Tertiary bark lice (Insecta: Psocodea) from the Insect Limestone (Bembridge Marls, Late Eocene) of the Isle of Wight, UK

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ABSTRACT: Late Eocene fossil Psocodea from the Isle of Wight are studied and classified within three new genera and seven species (Wightipsocus acourti (Cockerell 1921) gen. nov. et n. comb., Wightipsocus intasi gen. et sp. nov., Wightipsocus rossi gen et sp. nov., Awightipsocus jarzembowskii gen. et sp. nov., Awightipsocus megaloi gen. et sp. nov. Awightipsocus minimus gen. et sp. nov. and Wightimicropsocus inexpectatus gen. et sp. nov.) without however attributing them to any family. A key for fossil Psocodea from the Isle of Wight is given.





Psocodea is a small order with about 10,000 described Recent species. Its earliest record is supposed to be from the Permian of Kansas (USA), CIS (Commonwealth of Independent States), and New South Wales (Australia) (Carpenter 1992), but Mockford (1993, p. 2) considered that the earliest unquestionable fossil Psocodea known are those of Cretaceous amber.

Cockerell (1921) described very succinctly a Psocopteran (Psocus acourti) from the late Eocene (Hooker et al. 2007, 2009) or early Oligocene (Gale et al. 2006); concretions or tabular bands of very fine-grained micrite, identified as the Insect Limestone of the Isle of Wight. 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) (Gale et al. 2006). Latest studies date the Bembridge Marls as latest Priabonian (Hooker et al. 2009). The Isle of Wight specimens from the Insect Bed at the Natural History Museum belong to the E.J. A'Court Smith (purchased 1877, 1883), P.B. Brodie (purchased 1898) and R.W. Hooley (purchased 1924) collections. They are labelled "Gurnard Bay" or "Gurnet Bay" (which is an old name for Gurnard Bay). A'Court Smith collected specimens from West Cowes to Newtown River on the northwest side of the Isle of Wight (Jarzembowski 1980). Jarzembowski (1976) considered that most of the specimens probably came from Thorness Bay. The recent revision of the Isle of Wight fossil insect material kept in the Natural History Museum, London and the Maidstone Museum and Art Gallery, Maidstone revealed several new species of fossil Psocodea.

Fossil Psocodea preserved in amber are sufficiently well preserved in detail for accurate comparisons with the extant representatives of the order. Unfortunately, the study of Psocodea preserved as impressions in marl or limestone is mainly based on wing venations and, in many Psocodea belonging to the Psocomorpha suborder, even the wing venations are of limited value, as the classification within this suborder is based largely on other morphological details.

There have been historically several classifications of the Psocoptera, but the important revisions of the Psocoptera proposed by Smithers (1972, 1990), Mockford (1993) or Lienhard (1998) are fundamental tools for the systematics of the order.

This paper redescribes *Psocus acourti* Cockerell, 1921 = *Psocidus acourti* (Cockerell 1921) Lienhard & Smithers, 2002 and attributes it to a new genus, *Wightipsocus*. Six other new taxa (*Wightipsocus intasi*, *Wightipsocus rossi*, *Awightipsocus jarzembowskii*, *Awightipsocus megaloi*, *Awightipsocus minimus* and *Wightimicropsocus inexpectatus*) are also described. They are all placed in *incertae sedis* families. A key for fossil Psocodea from the Isle of Wight is given. All the drawings were made using a Leica binocular microscope with drawing tube.

The wing venation nomenclature and body structures follow that of Smithers (1972), Mockford (1993) and Lienhard (1998).

Institutional abbreviations: NHMUK, Natural History Museum, London; MNEMG, Maidstone Museum & Bentlif Art Gallery.

1. Systematic palaeontology

Order Psocodea Johnson, Yoshizawa & Smith, 2004 Suborder Psocomorpha (Roesler 1944) Family *incertae sedis*

Genus Wightipsocus gen. nov.

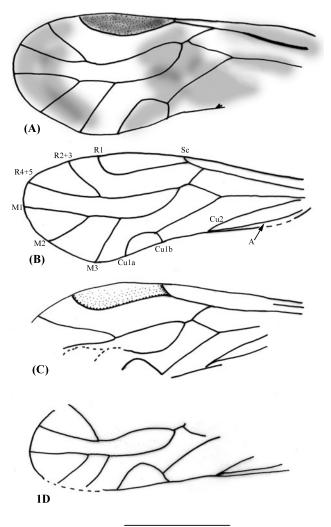
Type species. Psocus acourti Cockerell, 1921 = Psocidus acourti (Cockerell 1921) Lienhard & Smithers, 2002.

Etymology. After the Isle of Wight + *Psocus*.

Diagnosis. Legs with three tarsomeres. Forewing with veins bearing two rows of setae. Forewing with thickened and sclerotised free pterostigma; Rs merging with M for a small distance and forming Rs+M, free areola postica; nodulus present; and one anal vein. Hindwing with M bifurcated into M1 and M2.

Wightipsocus acourti (Cockerell 1921) new combination Text-figs 1, 2; Plate 1, figs 1–3

Holotype. Specimen number NHMUK In.24366 (Text-fig. 1A; Plate 1, fig. 1), Hooley collection, Insect Limestone, northwest Isle of Wight.



Text-Figure 1 Wightipsocus acourti (Cockerell 1921) new combination: (A) drawing of holotype, specimen NHMUK In.24366; (B) drawing of specimen MNEMG 2009.75 (BLS 551 A); (C) drawing of specimen NHMUK In.64128; (D) drawing of specimen NHMUK In.25370. Scale bar = 1 mm. Abbreviations: A = Anal vein; Cu = Cubitus vein; Cu1, Cu2 = Cubitus vein branches 1 & 2; M = Media vein; R = Radius vein; Sc = Subcosta vein.

