

# THE CONCHOSTRACAN FAUNA OF THE GREAT ESTUARINE GROUP, MIDDLE JURASSIC, SCOTLAND

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**ABSTRACT.** The Great Estuarine Group contains the most diverse conchostracan fauna so far described from the Jurassic or Cretaceous of Europe, comprising twelve species in seven genera. *Estheria munchisoniae* Jones was described in the last century; it is now referred to *Pseudograptia* Novojilov and is the youngest member (latest Bathonian?) of the fauna described here. *Euestheria trotternishensis* and *Neopolygrapta lealtensis* spp. nov. occur near the base of the Great Estuarine Group and probably close to the Bajocian–Bathonian boundary. *Dendrostracus hebridesensis* sp. nov. occurs towards the top of the Kildonnan Member, Lealt Shale Formation. In the overlying Lonfearn Member, *Skyestheria intermedia* sp. nov. appears (probably descended from *Neopolygrapta*) and itself gives rise to *Antronestheria praecursor* sp. nov. The higher parts of the Great Estuarine Group, including most of the Kilmaluag Formation, are dominated by *Antronestheria kilmaluagensis* sp. nov., with one occurrence of *Fibrestheria puncta* sp. nov. The *Pseudograptia* fauna (containing *P. orbita* Chen, *P. morrissi* sp. nov., *P. jonesi* sp. nov. and *P. munchisoniae* (Jones)) occurs in beds probably near the top of the Kilmaluag Formation. All the conchostracans inhabited shallow, freshwater to oligohaline, near-coastal, lagoons. Biogeographic comparisons with China show that the earlier faunas were distinct in the two areas, but the *Pseudograptia* fauna occurs in both. Details of the construction of conchostracan growth bands are revealed by stereo scanning electron micrographs.

CONCHOSTRACANS are small, bivalved branchiopod crustaceans with a non-mineralized carapace. They occur in non-marine facies from the Devonian to the present day, sporadically but often in great abundance; many palaeontologists still refer to them informally using the pre-occupied generic name '*Estheria*'. Jurassic and Cretaceous conchostracans have been little studied in Europe, no doubt partly because of the limited occurrence of suitable facies, but they have been extensively studied in Siberia and China, where they are important biostratigraphically within thick successions of non-marine strata deposited in large internal basins (e.g. Sichuan basin, Sungliao basin: Chen and Shen 1985; general summary in English, Chen *et al.* 1982, pp. 1011–1014). It is therefore important to examine conchostracan faunas in Europe that can be accurately dated by intercalation within marine sections.

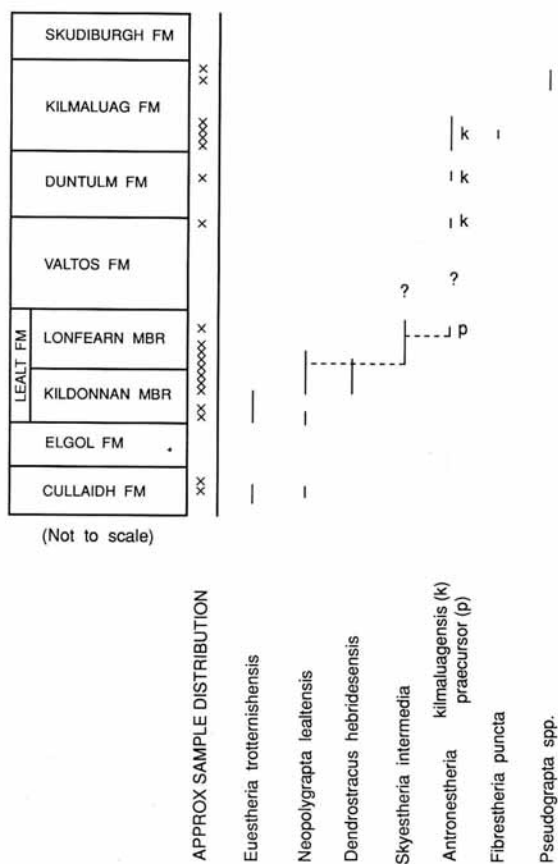
In Britain, conchostracans occur in the Triassic, including the Penarth Group ('Rhaetian'), sporadically in the Bathonian of central England, in the Purbeck Beds (top Jurassic-early Cretaceous) and in the Wealden Beds (early Cretaceous). By far the most abundant Jurassic faunas, however, are those of the Great Estuarine Group of the Inner Hebrides, NW Scotland, where conchostracans occur profusely, associated with the non-marine end of a series of faunal assemblages ranging from restricted-marine to freshwater (Hudson 1963*a*, 1963*b*, 1980). The age is late Bajocian–Bathonian. This occurrence is of interest from several points of view: local and worldwide biostratigraphical, palaeoecological, and palaeo-biogeographical. Our scanning electron microscope (SEM) studies have also enabled us to add important morphological details to existing knowledge of the conchostracan carapace, and we illustrate conchostracan sculpture stereoscopically for the first time.

## THE GREAT ESTUARINE GROUP

The Great Estuarine Group is an intercalation of varied paralic facies, up to 270 m thick, in the otherwise marine Jurassic succession of the Minch Basin (Hudson 1983). Its lithostratigraphy has

been reviewed by Harris and Hudson (1980). The base of the Group is defined at the upward passage from ammonite-bearing clays of the *garantiana* zone (late Bajocian) into dark shales, with a restricted fauna, of the Cullaidh Shale Formation. Its top occurs where the non-marine Skudiburgh Formation is abruptly overlain by the Upper Ostrea Member of the Staffin Bay Formation; this is dated palynologically as no older than the *discus* zone (latest Bathonian), and is overlain by the Belemnite Sands Member, *macrocephalus* zone, early Callovian (Bradshaw and Fenton 1982). The Great Estuarine Group may therefore include equivalents of the latest Bajocian *parkinsoni* zone, but most of it must be Bathonian. It can be divided into several distinctive formations that can be correlated lithostratigraphically (Harris and Hudson 1980; see Text-fig. 1),

### Stratigraphic Ranges of Conchostraca in the Great Estuarine Group



TEXT-FIG. 1. Stratigraphic subdivisions of the Great Estuarine Group (Harris and Hudson 1980), showing ranges of the main conchostracan species.

but no internal biostratigraphy is currently available. It seems likely, on grounds of regional event stratigraphy, that the Duntulm Formation correlates with the White/Blisworth Limestones of central England (Andrews 1985) and thus most probably with the *hodsoni* zone of the Bathonian (Torrens in Cope *et al.* 1980).

Within the Great Estuarine Group, the predominantly shale, low-salinity formations, especially the Lealt Shale Formation (both Kildonnan and Lonfearn Members) and the Kilmaluag Formation, contain abundant conchostracans. There are more limited occurrences in the Cullaidh Shale Formation, in the shale facies within the Valtos Formation, and in a freshwater intercalation within the Duntulm Formation. A definite stratigraphical arrangement of the conchostracan taxa emerges from our present sampling, and suggests that they will be useful in local and perhaps wider stratigraphical correlation.

#### PREVIOUS WORK ON CONCHOSTRACANS FROM THE GREAT ESTUARINE GROUP

Jones (1863) described the species *Estheria purchisoniae* from Skye; this was subsequently made the type species of the genus *Pseudograptia* Novojilov, 1954. No systematic descriptions or illustrations have appeared since, although conchostracans have been recorded from the Great Estuarine Group many times, variously as *Estheria*, *Euestheria* or *Cyzicus*, and gave their name to the Estheria Shales of Anderson (e.g. Anderson and Dunham 1964), now the Lealt Shale Formation of Harris and Hudson (1980). Hudson (1963b, p. 337) recorded conchostracans from several horizons within the Group and reported that 'each sample was reasonably homogeneous within itself, but that there was considerable variation between samples, especially in interspace ornament and also in size'. This suggested that several taxa were present, but in view of the then-prevailing confusion in conchostracan taxonomy, Hudson retained all the specimens in Jones's species *murchisoniae*, which he referred to *Euestheria* Deperet and Mazeran.

#### MATERIAL STUDIED

In 1988 we made two visits to the Hebrides specifically to collect material for this paper. We have also made extensive use of collections made by Hudson since 1963, in the collections of the Leicester University Geology Department, and between 1956-62, in the Sedgwick Museum, Cambridge. All material from the Great Estuarine Group used for this paper is listed in an Appendix, which is deposited at the British Library as Supplementary Publication No. SUP 14039 (11 pages). We have also re-studied the specimens described by Jones (1863) at the British Geological Survey, Keyworth, a limited amount of Geological Survey material from southern England, and some core material loaned by British Petroleum plc from the Porcupine Basin. Chen has made extensive use of the collections of the Nanjing Institute of Geology and Palaeontology for comparative purposes, and some material collected jointly in China in 1989, or presented to Hudson by Chen, is now in the Leicester University collections.

#### DISTRIBUTION OF CONCHOSTRACAN FAUNAS

The stratigraphy of the Great Estuarine Group and the distribution of conchostracans within it are summarized in Text-figure 1.

##### *Lealt Shale Formation and Cullaidh Shale Formation*

*Stratigraphy.* It is convenient to consider the two lowest shale formations together, because from the point of view of conchostracan distribution the unfossiliferous Elgol Sandstone Formation can be regarded as an intercalation within them. We have sampled the Cullaidh Shale Formation and the basal part of the Kildonnan Member of the Lealt Formation at two localities each. The middle part of the Kildonnan Member contains few, if any, conchostracans. Its upper part contains many,

and they continue into the lower part of the Lonfearn Member, which we have also sampled at several localities. The upper part of the Lonfearn Member contains conchostracans, but we have not sampled it adequately, and the same applies to the sparse conchostracan fauna of the basal Valtos Formation above.

In the Cullaidh Shale and basal Kildonnan Member, the genera *Euestheria* and *Neopolygrapta* occur, each represented by one species (when specifically identifiable). *Euestheria* is confined to these basal beds, except for one occurrence in the higher part of the Kildonnan Member, at which horizon *Neopolygrapta lealtensis* sp. nov. is joined by *Dendrostracus hebridesensis* sp. nov. These two species continue into the basal part of the Lonfearn Member, but have not been found more than about 3 m above the algal limestone that marks the contact between the members. Before the disappearance of *Neopolygrapta*, *Skyestheria* appears. Morphological features suggest it may have evolved from *Neopolygrapta*. *Skyestheria* is the commonest conchostracan in the middle part of the Lonfearn Member, including the shales in the Lealt River (immediately above and below a limestone with *Chara* fragments) from which conchostracans have most often been collected in the past. *Neopolygrapta* also occurs here. (This locality is mentioned in Hudson 1963b, p. 339; note that the new road bridge is a few metres upstream of the old one and stands on what were formerly the best exposures.)

A few metres higher, *Antronestheria praecursor* sp. nov. appears in abundance (noted as 'form with punctate ornament' by Hudson 1963b, p. 339). It probably evolved from *Skyestheria* and itself leads to *Antronestheria kilmaluagensis* sp. nov., which dominates the faunas of the higher Great Estuarine Group. Our data are insufficient to show whether or not *Skyestheria* and *Antronestheria* overlap stratigraphically. The species *Skyestheria elliptica* sp. nov. is only known from one sample; its horizon within the Lonfearn Member is unknown, but likely to be near the middle because of the occurrence of oolitic limestones nearby.

*Palaeoecology.* The Cullaidh Shale Formation has a sparse fauna mainly of fish scales and tiny gastropods, with occasional occurrences of bivalves including mytilids. We do not have sufficient information to relate the conchostracan occurrences to the rest of the fauna, which is clearly not a normal marine one. In the Raasay section, conchostracans occur near the passage into the Elgol Sandstone Formation and not in association with the marine-brackish faunas recorded by Forsyth (1960) from stratigraphically lower.

