Acta zoologica cracoviensia, **46**(suppl.– Fossil Insects): 311-318, Kraków, 15 Oct., 2003

Taphonomy and ecology of Purbeck fossil insects

Robert A. CORAM

Received: 10 Feb., 2002
Accepted for publication: 15 March, 2002

A. CORAM R. 2003. Taphonomy and ecology of Purbeck fossil insects. *Acta zoologica cracoviensia*, **46**(suppl.– Fossil Insects): 311-318.

Abstract. The basal Cretaceous Purbeck Limestone Group of southern England yields many fossil insects and study of their taphonomy allows a preliminary reconstruction of their life habitats. The aquatic fauna comprises a low diversity brackish water assemblage as well as transported remains of probably fresher water taxa. The terrestrial fauna comprises largely woodland inhabitants that generally became disarticulated prior to arrival at the site of deposition.

Key words: fossil insects, taphonomy, palaeoecology, Lower Cretaceous, southern England.

Robert A. CORAM, 6 Battlemead, Swanage, Dorset BH19 1PH and PRIS, The University, Reading, UK.
E-mail: rob@britishfossils.co.uk

I. INTRODUCTION AND GEOLOGICAL BACKGROUND

The Purbeck Limestone Group, best exposed in Dorset, southern England, consists mainly of lagoonal sediments currently considered to be basal Cretaceous (Berriasian) in age (ALLEN & WIMBLEDON 1991). Fossil insects are found at many horizons and can be very abundant, occurring in their hundreds on some bedding planes. They can be found at many coastal and inland quarry localities in Dorset, but the majority have come from the Purbeck type section at Durlston Bay, near Swanage (National Grid Reference SZ 035 780), which is still productive (Fig. 1). Seventeen orders of Purbeck insects have been recognised and about 200 species have been described, although a far greater number await description (CORAM & JARZEMBOWSKI 2002). This paper is a preliminary attempt to divide the Purbeck insect fauna into broad environmental categories on the basis of their taphonomy and to make some taphonomic comparisons with other deposits of similar age.

The Purbeck Limestone Group is divided into a lower Lulworth and upper Durlston formations. It is underlain by limestones of the Tithonian (Upper Jurassic) Portland Limestone Group containing a normal marine fauna, including giant ammonites, and is succeeded by non-marine, predominantly fluvial, deposits of the Wealden Group extending to the Upper Barremian/ earliest Aptian. These are also insectiferous (JARZEMBOWSKI 1984), providing the opportunity to track changes in the insect fauna through much of the Lower Cretaceous in southern England.

The Purbeck landscape was very flat, with distant massifs to the west, south and northeast. The lagoonal waters were probably never more than a few metres deep, and ranged in salinity from

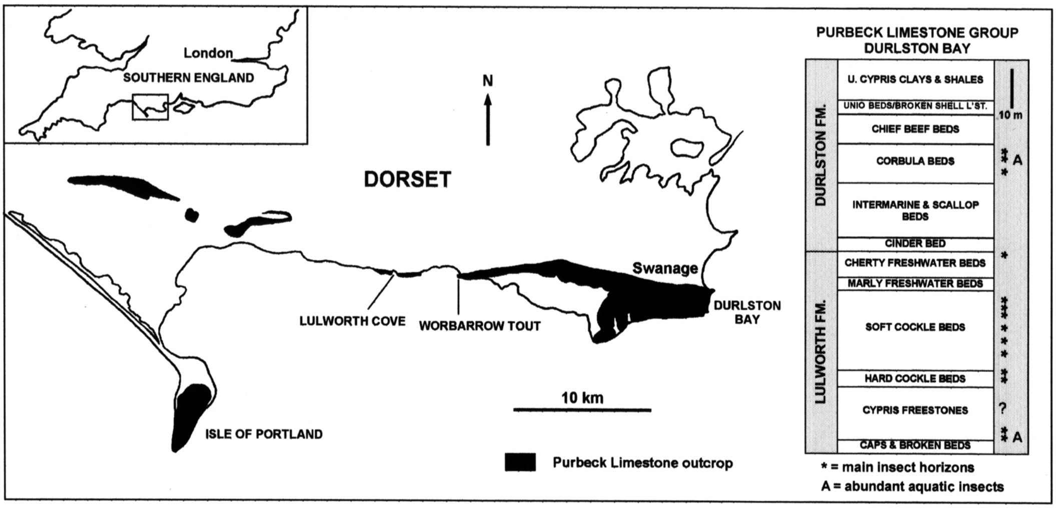

Fig. 1. Purbeck Limestone outcrop in Dorset, Southern England with distribution of insect horizons at Durlston Bay.

