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The stratigraphical potential of blattodean insects from the late Carboniferous of southern Britain

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Abstract – The Blattodea (cockroaches *sensu lato* or roachoids) from the southern coalfields of the UK are reviewed or examined, especially species occurring in more than one coal basin including *Mylacris abrupta* (Bolton, 1930) comb. nov., and undescribed material from Writhlington (Somerset). It is proposed that a derived mylacrid *Mylacris–Sooblatta* assemblage is used to extend the latest Westphalian and earliest Stephanian insect zonation from the continent to southern Britain, thus augmenting the European Pennsylvanian scheme.

Keywords: insects, Blattodea, Carboniferous, stratigraphy, UK.

1. Introduction

IGCP 469 is concerned with biotic change in the Pennsylvanian (Late Carboniferous) Subperiod (Bolsovian–Cantabrian subages) of the Variscan Zone. Biostratigraphy is an important tool, and fossil insects, especially from South Wales, can contribute here. The Welsh Pennsylvanian entomofauna includes extinct palaeopterous insects (palaeodictyopteroids), stem polyneopterans ('protorthopterans') and cockroaches *sensu lato* (blattodeans), and was last reviewed 75 years ago (North, 1931). By that time, Wales had already yielded a third of the British Carboniferous insect species and a Variscan fauna in northwest Europe had begun to be recognized. The fossils have stratigraphical significance because five out of six British species of Bolsovian–Stephanian insects found in multiple coal basins are recorded from the South Wales Coalfield. A seventh is known from the Duckmantian ('Westphalian B') Substage and is outside the scope of this project. These species are all blattodeans (Table 1), which is not surprising as the latter are the most abundant Carboniferous insects (Jarzembowski, 1987). Here we summarize our knowledge of these cockroaches (or roachoids) in the UK portion of the Variscan Foreland south of the Welsh-Brabant Massif (Fig. 1). This is to facilitate, and hopefully stimulate, taxonomic and biostratigraphical revision and study of new British material which has accumulated since the classical studies of the early twentieth century. Not least amongst this are finds from the upper Asturian Substage of the Somerset Coalfield (Jarzembowski, 1989).

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2. Insect stratigraphy

Pennsylvanian insect biostratigraphy is comparatively new and is being developed in conjunction with that of other non-marine animals, notably conchostracans (clam shrimps). The latter have a chitinous exoskeleton like insects and are often associated with them in the fossil record. A zonation has been proposed based on archimylacrid blattodeans for the Westphalian Stage, and on spiloblattinid blattodeans for the Stephanian Stage, continuing into the Permian System (Schneider, 1982; Schneider & Werneburg, 1993; Schneider *et al.* 2003; Schneider, Goretzki & Roessler, 2005). This insect zonation is recognized in Britain up to the *Archimylacris lubnensis* Zone (upper Bolsovian–lower Asturian substages) but no higher. Nevertheless, the upper Bolsovian–Asturian *Anomalonema reumauxi–Pseudestheria simoni* Assemblage Zone is recognized in the Somerset Coalfield based on the presence of the former distinctive conchostracan species (Jarzembowski, 2004, fig. 3). It may be noted that no Spiloblattinidae have yet been described from the UK and Mylacridae are an untapped potential in the Asturian–Cantabrian stratigraphical interval (see below).

3. Systematic palaeontology

The classification and taxonomy is based on Schneider (1983, 1984), who employed a broader species concept than previous workers, interpreted by Vršanský (2000) as superspecies; the latter's family nomenclature is given in parentheses. The critical material of UK Variscan blattodeans is dispersed throughout collections in Europe and North America so that a comprehensive revision has not yet been undertaken.

