

The Crustacea of the Insect Bed (latest Eocene) of the Isle of Wight, England, including the first spinicaudatan (clam shrimp) from the British Cenozoic

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ABSTRACT: The crustacean fauna of the Insect Bed (late Eocene), Isle of Wight is reviewed. The fauna comprises the branchiopod *Branchipodites vectensis* Woodward, 1879, ostracod *Potamocypris brodiei* Jones and Sherborn, 1889, and isopod *Eosphaeroma margarum* (Desmarest, 1822). In addition a new clam shrimp (Crustacea: Diplostraca: Spinicaudata) is described and named *Paraleptestheria mitchelli* sp. nov. This is the first record of the genus outside China and the first ‘conchostracan’ to be described from the European Cenozoic.

KEY WORDS: Anostraca, Arthropoda, Cenozoic palaeoenvironment, ‘Conchostraca’, Eocene-Oligocene, Isopoda, United Kingdom.

The Bembridge Marls Insect Bed crustacean fauna includes branchiopods (Anostraca, a fairy shrimp; and Spinicaudata, a clam shrimp), an ostracod (seed shrimp) and an isopod (relative of the woodlouse/sea slater); all except the first are scarce (Jarzembowski 1980). The fairy shrimp is the extinct branchiopod, *Branchipodites vectensis* Woodward, 1879 and abundant, complete examples of this crustacean are often associated with articulated insect bodies, but such rich layers appear to be very local (Jarzembowski 1976; Rogers 2009, 2013). The Insect Bed ostracod, *Potamocypris brodiei* Jones & Sherborn, 1889, has been compared more recently with another fresh water-brackish cypridid (*Cypridopsis* Brady: Haskins, 1968) and occasional ostracod valves may be found in silty laminae within the limestone (Jarzembowski 1980). In our opinion, Haskins’s ostracod does not resemble *P. brodiei* so it is not revised. The extinct, sphaeromid-like *Eosphaeroma margarum* (Desmarest in Brongniart & Desmarest, 1822) is a fresh water-brackish isopod also known from the continental late Palaeogene of France, and Germany (Martini 1972; Basso & Tintori 1995). The spinicaudatan (‘conchostracan’) *Paraleptestheria mitchelli* sp. nov. is described for the first time and is the main focus of the contribution as it is the only ‘Tertiary conchostracan’ (clam shrimp) described from Europe so far.

1. Locality and horizon

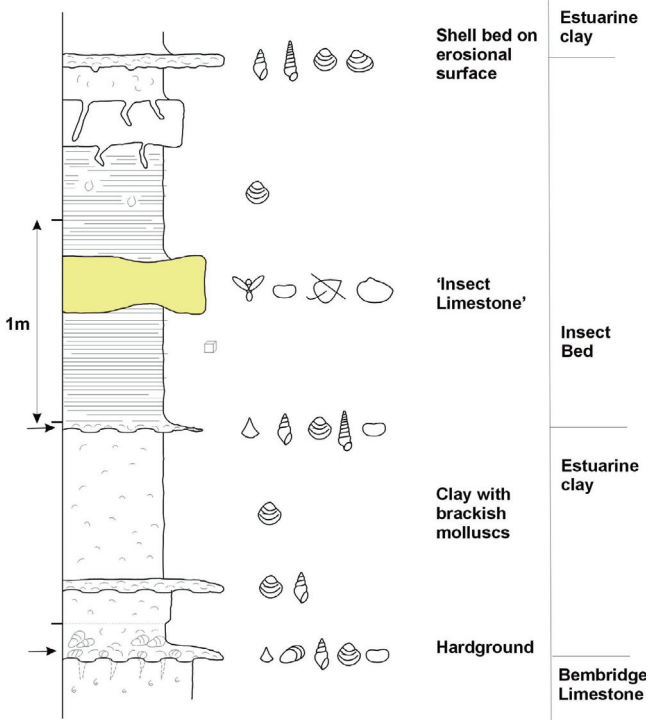
The specimens are from the Insect Bed of the Bembridge Marls Member, which outcrops along the NW and NE coasts



of the Isle of Wight. The Bembridge Marls are the basal member of the Bouldnor Formation and overlie the lacustrine Bembridge Limestone Formation (Daley 1972, 1999). The marls are an argillaceous sequence of muds and silts with occasional thin sands and limestones deposited in brackish to fresh water conditions (Insole *et al.* 1998). The term Insect Bed applies to a thin clay bed, near the base of the formation, with micritic limestones and hard marls under- and overlain by shell beds with a brackish/quasi marine fauna (Jarzembowski 1980; Ross & Self 2014). The micritic limestone (‘Insect Limestone’) occurs either as discrete concretionary lenses or as thin but continuous beds and contains aggregations of fossils including plant detritus, arthropods, molluscs, bird feathers and lizard scales. Fossil insects (Jarzembowski 1980; McCobb *et al.* 1998) and spiders (Selden 2001, 2002) are often found with exceptional three-dimensional preservation. The age of the Insect Bed was reviewed by Ross & Self (2014) and is now considered to be late Eocene.

Although the Insect Bed occurs at a number of exposures, conchostracans have only been found to date at St Helens on the NE coast (see Ross & Self 2014, fig. 1). Here a section of the lower Bembridge Marls, approximately 300 m long, is visible in the low-slipped cliffs between Node’s Point and the ruins of St Helen’s Church (Fig.1). The Insect Bed is approximately 8 m above the base of the cliffs at Node’s Point [national grid reference SZ 638 900] and dips southwards towards the axis of the Bembridge Syncline so that at the southern end [SZ 638 897] it lies 0.5 m above the cliff base

a



b

Symbols for graphic logs:

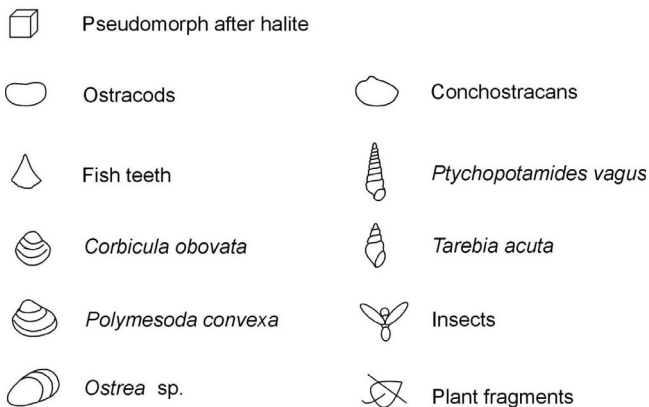


Figure 1 Stratigraphical section of the lower Bembridge Marls, in the low-slopped cliffs between Node's Point and the ruins of St Helen's Church.