Other material. NHMUK In.64128 (Text-fig. 1C; Plate 1, fig. 3), Hooley collection; NHMUK In.20559 (Text-fig. 2), Hooley collection; NHMUK In.25370 (Text-fig. 1D), Hooley collection; NHMUK In.25228, Hooley collection; MNEMG 2009.75 (BLS 551A) (Text-fig. 1B; Plate 1, fig. 2). Specimen NHMUK In.24508/NHMUK In.25677 (part and counterpart), Hooley collection, probably belongs to this species as well, and presents a three-tarsomere well preserved leg; but unfortunately the wing is too damaged to permit a positive identification.

Diagnosis. As for the genus, plus bifurcation of R2 + 3 and R4 + 5 very slightly basal to the level of bifurcation of M1 + 2 into M1 and M2.

Description. Measurements are made mainly from the holotype NHMUK In.24366 for the forewing, and from specimen NHMUK In.20559 for the head, antenna and hindwing. Head 0.65 mm wide. Eyes rounded, diameter 0.2 mm, separated by 0.2 mm. Antenna partially preserved with flagellomeres 0.1–0.15 mm long. Postclypeus 0.2 mm wide. Forewing glabrous and hyaline 3 mm long, 1.15 mm wide. Sc, 0.5 mm long (after specimen number In.64128), free and not reaching R. Distal free part of Sc (Sc' sensu Lienhard 1998) forming a sharp angle with the costal margin and reaching it 1.45 mm from

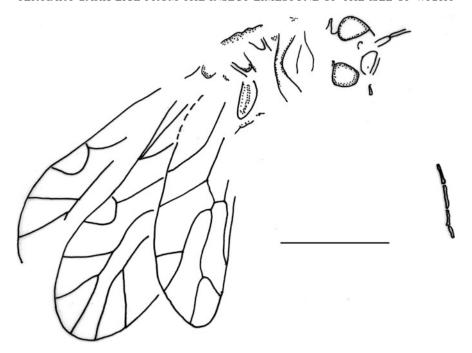
wing base; R1 simple, reaching nearly perpendicularly the costal margin at 2.30 mm from wing base. Pterostigma thickened, 0.85 mm long and 0.25 mm wide. Rs basally oblique, fusing with then branching from M; common portion Rs + M 0.1 mm long, at 1.3 mm from wing base; fork of R2 + 3 and R4 + 5 2.35 mm distal of wing base; R2 + 3 and R4 + 5slightly curved; reaching wing margin respectively at 2.7 and 2.9 mm from wing base. M basally fused with Cu1; fork of M1 + M2 and $M3 \ 2.05$ mm distal of wing base; M1 and M2separating 2.37 mm distal of wing base; M1 nearly straight, reaching wing apex, 0.6 mm long; M2 straight, 0.45 mm long; M3 straight, 0.56 mm long. Fork of Cu1 in Cu1a and Culb (sensu Mockford 1993) 1.45 mm from wing base; Cula strongly curved and longer than Cu1b. Areola postica (AP) free; no cross-vein between AP cell and M. Cu2 (from specimen MNEMG 2009.75 (BLS 551A)), 1 mm long; a distinct nodulus at 1 mm from wing base. 1A nearly straight, 0.9 mm long. Forewing must be originally coloured (but the pattern of preserved colouration as shown in the Plate 1, fig. 1, is weak and hardly discernable; it corresponds to indefinite shades in the basal anterior costal area, then around the bases of veins and in indefinite strips from the mid part of the wing to its distal part). Hindwing glabrous and hyaline, smaller than forewing, 2.35 mm long and 0.74 mm wide. Basal part of hindwing not preserved. Rs distally fused with M for 0.05 mm. R1 reaching anterior wing margin 1.65 mm from wing base. Bifurcation of Rs into R2 + 3 and R4 + 5 1.8 mm from wing base. $R2 + 3 \cdot 0.2 \text{ mm long}$; $R4 + 5 \cdot 0.5 \text{ mm long}$. Bifurcation of M into M1 and M2 1.55 mm from wing base; M1 0.4 mm long; M2 0.25 mm long. Cu1 and Cu2 reaching posterior wing margin respectively at 1·1 mm and 0·9 mm from wing base. Abdomen 0.75 mm wide.

Remarks. Wightipsocus acourti (Cockerell 1921) (= Psocus acourti Cockerell, 1921 = Psocidus acourti (Cockerell 1921) Lienhard & Smithers, 2002) was placed originally in the genus Psocus Latreille, 1794, without giving any reason for such attribution. The Recent Psocodea placed within this genus all have an areola postica attached to M, whereas Wightipsocus acourti has it free. Lienhard & Smithers (2002) placed it in the dustbin genus Psocidus Pearman, 1934 (without studying the material), as it does not fit in the genus Psocus. In any case, Wightipsocus acourti cannot belong to the family Psocidae (to which the genera Psocus and Psocidus belong), as it possesses trimere tarsi.

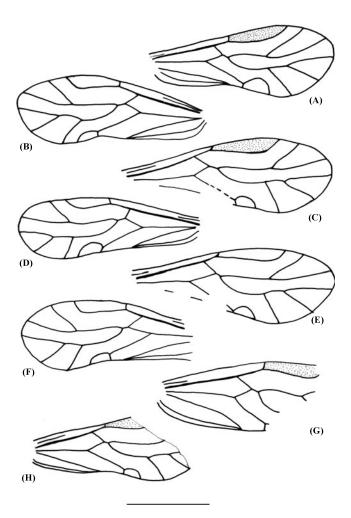
According to the keys to the families of Lienhard (1998) and Mockford (1993), Wightipsocus acourti falls in the sub-order Psocomorpha because of the combination of the following characters: (1) adult with legs with three tarsomeres; (2) forewing with thickened and sclerotised pterostigma; and (3) no scales.

