punctuation. Darker band at level of stem ScP + R forking, darker spot at level of vein $RA_2$ branching.

**Description.** Length of tegmen 6.5 mm, width of tegmen 1.9 mm.

**Remark.** Subfamilial and tribal assignment could not be given on the basis of preserved material.

*Blenniphora skaka* Szwedo sp. nov.
(Pl. 10: 2; Fig. 59)

**Etymology.** Specific epithet from Proto-Celtic word 'skak' meaning 'jump'.

**Holotype**. CAMSM X.50140.90 (TN 145), Smith Collection, Insect Limestone, NW Isle of Wight. Tegmen with clavus missing.

**Diagnosis.** Larger than *Blenniphora woodwardi* (Cockerell). Stem RP curved mediad in apical portion, forked slightly apicad of veinlet ir; anteriad branch forked again just before margin.

**Description**. Length of tegmen 7.2 mm, width 2.6 mm. Tegmen about 2.8 times as long as broad. Stem Sc about as long as common stalk ScP + R. Veins darker. Dark band slightly basad of stem ScP + R forking, continuing on stem MP+CuA forking, with more dark spot near costal margin. Darker spot on the vein MP at level of vein ScP + $RA_1$ branching. Two darker spots slightly basad of vein $RA_2$ forking.

*Blenniphora bikkanoa* Szwedo sp. nov.
(Pl. 10: 3; Fig. 60)

**Etymology.** Specific epithet from Proto-Celtic word 'bikkano' meaning 'small'.

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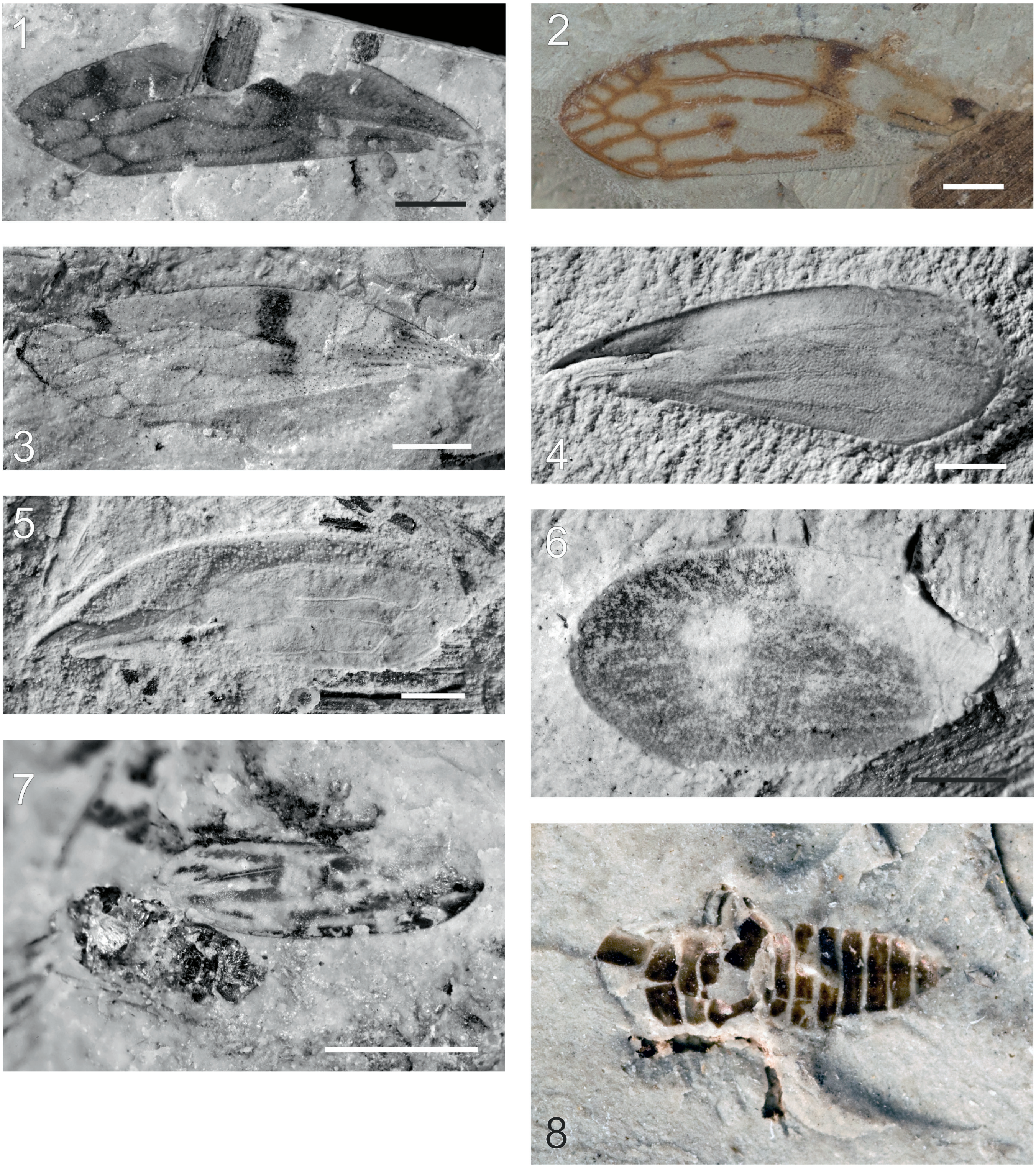



**Plate 10** (1) *Blenniphora woodwardi* (Cockerell, 1922), holotype, NHMUK In. 24363, tegmen, counterpart. (2) *Blenniphora skaka* Szwedo gen. et sp. nov., holotype, CAMSM X.50140.90, tegmen. (3) *Blenniphora bikkanoa* Szwedo gen. et sp. nov, holotype, NHMUK In.24503, tegmen. (4) *Luisphantyelus briwus* Szwedo gen. et sp. nov., holotype, NHMUK In. 24533, tegmen, part. (5) *Natajephora lijanka* Szwedo gen. et sp. nov., holotype, NHMUK I.8874, tegmen, part. (6) *Berro enissuextaensis* Szwedo gen. et sp. nov., holotype, NHMUK In.43467, tegmen. (7) *Teniwitta andrewrossi* Szwedo gen. et sp. nov., holotype, NHMUK In.20529, body and tegmen. (8) Cicadellidae nymph/exuvium, NHMUK I.9637.

**Holotype**. NHMUK In.24503, Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen with clavus missing.

**Diagnosis.** Smaller than *Blenniphora woodwardi* (Cockerell). Branch MP sinuate, branch RP in apical part curved mediad, forked at level of apical veinlet ir. Subapical cubital cell widest in apical portion.

**Description.** Length of tegmen 5.8 mm, width of tegmen 1.9 mm.

**Remark.** Subfamilial and tribal assignment could not be given on the basis of preserved material.

Genus *Luisphantyelus* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word 'luisphant' meaning 'toad, frog' combined with *Ptyelus*, genus name of cercopoid. Gender: masculine.

**Type species.** *Luisphantyelus briwus* sp. nov.; here designated.

**Diagnosis.** Tegmen similar to *Blenniphora* Szwedo, but differs in vein MP almost straight (stem MP distinctly curved in *Blenniphora*); stem ScP + R forked apicad of half of tegmen length (stem ScP + R forked basad of half of tegmen in *Blenniphora*); vein RP with single terminal (vein RP with three terminals in *Blenniphora*).

**Description.** Tegmen elongate, about three times as long as wide. Costal margin curved, apical margin rounded, clavus long. Stem Sc long. Common stem ScP + R forked distinctly apicad of half of tegmen length. Branch RA with three (?) terminals, branch RP single. Stem MP+CuA forked distinctly basad of half of tegmen length, branch MP nearly straight.

*Luisphantyelus briwus* Szwedo sp. nov.
(Pl. 10: 4; Fig. 61)

**Etymology.** Specific epithet from Proto-Celtic word 'briwo' meaning 'fragment'.

**Holotype**. NHMUK In. 24533/In. 24540 (part and counterpart), Hooley Collection, Insect Limestone, NW Isle of Wight.

**Diagnosis.** Apex of tegmen rounded; apical veinlet m-cu basad of apical veinlet ir; subapical median cell about as long as half of tegmen.

**Description.** Length of tegmen 6.5 mm, width of tegmen 2.3 mm. Other features as for the genus as it is the only included species.

Genus *Natajephora* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word 'nataje' meaning 'jump, fly', combined with suffix '~*phora*', common for cercopoids. Gender: feminine.

**Type species.** *Natajephora lijanka* sp. nov.; here designated.

**Diagnosis.** Similar to *Luisphantyelus* Szwedo, but tegmen slightly longer; stem ScP + R forked basad of half of tegmen length (stem ScP + R forked apicad of half of tegmen length in *Luisaphantyelus*); subapical veinlet mp-cua present (lack of such veinlet in *Luisaphantyelus*).

**Description.** Tegmen with costal margin distinctly curved at base, mildly curved in median portion, apical portion elongately rounded. Stem ScP long, common stalk ScP + R short, forked distinctly basad of half of tegmen length. Vein ScP + $RA_1$ reaching margin at level of claval apex, vein RA with two terminals; vein RP single. Stem MP nearly straight, with single terminal. Preapical and apical veinlets rp-mp oblique.

*Natajephora lijanka* Szwedo sp. nov.
(Pl. 10: 5; Fig. 62)

**Etymology.** Specific epithet from Proto-Celtic word 'lijank' meaning 'stone'.

**Holotype**. NHMUK I.8555/I.8874, Brodie Collection, Insect Limestone, NW Isle of Wight. Tegmen, clavus missing.

**Diagnosis.** Interradial cell slightly shorter than half of tegmen length

**Description.** Length of tegmen 7.3 mm, width 2.2 mm.

**Stratigraphical range.** Insect Limestone, Bembridge Marls, Bouldnor Formation, Priabonian, latest Eocene.

**Occurrence.** NW Isle of Wight, UK.

Gen. et sp. indet. 1
(Fig. 63)

**Material.** NHMUK In.24496, Hooley Collection, Insect Limestone, NW Isle of Wight. Part of hindwing, with apex missing.

**Description.** Preserved length 6.4 mm, width 3.4 mm. Hindwing with vein RP forked before apex, apicad of veinlet rp-mp. Vein CuA not forked before apex. Veinlet mp-cua short, placed slightly apicad of stem ScP + R forking. Anal field heavily wrinkled.

**Remark.** Specimens number In. 24515 and In. 24523 from the same locality and collector; may belong to the same taxon.

Gen. et sp. indet. 2
(Fig. 64)

**Material.** NHMUK In.24501, Hooley Collection, Insect Limestone, NW Isle of Wight. Part of hindwing, with base and anal portion missing.

**Description.** Similar to gen. et sp. indet. 1, but slightly smaller, preserved length 5.56 mm. Hindwing with vein RP single, vein CuA forked distinctly apicad of mp-cua veinlet. Apical portion at ambient vein darker.

**Remark.** CAMSM X.50140.145 (TN 203), Smith Collection, may also belong to this taxon.

Gen. et sp. indet. 3
(Fig. 65)

**Material.** NHMUK In.24560, Smith Collection, Insect Limestone, NW Isle of Wight. Part of hindwing, with base and anal portion missing.

**Description.** Preserved length 6.5 mm. Hindwing with vein RP single, vein MP single. Veinlet rp-mp close to the apex; veinlet m-cu at level of vein CuA forking.

Family Cercopidae Westwood, 1838

Genus *Berro* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic word 'berro' meaning 'short'. Gender: neuter.