In the Lealt Shale Formation conchostracans occur with the freshwater gastropods *Viviparus* and *Valvata* and the bivalve *Unio*, as well as commonly (from its incoming in the higher Kildonnan Member upwards) with the probably freshwater-brackish bivalve *Neomiodon*. The commonest associates of the conchostracans are freshwater to oligohaline ostracods of the genera *Limnocythere*, *Darwinula* and *Theriosynoecum*, with less commonly the euryhaline genus *Micropneumatocythere*. In the type section of the Kildonnan Member, Eigg, conchostracans do not occur in Beds 3–5 (Hudson 1966 and unpublished data) which are dominated by the brackish-water bivalve *Praemytilus strathairdensis*, nor in association with the marine-brackish *Plaucunopsis-Cuspidaria* faunas that occur in both members of the Formation. Walton (pers. comm. 1988) finds an excellent correlation between the proportion of the planktonic alga *Botryococcus* in palynological preparations and the presence of freshwater to oligohaline indicators (including conchostracans) in the macrofauna. In one bed in the Lonfearn Member in Trotternish (bed 1 of Hudson 1963b, p. 339) *Skyestheria* co-occurs with small mytilid bivalves. In general, the new data confirm that conchostracans inhabited the freshwater-brackish end of a spectrum of coastal lagoons of varying salinity (Hudson 1963a, 1963b, 1980; see also Tasch 1987, p. 139). Details will no doubt emerge from further collecting and from work in progress on the ostracod faunas and the palynology.

#### *Valtos and Duntulm Formations*

Few horizons in these formations yield conchostracans. We have studied only two samples, a bed 0.47 to 0.32 m below the top of the Valtos Formation on Muck, overlying a conspicuously yellow-weathering dolomitic limestone (Andrews and Walton 1990, p. 13, fig. 10), and Beds 6–7 of the

Duntulm Formation at Lon Ostatoin, Skye (the 'freshwater intercalation' of Andrews and Walton 1990, p. 8). Both yield *Antronestheria kilmaluagensis*, accompanied by *Neomiodon* and, in Muck, *Darwinula*.

#### *Kilmaluag Formation*

*Stratigraphy.* Conchostracans occur very commonly in the Kilmaluag Formation, wherever suitable lithologies (shales or fissile argillaceous limestones) are developed. With the exception of three localities, all the conchostracans belong to *Antronestheria kilmaluagensis* gen et sp. nov. This has been identified from the type section at Kilmaluag (beds 1, 3, 6, 7), bed 8 from Lon Ostatoin, and bed 4 from Prince Charles's Point; all bed numbers from Andrews (1985, p. 1122). Other Skye localities include the shore near the mouth of Lon Sgapail (Andrews, 1985, p. 1334), cliffs near Osmigarry (NG 390719), and slipped blocks on the shore of Lub Score (NG 404728). These occurrences span most of the exposed section of the Kilmaluag Formation, those at Kilmaluag being in its lower part and that at Prince Charles's Point probably in its upper part (Andrews 1985, p. 1134). In Strathaird, the Kilmaluag Formation is too metamorphosed to yield identifiable conchostracans. *A. kilmaluagensis* is abundant in its lower part at Laig Gorge, Eigg (beds 1, 2, 3, 5, 9 of Andrews, 1985, p. 1125).

One sample from bed 7 at Kilmaluag yielded the only other conchostracan species so far known from this horizon, *Fibrestheria puncta* sp. nov. Other samples from this bed yielded only *Antronestheria. Fibrestheria* also occur in the Blisworth Limestone of central England (see below).

Two localities have yielded a totally different conchostracan fauna consisting of species of *Pseudograptia* Novojilov. From one of these came the original material of *Estheria murchisonae* Jones: 'Mugstok' (Monkstadt), Trotternish (a locality also referred to as 'Icolmkill'). The specimens were collected by Murchison in 1826 from a temporary exposure made during the drainage of the former Loch Chaluis Cille, probably approximately NG 375695. Murchison (1829, p. 311) recorded, in blue shale, '*Ammonites Koenigi*, Ostracae in masses, many belemnites, flattened Tellinae (?), etc.' The 'flattened Tellinae' are the conchostracans subsequently described by Jones (1863), and preserved in the Geological Society Collections, now at the British Geological Survey, Keyworth, as No. 7296. The lithology, fine-grained grey argillaceous limestone with conchostracans almost covering one bedding plane, resembles typical Kilmaluag Formation. It is impossible to be sure how close the association with the other fauna recorded by Murchison was, but the presence of oysters suggests the Upper Ostrea Member, and the belemnites and ammonites the Belemnite Sands Member, both of the Staffin Bay Formation (Sykes 1975). It therefore seems most probable that the conchostracans occurred high in the Kilmaluag Formation or conceivably as an intercalation of 'Kilmaluag' facies within the Skudiburgh Formation.

The other *Pseudograptia* locality is in the Kilmaluag Formation of Muck, beds 13, 14 and 15 of Andrews (1985, p. 1125). Abundant and well preserved conchostracans occur in argillaceous dolomites, without macrofauna or ostracods. This outcrop is tectonically separated from the nearby Duntulm Formation and overlain by Palaeocene agglomerate. Lithological comparison with Strathaird suggests a high horizon with the Kilmaluag Formation (Andrews, 1985, p. 1128). Our suggestion, therefore, is that the *Pseudograptia* fauna is younger than the *Antronestheria* fauna and both are late Bathonian. At both localities *Pseudograptia murchisoniae* is accompanied by the species *P. orbita* Chen and *P. jonesi* sp. nov.; the Muck locality additionally yields *P. morrissi* sp. nov.

*Palaeoecology.* As in the Lealt Shale Formation, the occurrence of conchostracans in the higher Great Estuarine Group clearly correlates with non-marine facies, and it is likely that the Kilmaluag Formation lagoons were only tenuously connected to the open sea (Andrews 1985). *Antronestheria kilmaluagensis* is nearly always accompanied by ostracods (*Theriosynoecum*, *Darwinula*) that are considered to be freshwater or oligohaline (Kilenyi in Tan and Hudson 1974, p. 107); the *Theriosynoecum* show variations in node development. These forms are often accompanied by *Klieana*, which can also tolerate higher salinities. Some horizons additionally contain the brackish-marine ostracod *Progonocythere* (M. Wakefield pers. comm. 1989). Other associated fossils are

*Viviparus*, *Chara* oogonia, fish fragments and cuticular fragments of higher plants. The occurrence of *Pseudograptia* in ostracod-free dolomites from Muck may suggest tolerance of evaporated water and perhaps elevated (but non-marine) salinities by this genus (cf. Andrews *et al.* 1987). The Skye occurrence is in limestone, not dolomite (checked by X-ray diffraction), and also lacks associated ostracods, as do the occurrences of *Pseudograptia* spp. in Liaoning Province, China.

#### *Bathonian of Southern and Eastern England*

We have examined conchostracans from three localities in the Bathonian of England, using material from the BGS collections, Keyworth. Those from the top part of the Blisworth Limestone of Newport Pagnell, Bucks., may be assigned to *Fibresteria* cf. *puncta* sp. nov. The horizon is probably late Bathonian and about the same age as the occurrence of *F. puncta* in the Kilmaluag Formation, Skye. An occurrence in the Forest Marble near Cirencester is of poorly preserved specimens of *Dendrostracus*? This horizon is also late Bathonian, and if the occurrence is confirmed it will probably represent a later occurrence of *Dendrostracus* than in the Hebrides, where it is confined to the Lealt Shale Formation of probable early to mid Bathonian age. The Blisworth Clay of the Nettleton Bottom borehole yields *Antronestheria kilmaluagensis* and is probably of similar age to the Kilmaluag Formation, late Bathonian. Locality details of the English occurrences are given in the systematic section below.

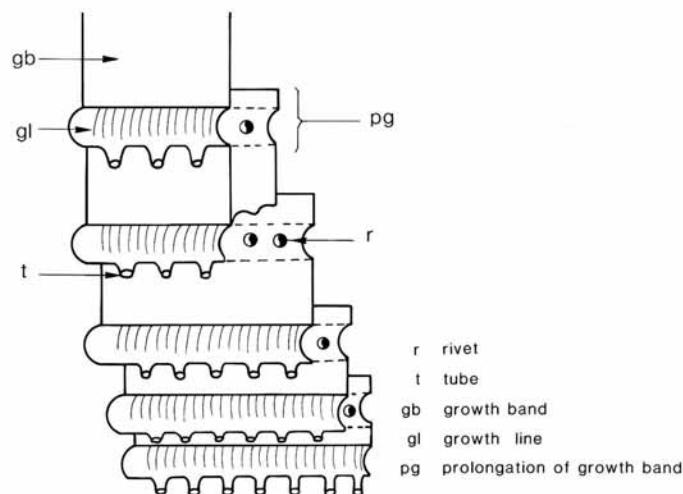
#### *Porcupine Basin*

A particularly interesting record of *Antronestheria kilmaluagensis* is in material loaned to us by the British Petroleum Company plc from a core taken in the northern part of the Porcupine Basin, offshore SW Ireland. The fossils and lithology are indistinguishable from typical Kilmaluag formation, and the horizon is independently dated as late Bathonian by ostracods (J. Athersuch pers. comm. 1988).

### MORPHOLOGY, TAXONOMY AND EVOLUTION

The taxonomy of fossil conchostracans is mainly based on the characteristics of their carapace and minute ornamentation of growth bands, because their soft bodies and appendages are seldom preserved in fossils (but see Zhang *et al.* 1987, for Jurassic soft-part preservation). The distinctive leads aside, many forms lack remarkable differences in shape of the carapaces, although some may have exceptional features of the umbo or dorsal margin (such as large umbo, umbonal node, reflected curved growth lines near dorsal margin). In most Jurassic and Cretaceous forms, the carapaces vary only from elliptical, oval, or subquadrate to subcircular, and their umbones are generally placed between the middle point and the anterior end of the dorsal margin, so the taxonomy is only dependent upon the variety of ornamentation. Sometimes, the evolution of ornamentation is very rapid and distinct in a particular basin or in a limited area belonging to the same river system. The non-marine Cretaceous of NE China has been successfully subdivided in this way (Zhang *et al.* 1976, pp. 44–45, 82–85, text-fig. 39; Chen and Shen, 1985, pp. 20–22, text-fig. 11). Thus we disagree with the low taxonomic status assigned to interspace ornament by Tasch (1969).

The variously developed growth lines of conchostracan carapaces are formed from the junction of neighbouring growth bands (Novojilov 1954, p. 96, text-fig. 69; Chen and Shen 1985, pp. 13–14; text-figs 7 and 8). These structures are clearly shown in SEM photographs in the present paper (Pl. 2, figs 8, 10, 11; Pl. 3, figs 6 and 9; Pl. 9, figs 9–12; pl. 10, figs 3–8). A row of tubes is situated on the lower margin of each growth band (= growth line), corresponding with a row of rivets on the prolongation of the next growth band (Text-fig. 2). The basal holes of these tubes are exposed on the interior surface of growth bands (Pl. 3, fig. 6). These tubes in *Dendrostracus* have a cross-bar in between (Pl. 3, figs 4 and 8), but those of *Neopolygrapta* are shorter and without the cross-bar (Pl. 2, figs 8, 10, 11; Pl. 10, figs 3–8). For *Skyestheria*, appearing in a higher horizon of the Lealt Shale Formation, these tubes contract and connect with each other to form beading on the lower margin of the growth lines (Pl. 4, figs 6 and 9).