The character "adult with legs with three tarsomeres" does not seem sufficient to assign our fossil to any of the Psocodea suborders. The character "thickened and sclerotised pterostigma" is the only and sufficient character that would orient the attribution rather to Psocomorpha; this same character is considered as being apomorphic of Psocomorpha by Yoshizawa (2002).

The type of venation that this species shows has been given the term "caeciliusid" by some authors (Garcia Aldrete 2005). This term means a forewing in which there is long basal common stem of M and Cu1, Rs and M fused for a short distance or at a point, Rs 2-branched, M is 3-branched, Cu1 has no connection to M and forms a rounded roof for the areola postica. This type of venation is certainly restricted to Psocomorpha; nevertheless, even if it is termed "caeciliusid", it does not corresponds obligatorily to the family Caeciliusidae, as the distinction between the different families of such type of venation is much more complex and requires body features as well.



Text-Figure 2 Wightipsocus acourti (Cockerell 1921), new combination, drawing of specimen NHMUK In.20559. Scale bar = 1 mm.



Text-Figure 3 Wightipsocus intasi gen. et sp. nov.: (A) drawing of holotype, specimen NHMUK In.24538; (B) drawing of paratype, specimen MNEMG 2009.78 (BLS 1608); (C) drawing of paratype, specimen MNEMG 2009.76 (BLS 1482 B); (D) drawing of paratype, specimen NHMUK In.17088; (E) drawing of paratype, specimen MNEMG 2009.77 (BLS 635 A); (F) drawing of paratype, specimen MNEMG 2009.79 (BLS 722); (G) drawing of paratype, specimen NHMUK I.9054; (H) drawing of paratype, specimen MNEMG 2009.80 (BLS 941). Scale bar = 1 mm.

According to Lienhard (1998), the following characters of *Wightipsocus acourti* would place it in either the family Pseudocaeciliidae or the family Philotarsidae: (1) a well developed macropterous wing; (2) trimere tarsi; (3) a free areola postica; (4) wings not glabrous; and (5) veins bearing two rows of setae.

According to Smithers' key (1990), Wightipsocus acourti would be attributed to Pseudocaeciliidae, Elipsocidae or Lachesillidae, due to: (1) being macropterous; (2) having tarsi 3-segmented; (3) wings without flattened scales; (4) forewing venation complex and not reduced to two parallel longitudinal veins; (5) thick pterostigma; (6) areola postica free; (7) Cu1a and Cu1b separate near wing margin; (8) forewing veins setose; and (9) forewing membrane glabrous.

As it is not known whether the hindwing is glabrous or not, attribution to either Lachesillidae or Elipsocidae is possible. The forewing character M + Cu, with two rows of setae, would orient the attribution to Pseudocaeciliidae. A minute examination of all the characters of Pseudocaeciliidae, Philotarsidae, Elipsocidae and Lachesillida would prove that Wightipsocus acourti doesn't belong to any of them. No member of those families possesses a hindwing with bifurcated M, but this character does occur in some modern Psocomorpha, notably in the entire family Calopsocidae and in some genera of family Epipsocidae; but here too the fossil does not fit into any of the later families. I think that W. acourti may be attributed to a new extinct family. However, most of the characters of W. acourti are pleisiomorphic within Psocomorpha, such as legs with three-segmented tarsi, pterostigma and a free areola postica. Even the very special character of a hindwing with bifurcated M, which seems apparently apomorphic for this group, and for Calopsocidae and some Epipsocidae in Psocomorpha (maybe this state has arisen several times as apomorphies in the group), is in reality a pleisiomorphy in Psocoptera. As I cannot find any real apomorphy with what is preserved in these fossils, it is not possible to allow the creation of a new family and I prefer the attribution of this taxon to an incertae sedis family, until the finding of more material that permits further consideration.

> Wightipsocus intasi gen. et sp. nov. Text-fig. 3; Plate 1, figs 4–11

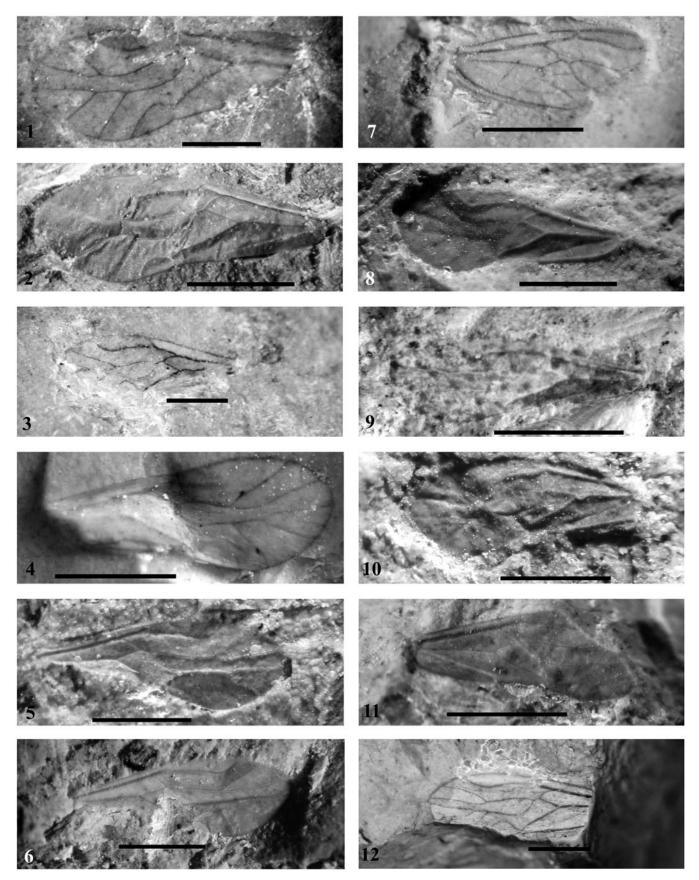
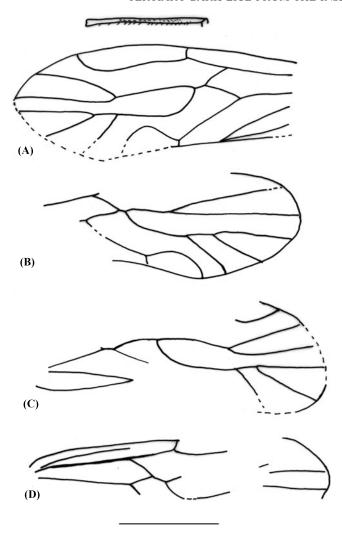