Table 1. Revised checklist of cockroaches (*sensu lato*) from the Upper Carboniferous of the British Variscan Foreland (south of the Wales-Brabant Massif) augmenting Schneider (1983)

Family	Species	South Wales	Forest of Dean	Bristol-Somerset	Kent	Other
Archimylacridae Handlirsch, 1906	*Archimylacris* '*regularis*' Bolton, 1934			X		
	Archimylacris lubnensis Kušta, 1883	X				France, Belgium
	Archimylacris calopteryx (Handlirsch, 1906)	X				USA
	Archimylacris scalaris Bolton, 1930	X				
	'Phylomylacris' parallelus Bolton, 1930	X				
	Archimylacris sp. n. 2 herein			X		
Archimylacridae?	'*Asemoblatta*' *glamorgana* Handlirsch, 1920	X				
Necymylacridae Durden, 1969	*Necymylacris hastata* (Bolton, 1911)	X				
Mylacridae Scudder, 1868	'*Drybrookia cubitalis*' Bolton, 1924		X			
	Mylacris abrupta (Bolton, 1930)	X				Canada, Zwickau
	Orthomylacris delicatula Bolton in Wallis, 1939	X				
	Orthomylacris hastata Bolton in Wallis, 1939	X				
	'*Orthomylacris*' *northi* (Bolton, 1930)	X				
	Sooblatta boltoniana Schneider, 1983	X				Canada, Zwickau, France
	Sooblatta burri (Bolton, 1912)	X			X	
	Sooblatta deanensis (Scudder, 1895)	X	X	X		France?
	Sooblatta? *nodulata* (Bolton, 1934)	X				
	Sooblatta ovata (Wallis nec Bolton, 1939)	X				
	Sooblatta strahani (Bolton, 1930)	X				
	Sooblatta villeti (Pruvost, 1912)	X				France
	'*Soomylacris*' *obesa* Bolton in Wallis, 1939	X				
Incertae sedis	'*Archimylacris*?' *celtica* Handlirsch, 1920	X				
	'*Archimylacris*?' *inversa* Handlirsch, 1920	X				
	'*Archimylacris*?' *obovata* Bolton, 1911	X				
	'*Hemimylacris*' *convexa* Bolton, 1911	X				
	'*Phyloblatta*?' *boltoniana* Handlirsch, 1920				X	
	'*Phyloblatta*?' *britannica* Handlirsch, 1920				X	
	'*Sooblattella*' *britannica* Handlirsch, 1920	X				

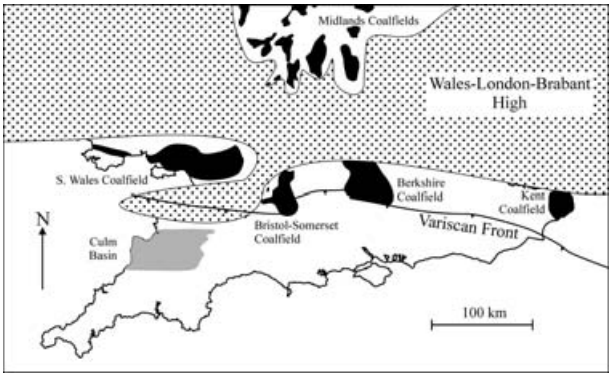

Figure 1. Main Upper Carboniferous coalfields (black) of the southern UK in their geological context. The Berkshire and Kent coalfields are concealed and insects are unknown from the former due to lack of collecting opportunities.

Schneider (1983) and Schneider, Goretzki & Roessler (2005) relied on the best available descriptions and re-examination of some types; detailed occurrences were given but not synonyms, which is rectified below.

Order BLATTODEA Brunner, 1882
Family ARCHIMYLACRIDAE Handlirsch, 1906
(Schneider, 1983)
(Archimylacrididae *sensu* Vršanský, 2000)

Comment. This monobasic family shows some archaic features in the wing venation including the connection of the median (M) with the anterior cubitus (Cu1) by a strong cross-vein close to the wing base, as well as a concentrically arranged, simple, striate cross-venation (archedictyon auct.). The latter becomes modified (during the late Westphalian) to increasingly anastomosing and reticulate patterns; for graphic definitions, see Schneider (1984, pl. V). Also, the wing outline becomes more elongate and main venation phyloblattoid-like. Archimylacrids are unknown after the Asturian except for *Archimylacris regularis* (Bolton, 1934) comb. nov. (*Archaeotiphe regularis* Bolton, 1934; *Parelthoblatta (Archaeotiphe) regularis* (Bolton, 1933 [sic]) ms name Durden (unpub. Ph.D. thesis, Yale Univ., 1972, p. 105, opp. p. 111)) from the lower Cantabrian Substage (Radstock Formation) of the Somerset Coalfield (Cleal, Dimitrova & Zodrow, 2003) and a paraphyletic relationship with Phyloblattidae remains possible. True transitional forms between the two families are, however, unknown, and early phyloblattids are coeval with archimylacrids in the Asturian.

