| Genus | Vol. 5(4): 307-347 | Wrocław, 28 XII 1994 |
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# British Upper Triassic and Lower Jurassic *Heteroptera* and *Coleorrhyncha* (*Insecta*: *Hemiptera*)

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ABSTRACT. The British Liassic *Heteroptera* and *Coleorrhyncha* are revised mostly on the basis of previously undescribed material reported by WHALLEY(1985). The specimens forming the basis of the few other published reports of *Heteroptera* from the British Triassic and Liassic were reexamined and either incorporated in the study or rejected as not being *Heteroptera*. The only Triassic heteroptera examined, *Pachymerus zucholdi* GIEBEL, is referred to *Pachymeridiidae*. A Triassic coleorrhynchan is tentatively referred to the genus *Archicercopis* (*Progonocimicidae*), but it is not formally named. The following new taxa are proposed: *Mesoscytina anglica* n.sp. (*Progonocimicidae*); *Britannicola senilis* n.sp. (*Archegocimicidae*); *Pterocimex jacksoni* n. gen. et sp. (*Pterocimicidae*, n.fam.); *Neomeridium trifurcum* n.gen. et sp. (*Pachymeridiidae*); *Protocoris indistinctus* n.sp. (*Protocoridae*); *Propreocoris maculatus* n.gen. et sp. (*Ochteridae*, *Propreocoridae* n.subfam.); *Liassocorixa dorsetica* n.gen. et sp. (*Corixidae*); *Lethonectes naucoroides* n.gen.et sp. and *Tarsabedus menkei* (*Belostomatidae*). The material representing four other species of *Pachymeridiidae* is described but the species themselves are not formally named.

Key words: Paleontology, entomology, new taxa, Britain, *Heteroptera*, *Coleorrhyncha*.

## INTRODUCTION

The Jurassic period beginning about 213 million years ago lasted for nearly 70 million years and saw profound evolutionary developments in the terrestrial *Heteroptera*. POPOV and WOOTTON, (1977) were unable to recognise any modern terrestrial families in two German Lower Liassic faunas that they studied. By contrast, POPOV's (1968) study of an Upper Jurassic assemblage of *Heteroptera* from Kazakhstan revealed a fauna of a much more modern aspect: two of the three terrestrial families that he found still have living representatives and the third, *Mesopentacoridae*, clearly belongs to the large, recent superfamily *Pentatomoidea*.

Triassic *Heteroptera* and *Coleorrhyncha* (the latter not recognized as such - no coleorrhynchan, living or fossil, had been described by that date) were first reported from Britain by BRODIE (1845) and WESTWOOD in BRODIE (1854). Subsequent publications by GIEBEL (1856), PHILLIPS (1871), BRODIE (1873, 1874) and HANDLIRSCH (1906) referred to the figures and descriptions in BRODIE's original work but added no new observations. The first records of Lower Jurassic *Heteroptera* from Britain appear in WHALLEY's (1985) work, which includes a synopsis of the Charmouth (Dorset) fauna of the group.

The Lower Liassic Charmouth fauna, which accounts for by far the greater part of the material studied by us, is about ten million years older than the Upper Liassic faunas of Mecklenburg and Saxony (Lower Toarcian) partially studied by POPOV and WOOTTON (1977) and POPOV (1989b, 1992). It contains a similar mixture of terrestrial and aquatic families with the former predominating. On the whole, it seems that the Lower Liassic fauna of *Coleorrhynha* and *Heteroptera* of Dorset is not as diverse and numerous as that of the German Upper Liassic (Dobbertin, Grimmen and East Lower Saxony), where the extinct terrestrial families *Progonocimicidae*, *Archegocimicidae* and *Pachymeridiidae* and the still extant aquatic families *Belostomatidae* and *Corixidae*, as well as the littoral *Ochteridae*, are well represented. Nevertheless, the Lower Lias of Great Britain has yielded the earliest known fossil representatives of *Cimicomorpha* (*Pterocimicidae*), *Pentatomomorpha* (*Pachymeridiidae*), and *Nepomorpha* (*Ochteridae*).

All specimen numbers mentioned in the article are NHM register numbers except in the case of the type-specimen *Tarsabedus menkei* which bears a registration number of the Bristol Museum and Art Gallery. Hand-drawn figures 1 to 3, 15, 21 to 24, 38 and 39 are by W.R. DOLLING ; figures 4, 5, 7, 9, 11, 12, 18, 27, 29, 31, 33, 36, and 37 were drawn by Yu.A. POPOV. The photographs were made by the NHM photographic service; the specimens were photographed immersed in water to enhance detail.

This joint article was in the main completed 8 years ago and we planned to publish it in Great Britain. Yet because of its size it could not be placed in a scientific journal for a long time, although it had already been referred to by some authors (WHALLEY, 1985; KUKALOVA-PECK, 1991; POPOV, 1992). New data and a series of new publications on fossil insects appeared during this period having somewhat transformed our notions about fossil *Hemiptera*. Hence, as compared to the pervious version, this text was considerably changed and supplemented.

## MATERIALS

An account of the JACKSON collection of Lower Liassic insects from Dorset, now in the Natural History Museum (formerly British Museum, Natural History) was made by WHALLEY (1985). In that publication the *Heteroptera* were only briefly described and not named. Now they are all named here and crossreferences to the earlier paper are inserted. Thirty five specimens of *Hemiptera* were collected by JACKSON from the Obtusum Zone of the Dorset Lias. Four of these were *Homoptera*; the remaining *Heteroptera* made up less than 8% of all fossil insect specimens from the Dorset locality. Fifteen of the Dorset specimens belong to a single species of the new family *Pterocimicidae* (fam.nov.), two to a species of *Corixidae*, three to two species of *Belostomatidae*, one to *Ochteridae* (*Propreocorinae* subfam.nov.) and eleven to various *Pachymeridiidae*.

In addition to the JACKSON collection, we also reviewed the Triassic and Liassic *Hemiptera* of the BRODIE collection in the Natural History Museum. This contained three specimens of *Progonocimicidae* (*Coleorrhyncha*), two of *Archegocimicidae* and two of *Pachymeridiidae* (*Heteroptera*). They are included in the following account together with a Liassic Protocorid from the TOMES collection in the Natural History Museum and a Belostomatid from the Liassic in the collection of the City of Bristol Museum and Art Gallery, Bristol. Thus all in all 41 remains of *Hemiptera* (*Coleorrhyncha* + *Heteroptera*) from the Upper Triassic and the Lower Liassic deposits of Britain were investigated which makes up about 10% of the total fossil insects assemblage.

There remain three other supposed *Heteroptera* from the British Lias. The "*Pentatomid*" mentioned by WESTWOOD (1854: 381, 396, pl. 18, fig. 2) and BRODIE (1874: 32) was catalogued in the *Odonata* by SCUDDER (1891: 167). *Belostoma liasina* GIEBEL (1856: 371) is currently listed in the genus *Dysmorphoptila* belonging to *Homoptera Cicadomorpha* (SHCHERBAKOV, 1984). Examination by one of us (PESW) of the type of *Mesohemipteron incertum* COCKERELL(1915: 476) has revealed that it is not a heteropteran but may probably be referred to *Fulgoroidea* (*Homoptera*).

## THE FOSSIL *HEMIPTERA* LOCALITIES

The term "insect limestone" used by BRODIE (1845) and others applies to beds of several ages from Upper Triassic to Lower Jurassic. Their stratigraphy is discussed by WHALLEY (1983), WARRINGTON et al. (1980) and COPE et al. (1981). The beds occur in a wide area in the counties of Avon, Gloucestershire, Somerset, Warwickshire and Hereford-and-Worcester. All the sites that have yielded *Heteroptera* and *Coleorrhyncha*, except for Strensham, Forthampton and Hasfield, which are of Upper Triassic age, are assigned to the Lower Lias and all are probably older than the Black Marl of Dorset from which most of the material in this paper originates. Many of the "insect limestone" sites were quarries that have now been filled and are inaccessible. The insect fossils as kept in the Natural History Museum are preserved on very small pieces of rock and few have associated zone fossils.

The insect-bearing strata at Strensham, in the county of Hereford-and-Worcester (formerly Worcestershire), and Forthampton and Hasfield, in Gloucestershire, belong to the Pseudomonotis Beds of the Upper Trias. WHALLEY (1983) reported a single species of the homopterous family *Cicadidae* from all three sites. We report a pachymeridiid and a progonocimicid from these beds.

The Planorbis Zone beds at Binton (Warwickshire), although rich in terrestrial insect fossils, particularly *Orthoptera* (WHALLEY, 1982), have so far yielded only one heteropteran - *Protocoris indistinctus*.

The only other "insect beds" localities to yield *Heteroptera* and *Coleorrhyncha* are Apperley in Gloucestershire and Morton Bagot in Warwickshire. Little or nothing is known of their stratigraphy or of the associated fauna. We assign them both to the Lower Lias, following tradition rather than evidence. The soft, white matrix in which the holotype of *Mesoscytina anglica* occurs is different from the harder, grey material of the other fossils.

The bulk of the material studied comes from the calcareous Lower Liassic mudstones (Black Marls) that outcrop on the beach to the East of Charmouth in Dorset. All the *Heteroptera* are from the Obtusum Zone. The Dorset *Heteroptera* are associated with a diverse insect fauna which has been studied in some detail (WHALLEY, 1985). Unlike many other Jurassic faunas, where the proportion of heteropteran species rarely reaches 6% of the total insect assemblage, the Dorset fauna comprises 14% of *Heteroptera*. This suggests that the faunal assemblage from which these fossils were derived was itself richer than usual in *Heteroptera*, since it is difficult to imagine any kind of differential preservation that might account for the difference. The insect fossils are closely associated with ammonites and with the plant beds of the Woodstone. The Lower Lias of Dorset has also yielded many marine reptiles and fish. The presence of these marine fossils implies that the insect thanatocoenosis was transported by water before being deposited. However, the condition of many of the fossil insects, with wings and other appendages not dissociated from the bodies, suggests that they were not transported any great distance (WHALLEY, 1985).

## SOME PHYLOGENETIC AND MORPHOLOGICAL INFERENCES

*Progonocimicidae* (Upper Permian to Upper Cretaceous). This Mesozoic family is assigned, on the evidence of the forewing venation and the dorsoventrally flattened body, to the suborder *Coleorrhyncha*, to which the recent family *Peloridiidae* also belongs. Modern *Peloridiidae* are cryptic, moss-inhabiting insects with a disjunct austral distribution. Studies of venation and the morphological features of both extinct *Progonocimicidae* and *Karabasiidae* and extant *Peloridiidae* show that the suborders *Coleorrhyncha* and *Heteroptera* are closely related and evolved as parallel stocks from common auchenorrhynchous ancestors (POPOV, SHCHERBAKOV, 1988, 1991). The morphology and taxonomy of Mesozoic *Coleorrhyncha* were also recently revised (POPOV, SHCHERBAKOV, 1991). *Progonocimicidae* are widespread throughout the Jurassic of Eurasia and are regularly met with in three wellknown Liassic faunas of

Western Europe. The family seems to be most diversified in the fauna of Mecklenburg (Dobbertin), where it is represented by five species of three genera including *Progonocimex* which clearly differs from all other Jurassic progonocimicids. Some undescribed progonocimicids are also known from the Upper Liassic fauna of Grimmen from Eastern Germany (J. ANSORGE, pers.comm.). In Saxony the group is represented by two or three species probably belonging to a single genus. In the British material they are represented only by a single species of the large genus *Mesoscytina* and a specimen dubiously assigned to *Archicercopis*. These two specimens are the only *Progonocimicidae* yet identified from the Jurassic of Britain; the Cretaceous ones were recently described by JARZEMBOWSKI (1991) and POPOV (KLIMASZEWSKI, POPOV, 1993).

Most progonocimicids are known only from detached forewings. In the specimen assigned by us to the genus *Archicercopis* both thorax and abdomen are present and the wings are folded over them in an apparently normal resting position. The forewings extend well beyond the lateral and posterior margins of the abdomen as in the macropter of the recent peloridiid *Peloridium hammoniorum* BREDDIN. The abdominal apex of the *Archicercopis* specimen is similar to that of *Mesoscytina* sp. (POPOV, SHCHERBAKOV, 1991).

*Archegocimicidae* (Lower Jurassic to Lower Cretaceous). Since the description of the first representatives of this family (HANDLIRSCH, 1906, 1925; PING, 1928) the systematic position of *Archegocimicidae* has for a long time been unclear. First it was considered to be close to *Pentatomidae* (HANDLIRSCH, 1906), then its representatives were described in the family *Lygaeidae* (PING, 1928). Still later this family was at first considered to be of unclear systematic position (HANDLIRSCH, 1939; BODE, 1953; BECKER-MIGDISOVA, 1962; POPOV, WOOTTON, 1977) and then tentatively included either in *Pentatomomorpha* (POPOV, 1980a, 1981), *Enicocephalomorpha - Dipsocoromorpha* (POPOV, 1980b), or in *Cimicomorpha* (WHALLEY, 1985). Many inconsistencies in the systematics and nomenclature of this family arose because of the appearance of recent works by Chinese paleontologists (HONG, 1981, 1984 a,b,c, 1988, 1992; HONG, WANG, 1976, 1990; LIN, 1982 a,b; ZHANG, 1986, 1991, 1992). The results of the study of the type-material of HANDLIRSCH and BODE (POPOV, WOOTTON, 1977) from the Jurassic and Cretaceous of Siberia and Mongolia (POPOV, 1985, 1986, 1988) confirmed that the Mesozoic family *Archegocimicidae* belongs to the infraorder *Leptopodomorpha* and is very similar to the modern family *Saldidae* (POPOV, 1985, 1989c). The first archegocimicid from the Siberian Jurassic, described as *Saldonia rasnitsyni* YU. POP., was placed in the family *Saldidae* (POPOV, 1973). As opposed to other more advanced Leptopodomorpha, Mesozoic archegocimicids (as well as *Pachymeridiidae* in *Coreoidea* s.l.) retain the costal fracture. An idea was also put forward about rather a smooth transition from the ancestral *Archegocimicidae* to the *Saldidae* (POPOV, 1988).