Plate 1 (1–3) Wightipsocus acourti (Cockerell 1921) new combination: (1) photograph of holotype, specimen NHMUK In.24366; (2) photograph of specimen MNEMG 2009.75 (BLS 551 A); (3) photograph of specimen NHMUK In.64128. (4–7) Wightipsocus intasi gen. et sp. nov.: (4) photograph of holotype, specimen NHMUK In.24538; (5) photograph of paratype, specimen MNEMG 2009.76 (BLS 1482 B); (6) photograph of paratype, specimen MNEMG 2009.77 (BLS 635 A); (7) photograph of paratype, specimen NHMUK I.9054. (8–11) Wightipsocus intasi gen. et sp. nov.: (8) photograph of paratype, specimen MNEMG 2009.78 (BLS 1608 A); (9) photograph of paratype, specimen NHMUK In.17088; (10) photograph of specimen MNEMG 2009.79 (BLS 722); (11) photograph of paratype, specimen MNEMG 2009.80 (BLS 941). (12) Wightipsocus rossi gen. et sp. nov., photograph of holotype, specimen NHMUK I.9276. Scale bars = 1 mm.



Text-Figure 4 Wightipsocus rossi gen. et sp. nov.: (A) drawing of holotype, specimen NHMUK I.9276; (B) drawing of paratype, specimen NHMUK I.10005; (C) drawing of specimen NHMUK I.8956(1); (D) drawing of paratype, specimen MNEMG I.8800. Scale bar = 1 mm.

Etymology. After the INTAS Project number 03-51-4367, which funded this study.

Holotype. Specimen number NHMUK In.24538 (Text-fig. 3A; Plate 1, fig. 4), Hooley collection, Insect Limestone, northwest Isle of Wight.

Paratypes. Specimens: NHMUK I.9054 (Text-fig. 3G; Plate 1, fig. 7), Brodie collection; NHMUK In.17088 (Text-fig. 3D; Plate 1, fig. 9), Smith collection; MNEMG 2009.76 (BLS 1482) (Text-fig. 3C; Plate 1, fig. 5); MNEMG 2009.77 (BLS 635) (Text-fig. 3E; Plate 1, fig. 6); MNEMG 2009.78 (BLS 1608) (Text-fig. 3B; Plate 1, fig. 8); MNEMG 2009.79 (BLS 722) (Text-fig. 3F; Plate 1, fig. 10) and MNEMG 2009.80 (BLS 941) (Text-fig. 3H, Plate 1, fig. 11).

Diagnosis. As for the genus (legs with three tarsomeres; forewing with veins bearing two rows of setae; forewing with thickened and sclerotised free pterostigma; Rs merging with M for a small distance and forming Rs + M, free areola postica; nodulus present; and one anal vein; hindwing with M bifurcated into M1 and M2), plus forewing with bifurcation of R2 + 3 and R4 + 5 at nearly the same level of bifurcation of M into M1 + M2 and M3.

Description. Measurements are mainly made from the holotype NHMUK In.24538. Forewing glabrous and hyaline, 2·3 mm long, 0·9 mm wide. Sc, 0·5 mm long (after specimen MNEMG 2009.78 (BLS 1608)), free and not reaching R. Distal free part of Sc (Sc' *sensu* Lienhard 1998) forming a sharp

angle with the costal margin and reaching it 1.35 mm from wing base; R1 simple, reaching obliquely the costal margin at 1.7 mm from wing base. Pterostigma thickened, 0.65 mm long and 0.15 mm wide. Rs basally oblique, branching slightly more distally with M; common portion Rs + M, 0.1 mm long, at 0.85 mm from wing base; fork of R2 + 3 and R4 + 5 1.4 mm distal of wing base; R2 + 3 nearly straight and R4 + 5 slightly curved basally; reaching wing margin respectively at 1.83 mm and 2.15 mm from wing base. M basally fused with Cu1; fork of M1 + M2 and M3 1.45 mm distal of wing base; M1 and M2 separating 1.67 mm distal of wing base; M1 nearly straight, reaching wing apex, 0.5 mm long; M2 straight, 0.4 mm long; M3 straight, 0.42 mm long. Fork of Cu1 in Cu1a and Cu1b (sensu Mockford 1993) 1.1 mm from wing base; Cu1a strongly curved and longer than Cu1b. Areola postica (AP) free; no cross-vein between AP cell and M. Cu2, 0.95 mm long; a distinct nodulus at 0.95 mm from wing base. 1A curved, 0.8 mm long.

Remarks. W. intasi differs from W. acourti by forewings of smaller size and bifurcation of R2 + R3 and R4 + R5 at nearly the same level of bifurcation of M into M1 + M2 and M3. Usually (but it is not a rule) in Recent Psocodea of such venation type, a smaller size suggests the family Caeciliusidae; but certainly such an assumption could not be applied to fossils without taking into account the remaining body features. Hindwings and legs are not preserved in W. intasi, but I consider that they are of the same type as W. acourti.

Wightipsocus rossi gen. et sp. nov. Text-fig. 4; Plates 1, fig. 12, 2, figs 1–2

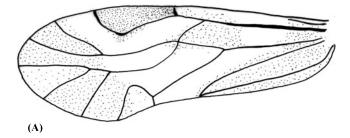
Etymology. After my friend Dr Andrew Ross, responsible for the INTAS Project number 03-51-4367, which funded this study.