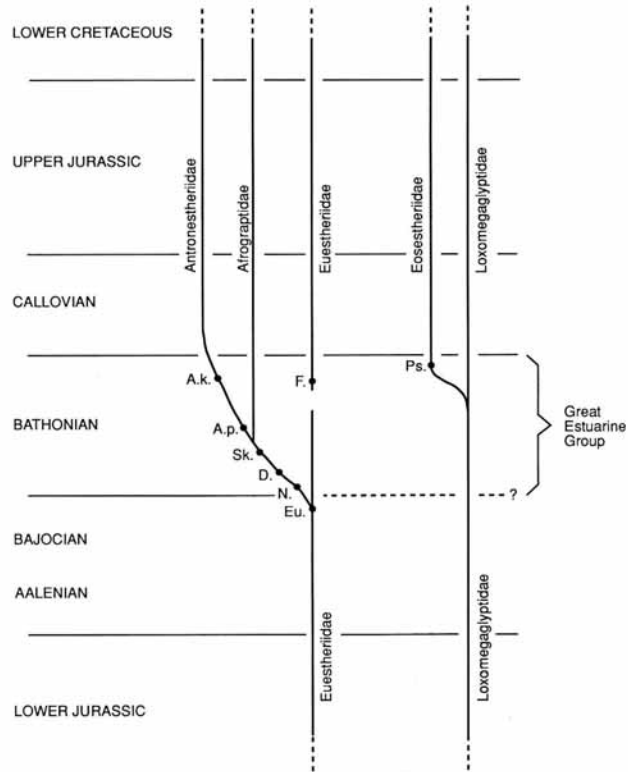
TEXT-FIG. 2. The construction of conchostracan growth bands and associated features.

Our morphological observations suggest some modifications to the classification of conchostracans given by Chen and Shen (1985) and to their evolutionary diagram (1985, p. 190, fig. 113). On the basis of the beading or serration along the lower margin of their growth lines, three genera erected herein (*Dendrostracus*, *Neopolygrapta* and *Skyestheria*) belong to the family Afrograptidae Novojilov, 1957. The origin of this family was regarded as uncertain by Chen and Shen (1985, p. 190, fig. 113). Our results suggest that these genera arose in the Middle Jurassic from members of the family Euestheriidae Defretin, 1965: *Dendrostracus* perhaps from *Euestheria* and *Neopolygrapta* from *Polygrapta*. The Afrograptidae (if monophyletic) thus originate in the Middle Jurassic and range into the lower Tertiary; they belong to the superfamily Eosestherioidea Zhang and Chen (*in Zhang et al.*, 1976) and there is no need for the superfamily Afrograptioidea Novojilov, 1957. According to interpretations in this paper, *Neopolygrapta* gave rise to *Skyestheria* in the Bathonian, and that in turn to the genus *Antronestheria* of the late Bathonian. *Antronestheria* is the type genus of the new family Antronestheriidae which includes other genera (see below) ranging from Middle Jurassic to Lower Cretaceous.

*Pseudograpta* Novojilov appears to be transitional between the families Loxomegaglyptidae and Eosestheriidae, a transition already dated as middle Jurassic by Chen and Shen (1985, p. 190, fig. 113). However, our new material suggests that *Pseudograpta* should be included in the latter family rather than in the former as in Chen and Shen (1985, p. 109). *Pseudograpta* is not closely related to the group of genera belonging to the Euestheriidae or originating from that family within the Middle Jurassic, and its incoming near the top of the Great Estuarine Group is probably the result of immigration. It corresponds to a uniting of formerly distinct faunal provinces, as discussed below. Text-figure 3 summarizes our present views on evolutionary relationships.

#### PALAEOBIOGEOGRAPHY

In this paper twelve conchostracan species in seven genera are described. Eight species in six genera (*Skyestheria*, *Dendrostracus*, *Neopolygrapta*, *Euestheria*, *Antronestheria* and *Fibrestheria*) form assemblages with overlapping stratigraphical ranges, belonging to or descended from the

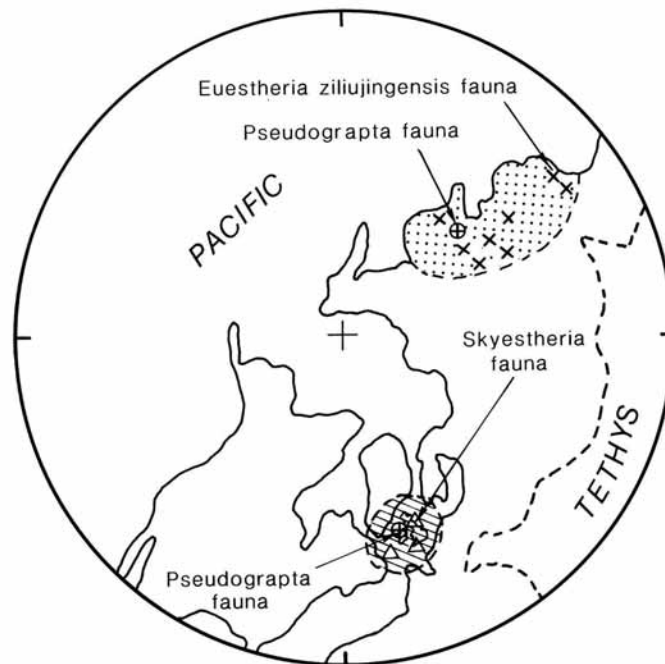


TEXT-FIG. 3. Possible evolutionary relationships among some Jurassic conchostracan families (superfamily Eosestherioidea Zhang and Chen, 1976), as illustrated by genera occurring in the Great Estuarine Group. Based on Chen and Shen (1985, p. 120, fig. 113), as modified herein. Direct descent is not necessarily implied; see discussion in text. Eu., *Eustheria*; N., *Neopolygrapta*; D., *Dendrostracus*; Sk., *Skyestheria*; A.p., *Antronestheria praecursor*; A.k., *A. kilmaluagensis*; F., *Fibresteria*; Ps., *Pseudograptus*.

Euestheriidae. They are mostly new forms with very complex dendritic or cavernous ornamentation in their growth bands. This fauna is here named the *Skyestheria* Fauna, so far known mainly from Scotland, but with some of its members also recorded from England and from the Atlantic west of Ireland. It occurs stratigraphically below a fauna containing four species of *Pseudograptus*.

The *Euestheria ziliujingensis* fauna is widely distributed in the Middle Jurassic deposits from E Asia (Chen and Shen 1982). Apart from the index species, the fauna includes *A. haifanggonensis* Chen, *E. yanjiawanensis* Chen, *E. complanata* Chen, *E. rotunda* Chen, *E. jingyuanensis* Chen, and *Paleoleptestheria chinensis* Chen. Their carapaces are generally small, elliptical or subcircular in outline, with simple small punctae or fine reticulate ornamentation of growth bands. *P. chinensis* from the Upper Shaximiao Formation of the Sichuan basin of SW China is a late member of this fauna and its cavernous ornamentation is similar to that of *Antronestheria*, described herein from late Bathonian deposits of Western Europe.





TEXT-FIG. 4. Map showing separate distribution of the early Middle Jurassic *Euestheria ziliujingensis* and *Skyestheria* faunas, and wide distribution of the later Middle Jurassic *Pseudograptia* fauna between China and western Europe. Polar projection based on Smith and Briden 1977.

By the end of the Middle Jurassic, the distinctness of the above-mentioned two conchostracan paleobiogeographic Provinces in the Euro-Asian continent (Text-fig. 4) disappeared, and they were replaced by a united *Pseudograptia* fauna. In this genus carapaces are large in size, with coarse hexagonal ornamentation of growth bands and very stout and convex growth lines (growth ridges). *P. orbita* and *P. murchisoniae* have been found in the Tuchengsz Formation of W Liaoning, NE China, as well as in Scotland (Zhang *et al.* 1976).

The two occurrences provide a remarkable example of the range of facies that conchostracans can inhabit, and of their wide dispersal. The Scottish occurrences are in near-coastal lagoonal dolomites, the Liaoning ones in thin green mudstones intercalated in thick, mainly fluvial, red-beds. They probably represent temporary pools or abandoned channels in flood-plains. And few places could be more different now than the shores of the Isle of Muck in the windy Hebrides, and the semi-arid uplands of Liaoning where the authors have jointly collected these conchostracans.

#### SYSTEMATIC PALAEOONTOLOGY

Order CONCHOSTRACA Sars, 1867

Superfamily EOESTHERIOIDEA Zhang and Chen, 1976 (*in* Zhang *et al.* 1976)

Family EUESTHERIIDAE Defretin, 1865

Genus EUESTHERIA Deperet and Mazeran, 1912

Type species. *Estheria minuta* (Zieten, 1833)

*Euestheria trotternishensis* sp. nov.

Plate 1, figs 1–6

*Etymology.* From Trotternish, the northernmost peninsula of the Isle of Skye, Scotland.

*Holotype.* A left valve (BMNH In 63723, Pl. 1, fig. 2) from 2.5 m above the base of the Kildonnan Member, Lealt Shale Formation at Lonfearn Cliff, Trotternish, Skye.

*Occurrence.* Limited to the basal part of the Kildonnan Member of their Lealt Shale Formation (early Bathonian) in Skye and Eigg, NW Scotland. *Euestheria* indet., possibly the same species, occurs also in the Cullaidh Shale Formation in Strathaird (LEIUG 108064–6), and *Euestheria?* in bed 5 of the Kildonnan Member in Trotternish (LEIUG 108069).

*Additional material.* Numerous specimens are from the same locality as the holotype, where *E. trotternishensis* ranges through at least 1 m of strata below the holotype horizon (BMNH In 63724, 5, LEIUG 108060–3, 108067, 108181). A few specimens are from bed 1 of the type section of the Kildonnan Member, Lealt Shale Formation, Eigg (SM J49383–7; LEIUG 108179, 80).

*Diagnosis.* This new species differs from *E. minuta* in possessing numerous flattened growth bands, and from *E. ziliujingensis* (Zhang *et al.* 1976) of the early Middle Jurassic in China in having a subquadrate carapace outline.

*Description.* All specimens are well preserved carapaces or external moulds. Carapace small, subquadrate in outline, 4.2–5.5 mm long 3.3–4.3 mm high; dorsal margin short, umbo projecting above its subcentral part; anterior and posterior margins relatively straight, ventral margin arched downward; 23–35 growth bands, flattened, and with many small punctae ornamenting the surface especially in lower parts of the growth bands (Pl. 1, figs 1, 5, 6) or appearing as small granules on the external mould (Pl. 1, figs 3 and 4).

Genus FIBRESTHERIA gen. nov.

*Etymology.* From the fibrous appearance of the growth bands.

Type species. *Fibrestheria puncta* sp. nov. from the Kilmaluag Formation of Skye.

*Occurrence.* Late Bathonian; NW Scotland and Central England.

*Diagnosis.* Carapace of moderate size, subcircular or elliptical in outline; growth bands flattened, ornamented by minute and crowded punctae which form vertical lines.

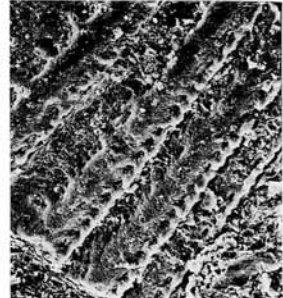
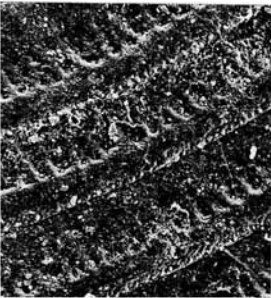
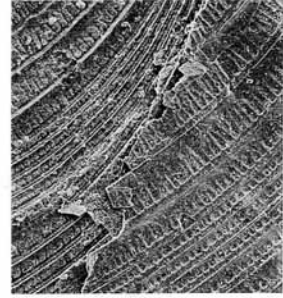
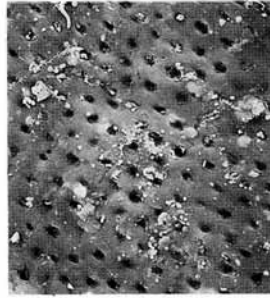
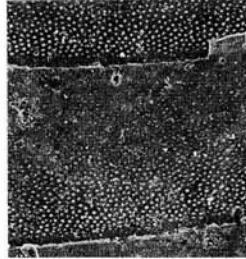
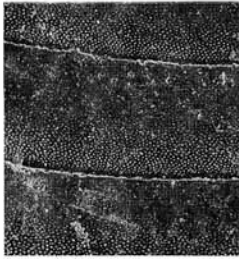
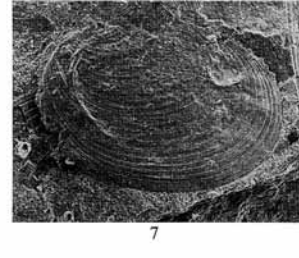
*Discussion.* Among all forms of the family Euestheriidae, *Tenuestheria* from the Upper Cretaceous is similar to this new genus in ornamentation, but differs in its thin carapace, few and broad growth bands, and especially in its punctate sculpture without vertical alignment.