fresh, through brackish and near-marine, to hypersaline. The climate is interpreted to have been seasonally semi-arid (ALLEN 1998), although there is evidence that it became rather more humid in the Durlston Formation: evaporites are much less frequent and there is a sustained increase in the clay mineral kaolinite (DECONINCK 1987), indicative of more intense weathering of the massifs supplying sediment to the basin. The insect fauna appears to support this climate change; for example, Recent empidid Diptera prefer moister environments and their proportional abundance in the brachyceran fly fauna increases in the Durlston Formation (CORAM et al. 2000).

Purbeck insect remains are found in fissile carbonates deposited in an 'intertidal/ supratidal' setting (the Purbeck probably did not experience true semi-diurnal tides, being only intermittently connected to the open sea; the 'tides' were wind or storm generated). In the Lulworth Formation such sediments often occur within evaporitic sabkha sequences such as are seen, for example, along parts of the Persian Gulf today and halite moulds are often found alongside the insect remains. The generally more hospitable fresh-brackish water conditions of the Durlston Formation allowed bivalves to thrive, with the consequent development of numerous shell limestone beds, including high intertidal-supratidal shell beaches (EL-SHAHAT & WEST 1983). In parts of the Durlston Formation such limestones are associated with insectiferous algal micrites which, being mainly lenticular, were probably mostly deposited in pools (ranging in size from metres to kilometres across) isolated from the main body of the lagoon.

A c k n o w l e d g e m e n t s. This is PRIS contribution No. 838.

II. PURBECK INSECT TAPHONOMY

A wide range of preservation is seen among Purbeck insects, ranging from completely intact to totally disarticulated (and often fragmentary) wings and sclerites (Figs 2 and 3). Study of the factors influencing the disarticulation of these insect remains is likely to provide information regarding the original provenance and life habitats of the various insect taxa.

Disarticulation of dead insects results from a combination of bacterially mediated decay processes (influenced by factors such as temperature and availability of oxygen) and mechanical de-

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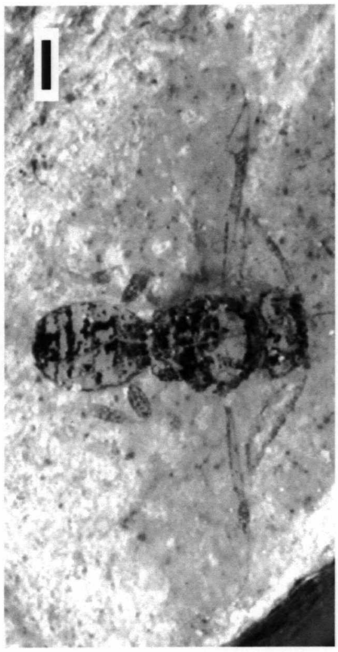

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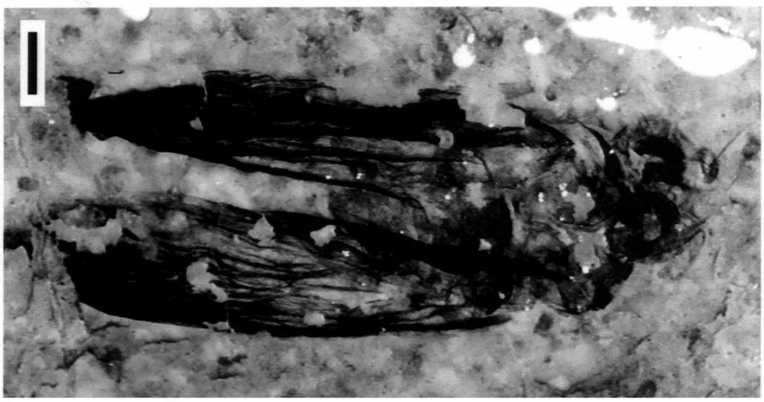