*Archegocimicidae* were widespread in the Early Jurassic of Western Europe (Dobbertin near Mecklenburg and East Lower Saxony of Germany), in the Middle and

the Late Jurassic of Siberia (Transbaikalia) and Northern China, in the Early Cretaceous of Eastern Siberia, Mongolia and China. Our *Britannicola senilis* is the first species of the family to be reported from Britain. Many undescribed archegocimicids are also known from the Upper Jurassic of Great Britain (Dinton and Durdlestone), the Lower Cretaceous of Siberia, Mongolia, China and apparently Brazil (Santana Formation).

*Pterocimicidae* (Lower Jurassic). We have found it necessary to errect this new family for our genus *Pterocimex*. This is a very distinctive bug, clearly separable from other Mesozoic *Heteroptera*. The *Pterocimicidae* are placed in the *Cimicomorpha* because of the long medial fracture situated from behind of R + M, retention of the costal fracture and sharp demarcation of the membrane from the corium. The same features are shared by the *Leptopodomorpha* but the modern species of that infraorder, with the exception of the specialised *Aepophilus* SIGN., have very large eyes, rather short heads and long legs, all contrasting with the *Pterocimicidae*. The female terminalia (Fig. 13) show little involvement of sternite VII and all that can be distinguished are a pair of broad sclerites (? gonoplacs or first valvulae) flanked by a pair of smaller ones (probably laterotergites VIII). The male abdominal segment VIII (Fig. 11) is much narrower and shorter than the preceding segments. The forewing venation resembles that of *Cimicomorpha*, on the one hand, and *Leptopodomorpha*, on the other. Among the modern cimicomorphan families the greatest similarity is found to the forewing of the modern but plesiomorphic *Velocipedidae*: Sc is free and diverges from R + M in the basal part of the wing; the basal cell is long and the discal cells of the corium are on the border with the membrane. However, the presence of two shorter and smaller closed medial cells together with one large basal one shows some similarity with *Archegocimicidae* (POPOV, 1985). *Pterocimicidae*, like *Archegocimicidae* and *Velocipedidae*, are characterized by such plesiomorphic features as a long rostrum, associated in *Cimicomorpha* with carnivory, simple forelegs, a long costal fracture and well developed precostal area. The presence of a complete set of closed cells (basal, medial, discal), of which the discal cells are still fully on the corium, and the preservation of both median cells, which are already lost in modern *Cimicomorpha*, clearly distinguish the Jurassic *Pterocimicidae* from all other known families of the infraorder. The certain similarities between the modern *Velocipedidae* and the Jurassic *Archegocimicidae* and *Pterocimicidae* allows to suppose that there is a link between *Cimicomorpha* and *Leptopodomorpha*, primarily through *Cimicoidea* and *Saldoidea*, suggesting that the cimicomorphans are a specialized line of *Leptopodomorpha*.

*Pachymeridiidae* (Upper Triassic to Lower Cretaceous). This diverse family, which belongs to the infraorder *Pentatomomorpha*, is well represented in the British material and in the Liassic faunas of Saxony and Mecklenburg. The lower Liassic material from Charmouth differs considerably from the Upper Liassic material of the two German localities. The latest Triassic "*Pachymerus*" *zucholdi* is the earliest known representative of its infraorder.

In the female *Pachymeridiidae* whose abdomen features were well preserved, the ovipositor turned out to be about half as long as the abdomen. We regard this as evidence that the plesiomorphic state of the ovipositor in *Pentatomomorpha* was lacinate, like in most modern *Lygaeidae*, rather than plate-like, as in *Pentatomidae* and *Coreidae*. The very long rostrum of our "*Pachymeridiidae* inc. sed. sp. 3" may be indicative of a predaceous habit. On the other hand, various recent plant-feeding *Heteroptera* in the families *Coreidae* and *Pyrrhocoridae* have long rostrum similar to the Upper Triassic species of *Cicadellidae* described by WHALLEY (1983). Most recent *Pentatomomorpha* are plant-feeders and the few predaceous groups within the infraorder are believed to have acquired this habit secondarily. If the earliest pentatomomorphans were predaceous, it may be that the early radiation of the group occurred before the shift to phytophagy, in which case the plant-feeding habit may have been acquired independently by several different lines within it.

Venation of the corium of the pachymeridiids is very similar to that of the modern relict *Idiostolidae* (POPOV, WOOTTON, 1977) which probably represent by themselves a group ancestral to *Idiostolidae* and all other *Coreoidea* (s.l.). Yet *Pachymeridiidae* still retain costal fracture lost by other more advanced *Pentatomomorpha*. They are abundant in some faunas through the Jurassic and the Early Cretaceous and prevail among terrestrial bugs.

*Protocoridae* (Lower Jurassic). This small family contains a single genus, *Protocoris*, which is otherwise known from the Lower Liassic of Switzerland (Aargau). A single specimen from Dorset is tentatively assigned to this genus, mainly on the basis of its general propositions. Like *Pachymeridiidae*, the family *Protocoridae* belongs to the infraorder *Pentatomomorpha* and it appears not to have survived into the latter half of the Jurassic. It should be noted that the Liassic family *Protocoridae* of West Europe has great resemblance with the Mesozoic family *Mesopentacoridae*, known from the Late Jurassic of the South Kazakhstan (POPOV, 1968) and Central Mongolia (POPOV, 1989a) and also from the Early Cretaceous of Transbaikalia (POPOV, 1990). There is also one more undescribed specimen (In.37178) from the Upper Lias of Germany (Dobbertin in Mecklenburg) apparently belonging to *Protocoridae* as well.

*Ochteridae* (Lower Jurassic to Recent). This family belongs to the infraorder *Nepomorpha* and the Early Liassic *Propreocoris maculatus* is the oldest member among ripicolous nepomorphan bugs. These bugs are one of the most ancient representatives of shore dwellers and may be looked upon as an initial group of *Heteroptera*. They have a long "probing" rostrum (similar to *Saldidae* and *Archegocimicidae* in *Leptopodomorpha* and *Velosipedidae* in *Cimicomorpha*) using it for feeding on immobile or dead soil microfauna and performing the role of scavengers (RIEGER, 1976; KERZHNER, 1981; POPOV, 1989c). The habitus, the character of the dorsal punctation of body, the posterior margin of pronotum with concavity in the middle, colour pattern of forewings, greatly widened costal area, long costal

(cuneal) fracture far removed from the base of the veined membrane with large cells, and relatively short membrane: all this shows that the *Propreocoris maculatus* should be regarded as a member of the littoral nepomorphan family *Ochteridae*.

There is a similar wide clavus in the related littoral nepomorphan family *Gelastocoridae* and two other leptopodomorphan families *Archegocimicidae* and *Saldidae*. Rather similar patterns of rounded pale spots are also encountered in some *Archegocimicidae* (e.g. *Progonocoris pictus* HANDL. and *Saldonia maculata* YU. POP.). However, the features that differ the new genus from *Archegocimicidae* and consequently from all *Leptopodomorpha* are as follows: a distinct differentiation of the forewing into corium and membrane with consequent obliteration of the corial venation, a widened costal area and the shortness of the membrane of macropterous forms. At the same time the extention of the apex of corium more than half way along the length of the forewing membrane is consistent with *Leptopodomorpha*. Unfortunately, the absence of the head and legs does not permit a complete comparison with other ochteroid *Gelastocoridae*. Yet some features suggest that it may be linked with littoral leptopodomorphan *Archegocimicidae* and *Saldidae*.

*Corixidae* (Upper Triassic to Recent). The main trends of the corixid evolution, in particular, the formation of specific head structures connected with the development of phytophagy (algo- and detritophagy, alongside with predation), the covering of scutellum by pronotum, formation of emboliar groove with frosted areas of hemelytra, development of various types of legs, and transformation of their structure have been briefly analyzed by POPOV (1986, 1989c). In the Early Jurassic, *Corixidae* are present in all three known European Liassic faunas, some of which (*Acromocoris angustus* BODE from Lower Saxony and *Acromocoris similis* YU. POP. from Mecklenburg) probably belong to the modern subfamily *Micronectinae* and the other (*Liassocorixa dorsetica* n.sp.) is a member of the Mesozoic subfamily *Archaecorixinae*. This latter primitive group of aquatic bugs was originally described from the lowermost Upper Jurassic of South-West Kazakhstan (POPOV, 1968). The oldest corixid *Lufengnacta corrigis* LIN is known from the uppermost Triassic (Yipinglang Formation) of China (LIN, 1977). This peculiar corixid most probably belongs to a specific new subfamily. In the Late Jurassic and Early Cretaceous faunas of Asia corixids become most diverse and numerous. They are geographically widespread throughout Mongolia and China. It is also noteworthy that the Late Mesozoic corixids belong mainly to the extinct subfamily *Velocoroxinae* and that they are often dominating among other water insects in freshwater biocoenoses.

*Belostomatidae* (Upper Triassic to Recent). Like the corixids, belostomatids (Giant Water bugs) belong to the Nepomorpha and are still widespread in Recent aquatic habitats, although the modern forms are mostly restricted to the tropical waters. *Belostomatidae* are found in the Liassic faunas of Saxony and Dorset but they are very different in the two localities. As in the case of *Corixidae*, the British material provides one of the earlier proven dates for the family than any previously known

occurrence, by about 10 million years. There are some undescribed belostomatids from the uppermost Triassic of USA (OLSON et al., 1978), the Upper Jurassic of New Mexico, USA (BRADBURY, KIRKLAND, 1966) and South Kazakhstan, and also from the Lower Cretaceous of Siberia and Mongolia except *Lethopterus multinervosa* YU. POPOV from the Mongolian Gobi Altai (POPOV, 1989a) and *Iberonepa romerali* MARTINEZ-DELCLOS, NEL, POPOV from the Lower Cretaceous (Barremian) of Spain (MARTINEZ-DELCLOS et al., 1993). It is noteworthy that the latter belostomatid bug is one more most specialized form with unusually well developed oar-shaped hind legs like in belostomatid *Stygeonepa foersteri* YU. POP. from the Upper Jurassic of Solnhofen (POPOV, 1971). This bug was an active, quick-swimming predator.

Both *Lethonectes* and *Tarsabedus* show some features similar to those of modern *Naucoridae*: the small, oval body and broad scutellum in the former and the short claval commissure in the latter. The dorsal flexure of the anterior tarsus at the tibio-tarsal articulation is a primitive trait unknown in any other *Belostomatidae*.

## EARLY JURASSIC EVOLUTION OF *HETEROPTERA* IN WEST EUROPE

Terrestrial *Heteroptera* are quite rare in Lower Jurassic fossil deposits and few of them have yet been described from Britain. Five infraorders of terrestrial bugs are currently recognized: *Cimicomorpha, Pentatomomorpha, Leptopodomorpha, Enicocephalomorpha* and *Dipsocoromorpha* (ŠTYS, KERZHNER, 1975). Members of the last two infraorders are generally small and delicate insects and they are unlikely to be found as fossils; neither was found to be represented among our material. As in POPOV and WOOTTON's (1977) study of German material of similar age, it has proven impossible to assign any of the British terrestrial bugs to modern families. We have found it justified to erect one new family and one new subfamily in the recent *Ochteridae* to accommodate *Pterocimex* and *Propreocoris*, which we place tentatively in the infraorders *Cimicomorpha* and *Nepomorpha* respectively. *Cimicomorpha* were not previously known to occur as early as this. We thus recognize one family of *Cimicomorpha* and two families each of *Nepomorpha* and *Pentatomomorpha* among the British material before us.

In the Liassic faunas of Germany and Great Britain, the aquatic bugs belong exclusively to the modern families *Corixidae, Belostomatidae* and *Naucoridae*. *Naucoridae* are recognized from the Mecklenburg deposits only, upon the basis of three rather featureless forewings. The British material confirms that the nepomorphan families were differentiated at this early date by providing material of undoubted *Belostomatidae* and *Corixidae*.

The picture that emerges of the heteropterous fauna of earliest Jurassic times is of one in which four modern infraorders are already present, three of them differentiated into families. The aquatic families in this fauna have persisted to the present day, whereas the terrestrial ones have all been supplanted by more modern forms. The persistence of the aquatic families and the dissappearance of the terrestrial ones is probably a reflection of the greater stability of aquatic habitats since the Early Jurassic.

The evolution of the two largest infraorders of *Heteroptera, Cimicomorpha* and *Pentatomomorpha*, has undoubtedly been greatly influenced by the changing terrestrial flora. Even the predaceous members of these groups hunt mainly on plants and must have the ability to exploit the architecture of plants as a hunting ground. Nevertheless, the extinction of the Early Jurassic families of these two groups and the earliest appearance of recent families clearly antedate the rise of the angiosperms.