(Jarzembowski *et al.* 2010). The Insect Bed here comprises a 0.65–0.85 m thick sequence of finely laminated silts and clays with a single 0.1 m band of micritic limestone. The 'Insect Limestone' is also found as loose blocks on the foreshore. At least six orders of insects are present, including beetles (Coleoptera), true flies (Diptera), ants and wasps (Hymenoptera), bugs (Hemiptera), dragonflies (Odonata) and termites (Isoptera). The insects are predominantly terrestrial and are often accompanied by plant remains, Crustacea and gastropods.

2. Material and methods

The electron microscope images of the uncoated spinicaudatan specimens were taken using a JEOL JSM 5310LV under low vacuum conditions. Elemental analysis was carried out using energy-dispersive X-ray microanalysis with an Oxford Instru-

ments ISIS system possessing a thin window SiLi X-ray detector. Areal distribution of the main components was assessed by X-ray dot mapping. Field numbers are given in parenthesis after museum registration numbers for continuity. The following abbreviations are used: coll., collected by; NHMUK, Natural History Museum London.

The taxonomy adopted herein follows Chen & Shen (1985) and Martin & Davis (2001). The methodology used for the spinicaudatan description follows partially the proposal of Scholze & Schneider (2015).

3. Spinicaudata

'Conchostracans' now formally called spinicaudatans (see Shen 2003; Gallego 2010; Astrop & Hegna 2015) are extant bivalved crustaceans that have inhabited fresh water to brackish environments throughout the Phanerozoic from the late Palaeozoic onwards. According to Gray (1988), spinicaudatans (among other branchiopods) have played an important part in fresh water ecosystems through much of the Phanerozoic. The world record of Cenozoic fossil spinicaudatans is limited to only a few countries: China, with many localities ranging from the late Palaeocene to the early Eocene (Hong *et al.* 1974; Chen 1975; Chen & Shen 1979, 1980, 1981, 1985; Shen & Chen 1979; Shen & Zhang 1979); Mongolia (late Palaeocene to early Eocene: Trusova & Badamgarav 1976); Brazil (Oligocene: Gallego & Mesquita 2000); Argentina (late Palaeocene and Miocene–Pliocene: Gallego & Mesquita 2000; Petrulevicius 2001) and North America (Eocene: Shen *et al.* 2006; early Oligocene: Stigall *et al.* 2017) (see Table 1).

In the present paper, we describe a new species, *Paraleptestheria mitchelli* sp. nov. assigned to the Family Loxomegalyptidae from the Insect Bed (Bembridge Marls), the latest Eocene transition in southern England. This is the first Cenozoic fossil spinicaudatan to be formally described from England and indeed from Europe.

4. Cenozoic 'conchostracan' distribution

In Asia, three Cenozoic 'conchostracan' faunas can be recognised: the *Perilimnadia* fauna, the *Fushunograptia changzhouensis* fauna (Palaeocene) and the *Paraleptestheria menglaensis* fauna (early Eocene) (Zhang *et al.* 1976; Chen & Shen 1981). In North America, Shen *et al.* (2006) reported the presence of *Cyclestherioides wyomingensis* Shen & Gallego (in Shen *et al.* 2006), and *Prolynceus laneyensis* Shen & Gallego (in Shen *et al.* 2006), in the Laney Member (Green River Formation, Wyoming, USA). These represent a new Eocene fauna (the *Cyclestherioides*–*Prolynceus* assemblage) belonging to *Cyclestheriida* and *Laevicaudata* respectively; these species have a close affinity to the extant species of *Cyclestheria* and *Lynceus*.

Recently, Stigall *et al.* (2017) described the first north-american cenozoic spinicaudatan, *Estherites? jocelynae* from Medicine Lodge Formation (early Oligocene, Beaverhead Basin) in southwestern Montana. Also it is the second-youngest fossil clam shrimp described globally, the first record of the genus *Estherites* outside China and finally it extends the range of the superfamily Estheriteoidea into the Paleogene.

In South America there are three 'conchostracan'-bearing formations. *Tremembeglypta saadi* Gallego (in Gallego & Mesquita 2000) has been reported from the Oligocene Tremembé Formation of the Taubaté Group, São Paulo State, Brazil. Petrulevicius (2001) mentioned 'conchostracans' (*Euestheria?*) in the Maíz Gordo Formation (late Paleocene) of Salta Province, Argentina. Neogene 'conchostracans' in the Upper Member of the San Roque Formation from San Luis, Argentina, represent two taxa probably belonging to the

Table 1 Stratigraphical distribution of the Cenozoic ‘conchostracans’ of the world (modified from Shen *et al.* 2006).

Age	China	Mongolia	North America	South America	Europe
PLIOCENE				Fushunograptidae? Loxomegaglytidae?	
MIOCENE	Messinian Tortonian Serravallian Langhian Burdigalian Aquitanian				
OLIGOCENE	Chattian Rupelian		<i>Estherites?</i> <i>jocelynae</i>	<i>Tremembeglypta saadi</i>	
EOCENE	Priabonian Bartonian Lutetian Ypresian	<i>Paraleptestheria menglaensis</i> fauna	<i>Cyclestherioides</i> – <i>Prolynceus</i> assemblage		<i>Paraleptestheria mitchelli</i> sp. nov. <i>Spinicaudata</i> indet.
PALAEOCENE	Thanetian Selandian Danian	<i>Fushunograptia changzhouensis</i> fauna <i>Perilimmadia</i> fauna	<i>Fushunograptia (=Altaestheria)</i> fauna	Euestheriidae?	