**Type species.** *Berro enissuextaensis* sp. Nov.; here designated.

**Diagnosis.** Tegmen with venation similar to extant genus *Aufidus* Stål, 1863, but smaller. Tegmen with three cells formed by terminals of stem ScP + RA (five or six cells in *Aufidus*). Four big apical cells as in *Aufidus.*

**Description.** Tegmen about twice as long as broad, apical margin rounded, with distinct appendix. Branch ScP + $RA_1$ forked slightly basad of branch $CuA_2$, vein RA with three terminals. Vein RP with single terminal, vein MP with single terminal. Apical veinlet ir slightly oblique. Apical cells slightly longer than wide.

*Berro enissuextaensis* Szwedo sp. nov.
(Pl. 10: 6; Fig. 66)

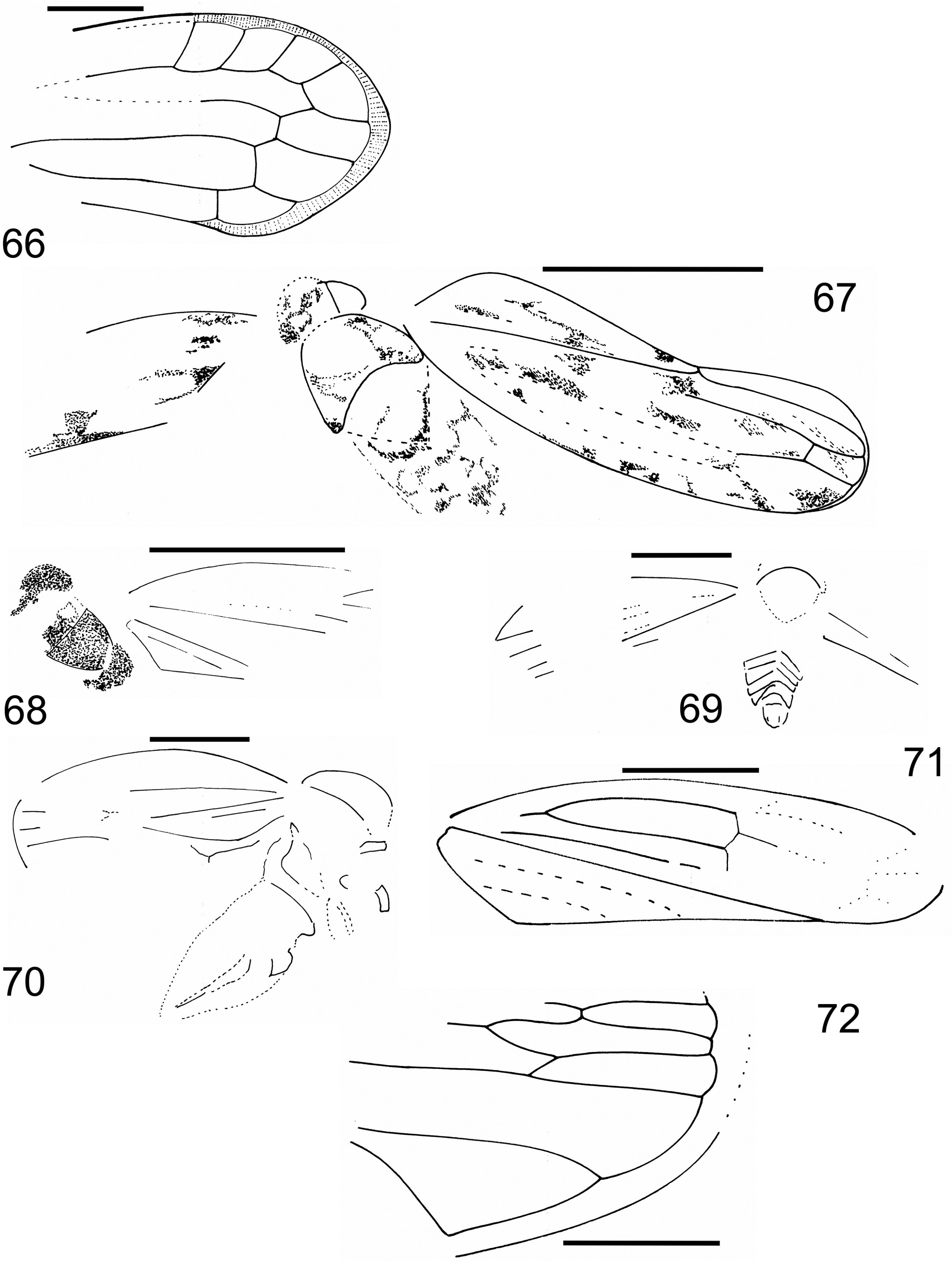
**Etymology.** Specific epithet from ancient British name of Isle of Wight – Eniss Uexta.

**Holotype**. NHMUK In.43467, Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen, with base and clavus missing

**Diagnosis.** Apical cells a2 and a3 of similar length; apical cells a1 and a4 shorter than cells a2 and a3.

**Description.** Length of tegmen. 4.7 mm, width of tegmen 2.3 mm.

**Remark.** Tribal assignment could not be given on the basis of preserved material.




**Figures 66–72** (66) *Berro enissuextaensis* Szwedo gen. et sp. nov., holotype NHMUK In.43467. (67) *Teniwitta andrewrossi* gen. et sp. nov., holotype NHMUK In.20529, parts of body and tegmina. (68) Cicadellidae: Typhlocybinae gen. et sp. indet., NHMUK In.17142(3). (69) Cicadellidae: Typhlocybinae gen. et sp. indet., NHMUK I.9720 , tegmen. (70) Cicadellidae: Typhlocybinae gen. et sp. indet., NHMUK I.9095. (71) Cicadellinae gen. et sp. indet. 1, NHMUK In.24507, tegmen. (72) Cicadellidae gen. et sp. indet. 2, NHMUK In.43466, part of hindwing. Scale bar = 1 mm.

Superfamily Cicadelloidea Latreille, 1802

Family Cicadellidae Latreille, 1802

Subfamily Mileewinae Evans, 1947

Tribe Mileewini Evans, 1947

Genus *Teniwitta* Szwedo gen. nov.

**Etymology.** Genus name derived from the Proto-Celtic words 'teni' meaning 'delicate' and 'witta' meaning 'vein'. Gender: feminine.

**Type species.** *Teniwitta andrewrossi* sp. nov.; here designated.

**Diagnosis.** In general habitus similar to extant genus *Ujna* Distant, 1908 and extinct genera *Eomileewa* Gebicki & Szwedo, 2001 and *Youngeewa* Gebicki & Szwedo, 2001, but distinctly smaller. Length of tegmen less than 2.5 mm (over 3 mm in *Ujna*, *Eomileewa* and *Youngeewa*). Tegmen uniformly narrow (more widened in postclaval portion in *Ujna*, *Eomileewa* and *Youngeewa*); head with apex more round than in *Ujna*, *Eomileewa* and *Youngeewa.*

**Description.** Vertex in mid line about as long as wide, compound eyes distinct. Pronotum in mid-line longer than vertex in mid-line. Tegmen uniformly wide, merely widened in post claval portion. Longitudinal veins delicate. Apex of clavus exceeding half of tegmen length.

*Teniwitta andrewrossi* Szwedo sp. nov.
(Pl. 10: 7; Fig. 67)

**Etymology.** Species named in honour of Dr Andrew J. Ross, eminent palaeoentomologist and Principal Curator of Palaeobiology at the National Museum of Scotland, Edinburgh, who made the studies of Insect Limestone material possible.

**Holotype**. NHMUK In.20529, Smith Collection, Insect Limestone, NW Isle of Wight. Right tegmen, body and part of left tegmen.

**Diagnosis.** Head and pronotum darkly coloured. Tegmen 3.75 times as long as wide, apex of clavus exceeding half of tegmen length, appendix narrow. Tegmen with indistinct patchy coloration.

**Description.** Length of preserved part of body 1.35 mm, head with compound eyes 0.47 mm, vertex in mid line 0.2 mm long. Length of tegmen 2.2 mm.

**Remark.** The Mileewinae were redefined by Dietrich (2011). Previously Mileewinae included only the nominotypical tribe, and redefined include tribes Mileewini, Tinteromini Godoy & Webb, 1994 and Makilingiini Evans, 1947 (both previously treated as separate subfamilies), as well as tribe Tungurahualini Dietrich, 2011.

Subfamily Typhlocybinae Kirschbaum, 1868

Gen. et sp. indet.
(Figs 68–70)

**Material.** NHMUK In.17142(3) (Fig. 68), (with a paratype of *Mastotermes anglicus* Rosen, 1913 and a cockroach tegmen (Blattodea: Ectobiidae) described by Ross (2019)), Smith Collection, Insect Limestone, NW Isle of Wight. Head, parts of thorax and abdomen, tegmen and hindwing partly preserved. NHMUK I.9720 (Fig. 69), remnants of head, thorax, abdomen and tegmina. NHMUK I.9095 (Fig. 70), remnants of body and tegmen.

**Remark.** These specimens belong to the subfamily Typhlocybinae, but the state of preservation does not allow the placement of these specimens in one of the recognised extinct or extant tribes (Gębicki & Szwedo 2006). The extant Typhlocybinae are leafhoppers distributed worldwide, with a known diversity of about 470 genera and 5200 species (Dietrich 2006). Fossil representatives of the group are poorly known and these scarce records needs to be reconsidered. The oldest known representatives of Typhlocybinae are placed in the extinct tribe Protodikraneurini Gębicki & Szwedo, 2006, from Eocene Baltic amber. Several other fossil taxa described from Late Eocene Baltic amber, Middle Eocene deposits of Roan Mountain, Colorado, Late Eocene deposits of Florissant, Colorado, USA, clearly represent Typhlocybinae, but need to be re-examined and redescribed (Gębicki & Szwedo 2006). The oldest representatives of the extant tribe Dikraneurini is a specimen mentioned and described by Dietrich & Vega (1995), from Miocene Dominican amber.

Subfamily Cicadellinae Latreille, 1802

Gen. et sp. indet. 1
(Fig. 71)

**Material.** NHMUK In.24507, Hooley Collection, Insect Limestone, NW Isle of Wight. Tegmen.

**Description.** Tegmen 3.8 mm long, 1.1 mm wide. Costal margin slightly arcuate, apex of clavus at about 3/4 of tegmen length. Stem ScP + R + MP forked basad of basal 1/4 of tegmen length. MP forked slightly basad of 2/3 of tegmen length.

**Remark.** Placement of this specimen in the subfamily Cicadellinae is only tentative. The interpretation of Cicadellinae follows Young (1968, 1977, 1986) in including only the tribes Cicadellini and Proconiini (Dietrich 2005).

Cicadellidae gen. et sp. indet. 2
(Fig. 72)

**Material.** NHMUK In.43466/II.2866 (part and counterpart), Hooley Collection, Insect Limestone, NW Isle of Wight. Part of hindwing, with base and anal portion missing.

**Description.** Preserved portion 3.5 mm long. Hindwing with vein RP single, vein MP single. Vein CuA forked basad of veinlet rp-mp. Veins RP and MP close each other, veinlet rp-mp short. Veinlet mp-cua long, oblique. Wing smoked.

Cicadellidae nymph/exuvium
(Pl. 10: 8)

**Material.** Nymph/exuvium, NHMUK I.9637, Brodie Collection, Insect Limestone, NW Isle of Wight.

**Discussion.** Over 220 specimens deposited in the NHM in London, Maidstone Museum and Sedgwick Museum, Cambridge were investigated. Eight families of Fulgoromorpha (Fulgoroidea) and four families of Cicadomorpha (Cicadoidea, Cercopoidea and Cicadelloidea) were identified. Thirty-five new species of Fulgoromorpha and Cicadomorpha are described (27 and eight respectively) in addition to four species formerly described.