## NOTE ON A FEATURE IN THE METATHORACIC REGION

In the material of *Tarsabedus menkei* there is a reddish patch in the metathoracic area. It is a very prominent feature in this fossil (Figs. 34, 35). It is divided, in section, into large, polygonal cells by narrow walls of calcite and contains scattered beads of colourless calcite embedded in a finely granular, reddish matrix. The latter has a high sulphur content. This patch was interpreted by WHALLEY (1985: 112, 146) as the remains of the metathoracic gland, basing this interpretation on its size and position. However, the stomach is located in the same area and it is by no means certain that the structure in question represents the former rather than the latter. POPOV (person. comm.), in his account of a new Early Cretaceous corixid, *Corixonecta hosbayari* YU. POP., noted an analogous reddish patch in the middle of the metathorax. A preliminary study of this patch revealed the so far undetermined remains of Cyanophyta and Protozoa. These groups are characteristic of the stomach contents of modern *Corixidae* and confirm that this Mesozoic corixid had a similarly mixed diet. STADDON (1971) reported that the metathoracic gland is absent from modern *Belostomatidae*. These facts lend support to the hypothesis that the structure seen in the metathorax of *Tarsabedus menkei* and also of some *Pterocimex jacksoni* (Fig. 8) and our "*Pachymeridiidae species* 3" (Fig. 23) is composed of crystalline stomach proteins rather than contents of the gland. The question cannot yet be regarded as settled either way in the case of these three species.

## CHECK-LIST OF LOWER MESOZOIC *COLEORRHYNCHA* AND *HETEROPTERA* IN BRITAIN

### *Coleorrhyncha*

| | | |
|---|---|---|
| *Progonocimicoidea* | | |
| *Progonocimicidae* | *Archicercopis* sp. | $T_3$ |
| | *Mesoscytina anglica* | $J_1$ |

### *Heteroptera*

| | | |
|---|---|---|
| *Leptopodomorpha* | | |
| *Archegocimicidae* | *Britannicola senilis* gen.et sp.n. | $J_1$ |

| | | |
|---|---|---|
| *Cimicomorpha* | | |
| *Pterocimicidae* | *Pterocimex jacksoni* gen.et sp.n. | $J_1$ |
| *Pentatomomorpha* | | |
| *Pachymeridiidae* | *Neomeridium trifurcum* gen.et sp.n. | $J_1$ |
| | *Pachymeridium* sp. 1 | $J_1$ |
| | *Pachymeridium* sp. 2 | $J_1$ |
| | *Pachymeridium* sp. 3 | $J_1$ |
| | *Pachymeridium* sp. 4 | $J_1$ |
| | "*Pachemerus*" *zucholdi* GIEBEL | $T_3$ |
| *Protocoridae* | *Protocoris indistinctus* sp.n. | $J_1$ |
| *Nepomorpha* | | |
| *Ochteridae* | *Propreocoris maculatus* gen.et sp.n. | $J_1$ |
| *Corixidae* | *Liassocorixa dorsetica* gen.et sp.n. | $J_1$ |
| *Belostomatidae* | *Lethonectes naucoroides* gen.et sp.n. | $J_1$ |
| | *Tarsabedus menkei* gen.et sp.n. | $J_1$ |

## SYSTEMATIC SECTION

### Order *Hemiptera*

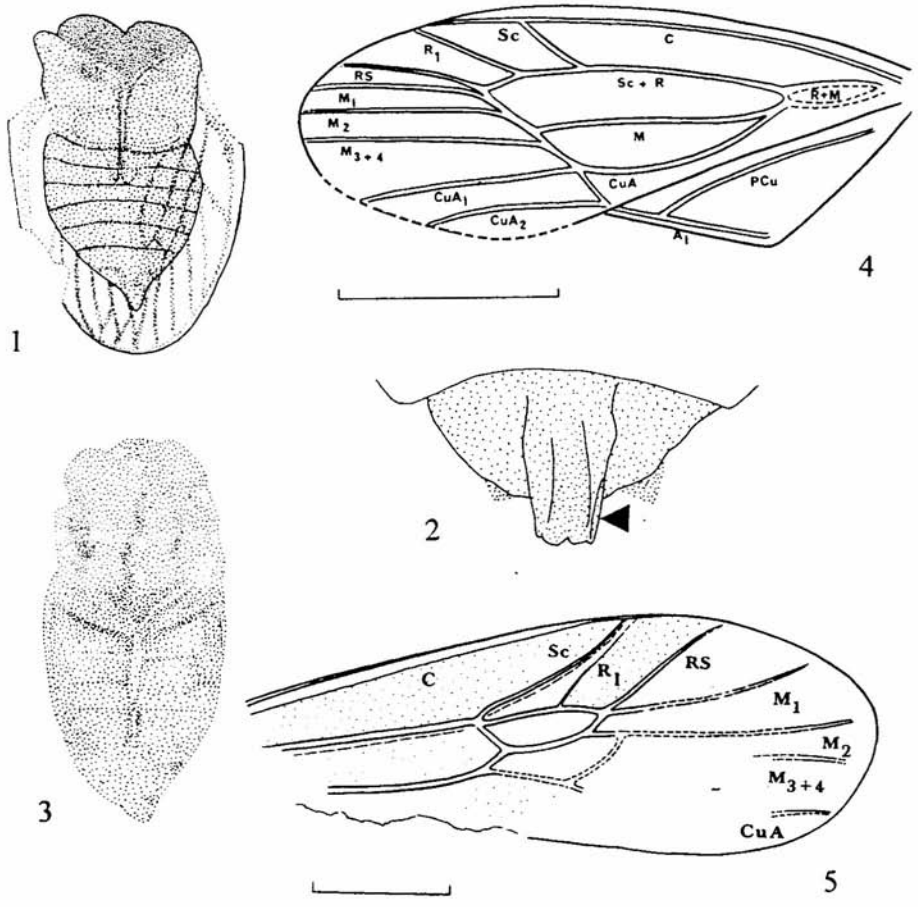
DIAGNOSIS. Hemimetabolous insects lacking cerci, with 4 wings (except some brachypterous and apterous forms). Head from hypognathous to prognathous, with mandibles and maxillae modified into two pairs of slender stylets ensheathed by labrum; palpi lost. Wings heteronomous (except in archescytinids) and coupled at flight; forewings more sclerotized and fixed on thorax; hindwings either diminished or with anal area expanded. Ovipositor lacinate, or variously modified, or reduced.

### Suborder *Coleorrhyncha*

DIAGNOSIS. Small, dorsoventrally flattened, initially jumping *Hemiptera* with tegmina folding flat, their commissural margins and apices overlapping in repose; wing-coupling mechanism consisting of a clip on under surface of apical part of clavus into which thickened margin of hind wing slides. Head opisthognathous with long rostrum directed backward and a fully developed tentorium including transverse bridge; antennae short and few segmented. Pronotum bears paranotal expansions. Coxae pagiopodous. Abdomen flattened with laterotergites facing ventrad and bearing spiracles.

## Superfamily *Progonocimicoidea*

DIAGNOSIS. *Coleorrhyncha* with forewing membrane almost wholly occupied by closed cells; basal cell small. For hindwing and body see POPOV, SHCHERBAKOV (1991).




1-3. *Coleorrhyncha*: 1 - *Archicercopis* sp. In. 3540, length 5.6 mm; 2 - *Archicercopis* sp., In. 3540, detail of abdominal apex, showing ovipositor ; 3 - "*Homopterous insect*" of BRODIE, In. 3565, length 5.8 mm 4. *Mesoscytina anglica* sp.n. Holotype, In.10988, forewing, 2.8 mm long; $A_1$ = first anal , C = costal vein, CuA = anterior cubital vein, $CuA_1$, $CuA_2$ = branches of anterior cubital vein, M = median vein, $M_1$, $M_2$, $M_{3+4}$ = branches of median vein, PCu = posterior cubital vein, R = radial vein, $R_1$ = first radial vein, RS = radial sector, Sc = subcostal vein. Scale bar = 1 mm5. *Britannicola senilis* gen et sp. n. Holotype, In. 11788, forewing; 5.5 mm long. Scale bar = 1 mm

## Family *Progonocimicidae* HANDLIRSCH, 1906

DIAGNOSIS. As superfamily, the only family with two subfamilies: *Progonocimicinae* and *Cicadocorinae*.

## Genus *Archicercopis* HANDLIRSCH, 1939

*Archicercopis* HANDLIRSCH, 1939: 142

TYPE SPECIES. *Archicercopis falcata* HANLIRSCH, by monotypy (HANDLIRSCH, 1939: 142; POPOV, WOOTTON, 1977: 337-338). Upper Lias, Germany.

DIAGNOSIS. Basal cell less than one-fifth of wing length; precostal strip broad; M three-branched, $M_{1+2}$ forking beyond r-m.

### *Archicercopis* sp.

(Figs. 1-2)

*Homopterous insect.* BRODIE, 1845: 101; pl.7, fig. 15.
*Homopterous insect.* WESTWOOD in BRODIE, 1845: 127.
*Homopterous insect.* PHILLIPS, 1871: 123.

DESCRIPTION. Head and legs missing. Main longitudinal veins of forewing visible (Fig. 1); C submarginal, at first strongly, then gradually approximated to costal margin; Sc and $R_1$ arise close together on R, but terminate much further apart on Sc. Anal tube (Fig. 2) short, apically exserted, ovipositor valves not projecting it, abdominal segment VIII with posterior margin weakly concave. Differs from the type--species of the genus, *A. falcata* HANDL. (Upper Lias, Dobbertin), in that the first and second veins joining R and C diverge strongly anteriorly, so that the cell bounded by them is much wider at the anterior margin than at the posterior margin.

MATERIAL. In. 3540, Forthampton (on label "Hasfield"), Gloucestershire; Uppermost Triassic, Pseudomonotis beds; BRODIE coll.; part and counterpart. Dimensions: 5.6 x 2.8 mm; forewing 4.2 x 1.7 mm.

NOTE. Hasfield and Forthampton are both in the county of Glocester, about 5 km apart, in the vicinity of Tewksbury. There is probably no inconsistency between the published and the label data. There is in the collection a specimen that was described by BRODIE, 1845, pl.7, fig. 21, as a "*Homopterous insect*" and WESTWOOD, op.cit.p. 127, commented that it is "possibly the pupa of the same (i.e. I. 35401) ... or a specimen destitute of wings". Both BRODIE's publication and the label of the specimen give the locality as Hasfield. We figure it here (Fig. 3) but do not consider that it can be assigned with any certainly to the *Heteroptera*. It superficially resembles also some *Auchenorrhyncha* but there is insufficient detail preserved to permit any definite identification. It bears the accession number I. 3565 and measures 5.8 x 3.0 mm.

## Genus *Mesoscytina* Hong, 1983

*Mesoscytina* Hong, 1983: 66.

Type species. *Mesoscytina brunnea* Hong, by original designation of Hong (1983: 66-67); Middle Jurassic, Haifanggou Formation, Beipiao Basin of North China.

Diagnosis. Basal cell short; precostal strip narrow; Sc and $R_1$ diverging toward apices; costal space rather parallel-sided, whereas radial one widening distally; M three-branched; $M_{1+2}$ forking before r-m.

Note. The limits and composition of the genus were revised by Popov, Shcherbakov (1991); most species now included were first described as *Olgamartynovia* spp., and the species groups proposed in the latter genus should be abandoned as artificial.

### *Mesoscytina anglica* n. sp.

(Fig. 4)

Diagnosis. Forewing less than 3 mm long; crossvein r-m very short; Sc and $R_1$ diverging apically.

Name. The name is self explanatory.

Description. Right forewing with veins thinner in its distal part; cross-vein cu-a and m-cu together with bases of $M_{1+2}$, $M_{3+4}$ and M forming an arc dividing the more sclerotized basal part of the forewing from the more membranous distal part. Sc an $R_1$ diverging apically, $R_1$ and RS not so widely spaced; Sc three times as far as from base of wing as from RS ($K_1 = 3.0$) *; base of $R_1$ closer to RS than to Sc ($K_2 = 1.65$); fork of $M_1+M_2$ of medium length ($K_3 = 0.16$); $K_4 = 0.26$; Pcu + $A_1$ ($A_1+A_2$ of Wootton, Betts, 1986) rather short ($K_5 = 6.0$); r-m very short.

Holotype (Fig. 4); In. 10988, Morton Bagot, Warwickshire; Lower Lias?; Brodie coll.; negative impression of right forewing. Dimension: forewing 2.8 x 1.0 mm.

Discussion. The species stands close to *M.abdita* Yu. Pop. from the Lower Jurassic of Central Asia (South Kirgizia), differing mainly by much smaller size (2.8 mm against 4.0 - 4.5 mm) and very short cross-vein r-m. This species from the England territory is the westernmost distributed member of the genus *Mesoscytina*.

## Suborder *Heteroptera*

Diagnosis. *Hemiptera* with distinct gula closing head capsule ventrally behind mouthparts; tentorium reduced, lacking a transverse bridge; left-right assymetry of maxillary stylets; left and right mandibular stylets are mirror images; forewings folded flat over body, often in form of hemelytra; wing-coupling mechanism consisting of a clip on under surface of apical part of clavus into which thickened margin of hind

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* For designation of veins see Popov, 1982: 83; for explanation of indices $K_1$ to $K_5$ see Popov, 1985: 31.

wing slides; forked cubital furrow of hindwing; presence of tracheo-spiraculus metamers (e.g. metathoracic scent apparatus in adults) and abdominal spiracles; concealed trochanter; abdominal terga almost flat, usually not strongly arched; present dorsal abdominal scent glands in nymphs.

### Infraorder *Leptopodomorpha*

DIAGNOSIS. *Heteroptera* with hemelytral membrane almost wholly occupied by a few closed cells; antennae longer than head; metathoracic gland with a single, median, ventral aperture; head with dorsal trichobotria; gonoplac usually present. Infraorder, including littoral, intertidial and sometimes terrestrial predators.