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Fig. 2. Massed beetle elytra, Lulworth Formation (Soft Cockle beds), Worbarrow Tout, Dorset; Maidstone Museum and Bentlif Art Gallery No. MNEMG 1999.32. Scale bar = 1.0 mm. Fig. 3. Whole wasp, Durlston Formation (Corbula beds), Durlston Bay, Dorset; MNEMG 2002.5. Scale bar = 0.5 mm. Fig. 4. Newly emerged caddis fly, Durlston Formation (Corbula beds), Durlston Bay, Dorset; MNEMG 2003.6. Scale bare = 0.5 mm.

struction, which can be physical in origin (e.g. transport) or biological (e.g. predation or bioturbation). The amount of disarticulation that occurs will generally be positively linked to the time available for these processes to operate between death and burial. There are also three basic sites at which disarticulation can occur: on the land, on the water surface and on (or in) the submerged sediment. Following death time will be spent in differing proportions at some or all of these sites, depending largely on the original life habitats of the insects.

Fig. 5 shows how the different insect orders are represented in terms of preserved number of fossils. The data is taken from a sample of 2600 specimens from the Corbula beds in the Durlston Formation of Durlston Bay. It is divided into terrestrial and aquatic components; the former is fairly typical for the Purbeck in general, the latter, comprising mostly well-preserved remains of few species, is only found in abundance at a limited number of horizons (see Fig. 1). Terrestrial and aquatic Coleoptera (beetles) have not been separated since it is often difficult to establish original mode of life from isolated elytra and some Purbeck beetle families (e.g. the abundant Hydrophilidae) today include both terrestrial and aquatic taxa. The terrestrial insect remains have been subdivided into those that still show some articulation (ranging from completely entire, e.g. wasp in Fig. 3, to associated portions, e.g. wings attached to isolated thoraxes) and those that are totally disarticulated, i.e. isolated wings or elytra (other sclerites are ignored due to the difficulty of assigning them to insect orders). The disarticulated component of Thysanoptera (thrips) is an estimate only because their detached wings are particularly small and indistinct, and hence easily overlooked.

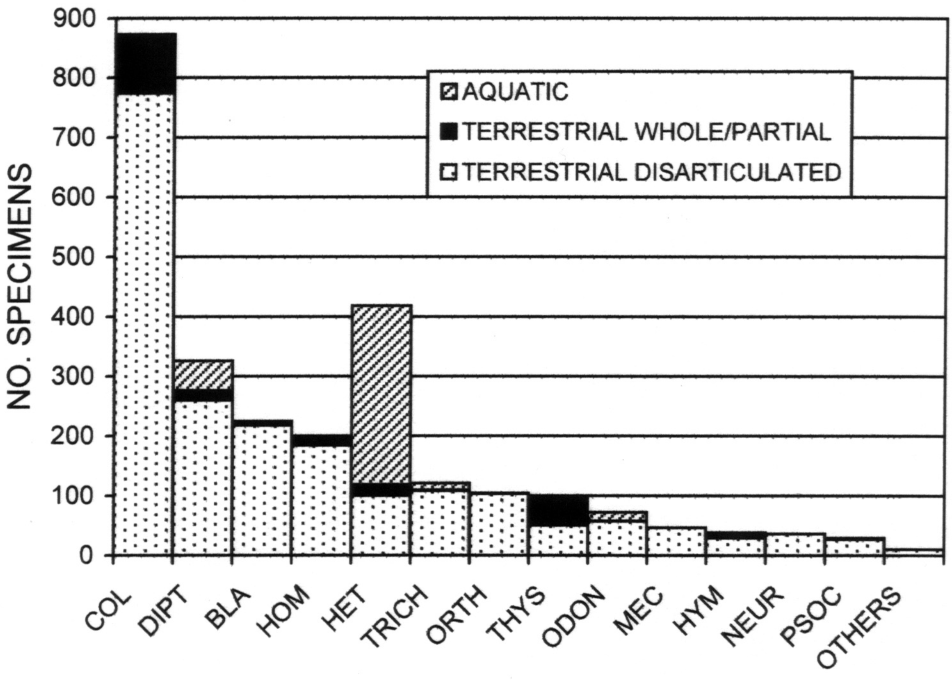

Fig. 5. Ordinal representation of insect fossils in the Corbula beds (Durlston Formation) at Durlston Bay.