Fushunograptidae and Loxomegaglyptidae (Gallego & Mesquita 2000). New geological studies of these lithostratigraphic units tentatively changed previous interpretation on the assignment to the San Roque Formation, but new studies are necessary to obtain more accurate data (Rivarola *et al.* 2016).

In Germany, Middle Eocene juvenile ‘conchostracans’ were identified in fish coprolites from Eocene Lake Messel by Richter & Baszio (2001) and were listed by Wedmann (2005), but have not been formally described.

As far as we know, no definite Quaternary fossil ‘conchostracans’ have yet been reported anywhere in the world.

5. Systematic description

Phylum Arthropoda von Siebold, 1848

Subphylum Crustacea Brünnich, 1772

Class Branchiopoda Latreille, 1817

Subclass Phyllopoda Preuss, 1951

Order Diplostraca Gerstaecker, 1866

Suborder Spinicaudata Linder, 1945

Superfamily Eosestherioidea Zhang & Chen
(in Zhang *et al.* 1976)

Family Loxomegaglyptidae Novojilov, 1958

Genus *Paraleptestheria* Chen (in Zhang *et al.* 1976)

Type species. *Paraleptestheria menglaensis* Chen
(in Zhang *et al.* 1976), from the early Eocene, China.

Paraleptestheria mitchelli nov. sp.
Figs 2–4

‘Clam shrimp (Crustacea, Conchostraca)’ Jarzembowski *et al.* 2010, p. 242, fig. 5.28.

Type specimens. Holotype NHMUK IC.1269 (BLN 4427) Paratypes IC.1270 (BLN 4470), IC.1271 (BLN 4405), IC.1272 (BLN 4401).

Etymology. After Mr A. A. Mitchell (Gillingham) who found this species.

Diagnosis. Carapace oval, large, submedial and supramarginal umbo, maximum height in middle of valve; seven or eight wide and smooth growth lines; broad growth bands ornamented with irregular reticular meshwork; meshes filled with small punctae which in external mould appear as nodular sculpture;

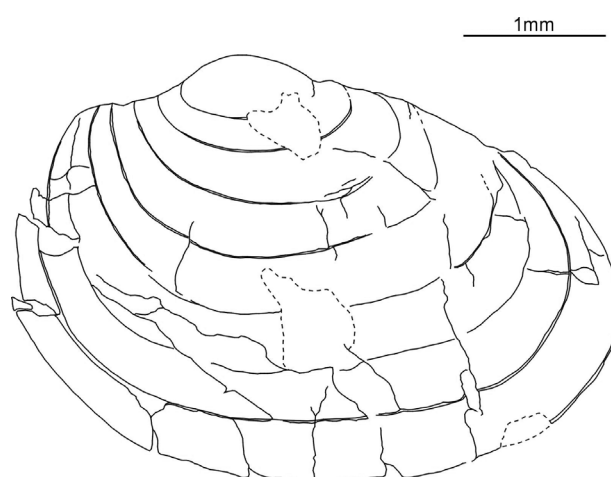


Figure 2 *Paraleptestheria mitchelli* sp. nov. drawing of NHMUK IC.1269 (BLN 4427) (coll. A. Mitchell) (Scale bar = 1 mm).

areolae isodiametric in middle of carapace or elongated antero-posteriorly in ventral area, 0.01–0.05 mm wide.

Occurrence. ‘Insect Limestone’, Insect Bed (late Eocene); St Helens, NE Isle of Wight, National Grid Reference SZ 638898

Description and measurements. Spinicaudata ‘conchostracan’ with large carapace oval in outline (ratio H/L 0.74), strongly convex, up to 4.2 mm long (L) and 3.1 mm high (H). Submedial and supramarginal umbo with elliptical outline. Umbonal area very small. Short dorsal margin (l/L 0.58) slightly convex comprising one third of total length of carapace, slightly sloping in front and behind. Anterior margin less convex and higher than posterior margin. Ventral margin slightly convex. Maximum height in middle part of carapace. Growth lines either seven or eight in number, broad and smooth. Growth bands broad and ornamented with irregular reticular meshwork. Each mesh is 0.01–0.05 mm wide and varies from isodiametrical in the mid carapace to elongated antero-posteriorly in ventral area and is filled with small punctae, which in external mould appear as a nodular sculpture.

Remarks. The type species *Paraleptestheria menglaensis* Chen (in Zhang *et al.* 1976, pl. 37, figs 1–8) differs from the new species in its oval outline, long and straight dorsal margin, small anterior umbo, greater anterior height, posterior margin contracted and 10–16 growth bands with large, horizontal, polygonal ornamentation (polygons 0.05–0.75 mm