### Family *Archegocimicidae* HANDLIRSCH, 1906

*Archegocimicidae* HANDLIRSCH, 1906: 493.
*Enicocoridae* POPOV, 1980: 50 (syn. by HONG, 1990).
*Xishaniidae* HONG, 1981: 87-88 (*Xishanidae*, emend. and syn. by POPOV 1988).
*Mesolygaeidae* HONG, REN, 1990: 0; **n.syn.**
*Mesolygaeidae* ZHANG, 1991: 682-683.
*Mesolygaeidae:* HONG, WAN, 1990: 96-100.
*Mesolygaeidae*: HONG, 1992, 45-50.

DIAGNOSIS. *Saldoidea* with pronotum coarsely warty, with a pronounced collar and with a transverse furrow one-third of the way back. Forewing weakly differentiated into corium and membrane, with a slight costal fracture and with a narrow costal strip; venation of corium prominent, main veins form three large cells and diverge almost from a single point; clavus relatively narrow. Legs thin and long. The female abdomen with ovipositor elongated into a small appendage.

### Genus *Britannicola* n. gen.

TYPE SPECIES. *Btitannicola senilis* n.sp.; Lower Lias; U.K.

DIAGNOSIS. Radial and medial cells of forewing small and short in relation to length of basal cell. Sc oblique.

NAME. Derived from "*Britannia*" (Lat.), Britain and "*cola*" (Lat.), inhabitant.

DESCRIPTION. Forewing with well developed but narrow costal strip. Costal and medial fractures distinct. The main veins thickened; Sc ($R_1$), R and M diverge from one point. Costal fracture closely approximated to Sc; medial fracture occupying about one-third of the forewing length. Basal cell R + M, parallel-sided, very large.

DISCUSSION. *Britannicola* differs from other genera of its family by forewing cells M and especially R which is much shorter in relation to the length of basal cell, and r-m cross-vein replaced with short anastomosis.

### *Britannicola senilis* n. sp.

(Fig. 5)

DIAGNOSIS. As genus; the only species.

NAME. Derived from "*senilis*" (Lat.), senile.

DESCRIPTION. Forewing unicolored, without distinct pattern. Venation indistinct in apical and posterior parts of wing, probably due to poor preservation. An oblique Sc and all branches of R reaching costal margin. Radial cell particularly small. CuA rather distanced from posterior margin of wing.

HOLOTYPE. (Fig.5); In. 11788, U.K. (no locality stated); "Lower Lias"; BRODIE coll. Dimensions: 5.5 x 1.8 mm.

PARATYPE. In. 10941, Apperley, Clouchester; Lower Lias ?; BRODIE coll. Dimensions: 4.6 x 1.5.

DISCUSSION. The venation of these specimens, especially that of the paratype, is in some parts indistinct. The following features are characteristic of *Archegocimicidae*: an even sclerotization of forewings, except for the stronger sclerotized costal area of corium, which is limited apically by a distinct costal fracture close to Sc; indistinct membrane; the course of R + M immediately in front of the medial fracture in the basal part of wing; the divergence of Sc, R and M almost from a single point; the remoteness of CuA from the claval fracture; the three closed cells of corium; the large basal cell (shorter than clavus); and the divergence of branches of R from each other and from M.

## Infraorder *Cimicomorpha*

DIAGNOSIS. *Heteroptera* lacking both true arolia and true pulvilli; metathoracic gland with paired, lateral apertures; forewing membrane with closed cells absent or confined to base; hindwing with non-branching distal sector R + M and not separating beyond basal cell; costal fracture usually present; gonoplac usually present.

### Family *Pterocimicidae* n. fam.

"Family nov. 1" WHALLEY, 1985: 143.

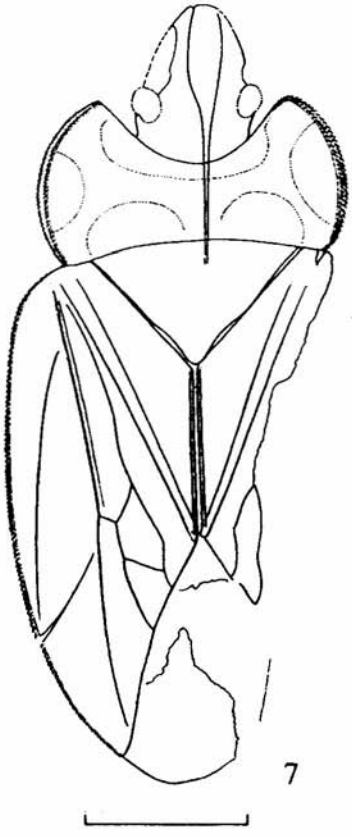
TYPE GENUS. *Pterocimex* n. gen., Lower Lias, U.K.

DIAGNOSIS. *Cimicomorpha* with elongate, prognathous head and broad, laterally explanate pronotum; forewing with a complete set of closed cells; male segment VIII not telescoped within VII at rest; ovipositor short.

DESCRIPTION. Head elongate, prognathous, tylus and juga projecting well in front of eyes; eyes small, not adjacent to anterior margin of pronotum; rostrum very long, projecting far beyond posterior margin of thorax. Pronotum transverse, not divided by transverse suture into anterior and posterior lobes. Scutellum triangular, of medium size, exposed, lacking transverse sulcus. Legs slender and rather short with femora scarcely reaching beyond body margin. Forewing complete, covering whole abdomen, with costal and medial fractures pronounced, differentiated into sclerotized

clavus and corium and unsclerotized membrane; precostal area (epipleura) broad. Sc leaving R + M about one quarter of the way from base of wing, becoming narrower distally, perhaps terminating on costal margin close to costal fracture; basal cell, between R + M and CuA, long; two medial and three discal closed cells present; RS and M running close together and approximately parallel distad of costal fracture; venation of membrane not apparent (possibly with numerous thin veins). Abdomen distinctly narrower basally, broadly rounded apically, with narrow connexivum. Male with well developed genital capsule, apparently completely covering genitalia ventrally; male segment VIII not telescoped within VII at rest (Fig. 11). Ovipositor short (Figs. 12, 13).

A single genus, *Pterocimex*, with one included species, is known from the Lower Lias of Dorset.



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6-7. *Pterocimex jacksoni* gen et sp. n. 6. Paratype, In. 59104, length 8.75 mm ( x 13.7), 7. Paratype, In. 59104, scale bar = 2 mm

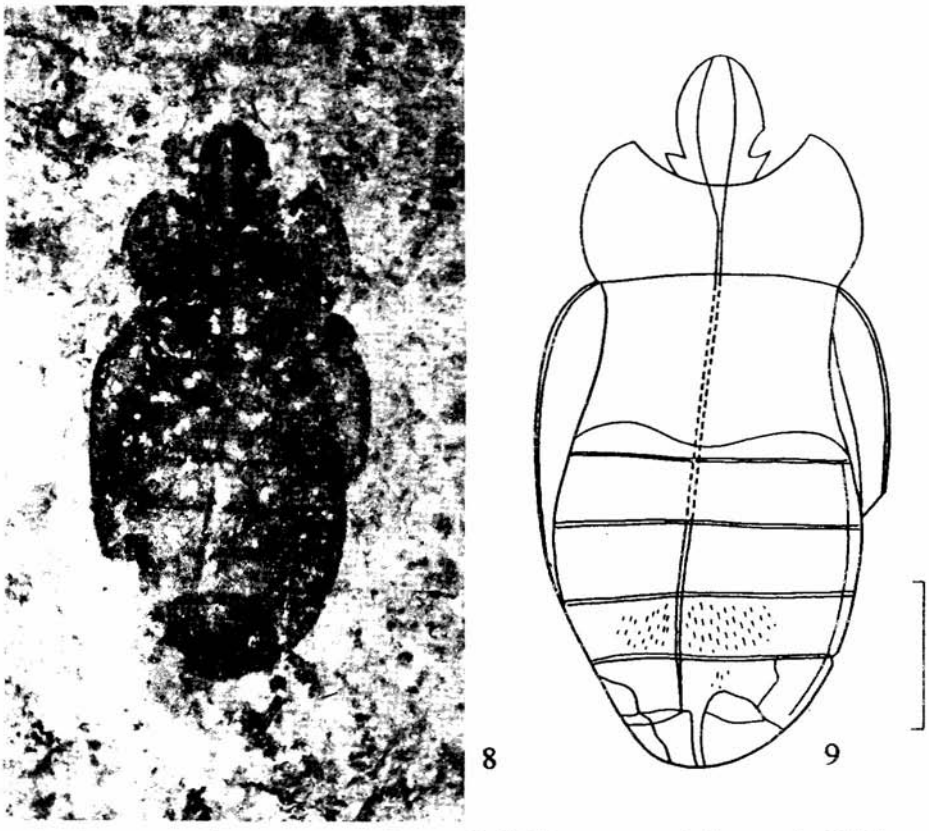
## Genus *Pterocimex* n. gen.

TYPE SPECIES. *Pterocimex jacksoni* n.sp.; Lower Lias, Dorset, U.K.

DIAGNOSIS. As family. Head slightly longer than pronotum; eyes small, hairy, close but adjacent to anterior margin of pronotum; rostrum long, reaching posteriorly almost to apex of abdomen; differentiation into clavus, corium and membrane pronounced.

NAME. Derived from "*pteros*" (Gr.), wing and "*cimex*" (Lat.), bug.

DESCRIPTION. Body elongate-oval, about half as wide as long, dorsoventrally flattened, of moderate size (8.5-10 mm). Monochromatic, dark-coloured. Head, thorax, abdomen and forewing, including membrane, covered with short,curved bristles. Pronotum sculptured, strongly transverse, about twice as broad as long, its lateral margins explanate and embracing head. Scutellum broader than long, shorter than pronotum. Forewing with three branches of R entering cuneal area, the fourth continuing along line of main stem of R parallel with M; basal cell about half as long as wing; membrane short, about equal in area to clavus and only about one third of

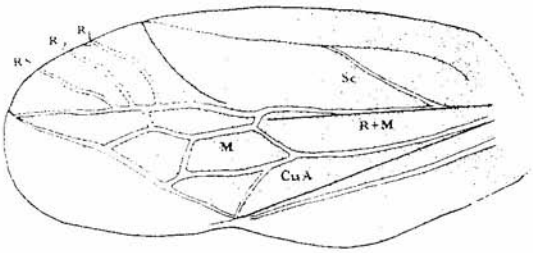


8-9. *Pterocimex jacksoni* gen.et sp.n. 8. Paratype, In. 59104, counterpart. 9. Paratype, In. 59104, counterpart, scale bar = 2 mm

the area of corium; venation of membrane not distinct. Abdomen slightly longer than wide, pre- genital segments longitudinally sulcate in midline.

***Pterocimex jacksoni* n. sp.**

(Figs. 6-13)

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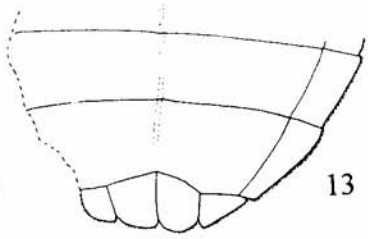

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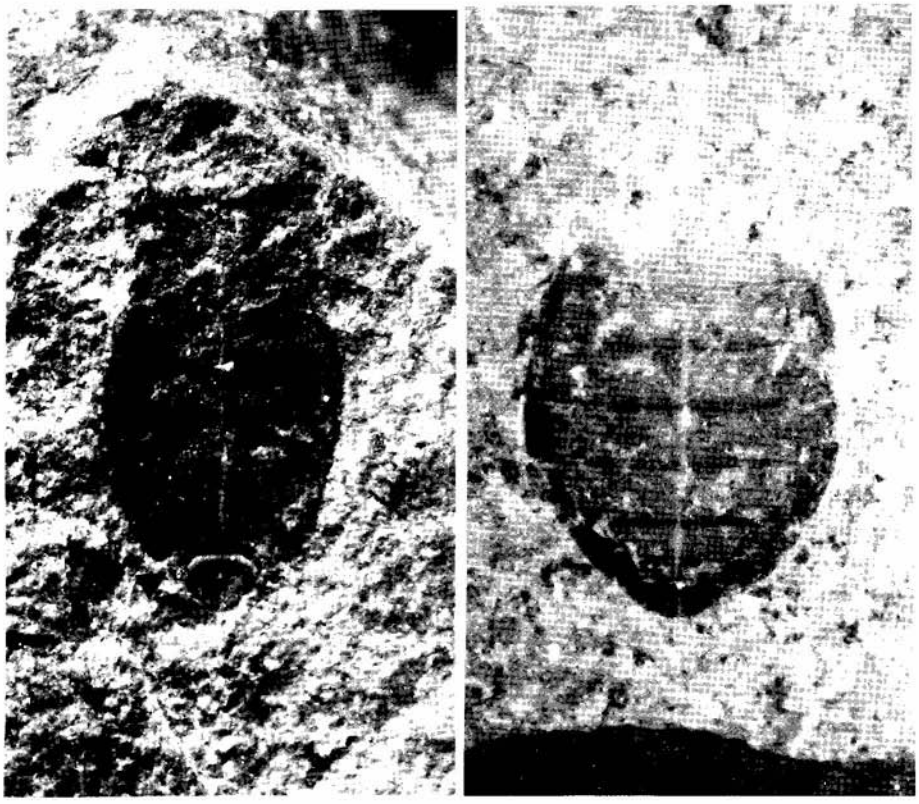


10-13. *Pterocimex jacksoni* gen et sp. n. 10. Paratype, In. 59359, forewing, 6.25 mm long, 11. Paratype, In. 59147, male abdomen, length 5.4 mm; eighth abdominal segment arrowed (x 17.8), 12. Paratype, In. 49567, female abdomen, length 5.1 mm; note pubescence (x 15.6), 13. Paratype, In. 49216, detail of apex of female abdomen, width 4.1 mm (x 30)

"Gen. et sp.nov. 1A" WHALLEY, 1985: 145 and 144, figs. 39-40.