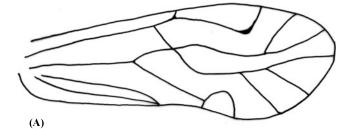
Holotype. Specimen NHMUK I.9276 (Text-fig. 4A; Plate 1, fig. 12), Brodie collection; Insect Limestone, northwest Isle of Wight.

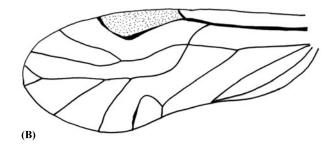
Paratypes. Specimens numbers: NHMUK I.10005 (Text-fig. 4B), Brodie collection; NHMUK I.8956(1) (Text-fig. 4C, Plate 2, fig. 1), Brodie collection; NHMUK I.8800 (Text-fig. 4D; Plate 2, fig. 2), Brodie collection.

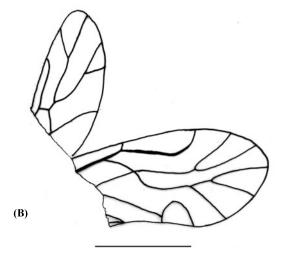
Diagnosis. As for the genus, plus forewing larger than 3 mm and bifurcation of R2 + R3 and R4 + R5 at the same or just before the level of bifurcation of M into M1 + M2 and M3.

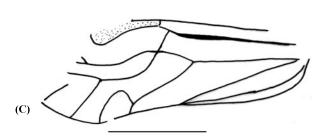
Description. Measurements are mainly made from the holotype specimen NHMUK I.9276. Forewing glabrous and hyaline 3.2 mm long, 1.25 mm wide. Sc, 0.95 mm long (from specimen NHMUK I.8800), free and not reaching R. Distal free part of Sc (Sc' sensu Lienhard 1998) forming a perpendicular angle with the costal margin and reaching it 1.35 mm from wing base; R1 simple, reaching obliquely the costal margin at nearly 2.45 mm from wing base. Pterostigma thickened, 1.1 mm long and 0.25 mm large. Rs basally oblique, branching slightly more distally with M; common portion Rs + M 0.15 mm long, at nearly 1.25 mm from wing base; fork of R2 + 3 and R4 + 5 2·15 mm distal of wing base; R2 + 3nearly straight and R4 + R5 slightly curved basally, reaching wing margin and wing apex respectively at 3 mm and 3.2 mm from wing base. M basally fused with Cu1; fork of M1 + M2 and M3 2·13 mm distal of wing base; M1 and M2 separating 1.67 mm distal of wing base; M1 and M2 straight, respectively 0.75 mm and 0.55 mm long. M3 straight, 0.55 mm long. Fork of Cu1 in Cu1a and Cu1b (sensu Mockford 1993) 1.6 mm from wing base; Cu1a strongly curved and much longer than Culb. Areola postica free; no cross-vein between AP cell and M. Cu2 1·1 mm long; a distinct nodulus at 1·2 mm from wing base. 1A curved. Tibia preserved on the holotype specimen.











Text-Figure 6 Awightipsocus jarzembowskii gen. et sp. nov.: (A) drawing of paratype, specimen NHMUK In.24579; (B) drawing of paratype, specimen NHMUK In.24788. Scale bars = 1 mm.

Text-Figure 5 Awightipsocus jarzembowskii gen. et sp. nov.: (A) drawing of holotype, specimen MNEMG 2009.81 (BLS 439 A); (B) drawing of paratype, specimen NHMUK I.9528; (C) drawing of paratype, specimen NHMUK In.24536. Scale bar = 1 mm.

Remarks. W. rossi differs from W. acourti and W. intasi in its larger forewings and bifurcation of R2 + 3 and R4 + 5 at nearly the same level or slightly before the bifurcation of M

Genus Awightipsocus gen. nov.

into M1 + M2 and M3.

Etymology. After the Greek "a" = not and the genus Wightipsocus.

Diagnosis. Forewing venation very similar to the genus *Wightipsocus*, except Rs meeting with M in a point forming an X shape. Hindwing as in *Wightipsocus*, with M bifurcated into M1 and M2.

Awightipsocus jarzembowskii gen. et sp. nov. Text-figs 5, 6; Plate 2, figs 3–5

Etymology. After my friend Professor Ed Jarzembowski, Curator of the MNEMG.

Holotype. Specimen MNEMG 2009.81 (BLS 439 A) (Text-fig. 5A, Plate 2, fig. 3) and its counterpart MNEMG 2009.81 (BLS 434 B) deposited in the MNEMG; Insect Limestone, northwest Isle of Wight.

Paratypes. Specimens: NHMUK I.9528 (Text-fig. 5B; Plate 2, fig. 4), Brodie collection; NHMUK In.24536 (Text-fig. 5C; Plate 2, fig. 5), Hooley collection; NHMUK In.24579 (Text-fig. 6A), Hooley collection; NHMUK In.24788 (Text-fig. 6B), Hooley collection.

Diagnosis. As for the genus, plus bifurcation of R2 + 3 and R4 + 5 at the midlevel between the bifurcation of M1 + M2 into M1 and M2 and M3.