EXPLANATION OF PLATE 1

Figs 1–6. *Euestheria trotternishensis* sp. nov., from the basal Kildonnan Member, Lealt Shale Formation, Lonfearn Cliff, Skye. 1, 3, 4, BMNH In 63724; 1,  $\times 42$ ; 3,  $\times 72$ ; 4,  $\times 120$ . 2, holotype, BMNH In 63723,  $\times 7.7$ . 5 and 6, BMNH In 63725; 5,  $\times 180$ ; 6,  $\times 600$ .

Figs 7–12. *Skyestheria elliptica* gen. et sp. nov., from the Lonfearn Member, Lealt Shale Formation, Rigg Burn, Skye. 7 and 8 holotype, BMNH In 63742; 7,  $\times 12$ ; 8,  $\times 180$ . 9–11, BMNH In 63743; 9,  $\times 42$ ; 10,  $\times 120$ ; 11,  $\times 180$ . 12, BMNH In 63744,  $\times 240$ .

PLATE I



*Fibresteria puncta* sp. nov.

Plate 4, figs 1, 8, 11

*Etymology.* From the punctate nature of the growth band sculpture.*Holotype.* An external mould of a right valve with some pieces of surviving shell (SM J49594-604I, Pl. 4, figs 1, 8, 11), from the Kilmaluag Formation of Skye.*Occurrence.* Kilmaluag Formation, Trotternish, Skye; so far known from one hand specimen only. *Fibresteria* cf. *puncta* occurs in the top 30 cm of the Blisworth Limestone (late Bajocian) on the M1 motorway near Newport Pagnell, Bucks (SP 8564 3840); BGS collection WA 908-910. This is probably within the *aspidioides* zone, late Bathonian (Cope *et al.* 1980, p. 39, fig. 6b).*Additional material.* Many individuals in the same slab (SM J49594-604) from Kilmaluag, Trotternish, Skye, bed 7 of Andrews (1985, p. 1122).*Diagnosis.* As for the genus.*Description.* Carapace of moderate size, elliptical to subcircular in outline, 8-11 mm long, 5-7 mm high; dorsal margin somewhat broken, umbo narrow and small, situated between its central and anterior end; anterior margin straight, posteroventral margin rounded; more than 30 growth bands with overlapping junctions, ornamented with minute and crowded punctae that are vertically aligned.

## Family AFROGRAPTIDAE Novojilov, 1957

## Genus NEOPOLYGRAPTA gen. nov.

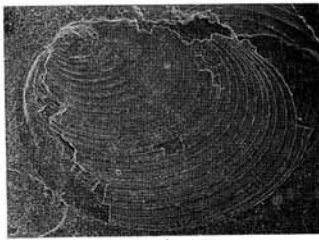
*Etymology.* This genus resembles *Polygrapta* Novojilov, 1957, but is younger.*Type species.* *Neopolygrapta lealtensis* sp. nov. from the Lealt Shale Formation and Cullaidh Shale Formation in Skye.*Occurrence.* Early Bathonian; NW Scotland.*Diagnosis.* Carapace small, elliptical or oval in outline; numerous growth bands with radial striae and cross bars, forming irregular reticulations with each other; growth lines with tubiform serrations of the lower margin.*Discussion.* The new genus and *Polygrapta*, distributed in the Euro-Asia continent during the Permian and Triassic, are much alike in ornamentation and growth bands, but the former differs from the latter in its tubiform serrations of the lower margin of the growth lines.*Neopolygrapta lealtensis* sp. nov.

Plate 2, figs 1-12; Plate 10, figs 1-12

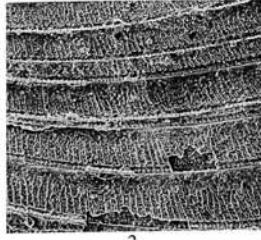
*Etymology.* From the Lealt River in Trotternish, Isle of Skye, Scotland.

## EXPLANATION OF PLATE 2

Figs 1-12. *Neopolygrapta lealtensis* gen. et sp. nov., from the Lealt Shale Formation of the Rudha nam Braithairean area, Skye; BMNH In 63728 and 63730 from the Lonfearn Member, BMNH In 63726,7 from the Kildonnann Member. 1, holotype, BMNH In 63726,  $\times 12$ . 2 and 9, BMNH In 63727; 2,  $\times 42$ ; 9,  $\times 120$ . 3-6, 12, external mould, BMNH In 63728; 3,  $\times 42$ ; 4,  $\times 12$ ; 5,  $\times 90$ ; 6,  $\times 90$ ; 12,  $\times 420$ . 7, BMNH In 63729,  $\times 180$ . 8, 10, 11, BMNH In 63730; 8,  $\times 72$ ; 10,  $\times 60$ ; 11,  $\times 420$ .



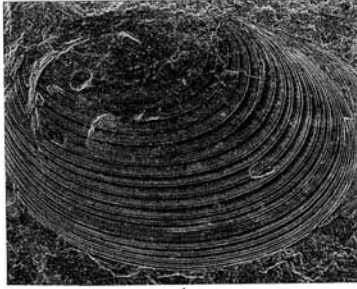
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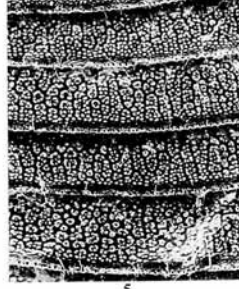
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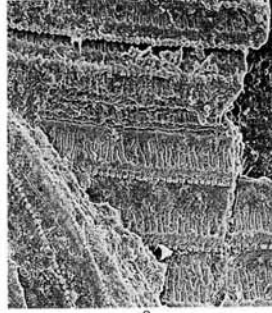
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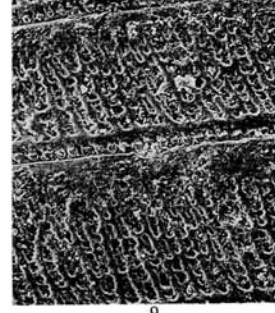
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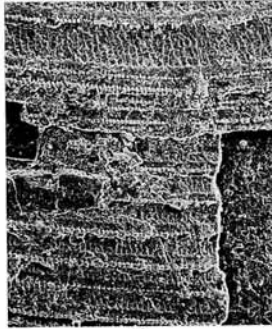
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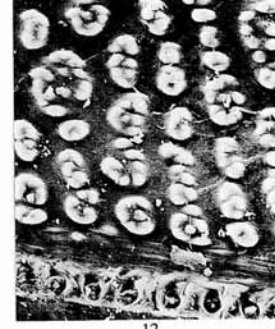
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*Holotype.* A left valve (BMNH In 63726, Pl. 2, fig. 1) from Upper Kildonnan Member of the Lealt Shale Formation, Lonfearn Cliff, Skye.

*Occurrence.* Kildonnan Member to lower Lonfearn Member of the Lealt Shale Formation, Isle of Skye.

*Additional material.* Many specimens from the Kildonnan and lower Lonfearn Members of the Lealt Shale Formation, Trotternish, Skye. Kildonnan Member: LEIUG 108082-4 from Rudha nam Braithairean; LEIUG 108085,6 from Lonfearn Cliff; LEIUG 108087-9 from South Rigg. Lonfearn Member: LEIUG 108070-81, 108184,5 from Rudha nam Braithairean; BMNH In 63728, LEIUG 108182,3 from Lonfearn Cliff; LEIUG 108194 from the Lealt River; LEIUG 108090,1, 108186-9 from North Rigg.

*Diagnosis.* As for the genus.

*Description.* Most specimens are well preserved carapaces or external moulds. Carapace small, oval or elliptical in outline, 4-5.5 mm long, 3-4 mm high; dorsal margin short and straight, umbo small, situated near its anterior end; anterior, posterior and ventral margins rounded; about 30 growth bands covered with radial striae and cross bars, striae simple and sometimes branching, cross bars fine and separating the interspace between striae into irregular reticulation; growth lines with short tubiform serrations of the lower margin. In external moulds of the carapace, growth bands with dotted ornamentation, radially arranged vertically, each dot consisting of several granules.

#### Genus DENDROSTRACUS gen. nov.

*Etymology.* From the dendritic appearance of the growth band sculpture.

*Type species.* *Dendrostracus hebridesensis* sp. nov. from the Lealt Shale Formation in the Isle of Skye.

*Occurrence.* Bathonian of Britain; the type species known only from the Great Estuarine Group of Scotland (see below).

*Dendrostracus?* also occurs in the Forest Marble, from 3-4 m beneath the Cornbrash, in the BGS Sandpool Farm borehole (SU 0122 9427) between Cirencester and Swindon. These strata most probably belong to the *aspidioides* zone, late Bathonian (Cope *et al.* 1980, p. 32).

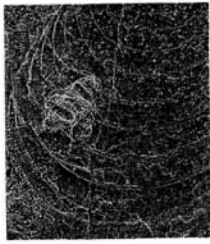
*Diagnosis.* Carapace small, elliptical or oval in outline; growth bands flattened and ornamented by dendritic striae and small reticulations, reticulation separated by dendritic striae into many groups of meshwork patterns. Growth lines with tubiform serrated lower margins.

*Discussion.* This genus is similar in size and shape of carapace to *Neopolygrapta*, but differs from the latter in broader growth bands with dendritic ornament, and in the longer tubes forming the serrated lower margin of the growth lines, with a few cross bars between the tubes. The new genus is also somewhat similar in ornamentation of growth bands to *Jilinstheria*, *Plectestheria* and *Glyptostracus* (Zhang *et al.* 1976, pl. 82, fig. 2; pl. 84, figs 5 and 6; pl. 133, figs 1-5) from the Upper Cretaceous of NE China, but differs from them chiefly in having a tubiform serrated lower margin to its growth lines. In addition, the dendritic striae of three Upper Cretaceous forms are much stronger and more thickened than these of *Dendrostracus*, and their reticulations between dendritic striae are of clearly different origin.

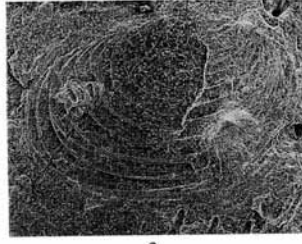
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#### EXPLANATION OF PLATE 3

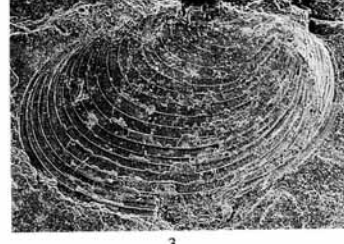
Figs 1-9. *Dendrostracus hebridesensis* gen. et sp. nov., from the Kildonnan Member, Lealt Shale Formation, south Rigg, Skye. 1 and 2 holotype, BMNH In 63731; 1,  $\times 18$ ; 2,  $\times 12$ . 3 and 5, BMNH In 63732; 3,  $\times 12$ ; 5,  $\times 180$ . 4 and 7, BMNH In 63732; 4,  $\times 240$ ; 7,  $\times 600$ . 6, BMNH In 63733,  $\times 120$ . 8, BMNH In 63735,  $\times 420$ . 9, BMNH In 63736,  $\times 200$ .