DIAGNOSIS. As genus; the only species.

NAME. Named after James F. JACKSON, who made a remarkable collection of fossil insects from Dorset Lias.

DESCRIPTION. Width of head including eyes divided by length, 0.93. Width of pronotum divided by length in midline, 2.8. Width of scutellum divided by length, 1.4. Length of corium divided by length of forewing 0.71. Greatest width of corium divided by its total length, 0.41. Length of clavus divided by length of forewing, 0.52. Greatest width of clavus divided by its length, 0.23. Length of claval commissure divided by length of scutellum, 1.1. Length of membrane divided by length of forewing, 0.46. Width of membrane divided by its length, 0.41. Greatest width of closed forewings at level of scutellum, this width divided by width of pronotum, 1.2.

Total length, 8.8 - 10 mm (mean 9.2, n=4). Head length, 1.6-1.8 mm; width, 1.5-1.7 mm. Pronotum length, 1.2-1.7 mm; width, 3.5-5.2 mm. Scutellum length, 1.1-1.4 mm; width, 1.5-1.9 mm. Forewing length, 5.7-6.9 mm. Corium length (including cuneus), 5.0-6.1 mm; greatest width, 1.9-2.3 mm. Clavus length, 2.3-3.8 mm; greatest width, 0.67-0.83 mm; claval commissure length, 1.2-1.9 mm. Membrane length, 2.7-3.3 mm; width 0.92-1.4 mm. Greatest width across closed forewings, 4.2-4.7 mm. All dimensions and ratios, except total body length, based on five to nine examples.

HOLOTYPE. In. 53909. The Woodstone, Black Ven, Charmouth, Dorset; Lower Lias; JACKSON coll.; part and counterpart. Dimensions: 9.25 x 4.33 mm.

PARATYPES. The Woodstone, Black Ven, Charmouth, Dorset; Lower Lias; JACKSON coll.: In.49589; In.51048*; In.59359 (Fig. 10). The Flatstones, Stonebarrow, Charmouth, Dorset; Lower Lias; Jackson coll.: In.49216* (Fig. 13); In.49243*; In.49567* (Fig. 12); In.49576; In.53986; In.53995*; In.59104* (Figs. 6-9); In.59128*; In.59137*; In.59147* (Fig. 11); Charmouth, Dorset (no further detail). In.59358B. (Asterisks indicate specimens with counterparts). Halftone figures of In.59128 and 59137 published by WHALLEY, 1985: 144, figs. 40 and 39 respectively. In.53986 preserved in the collection of the Paleontological Institute, Russian Academy of Sciences, Moscow.

NOTE. In.59137 has a group of three spots of a resinous-looking, reddish-brown deposit at the apex of scutellum, in the position of metathoracic gland or stomach, and similar, but less obvious, traces are visible in some other specimens of this species. In.49576 is a forewing which is narrower than the others, especially in the epipleural area. The venation is also very distinct, and for these reasons we believe it may have come from a teneral individual and is not fully expanded.

## Infraorder *Pentatomomorpha*

DIAGNOSIS. *Heteroptera* lacking arolia; pulvilli present; metathoracic gland with paired, lateral apertures; forewing membrane with closed cells absent or confined to base; costal fracture of recent representatives absent; hindwing with R and M separating beyond basal cell; gonoplac absent; possesion of ventral abdominal trichobotria (except in *Aradoidea*).

## Family *Pachymeridiidae* HANDLIRSCH, 1906

DIAGNOSIS. *Coreoidea* with forewings differentiated into clavus, corium and membrane; costal and medial fracture present; costal fracture short and often weakly indicative, medial fracture long; Sc, R and M diverging from almost the same point; clavus, corium and pronotum usually distinctly sculptured; claval commissure shorter than scutellum or equalling it in length.

NOTE. This rather large Mesozoic family of terrestrial coreid-lygaeid bugs is widespread in the Lower Jurassic of West Europe and the late Mesozoic of Asia. All previously described representatives of the family, with the exception of "*Pachymerus*" *zucholdi* GIEB. (GIEBEL, 1856) from the Upper Jurassic (the latest Rhaetian) of England, were found in the Upper Liassic deposits in Germany (Dobbertin, Mecklenburg) (HANDLIRSCH, 1906, 1925, 1939) and in the Upper Jurassic of South Kazakhstan (POPOV, 1961). The family is very inadequately known at present and a reliable diagnosis of it cannot be given yet. The main diagnostic features, by which *Pachymeri*diidae are determinated, are: the divergence of Sc, R and M veins of forewings from nearly one point and the presence of costal fracture. For the last one and a half decades, numerous pachymeridiids and their stratigraphic distribution have been described from the Lower Cretaceous of the eastern Transbaikalia of Siberia (POPOV, 1990), West Mongolia (POPOV, 1986) and the Jurassic-Cretaceous deposits of North and South China (HONG, 1983, 1984a,b, 1987; HONG, WANG, 1990; LIN, 1986; ZHANG, 1992). Judging by some external structures, for example, the laminate lateral margins of pronotum, the more recent pachymeridiids had already acquired typically lygaeoid appearence. Up till now 8 genera and about 10 species were described in this family from the Lias of West Europe and over 15 genera and about 30 species from Asia. Moreover, there are a lot of undescribed pachymeridiids from Siberia, Mongolia and, apparently, from China.

### Genus *Neomeridium* n. gen.

"Gen. et sp.nov. 3A" WHALLEY, 1985: 145.

TYPE SPECIES. *Neomeridium trifurcum* n.sp.; Lower Lias;U.K.

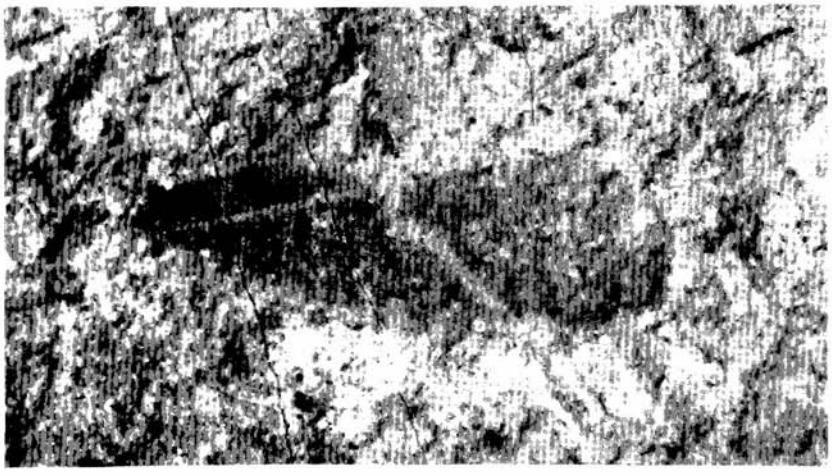
DIAGNOSIS. Forewing narrow as in *Pachymeridium* GEINTZ but with three branches of the radius arising close together near apex of medial fracture. CuA remote from claval fracture.

NAME. Compound of "*neo*" (Lat.), new and "*meridium*" (Lat.), element of name of type genus of the family, *Pachymeridium*.

### *Neomeridium trifurcum* n. sp.

(Figs. 14-16)

"*Archegocimicidae*, gen. et sp. indet."(In.51007), WHALLEY, 1985: 143; "Gen. et sp.nov. 3A" WHALLEY, 1985: 145.



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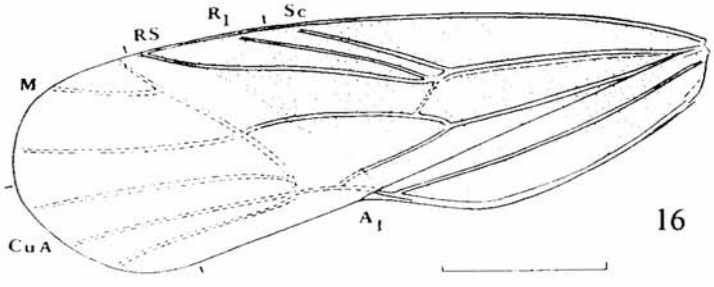


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14-16. *Neomeridium trifurcum* gen. et sp. n., 14. Holotype, In. 59151, forewing, 8.75 mm long (x 13.4), 15. Paratype, In. 49566, forewing, 8.2 mm long (x 13.4), 16. Holotype, In. 59151, forewing; scale bar = 2 mm

DIAGNOSIS. As genus; three only species.

NAME. Derived from "*trifurcum*" (Lat.), three branches.

DESCRIPTION. Total length of forewing 8-9 mm. Clavus and corium punctate; corium with cross-markings in "herring-bone" pattern. Proportions as other *Pachymeridiidae*. Corium length divided by total length of forewing, 0.73; corium greatest width, 0.33 times its length. Clavus length divided by total length of forewing, 0.45; clavus greatest width divided by its length, 0.22. Claval commissure length divided by claval length, 0.39. Membrane length divided by total of forewing, 0.54; membrane width divided by its length, 0.60. Four (possibly five) longitudinal veins can be discerned in the membrane.

HOLOTYPE. (Figs. 14, 16); In.59151. The Woodstone, Black Ven. Charmouth; Lower Lias; JACKSON coll. Dimentions: Length, 8.75 mm; corium, 6.75 x 2.25 mm; clavus, 4.08 x 0.83 mm; membrane, 4.92 x 2.92.

PARATYPES. In.51039*, In.53901*, In.64014*. The Woodstone, Black Ven, Charmouth, Dorset; Lower Lias; JACKSON coll.; In.49566* (Fig. 15). In.51007, In.53941, In.59105*. The Flatstones, Stonebarrow, Charmouth, Dorset; Lower Lias; JACKSON coll. (Asterisks indicate specimen with part and counterpart).

DISCUSSION. The venation of this species appears sufficiently different from that of other *Pachymeridiidae* to warrant the erection of a new genus. This is generally a larger species than most pachymeridiids but there is considerable variation in size amongst the specimens examined (as noted above, the length of the forewing varies from 8 to 9 mm). The three specimens treated below are all smaller than any of these.

## *Pachymeridiidae* incertae sedis

### Gen. sp. 1

(Fig. 17)

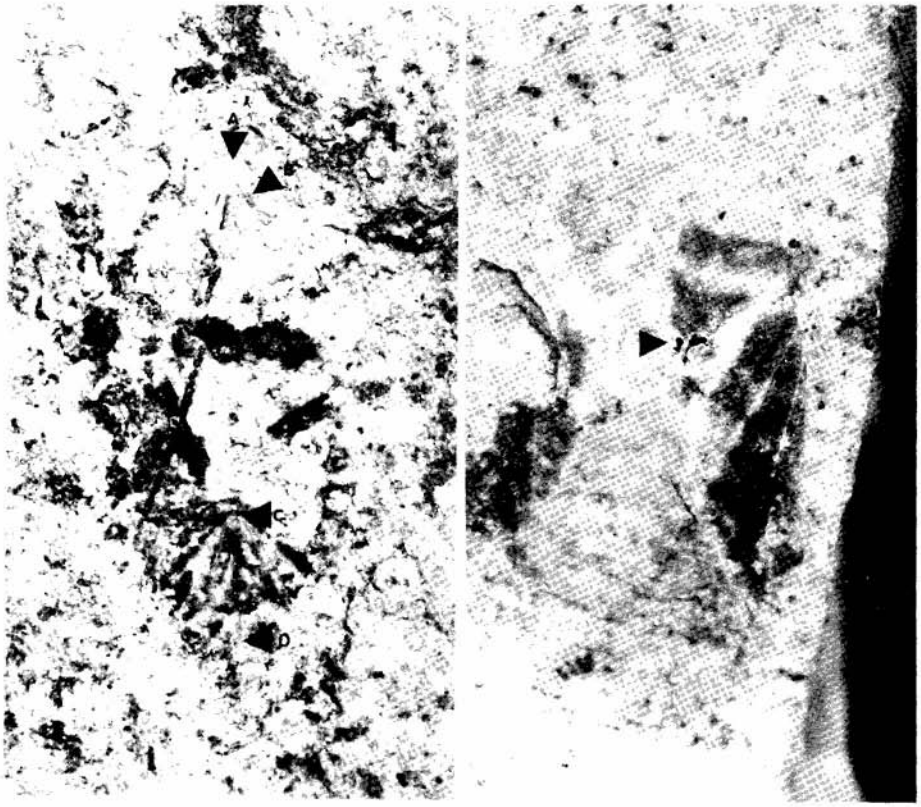
"*Pachymeridiidae* species 4A" WHALLEY, 1985: 146.

DESCRIPTION. A female specimen consisting of head, thorax, abdomen and some appendages. Head approximately quadrate, apically pointed. Rostrum very long, reaching to base of ovipositor. Antennal segment 1 not reaching apex of head (possibly incomplete in fossil). Pronotum short, greatly widened posteriorly. Forewing membrane extending beyond apex of abdomen at rest. Posterior femora extending well beyond margins of body. Pronotum, scutellum, corium and posterior femur rather coarsely sculptured. Abdomen slightly broader than long, ovipositor more than half as long as abdomen.