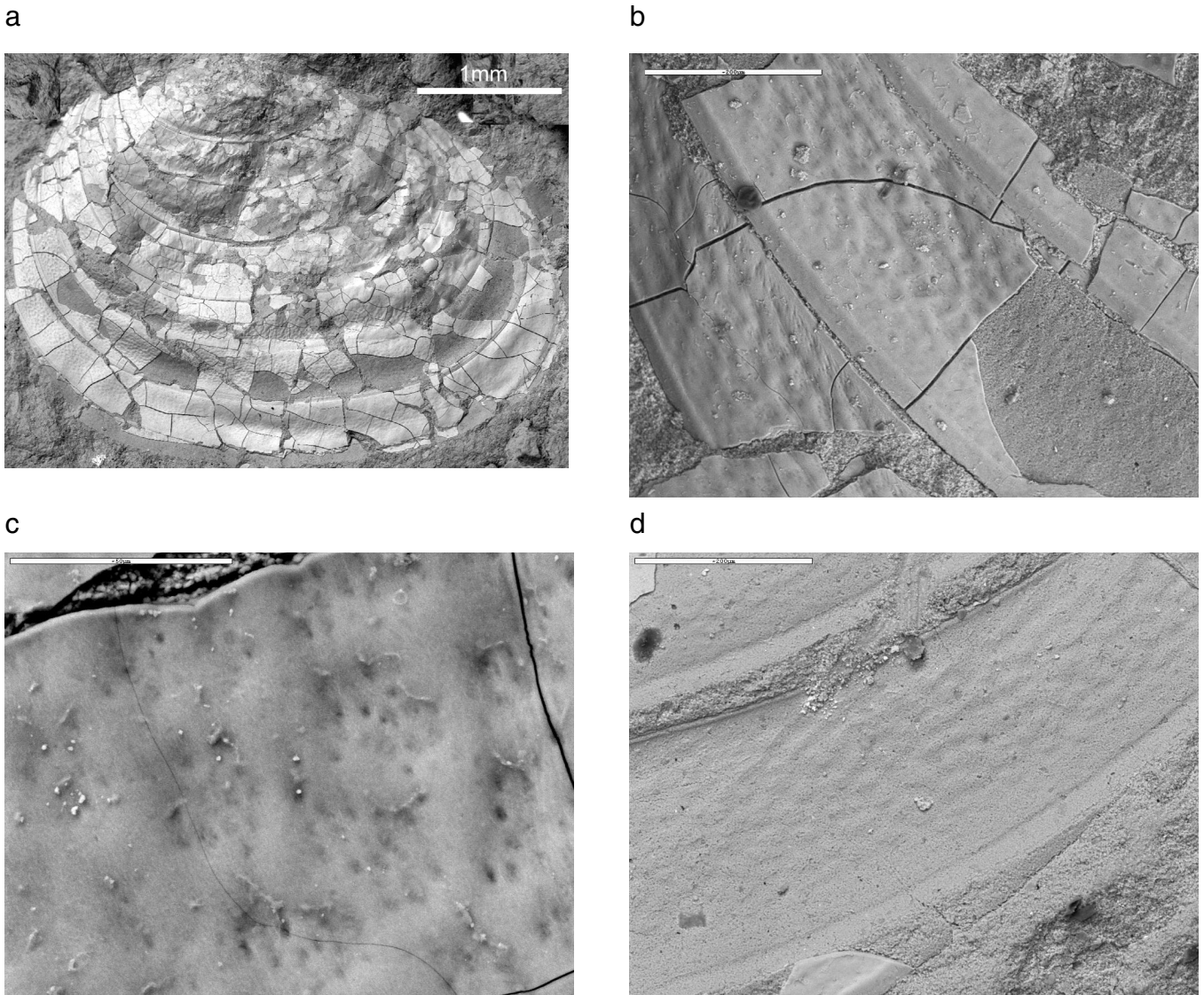


Figure 3 *Paraleptestheria mitchelli* sp. nov., SEM photographs NHMUK IC.1269 (BLN 4427) montage + 2 close-ups, IC.1271 (BLN 4401) matrix impression. (a) General ovate outline, subcentral umbo, few growth lines and irregular meshwork ornamentation pattern, SEM image (Scale bar = 1 mm). (b) Detail of the last two anterior growth bands with irregular meshwork ornamentation (Scale bar = 200 µm). (c) Detail of b with few meshes filled with small punctae (Scale bar = 50 µm). (d) Detail of postero-ventral growth band without whitest layer and showing a poor, well-preserved ornamentation pattern.

across) which are weaker posteriorly. Both species share the anterior margin being broadly rounded, a low number of stout growth lines, and broad growth bands with areolar ornamentation. There are nine species attributed to the genus *Paraleptestheria* (Chen 1975; Zhang *et al.* 1976; Shen & Zhang 1979). The key characters of these species are given in Table 2.

From Table 2 we can see that this new species is chiefly distinguished from the others by its subcentral umbo, which rises above the dorsal margin, and fewer growth lines; moreover, the mesh is filled with punctae.

Discussion. The only other European occurrence of a ‘conchostracan’ from the Cenozoic, from Messel (Germany), is rather poorly known as there are few morphological characters given by Richter and Baszio (2001, p. 351): ‘...The specimens are egg-shaped, small (body length ca. 150–200 µm) and clearly segmented. In some cases, a bifurcated antenna is visible on the largely expanded and ventrally bent anterior end. At the posterior end, a bifurcated furca is sometimes visible. The whole body including the head is covered by a carapace and bears a large number of thoracic leg pairs (up to 13 visible). The last two characters prove that these are not

juvenile Cladocera, but rather very small, fully developed juvenile Conchostraca.’ We speculate that they perhaps belong to a spinicaudatan ‘conchostracan’. But we do not know whether the carapace is with or without growth lines. Such a very small carapace (ca. 150–200 µm) has never been found in either fossil or living specimens before.

The genus *Paraleptestheria* has so far only been found in China and *P. menglaensis* Chen is considered as an index member of the early Eocene *Paraleptestheria* fauna. *Paraleptestheria* was found in association with the subgenus *P. (Nanhaiestheria)* (Shen 2003) in the Buxing Formation in the Sanshui basin of Guangdong, southern China (Shen & Zhang 1979). The subgenus is characterised by having a beaded structure along the lower margin of the growth lines (Shen & Zhang 1979, pl. 2 figs 1–4).

The rare carapaces from St Helens are broken or cracked; X-ray elemental analysis (Fig. 4) shows that they are calcium phosphate (probably apatite) embedded in clayey limestone.

Ostracods, probably *Potamocypris brodiei*, are lying near the specimens of *P. mitchelli* in the same pieces of limestone (Fig. 5).