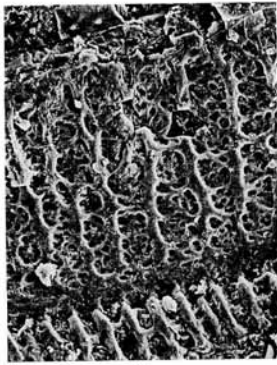
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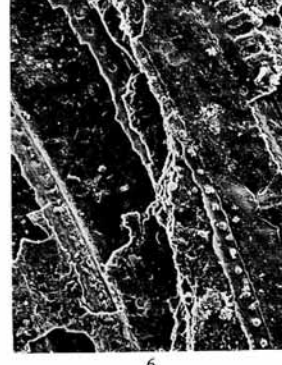
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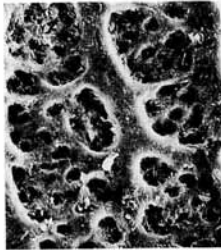
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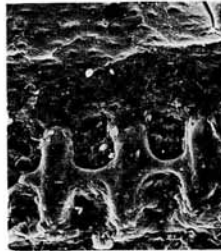
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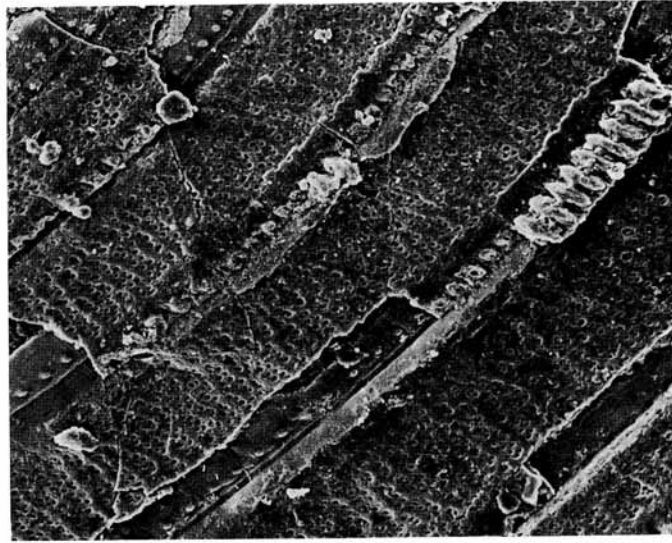
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*Dendrostracus hebridesensis* sp. nov.

Plate 3, figs 1-9; Plate 9, figs 9-12

*Etymology.* From the Hebrides, islands off NW Scotland.*Holotype.* An external mould of a left valve (BMNH In 63731, Pl. 3, fig. 2) from the Kildonnan Member, Lealt Shale Formation, in S Rigg, Skye.*Occurrence.* The species has a short recorded range in the upper Kildonnan and lower Lonfearn Members of the Lealt Shale Formation, Skye.*Additional material.* At least 21 specimens from the upper Kildonnan and lower Lonfearn Members of the Lealt Shale Formation, Trotternish, Skye. Kildonnan Member: LEIUG 108086, 108095-7 from Rudha nam Braithairean; LEIUG 108099, 100 from Lonfearn Cliff; BMNH In 63732-6, LEIUG 108098, 108190-3 from South Rigg, Lonfearn Member: LEIUG 108094 from Rudha nam Braithairean.*Diagnosis.* As for the genus.*Description:* Most specimens are poorly preserved internal or external moulds, but a few well preserved carapaces or external moulds show excellent ornamentation. Carapace small, oval or elliptic in outline, 3.5-4.6 mm long, 2.6-3.3 mm high; dorsal margin short and slightly arched upward; umbo small, situated subcentrally; anterior, posterior and ventral margins rounded, postventral margin obviously expanded; 15-30 growth bands, flattened and ornamented with dendritic striae and small reticulations which are separated by dendritic striae into many groups of mesh (each group generally including 6-8 meshes); occasionally only small reticulations in one or two growth bands near the ventral margin of carapace and without dendritic striae; a row of long tubiform structures attached to the lower margin of each growth line near the ventral side of the carapace, and a few cross bars between the tubes (Pl. 3, figs 4 and 8).

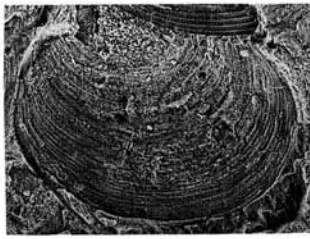
## Genus SKYESTHERIA gen. nov.

*Etymology.* From the Isle of Skye, Scotland.*Type species.* *Skyestheria intermedia* Chen and Hudson sp. nov. from the Lonfearn Member, Lealt Shale Formation in Skye.*Occurrence.* Bathonian, Isle of Skye.*Diagnosis.* Carapace small, oval, elliptical or subcircular in outline; numerous growth bands with *Neopolygrapta*-type ornamentation which crosses the whole band near the dorsal side of the carapace, but only occurs in the lower part of each band near the ventral side; growth lines with beaded lower margin.*Discussion.* This genus originates directly from *Neopolygrapta*. Its ornamentation of radial striae with cross bars shrinks back to the lower part of each growth band near the ventral side of the carapace and the upper part of the growth band is smooth. Along the lower margin of each growth

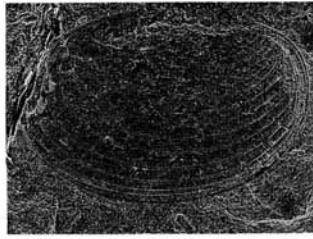
## EXPLANATION OF PLATE 4

Figs 1, 8, 11. *Fibrestheria puncta* gen. et sp. nov., holotype, SM J49594-604I, from the Kilmaluag Formation, Kilmaluag, Skye. 1,  $\times 5.5$ . 8,  $\times 42$ . 11,  $\times 414$ .Figs 2, 3, 5, 6, 9, 12. *Skyestheria intermedia* gen. et sp. nov., from the Lonfearn Member, Lealt Shale Formation, Skye. 2, BMNH In 63738,  $\times 12$ . 3 and 5, holotype, BMNH In 63737; 3,  $\times 72$ ; 5,  $\times 12$ . 6, BMNH In 63739,  $\times 120$ . 9, BMNH In 63740,  $\times 420$ . 12, BMNH In 63741,  $\times 900$ .Figs 4, 7, 10. *Antronestheria praecursor* gen. et sp. nov., from the upper part of the Lonfearn Member, Lealt Shale Formation, Lealt River, Skye. 4, holotype, SM J49409,  $\times 4.8$ . 7, BMNH In 63751,  $\times 60$ . 10, SM J49398,  $\times 72$ .

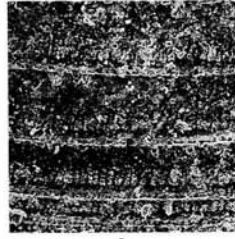




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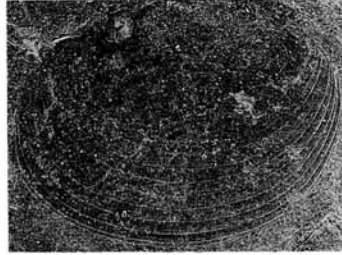
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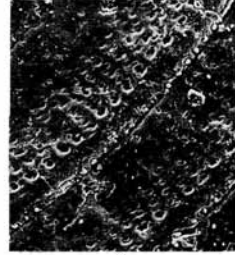
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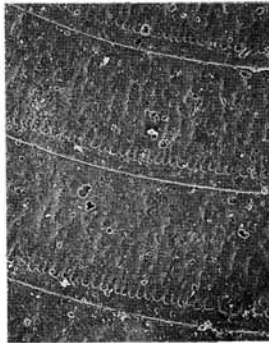
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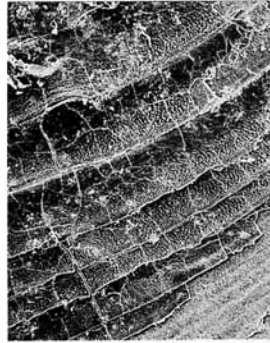
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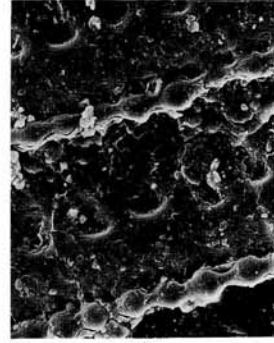
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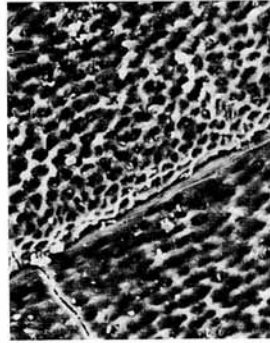
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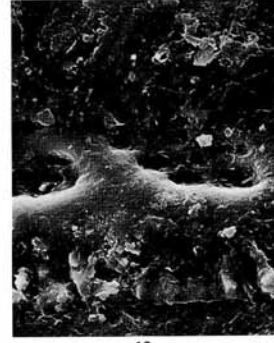
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line, the tubiform structure has been replaced by beading, presumably for consolidating the carapace, and the growth lines have thickened.

*Skyestheria intermedia* sp. nov.

Plate 4, figs 2, 3, 5, 6, 9, 12; Plate 9, figs 5–8

*Etymology.* This species is believed to occupy an intermediate position in the evolution of these conchostracans.

*Holotype.* An external mould of a left valve (BMNH In 63737, Pl. 4, figs 3 and 5) from the middle Lonfearn Member of the Lealt Shale Formation in the Lealt River, Skye.

*Occurrence.* Lonfearn Member of the Lealt Shale Formation in Skye.

*Additional material.* At least 32 specimens from the Lonfearn Member of the Lealt shale formation in Skye. BMNH In 63738, LEIUG 108104,5, 108198,9, from Rudha nam Braitharean; LEIUG 108112–4 from Lonfearn Cliff; BMNH In 63739, LEIUG 108102,3, 1081101,1, 108195–7 from Lealt River; BMNH In 63741, LEIUG 108106–9, 108200–5, from North Rigg; LEIUG 108115,6 from Elgol.

*Diagnosis.* *Skyestheria* with radial striae and cross bars in interspace sculpture of approximately equal strength.

*Description.* Carapace small, oval, elliptical or subcircular in outline, 3.5–4.5 mm long, 2.3–3.6 mm high; dorsal margin short and straight, umbo small and situated between its central and anterior end; anterior and ventral margins relatively straight, post-ventral margin rounded and slightly expanded; about 20–30 growth bands, ornamented by radial striae with cross bars through whole intervals in dorsal side, or only occupying the lower part of interval in ventral side; near ventral margin of carapace, thickened growth lines with beading along its lower margin and a row of shallow cavernous sculpture along its upper margin, several minute punctae surrounding the major structures in each case.

*Skyestheria elliptica* sp. nov.

Plate 1, figs 7–12

*Etymology.* From the shape of the carapace.

*Holotype:* A left carapace (BMNH In 63742, Pl. 1, figs 7, 8, 10) from the Lonfearn Member of the Lealt Shale Formation in Rigg Burn, Skye.

*Occurrence.* Lonfearn Member of the Lealt Shale Formation in Skye, from one bed only so far.

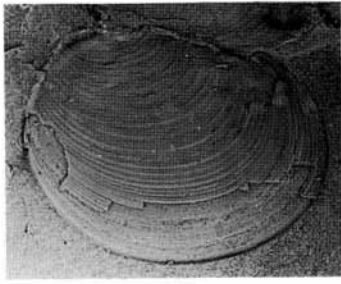
*Additional material.* Five specimens BMNH In 63743,4, LEIUG 108117,8, 108206 from same locality and same horizon as the holotype.

*Diagnosis.* *Skyestheria* with radial striae markedly stronger than cross bars in interspace sculpture.

