THE ECOLOGY AND STRATIGRAPHICAL DISTRIBUTION OF THE INVERTEBRATE FAUNA OF THE GREAT ESTUARINE SERIES

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ABSTRACT. The invertebrate macrofauna of the Great Estuarine Series is reviewed, with special reference to the ecological inferences which can be drawn from it. Evidence from modern relatives, and from association with other fossils, is used to deduce the probable ecological preferences, especially of salinity, of each of the common species. The stratigraphical distribution of the fauna among the formations of the Series is comprehensively described for the first time. *Unio andersoni* sp. nov. is described and figured.

THIS paper records the stratigraphical distribution of the more important faunas of the Great Estuarine Series (Middle Jurassic) of north-west Scotland, and reviews the evidence for the ecology of the fossils concerned. The stratigraphy of the Series has been described elsewhere (Hudson 1962), and is summarized in text-fig. 1.

The fauna is dominated by the Mollusca. As systematic descriptions of most species have recently been published or are readily available, I have only included morphological descriptions and taxonomic discussions where my own work has added materially to existing knowledge. Ecological information, on the other hand, is very scattered in the literature; part of it comes from modern representatives of fossil groups, and part from association with other fossils. This information is brought together here, attention being concentrated on the commonest species or those giving a clear ecological indication, especially of palaeo-salinity (Hudson, this journal, p. 318).

In the stratigraphical section, all the important invertebrate macro-fossils are listed (Table 1); this is the first such survey for the whole Great Estuarine Series.

THE INVERTEBRATE FAUNA

The restricted nature of the invertebrate fauna of the Great Estuarine Series as compared with that of the equivalent marine beds of the English Great Oolite Series is immediately apparent even when allowance is made for deficient collecting.

The common mollusc species of the Great Estuarine Series were mostly described by Forbes (1851) and Tate (1873). They also identified some fossils with already described English species. Anderson and Cox (1948) redescribed Forbes's and Tate's species, and assigned them to their correct stratigraphical horizons. They also described some new species, and reviewed the fauna of the Great Estuarine Series as then defined. In fact most of this discussion refers to the Staffin Bay Beds of my classification (Hudson 1962), the faunas of which are more marine than those of the Great Estuarine Series *sensu stricto*, and which are not dealt with in detail here. Some of the lamellibranchs were further revised by Casey (1952, 1955), and British Great Oolite mollusca generally have been revised by Cox and Arkell (1948–50). Yen (1948) redescribed some gastropods, but his conclusions have been disputed. Forsyth (1960) records a few fossils new to the 'Series'.

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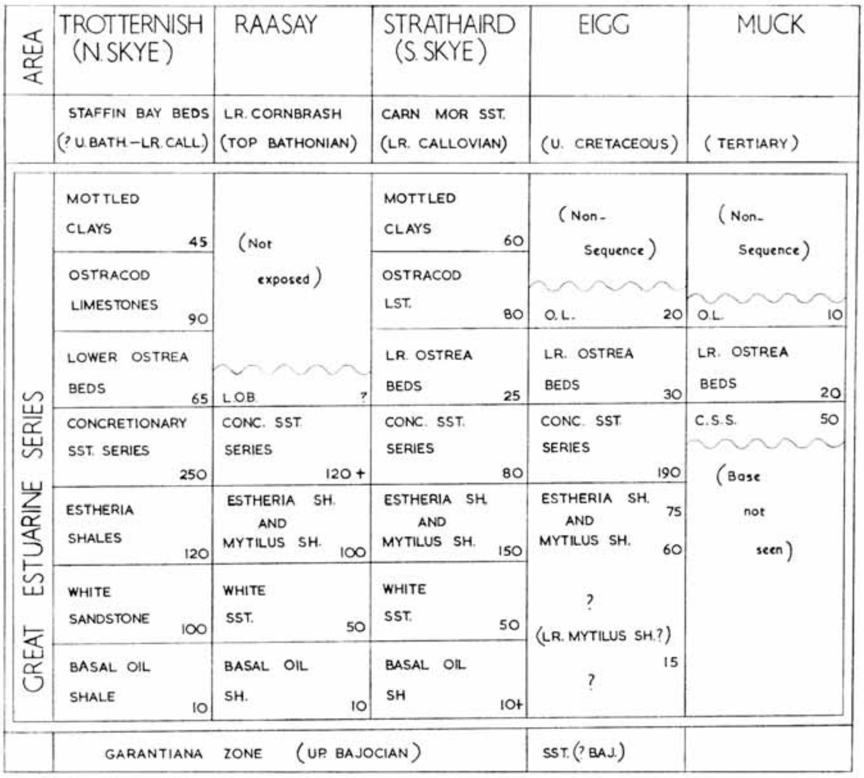
TABLE 1. *List of invertebrate fossils from the Great Estuarine Series*

*Formation abbreviations from text-fig. 1. * = new record for Great Estuarine Series; † = single occurrence only.*

	Formation
Foraminifera: Miliolids, and family indet.*	L.O.B.
Echinoderma: Regular echinoid, plate and spines*	L.O.B.
Isocrinus?†	B.O.S.
Annelida: '*Serpula*' *sp.**†	L.O.B.
Brachiopoda: *Discinisca sp.**†	L.O.B.
'*Rhynchonella*' cf. *concinna* (J. Sow.)	L.O.B.
Polyzoa: Cyclostome indet.*†	L.O.B.
Lamellibranchia:	
Modiolus cf. *imbricatus* J. Sow.	M.S., E.S., L.O.B.
Mytilus (*Praemytilus*) *strathairdensis* Anderson and Cox	M.S.
*Meleagrinella sp.**†	B.O.S.
*Pteroperna sp.**	M.S.
Placunopsis socialis Morris and Lycett*	M.S., E.S., L.O.B.
Placunopsis aesturina (Tate)	M.S., E.S.
Liostrea hebridica (Forbes)	E.S., L.O.B.
Lopha sp.†	M.S.
Unio andersoni sp. nov.	M.S., L.O.B.
Neomiodon brycei (Tate) and *N. spp.*	M.S., L.O.B. incl.
Anisocardia (*Antiquicyprina*) *cucullata* (Tate)	L.O.B.
Quenstedtia cf. *bathonica* (Morris and Lycett)	B.O.S.
Quenstedtia? staffinensis (Forbes)	O.L.
'*Quenstedtia*' *forbesi* Anderson and Cox*	L.O.B.
Pleuromya robusta (Tate)	L.O.B.
Corbula hebridica Tate	L.O.B.
Myopholas acuticostata (J. de C. Sowerby)	L.O.B.
Cuspidaria ibbetsoni (Morris)*	M.S., E.S., L.O.B.
Gastropoda:	
Neridomus arata (Tate)	L.O.B.
Hydrobia praecursor Sandberger†	O.L.
Zebina caledonica (Tate)	L.O.B.
Tornus praecursor (Tate)	M.S., E.S.
Assiminea skyensis Anderson and Cox†	O.L.
Procerithium cf. *pisoliticum* (Hudleston)†	O.L.
Procerithium (*Rhabdocolpus*) cf. *vetustum* (Phillips)†	O.L.
Globularia formosa? (Morris and Lycett)*†	L.O.B.
Globularia hebridica Anderson and Cox	M.S., E.S.
Viviparus scoticus (Tate)	M.S.–O.L. incl.
Viviparus bithnyoides (Yen)†	O.L.
Cylindrobullina inermis (Tate)	M.S., E.S., C.S.S.
Arthropoda:	
Phyllopoda: *Euestheria murchisoniae* (Jones)	B.O.S.–O.L. incl.
Ostracoda: Ostracods including Metacyprids	B.O.S.–O.L. incl.
Bairdia sp.†	B.O.S.
Trace fossils: *Pelecypodichnus amygdaloides* Seilacher*	C.S.S.