Description. Measurements of the forewing are made from the holotype MNEMG 2009.81 (BLS 439 A) and its counterpart MNEMG 2009.81 (BLS 434 B); and for the hindwing from the specimen NHMUK In.24788. Forewing glabrous and hyaline 3.3 mm long, 1.25 mm wide. Sc 0.5 mm long. Distal free part of Sc (Sc' sensu Lienhard 1998) forming a sharp angle with the costal margin and reaching it 1.65 mm from wing base; R1 simple, reaching obliquely the costal margin at 2.6 mm from wing base. Pterostigma thickened, 0.85 mm long and 0.3 mm wide. Rs basally oblique, meeting with M in one point; fork of R2 + 3 and R4 + 5 2.45 mm distal of wing base; R2 + 3 and R4 + 5 curved; reaching wing margin respectively at 2.9 mm and 3.25 mm from wing base. M basally fused with Cu1; fork of M1 + M2 and M3 2.45 mm distal of wing base; M1 and M2 separating 2.6 mm distal of wing base; M1 and M2 slightly curved. M1 0.75 mm long; reaching wing margin slightly before the apex, M2 0.5 mm long; M3 straight, 0.55 mm long. Specimen NHMUK I.9528 presenting teratology in M1 which is bifurcated apically. Fork of Cu1 in Cu1a and Cu1b (sensu Mockford 1993) 1.9 mm from wing base; Cu1a strongly curved and longer than Cu1b. Areola postica (AP) free; no cross-vein between AP cell and M. Cu2 1.6 mm long; a distinct nodulus at 1.9 mm from wing base. 1A curved basally, 1.5 mm long. Forewing must be coloured. Hindwing glabrous and hyaline, smaller than forewing and only apical half preserved, 0.65 mm wide. Rs distally fused with M for 0.05 mm. R1 reaching anterior wing margin. Rs bifurcated into R2 + 3 and R4 + 5. R2 + 3 0.3mm long; R4 + 5 0.45 mm long. Bifurcation of M into M1 and M2 0.6 mm from wing apex; M1 0.35 mm long; M2 0.2

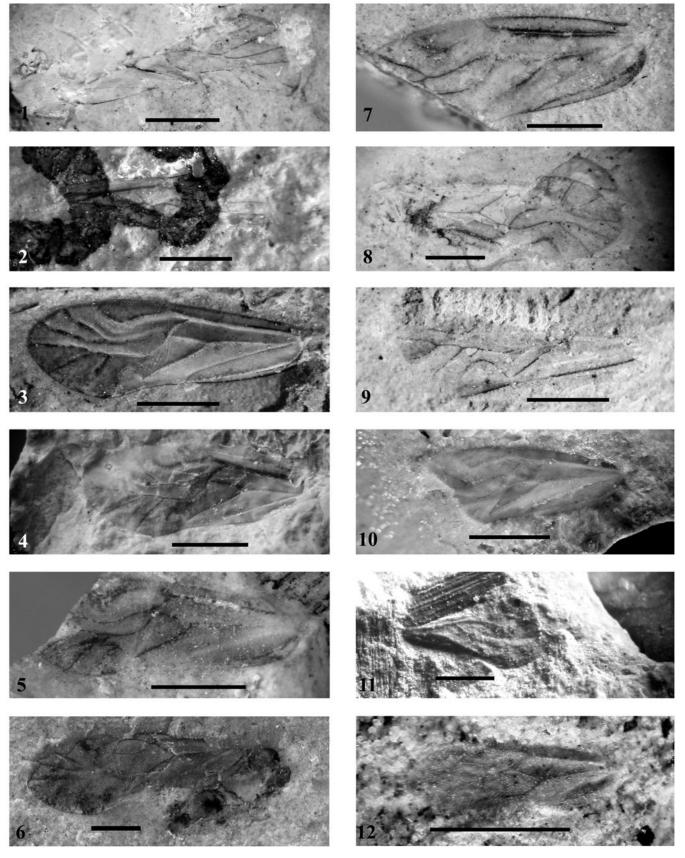
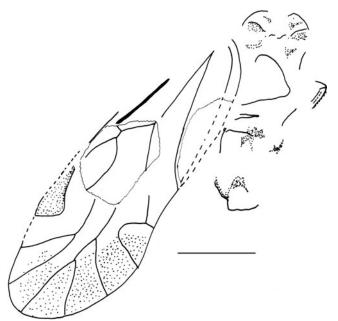


Plate 2 (1–2) Wightipsocus rossi gen. et sp. nov.: (1) photograph of paratype, specimen NHMUK I.8956(1); (2) photograph of paratype, specimen NHMUK I.8800. (3–5) Awightipsocus jarzembowskii gen. et sp. nov.: (3) photograph of holotype, specimen MNEMG 2009.81 (BLS 439 A); (4) photograph of paratype, specimen NHMUK I.9528; (5) photograph of paratype, specimen NHMUK In.24536. (6–8) Awightipsocus megaloi gen. et sp. nov.: (6) photograph of holotype, specimen NHMUK In.17187; (7) photograph of paratype, specimen NHMUK In.24601; (8) photograph of paratype, specimen NHMUK In.24532. (9–10) Awightipsocus minimus gen. et sp. nov.: (9) photograph of paratype, specimen MNEMG 2009.82 (BLS 985 B); (10) photograph of holotype, specimen MNEMG 2009.83 (BLS 981). (11) Wightimicropsocus inexpectatus gen. et sp. nov., photograph of paratype, specimen NHMUK In.25108. (12) Awightipsocus minimus gen. et sp. nov., photograph of holotype, specimen MNEMG 2009.84 (BLS 1501). Scale bars = 1 mm.



Text-Figure 7 Awightipsocus megaloi gen. et sp. nov., drawing of holotype, specimen NHMUK In.17187. Scale bar = 1 mm.

mm long. Cu1 reaching posterior wing margin at 0.9 mm from wing apex.

Remarks. As for *Wightipsocus*, according to the keys to the families of Lienhard (1998) and Mockford (1993), *Awightipsocus* would fall in the suborder Psocomorpha.

Awightipsocus is very similar to Wightipsocus, but in the forewing Rs meets with M in one point, forming an X shape instead of merging with it for a distance. It seems quite possible that Wightipsocus and Awightipsocus, both with bifurcate M in the hindwing, are primitive relatives of the living Calopsocidae, with plesiomorphies of three tarsomeres (calopsocids have two) and simple forewing venation. The two rows of setae on the forewing veins also conform to this idea. For the same reason as for Wightipsocus, I prefer to attribute Awightipsocus to the family incertae sedis.