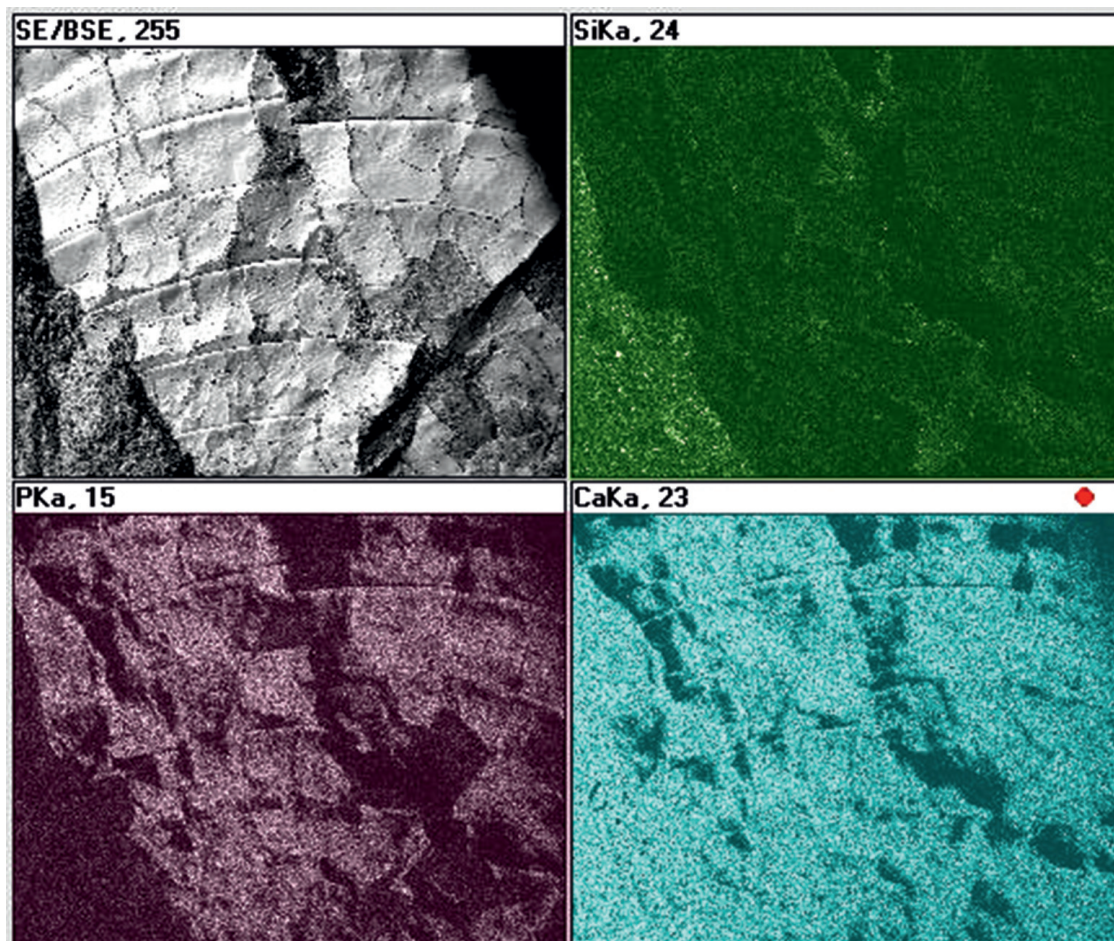


Figure 4 X-ray elemental analysis showing that the *P. mitchelli* carapaces are calcium phosphate (probably apatite) embedded in clayey limestone (IC.1270 (BLN 4470)).

Table 2 Key characters of the species of *Paraleptestheria*.

Genus and species	Characters				
	Shape	Umbonal position	Carapace height	Growth lines	Others
<i>P. mitchelli</i> sp. nov.	Oval	Subcentral	Anterior height > posterior	7–9	
<i>P. menglaensis</i> Chen	Oval	Anterior	Anterior height > posterior	c. 13	
<i>P. lanpingensis</i> Chen	Subrectangular	Anterior	Anterior height < posterior	>13	
<i>P. mohanensis</i> Chen	Elliptical	Anterior	Anterior height \approx posterior	c. 20	
<i>P. triangularis</i> Chen	Subtriangular	Anterior	Anterior height > posterior	>20	
<i>P. yunlongensis</i> Chen	Subquadrate	Mid-anterior	Anterior height \approx posterior	>16	
<i>P. aquilonaria</i> Zhang & Chen	Elliptical	Subcentral	Anterior height < posterior	c. 12	
<i>P.?</i> jintanensis Chen	Oval	Subanterior	Anterior height < posterior	c. 30	
<i>P. baoyuensis</i> Shen & X. Zhang	Elliptical	Subcentral	Anterior height \approx posterior	12–14	
<i>P. (Nanhaiestheria) sanshuiensis</i> Shen & X. Zhang	Elliptical	Subcentral	Anterior height < posterior	c. 13	Beaded growth lines



Figure 5 *Paraleptestheria mitchelli* sp. nov., photograph of NHMUK IC.1269 associated with ostracods, probably *Potamocypris brodiei* Jones & Sherborn, 1889.

6. Anostraca

Anostracans are commonly known as fairy shrimps, this group (order Anostraca) being included by Tasch (1969) in the subclass Sarsostraca (a name resurrected by Martin & Davis, 2001). These small crustaceans are characterised by an elongated body without a carapace, commonly with 11 thoracomeres with appendages modified for swimming and occasionally 17 or 19 thoracopods (in the atypical *Polyartemia*), eight abdominal segments generally without appendages, the body ending with a caudal furca with an unsegmented stylus, stalked eyes, short antennule and long prehensile antennae in males which are reduced in females. Of the 10 recognised families (Tasch 1969; Rogers 2013) only two are exclusively fossil (Gilsonicarididae and Palaeochirocephalidae) and considered as Incertae Sedis (Rogers 2013), and the families Artemiidae, Parartemiidae (suborder Artemiina) and Streptocephalidae, Tanymastigidae, Branchipodidae, Thamnocephalidae, Branchinectidae and Chirocephalidae (suborder Anostracina) are extant (Rogers 2013). They usually inhabit small, temporary, alkaline fresh water bodies (although *Artemia salina* Linnaeus, Eocene to Recent, and *Branchinecta campestris* Lynch are adapted to a high degree of salinity in saline lakes and lagoons), also occurring in pools after rain or those formed by the melting of ice or snow. In the Antarctic continent, they can survive under the ice cap. Other species at the opposite extreme can survive temperatures up to 41 °C. Anostraca range from the Lower Devonian to Recent.

Systematically, Martin & Davis (2001) considered that the anostracans constitute a clearly separate lineage from the rest of the branchiopods as this is an old group with a slow evolutionary rate. They should be treated as a separate subclass (Sarsostraca) that probably in future could include the extinct order Lipostraca (including *Lepidocaris rhyniensis* Scourfield from the Devonian) and the Cambrian genus *Rehbachtiella* Müller. But recently, Olesen (2009) considered that Lipostraca is the sister group of Anostraca and *Rehbachtiella* the sister taxa or all branchiopods (Sarsostraca and Phyllopoda).