It can be seen that in terms of number of preserved specimens Coleoptera are most abundant, followed by Heteroptera (including aquatic) and Diptera. Preserved abundance does not, of course, necessarily equate with live abundance due to the multitude of taphonomic influences on the insects between death and fossilisation. Thus the numerical dominance of beetle remains could be a consequence of the sturdiness and transportability of their elytra rather than an actual living preponderance in the local environment. Additionally, the abundance of remains from a particular order need not relate to their diversity. The abundant aquatic Heteroptera, for example, are vastly dominated by a single species (see below), whereas the relatively uncommon Hymenoptera (wasps) are nevertheless of high diversity, approximately 30 species being represented in the sample.

III. AQUATIC INSECTS

An important determinant of degree of disarticulation is whether fossil insects are aquatic or terrestrial. In the absence of transport aquatic insects have a better chance of being preserved entire since they are less likely to spend time decaying and disarticulating on the land or water surface. Aquatic insect remains are found throughout the insectiferous Purbeck and show a whole range of preservation from intact with no discernible damage to disarticulated fragments, almost certainly reflecting a spectrum of taphonomic histories.

Well-preserved aquatic insects are found mainly near the base of the Lulworth Formation (Cypris Freestones) and in the Durlston Formation (Corbula beds) – see Fig. 1. The fauna comprises abundant nymphs and winged adults of *Nepidium stolones* WESTWOOD 1854, a heteropteran bug of uncertain affinities (POPOV et al. 1999), dipteran (chironomid) pupae, newly emerged adult trichopterans (caddis flies) sometimes still associated with their pupal cases (Fig. 4), and occasional odonate (dragonfly) nymphs. The generally good preservation suggests little or no transport and that the insects are therefore probably autochthonous, or nearly so. The *Nepidium* bugs are additionally very common and represented by several life-stages.

These insects are interpreted as brackish water inhabitants because they are of low diversity and found alongside organisms such as the still-extant gastropod *Hydrobia* indicative of brackish conditions (CORAM & JARZEMBOWSKI 2002). Other uncommon whole aquatic insects found in the same deposits, including small coptoclavid beetles (PONOMARENKO et al. 2000), are not represented by immature stages. It is likely that rather than being components of this brackish fauna, these were merely occasional visitors to the water bodies (in which they may not have survived long).

Various other aquatic insects are known only from generally uncommon disarticulated remains that are, however, relatively diverse and include a number of taxa, e.g. several Coleoptera (hydrophilids, gyrinids, dytiscids), Heteroptera (belostomatids, gerrids) and Ephemeroptera, not known from better preserved material. These insects are almost certainly allochthonous, especially in view of the fact that their remains occur even in evaporite-bearing beds in the Lulworth Formation deposited in hypersaline conditions unsuitable for most or all aquatic insects. On the basis of their fairly high diversity and the salinity preferences of Recent representatives they are interpreted as inhabitants of relatively fresh water that were transported to the brackish or hypersaline deposits in which they were buried. Their remains, as well as those of adult insects (e.g. chaoborid and ptychopterid flies) known to have aquatic pre-imaginal stages, indicate that even during periods of maximum aridity there were still low salinity water bodies in the region.