My own collection (in the Sedgwick Museum, Cambridge) contains specimens of all the important species and some additions to the fauna. I have also examined the collections in the Geological Survey Museum, Edinburgh (through the kindness of Mr. R. B. Wilson), and have redetermined some of the fossils. I have also been able to correct the stratigraphical assignment of a few groups of specimens.



TEXT-FIG. 1. Stratigraphy of Great Estuarine Series. Thicknesses in feet.

THE ECOLOGY OF THE INVERTEBRATE FAUNA

The fauna listed in Table 1 may be readily divided into ecological groups.

(*a*) The typical fossils of the Great Estuarine Series. Certain species may be considered with more abundant species of the same genus, so that the ecological interpretation of the 'Series' turns very largely on the interpretation of only twelve species or groups: *Modiolus* cf. *imbricatus*, *Mytilus* (*Praemytilus*) *strathairdensis*, *Placunopsis socialis*, *Liostrea hebridica*, *Unio andersoni* sp. nov., *Neomiodon brycei*, *Cuspidaria* *ibbetsoni*; *Viviparus scoticus*; *Tornus praecursor*, *Globularia hebridica*, and *Cylindrobullina inermis*; *Euestheria murchisoniae*.

These species are discussed in detail below. Taxonomic discussion is included where necessary.

(*b*) Six records of marine stenohaline major taxa and eight species of marine mollusca, confined to the marine horizon of the Lower Ostrea Beds. These are listed and discussed under Lower Ostrea Beds on p. 340. They were normal shallow-water marine animals.

(*c*) Three species of marine genera confined to the Basal Oil Shale, a transition bed at the base of the Series.

(*d*) The remaining seven species are single records or of very restricted occurrence (Table 1), so that extended discussion is not possible.

LAMELLIBRANCHS

Modiolus cf. *imbricatus* J. Sowerby

Occurrence. A *Modiolus* comparable to this species, but generally smaller, has been recorded from several localities and horizons (e.g. Lee 1920, p. 54). I have collected it from three horizons: from just below the Mytilus Shales algal bed with *Placunopsis* and *Cuspidaria*, from the algal bed horizon of the Lower Ostrea Beds with *Rhynchonella* and marine mollusca, and from the Estheria Shales in Raasay alone.

Ecology. *Modiolus* belongs to a very ancient group, which has always been shallow-water marine, or even littoral (Newell 1942). Data on modern *Modiolus* are not so abundant as on *Mytilus*, but at least in Britain it apparently lives in somewhat deeper water, below the littoral zone proper (Yonge 1949), and in the Baltic it does not extend into water of such low salinity as *Mytilus edulis* (Sorgenfrei 1958). The genus is thus marine, shallow-water but not littoral, and able to tolerate limited reduction in salinity. Its occurrence in the Great Estuarine Series is consistent with this, since it occurs principally in the more marine beds.

Mytilus (*Praemytilus*) *strathairdensis* Anderson and Cox

Preservation. This species (Pl. 53, fig. 6) was described by Anderson and Cox (1948) from near the base of the Estheria Shales of Strathaird. Their material consisted of internal and external moulds in hard black shale. No further occurrences were known, and none has since been described. The species is, however, abundant on the same horizon in Eigg, where it characterizes the Mytilus Shales (Hudson 1962). In Eigg the shell is preserved; except for a very thin outer layer, which may be calcitic, it is composed of nacreous aragonite (checked by X-ray powder photograph by Dr. P. Gay). The *Myoconcha* n.sp. of Kitchin (in Barrow 1908, pp. 21–23) and Lee (1920, p. 54) belongs to this species (Geological Survey Museum, Edinburgh, T 2963A–T 2968A, from Eigg, and T 215E, from Raasay).

Occurrence. Except for one doubtful record from the Upper Estheria Shales of north Eigg, this species is confined to the Mytilus Shales of Eigg, Skye, and Raasay. In these it is extremely abundant, and except for a few thin beds it dominates the fauna. It usually occurs in monotypic shell beds, never with *Unio* or *Viviparus*, and doubtfully with *Neomiodon*.

Ecology. M. strathairdensis is one of the earliest representatives of its genus, although subgenerically distinct from *Mytilus* s.s. At the present day *Mytilus* is one of the best examples of a euryhaline marine mollusc. In the Baltic area *M. edulis* inhabits the Gulf of Finland, one of only four lamellibranchs, out of ninety-two inhabiting the Kattegat, to do so. The mean salinity at the limit of its range is 6–10‰; there is no doubt that salinity is the limiting factor (Segestråle 1957, Sorgenfrei 1958). *M. edulis* is also a common littoral species in waters of normal salinity. It is extremely gregarious (Newell 1942). There is every reason to suppose that *M. strathairdensis*, like *Midiolus*, shared the general preferences of the Mytilacea, and it almost certainly resembled *Mytilus* s.s. in tolerating extreme conditions of salinity and in being gregarious. Its exclusion from the more certainly marine beds with *Placunopsis*, *Cuspidaria*, and *Modiolus* supports this. On the other hand, *Mytilus* has always been a marine-euryhaline, rather than a fresh or true brackish-water genus, and this is supported by the absence of *M. strathairdensis* from beds with *Unio* and *Viviparus*. The species does not overlap in stratigraphical range with *Liostrea hebridica*, which may have had similar ecological requirements.

Placunopsis socialis Morris and Lycett

Placunopsis aesturina Tate

Previous records. Placunopsis socialis (Pl. 53, figs. 3, 4) is a well-known species in the Great Oolite, especially in the Upper Estuarine Series of the Midlands. It has not been recorded from the Hebrides before. *P. aesturina* was described by Tate (1873, p. 349, pl. 12, fig. 12) from the Estheria Shales, and has been recorded from various horizons and localities in the Great Estuarine Series.

Tate's description of *P. aesturina* mentions central umbones, whereas his figure shows an inequilateral shell. The holotype is in fact inequilateral, like the figure (Geological Survey Museum, London, 8621). Most of the records from the Great Estuarine Series are of specimens with central umbones, better referred to *P. socialis*, or are not specifically determinable. *P. socialis* is a very variable species. An inflated form, very common in the Mytilus Shales, is rather distinct, but also occurs in the Upper Estuarine Series of the Midlands.