Awightipsocus megaloi gen. et sp. nov. Text-figs 7, 8A-C; Plate 2, figs 6-9

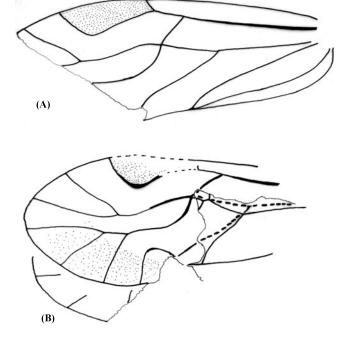
Etymology. After the Greek "megalo" = large.

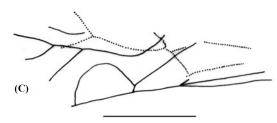
Holotype. Specimen number NHMUK In.17187 (Text-fig. 7, Plate 2, fig. 6), Smith collection; Insect Limestone, northwest Isle of Wight.

Paratypes. Specimen numbers: NHMUK In.24601 (Text-fig. 8A, Plate 2, fig. 7), Hooley collection; NHMUK In.24532 (Text-fig. 8B, Plate 2, fig. 8), Hooley collection; MNEMG 2009.82 (BLS 985 B) (Text-fig. 8C, Plate 2, fig. 9).

Diagnosis. As for the genus, plus bifurcation of R2+3 and R4+5 very slightly beyond the level of bifurcation of M1+M2 and M3. Tibia with series of aligned setae.

Description. Measurements were made from several specimens, as none is well preserved, but mainly from the holotype. Forewing glabrous and hyaline, 4·5 mm long, 1·5 mm wide (after the holotype). Sc not preserved in any specimen. Distal free part of Sc (Sc' sensu Lienhard 1998) forming a sharp angle with the costal margin and reaching it 2·05 mm from wing base (after specimen number NHMUK In.24601); R1 simple, reaching obliquely the costal margin at 3·4 mm (for holotype) and 3·1 mm (for specimen NHMUK In.24601) from wing base. Pterostigma thickened, 1 mm long and 0·35 mm wide. Rs basally oblique, meeting distally with M in a single





Text-Figure 8 Awightipsocus megaloi gen. et sp. nov.: (A) drawing of paratype, specimen NHMUK In.24601; (B) drawing of paratype, specimen NHMUK In.24532; (C) drawing of paratype, specimen MNEMG 2009.82 (BLS 985 B). Scale bar = 1 mm.

point; fork of R2 + 3 and R4 + 5 3·3 mm distal of wing base; R2 + 3 and R4 + 5 slightly curved, reaching wing margin respectively at 3·8 mm and 4·23 mm from wing base. M basally fused with Cu1; fork of M1 + M2 and M3 3·1 mm distal of wing base; M1 and M2 separating 3·5 mm distal of wing base; M1 reaching wing apex; M2 0·7 mm long; M3 0·75 mm long. Fork of Cu1 in Cu1a and Cu1b (sensu Mockford 1993) 2·55 mm from wing base; Cu1a strongly curved and longer than Cu1b. Areola postica (AP) free; no cross-vein between AP cell and M. Cu2 1·9 mm long; a distinct nodulus at 1·9 mm from wing base. 1A 1·95 mm long. Forewing must be coloured (Text-fig. 8B). Hindwing glabrous and hyaline, only parts are preserved. Rs distally fused with M for 0·05 mm. Thorax 0·75 mm long and 0·9 mm wide. Abdomen 1·8 mm long and 0·9 mm wide.

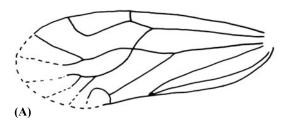
Awightipsocus minimus gen. et sp. nov. Text-fig. 9A-B, Plate 2, figs 10-11

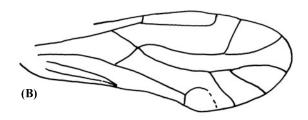
Etymology. After the Latin "minimus" = small.

Holotype. Specimen number MNEMG 2009.83 (BLS 981) (Text-fig. 9A, Plate 2, fig. 10); Insect Limestone, northwest Isle of Wight.

Paratype. Specimen NHMUK In.25108 (Text-fig. 9B, Plate 2, fig. 11), Hooley collection.

Diagnosis. As for the genus, plus bifurcation of R2 + 3 and R4 + 5 on the same level as the bifurcation of M1 + M2 into M1 and M2.







Text-Figure 9 (A–B) *Awightipsocus minimus* gen. *et* sp. nov.: (A) drawing of holotype, specimen MNEMG 2009.83 (BLS 981); (B) drawing of paratype, specimen NHMUK In.25108. (C) *Wightimicropsocus inexpectatus* gen. *et* sp. nov., drawing of holotype, specimen MNEMG 2009.84 (BLS 1501). Scale bar = 1 mm.

Description. Forewing glabrous and hyaline, 2.4 mm long, 0.9 mm wide. Sc not preserved. Distal free part of Sc (Sc' sensu Lienhard 1998) forming a perpendicular angle with the costal margin and reaching it 1.35 mm from wing base; R1 simple, reaching obliquely the costal margin at 1.85 mm from wing base. Pterostigma 0.55 mm long and 0.2 mm wide. Rs basally oblique, meeting more distally with M in a single point; fork of R2 + 3 and $R4 + 5 \cdot 1.8$ mm distal of wing base; R2+3 and R4+5 slightly curved, reaching wing margin respectively at 2.2 mm and 2.4 mm from wing base. M basally fused with Cu1; fork of M1 + M2 and M3 1.6 mm distal of wing base; M1 and M2 separating 1.8 mm distal of wing base; M1 0.45 mm long; M2 0.4 mm long; M3 0.35 mm long. Fork of Cu1 in Cu1a and Cu1b (sensu Mockford 1993) 1.55 mm from wing base; Cu1a strongly curved and longer than Culb. Areola postica (AP) free; no cross-vein between AP cell and M. Cu2 1·15 mm long; a distinct nodulus 1·1 mm from wing base. 1A 1.25 mm long.