It is interesting to note that this presumed low salinity aquatic insect fauna is not known preserved *in situ*. A number of fresh or near-fresh Purbeck deposits occur in the upper part of the Lulworth Formation and in the Durlston Formation and have yielded a diverse freshwater biota including viviparid snails, charophytes and even amphibians, but no insects. The main reason for this seems to be that the fresher water conditions were more conducive to predators, scavengers and bioturbating organisms that consumed or destroyed insects before they could be preserved. The abundance of shells and burrows in these deposits also tends to obscure the good bedding surfaces required for recognising insect fossils. Study of the taphonomy of Purbeck insect fossils combined with geological evidence and knowledge of Recent insect lifestyles therefore allows some reconstruction of different Purbeck insect habitats (Fig. 6).

In general, therefore, Purbeck are found only in deposits in which brackish, hypersaline or rapidly fluctuating salinities suppressed benthic biota. Worldwide, a number of fresh or near-fresh Lower Cretaceous deposits do yield insect fossils and in these cases the benthos was restricted by other factors, such as a deeper, stratified water column leading to anoxic bottom conditions, as suggested, e.g., for Montsec, Spain (GIBERT et al. 2000) and Baissa, Transbaikalia (ZHERIKHIN et al. 1999).

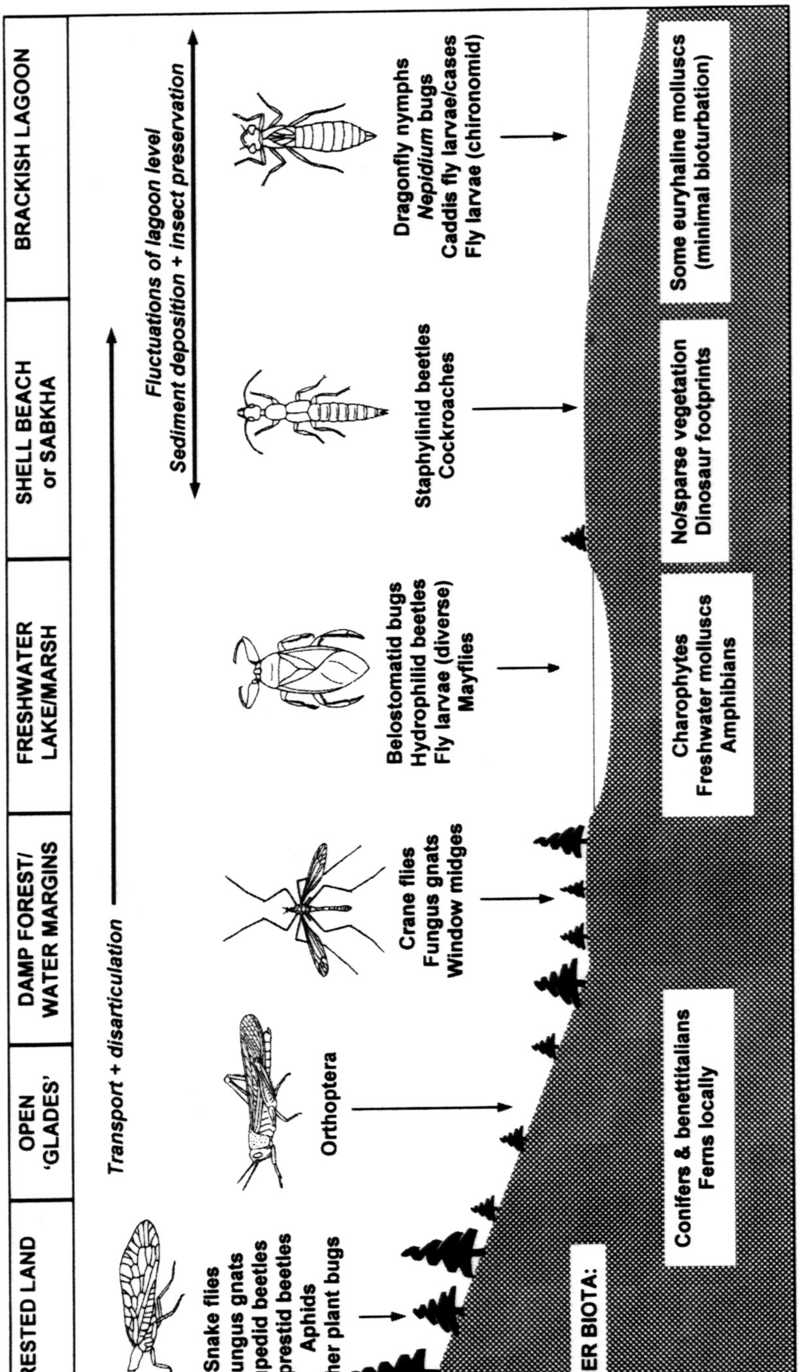

Fig. 6. Inferred life habitats of various Purbeck insects.