Schneider (1983) reduced about 10 genera (sometimes regarded as belonging to different families) including *Parelthoblatta* Handlirsch, 1904, to a single genus *Archimylacris* Scudder, 1868. The number of species was also reduced from about 25 to 17. Archimylacrids are known from nearly all Euramerican basins of Westphalian age, mostly as solitary wings. The continuing study of 240 *Archimylacris* wings from Writhlington (Section 4) offers a unique opportunity to investigate intraspecific variation and possible sexual

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dimorphism. This is of primary importance for the taxonomy of this stratigraphically useful genus (see Section 2).

Archimylacris lubnensis Kušta, 1883

Synonyms. Archimylacris belgica Handlirsch, 1904; *Parelthoblatta belgica* (Handlirsch, 1904) Laurentiaux, 1967; *Archimylacris desaillyi* Leriche, 1907; *Archimylacris woodwardi* Bolton, 1910; *Phyloblatta* (*Asemoblatta*) *humenryi* Pruvost, 1912; *Archimylacris atrebatica* Pruvost, 1919; *Archimylacris elbyi* Pruvost, 1919; *Archimylacris diensti* Guthörl, 1934 (Schneider, 1983; Schneider, Goretzki & Roessler, 2005).

Locality and horizon in UK. Clydach, Swansea Valley, South Wales; roof shale above the No. 2 Rhondda Seam, Rhondda Member, Lower Pennant Formation. Bolton (1910) noted that the 10 ft (3 m) thick shale thins eastwards and is replaced by sandstone within 2 miles (3.2 km).

Age in UK. Late Bolsovian Subage (Cleal, 1978).

Comment. Schneider (1983, p. 109) and Schneider, Goretzki & Roessler (2005) recorded this species from South Wales as well as the Bolsovian and early Asturian substages of France, Belgium and Germany; the latter also gave a new figure of *A. lubnensis* from the late Bolsovian of the Czech Republic (Lubná Seam, Radnice Formation). *Archimylacris acadica* Scudder, 1868 from the roof of the main seam of the Pictou Coal, Nova Scotia, Canada is another possible synonym. This species' extension of range to southern England is anticipated.

The British material (*A. woodwardi*) is referred to by Bassett (1972, p. 17), Durden (unpub. Ph.D. thesis, Yale Univ, 1972, p. 102, opp. pp. 111, 309, 313), Handlirsch (1922, p. 113), Jarzembowski (1988, p. 38), Laurentiaux (1967, pp. 61, 64) and North (1931, p. 42). A modern photograph (ammonium chloride-coated) of the holotype of *A. woodwardi* is in Owens & Bassett (1995, p. 9, fig. 5,1). The forewing is slightly shorter (1.8 × 1.0 cm) than typical *A. lubnensis* (2.7 × 1.1 cm) due to deformation, although the venation is similar.

Family MYLACRIDAE Scudder, 1868
(Mylacrididae *sensu* Vryšanský, 2000)

Comment. Schneider (1983) reduced the number of valid mylacrid genera from over 40 to 6, and the number of species from about 120 to 53. The genera were formerly distributed in various families and the reduction was done with some reservation because of poorly figured types and exceptional variation amongst mylacrids. The continuing investigation of a uniquely large collection of mylacrid cockroachoids from Writhlington (see Section 4) should improve our knowledge of intraspecific variation and aid taxonomy. The species of *Sooblatta* given below may well be reduced to one or two species in future.

Mylacris abrupta (Bolton, 1930) comb. nov.

Synonyms. Mylacris moriensis (Copeland, 1957), Schneider, 1983; *Phylomylacris abrupta* Bolton, 1930; *Phylomylacris* cf. *abrupta* Bolton, 1930 (Schneider, 1983); *Orthomylacris abrupta* (Bolton, 1929 [sic]) ms name Durden (unpub. Ph.D. thesis, Yale Univ., 1972).

Locality and horizon in UK. Beili Glas Colliery, Gorseinon, South Wales; shale associated with the Penyscallen Seam, Grovesend Formation.