The Bembridge Marls fauna, preserved in the late Eocene Insect Bed of the Isle of Wight, with regard to family composition differs from the fauna of the Eocene Baltic amber. Unfortunately, Baltic amber planthoppers (Fulgoromorpha) and leafhoppers (Cicadomorpha) are still insufficiently studied, which prevents simple comparison. The coeval fauna of planthoppers and leafhoppers of Florissant, Colorado is also insufficiently known (Scudder 1890, 1892; Cockerell 1906, 1908a; Lewis & Heikes 1991) and the taxa described require urgent revisionary studies. This fossil site presents representatives of Achilidae, Dictyopharidae, Fulgoridae, Nogodinidae *sensu lato*, Cicadidae, Aphrophoridae, Clastopteridae and Cicadellidae, similarly to the Bembridge Marls fauna. Unfortunately, the state-of-the art on planthoppers and leafhoppers from the

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Florissant beds precludes the detailed comparison with these insects preserved in the Bembridge Marls. Few species of planthoppers and leafhoppers have been reported form the earliest Miocene strata of Rott in Germany (Statz 1950); Cicadellidae are dominant in this fossil assemblage, but the material requires revision. Taphonomic conditions during fossilisation of planthoppers and leafhoppers in the Insect Bed of the Isle of Wight and in Baltic amber were different. However, both faunas share some common elements at the family level. Representatives of the family Cixiidae are most numerous in both faunas. Bothriocerine cixiids, recently limited in distribution to the New World, are present in Baltic amber and in the Insect Bed. The oldest record of Bothriocerinae is found in the Palaeocene Fur Formation of Denmark (undescribed), while the New World record is from Miocene Dominican amber (Schlee 1990). One may assume that the taxon originated in Europe, and migrated to North America, then spread to Central and South America. It could be hypothesised that this migration took place during the Palaeocene–Eocene Thermal Maximum, about 55.5 Mya, through the Thulean Bridge, a corridor connecting Europe, Greenland and North America (McKenna 1983; Sanmartín *et al*. 2001; Smith *et al*. 2006). Recent distribution and diversity of Bothriocerinae resulted rather from the reduction of the ancestral range and secondary diversification on the islands of the Caribbean (Szwedo 2002). The biology of Bothriocerinae is poorly known; host plants (Wilson *et al*. 1994) comprise the families Pinaceae (gymnosperms), Fagaceae, Rubiaceae, Polygonaceae, Chrysobalanaceae, Solanaceae, Asteraceae (dicotyledone angiosperms), Arecaceae, Juncaceae, Cyperaceae, Commelinaceae, Poaceae (monocotyledone angiosperms). Representatives of the subfamily Cixiinae found among the Bembridge Marls fossils are Mnemosynini, Pentastirini and Cixiini. The record of Mnemosynini is known since the Palaeocene Fur Formation of Denmark (undescribed), uppermost Palaeocene of Menat in France and Eocene Baltic amber (Szwedo 2004; Szwedo *et al*. 2006), and Miocene Mexican amber (Fennah 1963). Recent representatives of Mnemosynini are distributed in subtropical and tropical zones of the world, with only two host plant records on Poaceae and Cactaceae (Myers 1929; Stalle 1987; Wilson *et al*. 1994). Fossil representatives ascribable to Pentastirini are reported from mid-Cretaceous Burmese amber (Grimaldi *et al*. 2002); other undescribed forms are known from the Palaeogene of Denmark and described taxa from the Eocene Baltic amber (Szwedo & Stroiński 2002), Miocene Dominican amber (Szwedo 2000) and the earliest Miocene strata of Germany (Statz 1950). In respect to their host plants, Pentastirini are recorded from a wide spectrum of plant families: Agavaceae, Amaranthaceae, Arecaceae, Asteraceae, Batidaceae, Betulaceae, Blechnaceae (fern), Brassicaceae, Caricaceae, Chenopodiaceae, Convolvulaceae, Dicksoniaceae, Ebenaceae, Ericaceae, Euphorbiaceae, Fabaceae, Flacourtiaceae, Frankeniaceae, Gesneriaceae, Hydrangiaceae, Lamiaceae, Liliaceae, Malvaceae, Moraceae, Myrtaceae, Oleandraceae, Pinaceae, Poaceae, Rhizpohoraceae, Salicaceae, Solanaceae, Tamaricaceae, Urticaceae, Verbenaceae, Zygophyllaceae, but at the species level most Pentastirini are oligophagous. Representatives of the tribe Cixiini were previously known from Baltic amber and from Dominican amber (Szwedo *et al*. 2004). These planthoppers are related to plant families: Arecaceae, Chenopodiaceae, Cupressaceae, Ehteriaceae, Ericaceae, Fagaceae, Juglandacaea, Malvaceae, Oleaceae, Pinaceae, Plumbaginaceae, Poaceae, Rosaceae, Salicaceae, Sapindaceae and Tamaricaceae (Wilson *et al.* 1994). The host plants of Pintalini are virtually unknown; the only record comes from Alismataceae (Wilson *et al.* 1994). The family Achilidae is represented among the Bembridge palaeoentomofauna by *Hooleya indecisa* Cockerell of the tribe Achillini and two poorly preserved additional specimens. Most Achilidae are not phloem feeders like the majority of planthoppers but feed on the hyphae of fungi. Achillini are represented in the extant fauna by only two genera from Western and Central Africa, so the finding of another representative of the tribe in the Isle of Wight from Late Eocene deposits is very interesting. Achilidae are quite common in Eocene Baltic amber, but represented by taxa of other tribes including two extinct ones (Szwedo 2006a). The sole achilid described from the Late Eocene of Florissant requires revision. Inclusions in Miocene Dominican amber are representative of the most numerous recent tribe, Plectoderini Fennah, 1950. Among the Bembridge palaeoentomofauna the family Tropiduchidae is represented by the extant tribes Catullini and Trypetimorphini and by a very interesting find of the tribe Jantaritambini, previously known only from Baltic amber. Host plant range of recent Catullini comprises Rutaceae, Poaceae and Cyperaceae, and genera of the tribes occur in Afrotropical and Oriental Regions. The Trypetimorphini host plant range comprises Arecaceae, Poaceae and Cyathaceae and today the tribe is widely distributed in Afrotropical, Palaearctic, Oriental and Australian regions (Metcalf 1954; Fennah 1982; Wilson *et al*. 1994). Genera of Tropiduchidae: Gaetulini are recently distributed in tropical and subtropical zones all around the world (Fennah 1984). The fossils from the Bembridge Marls seem to be related to extant taxa from the Oriental region. The family Issidae is distributed worldwide with widely known host plant ranges (Wilson *et al*. 1994): Arecaceae, Asteracae, Chenopodiaceae, Clusiaceae, Corylaceae, Cupressaceae, Cyathacae, Ericaceae, Ephedraceae, Euphorbiaceae, Fabaceae, Fagaceae, Hypericaceae, Moraceae, Pinaceae, Piperaceae, Poaceae, Polygonaceae, Rosaceae, Santalaceae, Scrophulariaceae, Solanaceae, Tamaricaceae, Verbenaceae and Vitaceae, with a number of polyphagous forms. The host plant spectrum of Nogodinidae is poorly known; it comprises Apocynaceae, Asteraceae, Myrtaceae and Steruliacae (Wilson *et al*. 1994). The tribe Ambitaktoini are known only from the Insect Bed of the Isle of Wight. The fossil record of Nogodinidae is relatively rich (Szwedo *et al*. 2004; Shcherbakov 2006). Host plant records of the family Lophopidae comprise Arecaceae, Bignoniaceae, Fabaceae, Poaceae, Myrtaceae and Rubiaceae (Wilson *et al*. 1994; Soulier-Perkins *et al.* 2007), but lophopids are believed to feed mainly on the monocot families Arecaceae, Musaceae and Poaceae (Soulier-Perkins 1998, 2000; Soulier-Perkins *et al.* 2007). Recently, the family is distributed in the tropical zone of the Afrotropical, Oriental, Australian and Neotropical Regions. Known fossils occur in the Palaeocene of Menat in France, Palaeocene deposits of Tibet and the Middle Eocene Messel Maar in Germany (Szwedo & Wappler 2006; Stroiński & Szwedo 2012; Szwedo *et al*. 2015). The host plant range of recent Ricaniidae comprises the families Araceae, Arecaceae, Canabidaceae, Fabaceae, Flacourtiaceae, Malvaceae, Moraceae, Myrtaceae, Oleaceae, Pandanaceae, Pittosporaceae, Poaceae, Rubiaceae, Santalaceae and Theaceae. The fossil record of the family needs reconsideration and revision as numerous taxa previously placed in the Ricaniidae were proposed to belong to Nogodinidae (Shcherbakov 2006).

In contrast to phloem-feeding Fulgoromorpha, cicadomorphan Cicadidae (singing cicadas) are notable xylem-feeders. Singing cicadas are peculiar with endogeic nymphal life habits, with prolonged nymphal development lasting up to 17 years in some recent Nearctic species (Karban 1986). It is noteworthy that for cicadas (and other xylem feeders as well) woody and tall-growing species of host plants do not play a role. In particular, the nymphs are seldom recorded from woody plants, although after emergence relatively numerous species perform an obligate stratum shift from the soil or herbaceous layer up to tall herbs or up to the canopies (Nickel 2003). Another group of Cicadomorpha – Cercopoidea – feed almost exclusively on xylem sap and are believed to be oligophagous to widely polyphagous on a wide variety of host plants. Very generally speaking, Aphrophoridae are regarded as feeding on conifers and herbaceous dicotyledones, while Cercopidae tend to feed on herbaceous monocotyledones (Carvalho & Webb 2005). Within the diversity of host plants, numerous cercopoids have a predilection for nitrogen-fixing plants. The Cercopidae prefer plants with associative nitrogen fixation through root zone bacteria (Thompson 2004), while Aphrophoridae prefer legumes, plants of the Fabaceae and related families (Carvalho & Webb 2005).

Phloem feeding is widespread among the biggest cicadomorphan family, Cicadellidae, with some exceptions. The subfamily Typhlocybinae is the only group adapted to mesophyll feeding, which required dramatic morphological and physiological adaptations. Within Cicadellidae numerous phloem-feeding subtaxa are largely arboreal (e.g., Fagacae, Betulaceae, Tiliaceae, Aceraceae, Salicaceae) while others predominate on Poaceae, Cyperaceae and Juncaceae (Nickel 2003). Very little is known about host plants of Mileewinae, only a scant record on Asteraceae and Urticaceae exists (Chiang & Knight 1991) and they are found in moist habitats in the understory of shrubs and small trees in montane tropical and subtropical forest regions (Linnavuori 1979; Nielson & Godoy 1995). The tribe is recently widespread in the Ethiopian, Oriental and Neotropical Regions, and comprises only four endemic genera with 90 species (Nielson & Knight 2000; Dietrich 2006), plus three extinct genera are known from European deposits. Mesophyll feeding Typhlocybinae, exploiting advanced herbaceous angiosperms such as Lamiaceae, Asteraceae, Poaceae, Cyperaceae, which are likely to constitute a more recent evolutionary trend. However, more basal tribes – Empoascini and Dikraneurini – seem to present a more general, ancestral trait in comparison to 'higher' Typhlocybinae (Nickel 2003). Typhlocybinae is a large, distinctive, cosmopolitan group, that is especially rich in the Oriental region (Nielson & Knight 2000), with a relatively rich fossil record (Gębicki & Szwedo 2006).