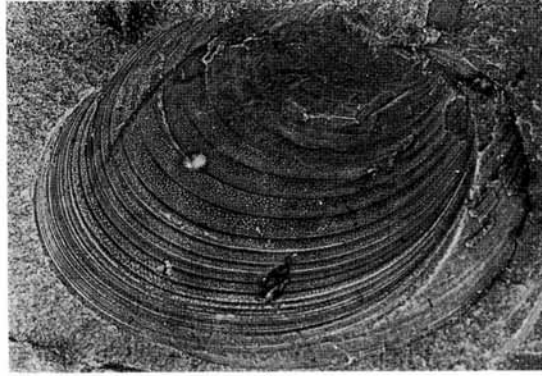
*Description.* This species is very similar in shape and size of carapace to *S. intermedia*, but differs chiefly in ornamentation. Its radial striae are consistently stronger and cross bars are weaker than those of *S. intermedia*: compare Plate 1, figures 9, 10, 11 with Plate 4, figure 6 and Plate 9, figures 5, 6, 7, 8. The carapace of the holotype is 3.2 mm long and 2.3 mm high. There are about 30 growth bands.

EXPLANATION OF PLATE 5

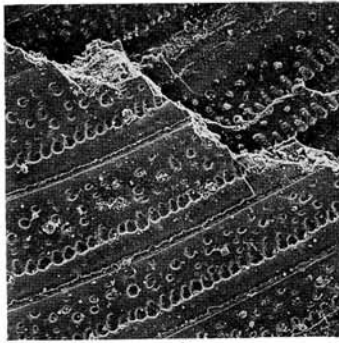
Figs 1–8. *Antronestheria kilmaluagensis* gen. et sp. nov., from the Kilmaluag Formation, Trotternish, Skye.  
1, BMNH In 63746,  $\times 9.6$ . 2, holotype, BMNH In 63745,  $\times 13.5$ . 3–5 BMNH In 63747; 3,  $\times 90$ ; 4,  $\times 300$ ;  
5,  $\times 300$ . 6, BMNH In 63748,  $\times 600$ . 7, BMNH In 63749,  $\times 600$ . 8, paratype, left valve BMNH 63750,  $\times 20$ .



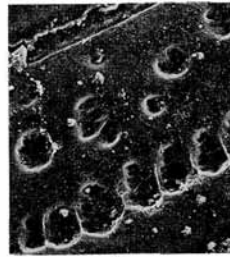
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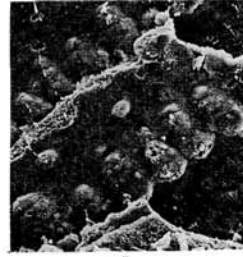
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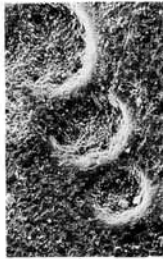
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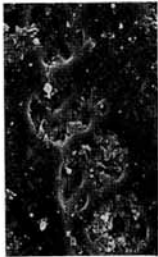
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CHEN and HUDSON, *Antronestheria kilmaluagensis*

## Family ANTRONESTHERIIDAE nov.

Carapace elliptical or subcircular in outline; numerous growth bands with cavernous ornamentation; fossae of moderate or large size, simple or consisting of small punctae. Includes *Antronestheria* Chen and Hudson (gen. nov.), *Pseudestherites* Chen, 1976 (in Zhang *et al.* 1976), *Paleoleptestheria? chinensis* Chen, 1976 (in Zhang *et al.* 1976). Middle Jurassic to Lower Cretaceous.

## Genus ANTRONESTHERIA gen. nov.

*Etymology.* From the Greek *antron*, a cave or cavity, in reference to the interspace sculpture.

*Type species.* *Antronestheria kilmaluagensis* sp. nov. from the Kilmaluag Formation (Bathonian) in NW Scotland and late Bathonian strata in the Porcupine Basin, NE Atlantic off Ireland.

*Occurrence.* Middle to upper Bathonian; NW Scotland, eastern England and Porcupine Basin off Ireland.

*Diagnosis.* Carapace moderate in size, oval to subcircular in outline; growth bands broad and flattened, with large cavernous ornamentation; fossae, consisting of several punctae, deepened and crowded along upper margin of each growth line; growth lines smooth and thickened.

*Discussion.* The new genus resembles *Paleoleptestheria chinensis* from the late middle Jurassic of SW China, and *Pseudestherites* from early Lower Cretaceous of NE China (Zhang *et al.* 1976, pl. 34, figs 1–8; pl. 39, figs 1, 2, 7, 8) in cavernous ornamentation, but differs from them in possessing several punctae in each fossa, and a row of crowded and deepened fossae along the growth line. *Antronestheria* probably evolved from *Skyestheria* of the Lonfean Member, but the latter differs from the former in having the beading along lower margin of each growth line and radial striae with cross bars in between.

*Antronestheria kilmaluagensis* sp. nov.

Plate 5, figs 1–8; Plate 9, figs 1–4

*Etymology.* From Kilmaluag, a village in north Trotternish, Isle of Skye, Scotland.

*Holotype.* An external mould of a left valve (BMNH In 63745, Pl. 5, fig. 2) from the Kilmaluag Formation in Kilmaluag Bay, Skye.

*Occurrence.* Commonly in the Kilmaluag Formation in Skye, NW Scotland; also in the same formation, Eigg (beds 1–9 of Andrews, 1985, p. 1125; LEIUG 108144–6). One recorded occurrence each from the Duntulm Formation, Lon Ostatoin, Skye, and the top of the Valtos Formation, Muck (LEIUG 108142–3). Also recorded from the late Bathonian, Porcupine Basin, and from the Blisworth Clay of the BGS Nettleton Bottom borehole, Lincolnshire (BGS BLJ 7762).

*Additional material.* At least 28 specimens from the Kilmaluag Formation, Trotternish, Skye. From Beds 1–7 of Andrews (1985, p. 1122) in Kilmaluag Bay: BMNH In 63746, LEIUG 108207–10, 108119–32. LEIUG 108133 from Lub Score. BMNH In 63747–50, LEIUG 108211–4 from Lon Spapail.

## EXPLANATION OF PLATE 6

Figs 1, 3, 5, 6b, 8. *Pseudograptia orbita* Chen, 1976, from the Kilmaluag Formation(?) near Monkstadt, Trotternish, Skye. 1 and 8, left valve, BGS, GSC 7296c; 1,  $\times 6$ ; 8,  $\times 22$ . 3, 5, 6b, right valve, BGS, GSC 7296b; 3,  $\times 6$ ; 5,  $\times 22$ ; 6b,  $\times 2.4$ .

Figs 2, 4, 6a, 7. *Pseudograptia murchisoniae* (Jones, 1863), from the Kilmaluag Formation(?), near Monkstadt, Trotternish, Skye. 2 and 6a, lectotype, BGS, GSC 7296a; 2,  $\times 6$ ; 6a,  $\times 2.4$ . 4, BGS, GSC 7296e,  $\times 22$ . 7, BGS, GSC 7296f,  $\times 22$ .

Fig. 6d. *Pseudograptia jonesi* sp. nov., BGS, GSC 7296d, from the Kilmaluag Formation (?), near Monkstadt, Trotternish, Skye,  $\times 2.4$ .



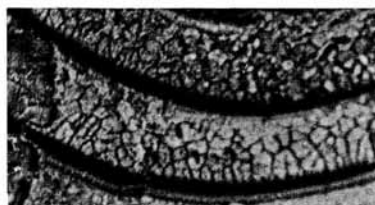
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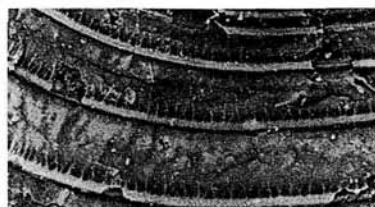
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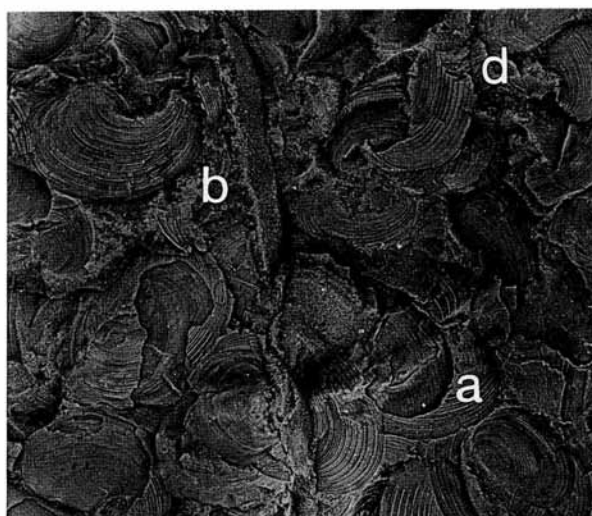
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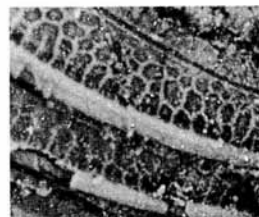
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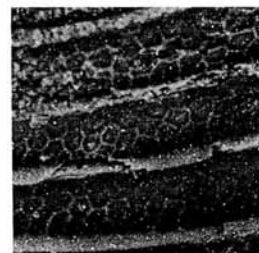
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*Diagnosis.* *Antronestheria* with large fossae in growth bands that are not aligned.

*Description.* Specimens are well preserved carapaces or external moulds. Carapace of moderate size, subcircular in outline, 3.8–8 mm long, 3–6 mm high; dorsal margin short, small umbo located near its centre; anterior and posterior margins relatively straight, postero-ventral margin rounded and slightly expanded; about 30 growth bands on carapace of adult, ornamented by cavernous sculpture; fossae subcircular or irregular-elliptical; each big fossa including several small punctae (Pl. 5, figs 4, 6, 7); a row of crowded and deepened fossae along upper margin of each growth line (Pl. 5, fig. 3); growth lines smooth and thickened, without beading or tubiform serrated lower margin. In external moulds, fossae appear as large pits which contain small granules (Pl. 5, fig. 5).

*Antronestheria praecursor* sp. nov.

Plate 4, figs 4, 7, 10

*Etymology.* This species is a precursor of the type species stratigraphically.

*Holotype.* An external mould of a right valve (SM J49409, Pl. 4, fig. 4) from upper Lonfearn Member of the Lealt Shale Formation in Lealt River, Isle of Skye.

*Occurrence.* Upper Lonfearn Member of the Lealt Shale Formation, Skye.

*Additional material.* Specimens are poorly preserved carapaces or exterior moulds (SM J49397–49414 (this series includes the holotype), BMNH In 693751, LEIUG 108136, 108215,6) from the upper Lonfearn Member of Skye.

*Diagnosis.* *Antronostheria* with fossae in growth bands aligned in vertical rows.

*Description.* Carapace subcircular in outline, 6.5–8 mm long, 4.75–5.9 mm high; anterior, posterior, and ventral margins all rounded; dorsal and umbonal area always poorly preserved, so growth lines not counted exactly; growth bands broad and flattened, covered with cavernous ornamentation; fossae vertically extended, crowded and deepened along upper margin of each growth line; growth lines thickened, without beading in their lower margins.

*Remarks.* *Antronestheria kilmaluagensis* is the dominant conchostracan of the upper Great Estuarine Group (see above), and *A. praecursor* from the upper part of the Lonfearn Member could be the earliest species of the genus.