MATERIAL. (Fig. 17); In.51028. The Flatstones, Stonebarrow, Charmouth, Dorset; Lower Lias; JACKSON coll.; part and counterpart. Dimensions: Total length from apex of head to apex of folded forewings, 11.3 mm. Head length, 1.8 mm; rostrum length, 7.3 mm. Pronotum length in mid-line, 2.2 mm; width of anterior margin, 2.0 mm; width of posterior margin, 3.6 mm. Total length of forewing, 7.5 mm. Length of

posterior femur, 3.8 mm. Abdomen length, 4.8 mm; width, 5.0 mm; ovipositor length, 3.2 mm.

DISCUSSION. The forewing is insufficiently well-preserved for this specimen to be allocated to a genus. Its total forewing length is less than any of the detached forewings




17 18

17. *Pachymeridiidae* species 1. In. 51028, length 11.3 mm (x 9.7). Arrows: A = apex of head, B = first joint of antenna, C, D = base, apex of ovipositor, 18. *Pachymeridiidae* species 3, In. 50999, length of forewing 6.3 mm(x 15.8). Arrow indicates crystalline body, probably stomach contents

described above as *N. trifurcum*. As it is a female it would be expected to be larger than the average for its species and we therefore exclude it from *N. trifurcum*. Its general body proportions and coarse body sculpture leave no doubt that it is a member of the same family.

### Gen. sp. 2

"*Pachymeridiidae* species 5A" WHALLEY, 1985: 146.

DESCRIPTION. A female without head or legs. Pronotum and scutellum more coarsely sculptured than corium or clavus. Abdomen as broad as long, ovipositor more than half as long as abdomen.

MATERIAL. In.51005. The Flatstones, Stonebarrow, Charmouth, Dorset; Lower Lias; JACKSON coll. Dimensions: Length, 7.7 mm. Pronotum length, 1.6 mm; width at base, 2.9 mm. Scutellum length, 1.4 mm; width, 1.8 mm. Total forewing length (estimate), 6.7 mm. Abdomen length, 4.1 mm; width, 4.1 mm; ovipositor length, 2.2 mm.

DISCUSSION. Considerably smaller than species 1 (whose length from anterior margin of pronotum to the apex of the abdomen is 8.9 mm) but otherwise of the same general proportions. The long ovipositor of these two *Pachymeridiidae* is noteworthy. Insufficient details of the forewing are visible to enable us to place this specimen to genus.

### Gen. sp. 3

(Fig. 18)

"*Pachymeridiidae* species 6A" WHALLEY, 1985: 146.

DESCRIPTION. A body, sex unknown, with forewings attached. Pronotum, scutellum, clavus and corium rather coarsely sculptured. There is a deposit of a red substance at the level of the apex of the scutellum in the position usually occupied by the metathoracic scent gland in *Heteroptera*. Proportion of length to breadth and relative lengths of corium, clavus and membrane very close of *N. trifurcum*.

MATERIAL. (Fig. 18). The Flatstones. Stonebarrow, Charmouth, Dorset; Lower Lias; JACKSON coll. Dimentions: Total length of forewing, 6.3 mm; corium, 4.4 x 1.5 mm; clavus, 2.9 x 0.64 mm; membrane, 3.6 x 2.0 mm.

DISCUSSION. Details of the forewing venation are insufficient to place the species to a genus. We have seen deposits of reddish material at the site of the metathoracic gland in fossil *Heteroptera* of other families (e.g. corixids *Corixonecta hosbayari* YU. POP. from the Early Creatceous of West Mongolia or see notes under *Tarsabedus menkei*). On the grounds of size (and parsimony) we feel that this specimen may be the same species (perhaps a male) as species 2.

### Gen. sp. 4

(Fig. 20)

DESCRIPTION. A detached forewing, almost complete. Differentiation into clavus, corium and membrane apparent. Surviving venation fragmentary, in part indicated by organic pigment on clavus and corium. Medial fracture present, costal fracture not apparent.

MATERIAL. (Fig. 20). In.10947. Apperley, Gloucestershire; Lower Lias?; BRODIE coll. Dimensions: 4.7 x 1.3 mm.

DISCUSSION. Tentatively assigned to *Pachymeridiidae* on the basis of the character given above. The claval commissure is less than half as long as the posterior margin of clavus, as in *Neomeridium* and most modern *Lygaeidae*. This specimen is smaller than all other known Liassic *Pachymeridiidae*.

### *"Pachymerus" zucholdi* GIEBEL, 1856

(Fig. 19)

"*Cimicideous insect*" BRODIE, 1845: 101, pl.7, fig.22.

"Apparently a cimicideous insect" WESTWOOD in BRODIE, 1845: 128.

*Pachymerus zucholdi* GIEBEL, 1856: 356.

"*Cimicideous insect*" PHILLIPS, 1871: 123.

*Cimex* BRODIE, 1873: 25.

*Cimex* BRODIE, 1874: 33.

*(Pachymerus zucholdi* GIEBEL); HANDLIRSCH, 1906: 504 (excludes species from *Pachymerus*).

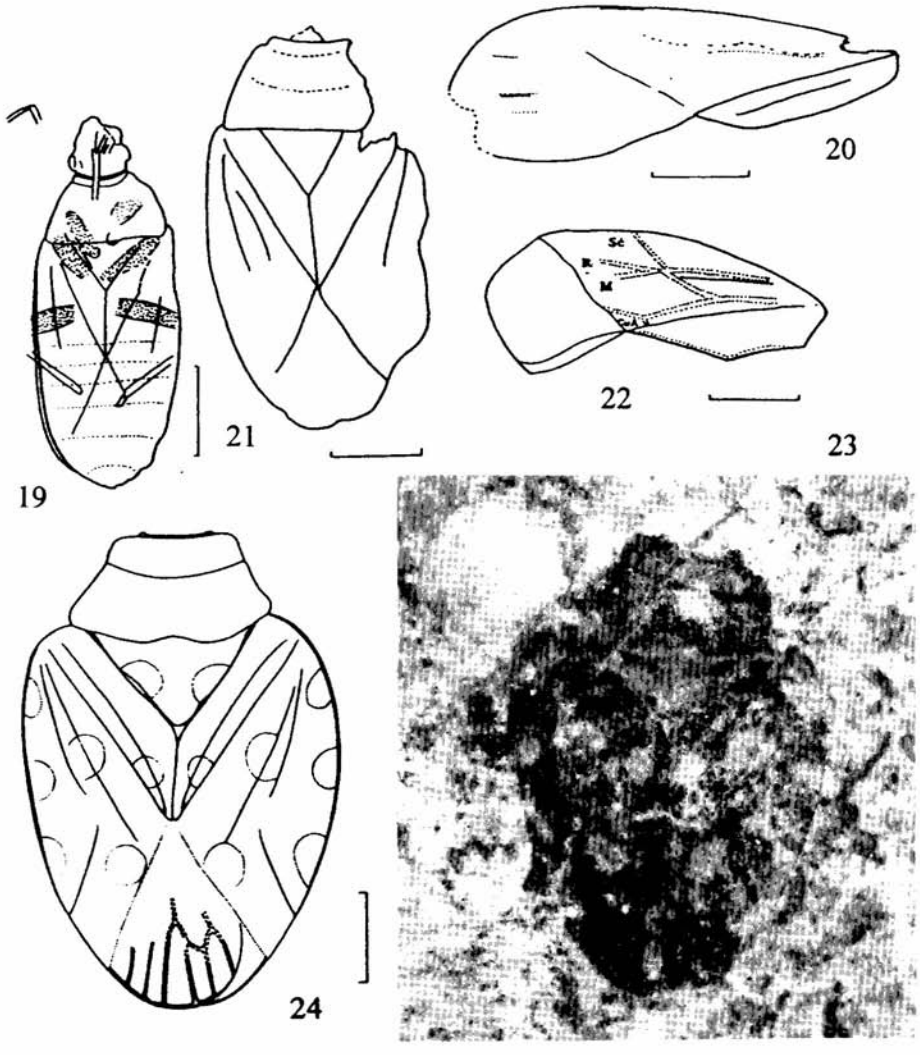
DIAGNOSIS. It is not possible to provide a diagnosis differentiating this insect from its relatives because of the imperfect state of preservation.

DESCRIPTION. Head, including eyes, about as wide as long, nearly equal in length to pronotum; pronotum twice as wide as long, with wide anterior collar; scutellum slightly wider than long, shorter than claval commissure. Forewing well differentiated into clavus, corium and membrane; medial fracture reaching to level of apex of clavus, costal fracture not apparent; corium length divided by total length of forewing, 0.82; corium greatest width, 0.36 times its own length; clavus length divided by total length of forewing, 0.48; clavus greatest width divided by its own length, 0.25; claval commissure divided by length of clavus, 0.55; membrane length divided by total length of forewing, 0.62; membrane width divided by its own length, 0.67. Femora short, posterior pair reaching slightly beyond lateral margins of body, nearly equal in length to posterior tibiae. Abdomen slightly longer than broad, about as broad as closed forewings.

HOLOTYPE. (Fig. 19). In.3567. Strensham (Hereford-and-Worcester); Upper Triassic; BRODIE coll. Dimensions: 8.3 x 3.1 mm., total length of forewing, 5.6 mm.

DISCUSSION. The type shows little detail but the general proportions are sufficient to enable it to be placed in *Pachymeridiidae* with confidence. The femora are all preserved as dark shadows, the posterior pair lying transversely across the body and

evidently because of the line taken by the preserved parts of the posterior tibiae, they cannot in life have projected much beyond the body margin. The other femora




19. "*Pachymerus*" *zucholdi* GIEBEL. Holotype, In. 3567, length 8.3 mm. Scale bar = 2 mm, 20. *Pachymeridiidae species* 4. In. 10947, forewing, 4.7 mm long. scale bar = 1 mm; 21-22. *Protocoris indistinctus* sp. n. Holotype, In.6722, length 4.6 mm, scale bar = 1 mm, 22. detail of forewing; 23-24. *Propreocoris maculatus* gen.et sp. n. Holotype. In.59152, length 5.4 mm (x 18,5), 24. Holotype, In. 59152, scale bar = 1 mm

its less strongly transverse pronotum and smaller size. *Pallicoris firmis* LIN from the Lower Jurassic of South China (Guangxi province), once placed to *Protocoridae* (LIN, 1986), actually belongs to *Pachymeridiidae*. In addition to an unusual similarity between the Early Jurassic species of *Protocoris* and *Probascanion megacephalum* HANDL. pointed out by POPOV (1992), the above arguments allow to reexamine the interrelationship of Jurassic *Probascaniidae* and *Protocoridae* in future.

## Infraorder *Nepomorpha*

DIAGNOSIS. Aquatic and littoral *Heteroptera* with antennae shorter than head, trend toward a decrease in the number of antennal segments; cephalic trichobotria reduced; metathoracic gland with a single, median, ventral aperture; subgenital plate of sternum VII elongated backward and conceals ovipositor; mostly carnivorous (except *Corixoidea*); tarsal claw without arolia.

## Family *Ochteridae* KIRKALDY, 1897

DIAGNOSIS. Body small, oval, short, flattened out, resembling *Saldidae* living in similar biotopes; head short, eyes large, ocelli present, four-segmented rostrum very long; forewing divided into clavus, corium, large embolium (costal area), and membrane,the latter with cells and radial grooves along outer margin (peripheral membrane); male abdominal segments asymmetrical and ovipositor in female reduced.

### Subfamily *Propreocorinae* n. subfam.

"Family nov. 2" WHALLEY, 1985: 145.

TYPE GENUS. *Propreocoris*, n.gen.; Lower Lias; U.K.

DIAGNOSIS. *Ochteridae* with pronotum considerably narrower than width across forewings, with a narrow collar and with a transverse sulcus about one third of the way back; pronotum, scutellum, clavus, and corium finely punctate; forewing distinctly differentiated into corium and membrane, venation of corium indistinct; clavus broad.

DESCRIPTION. Width of pronotum considerably less than width across forewings at rest, with a narrow anterior collar and transverse sulcus dividing it into a smaller anterior and larger posterior lobes. Forewing strongly sclerotized with costal and medial fractures pronounced, costal stir very narrow, costal fracture reaching approximately to the middle of wing; veins of corium very indistinct; membrane clearly differentiated from corium, its veins parallel, reaching its apical margin and forming some large cells, peripheral membrane very narrow.

A single genus with one species is known.

NOTE. The narrower pronotum without distinct laminate extentions of the lateral margins and strongly contracted precostal stir of the forewing clearly separate

*Propreocoris* from other ochterid bugs and permit to erect this new subfamily for our new genus.

### Genus *Propreocoris* n. gen..

TYPE SPECIES. *Propreocoris maculatus* n. sp., Dorset, Lower Lias.

DIAGNOSIS. As subfamily; the only genus.

NAME. Derived from "*proprius*' (Lat.), characteristic, distinctive and "*coris*" (Lat.), bug.

DESCRIPTION. Width of body across firewings in resting position 1.6 times width of pronotum; pronotum with lateral margins narrowing towards posterior margin very weakly concave in the middle; ratio of length of anterior lobe to length of pronotum about 3.7; anterior margin about as wide as median length, posterior margin more than twice as wide as median length. Scutellum about 1.7 times as wide as long, half as wide as posterior margin of pronotum and almost as long as length of claval commissure. Forewing greatly widened in costal area; costal fracture long and curved, commencing at point on costal margin about two fifth of the way along length of membrane; apical margin of corium slightly concave, apex of corium about three fifths of the way along membrane; area of membrane about half that of corium, membrane with about six longitudinal veins (but see note under description of species). Pronotum, scutellum, clavus, and corium finely punctate.

### *Propreocoris maculatus* n. sp.

(Figs 23, 24)

"Gen. et sp. nov. 2A" WHALLEY, 1985: 145 and 144, fig. 41.