It could be hypothesised that planthoppers and leafhoppers of the Bembridge Marls Insect Bed present a non-homogenous picture of taxa inhabiting more open habitats, shrubland and or woodland during the Late Eocene. Taxa supposed to live in more open habitats, related to herbaceous plants and mainly xylem feeders, constitute at least about 20%. It is difficult to make the same estimation for phloem feeders, but the ratio of planthoppers (and possibly also cicadellids) living in open habitats seems to be rather high. However, some forms believed to be restricted or closely related to woody plants also occur in the sample. The lack of the evidence precludes a conviction on the exact types of habitats just on the basis of taxic diversity of Fulgoromorpha and Cicadomorpha. Some distributional patterns observed on the basis of planthoppers and leafhoppers from the Insect Bed assemblage of the Isle of Wight could be related to changes of vegetation and habitat conditions in the Palaeogene and Neogene. Cooling climates in the Late Palaeogene–Early Neogene forced large assemblages of warm temperate to subtropical biotas to retreat from medium- to high-latitude circumboreal distribution southwards, to large refugial regions that preserved the warm wet climate that they needed. These refugia, termed Tertiary relict floras, are found in East Asia, SE North America, western North America and SW Eurasia (Milne 2006). It seems reasonable to hypothesise that the plant feeding taxa migrated with their host plants and part of the recent diversity of planthoppers and leafhoppers in the tropics and subtropics originated due to these migrations. Notwithstanding the scarce data and still weak knowledge of fossil planthoppers and leafhoppers, unknown ancestral areas of the higher taxa and dispersal routes, it seems that migration, resulting in wide ranges of higher taxa, was an important process in the past. The biogeographic scenario proposed for Lophopidae (Soulier-Perkins 2000) could be tested in respect to the Bembridge Marls fossils and other fossils of the family as well. The oldest fossil species of Lophopidae comes from Palaeocene deposits of Tibet and France (Stroiński & Szwedo 2012; Szwedo *et al*. 2015). It could be assumed that Lophopidae separated in the Late Cretaceous. These planthoppers benefited from exploitation of the host plant's expansion and availability of new habitats due to the Mid-Cretaceous re-organisation of biosphere (Szwedo & Soulier-Perkins 2010; Stroiński & Szwedo 2012). This separation took place probably somewhere in the ancestral area of Arecaceae, their presumed ancestral host plants. Lophopidae committed a rather rapid diversification and spreading coincident with them. The ecological shift of the Sarebasa$^{+}$ clade to Poaceae was postulated to take place in Southeast Asia (Soulier-Perkins *et al*. 2007). This shift could be related to Poaceae massive diversification and expansion in the Palaeogene (Jones *et al*. 2014; Magallón *et al.* 2015). The finding of Lophopidae from the Sarebasa$^{+}$ group among Bembridge Marls fossils could support this opinion. The tempo of insect migrations could be estimated only by comparison with other better sampled groups with more fossils (and fossil sites) elaborated. Some assumptions could be present for example on the basis of rapid expansion of true primates during 100,000 years duration of the Palaeocene–Eocene Thermal Maximum (Smith *et al*. 2006). In respect to this, the understanding of the recent distribution (and phylogeny) of planthoppers and leafhoppers cannot ignore fossil data. The entomofauna preserved in the Bembridge Marls Insect Bed could be regarded as representative of the Palaeogene hothouse world and together with other fossil assemblages of these times is a precious source of phylogenetic, biogeographic, palaeoclimatic and palaeoecological information.

## True bugs (Heteroptera)

by *Yuri A. Popov*

During my visit to the NHM (London) I examined and studied the collection of true bugs from the Bembridge Marls (Insect Limestone) containing early findings (120 specimens), the finds made during fieldwork (under the guidance of Dr A. J. Ross) in May of 2005, and nine specimens from the collection of the Sedgwick Museum (Cambridge) belonging to Corixidae (one hemelytron), Gerridae (one hemelytron), Lygaeidae (two), Cydnidae (one) and Pentatomidae (two in the genus *Podopinites* Popov gen. nov. and one hemelytron probably belonging to the genus *Teleoschistus* Scudder, 1890). One specimen of Cydnidae was also found in the collection of Mr Andy Yule (the Dinosaur Isle Museum). Altogether about 150 fossils of these hemipteran insects have been examined.

It is apparent that there is a low taxonomic diversity of Heteroptera in the Insect Limestone, represented by fewer than a dozen families (compared to about 100 recent and extinct families known so far). The fauna is dominated by the Pentatomidae (64 specimens) and Lygaeidae (30 specimens), which are among the largest extant families with more than 10,000 recent species each. Pentatomidae are represented by no more than two or three genera, mostly represented by large hemelytra (10–15 mm) and probably can be referred to as the genus *Teleoschistus* widespread in the middle Cenozoic (e.g., Florissant, USA; Mo Clay, Denmark; Oeningen, Germany). There is an analogous situation with Lygaeidae in that the fossils are represented almost exclusively by bodies. The third group of bugs is represented by the relatively small pentatomoid family Cydnidae (over ten specimens), comprising only about 90 genera and 680 living species (Lis 2006). The rest of the heteropteran families have a few specimens: Belostomatidae (one), Corixidae (six), Gerridae (one), Anthocoridae? (one), Miridae (three), Alydidae (one), and Coreidae (two). Here the only representative of the first family may definitely be referred to the modern genus *Lethocerus* Latreille, 1802 (giant water bugs). Aquatic Corixidae are similar to the Miocene genus *Diacorixa* Popov, 1971, numerous representatives of which are known from the southern Germany (Randeck Maar) and northern Kirghizia (Popov 1989), but these represent another, new genus.

It is interesting to note that the first fossil findings of the pentatomid subfamily Podopinae are represented by the new (formal) genus *Podopinites* Popov gen. nov. consisting of *P. acourti* (Cockerell, 1921c) and *P. coloratus* Popov sp. nov. Lace bugs (Tingidae) are of a special interest here. One of them belongs to the extant genus *Parasinalda* (Cantacaderinae, Phatnomini), whose recent species (14) are exclusively distributed in the tropics and subtropics (mainly in South Africa), and three species are known from Eocene Baltic amber (Golub & Popov 2005a). The presence of the genus *Parasinalda* Heiss & Golub, 2013 in the Eocene of Europe tells us about correspondence of climatic conditions in this period to ecological requirements of the species of this genus. Only very wide biogeographical connections for a long time between Europe and Africa could provide such a great shift of the genus southward (Golub & Popov 2005a) and these changes are probably related to the temperature reduction during the Neogene and Pleistocene (Nel *et al.* 2004). The present discovery of a Late Eocene European tingid belonging to the Phatnomini supports the opinion (Golub & Popov 1999) about the significance and diversity of the Cantacaderinae among the lace bug fauna of the European Paleogene (Heiss 2002; Wappler 2003; Nel *et al.* 2004; Golub & Popov 2005a, b). In the Eocene fauna of East Europe representatives of the subfamily Cantacaderinae, especially of the tribe Phatnomini, were widespread and highly diverse. In particular, only from Baltic amber do three genera of Phatnomini occur (*Parasinalda, Intercader* Golub & Popov, 1998 and *Tingicader* Golub & Popov, 1998) and two genera of Cantacaderini (*Paleocader* Froeschner, 1996 and *Weitschatiella* Heiss, 2002). The morphological features of the species in *Intercader* and *Tingicader* genera combine features of two related taxonomic groups of a higher rank: *Intercader* – Phatnomini and Cantacaderini, *Tingicader* – Phatnomini and the subfamily Tinginae (Golub & Popov 1998, 2002; Golub 2001). Thus, in the Eocene, judging from the diversity of some genera and the representations of intermediate forms between the Tingidae taxa on tribal and subfamily levels in the territory of Central Europe, there have probably been intensive form developing processes. In the Eocene or maybe even in the Paleocene the differences between the highest taxa of the family (Cantacaderini, Phatnomini and Tinginae) reached the modern level. Later on, such intensive processes of adaptive radiation in the subfamily Cantacaderinae (Cantacaderini and Phatnomini) moved southward. In the modern fauna both tribes Cantacaderinae (Cantacaderini and Phatnomini) are represented exclusively in the tropics and only partially in the subtropics. As compared to the Eocene, by the present time in Eurasia the northern limit of the range of Cantacaderini has moved to the south by approximately 15 latitudinal degrees, while Phatnomini by approximately 25 degrees (Golub & Popov 2005b).

From the late Middle Eocene of Grube Messel (Germany) another cantacaderid, *Exmesselensis disspinosus* Wappler, 2003, was also found and placed in Phatnomini (Wappler 2003). One more very peculiar cantacaderine (?Phatnomini) lace bug *Parazetekella eocenica* Nel *et al.*, 2004 was described from the lowermost Eocene amber of the Paris Basin (Nel *et al.* 2004). A new genus *Viktorgolubia* Popov gen. nov. is being established within the subfamily Tinginae for *Celantia* (?) *seposita* (Cockerell 1921c) from the Bembridge Marls. A specimen identified as Tingidae *incertae sedis* by Nel (1992) from the uppermost Eocene of France also belongs to this genus.

Suborder Heteroptera, Latreille, 1810

Infraorder Nepomorpha Popov, 1968

Superfamily Corixoidea Leach, 1815

Family Corixidae Leach, 1815

Subfamily Corixinae Leach, 1815

Genus *Diacorixites* Popov gen. nov.

**Etymology.** After the Miocene genus *Diacorixa* Popov, 1971. Gender: masculine.

**Type species.** *Diacorixites szwedoi* sp. nov.; here designated.

**Description.** Hemelytra medium sized (5–6 mm), smooth, finely punctate, sclerotised, not differentiated into proximal coriaceous and distal membranaceous part; transverse dark stripes, outer border of membrane dark; embolium (embolar groove) quite wide and rather flattened; white frosted (pruinous) area (prenodal and postnodal pruinoses) well developed; postnodal pruina quite short, less than two times as long as prenodal pruina; embolium rather flattened and wide; costal fracture (nodal furrow) almost vertical; border between corium and membrane hardly distinguished.

**Remarks.** This formal genus is the closest to the Miocene genus *Diacorixa* Popov (Popov 1971, 1989) – whose species are known from the Miocene sediments of North Kirghizia (*D. miocaenica* Popov, 1971) and southern Germany (*D. germanica* Popov). The greatest similarities of its melytral features are as follows: rather flattened costal margin (especially embolium) and clavopruinous area of hemelytra, as well as the dark outer border of membrane (as in *D. germanica*). Yet the differences, more sclerotised hemelytra, different ration of pruinose areas (very short postnodal pruina), transversal position of costal fracture, and well-developed dark stripes, clearly distinguish it from the species of the genus *Diacorixa*.

*Diacorixites szwedoi* Popov sp. nov.
(Pl. 11: 1–3)

**Etymology.** Species is named after my friend and colleague Dr Jacek Szwedo (Department of Invertebrate Zoology and Parasitology, University of Gdańsk, Gdańsk, Poland), an eminent specialist on the fossil hemipterans.