IV. TERRESTRIAL INSECTS

Purbeck terrestrial vegetation was relatively undiverse, comprising conifer trees (predominantly one species), with less common bennettitaleans, ferns and lycopods (FRANCIS 1984). The overall character of the terrestrial insect fauna, based on the preferred habits of Recent relatives, suggests a wooded habitat, including, for example, xylophagous cupedid beetles, herbivorous fulguroid bugs (planthoppers), and predatory Raphidioptera (snake flies). The occurrence of fine charcoal in the insect beds (particularly in the Lulworth Formation) attests to frequent forest fires. The presence of woodland insects preferring moist conditions (e.g. Mycetophilids – 'fungus gnats') indicates that there were also areas of damper woodland, perhaps bordering fresh water bodies. More open habitats are suggested by relatively frequent Orthoptera (crickets, etc.).

It can be seen from Fig. 5 that terrestrial Purbeck insect remains are virtually all disarticulated. This contrasts with a number of lacustrine deposits of similar age in which a higher proportion of the terrestrial insects are preserved whole. These fossil lakes are often reported to have had vegetated margins that would have been good insect habitats, e.g. Baissa (ZHERIKHIN et al. 1999) and Crato, Brazil (GRIMALDI & MAISEY 1990). Thus dead terrestrial insects would often not have travelled far to the depositional site, and indeed many insects may have flown or jumped directly into the water and hence spent no time decaying on land.

Since Purbeck aquatic insects are often well preserved, it is likely that most disarticulation of terrestrial remains occurred on the land or water surface. Although remains of trees are found *in situ* in the basal Purbeck (not in association with insect fossils), the water bodies in which the insects were preserved were typically bordered by barren sabkhas or shell beaches; the nearest vegetated land suitable for supporting insects in large numbers was often many kilometres away. Most dead terrestrial insects are likely to have undergone a period of decay and disarticulation on the sabkhas/beaches before being washed into pools or collected up by rising lagoon waters.

Further disarticulation probably occurred on the water surface. In laboratory experiments dead insects will usually float for many weeks or months before settling through the water column (DUNCAN 1997) and inevitably some disarticulation occurs in this time. For insects to be preserved whole they therefore need to break through the surface tension of the water relatively soon after arrival. Larger live insects can achieve this through their own struggles (MARTÍNEZ-DELCLÓS & MARTINELL 1990); dead floating insects require some sort of physical disturbance, such as rainfall. The Purbeck climate was semi-arid, almost certainly with long periods of no rainfall, especially during deposition of the Lulworth Formation hypersaline beds in which insect remains are particularly highly disarticulated. The often high salinity of the water is likely to have been an additional factor; being denser this would have rendered insect remains even less liable to settling. Finally, since the Purbeck water bodies were invariably shallow and often relatively small, floating insects would have been subjected to destructive processes such as wave action at the strandline, which probably at least partly explains why terrestrial insects are often more completely preserved in deeper-water offshore lacustrine settings (WILSON 1980).

Other well-preserved Purbeck terrestrial insects, rather than living in the comparatively distant woodland may instead have lived on the sparsely vegetated lagoon margins themselves, and hence undergone little transport prior to fossilisation. For example, staphylinid beetles, although relatively uncommon, are more often preserved whole than other terrestrial beetle taxa. By analogy with some modern staphylinids, these Purbeck examples may well have been shoreline scavengers/predators. The occasional whole or near-whole Purbeck blattids (cockroaches) may have had a similar lifestyle.