DIAGNOSIS. As genus; the only species.

NAME. Derived from "*maculatus*" (Lat.), spotted.

DESCRIPTION. Head and legs missing. Venation of corium not distinct, that of membrane consisting of six parallel veins. This may be the case when there are only three veins on each forewing, the two sets of veins being superimposed. If this is so, then the three veins are restricted to the anterior half of each membrane. Pronotum, scutellum, clavus, and corium dark-coloured, there is a pattern of large, round, and pale spots on clavus and corium.

HOLOTYPE. In.59152 (Figs. 23, 24). The Woodstone, Black Ven, Charmouth, Dorset; Lower Lias; JACKSON coll.; part and counterpart. Dimensions: 5.4 x 3.5 mm. Figured by WHALLEY , 1985: 144, fig. 41 (halftone).

### Family *Corixidae* LEACH, 1815

DIAGNOSIS. *Nepomorpha* has hypognathous head with labrum greatly developed, concealing short rostrum; antennae short, completely hidden, forewing not foliaceously

expanded at costal margin; fore legs not grasping, hind legs natatory with two-segmented tarsi considerably flattened; nymphs with dorsal abdominal glands. True aquatic insects, basically, algo- or detritophagous, rearly predators or phytozoophags.

### Subfamily *Archaecorixinae* Popov, 1968

Diagnosis. Body elongate-oval, moderately large; pronotum short, scutellum free; forewing venation well developed, clavus short; male genital segments symmetrical.

Note. This primitive group of aquatic bugs was originally described from the bottom of the Upper Jurassic of south-West Kazakhstan (Popov, 1968). They are chiefly characterized by weakly elongated oval body shape, strongly transverse pronotum, broadly triangular scutellum, short clavus with two longitudinal veins,, correspondingly short claval commissure and symmetrical genital segments. However, the definition of the relation of *Archaecorixinae* to other subfamilies, primarily *Micronectinae* and *Velocorixinae*, may be done after a final revision of Late Jurassic *Archaecorixinae* and *Velocorixinae* and correction of previous tentative phylogenetic schemes of both fossil and recent subfamilies of *Corixidae* (Popov, 1989d, 1992).

### Genus *Liassocorixa* n. gen.

Type species. *Liassocorixa dorsetica* n. sp..

Diagnosis. Differs from *Archaecorixa* by its less strongly transverse pronotum and longer claval commissure.

Name. Derived from "*Lias*", Liassic and "*Corixa*", a genus of waterbugs.

Description. Body moderately large (about 10 mm long), elongate-oval, about 1.7 or 1.8 times as long as broad. Pronotum strongly transverse, three times as wide as long, almost as long as scutellum, weakly sculptured anteriorly. Scutellum broadly triangular, about twice as broad as long. Corium with a very short costal fracture; venation indistinct. Clavus with two longitudinal veins; length of claval commissure almost 1.5 times length of scutellum. Male genital segments symmetrical.

Discussion. This new genus is quite similar to *Archaecorixa* Yu. Pop., from the Upper Jurassic of Karatau (South Kazakhstan). It differs from that genus by a less strongly transverse pronotum (more than 3.5 times as wide as long in *A. lata* Yu. Pop.) and longer claval commissure (equal in length to scutellum in *A. lata* Yu. Pop.).

### *Liassocorixa dorsetica* n. sp.

(Fig. 25-27)

Diagnosis. As genus; the only species.

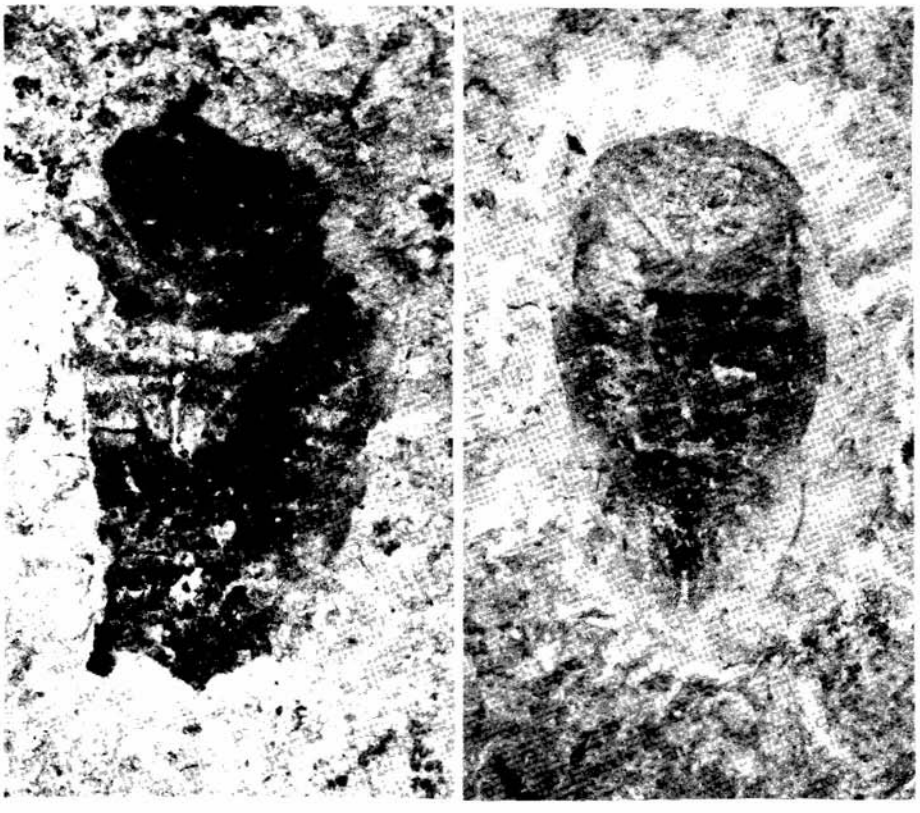
Name. Derived from the locality "Dorset".

Description. In both specimens the head is missing. The short, broad pronotum is missing in the paratype; in the holotype it shows trace of striations near the anterior margin, its posterior margin is straight and the anterolateral angles are distinct.

Scutellum with lateral margins slightly flexuous and apex weakly mucronate. In.59140 (figured) has a single, long slender leg visible close to the lateral margin of the abdomen posteriorly, but it is not possible to trace its connection with the thorax; it resembles in thickness mesothoracic legs of modern corixids. The last visible abdominal segment is deeply cleft. Length, 8.5-9.9 mm. Length of pronotum, 1.4 mm; breadth, 4.4 mm. Length of scutellum, 1.3-1.4 mm; breadth, 2.5-2.6 mm. Length of forewing, 7.0-7.5 mm. Length of claval commissure, 2.0 mm.

HOLOTYPE. (Figs. 25-27). In.59140. The Flatstones, Stonebarrow, Charmouth, Dorset; Lower Lias; JACKSON coll., part and counterpart. Dimensions: 9 x 9 mm. Length of pronotum, 1.4 mm; width 4.5 mm. Length of scutellum, 1.5 mm; width 2.7 mm. Length of claval commissure, 2.1 mm.

PARATYPE. In.59166. The Woodstone, Black Ven, Charmouth, Dorset; Lower Lias; JACKSON coll. Dimensions: 9.0 x 5.7 mm.



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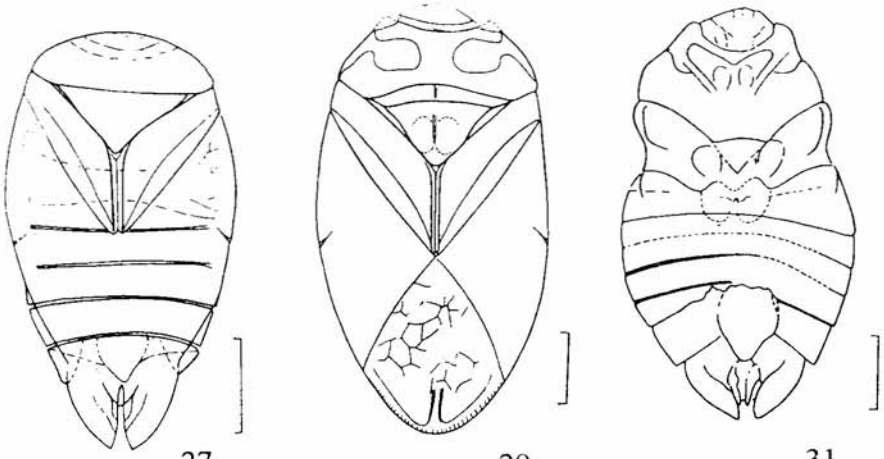
25-26. *Liassocorixa dorsetica* gen. et sp. n. Holotype, In. 59140, length 9.9 mm (x 13.1), 26. counterpart (x 13.1)



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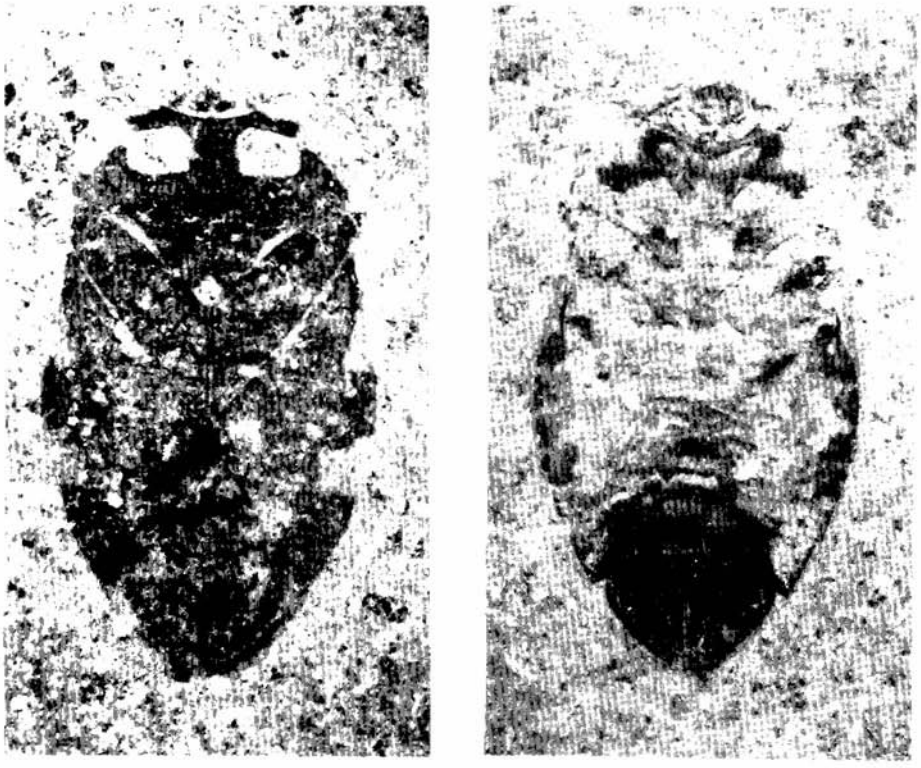

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27. *Liassocorixa dorsetica* gen. et sp. n. Holotype, In. 59140, scale bar = 2 mm, 28-31. *Lethonectes naucoroides* gen.et sp. n. Holotype, In. 49615, length 13 mm (x 11.2), 29. Holotype, In. 49615, scale bar = 2 mm, 30. counterpart (x 11.2), 31. Counterpart, scale bar = 2 mm

## Family *Belostomatidae* Leach, 1815

Diagnosis. *Nepomorpha* with a pair of retractable respiratory straps at apex of abdomen; forewings with distinct venation, claval commissure about equal in length to scutellum. Predatory aquatic bugs.

## Subfamily *Belostomatinae* Leach, 1815

Diagnosis. *Belostomatidae* without longitudinal sutures on the abdominal sternites.

Note. In three of four specimens of broadly oval water bugs examined, the siphon is visible (Figs. 29, 30, 33, 35). The scutellum of the smaller species before us is only about half as long as wide, a feature which is unique in the family. As we can find no trace of longitudinal sutures on the abdominal sternites we place both species in the subfamily *Belostomatinae*, in which the only described Jurassic genera are *Mesonepa* Handl., *Nepidium* Westw., *Megalocoris* Bode and also Cretaceous *Lethopterus* Yu. Pop. We erect new genera for both of species now before us.

## Genus *Lethonectes* n. gen.

Type species. *Lethonectes naucoroides* n.sp..

Diagnosis. Small *Belostomatidae* with scutellum more than twice as broad as long; costal fracture level with apex of clavus.

Name. derived from "*lethos*" (Greek), death and "*nectos*" (Greek), swimmer.

Description. Small belostomatids, less than 13 mm long; form elongate-oval. Head small, much narrower than pronotum. Pronotum broadly transverse, more than 2.5 times as wide as long, without transverse suture. Scutellum broad, more than twice as wide as long and with distinct transverse suture. Forewing with very short, oblique costal fracture at level of apex of clavus; corium clearly differentiated from membrane. Clavus broad, with two longitudinal veins. Claval commissure rather short, equal in length to scutellum. Membrane covered with finely reticulate venation except for very narrow peripheral membrane. Abdomen without longitudinal ventral sutures. Respiratory straps rather short.