Martin & Davis (2001) cited the mistake of including a non-crustacean and an insect nymph in this group. Thus Tasch (1969, p. R183) mentioned that Rolfe (1967) called attention to the genus *Rochdalia* Woodward not being an anostracan and indistinguishable from a breyeriid nymph (Insecta: Palaeodictyoptera) from the Carboniferous (Wootton 1972). Belk &

Schram (2001) also incorrectly considered that *Rochdalia parkeri* Woodward from the Upper Carboniferous has 11 thoracic segments and anostracan affinities. Tasch (1969) also suggest that Rolfe (1967) mentioned that *Gilsonicaris* van Straelen and *Branchipusites* Goldenberg could be a myriapod and an arthropleurid respectively (*sensu* Belk & Schram, 2001).

The fossil record of anostracans is sparse and discontinuous, and their preservation and assignment to known families is very problematic, when the sexual organs are not preserved, any systematic interpretation is doubtful. Belk & Schram (2001) argued that due to the delicate exoskeleton they are rare as fossils and that in the literature there are only a few ambiguous records. Schram (1986) considered that the Palaeozoic record of the anostracans is unconvincing; nevertheless, he gave a possible example from the Upper Silurian of Indiana. Belk & Schram (2001) described *Branchinecta barstowensis* Belk and Schram from the middle Miocene of California and a doubtful, unidentified anostracan has been described from the Cretaceous of Australia (Jell & Duncan 1986).

On balance, the Anostraca–Lipostraca group has a scarce record (Tasch 1963) and the most ancient fossil is *Gilsonicaris rhenana* van Straelen (Upper Devonian) with 18 thoracic segments, 11 of them with appendages, and close affinities with *Branchipodites vectensis*, differing only in the larger number of segments. Schram (1986) also considered this taxon was doubtful. On the other hand, *Branchipusites anthracinus* Goldenberg (Upper Carboniferous) has got only eight segments with appendages that resemble the branchial lamella of the living *Branchipus* (Goldenberg 1873). Belk & Schram (2001) suggested that it could be a juvenile insect, however it was recently considered to be an arthropleurid (Paleobiology Database 2015).

Subclass Sarsostraca Tasch, 1969

Order Anostraca Sars, 1867

Family Branchipodidae Simon, 1886

Diagnosis (*sensu* Tasch, 1969). Like Artemiidae in number of somites and genital organs except that the apical parts of the penes bear several spines. Basal segments of antennae in males coalesce medially in so-called clypeus. ?Upper Carboniferous, late Eocene, Recent.

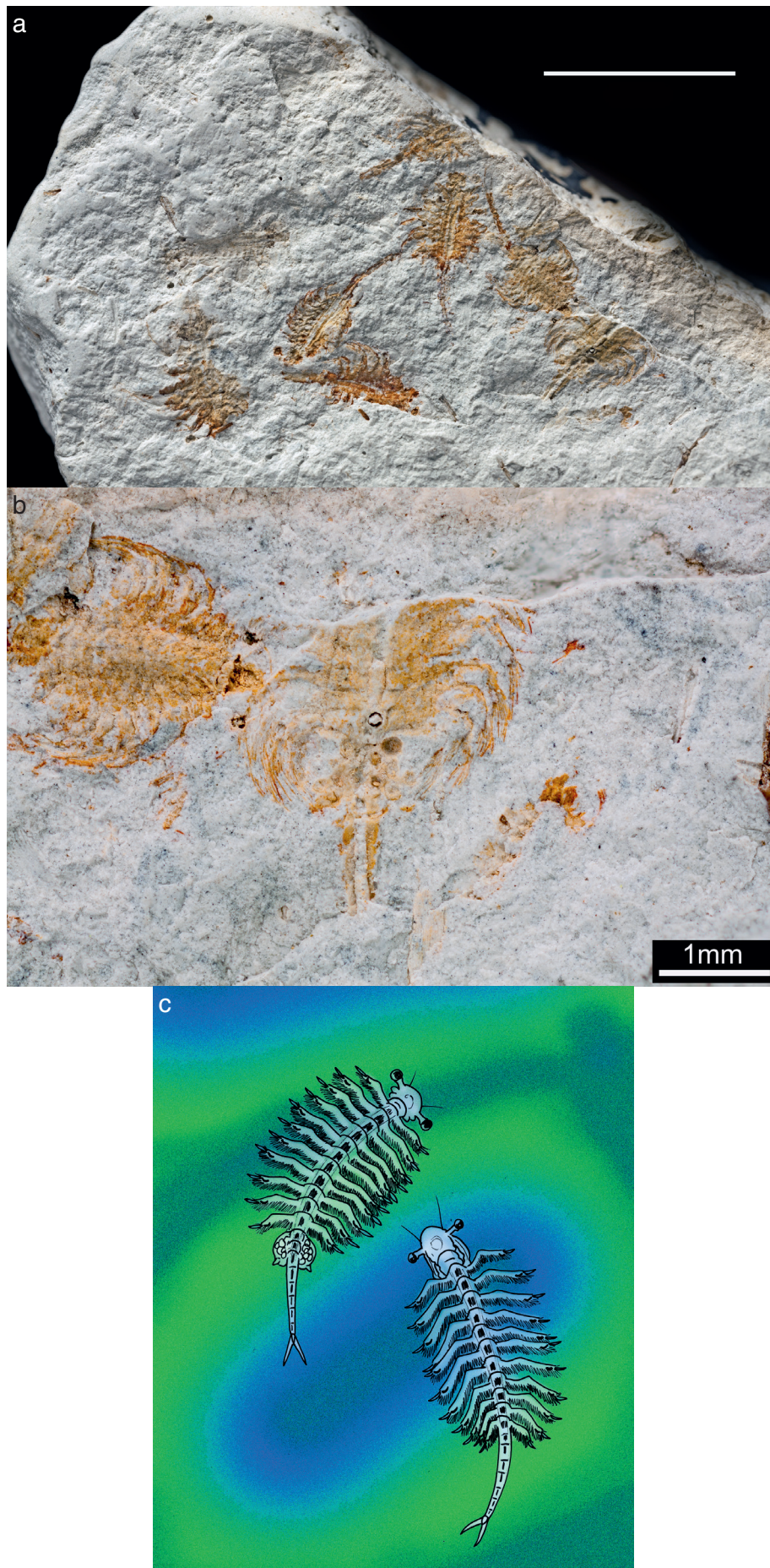


Figure 6 (a–c) *Branchipodites vectensis* Woodward, 1879 group photo (Scale bar 5 mm) and close-up showing ovisac IC.1267 (coll. A. Yule). c. Reconstruction (reproduced with permission from Avancna © 2014 deviantART).