The terrestrial insect fossils of the succeeding Wealden, mainly found in southeast England, are similarly mostly disarticulated. They, too, may have usually spent time decaying on land (on river floodplains rather than beaches/flats), although much fragmentation is also likely to have occurred during river transport, and their remains are often found concentrated in fluvial scour-fills (JARZEMBOWSKI 1984). River activity was, in contrast, much more limited in the Purbeck.

REFERENCES

ALLEN P. 1998. Purbeck-Wealden (early Cretaceous) climates. *Proceedings of the Geologists' Association*, **109**: 197-236.

ALLEN P., WIMBLEDON W. A. 1991. Correlation of NW European Purbeck-Wealden (nonmarine Lower Cretaceous) as seen from the English type-areas. *Cretaceous Research*, **12**: 511-526.

CORAM R., JARZEMBOWSKI E. A., MOSTOVSKI M. B. 2000. Two Rare Eremoneuran Flies (Diptera: Empididae and Opetiidae) from the Purbeck Limestone Group. *Paleontological Journal*, **34** (Suppl. 3): S370-S373.

CORAM R., JARZEMBOWSKI E. A. 2002. Diversity and ecology of fossil insects in the Dorset Purbeck succession, southern England. [In:] A. R. MILNER, D. J. BATTEN (eds) – Life and environments In Purbeck times. *Special papers in Palaeontology*, **68**: 257-268.

DECONINCK J. F. 1987. Minéraux argileux des faciès Purbeckiens: Jura suisse et français, Dorset (Angleterre) et Boulonnais (France). *Annales de la Societé Géologique du Nord*, **106**: 285-297.

DUNCAN I. J. 1997. The taphonomy of insects. Unpublished PhD thesis, University of Bristol. 324 pp.

EL-SHAHAT A., WEST I. M. 1983. Early and late lithification of aragonitic bivalve beds in the Purbeck Formation (Upper Jurassic - Lower Cretaceous) of southern England. *Sedimentary Geology*, **35**: 15-41.

FRANCIS J. E. 1984. The seasonal environment of the Purbeck (Upper Jurassic) fossil forests. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **48**: 258-307.

GIBERT J. M. DE, FRENEGAL-MARTINEZ M. A., BUATOIS L. A., MÁNGANO M. G. 2000. Trace fossils and their palaeoecological significance in Lower Cretaceous lacustrine conservation deposits, El Montsec, Spain. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **156**: 89-101.

GRIMALDI D., MAISEY J. 1990. Introduction. [In:] D. A. GRIMALDI (ed.) – Insects from the Santana Formation, Lower Cretaceous, of Brazil. *Bulletin of the American Museum of Natural History*, **195**: 5-15.

JARZEMBOWSKI E. A. 1984. Early Cretaceous insects from southern England. *Modern Geology*, **9**: 71-93, pls I-IV.

MARTÍNEZ-DELCLÓS X., MARTINELL J. 1990. Insect taphonomy experiments. Their application to the Cretaceous outcrops of Lithographic Limestones from Spain. *Kaupia,* **2**: 133-144.

PONOMARENKO A. G., CORAM R., JARZEMBOWSKI E. A. 2000. Fossil beetles (Insecta: Coleoptera) from the Purbeck Limestone Group of Dorset - a Preliminary Report. *Proceedings of the Dorset Natural History and Archaeological Society*, **121** (for 1999): 107-112.

POPOV YU. A., CORAM, R., JARZEMBOWSKI, E. A. 1999. Fossil heteropteran bugs from the Purbeck Limestone Group of Dorset. *Proceedings of the Dorset Natural History and Archaeological Society*, (1998) **120**: 73-76.

WILSON M. 1980. Eocene lake environments: depth and distance-from-shore variation in fish, insect, and plant assemblages.

ZHERIKHIN, V. V., MOSTOVSKI, M. B., VRSANSKY, P., BLAGODEROV V. A., LUKASHEVICH E. D. 1999. The unique Lower Cretaceous locality Baissa and other contemporaneous fossil insect sites in North and West Transbaikalia. Proceedings of the First International Palaeoentomological Conference, Moscow 1998: 185-191.