Age in UK. Late Asturian (late 'Westphalian D') Subage (Cleal, 1978).

Comment. Schneider (1983, pp. 112, 115) recorded this species as *Mylacris moriensis* from South Wales, and from the Asturian of Canada (Nova Scotia) and eastern Germany (Zwickau Basin). *P. abrupta,* however, has date priority. The UK type (no. 27.177.G10/36) and figured material is in the National Museum of Wales (Bassett, 1972, p. 19), and a modern photograph is in Owens & Bassett (1995, p. 9, fig. 5,5).

Sooblatta boltoniana Schneider, 1983

Synonyms. Stenomylacris? *lanceolata* (Bolton, 1911) Handlirsch, 1922; *Orthomylacris lanceolata* Bolton, 1911 (Schneider, 1983); *Quasimylacris lanceolata* (Bolton, 1911) Durden, 1984.

Locality and horizon in UK. Clydach Merthyr Colliery, Clydach, Swansea Valley, South Wales; shales associated with the Graigola Seam, Pennant Formation.

Age in UK. Late Asturian (late 'Westphalian D') Subage (C. Cleal, pers. comm.).

Comment. Schneider (1983, p. 112) also recorded this species from the Asturian Substage of eastern Germany. Durden (1984 ex unpub. Ph.D. thesis, Yale Univ., 1972, p. 103, opp. p. 111, 237–42, 244, opp. 349; pl. 8, figs 69a–d, 70–1a, captions 396–7) previously recorded it from northern France plus the Stellarton Group of Nova Scotia, Canada (Bolsovian Substage).

Bolton's type is No. 24511 in the British Geological Survey collections, as indicated by North (1931, p. 42).

Sooblatta burri (Bolton, 1912)

Synonyms. Soomylacris burri Bolton, 1912 and *Soomylacris truncata* Bolton, 1934 (Schneider, 1983, by implication); *Mylacris burri* (Bolton, 1912) Durden, 1969 (also unpub. Ph.D. thesis, Yale Univ., 1972); *Trilophomylacris burri* (Bolton) Handlirsch, 1922; *Orthomylacris truncaluta* (Bolton, 1933 [sic]) Durden, 1969; *Orthomylacris truncata* (Bolton, 1933 [sic]) Durden (unpub. Ph.D. thesis, Yale Univ., 1972).

Localities and horizons. Barfreston[e] borehole, Kent; dark shale at −1208 ft (368 m), upper Upper Coal Measures (Gallois & Edmunds, 1965, fig. 21). Pentre Colliery, Landore, Swansea, South Wales;

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plant-bearing ironstone over Swansea Five Foot Seam, Grovesend Formation.

Age. Late Asturian Subage (see below).

Comment. The present depository of the material belonging to this species is unknown. It was originally unnumbered in the Museum of the Kent Coal Concessions Company, Dover, and Dix Collection, respectively. The species occurs well above the base of the Asturian Substage as currently understood in both the Kent and South Wales coalfields (e.g. Cleal, Fraser & Thomas, 2005).

Sooblatta deanensis (Scudder, 1895)

Synonyms. Soomylacris deanensis (Scudder, 1895) and *Discomylacris obtusa* (Bolton, 1911) Handlirsch, 1922; *Soomylacris celtica* Bolton, 1934; *Hemimylacris obtusa* (Bolton, 1911) North, 1931; *Soomylacris stocki* Bolton, 1922; *Phylomylacris membranacea* Bolton, 1930; *Mylacris deanensis* (Scudder, 1895), *Orthomylacris celtica* (Bolton, 1933 [sic]), *Mylacris obtusa* (Bolton, 1911) and *Mylacris stocki* (Bolton, 1922) Durden, 1969; *Mylacris celtica* (Bolton, 1933 [sic]), *Orthomylacris obtusa* (Bolton, 1911) and *Aphelomylacris membranacea* (Bolton, 1929 [sic]) ms names Durden (unpub. Ph.D. thesis, Yale Univ., 1972).