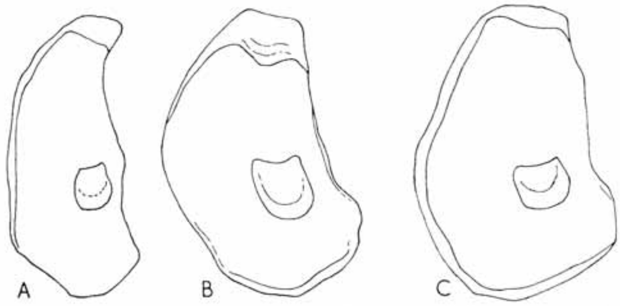
Occurrence. Placunopsis occurs at various horizons in the Mytilus and Estheria Shales, and in the Lower Ostrea Beds. In the limestones just below the Mytilus Shales algal bed *P. socialis* is almost a rock-former, especially the inflated form. It is associated with *Cuspidaria ibbetsoni*, *Modiolus*, *Lopha*, and rare *Neomiodon*.

Ecology. Placunopsis is undoubtedly a marine genus. It is gregarious and common in restricted assemblages, and may have been tolerant of very shallow water and variable salinity.

Liostrea hebridica (Forbes)

Discussion. This is one of the most important fossils (text-fig. 2) of the Great Estuarine Series, where it dominates the fauna of the Lower Ostrea Beds. A discussion of the species, with synonymy and excellent figures, is given by Arkell (1934). In the Great Oolite Series it was long known as *Ostrea sowerbyi*. The variety *rugosa* is not known in the Hebrides. Most specimens are moderately elongated, but the extreme variety *elongata*, which is the commonest form in the Fuller's Earth at Langton Herring in Dorset, is uncommon.

The genus *Liostrea* Douvillé may conveniently be used for smooth and not strongly curved Mesozoic oysters, but it is probably only a form genus, as are other 'genera' of oysters based on shell form and sculpture. As is becoming well known, living oysters can be distributed among three genera—*Pycnodonte*, deep-water and non-gregarious; *Ostrea* s.s., with type species *O. edulis*; and *Crassostrea*, type species the American oyster, *C. virginica* (Yonge 1960). The biological differences are considerable, and are correlated with ecological station: *Ostrea* is smaller, rounded, larviparous, and marine, while *Crassostrea* is larger, elongated, oviparous, and estuarine. It possesses a structure,



TEXT-FIG. 2. Interiors of right valves of *Liostrea hebridica* (A, B) and *Crassostrea virginica* (C), to show similarity of shell form and position of muscle-scar. A, Langton Herring (tracing of Arkell 1934, pl. iv, fig. 6; *L. hebridica* var. *elongata*, × 1. B, Ketton, Upper Estuarine Series, original, × 1. C, After Orton, × ½.

the promyal chamber, for removing suspended mud from its system. Correlated with this is the position of the muscle-scar well back from the hinge-line, as opposed to its central position in *Ostrea*. Ranson (1939, 1942) showed that the larval shells, or prodissoconchs, afforded a clear distinction between the oyster genera, and demonstrated by this criterion that some fossil genera could be assigned to either *Ostrea* or *Crassostrea* (*Gryphaea* of Ranson).

In general shape and position of muscle-scar *L. hebridica* closely resembles *Crassostrea virginica*, though it is only about half as large (text-fig. 2). The muscle-scar is regarded as significant in fossils by Gunter (1950) and Yonge (1960). Hallam (1959) relates *L. irregularis* to *Ostrea* by this criterion. Preliminary work has been done on separating prodissoconchs from the matrix of *L. hebridica* shell-beds, especially that of Langton Herring in the Fuller's Earth of Dorset. A few have been found which are strongly inequilateral, like those of *Crassostrea* and unlike *Ostrea* (Yonge 1960). It is hoped to continue this work, but at present both lines of evidence suggest that *L. hebridica* was more closely related to *Crassostrea* than to *Ostrea*.

Occurrence. The chief occurrence of *L. hebridica* is in monotypic shell-beds in the Lower Ostrea Beds. Less often, the shell beds also contain *Neomiodon*, and this lamellibranch is perhaps more common in the associated shales. At the marine Algal Bed horizon *L. hebridica* occurs with a much greater variety of lamellibranchs (listed in next section) and with *Rhynchonella*. Very similar assemblages occur in the Upper Estuarine Series of the Midlands. In the Staffin Bay Beds *L. hebridica* is common, but less completely dominant.

Ecology. Summaries of the vast literature on oyster ecology are given by Korringa (1952) and Yonge (1960). *Crassostrea*, to which *L. hebridica* is thought to have been related, has a narrower temperature range than *Ostrea*, but is much more tolerant of low and fluctuating salinities; *Ostrea* extends to salinities of 23‰, *Crassostrea* to 12‰ (Yonge 1960). *Crassostrea* in fact does not normally form reefs except in reduced salinities. In the enclosed bays of Texas the pure *C. virginica* reefs which flourish in salinities of 12–20‰ are invaded at higher salinities by marine forms, including *Ostrea*.

The morphological and ecological analogies between *L. hebridica* and *C. virginica*, further discussed in the accompanying paper (p. 323), are so close that it seems reasonable to infer that *L. hebridica*, in the form of pure oyster reefs, inhabited shallow, partially enclosed bays with salinity about half that of sea water.

Unio andersoni sp. nov.

This species (Pl. 53, figs. 1, 2) is described at the end of the paper.

Previous records. There has been some doubt about the occurrence of *Unio* in the Great Estuarine Series; as Anderson and Cox (1948) show, most of the early records were erroneous. *Unio* was, however, correctly identified from Eigg by Kitchin (in Barrow 1908), but was not described. Jackson (1911*a*, p. 120) records *Unio*, compared to *U. distortus* Bean, from Eigg. I have examined the specimen (Manchester Museum, L.10504), and do not accept the pseudocardinal tooth mentioned by Jackson. There is no proof that the shell is a *Unio*.

Occurrence. Reptile Bed and Unio Bed, Mytilus Shales, Eigg; Lower Ostrea Beds (?), Trotternish.

Ecology. *Unio* is perhaps the best known of all freshwater lamellibranchs, and the Unionidae have been exclusively freshwater at least as far back as the Jurassic. The typical occurrence of present-day Unionidae is in freshwater lakes and rivers. However, *U. andersoni* certainly did not live in inland waters, since both the Reptile Bed and the Unio Bed are followed without a break by beds with marine-brackish fossils. It is therefore interesting to note that *Unio* occurs at the present day in the shallow coastal waters of the Gulf of Finland, with salinities up to a maximum of 3–4‰ (Segerstråle 1957). Therefore, if modern *Unio* is taken as a guide, *U. andersoni* could have inhabited coastal lagoons like those envisaged for the deposition of the Great Estuarine Series, but these must have become temporarily almost freshwater.

The Reptile Bed occurrence, with gastropods usually regarded as marine (see under *Tornus praecursor*, below), may be an ecologically mixed one in a condensed deposit, and in any case I prefer to regard the gastropods, rather than *Unio*, as euryhaline.

Neomiodon brycei (Tate) and *Neomiodon spp*.