Comments. As mentioned by Tasch (1969), this branchiopod family is morphological similar to Artemiidae, and only differs in just two penes with several spines in the apical portion. On the other hand, the male antennae are basally coalesced until the middle portion. The genus *Branchipodites* Woodward is recorded from the late Eocene of England and *Branchipusites* Goldenberg from the Carboniferous of Germany. Two other genera are living ones, *Branchipus* Shäffer from Europe, Asia and Africa and *Branchipodopsis* Sars from Asia and Africa.

Genus *Branchipodites* Woodward, 1879

Type species. *Branchipodites vectensis* Woodward, 1879, OD, pp. 345–46, plate XIV, figs 6–9, latest Eocene Insect Bed (Bembridge Marls), Isle of Wight, England.

Branchipodites vectensis Woodward, 1879
Fig. 6a–c

Diagnosis (*sensu* Tasch, 1969). Males with large clasping antennae, females with small antennae and egg pouches; female trunk with eight pairs of legs; abdominal somites narrow, elongated. Eyes stalked.

Occurrence. ‘Insect Limestone’, Insect Bed (latest Eocene), NW Isle of Wight, England.

Remarks. Often small spherical cavities are found in pieces of ‘Insect Limestone’. These are consistent in size and shape with the eggs in the egg pouches of *B. vectensis*.

Peloids, thought to be anostracan faecal pellets, are the most abundant allochem in the limestone. These are locally concentrated and frequently co-occur with fossilised *B. vectensis* (see Ross & Self, 2014).

7. Isopoda

Aquatic isopods are woodlouse-like crustaceans with a dorsal-ventrally flattened body comprising a cephalothorax, seven

free thoracic segments (each with a pair of limbs, the first for grasping, the others for walking) and a reduced abdomen covered dorsally by a single plate (with a pair of branched uropods). They are known from the Upper Carboniferous onwards (Wilson 2012).

Today, terrestrial isopods include the domestic woodlice and pill bugs, but there is no common name for all the diverse aquatic isopods: some more familiar marine species include the sea slater (a ligiid), speckled sea louse (a cirrolanid) and sea pill bug (a sphaeromatid). The latter, like the Insect Bed isopod, is considered to be a sphaeromatoid in the suborder Sphaeromatidea, previously Flabellifera (Brandt & Poore 2003). Sphaeromatids are so called because the oval body is readily rolled into a ball as in pill bugs and some trilobites. The family name is Latinised as Sphaeromidae, but was altered to Sphaeromatidae (to reflect the Greek stem of *Sphaeroma*) by Dahl (1916). We have retained the latter for nomenclatural stability.

Extant species of the typical genus *Sphaeroma* are good swimmers and live in estuaries and saltmarsh pools, as well as on the seashore, and can even occur in fresh water, although are only transitory in the latter.

Fossil sphaeromatoids are known from the Triassic onwards. The Insect Bed isopod belongs to the fossil taxon *Eosphaeroma* that was considered a ‘basket genus’ by some 20th-Century workers, e.g., Basso & Tintori (1995). Assigning fossil species to natural genera in the absence of some fine details, e.g., in the appendages, can be a problem for the palaeontologist, but can be overcome by placing them in collective groups (Jarzembowski *et al.* 2014). In this case, we suggest that the genus *Eosphaeroma* is treated as a collective of possible sphaeromatid morphospecies with a broad, ovoid body; small head much narrower than and sunk into the thorax; subequal, ‘sickle’-shaped uropods; and a nearly semicircular abdominal plate (pleotelson), broadly rounded posteriorly (Fig. 7).