**Holotype.** NHMUK II.3045, Yule Collection, Insect Limestone, NW Isle of Wight.

**Paratypes**. NHMUK I.8943, hemelytron part (membranous part is not preserved); I.10371 (labelled as ‘Coleoptera’), both Brodie Collection and In.24561 Hooley Collection

**Diagnosis**. As for genus. Holotype length 6.6 mm, width 1.6 mm.

**Description.** As for the genus.

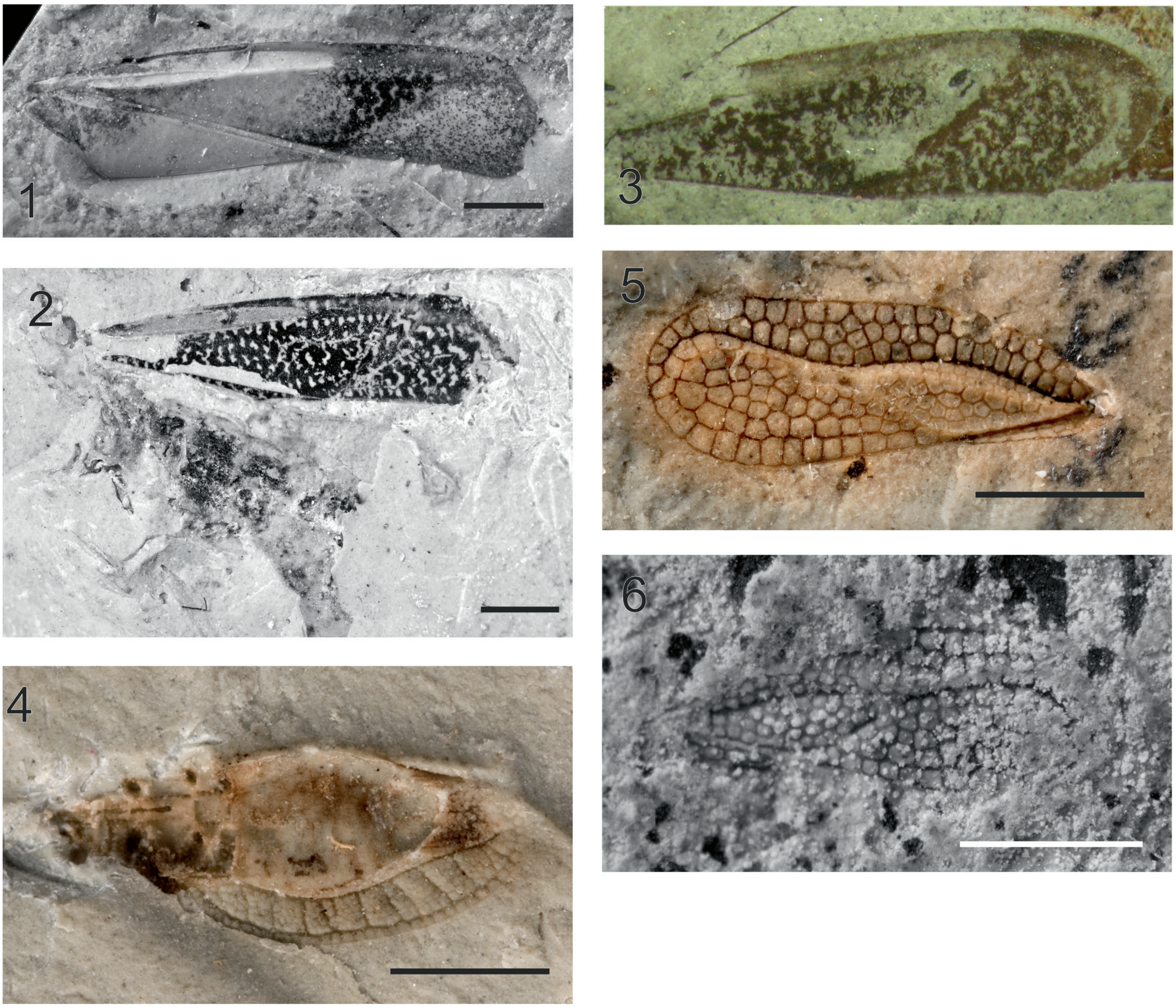


**Plate 11** (1–3) *Diacorixites szwedoi* Popov gen. et sp. nov.: (1) holotype, NHMUK II.3045, tegmen; (2) paratype, NHMUK I.8943, tegmen and body remains; (3) paratype, NHMUK I.10371, tegmen. (4) *Parasinalda wappleri* Popov sp. nov., holotype, NHMUK I.9644. (5) *Viktorgolubia seposita* (Cockerell, 1921c) gen. nov., comb. nov., holotype, NHMUK In.24360, tegmen. (6) *Viktorgolubia* sp., NHMUK In.24361.

Infraorder Cimicimorpha Leston *et al.*, 1954

Superfamily Tingoidea Laporte, 1833

Family Tingidae Laporte, 1833

Subfamily Cantacaderinae Stål, 1873

Tribe Phatnomatini Drake & Davis, 1960

Genus *Parasinalda* Heiss & Golub, 2013

**Type species.** *Phatnoma baltica* Drake, 1950; by original designation.

**Emended diagnosis** (for fossil species). The genus is recognised by the presence of a dorsomedial tubercle or spine of head, quite narrow paranota (not recurved above itself) with only one or two rows of areolae along most of its length and usually also narrow costal area containing one or two rows of areolae which are larger than the areolae of subcostal area. Rostrum surpassing fore coxae or extending middle coxae reaching hind ones sometimes.

**Remarks.** Such characters as the narrow and somewhat oblique, very weakly bilobed paranota with only two rows of areolae and also narrow costal area of hemelytra containing usually one or two rows of areolae (like in the recent type species *Sinalda elegans* Distant, 1904 and also *S. sinuaticollis* Linnavuori, 1977 or *S. haplotaxis* Froeschner, 1968) strongly differentiate them from the fossil species from Eocene Baltic amber placed in the genus *Sinalda* by Froeschner (1996) and Golub & Popov (1998). After studies of additional material of *S. baltica* (Drake 1950), Heiss & Golub (2013) transferred Baltic amber species *S. baltica, S. froeschneri* Golub & Popov, 1998 and *Parasinalda groehni* Heiss & Golub, 2013 to the genus *Parasinalda*. Nevertheless, for a resolution of taxonomical generic problem between *Sinalda* and *Parasinalda* all fossils and recent species referred to these genera should be restudied.

*Parasinalda wappleri* Popov sp. nov.
(Pl. 11: 4; Fig. 73)

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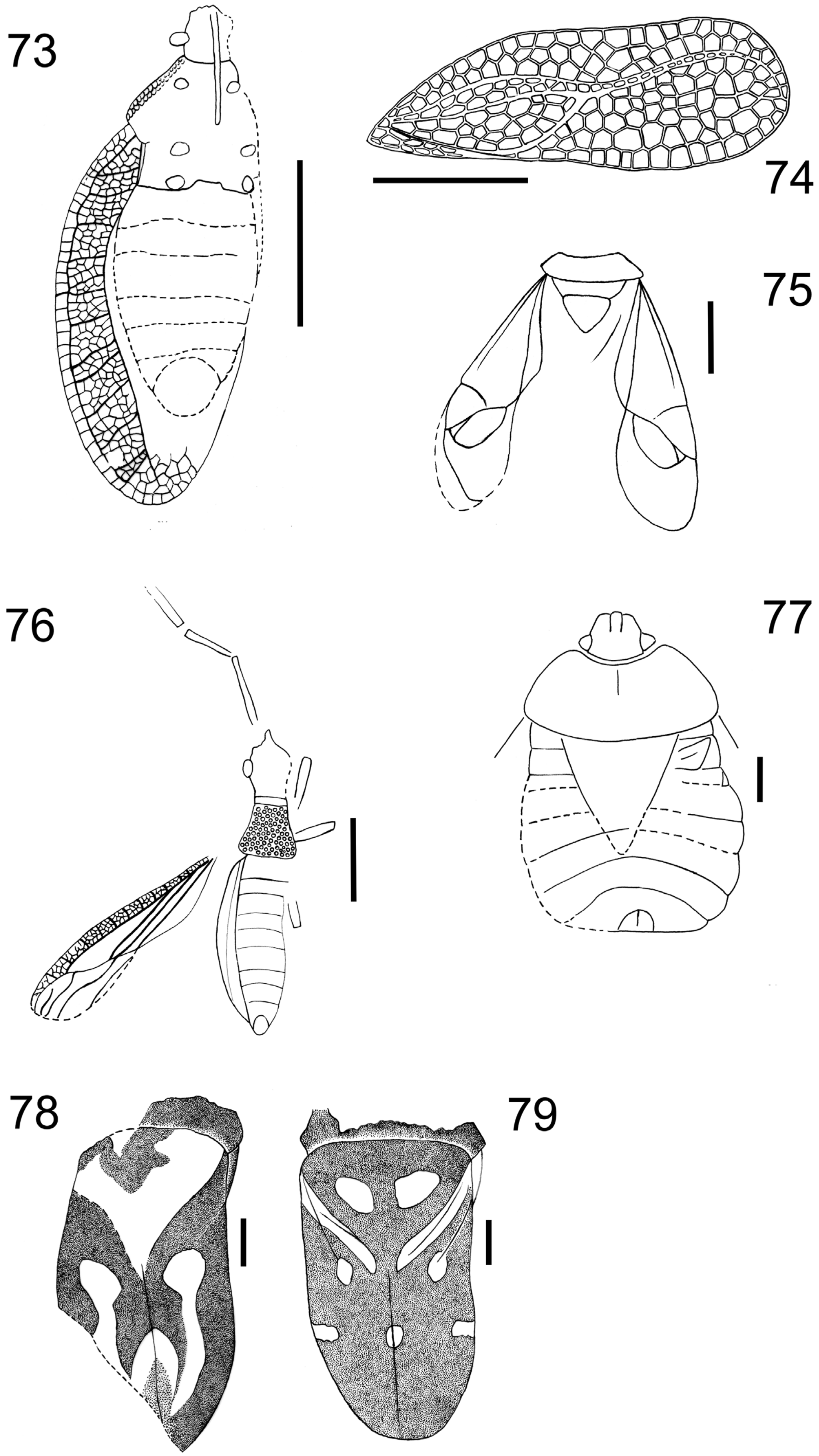


**Figures 73–79** (73) *Parasinalda wappleri* Popov sp. nov., holotype, NHMUK I.9644. (74) *Viktorgolubia seposita* (Cockerell, 1921c), holotype, NHMUK In.24360. (75) *Gurnardinia herczeki* Popov sp. nov., holotype NHMUK In.17232. (76) *Gurnardobaya rossi* Popov sp. nov, holotype, NHMUK I.9074. (77) *Eocenocydnus lisi* Popov gen. et sp. nov., holotype, MIWG DIX 205.36. (78) *Podopinites coloratus* Popov gen. et sp. nov., holotype, NHMUK In.24516. (79) *Podopinites acourti* (Cockerell 1921c) gen. nov, comb. nov., holotype, NHMUK I.8658. Scale bar = 1 mm.

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**Etymology.** After Torsten Wappler (Bonn), the German palaeoentomologist famed for his excellent monograph on the Eocene insects from Eckfelder Maar, SW Germany (Wappler 2003) and some publications on fossil Tingidae.

**Holotype.** NHMUK I.9644, Brodie Collection, Insect Limestone, NW Isle of Wight, old label 'Coleoptera'. Female (?), macropterous form, counterpart (ventral), moderately preserved insect (head partly preserved, legs and most of right side of body missing).

**Description.** Body oblong oval, twice as long as wide, length from head (apparently longer than preserved) to apices of hemelytra 3.2 mm, preserved width 1.3 mm. Eyes moderate size, weakly protrude laterally; rostrum quite short, slightly extended beyond middle of mesothorax. Pronotum relatively short, narrowing apically, anterior pronotal margin distinctly concave, paranota no projecting anterior angles, narrow, with probably two cell rows. Hemelytra very long and extended much beyond abdominal apex; outline of hemelytra arc-like; costal area narrow, with one regular row of rectangular cells of middle size along its almost full (except in basal part) length; subcostal area very wide, with not less than ten transversal thick veins and with five or six rows of quite small, irregular pentagonal or quadrangular cells; hemelytral membrane rather wide, with about ten cell rows in the widest part.

Subfamily Tinginae Laporte, 1832

Genus *Viktorgolubia* Popov gen. nov.