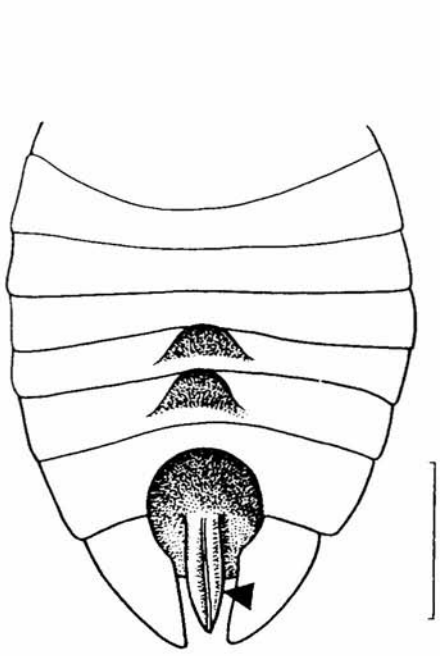
Discussion. This genus contains one of the smallest *Belostomatidae* known; few modern species are small or even smaller. The broad scutellum is a feature unique to this genus and suggests that the earliest belostomatids may have resembled *Naucoridae*. The costal fracture is situated more distally than in *Belostomatidae* known to us. The small head and the presence of a breathing siphon nevertheless unequivocally place this genus in *Belostomatidae*. The small size and the very short pronotum lacking a transverse suture ally it with the Late Jurassic *Nepidium stolones* Westw., which was erroneously placed by one of us in *Notonectidae* (Popov, 1971). The more broadly oval body and even shorter pronotum of *Nepidium* distinguish it from *Lethonectes*. Still greater differences exist between the new genus and the well known belostomatid *Mesonepa primordialis* (Germ.) from the Upper Jurassic of Solnhofen (Germany).

*Lethonectes* differs from it in its more transverse, unsculptured pronotum and scutellum, the absence of a transverse pronotal suture, the lack of obvious venation on the corium, its less elongated and rather naucorid-like body and, finally, the smaller size (*Mesonepa* is 2.5 to 3 times as long). However, the two genera are similar in that the claval commissure is of the same length as the scutellum in both. The new genus also well differs from the other genus *Lethopterus*, described from the Lower Cretaceous of Central Mongolia (Popov, 1989a), by incomplete venation of forewing and much smaller size.

### *Lethonectes naucoroides* n. sp.

(Figs. 28-33)

"*Mesonepa* species 7A" Whalley, 1985: 146.



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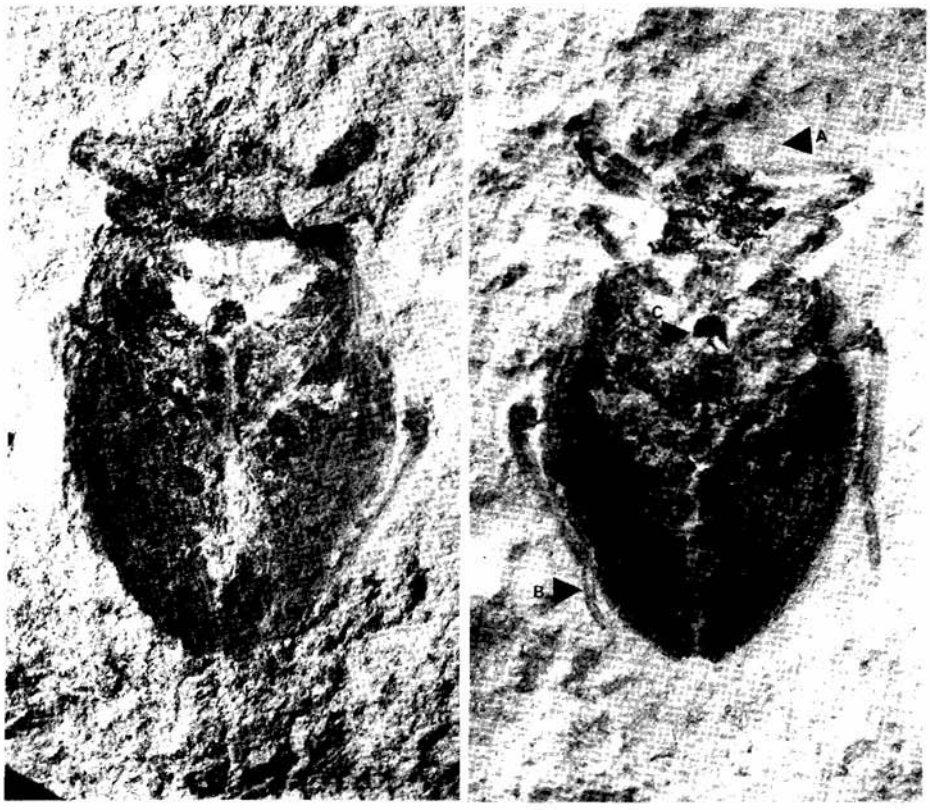
32-33. *Lethonectes naucoroides* gen. et sp. n. Paratype, In. 51014, length 11.6 mm (x 11.2),
33. interpretation of abdomen; respiratory straps arrowed, scale bar = 2 mm

DIAGNOSIS. As genus; the only species.

NAME. Denotes superficial resemblance to the water bug *Naucoris*.

DESCRIPTION. Pronotum with two large, pale lateral spots (Fig. 28), perhaps indicating position of dorsoventral indirect flight muscles or anterior coxal cavities. Anterior and posterior margins of pronotum concave. Scutellum with apex rounded. Clavus with $A_1$ about twice as remote from posterior margin as from anterior margin. Apex of corium with trace of mottled pattern. Length, 12.0 mm; width, 6.6-7.0 mm. Pronotum length, 2.0 mm; width, 6.8-7.0 mm. Scutellum length, 2.0-2.2 mm; width, 4.2-4.4 mm. Forewing length, 9.4-10.0 mm. Claval commissure, 2.2 mm.

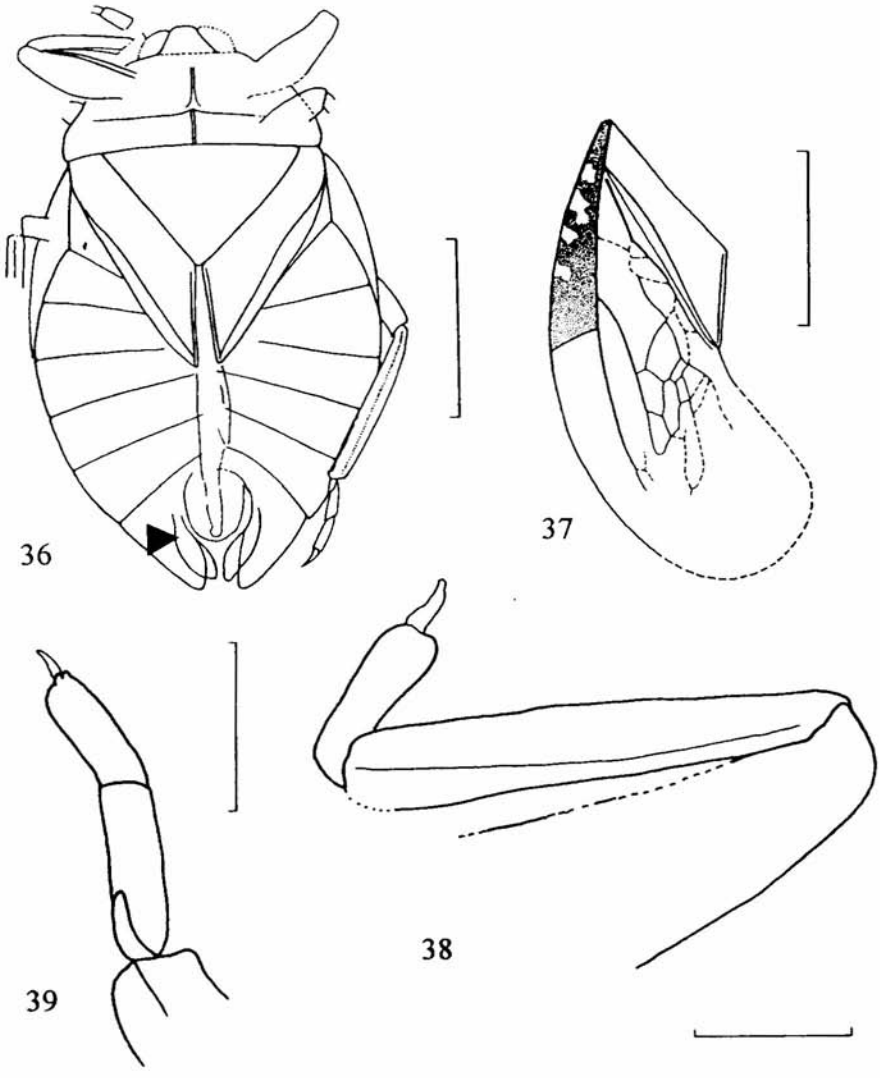
HOLOTYPE. (Figs. 28-31). In.49615. The Flatstones, Stonebarrow, Charmouth, Dorset; Lower Lias; JACKSON coll.; part and counterpart.Dimensions: 12.5 x 6.8 mm. Length of pronotum, 2.2 mm; width, 5.8 mm. Length of scutellum, 1.8 mm; width, 3.7 mm. Length of forewing, 10.1 mm. Length of claval commissure, 2.4 mm.




34 35

34-35. *Tarsabedus menkei* gen. et sp. n. Holotype, BRSMG Cc688, length 33 mm (x 3.6), 35. counterpart ; arrows: A = anterior tarsus (see Fig. 38), b = posterior tarsus (see Fig. 39), C = crystalline body, probably stomach contents (x 3.6)

PARATYPES. (Figs. 32-33). In.51014 and In.59383 (part and counterpart); data of both as holotype. Dimensions: 12.3 x 7.3 mm. Pronotum, 2.4 x 5.9 mm. Scutellum, 2.0 x 3.8 mm. Forewing, 10.8 mm. Claval commissure, 2.8.




36-39. *Tarsabedus menkei* gen. et sp. n. Holotype, BRSMG Cc688: 36. Respiratory straps arrowed; 37. Detail of forewing, scale bar = 10 mm, 38. Detail of foreleg; 39. Detail of posterior tarsus, scale bar = 2 mm

## Genus *Tarsabedus* n. gen.

TYPE SPECIES. *Tarsabedus menkei* n.sp., Lower Lias, U.K.

DIAGNOSIS. *Belostomatidae* retaining mobility at articulation of anterior tibia and tarsus; claval commissure shorter than scutellum.

NAME. Derived from "*tarsus*" (Lat.) and *Abedus*, a genus of extant *Belostomatidae*.

DESCRIPTION. Medium-sized *Belostomatidae* of oval outline. Head small, much narrower than pronotum. Pronotum broadly transverse, about three times as wide as long, with transverse suture dividing it into anterior and posterior lobes. Scutellum short and broad, more than 1.5 times as wide as long and 1.2 times as long as claval commissure. Corium not clearly differentiated from membrane; costal fracture slightly basad of level of clavus apex; venation in greater part of corium somewhat reticulate (Fig. 37). R long, parallel with costal margin. Clavus broad, with two longitudinal veins; claval commissure short. Anterior tibia (Fig. 38) gradually widening towards apex, anterior tarsus (Fig. 38) capable of dorsad flexure at tibio-tarsal articulation, perhaps 2-segmented, claws stout, curved. Posterior tarsus (Fig. 39) three-segmented, first segment very short with dorsal surface greatly reduced, second segment the longest, claws stout, curved. Straps of respiratory siphon short, broad.

DISCUSSION. We consider it necessary to erect a new genus for this species because of the mobility of the anterior tarsus. We know of no other *Belostomatidae* with this feature. It indicates that *Tarsabedus* represents a stage in the evolution of the family where reduced mobility at the anterior tibio-tarsal articulation had not been acquired. The very short claval commissure of *Tarsabedus* approaches the relative length of the longest commissures found among modern naucoroids (*Potamocoridae* and *Aphelocheiridae*); we know of no other belostomatids with the claval commissure shorter than scutellum.

### *Tarsabedus menkei* n. sp.

(Figs. 34-39)

"Gen. et sp. nov. 8A" WHALLEY, 1985: 146; 144, fig. 42.

DIAGNOSIS. As genus; the only species.

NAME. Named after the wellknown American entomologist Arnold MENKE, who made a great contribution to the study of belostomatid bugs.

DESCRIPTION. As genus. Exocorium with marbled pattern of pigmentation (Fig. 37).

HOLOTYPE. BRSMG Cc 688 (Fig. 34-39; figured by WHALLEY, 1985: 144, fig. 42); 1/4 mile (0.6 km) east Charmouth, Dorset; Lower Lias; I.S. LOWPEKINE coll.; Sinemurian, *Asteroceras obtusum* zone; part and counterpart. In City of Bristol Museum and Art Gallery. Dimensions: Length, 33 mm; greatest width, 20 mm. Pronotum length, 5.0 mm; width, 15 mm. Forewing length, 26 mm; width, 15 mm.

Anterior tibia: length, 6.75 mm, greatest width (at apex), 1.25 mm. Anterior tarsus: length, 1.5 mm; width, 0.70 mm; claw length, 0.80 mm. Posterior tibia: length, 10.8 mm; width, 2.0 mm. Posterior tarsus: length of segment 1, 1.0 mm; length of segment 2, 2.2 mm; length of segment 3, 2.0 mm; length of claws, 1.3 mm; width of segment 2, 0.80 mm; width of segment 3, 0.72 mm.

NOTE. The nodule containing the type-specimen also contained a specimen of the ammonite *Promicroceras planicosta* (J. SOWERBY)

ACKNOWLEDGEMENTS

We are very indebted to Dr.D.E. SHCHERBAKOV (Paleontological Institute, Russian Academy of Sciences, Moscow) for providing critical review of the manuscript, which helped to make significant improvements in the final version and Dr. Grzegorz GABRYŚ, Wrocław, for his invaluable comments on the manuscript and his kind support in the matter of publication of it in this Journal.

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