Family EOSESTERIIDAE Zhang and Chen, 1976 (*in* Zhang *et al.* 1976)

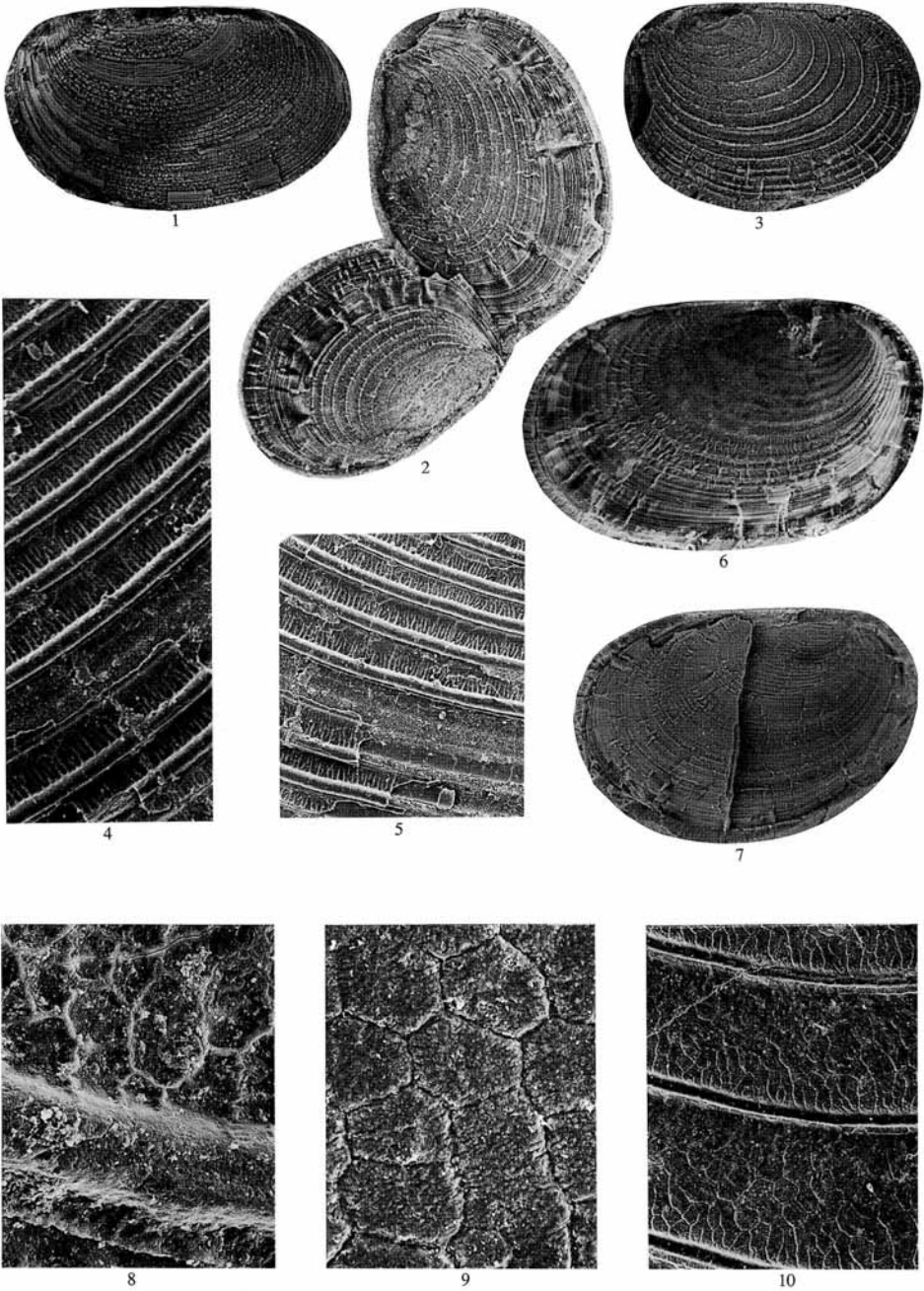
Genus PSEUDOGRAPTA Novojilov, 1954

*Type species.* *Estheria murchisoniae* (Jones, 1863), from Upper Kilmaluag Formation (?) in Skye and Muck, NW Scotland.

*Occurrence.* Late Middle Jurassic; W Europe and E Asia.

#### EXPLANATION OF PLATE 7

Figs 1, 4, 5, 7. *Pseudograptia jonesi* sp. nov. 1, holotype, BGS, GSC 7296g, from the Kilmaluag Formation(?), Skye (associated with lectotype of *P. murchisoniae*), × 6; 4 and 5, BGS, GSC 7296h, fragments of same shell; 4, × 96; 5, × 42. 7, BMNH In 63752, from the Upper Kilmaluag Formation, Camas Mor, Muck, × 4.3.  
Fig. 2. *Pseudograptia orbita* Chen, 1976, from the Upper Kilmaluag Formation, Camas Mor, Muck, BMNH In 63754, × 5.6.  
Figs 3, 6, 8–10. *Pseudograptia murchisoniae* (Jones, 1863), from the Upper Kilmaluag Formation, Camas Mor, Muck. 3 and 6, BMNH In 63753; 3, × 5.6; 6, × 6. 8–10, BMNH In 63755–7, respectively; 8, × 420, 9, × 420, 10, × 42.



CHEN and HUDSON, *Pseudograptia*

*Diagnosis.* Carapace large, elliptical or subcircular in outline; growth bands broad and flattened, ornamented by bold polygonal reticulations in dorsal and central parts of carapace, and radial striae in ventral or postero-ventral parts; growth lines stout and convex (growth ridges), without beading or tubiform marginal structures.

*Discussion.* This genus is similar in ornament to *Eosestheria*, but differs in its stout and convex growth ridges and in the coarser polygonal reticulations of its growth bands. In general, the change from reticulation near the dorsal side into radial striae near the ventral side is abrupt for *Pseudograptia* (except *P. morrisoni* sp. nov.), but for *Eosestheria* there is a transitional area of two types of ornament in the carapace. This genus has a strong resemblance to *Nestoria* in stout and convex growth ridges and bold polygonal reticulation, but the latter differs from the former in not having radial striae on its growth bands near the ventral margin of the carapace. Novojilov (1954, pp. 81–82, pl. 15, fig. 10; pl. 16, fig. 1) referred another three species to this genus: *P. andrewsi* (Jones), *P. orientalis* (Eichwald), and *P. olonchurenensis* Novojilov, but unfortunately so far no bold polygonal reticulations or stout convex growth ridges are to be found among them.

*Pseudograptia muchisoniae* (Jones, 1863)

Plate 6, figs 2, 4, 6a, 7; Plate 7, figs 3, 6, 8–10

- 1863 *Estheria muchisoniae* Jones, pp. 100–101, pl. 3, figs 1–12.  
 1946 *Bairdestheria muchisoniae* (Jones); Raymond, p. 227.  
 1954 *Pseudograptia muchisoniae* (Jones); Novojilov, p. 81.  
 1976 *Pseudograptia* aff. *muchisoniae* (Jones); Zhang *et al.*, p. 173, pl. 56, figs 1–8.

*Lectotype.* An external mould of a left valve from the syntype (British Geological Survey, Geological Society Collection (BGS, GSC) 7296a, Pl. 6, figs 2 and 6a) figured by Jones in 1863 (pl. 3, fig. 2) from the Upper Kilmaluag Formation (?) in the canal, Icolmkill, Skye.

*Occurrence.* Upper Kilmaluag Formation (?) from 'Icolmkill', Skye and Camas Mor, Muck, NW Scotland.

*Material.* Eleven specimens: syntype (BSG, GSC 7296) from Skye; BMNH In 63753, 63755–7, LEIUG 108137–41, 108217 from Camas Mor, Muck. Muck specimens from Beds 13 and 15 of the Kilmaluag Formation (Andrews 1985 p. 1125).

*Original Description.* This species was described by Jones (1863 p. 100) as follows: 'carapace-valve nearly elliptical, the straight hinge-line interfering with the symmetry of the outline. The umbo is forward, at the end of the hinge-line, and scarcely affects the outline. The anterior extremity has a flatter curve than the posterior. About eighteen delicate concentric ridges are usually distinctly to be observed, with their rather wide interspaces; but some carapaces have nearly thirty ridges, with very narrow interspaces. The ornament of the interspaces is essentially a bold, irregularly hexagonal reticulation, like that of *E. minuta*; but it generally takes on a distinct, short, vertical wrinkling of the lower part of the interspace. This sometimes presents the modification seen in figs 3 and 8, where the wrinkling is of a much smaller pattern, and reached half way up, or all across the interspace. Sometimes a delicate, horizontal wrinkling, without hiding altogether the reticulate structure of the shell. Not infrequently, both the broad and the narrow interspaces are blank (figs 6 and 10).' Judging from this description, and new observations on the slab bearing Jones's syntype specimens, there are at least three different forms: the first form is elliptical in outline of carapace, with 16–32 growth bands ornamented by bold irregular hexagons near dorsal side and radial striae near ventral side; the second form is subcircular in outline, with 15–20 growth bands and ornamentation as the first; the third form is also

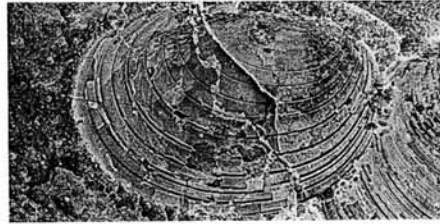
EXPLANATION OF PLATE 8

Figs 1–9. *Pseudograptia morrisoni* sp. nov., from the Upper Kilmaluag Formation, Camas Mor, Muck. 1, BMNH In 63758,  $\times 8.4$ . 2, holotype, BMNH In 63759,  $\times 8$ . 3, BMNH In 63760,  $\times 5$ . 4–9, BMNH In 63751; 4,  $\times 24$ ; 5,  $\times 12$ ; 6,  $\times 24$ ; 7,  $\times 60$ ; 8,  $\times 240$ ; 9,  $\times 420$ .





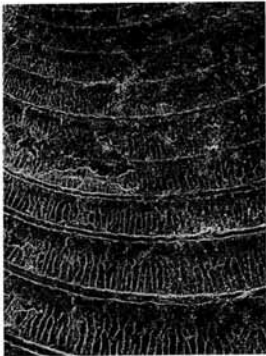
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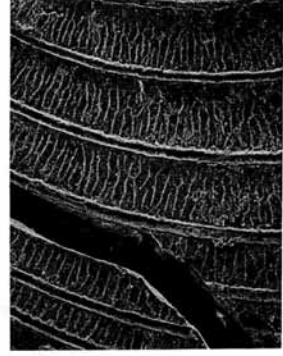
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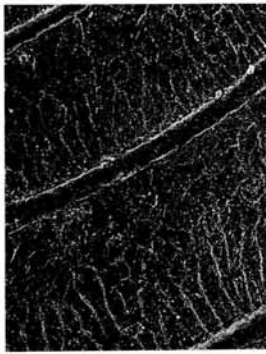
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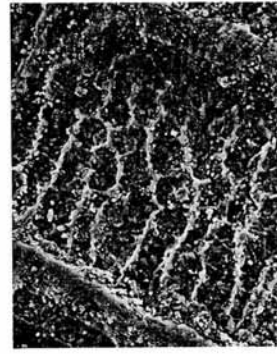
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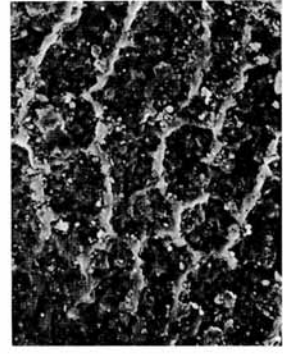
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elliptical in outline, but with about 40 narrow growth bands, ornamented mostly by short radial striae. The present authors consider that this famous conchostracan species should be represented by the first elliptical form, and assign an exterior mould of left carapace from Jones's slab (Pl. 6, figs 2 and 6a) as the lectotype. The second form is referred to *P. orbita* Chen, and the third described herein as *P. jonesi* sp. nov. (see below).

*Revised description.* Carapace large, elliptical in outline, 7.5–10.3 mm long, 5–6.2 mm high; dorsal margin long and straight, umbo small and subanterior; anterior margin straight, the posterior rounded, the ventral arched downward; broad growth bands ornamented by bold polygonal reticulations, mesh mostly irregular hexagonal, mesh wall thin, mesh base shallow and flattened with short septum-like structure (Pl. 7, fig. 9); radial striae frequently developed in the lower part of each growth band near ventral side of carapace; growth ridges stout and smooth.

*Remarks.* Novojilov (1954, pl. 11, fig. 2; pl. 15, figs 5–9) described some specimens from the Upper Jurassic in Mongolia, referring them to this species, but they may belong to *Eosestheria* according to their ornament.