2016 *Viktorgolubia* 'Popov gen. nov. (in press)': Golub & Popov, 2016, p. 70 – *nomen nudum.*

**Etymology.** The specific epithet is a patronymic honouring my old friend and colleague, Russian Heteropterist Viktor B. Golub, the World's eminent specialist on the family Tingidae.

**Type species.** *Celantia* (?) *seposita* Cockerell, 1921c; here designated.

**Diagnosis** (hemelytron). Hemelytral areolae mostly moderately large and mainly pentagonal and rectangular areolae; hemelytra clearly subdivided by raised veins into costal, subcostal and discoidal areas, and membrane, without stenocostal area and distinctly elevated transverse veins; hypocostal (Sc) vein delimiting costal and subcostal areas; costal area very wide (especially along preapical sinus), with three rows of areola in its widest part; subcostal area very narrow, raised to a vertical position and therefore weakly visible from above, with one or two rows of areolae; discoidal area short, slightly shorter of half length of hemelytron (R + M and Cu fused at middle of hemelytron) and almost flat; membrane wide; clavus clearly separated from corium by suture; hypocostal and R + M + Cu reaching hemelytron apex.

**Remarks.** Judging from the absence of the stenocostal area and elevated prominent transversal veins of hemelytra *Viktorgolubia* Popov gen. nov. belongs to the subfamily Tinginae. The presence of a strongly reduced clavus, separated from the corium by a groove, does not contradict the placement of this genus in this subfamily, because the clavus is also separated from the corium by the suture or a fracture in representatives of some genera of the Tinginae. The type of areolae and the relation of the length between hemelytral areae (a short discoidal area) show that the new genus may be similar to the following four recent American genera: *Corythucha* Stål, 1873 (North and South America), *Gargaphia* Stål, 1862b (North and South America), *Leptopharsa* Stål, 1873 (North and South America) and *Pliobyrsa* Drake & Hambleton, 1946 (Central and South America). In this case *Leptophars*a is also known from Dominican amber (Golub & Popov 2003). The general form of the hemelytron *Viktorgolubia* is reminiscent of the cosmopolitan genus *Tingis* Fabricius, 1803 differing from it by the narrower subcostal area and the shorter discoidal area.

Cockerell's (1921c) placement of the species *seposita* in the recent genus *Celantia* Distant, 1903, whose recent species are known from India, Ceylon, Bismarck Archipelago and Australia, was incorrect. In the type species, *C. vagans* Distant, 1903 the discoidal area of hemelytra is much longer and comprises over a half of the hemelytron length, while in species of the genus *Viktorgolubia* the subcostal area is much shorter than half the length of the whole hemelytron. Also in *C. vagans* the subcostal area is considerably broader than in the extinct species of the new genus and more flattened (not recurved above itself).

In addition, the new genus differs from *Corythucha*, *Gargaphia*, *Leptopharsa* and *Pliobyrsa*, primarily by its narrow subcostal area, located almost vertically, which from above it is almost not visible, that is why Cockerell (1921c), in his drawing of *Celantia* (?) *seposita* missed the subcostal area. In the representatives of the above four genera it is broader and much more flattened. In *Corythucha*, *Gargaphia, Leptopharsa* and *Pliobrysa* the discoidal area is more or less concave, while in the species of the genus *Viktorgolubia* it is practically flat.

*Viktorgolubia seposita* (Cockerell, 1921c) comb. nov.
(Pl. 11: 5; Fig. 74)

1921 *Celantia* (?) *seposita* Cockerell, 1921c, p. 542, fig. 1.
1960 *Celantia* (?) *seposita*; Drake & Ruhoff, p. 11.
1965 *Celantia* (?) *seposita*; Drake & Ruhoff, p. 118.
1992 *Celantia* (?) *seposita*; Nel, p. 103.
1999 *Celantia* (?) *seposita*; Golub and Popov, p. 36.
2003 *Celantia* (?) *seposita*; Wappler, p. 26.
2016 *Viktorgolubia seposita* Cockerell, 1903 [sic]: Golub & Popov, p. 70.
2016 *Viktorgolubia seposita*: Popov, comb. nov. (in press): Golub & Popov, p. 70.

**Holotype.** NHMUK In.24360, Hooley Collection, Insect Limestone, NW Isle of Wight.

**Description** (left hemelytron, measurements in mm). Length 2.8, width 1.0; width of costal area 0.4; width of subcostal area 0.1; discoidal area: length 1.5, width 0.3; width of sutural area (membrana) 0.6; clavus: length 0.9, width 0.15. All hemelytral areolae large and almost the same size. Subcostal area with two rows of areolae along R + M vein and one row of areolae along R + M + Cu. Discoidal area with four rows of areolae in the widest part of it. Clavus distinctly narrowing to its apex, with three rows of areolae at base, two rows of areolae in other part and one areola at apex.

**Remark**. Another specimen, NHM In.24361 (Pl. 11, fig. 6) Hooley Collection, length 2.3 mm, width 0.9 mm, probably belongs to the same genus.

Family Miridae Hahn, 1833

Subfamily Phylinae Douglas & Scott, 1865

Genus *Gurnardinia* Popov gen. nov.

**Etymology.** Derived from the locality Gurnard Bay. Gender: feminine.

**Type species.** *Gurnardinia herczeki* sp. nov.; here designated.

**Diagnosis.** Medium sized, not more 5 mm; generally oblong-oval body; dorsal surface smooth and bare. General coloration dark-brown. Antennae long and thin. Pronotum small, more than seven times shorter of body length; trapezoidal, clearly transverse, more than twice as wide as long. Mesoscutum narrowly exposed. Hemelytral membrane biareolate, minor cell weakly marked.

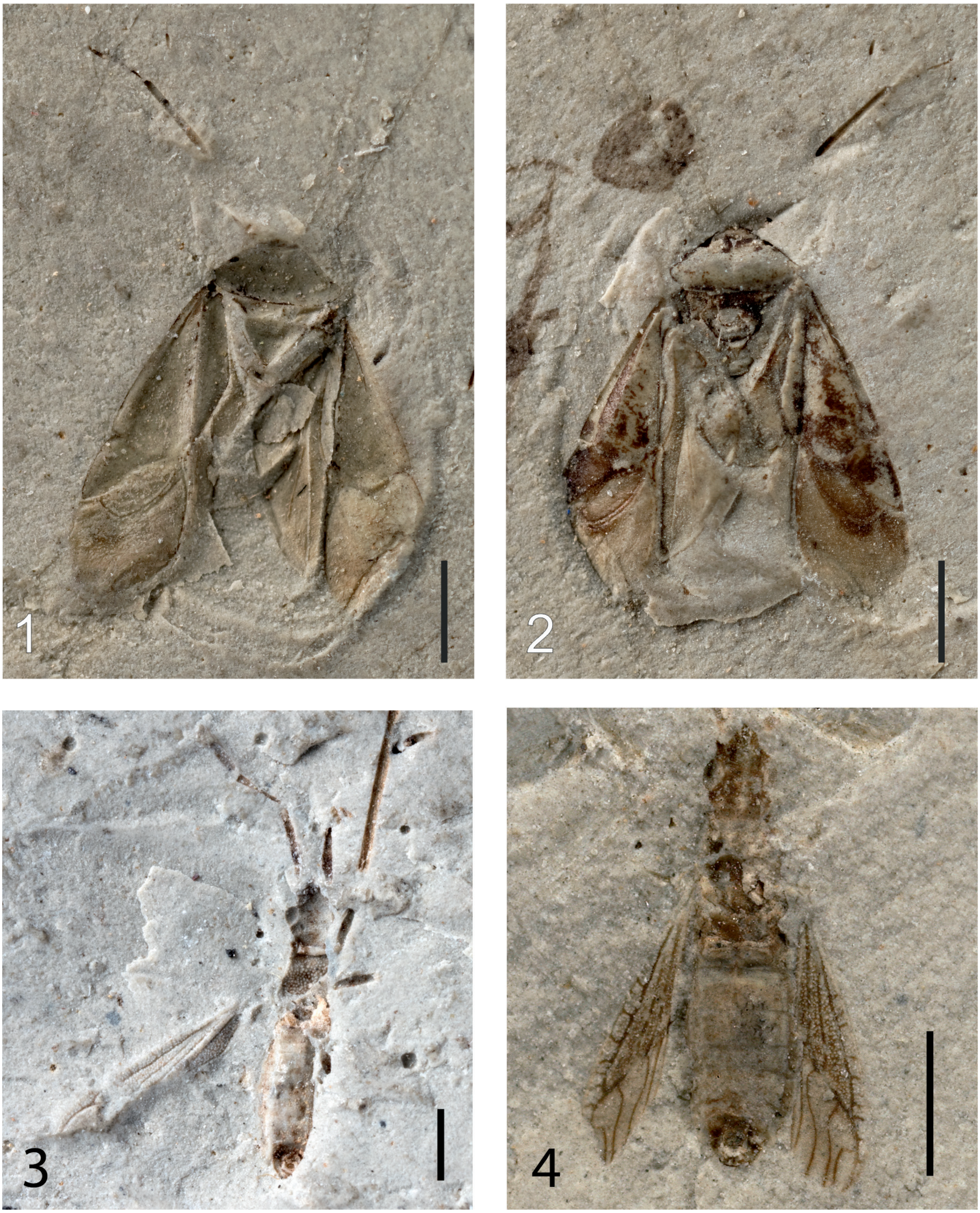


**Plate 12** (1–2) *Gurnardinia herczeki* Popov gen. et sp. nov.: (1) holotype, NHMUK In.17231, counterpart; (2) holotype, NHMUK In.17232, part. (3–4) *Gurnardobaya rossi* Popov gen. et sp. nov.: (3) holotype, NHMUK I.9074; (4) paratype, CAMSM X.50140.71.

**Remarks.** The main characters typical for genera of the Phylinae, such as the absence of pronotal collar and calli, and also the impunctate body, are sufficient to place the new genus in this subfamily and possibly the tribe Phylini. The recent taxonomy of all recent mirid subfamilies is mainly based on the pretarsal structures and modifications of the male genitalia.

*Gurnardinia herczeki* Popov sp. nov.
(Pl. 12: 1–2; Fig. 75)

**Holotype.** In.17231/In.17232 (part and counterpart), Smith Collection, Insect Limestone, NW Isle of Wight.

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**Etymology.** Named in honour of my old best friend and colleague Prof. Dr hab. Aleksander Herczek (Silesian University, Katowice, Poland), a well-known specialist on the family Miridae.

**Description**. Macropterous. Body length *ca.*4 mm. Pronotum convex; strongly transverse, 2.36 times as wide as long; lateral margins strongly narrowing toward (LSP = 3.25), posterior margin straight. Outer margin of hemelytra parallel and almost straight; proportion of hemelytron, corium and cuneus length along outer side 4.8–3.4–1.4. maximal length of cuneus almost 2.5 times less than corium length; large membrane cell 1.7 times shorter than membrane length.

**Measurements** (in mm). Body length including hemelytra 4 mm (3.8 without head), width 1.7; antennal joints II: III: IV = ~0.9: 0.9: 0.6; pronotum: length 0.55, width 0.4 (ant.) and 1.3 (post.); mesoscutum length 0.15; scutellum: length 0.5, width 0.7.

Infraorder Pentatomomorpha Leston *et al.*, 1954

Superfamily Lygaeoidea Schilling, 1829

Family Lygaeidae Schilling, 1829

Subfamily Lygaeinae? Schilling, 1829

Tribe Gurnardobayini Popov, trib. nov.