Localities and horizons. Foxe's Bridge, Forest of Dean, Gloucestershire; 'Coal Measures'. Crump Meadow, Forest of Dean, Gloucestershire; 'Coal Measures'. Gladys Colliery near Penllergaer Church, West Glamorgan, South Wales; shales associated with Swansea Four Foot Seam, Grovesend Formation. Cily bebyll, near Swansea, South Wales; shales associated with Pretoria Seam, Grovesend Formation. Mountain Colliery, Gorseinon, South Wales; shales associated with Penyscallen Seam, Grovesend Formation. Bromley Colliery, Pensford, Somerset; above the No. 6 Seam, Farrington Formation.

Age. Late Asturian (South Wales and Somerset) and Early Cantabrian (Forest of Dean) subages (C. Cleal, 1978, and pers. comm. 2005).

Comment. The synonymy is based on Schneider (1983, pp. 112, 116) and *S. deanensis* might extend its range to France (Bolton, 1934, p. 293). *Sooblatta boltoniana* (see above) and *S. lanceolata* (Sterzel, 1881) from the Zwickau Formation (late Asturian) of eastern Germany have a similar venation.

Specimens are deposited in various museums. *S. deanensis* and *M. stocki* are in the United States National Museum and *M. obtusa* is in the British Geological Survey. *P. membranacea* is in the National Museum of Wales and a modern photograph of the type was published by Owens & Bassett (1995, fig. 5,4). The type of *O. celtica* was in the Dix Collection but its present location is unknown. The Bristol City Museum & Art Gallery has, however, additional material of this species.

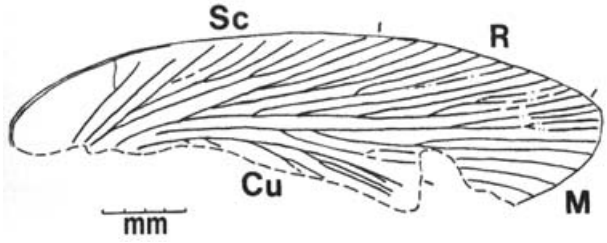

Figure 2. *Sooblatta villeti* (Pruvost, 1912), Beili Glas Colliery, Gorseinon, Swansea, South Wales; shales associated with the Penyscallen Seam, Grovesend Formation (late Asturian Substage), left forewing venation.

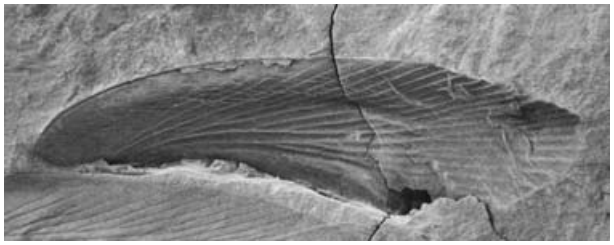

Figure 3. *Sooblatta villeti* (Pruvost, 1912), Beili Glas Colliery, Gorseinon, Swansea, South Wales; shales associated with the Penyscallen Seam, Grovesend Formation (late Asturian Substage), left forewing, × 2.6.

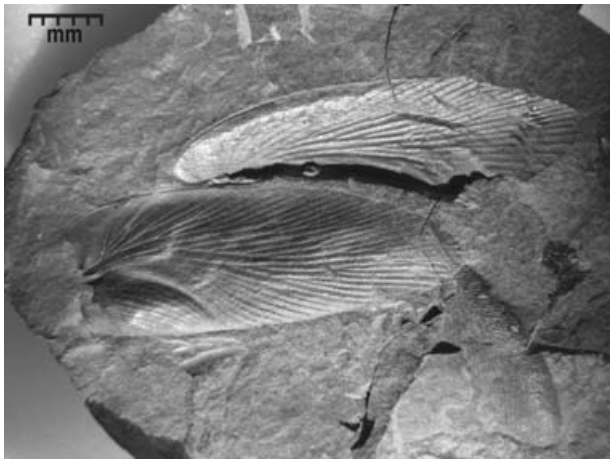

Figure 4. *Sooblatta villeti* (Pruvost, 1912), Beili Glas Colliery, Gorseinon, Swansea, South Wales; shales associated with the Penyscallen Seam, Grovesend Formation (late Asturian Substage), whole fossil.