*Pseudograptia orbita* Chen, 1976 (in Zhang *et al.* 1976)

Plate 6, figs 1, 3, 5, 6b, 8; Plate 7, fig. 2

1976 *Pseudograptia orbita* Chen; Zhang *et al.* pp. 173–174, pl. 55, figs 1 and 2.

*Holotype.* An exterior mould of a left carapace from the Middle Jurassic Tuchengzi Formation at Cajiagou near Jinlingsi, W Liaoning, China.

*Occurrence.* Upper Kilmaluag Formation (?) in 'Icolmkill', Skye and Camas Mor, Muck.

*Additional material.* A right valve and another left valve from the same slab as *P. murchisoniae* (BGS, GSC 7296b, c), Skye; five specimens BMNH In 63754, 63762, LEIUG 108139 (two specimens), LEIUG 108141 (M88-CPJ2) from the Upper Kilmaluag Formation at Camas Mor, Muck.

*Description.* Carapace large, subcircular in outline; 8.5–12 mm long, 6.5–8.5 mm high; dorsal margin short, small umbo located between its centre and anterior end; anterior, posterior and ventral margins rather rounded, postero-ventral margin slight expanded; growth ridges stout and convex; 16–32 growth bands broad and flattened, ornamented with bold irregular hexagons in dorsal and middle parts of carapace, and short radial striae in ventral part.

*Remarks.* This species is frequently associated with *P. murchisoniae* and it is very similar to the latter in ornamentation, but differs in outline of carapace. They might be sexual dimorphs, but so far there is no evidence of appendages or eggs in the fossils.

*Pseudograptia jonesi* sp. nov.

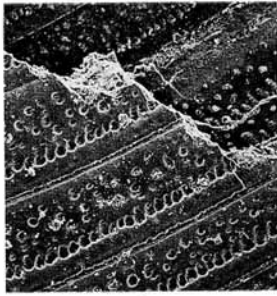
Plate 6, fig. 6d; Plate 7, figs 1, 4, 5, 7

*Etymology.* In honour of Professor T. R. Jones, author of the first monograph on fossil conchostracans.

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EXPLANATION OF PLATE 9

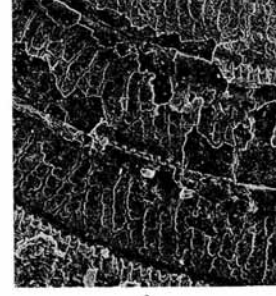
- Figs 1–4. *Antronestheria kilmaluagensis* gen. et sp. nov., BMNH In 63747, Kilmaluag Formation, Trotternish, Skye. Stereo pairs. 1 and 2,  $\times 90$ . 3 and 4,  $\times 180$ .  
 Figs 5–8. *Skyestheria intermedia* gen. et sp. nov., BMNH In 63739 Lonfearn Member, Lealt Shale Formation, Lealt River, Skye. Stereo pairs. 5 and 6,  $\times 90$ . 7 and 8,  $\times 180$ .  
 Figs 9–12. *Dendrostracus hebridesensis* gen. et sp. nov., BMNH In 63733, Kildonnan Member, Lealt Shale Formation, south Rigg, Skye. Stereo pairs. 9 and 10,  $\times 90$ . 11 and 12,  $\times 180$ .



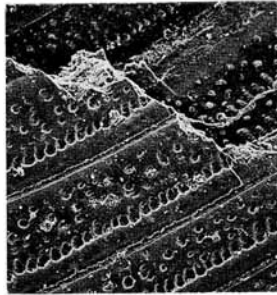
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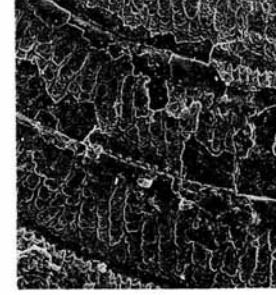
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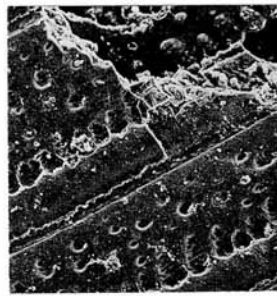
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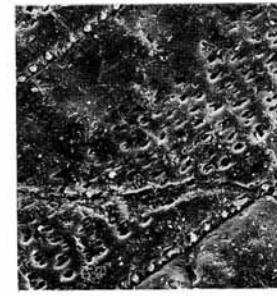
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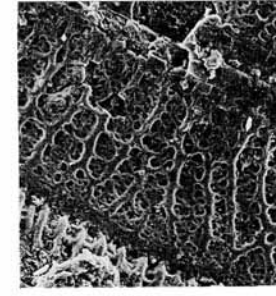
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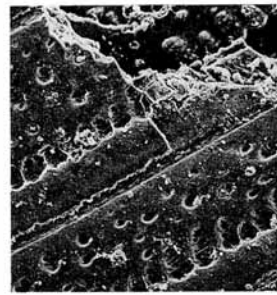
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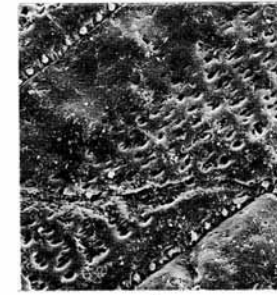
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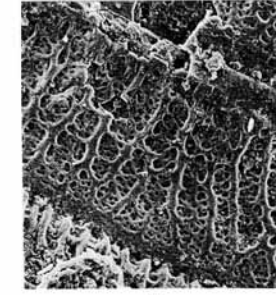
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*Holotype.* An external mould of a right valve with a few pieces of surviving 'chitinous' shell in lower surface of the syntype slab (BGS, GSC 7296g, Pl. 7, fig. 1), from the Upper Kilmaluag Formation (?) at Icolmkill, Isle of Skye; fragments from the same shell showing ornament (BGS, GSC 7296h, Pl. 7, figs 4 and 5).

*Occurrence.* Upper Kilmaluag Formation (?); 'Icolmkill', Skye and Camas Mor, Muck.

*Additional material.* Apart from the holotype, there are two specimens: one from the slab's upper surface (BGS, GSC 7296d, Pl. 6, fig. 6), another (BMNH In 63752) from upper Kilmaluag Formation at Camas Mor, Muck (bed 15 of Andrews 1985).

*Diagnosis.* *Pseudograptia* with narrow and numerous growth bands, and dominant short radial striae on the growth bands.

*Description.* Carapace moderate to large, elliptical in outline, 7.7–11 mm long, 4.7–7.5 mm high; dorsal margin poorly preserved, umbo situated subcentrally or near its anterior end; anterior and posterior margins somewhat straight, ventral margin broadly arched downward; narrow growth bands about 40 in number, ornamented with short radial striae in lower part of each interval, and reticulation only in dorsal region of carapace; growth ridges stout and smooth.

*Pseudograptia morrиси* sp. nov.

Plate 8, figs 1–9

*Etymology.* For Mr S. Morris of the Natural History Museum, London, who collected these conchostracans with us in August 1988.

*Holotype.* An external mould of a left valve (BMNH In 63759, Pl. 8, fig. 2) from the Upper Kilmaluag Formation at Camos Mor, Muck.

*Occurrence.* Upper Kilmaluag Formation, Camas Mor, Muck.

*Additional material.* Six specimens (BMNH In 63758, 63760,1; LEIUG 108218–20); locality and horizon same as holotype (beds 13–15 of Andrews 1985).

*Diagnosis.* Small *Pseudograptia* with reticulation in dorsal growth bands passing into radial striae in ventral growth bands.

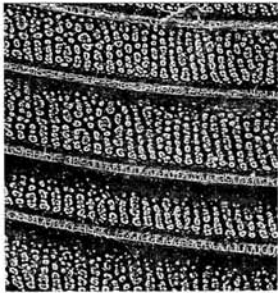
*Description.* Most specimens are poorly preserved internal or external moulds, and only a few with 'chitinous' shell and ornamentation on growth bands. Carapace of moderate size, elliptical in outline, 5.4–9.8 mm long, 3.8–6.5 mm high; dorsal margin straight and long, small and narrow umbo situated near its anterior end; anterior and posterior margins curved symmetrically, ventral margin arched broadly and downward; growth lines thickened; 15–21 growth bands, broad and flattened, ornamented by very irregular polygons near dorsal side and gradually changed into striae near ventral or postero-ventral parts of carapace.

*Discussion.* This species is the smallest of the genus *Pseudograptia*, and might be referred to *Eosestheria* based on the transitional ornament from reticulation in the dorsal side to radial striae in the ventral side, but for the thickened growth lines. *Eosestheria* was widely distributed in E Asia during the late Jurassic and it was considered to evolve from *Nestoria* (Zhang *et al.* 1976, pp. 79–80,

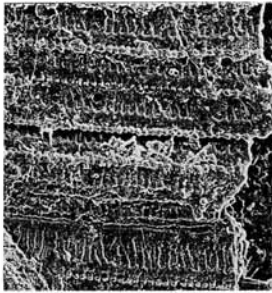
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EXPLANATION OF PLATE 10

Figs 1–12. *Neopolygraptia lealtensis* gen. et sp. nov., Lealt Shale Formation, Lonfearn, Skye. Stereo pairs. 1, 2, 9–12, BMNH In 63728; 1 and 2,  $\times 90$ ; 9 and 10,  $\times 90$ ; 11 and 12,  $\times 180$ . 3–8, BMNH In 63730; 3 and 4,  $\times 180$ ; 5 and 6,  $\times 90$ ; 7 and 8,  $\times 180$ .



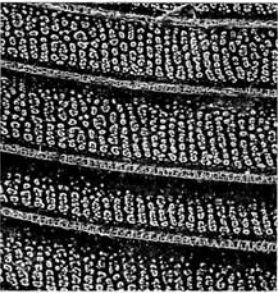
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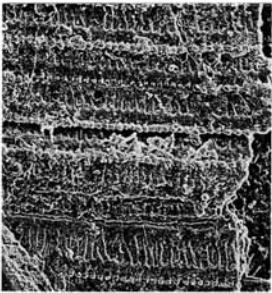
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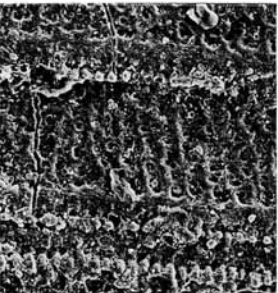
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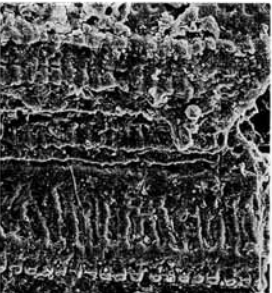
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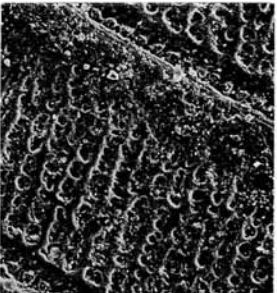
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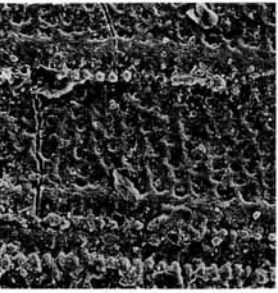
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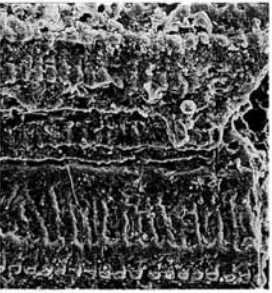
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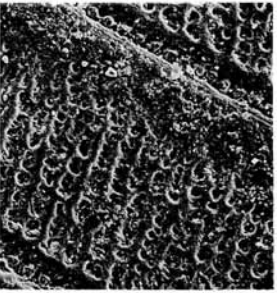
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text-fig. 38). Based on the new material from the Isle of Muck, there is a greater possibility that *Pseudograptia morrissi* sp. nov. is the ancestor of *Eosestheria*.

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