Discussion. The genus *Neomiodon*, the *Cyrena* of earlier authors, may be considered as a whole. It is the commonest mollusc of the Series; it dominates the faunas of the Estheria Shales and Concretionary Sandstone Series, where it forms monotypic shell-beds and is a rock-former in the limestones. It also occurs in the Mytilus Shales and the Lower Ostrea Beds. In the Staffin Bay Beds it forms part of a more varied and more marine fauna.

The taxonomic history of the Great Estuarine Series *Neomiodons* is complicated. Forbes and Tate described several species of '*Cyrena*', mostly from the Staffin Bay Beds. These were redescribed by Anderson and Cox (1948), who referred some to marine genera, and erected a new genus *Protomiodon*, for *Cyrena brycei* Tate and species considered congeneric with it. Casey (1955), in a comprehensive paper on the Neomiodontidae, showed that *Protomiodon* was a synonym of *Neomiodon*. Casey (1952) has also demonstrated extensive external homeomorphy among such smooth, trigonal-ovate lamellibranchs as *Neomiodon* and *Staffinella* [*Protomiodon*] *staffinensis*. Fortunately this problem concerns mainly the Staffin Bay Beds; the forms which dominate the fauna of the middle part of the Great Estuarine Series are undoubtedly *Neomiodon*. Most can be referred to *N. brycei* (Tate) and its variety *quadrata* on shell outline (Anderson and Cox 1948), but other species, including *N. cunninghamii* (Forbes), are probably present.

Occurrence and ecology. Since the Neomiodontidae are extinct, it is not possible to draw ecological conclusions from close modern relatives, and arguments must be based on associations with other fossils. Casey (1955) considers the family to be the ecological forerunners, but not the direct ancestors, of the fresh- and brackish-water Corbiculidae, of the Tertiary and the present day, which they so closely resemble. He sums up the ecology of *Neomiodon* itself as 'fresh or brackish water, gregarious, sometimes associated with members of marine genera'. He cites evidence from the Purbeck and Wealden of frequent association with *Unio* and *Viviparus*, and much less frequent occurrence with *Modiolus*, *Corbula*, and *Pecten*. Despite association with marine genera in the Staffin Bay Beds, Casey considers Middle Jurassic *Neomiodon* to have had the same ecological preferences. It is now possible to cite evidence, similar to Casey's from the Purbeck, from the Great Estuarine Series itself. *Neomiodon* occurs with *Viviparus*, *Euestheria*, and metacyprid ostracods at many horizons, and with *Unio* at two, as well as with *Liostrea*. As in the Purbeck, however, it is not usually abundant in precisely the same bed as marine-brackish genera. The analogy with the Middle Purbeck is the more striking as the facies is so similar. I therefore support Casey's conclusions on the ecology of *Neomiodon*. The extensive beds with *Neomiodon* alone may have been deposited in water just saline enough to exclude *Unio* and *Viviparus*, but still too dilute to admit marine genera; this is the 'species minimum' of the Great Estuarine Series.

The trace fossil *Pelecypodichnus amygdaloides* Seilacher is extremely common in the thin-bedded sandstones and shales of the Concretionary Sandstone Series. It is formed as the 'resting trace' of a lamellibranch inhabiting shallow, temporary burrows in a thin layer of sand over mud (Seilacher 1953). In this case *Neomiodon* was undoubtedly the lamellibranch responsible, and the occurrence confirms the mode of life of *Neomiodon* which could also be predicted from its typically 'active lamellibranch' morphology (cf. Yonge 1949, pp. 228–9).

Cuspidaria ibbetsoni (Morris)

This species (Pl. 53, fig. 5) has not previously been positively identified from the Series, though Anderson and Cox (1948, p. 120) record a probable fragment.

Occurrence. *C. ibbetsoni* is abundant at several horizons in the Mytilus and Estheria Shales, especially just below the algal bed, and also occurs in the Lower Ostrea Beds. It is associated especially with *Placunopsis socialis*, an association also characteristic of the Upper Estuarine Series of the Midlands.

Ecology. Modern *Cuspidaria* is deep-water marine, and Cox (1960) has questioned whether the Jurassic species, which are all shallow-water forms, were related to it, or were septibranchs at all. *C. ibbetsoni* occurs widely in the Great Oolite Series in England, and is especially abundant in the Upper Estuarine Series of the Midlands. The forms in the clays there have long rostra, like my specimens and unlike those from the Great Oolite limestones (Cox and Arkell 1948)—a fact which may be ecologically significant. The occurrence and associations of *C. ibbetsoni* suggest a shallow marine habitat, and tolerance of muddy and perhaps brackish conditions.

GASTROPODS

Viviparus scoticus (Tate)

Previous records. This is by far the most important gastropod in the Great Estuarine Series, occurring in all formations from Mytilus Shales to Ostracod Limestones, and it has given rise to much controversy. It was described as a *Paludina* (= *Viviparus*) by Tate (1873), and considered as freshwater until Yen (1948) proposed a new genus *Bathonella* for it, and claimed that it was marine. The ecological and taxonomic arguments are linked, since many palaeontologists are unwilling to admit that a marine shell was a *Viviparus*, or vice versa. The purely morphological differences between *Bathonella* and *Viviparus* have been very differently assessed by different authors. Yen (1948) placed it in a different family from *Viviparus*; this was accepted by Anderson and Cox (1948). Arkell (1948) doubted the generic separation, and Watson (1950) firmly rejected it. Cox (1950) admitted that the distinction could be specific only, but held that since *Bathonella* was marine the generic distinction was desirable. Since I do not consider that the ecology of *Bathonella* differed materially from that of other *Viviparus*, I propose to reject the name, regarding the slight morphological differences listed by Yen as of specific rank only (Watson 1950). *Bathonella bithnyoides* Yen 1948 is assumed to be congeneric with *V. scoticus*.

Occurrence. Yen (1948), who was originally responsible for the view that *V. scoticus* was marine, did not in fact record marine fossils from the same bed, but only from an adjacent one (see Stratigraphical section). In view of the repeated oscillations of conditions known in the Great Estuarine Series this cannot count as a true association. Cox (1950) drew up a list of occurrences of *V. scoticus* in the Great Estuarine Series, mainly from Anderson's unpublished records, but including two of Tate's (1873) lists, which alone contain undoubtedly marine genera. Cox admits that these may have been compiled from more than one bed, and from field experience of the localities concerned I should regard this as certain. This reduces Cox's list of associates to *Neomiodon*, *Euestheria* and ostracods, all at many localities, and *Hydrobia praecursor* and *Quenstedtia? staffinensis* at one each. The only marine genus here is *Questedtia*, and the generic attribution of the species is quite uncertain (Anderson and Cox 1948). To this list I can add, from my own collecting, *Unio* in two localities, both with *Neomiodon* also. I can also add several more occurrences of *V. scoticus* alone or with *Neomiodon*, *Euestheria*, and ostracods, and a great deal of negative evidence, on the non-occurrence of *V. scoticus* with marine or marine-brackish genera.