Sooblatta villeti (Pruvost, 1912)
Figures 2–4

Synonyms. Phylomylacris cf. *villeti* Pruvost (Bolton, 1930; North, 1931 pars; Bassett, 1972); *Aphelomylacris villeti* (Pruvost) ms name Durden (unpub. Ph.D. thesis, Yale Univ., 1972).

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Locality and horizon. Beili Glas Colliery, Gorseinon, South Wales; shales associated with the Penyscallen Seam, Grovesend Formation.

Age. Late Asturian Subage (Cleal, 1978).

Comment. Originally described from Lens (northern France) in the Faisceau d'Edouard member (Assise de Bruay), this species is sometimes cited as 'cf.' in the UK following Bolton (1930, p. 30). This is because he regarded it as a variant form but, as such, it falls outside the provisions of formal zoological nomenclature. Schneider (1983, pp. 112, 115–16, pl. 2, fig. 4; 1984, p. 6, pl. 2, fig. 7) has discussed and figured the Bolsovian–Asturian French material.

The British record (National Museum of Wales specimen no. 27.177.G12 (DD 02655)) is preserved in grey, possibly ferruginous, mudstone with plant remains including two 'fern' pinnules. It is a taphonomically unusual specimen in that the right forewing overlies the left one and the wings are displaced anteriorly and apically, the rest of the animal between them being missing. The base of the right forewing is also missing, but so is the counterpart, so we cannot tell if this is due to palaeopredation or natural fracture. Bolton's venation diagram (based on the right forewing: Bolton, 1930, fig. 10) is basically correct except for the wing proportions and that the anal veins have two extra end twigs not shown. The wing membrane has an irregular, slightly cellular, transverse reticulation.

The left forewing is incompletely exposed and was not drawn by Bolton, so it is illustrated here (Figs 2, 3). It is unusual in being preserved in ventral aspect. Further examination under polarized light or in liquid immersion may reveal additional details, although any preparation to expose the posterior half could risk damaging the figured opposite wing. The two wings show differences in the branching of the veins (cf. Fig. 2 with Bolton's fig. 10). The left subcostal area (with only nine branches of Sc towards the wing margin) is distinctly smaller and more triangular than the right one. The left radial sector (the first main branch of R with four apical branches) is also better developed. These differences are consistent with the variability noted in other early blattodeans by Vršanský (2000), who hypothesized that they became more specialized during the Phanerozoic with attendant loss of variation. This species, *S. burri*, *S. deanensis, M. abrupta* and *A. lubnensis* are quite variable on Schneider's taxonomy. Such variation has, unfortunately, been the basis of new species in the past. Modern cockroaches can show similar and indeed greater individual and specific variation seen in *Periplaneta americana* and *P. australasiae*: forewings adapted for flight show low variability, whereas those functioning as protective tegmina (leathery covers) are highly variable (Schneider, 1977, 1978). Mylacrid forewings become increasingly elytra (wing case)-like during late Carboniferous–early Permian times with correspondingly greater variation in venation (Schneider, 1980). Vršanský's hypothesis is therefore not supported.

4. Preliminary account of the Writhlington blattodeans (Radstock 'Basin')

Writhlington is a good example of a late Westphalian entomofauna associated with swamp vegetation (Thomas & Cleal, 1994). This analysis is based on a sample of around 800 blattodeans from Writhlington Geological Nature Reserve, Somerset Coalfield (OS grid reference ST 703553), examined in 1994. The specimens were mainly those presented to the Bristol City Museum & Art Gallery. A breakdown of the total and identified material is given in Table 2; the latter is based on forewings/forewing fragments briefly described below. The insects are thought to have been predated by arachnids and then mostly broken up on the contemporary forest floor, only a few being rapidly buried intact (Duncan, Titchener & Briggs, 2003). The probably acidic swamp water was, however, not taken into account as a decay agent, for example, on the wing/thorax articulation (Dr X. Martínez-Delclós, pers. comm.).