Remarks. In addition to the differences cited in the diagnosis of the three species concerning the level of bifurcation of R2+3 and R4+5 compared to the level of bifurcation of M1+R2 and M3, the main other differences between A. *jarzembowskii*, A. *minimus* and A. *megaloi* are in wing venation measurements. A. *megaloi* is the largest one and A. *minimus* the smallest.

Suborder Psocomorpha ? (Roesler 1944) Family *Incertae sedis*

Genus Wightimicropsocus gen. nov.

Etymology. After the Isle of Wight + the Greek "micro" = very small + Psocus

Diagnosis. Forewing with free Pterostigma; Rs merging with M for a small distance and forming rs + m; bifurcation between R2 + 3 and R4 + 5 at the same level as bifurcation between M1 + R2 and M3; wing apex between M1 and M2; free elongated areola postica much longer than Pterostigma; nodulus present; one anal vein.

Wightimicropsocus inexpectatus gen. et sp. nov. Text-fig. 9C; Plate 2, fig. 12

Etymology. After the unexpected finding of this taxon. **Holotype.** Specimen number MNEMG 2009.84 (BLS 1501); Insect Limestone, northwest Isle of Wight.

Diagnosis. As for the genus.

Description. Forewing maybe setose, 1.57 mm long, 0.5 mm wide. Sc 0.27 mm long. Distal free part of Sc (Sc' sensu Lienhard 1998) forming a sharp angle with the costal margin and reaching it 0.67 mm from wing base; R1 simple, reaching obliquely the costal margin at 0.9 mm from wing base. Pterostigma 0.27 mm long and 0.075 mm wide. Rs basally oblique, branching slightly more distally with M; common portion Rs + M 0.07 mm long, at 0.725 mm from wing base; fork of R2 + 3 and R4 + 5 1·1 mm distal of wing base; R2 + 3 and R4+5 reaching wing margin respectively at 1·12 mm and 1.35 mm from wing base. M basally fused with Cu1; fork of M1 + M2 and $M3 \cdot 1\cdot 12$ mm distal of wing base; M1 and M2separating 1.32 mm distal of wing base; M1 nearly straight, 0.22 mm long; M2 straight, 0.22 mm long; M3 straight, 0.3 mm long. Fork of Cu1 in Cu1a and Cu1b (sensu Mockford 1993) 0.72 mm from wing base; Cu1a elongated and much longer than Cu1b. Areola postica (AP) free, 0.42 mm long; no cross-vein between AP cell and M. Cu2 0.6 mm long; a distinct nodulus at 0.6 mm from wing base. 1A curved, 0.65mm long.

Remarks. As only one specimen is preserved for this taxon, no positive determination is possible (although size and venation suggest Archipsocidae, as no modern archipsocid shows branches of M). This species is notable for having a well elongated "special" areola postica that is nearly twice as long as the pterostigma. This taxon certainly belongs to a different family from the other fossil psocids of the Isle of Wight, but here too, the lack of characters does not allow any family level attribution.

2. Conclusion

The relatively well diversified fossil Psocodea fauna from the late Eocene Bembridge Marls of the Isle of Wight greatly increases our knowledge of the biodiversity of Psocodea. This diversity indicates a warmer climate than that of today for the same area, as it is known that the multiplicity of species increases with high temperatures. It also reflects a sylvan or forest habitat, as the species found in the Bembridge Marls of the Isle of Wight belong to families or groups that usually live on dead or living leaves, on bark surfaces and in leaf litter; and that feed on lichen, decomposed leaves and wood and/or fungi.

A comparison between the fossil Psocodea of the Isle of Wight and all the known Cenozoic psocomorphan fossils com-

firms that the Psocodea of the Isle of Wight are peculiarly different. They look, at first examination, very similar to Recent psocomorphan families, without really fitting into any of them. They have a number of presumably primitive features, such as hindwing M bifurcated and legs with tarsi three-segmented. These characters either put them very basally in the evolutionary tree of Psocomorpha, or very derived, if these characters are considered as reversions.

Although Yoshizawa (2002) made a good phylogeny of the Psocomorpha based on Recent species, his study alone seems insufficient without including fossils. In my opinion, a very thorough phylogenetic analysis, including Recent and fossil species, is needed to clarify the classification of the whole order Psocodea.

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4. Appendix I. Key to the fossil Psocodea of the Isle of Wight

- 1 Areola postica elongated, longer than pterostigma = Wightimicropsocus inexpectatus.
 - Areola postica relatively shorter go to 2.
- 2 Rs merging with M for a small distance and forming rs + m = Wightipsocus..... go to 3.
 - Rs meeting M in a single point = Awightipsocus..... go
- 3 Forewing 3 mm long, with bifurcation of R2 + 3 and R4 + 5 very slightly basal to the level of bifurcation of M1 + R2 into M1 and M2 = Wightipsocus acorti.
 - Forewing 2·3 mm long, with bifurcation of R2 + 3 and R4 + 5 at nearly the same level of bifurcation of M into M1 + M2 and M3 = Wightipsocus intasi.
 - Forewing larger than 3 mm and bifurcation of R2+3 and R4+5 at the same or just slightly before the level of bifurcation of M into M1+M2 and M3 = Wightipsocus rossi
- 4 Forewing 3.3 mm long and bifurcation of R2 + 3 and R4 + 5 at the midlevel between the bifurcation of M1 + M2 into M1 and M2 and M3 = Awightipsocus jarsembowskii.

- Forewing 4.5 mm long and bifurcation of R2 + 3 and R4 + 5 very slightly beyond the level of bifurcation of M1 + M2 and M3 = Awightipsocus megaloi.
- Forewing 2.4 mm long and bifurcation of R2+3 and R4+5 on the same level as the bifurcation of M1+M2 into M1 and $M2=Awightipsocus\ minimus$.

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