The other well-known occurrences of *V. scoticus* (or species regarded by Anderson and Cox (1948) as synonymous with it) are in Oxfordshire (Watson 1950) and Indre, France (Fischer 1961). Neither yields acceptable evidence of marine associates. Fischer shows clearly that *Viviparus* occurs immediately above a lignite bed which rests on an erosion surface, that it is associated with '*Valvata*' and '*Planorbis*', and that none of these gastropods is found in the marine beds above and below.

Ecology. Present-day *Viviparus* is one of the best known of all freshwater gastropods. There is therefore a presumption that beds containing shells which appear to be fossil *Viviparus* are also freshwater, especially if they contain other freshwater fossils. This conclusion has always been accepted, for instance, in the Wealden Beds. On the basis of the above review, there seems no reason to depart from it in the case of the Great Estuarine Series. There only remains, as with *Unio*, the possibility that *Viviparus*, since its habitat in this case was certainly coastal, could tolerate a slight degree of brackishness in the water. This is quite possible; but the total exclusion of marine genera shows that salinity stayed on the freshwater side of the 'species minimum'.

Tornus praecursor (Tate)
Globularia hebridica Anderson and Cox
Cylindrobullina inermis (Tate)

These three small gastropods may be considered together. The type localities are all in the Estheria Shales of the Portree district, Skye, where the species occur together and with *Modiolus* (Tate 1873, Anderson and Cox 1948). Tate referred the species to *Valvata*, *Neritina* (*G. hebridica* = *N. staffinensis* Tate non Forbes), and *Melania* respectively. In referring them to marine genera, Anderson and Cox comment on the difficulty of generic assignment of imperfectly preserved small gastropods, and in the case of *T. praecursor* they were influenced by association with other marine fossils.

Occurrence. Most small gastropods in my collection do not show apertural characters, and are therefore difficult to determine. However, all three species mentioned above probably occur in the Reptile Bed of the Mytilus Shales. *G. hebridica* is the abundant small naticoid shell of Kitchin (in Barrow 1908, p. 22). Here they are associated with *Unio*, as well as with numerous fish scales and teeth and disaggregated reptilian bones, so the assemblage is an ecologically mixed one if the gastropods were truly marine. I have also found *Cylindrobullina sp.* with young *Mytilus strathairdensis* and with *Neomiodon brycei*. Small, low-spired gastropods, possibly referable to *T. praecursor*, occur associated with *Neomiodon* and *Euestheria* at several localities in the Estheria Shales of Skye.

It is possible that these small gastropods were euryhaline, as many small gastropods are today, but until more taxonomic work has been done on better-preserved material they are unsafe environmental indicators.

PHYLLOPODA

Euestheria murchisoniae (Jones)

Previous records. In 1862 Jones described this species of '*Estheria*' from material collected by Murchison in 1826. His type material appears to be lost. Subsequently the species, or the genus '*Estheria*', has been recorded several times from the Great Estuarine Series, but no further descriptions or figures have been published. The classification of fossil '*Estheria*' (itself a preoccupied name) is in a confused state; the genus accepted here for *E. murchisoniae* is *Euestheria* Déperet and Mazeran, of which the type species is *Eu. minuta* of the Triassic (Kobayashi 1954).

Occurrence. *Euestheria* is most abundant in the Estheria Shales, where bedding planes may be covered by its carapaces. It is associated with *Neomiodon*, ostracods, fish fragments, and oogonia of *Chara*. In the Ostracod Limestones it is again very common, but less universally present, accompanied by ostracods and fish fragments. It occurs more locally in the Basal Oil Shale, the Mytilus Shales, and the Concretionary Sandstone Series.

I have collected twelve samples with abundant *Euestheria* from the Estheria Shales and the Ostracod Limestones, and studied the variation within and between them (210 specimens were examined). Carapace outline, position of umbo, number of growth-rings, and interspace ornament are among rather few features of fossil '*Estheria* 'which can be used in classification, but there has been no agreement as to which of them is most important (compare Raymond 1946, Bock 1953, Kobayashi 1954, Tasch 1956). My study showed 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 suggests that several taxa are present—these range from varieties or subspecies to genera or even families, depending on the classification employed. In general the specimens were smaller and less elongated than those figured by Jones, but their general outline and number of growth-rings were similar. At present I propose to retain all the specimens in *Eu. murchisoniae*. The variations did not have any obvious stratigraphical significance, but the largest specimens were from the Ostracod Limestones.

Ecology. Modern '*Estheria*' species are most common in very shallow ponds, including temporary 'playas', in inland basins in warm temperate areas. They mostly inhabit fresh waters, occasionally brackish lagoons, but never live in the sea (Kobayashi 1954, Jones 1862, pp. 5–7). The vast majority of fossil '*Estherias*' come from continental formations. It is certainly significant that they are completely absent from the marine Jurassic and Cretaceous of north-west Europe, but occur in the Triassic (including the Rhaetic), the Great Estuarine Series, the Purbeck, and the Wealden. In the Great Estuarine Series the associates listed above are all freshwater or freshwater-brackish.

THE STRATIGRAPHICAL DISTRIBUTION OF THE FAUNA

The faunas of the formations of the Great Estuarine Series are here described in stratigraphical order. All macro-invertebrate species are listed (apart from a few early records which have not been confirmed); vertebrates and microfossils are only mentioned in passing. Measured sections are given of a few important localities; much fuller stratigraphical information, including many more measured sections, is in my thesis (University of Cambridge, Ph.D. 1962). Figures in brackets after locality names refer to the National Grid.

a. Basal Oil Shale

The Garantiana Clay, the last marine formation below the Great Estuarine Series, passes gradually up into the Basal Oil Shale. The lithology changes from blue, blocky clay to black fissile shale, and the fauna changes from one of ammonites to a peculiar and restricted assemblage in which fish scales are the commonest fossils.

The gradual passage is best seen in the cliffs above Prince Charles's Cave, north of Portree, Skye (513477 to 515490). The Oil Shale here contains *? Quenstedtia* cf. *bathonica* (Morris and Lycett), with valves attached (cf. Forsyth 1960), *Meleagrinella* sp. indet., indeterminate tiny gastropods and ostracods, in addition to numerous cycloid and ctenoid fish scales and one almost complete leptolepid fish (identified by Mr. H. A. Toombs; Sedgwick Museum J.29055). In Raasay the Quenstedtia Shale of Forsyth (1960), the equivalent of the Basal Oil Shale, contains *Isocrinus* in its lower part and *Quenstedtia* alone in its upper part; just below the White Sandstone *Euestheria* occurs. At Port na Cullaidh, Elgol, Strathaird, the Basal Oil Shale is intermittently exposed; it is very similar to the Trotternish development and yields abundant fish scales, *Euestheria*, ostracods, gastropods, and ? *Mytilus*. The abundance of fish material contrasted with the paucity of mollusca, together with the high carbon content, suggest that the bottom water may have become stagnant at this time. There was probably also a gradual decline in salinity.

b. The *White Sandstone* is unfossiliferous.

c. Mytilus Shales

These form the lower part of the Estheria Shales of Eigg, Strathaird, and Raasay (Hudson 1962). The type section in Eigg, north of Kildonnan (495870), gives the best record of rapid vertical variations in lithology and fauna in the Great Estuarine Series. A detailed account will be published elsewhere; the following is a summary of the faunas, from top to bottom.