**Type genus.** *Gurnardobaya* Popov gen. nov.; here designated.

**Diagnosis.** Body slender; antennae long, eyes rather small and weakly projecting; hemelytra narrow, subcostal area with numerous transversal short veins, veins R, M and Cu almost parallel each other.

**Remarks.** The peculiar venation of this form strongly differing from all other lygaeids allows the erection of a new taxon at tribal level.

Genus *Gurnardobaya* Popov gen. nov.

**Etymology.** The generic name is derived from the place Gurnard Bay where Joseph A'Court Smith lived.

**Type species.** *Gurnardobaya rossi* sp. nov.; here designated.

**Description**. Medium sized, not more than 5 mm. Body elongate, slender, granular, six times as long as wide. Head quite long, somewhat longer than wide and pronotum length; antennae long and quite thin. Pronotum roughly granulate, convex and relatively elongate, slightly longer than wide or equal size of length and width; pronotal collar well developed and the same thickness as antennal joints; lateral margins weakly narrowing toward and slightly emarginated, posterior one straight; its posterior angles rounded. Hemelytra strongly elongated, about four times as long as wide; three main veins R, M and Cu distinctly expressed along of all wing length, R and M are fused at distal part of wing; membrane with four free parallel veins. Scutellum medium size. Legs slender and femora of all legs are equal thickness.

*Gurnardobaya rossi* Popov sp. nov.
(Pl. 12: 3–4; Fig. 76)

**Etymology.** Named after Dr Andrew J. Ross, palaeoentomologist at the National Museum of Scotland, Edinburgh.

**Holotype.** NHMUK I.9074a, b (part and counterpart) (Fig. 3); Brodie Collection, Insect Limestone, NW Isle of Wight. Male.

**Paratype**. CAMSM X.50140.71 (TN122) (Fig. 4), Smith Collection. Male.

**Description.** Macropterous. Body length *ca.* 4 mm., elongate body almost six times as long as wide; general coloration pale-yellowish, antennae and legs dark-brown; dorsal surface bare. Antennal joints II–IV of equal thickness, second joint longest. Hemelytra slightly longer than abdomen.

**Measurements** (in mm). Body length 4.0 mm, width 0.65; head: length 0.7, width 0.6; pronotum: length 0.65, width 0.6; hemelytron: length 2.7, width 0.7; abdomen: length 2.0, width 0.7.

**Remarks.** There is another specimen from the Sedgwick Museum, Cambridge, whose main characters (same size of body, slender and granulate surface of body, somewhat elongate head and pronotum, and especially the same peculiar venation of hemelytra) correspond well (Pl. 12: 4) with the type specimen (Pl. 12: 3). However, the apical parts of corium of these specimens are somewhat different them. Unfortunately, the incomplete preservation of both of them does not allow to solve their taxonomical position. Therefore this specimen is tentatively included into this species as a paratype.

Family Lygaeidae Schilling, 1829? *incertae sedis*

Genus *Lygaeites* Heer, 1853

*Lygaeites amabilis* Cockerell, 1921
(Pl. 13: 1)

1921 *Lygaeites amabilis* Cockerell, 1921c, p. 542; fig. 1., pl. 2, fig. 1.
1927 *Lygaeites amabilis*; Cockerell, p. 590
1964 *Lygaeites amabilis*; Slater, p. 1503.

**Holotype.** NHMUK In.24362, Hooley Collection, Insect Limestone, NW Isle of Wight. Hemelytron.

**Description.** (after Cockerell 1921c): Tegmen length 2.9 mm, width 1.2 mm, beautifully marked as shown in the figure. The corium has white marks on a black ground; the membrane is light reddish brown, with four curved, broad, white lines.

Superfamily Pentatomoidea Leach, 1815

Family Cydnidae Billberg, 1820

Subfamily Sehirinae? Amyot & Audinet-Serville, 1843

Genus *Eocenocydnus* Popov gen. nov.

**Etymology.** From the geological name and the genus *Cydnus* Fabricius, 1803. Gender: masculine.

**Type species.** *Eocenocydnus lisi* sp. nov.; here designated.

**Diagnosis.** Large size, more than 5 mm. Body oval, deeply punctate, less than 1.5 times as long as wide. Head markedly transverse, without spinules at anterior margin; clypeus quite narrow, slightly projecting beyond jugal plates; eyes of moderate size, almost transversely triangular, touching anterior pronotal margin, vertex rather broad. Pronotum convex, markedly transverse, only less than 1.5 times as wide as long, with anterior margin distinctly sinuate, posterior one weakly concave, lateral margins clearly convex; its anterior angles subacuate, posterior ones weakly rounded. Scutellum triangular, apparently a little wider than long. Abdomen very broad, distinctly wider than length.

**Remarks.** This genus is distinct from other Palaeogene cydnids and probably from all known Neogene ones by the strongly transverse vertex, pronotum and abdomen, and also coarsely punctured body. The incomplete preservation of body (antennae, legs, and hemelytra are missed) does not allow to put this Oligocene cydnid in a definite subfamily. But judging from the large size of this burrower bug, open anteriorly clypeus and absence of spinules along the anterior margin of the head, it may apparently be placed in the subfamily Sehirinae and one can compare it with the recent genus *Sehirus* Amyot & Audinet-Serville, 1843 having similar features. However, the

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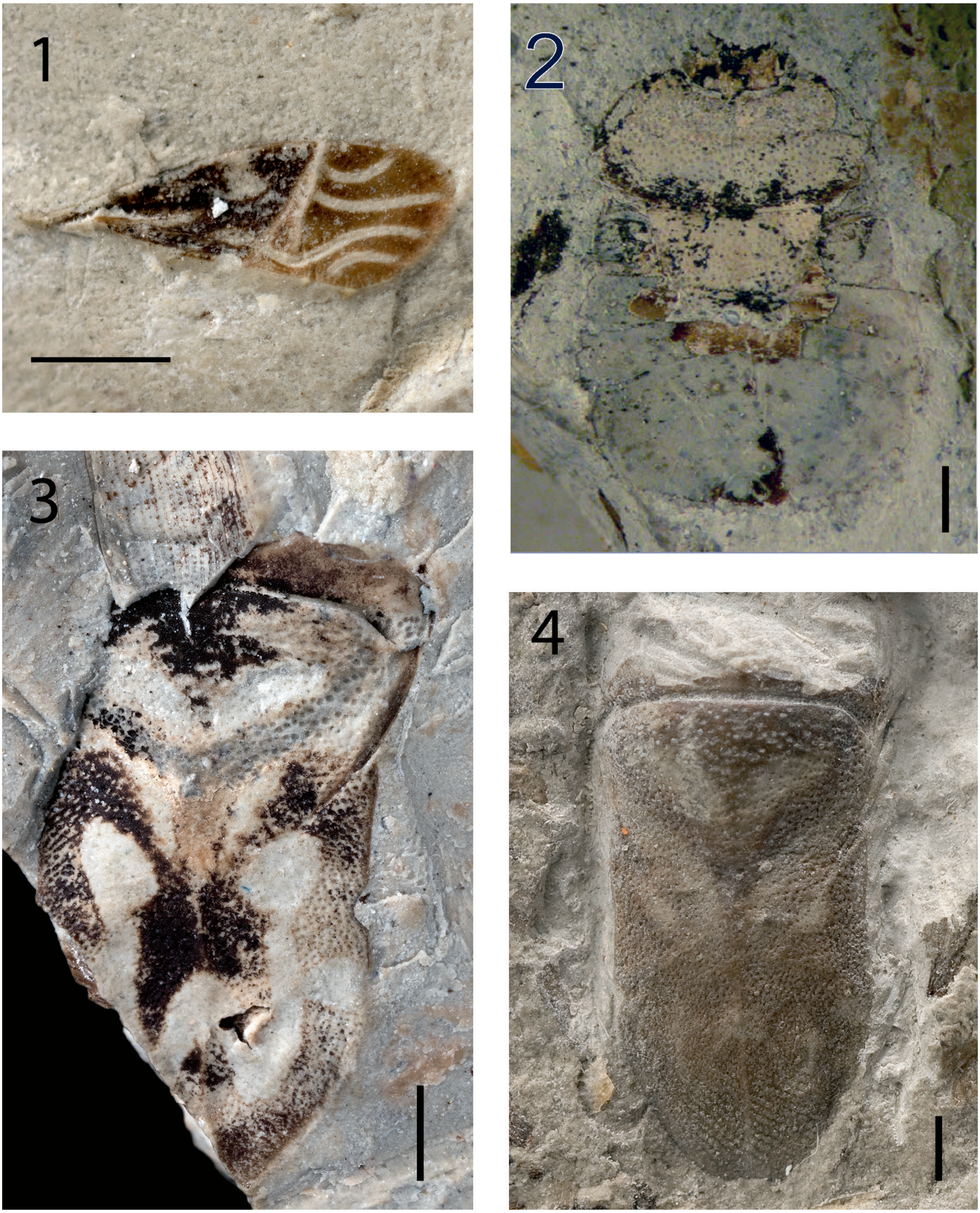


**Plate 13** (1) *Lygaeites amabilis* Cockerell, 1921c, holotype, NHMUK In.24362, hemelytron. (2) *Eocenocydnus lisi* Popov gen. et sp. nov., holotype, MIWG DI.X.205.36. (3) *Podopinites coloratus* Popov gen. et sp. nov., holotype, NHMUK In.24516. (4) *Podopinites acourti* (Cockerell, 1921c) comb. nov., holotype, NHMUK I.8658.

triangular eyes of this Eocene cydnid clearly distinguish it from the species of *Sehirus*.

*Eocenocydnus lisi* Popov sp. nov.
(Pl. 13: 2; Fig. 77)

**Etymology.** After the well known heteropterologist Professor Dr hab. Jerzy A. Lis, outstanding specialist of the burrow bugs (Cydnidae).

**Holotype.** MIWG DI.X 205.36, female, part, Insect Limestone, NW Isle of Wight.

**Description.** The head almost twice as wide as long. Vertex more than five times wider than eye; pronotum nearly twice as wide as long and abdomen; very broad abdomen, some more 1.5 times as wide as long.

**Measurements** (in mm). Body length 7.5, width 5.5; head: length 1.1, width (across eyes) 1.6; eye width 0.25; vertex width 1.25; pronotum: length 2.25, width 2.0 (ant.) and 4.5 (post.); scutellum width 3.6; abdomen: length 3.5, width 5.5.

Family Pentatomidae Leach, 1815

Subfamily Podopinae Amyot & Audinet-Serville, 1843

**Remarks**. Of great interest is the presence of the new (formal) genus *Podopinites* Popov gen. nov. based on *P. acourti* (Cockerell 1921c) and the newly discovered *P. coloratus* Popov sp. nov. The humeral angles of pronotum, strongly convex and large scutellum covering the abdomen, which is shorter than the posterior margin of the pronotum definitely point to them being members of the pentatomid subfamily Podopinae – the first fossil representatives of this peculiar subfamily. This widely distributed subfamily has 65 genera and 255 species (Davidová-Vilímová 1993; Schuh and Slater 1995).

Genus *Podopinites* Popov gen. nov.

**Etymology.** From the generic name of a true bug – *Podops* Laporte, 1832 and ending '*ites*'. Gender: masculine.

**Type species**. *Podopinites coloratus* Popov sp. nov.; here designated.

**Diagnosis.** Body elongated, distinctly convex, about 10 mm. Scutellum very large and reaching apex of abdomen, almost twice as long as wide; surface distinctly dark-coloured and deeply punctuate, with distinct longitudinal medial carina; base of scutellum almost the same size as posterior margin of pronotum, the latter straight along almost all of its length.

**Composition.** The genus contains the type species which is described below and one other form which was described as *Pentatomites acourti* Cockerell, 1921c.