Archimylacris n. sp. 2 ♂
Figure 5

Description. Archimylacrid forewings 12–15 mm long, 5 mm wide, with elongate 'phyloblattoid' outlines and tips above the mid-longitudinal axes. Unfortunately, nearly all the wings from Writhlington show some degree of tectonic deformation, which particularly affects the delicate cross-venation (archedictyon auct.). The observable cross-venation of the male of this

Table 2. Composition of Writhlington blattodean fauna

Faunal composition (N = 802)	
Part	Number
Forewings (fw)	474
Hindwings (hw)	77
Wing fragments	152
Pronota (headshields, p)	25
Clavi (fw)	17
Specimens with fw + hw	10
Specimens with fw – hw	8
Specimens with fw + p	3
Adult body fragments	6
Larval remains	30
Associated non-blattodean insect wings	5

Number and percentage of species (N = 388)		
Species	Number of specimens	Percentage
Archimylacris sp(p).	273	70
Sooblatta sp(p).	85	22
Phyloblatta? sp.	30	8

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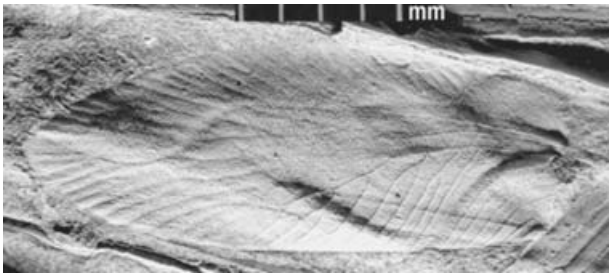

Figure 5. *Archimylacris* n. sp. 2 ♂, Writhlington Geological Nature Reserve (W 361, Bristol City Museum); Farrington Formation (late Asturian Substage). Ammonium chloride coated.

species is transitional between the simple striate pattern of primitive archimylacrids and the anastomosing to increasingly reticulate one of advanced forms.

Comment. The cross- and longitudinal venation is very close to *Archimylacris* 'form Zwickau' (Schneider, Goretzki & Roessler, 2005; = *Archimylacris* n. sp. 1 Schneider, 1983). The only remarkable difference is size (21 × 8 mm in the German form), although intraspecific size differences varying by 100 % are common in fossil and Recent cockroach wings. The degree of reticulation of the cross-venation is, however, a little higher (more advanced) in the Writhlington material, which suggests a younger, more derived species compared to Zwickau. Unfortunately, the precise horizon of the Zwickau form is unknown although palynological evidence indicates that the Zwickau section could range from the Asturian to the Cantabrian (Döring *in* Schneider *et al.* 2005). The *Archimylacris* wing figured by Duncan, Titchener & Briggs (2003, fig. 4B) possibly belongs to this species as well as '*Phylomylacris*' *parallelus* Bolton, 1930 from South Wales.

Archimylacris n. sp. 2 ♀

Description. Archimylacrid forewings 10–12 mm long and 5–6 mm wide, with short, ovoid outlines and rounded wing tips. Longitudinal and cross-venation generally identical to n. sp. 2 ♂.

Comments. These are probably female forewings of the same species as n. sp. 2 ♂. They resemble the longitudinal venation of *Archimylacris* '*woodwardi*' (see Section 3) but differ significantly in the cross-venation. A specimen of n. sp. 2 ♀ (Booth Museum Brighton 014937,−8 [W 829a,b]) has been figured by Jarzembowski (1994, fig. 9, 2004, pl. 1, fig. 6) and Jarzembowski & Ross (1993, fig. 5). The first (A) of the archimylacrid wings illustrated by Duncan, Titchener & Briggs (2003, fig. 4) may be very deformed examples of this species; *Archimylacris* '*regularis*' Bolton, 1934 comb. nov. from Somerset may be conspecific.

Sooblatta sp(p).

Description. Mylacrid wings from 18 × 8 mm to 26 × 11 mm across. The longitudinal venation resembles *Sooblatta deanensis* (Scudder, 1895) and *Sooblatta villeti* (Pruvost, 1912), two similar species. The cross-venation is transitional, anastomosing to (?) incipient reticulate in the central part of the wing, and the degree of reticulation is slightly less than in *S. villeti*.

Comments. The taxonomy of *Sooblatta* species needs detailed re-examination of type material from the UK. Two specimens from Writhlington have been widely figured: BMB 014863,-4 [W 48a,b] (Austen, 2001, fig. 40; Jarzembowski, 1985, fig. 1, 1988, fig. 3, 1994, fig. 5) and 014844 [W 653a,b] (Freeman, 2005, fig. 32.8(b); Jarzembowski, 1989, fig. 13, 1991, p. 13); they are provisionally referred to *Sooblatta* cf. *deanensis*.