9. *Algal Bed*, 1 ft. 4 in. An 'algal-dome' bed partly composed of faecal pellets (Hudson 1962). *Placunopsis socialis* near the base.

8. *Placunopsis Limestones*, 6 ft. Hard blue limestones separated by shales. *P. socialis*, *P. aesturina?*, *Cuspidaria ibbetsoni*, *Modiolus sp.*, *Lopha sp.*, *Neomiodon sp.* (rare). Following the interpretations of Section III, this is a high-salinity fauna.

7. *Unio Bed*, 8 in. Sandy argillaceous limestone. *Unio andersoni*, common; *Neomiodon*, *Viviparus*. A freshwater fauna.

6. Limestones and shales, 5 ft. *Cuspidaria ibbetsoni* near base, *Neomiodon brycei* near top. First occurrence of these two species. Last occurrence of *Mytilus strathairdensis*.

5. Silty shale with thin limestones, 30 ft. The main mass of the Mytilus shales; fauna dominated by *M. strathairdensis*, forming 'mussel beds'.

4. Complex Bed, 3 ft. Coarse sandstone with common fish remains. First occurrence of fully grown *M. strathairdensis*.

3. Shale, 8 ft. Very abundant *M. strathairdensis*, but nearly all young individuals. Near the base a 1-in. bed with *Viviparus* but no *Mytilus*.

2. Reptile Bed, 4 in. Hard sideritic limestone. Abundant small gastropods (*Globularia hebridica*, *Tornus praecursor*, *Cuspidaria ibbetsoni*), common *Unio andersoni*.

Abundant fish teeth, scales and fin-spines, reptile vertebrae, and limb bones. Possibly a condensed deposit.

1. Shale, 8 ft. Sparsely fossiliferous. Near base, *Euestheria murchisoniae* (therefore low salinity) and fish scales like those from the Basal Oil Shale. Base not seen.

These rapid changes of fauna within a fairly constant gross lithology are regarded as characteristic of lagoonal conditions, and due to salinity changes (see accompanying paper). The above succession records a gradual (and fluctuating) increase in salinity from bed 1 to bed 5, to perhaps half the salinity of sea water; a decline in beds 6–7 to almost fresh water, and a more sudden increase in beds 8–9 to definite marine-brackish salinities, as judged by the ecology of the fossils deduced in the previous section of this paper.

In Strathaird *M. strathairdensis* is common, and the Placunopsis limestone below the algal bed is well developed. It is exposed north of Elgol (Anderson 1948, Hudson 1962), where it yields *Placunopsis socialis, Cuspidaria ibbetsoni, Pteroperna sp.*

In Raasay the Mytilus Shales are not well known, but *M. strathairdensis* occurs and loose blocks of the Algal Bed and of the Placunopsis limestones have been found (Lee 1920).

d. Estheria Shales

The typical Estheria Shales have an abundant and highly characteristic fauna of *Euestheria, Neomiodon*, ostracods, and scattered fish fragments; in certain beds these are accompanied by *Viviparus* and small gastropods.

At the Lealt River in Trotternish, the type locality (Anderson 1948, pp. 125–6, with map), the typical lithology is well seen. The black shale immediately overlying Anderson's algal limestone, on the south bank of the river just above the road-bridge, yields *Euestheria murchisoniae*, a form with radial-linear interspace ornament (in great abundance and well preserved), *Neomiodon*, ostracods, and fish scales. Similar shale a few feet higher in the succession, on the north bank, yields *Eu. murchisoniae*, form with punctate ornament, *Neomiodon, Viviparus*, and very abundant ostracods.

The burn north of Rigg Burn (crosses road at 518571) gives a good section, which affords an excellent example of the characteristic rapid variation of fauna. The following section is about 100 yards west of the road, and 30 ft. above the base of the Estheria Shales:

	ft.	*in.*
3. Shale with *Cuspidaria ibbetsoni, Placunopsis socialis*, cf. *Quenstedtia, Procerithium spp.*	1	0
2. Shell limestone, *Cuspidaria*, with shale partings	1	0
1. Shale with *Euestheria murchisoniae*, ostracods, fish fragments, *? Mytilus*	2	0

A similar shale to bed 1, about 10 ft. lower in the succession, yielded *Eu. murchisoniae*, ostracods, *Neomiodon sp., Viviparus scoticus, ? Tornus praecursor*. This is a complete low-salinity assemblage; it is notable that bed 1 above contains *Euestheria* and Mytilid shells, but not *Viviparus*, and may thus represent somewhat higher salinity. Bed 3 is definitely brackish-marine, with no freshwater-brackish indicators.

In Raasay the shales are identical to those of Trotternish, with abundant *Euestheria*. Oolitic limestones are well represented; one of these yielded *Modiolus* cf. *imbricatus*.

In Strathaird the beds are baked by intrusions, and less amenable to search for fossils. The most notable feature is the occurrence of *Liostrea hebridica* just above the algal bed (Anderson 1948, p. 127). Higher up, some *Viviparus* beds occur. In Eigg the shales yield *Euestheria*, *Neomiodon*, ostracods, and *Viviparus*, with no additions to the Trotternish fauna. *Cuspidaria ibbetsoni* and *Placunopsis sp.* occur a short way above the algal bed on the north coast (474907), and I have a queried record of *Mytilus* from here. Immediately above is a *Viviparus* bed.

e. Concretionary Sandstone Series

This is the thickest formation in the Great Estuarine Series, and it is very variable. Its deposition is an involved study in sedimentary petrology and sedimentation. Its fauna, however, is monotonous. *Neomiodon* is the only macrofossil in many beds; *Viviparus* is the only other common mollusc. A few beds contain ostracods; *Euestheria* is rare. There are isolated records of *Placunopsis* (from Strathaird, T 4311, T 4318; Wedd 1910, p. 124), and *Cylindrobullina?* (from Eigg, T 719A, T 720A, two forms; Kitchin in Barrow 1908, p. 24); these are in the Survey Museum, Edinburgh.

My collection includes well-preserved *Neomiodon brycei* and *Neomiodon sp.* from the Lealt River, Trotternish (with brown on white colour banding), from the Valtos shore section, Trotternish, from Eist, Duirinish (associated with small *Cylindrobullina sp.*), and from Raasay. The best-preserved *Viviparus scoticus* are from Eist and from Strathaird, where they occur near the top of the formation on the shore at Cladach a' Ghlinne (Wedd 1910, p. 124). The trace fossil *Pelecypodichnus amygdaloides* is abundant, especially in Trotternish.

f. Lower Ostrea Beds

These beds, with their extraordinary abundance of oysters, have attracted attention and comment from the earliest investigators onwards. Everywhere limestones composed of *Liostrea hebridica*, alternating with shales, are the dominant lithology. The beds are exposed over a wider area than any other formation of the Series, and are fairly constant, though thicker and sandier in Trotternish than elsewhere (Hudson 1962). Exposures yielding *L. hebridica* are far too numerous to list here. This account concentrates on the more extensive fauna of the marine horizon which is constantly associated with Anderson's (1948) Algal Bed. The important exposures are described below. Since knowledge of the distribution of this fauna at present depends more on the vagaries of collecting than on true geographical variation, it is convenient first to review the fauna as a whole.