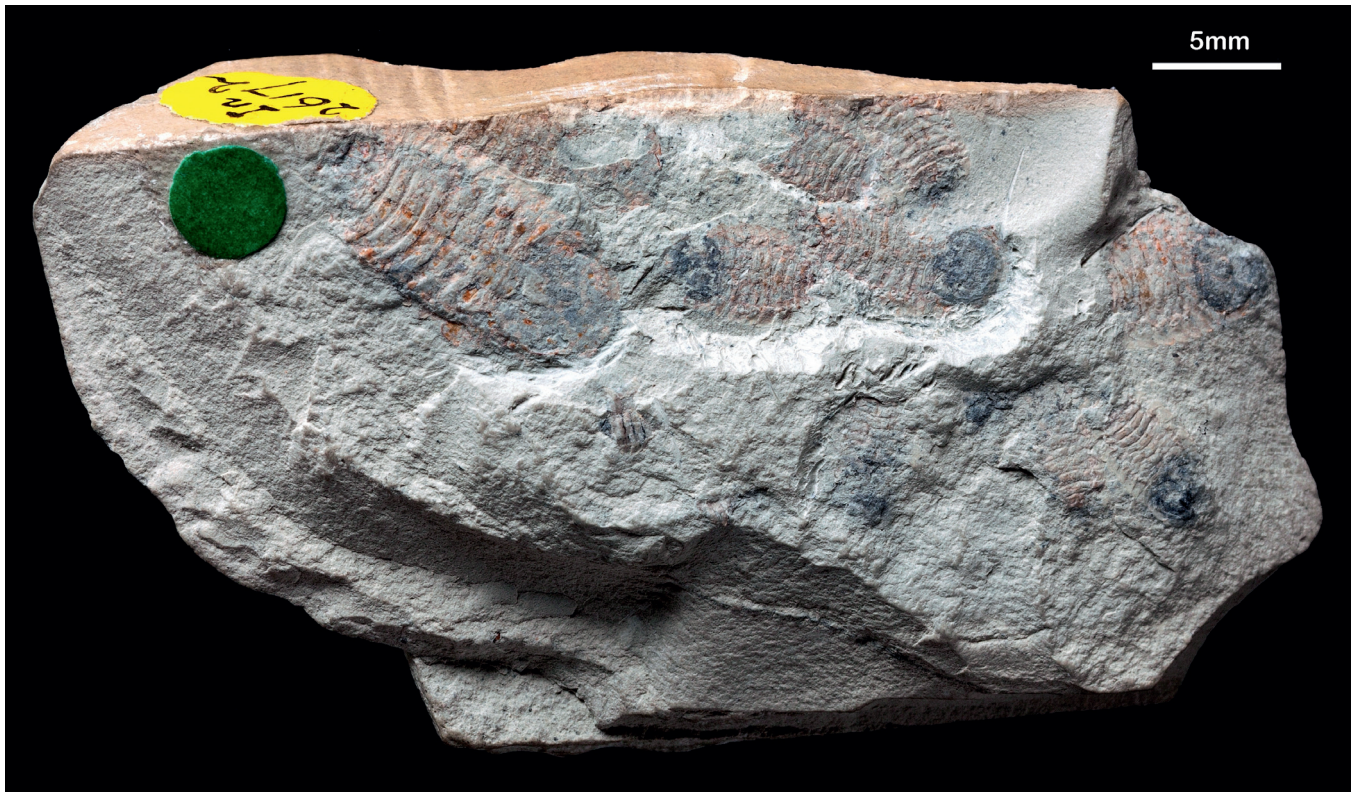


Figure 7 *Eosphaeroma margarum* (Desmarest, 1822) group photo in 26172b: green spot indicates specimen figured by Martini (1972, pl. 2, fig. 3). The dark grey patches are pleotelsons.

Martini (1972) revised the Insect Bed isopod, considering it to belong to a French fresh water–brackish species, *Eosphaeroma margarum* (Desmarest). Fossils are uncommon and only occur locally in the ‘Insect Limestone’, individuals varying in size.

He also revised *Eosphaeroma obtusum* (von Meyer) considering it to occur in the higher part of the Bembridge Marls, as well as in the Lower Oligocene of France and Germany. More recently, *E. obtusum* has been reported from Italy (De Angeli & Quaggiotto 2014).

Class Malacostraca Latreille, 1802

Order Isopoda Latreille, 1817

Suborder Sphaeromatidea Wägele, 1989

Superfamily Sphaeromatoidea Latreille, 1825

?Family Sphaeromatidae Latreille, 1825

Genus *Eosphaeroma* Woodward, 1879

Type species. *Eosphaeroma fluviatile* Woodward, 1879 by subsequent designation (Van Straelen, 1931); ‘Insect Limestone’, Insect Bed (latest Eocene), NW Isle of Wight, England

Eosphaeroma margarum
(Desmarest in Brongniart & Desmarest, 1822)
Fig. 7

Diagnosis (after Martini, 1972; De Angeli & Quaggiotto, 2014). Small to medium sized isopod with elongate-oval body, slightly convex in cross section; comparatively small head with laterally located eyes; head enclosed posteriorly and laterally by first pereonite; pereonites expanded laterally and seven visible but only one free pleonite with continuous transverse suture; large, subcircular pleotelson, rounded posteriorly and comprising about one third of body length; pair of biramous uropods, laterally located on pleotelson, with subequal branches and relatively wide endopod and leaf-shaped exopod.

Occurrence. Late Palaeogene of France, Germany and England (Martini 1972).

Comments. This species is the senior synonym of *E. fluviatile* and differs from *E. obtusum* (von Meyer 1858) in the shape of the uropods and possession of an uninterrupted transverse suture on the free pleonite (von Meyer 1858).

8. Palaeoecology

The fine grain size and planar laminations indicate that the Insect Bed at St Helens was deposited in a low-energy environment. Halite pseudomorphs are present in the laminated clays and limestone suggesting that the sequence was deposited in a hypersaline lagoon. However, the pseudomorphs are rare so that super-saturation may have only occurred sporadically.

Extant ‘conchostracans’ and anostracans generally live in transient aquatic environments. ‘Conchostracans’ are mainly benthic and affected at an early stage by declining oxygen levels as the pools desiccate. Weak-swimming ‘conchostracans’ are unable to utilise oxygen in the sub-surface layer due to the high-energy expenditure required to swim to the air-water interface whereas anostracans are nektonic (Brendonck 1999). Extant ‘conchostracans’ therefore develop and attain sexual maturity earlier than anostracans. Benthic conditions suitable for colonisation may, however, have been short lived. The low abundance of ‘conchostracans’ cannot be attributed to palaeopredation as fish are very rare in the Insect Bed (see Hooker *et*

al. 2019). Alternatively, the carapaces may have been washed in to the site of deposition, but not far from their natural habitat.

In China, *Paraleptestheria* often occurs in red beds in which gypsum or rock salt is common. This indicates that the animals could adapt to a saline or brackish water environment (Chen & Shen 1981). This is consistent with the lagoonal setting of the British occurrence (see above).

9. Conclusions

‘Conchostracans’ decline generally after their Mesozoic heyday (possibly due to the rise of teleost fish) and are absent from the modern British fauna (although still surviving in continental Europe). This first British Cenozoic find is therefore significant. Extant branchipodid fairy shrimps are marginalised too in Europe, e.g., occurring in rain-filled tank tracks on Salisbury Plain in England (English Nature 1993). The Insect Bed is their only record in the British ‘Tertiary’. The occurrence of these branchiopods is ecologically significant (representing succession in the water body) as discussed above. The generic placement of the Insect Bed ostracod needs confirmation as mentioned above, despite occurring in a limestone matrix (modern ostracod investigators prefer to work with freshly sieve samples). Also, the family placing of the rare and somewhat elusive isopod needs confirmation, especially as it is stratigraphically replaced by another congener in the European Palaeogene (Martini 1972). In view of the exceptional preservation of the ‘Insect Limestone’, other crustaceans such as water fleas (Cladocera) should be looked out for.

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