**Remarks.** Despite the incomplete preservation of the body (head, basal part of the pronotum and legs are missing) of these specimens, it is possible to put them in the Pentatomidae. The scutellum covering the whole abdomen is known only in two pentatomoid families: Scutelleridae Leach, 1815 and Podopinae (Pentatomidae). But the base of the scutellum, which is not broader than the posterior margin of the pronotum is the main feature for members of the pentatomid subfamily Podopinae and it allows these fossils to be placed here. However, the equal length of the posterior margin of the pronotum and the base of the scutellum and also strongly convex and significantly elongate, especially *P. acourti* (Cockerell), body are features that taxonomically might bring them close to the Scutelleridae.

*Podopinites coloratus* Popov sp. nov.
(Pl. 13: 3; Fig. 78)

**Etymology.** Derived from '*coloratus*' (Latin), coloured.

**Holotype.** NHMUK In.24516, Hooley Collection, Insect Limestone, NW Isle of Wight.

**Diagnosis.** This new species clearly differs from *P. acourti* in the angular humeral angles of pronotum and the type of coloration (first of all by two longitudinal stripes of the scutellum); also the body is less convex in *P. coloratus*.

**Description.** Head and most of part of pronotum, and legs missing. Humeral angles of pronotum broadly rounded. Scutellum moderate convex, 1.89 as long as wide; strongly pigmented, with two clearly expressed longitudinal white stripes; apex moderately rounded.

**Measurements**. Preserved length 7.8 mm, width 3.7 mm.

*Podopinites acourti* (Cockerell, 1921c) comb. nov.
(Pl. 13, fig 4; Fig. 79)

1921 *Lygaeites acourti* Cockerell, 1921c, p. 543, fig. 3.
1927 *Pentatomites acourti*: Cockerell, p. 590.
1964 *Lygaeites acourti*: Slater, p. 1503.

**Holotype.** NHMUK I.8658, Brodie Collection, Insect Limestone, NW Isle of Wight.

**Redescription.** Head and most part of pronotum, and legs missing. Humeral angles of pronotum angularly rounded. Scutellum strongly convex, 1.88 as long as wide; coloured, there is a pattern of quite large, mainly round and pale spots; apex widely rounded.

**Measurements.** Width of pronotum 4.6 mm; length of scutellum 7.5 mm, width 4 mm.

**Remark.** Undescribed representatives of the Heteroptera are presented on Plate 14. Water true bugs are represented by Gerridae – sole tegmen, preliminarily identified as belonging to the genus *Gerris* Fabricius, 1794 (Pl. 14: 1) and Belostomatidae Leach, 1815, probably belonging to the genus *Lethocerus* Mayr, 1853 (Pl. 14: 7) – I.9425, tegmen length 42 mm, width 24 mm. Land bugs are represented by the families Coreidae (Pl. 14: 2) – In.24505, tegmen length 6.4 mm, width 2.0 mm, Lygaeidae (Pl. 14: 3–4) – I.8856, tegmen length 4.0 mm, width 1.2 mm; In.24505 tegmen length 6.4 mm, width 2.0 mm, Cydnidae (Pl. 14: 5) – In.17441b, tegmen length 5.8 mm, preserved width of abdomen 2.5 mm and Pentatomidae, tentatively identified as belonging to the extinct genus *Teleoschistus* Scudder, 1890 (Pl. 14: 6) – II.2713a tegmen length 12 mm, width 6 mm.

**Discussion.** By composition, the Bembridge Marls Heteroptera fauna differs considerably from the family composition in Baltic amber. Partially this may be explained by taphonomic reasons. Unfortunately, Heteroptera of Baltic amber are still in the early stage of study and one can compare only individual groups. Primarily this refers to the main thermophilous Tingidae, which are represented by subfamily Tinginae, dominating in the modern fauna, and the genus *Viktorgolubia* is close to the genera spread predominantly in the tropics and subtropics of the Eastern Hemisphere. One of them (*Leptopharasa*) is rather common in Dominican amber (Golub and Popov 2000, 2003). Yet other specimen belonging to this genus (identified as Tingidae incertae sedis by Nel (1992) is known from the uppermost Eocene of France. It also became clear that the genus *Parasinalda* of the subfamily Cantacaderinae is present only in the Insect Limestone of the Bembridge Marls and Baltic amber. Hemelytra of the water family Corixidae closely resemble those of the Miocene genus *Diacorixa* known from southern Germany (Randecker Maar) and Kirghizia (Popov 1971, 1989). Representatives of two terrestrial bug families Pentatomidae and Lygaeidae are dominant among all other heteropterans. Most of them resemble pentatomids and lygaeids from the Late Eocene of Florissant (Colorado, USA). One can note that the heteropteran assemblage of the Bembridge Marls looks rather poor

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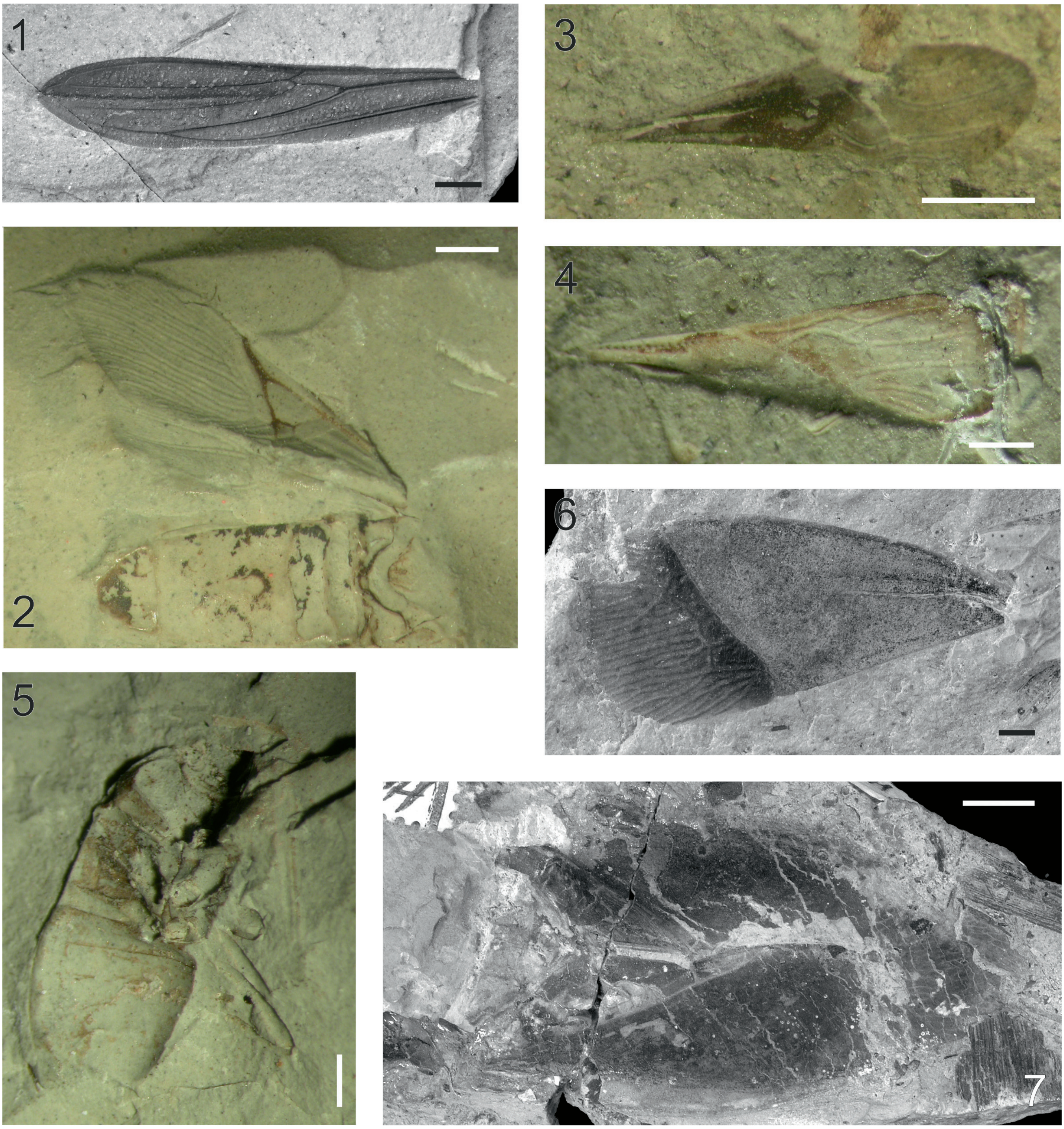


**Plate 14** (1) Tegmen of Gerridae: *Gerris* sp., CAMSM X.50140.44 (TN94) (Smith Collection). (2) Tegmen of Coreidae, NHMUK In.24505 (Hooley Collection). (3) Tegmen of Lygaeidae, NHMUK I.8856 (Brodie Collection). (4) Tegmen of Lygaeidae, NHMUK I.8857 (Brodie Collection). (5) Cydnidae, NHMUK In.17441b (Smith Collection). (6) Tegmen of Pentatomidae: ?*Teleoschistus* sp., NHMUK II.2713a (Collection Polish Team). Scale bar = 1 mm. (7) Belostomatidae; *Lethocerus* sp., NHMUK I.9425 (Brodie Coll). Scale bar = 5 mm.

in taxonomic composition – its fauna is represented by less than a dozen families (compared to about 100 recent and extinct families known so far). Among them, dominating are Pentatomidae (64 specimens) and Lygaeidae (30 specimens) which belong to the largest extant families including more than 10,000 recent species each. There is poor taxonomic diversity in the Bembridge Marls fauna. In addition to *Podopinites* gen. nov. Pentatomidae are represented by large hemelytra (10–15 mm) that most probably can be referred to the genus *Teleoschistus*, though *Polioschistus* Scudder, 1890, *Poteschistus* Scudder, 1890 and *Pentatomites* Scudder, 1890 from the Late Eocene of Florissant (Scudder 1890) are other possibilities. There is an analogous situation in Lygaeidae (Pl. 14: 3–4). The difference is that the fossils are represented almost exclusively by bodies. The third group of bugs is represented by the pentatomoid family Cydnidae (a dozen specimens; Pl. 14: 5) comprising only about 600 living species. The rest of the Heteroptera families usually have few specimens: Coreidae Leach, 1815 (two; Pl. 14, fig. 2), Alydidae (one), Miridae (three), Tingidae (two), ?Anthocoridae (one), Gerridae (one), Corixidae (six) and Belostomatidae (one). The representative of the Belostomatidae (giant water bugs) can be identified

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as belonging to the recent cosmopolitan genus *Lethocerus* (Pl. 14: 7), whose representatives prefer staying in water habitats. Sometimes they can exist in saline estuaries draining into a sea or even ocean. Therefore *Lethocerus* could have lived in the brackish lagoon and estuarine environment of Bembridge Marls, though the presence of only adult specimens and the absence of nymphs does not support this. Specimens belonging to the Corixidae are distributed worldwide, but predominantly found in temperate and subtropical areas. Various corixids (e.g., species of the subgenus *Sigara* (*Vermicorixa*)) survive well in salt water (e.g., salt lakes). It should be noted that corixids from Bembridge Marls are only represented by hemelytra. If one presumes that water boatmen are autochthonous then their hemelytra could be transported by local currents. It is also possible that a single hemelytron of the water strider (Gerridae) from the Sedgwick Museum, Cambridge, belongs to the modern genus *Gerris* (Pl. 14, fig. 1), which are almost exclusively confined to stagnant (lentic) freshwater, such as pools, ponds, and smaller lakes. Some species inhabit temporary pools and these are usually long-winged (Andersen 1973).

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