The greatest thickness of the marine beds is not more than 10 ft., in Trotternish and Waternish, and these beds are always underlain and overlain by ordinary *Liostrea* beds. The Algal Bed usually occurs towards the top of the marine beds.

The following members of marine stenohaline groups are confined to this horizon: foraminifera (several records, mostly of miliolids), echinoids (regular, plates and spines, 2 records), '*Serpula*' (1 record), *Discinisca* (1 record), *Rhynchonella* cf. *concinna* (common in north Skye), polyzoan (cyclostome, 1 record).

Of the mollusca, *Liostrea hebridica*, *Modiolus imbricatus*, *Cuspidaria ibbetsoni*, and *Placunopsis socialis* were dealt with above, and the following are confined to this horizon: *Anisocardia* (*Antiquicyprina*) *cucullata* (Tate), '*Quenstedtia*' *forbesi* Anderson and Cox, *Pleuromya robusta* (Tate), *Corbula hebridica* Tate, *Myopholas acuticostata* (J. de C. Sowerby); *Neridomus arata* (Tate), *Zebina caledonica* (Tate), *Globularia* *formosa?* (Morris and Lycett). These are discussed below. In addition there are fragments of *Mytilus* (*Falcimytilus*) sp. in my collection (see also Tate 1873, p. 346), and indeterminate lamellibranchs and gastropods. It is doubtful if *Neomiodon* occurs. The smooth, trigonal ovate lamellibranchs ('*Cyrenas*' of the old authors) in these beds are usually larger than typical *Neomiodon*, and in the absence of preserved dentition are very difficult to determine. Most are probably members of marine genera, like *Anisocardia cucullata*, which was itself one of Tate's '*Cyrenas*' (cf. Cox 1947, Anderson and Cox 1948, Casey 1952, 1955).

Anisocardia (*Antiquicyprima*) *cucullata* (Tate). The specimens recorded here do not show dentition, but may be referred to this species on shell outline. Some are not distinguishable from small specimens of *A.* (*A.*) *loweana* (Morris and Lycett) from the Great Oolite.

'*Quenstedtia*' *forbesi* Anderson and Cox. One specimen from Duntulm agrees with Anderson and Cox's figure (1948, pl. 2, fig. 9). The dentition is unknown and the shell may not be a *Quenstedtia* (Casey, personal communication).

Pleuromya robusta (Tate). Several specimens from Lovaig Bay, of which the best is figured (Pl. 53, fig. 8), appear to confirm Anderson and Cox's tentative conclusion that this species is distinct from *P. uniformis* (J. Sow.), being shorter and relatively higher.

Corbula hebridica Tate. This small species is quite common at this horizon.

Myopholas acuticostata (J. de C. Sowerby). This distinctive lamellibranch (Pl. 53, fig. 7) was recorded by Tate (1873, p. 346), but not mentioned by Anderson and Cox. It is quite common at Duntulm and at Loch Bay. It is widespread in the Great Oolite Series, including the Upper Estuarine Series of Northants.

Neridomus arata (Tate) and *Zebina caledonica* (Tate). Two of Tate's species, revised by Anderson and Cox (1948). I have no further records.

Globularia formosa? (Morris and Lycett). Two specimens from Loch Bay are doubtfully referable to this common Great Oolite species.

These are all normal, shallow-water, marine fossils, either identical with or closely related to species of the English Great Oolite Series. The marine incursion was short-lived, however, and it seems likely that the lagoons reached almost marine salinity for a while, rather than that truly open-sea conditions were established. A closely analogous case is the invasion of the Texas *Crassostrea* reefs by a more saline fauna, of species which also inhabit the open Gulf, when salinity rises above 25‰ (see Hudson, this journal, p. 318).

Trotternish succession

The best exposure of the marine horizon is the shore section at Cairidh Ghlumaig, Duntulm (410737), where Macgregor first discovered *Rhynchonella* in the Great Estuarine Series (Macgregor 1934, Anderson 1948). The section shows, in summary:

	ft.	*in.*
3. Shale and limestone, alternating, with *Liostrea*	10	0
2. Shale, sandstone, and limestone with *Liostrea* and *Rhynchonella*, algal bed 3 in. below top	7	7
1. Sandstone with plant remains and *Liostrea*	11	0

The marine beds, as defined by the range of *Rhynchonella* (*R.* cf. *concinna*, Macgregor 1934), are no. 2 of the above succession. A bed of sandy shale, 2 ft. above the base of bed 2, yielded, in addition to *L. hebridica*, *Myopholas acuticostata*, *Anisocardia cucullata*, *Quenstedtia forbesi*, and indeterminate heterodonts. From bed 2 generally come *Discinisca sp.*, *Serpula sp.* and, according to Macgregor (1934), *Modiolus sp.*

A stream section ½ mile SSW. of the above locality (406728), above the road-bridge, is in beds probably entirely above those just described. It shows 7 ft. of green silty shales, with *Neomiodon*, overlain by 5 ft. of *Liostrea* beds, which also contain *Placunopsis*. This section is important as showing *Neomiodon* shales within the Lower Ostrea Beds. Loose blocks of sideritic mudstone, apparently nodules, yielded a well-preserved fauna of *Neomiodon brycei* and *N. sp.*, *Unio andersoni*, and *Viviparus scoticus*. All three genera occur in one hand specimen. This is one of the best freshwater faunas from the Great Estuarine Series. The loose blocks almost certainly came from the green *Neomiodon* shales within the Lower Ostrea Beds, and thus imply a very marked oscillation in salinity. It is notable that *L. hebridica* does not occur with the freshwater fossils. It is just possible, but unlikely, that the blocks came from the Ostracod Limestones higher up the stream.

Waternish succession

The small inlier at Loch Bay gives excellent exposures of the marine horizon. There are three sections showing algal beds in the Bay River and its tributaries. They differ in details but agree in showing two algal beds, separated by 1 to 2½ ft. of shale and oyster limestone, and probably are all on the same horizon. Anderson (1948, pp. 133–4) gives a map of the exposures, but only records one algal bed.

The following section is seen in the tributary to the Bay River at grid reference 271537; beds 1–3 in the right bank at a bend in the stream, beds 4–7 in the stream itself a little farther downstream:

	ft.	*in.*
7. Shale and limestone with *Liostrea*	3	9
6. Algal bed, brecciated	0	9
5. Shale with *Liostrea*	1	0
4. Algal bed, laminated, with *Rhynchonella* and foraminifera	0	9
3. Shale and limestone with well-preserved *Liostrea*	6	3
2. Sandstone, grey, fine-grained, uncemented	3	6
1. Clay, grey, sandy, base not seen	3	0

The top of bed 2 is somewhat hardened and yields abundant but fragile *Placunopsis socialis*, *Cuspidaria ibbetsoni*, and numerous ostracods.