Phyloblatta? sp.

Description. Phyloblattid forewings about 20 mm long with non-striate cross-venation and a more sigmoidal anterior cubital vein (Cu1) than in *Archimylacris*, possibly belonging to *Phyloblatta* Handlirsch, 1906. The material could represent one species but needs further (fine) preparation.

4a. Composition of the Writhlington blattodean fauna

The percentages (Table 2) give an archimylacrid:mylacrid:phyloblattid ratio of about 7:2:1. No other Carboniferous site has been sampled so extensively, thus comparison with other localities is difficult. Nevertheless, the assemblage is unusual because most Westphalian entomofaunas are mylacrid-dominated. It resembles Pas-de-Calais but *Sooblatta* is more common there. Stephanian faunas are phyloblattid-dominated except for some Moroccan localities (Stephanian B, Souss Basin, High Atlas Mountains: Hmich *et al.* 2003). The archimylacrid dominance at Writhlington is probably ecological, as the Writhlington blattodeans are autochthonous/parautochthonous (Duncan, Titchener & Briggs, 2003).

5. Conclusion

In Southern Britain, blattodeans were evidently more abundant and diverse during late Westphalian times than their descendants, the true cockroaches, are today. Mylacrids were especially widespread, notably species of the genus *Sooblatta* (*S. boltoniana, S. burri*, *S. deanensis* and *S. villeti*), plus *Mylacris abrupta*. This contrasts with there being only one multibasinal archimylacrid, *Archimylacris lubnensis*, although this

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Table 3. Synopsis of Bolsovian–Cantabrian insect (blattodean)/conchostracan (I/C) zonation after Schneider, Goretzki & Roessler (2005)

Blattodean/conchostracan biozones	Chronostratigraphy
Other spiloblattinid zones (I)	Stephanian Stage
Syscioblatta corsini Zone (I)	?Cantabrian Substage
Archimylacris f. Zwickau Zone (I)	Asturian–?Cantabrian substages
Kinklidoblatta morini Subzone stat. nov. (I)	middle–upper Asturian Substage
Mylacris–Sooblatta Zone nov. (I): *Mylacris abrupta–Sooblatta burri–Sooblatta deanensis* Assemblage Zone	Asturian–lower Cantabrian substages
Anomalonema–Pseudestheria (Assemblage) Zone (C)	upper Bolsovian–Asturian substages
Archimylacris lubnensis Zone (I)	upper Bolsovian–lower Asturian substages
Megasitum–Pseudestheria (Assemblage) Zone (C)	Bolsovian Substage
Other archimylacrid zones (I)	lower Westphalian Stage

The '*morini*' Zone is here considered as a subzone and a new mylacrid zone is proposed (see Section 5).

Bolsovian–early Asturian species belongs to a family used for Westphalian biochronozonation (Table 3). The upper Asturian–Cantabrian interval is, however, less well correlated in Europe with the *Archimylacris* 'form Zwickau' Zone (Asturian–?Cantabrian). The archimylacrid *Kinklidoblatta morini* commonly occurs in the middle–late Asturian (ranging from the top of the Faisceau de Dusouich up to the Faisceau d'Edouard, Nord-Pas-de-Calais, France) and with *Sooblatta villeti* in the late Asturian (Faisceau d'Edouard). It can therefore form a subzone within the Form Zwickau Zone (Table 3). *Archimylacris* n. sp. 2 suggests a late Asturian to possibly early Cantabrian date for Writhlington (Section 4). The above five mylacrid species are all found in the upper Asturian Substage of Wales. One (*S. deanensis*) continues into the lower Cantabrian Substage (in Gloucestershire), and two more or less related species (*S. villeti* and *S. boltoniana*) range down into the Bolsovian outside the UK. *M. abrupta*, *S. burri* and *S. deanensis* are, however, coeval with the '*morini*' and Form Zwickau zones. This mylacrid assemblage therefore forms a convenient proxy for the unrecognized archimylacrid zones in the UK and elsewhere and is proposed as the *Mylacris–Sooblatta* Zone in Table 3.

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