Near the mouth of the Bay River a richly fossiliferous white limestone outcrops, overlain by the algal beds and *Liostrea* beds. It probably yielded many of the fossils listed by Tate (1873, pp. 346–7) from Loch Bay. My collection includes *L. hebridica*, *Myopholas acuticostata*, *Modiolus* cf. *imbricatus*, *Anisocardia cucullata*, *Corbula hebridica*, heterodont lamellibranchs, *Globularia formosa?* The top of this bed yielded the only polyzoan from the Great Estuarine Series, a cyclostomatous form revealed by a thin section.

At Lovaig Bay, about 2 miles WNW. of Loch Bay, there is a small outcrop of Lower Ostrea Beds below basalt, and richly fossiliferous blocks of limestone are strewn on the beach. One of these yielded *L. hebridica*, *Pleuromya robusta* (abundant), *Corbula hebridica*, *Anisocardia cucullata*, *Mytilus* (*Falcimytilus*) *sp*. Blocks of the algal bed also occur.

Duirinish succession

Only loose blocks of the Lower Ostrea Beds occur at Eist, in the stream draining Loch Mor and on the shore. They include the algal bed. One block of limestone yielded *Corbula hebridica*, *Pleuromya robusta*, and echinoid spines (in thin-section).

Raasay, Strathaird, and Eigg make no additions to the faunas from north Skye. *A. cucullata* is recorded from Raasay (Lee 1920). A thin-section from Eigg showed a regular echinoid plate and spine. This occurrence of regular echinoids in the oyster beds recalls the well-known association of *Hemicidaris* with the Cinder Bed in the Purbeck.

Muck succession

The typical oyster beds are better exposed in Camas Mor, Isle of Muck, than anywhere else (Hudson 1962). The transition from Concretionary Sandstone Series shales, with *Neomiodon*, is also well seen. Harker (1908) included these shales in the Ostrea Beds, and said that the oysters increased in size up the succession. According to my observations, *L. hebridica* comes in sharply, and is its normal size at the base. The algal bed occurs near the top of the exposed succession. A limestone about 5 ft. below this reveals numerous foraminifera in thin-section, mostly Miliolids.

Some of the fossils collected by the Geological Survey are wrongly listed in the Memoir (Harker 1908, p. 33). Lithologies and catalogue entries show that the following groups of specimens are truly from the Lower Ostrea Beds. I have revised the identifications. All are in the Survey Museum, Edinburgh.

1. T 3238A–T 3247A. Base of Ostrea Beds.
   Modiolus sp., *Placunopsis socialis*, fish scales.
2. T 3227A–T 3237A. Probably about 5 ft. below the algal bed.
   Liostrea hebridica, *Placunopsis sp.* or *spp.*, small lamellibranchs and gastropods; *Pholidophorus sp.* (ident. by Kitchin).
3. T 3221A–T 3226A. Ostrea Beds isolated among dolerite intrusions, i.e. near top of formation.
   Liostrea hebridica, including some very large specimens.

g. Ostracod Limestones

The fauna of this formation is extremely restricted. The typical lithology is alternating shale and argillaceous limestone, but the limestones are more muddy and the shales usually more calcareous than in the Estheria Shales. Mudcracks are very common. Many of the limestones are crowded with ostracods, and *Euestheria* is common; *Viviparus scoticus* is common in certain beds but other molluscs (notably *Neomiodon*) are rare. Scattered fish remains are frequent.

The most important exposure in Trotternish is at Kilmaluag Bay (437751, map in Anderson 1948, p. 129). Near the base of the formation, grey sandy shales with plant remains (5 ft.) are overlain by white calcareous shales with pyrite nodules and mudcracks

(2 ft.). Both these beds yield ostracods, *Euestheria murchisoniae* (unusually large in the calcareous shale) and lamellibranchs comparable to *Quenstedtia? staffinensis*, but generically uncertain. Higher up a limestone with *Viviparus* is interbedded with ripple-marked sandstone; the exact succession is difficult to determine because of discontinuous exposures. Yen (1948) collected fossils from here, but I have been unable to locate the beds in my succession. They were said to be 9 ft. above the Lower Ostrea Beds. Yen's succession, written out from his description (1948, p. 167), is:

	ft.	*in.*
4. Sandy limestone	1	0
3. Black shale	0	1½
2. Fine-grained cementstone	0	4
1. Sandy limestone	1	0

Bed 2 yielded two species of *Procerithium*, 'the sandy limestone' (it is not stated which) yielded *Viviparus scoticus*, *V. bithnyoides* (*Bathonella* of Yen), and *Neomiodon sp.* (*Cyrena jamesoni* Forbes). These *Procerithiums* are the only marine fossils from the Ostracod Limestones. I have not found a rock like that containing them elsewhere in the Great Estuarine Series, but similar small gastropods occur in the Estheria Shales with *Cuspidaria* and *Placunopsis*. They do not occur in the same bed as *Viviparus*. Anderson and Cox (1948) record *Assiminea skyensis* from 5 ft. above the base of the Ostracod Limestones here, and Cox (1950) records *Hydrobia praecursor* from the Ostracod Limestones of Skye, locality unspecified but probably from Trotternish. Both these genera of small gastropods inhabit brackish water today (Anderson and Cox 1948).

In Strathaird, Eigg, and Muck the Ostracod Limestones yield only ostracods, *Euestheria*, *Viviparus scoticus*, and fish fragments *V. scoticus* ('Paludina') gives its name to the Paludina Limestones of Wedd (1910). The Geological Survey's specimens from Muck are wrongly listed in the Memoir (Harker 1908, p. 33) as from the Ostrea Beds. Their true source is easily established from lithology. The fossils (T 3199A–T 3220A) comprise ostracods, fish fragments, *Euestheria murchisoniae*, and *Viviparus scoticus*.

Thus, except for one thin bed at Kilmaluag, the Ostracod Limestones contain a low-salinity assemblage throughout. The water must have been almost continuously muddy, and mudcracks show that it very frequently dried up. These facts may account for the

EXPLANATION OF PLATE 53

Figures natural size except 3, 4; figs. 1, 4, 5, 6 coated with ammonium chloride. Sedgwick Museum registered numbers.

Figs. 1, 2. *Unio andersoni* sp. nov. 1*a*, *b*, Holotype, Lower Ostrea Beds?, near Duntulm, Skye; J.48684. Reversed stereo-pair, separation 6·5 cm. The specimen is an internal mould. 2, Mytilus Shales, near Kildonan, Eigg; J.48685. Left valve with nacreous shell preserved.

Figs. 3, 4. *Placunopsis socialis* Morris and Lycett. Mytilus Shales, near Kildonan, Eigg. 3, J.48686, left valve. 4, J.48687, left valve of large specimen of inflated form. Both × 2.

Fig. 5. *Cuspidaria ibbetsoni* (Morris). Mytilus Shales, near Kildonan, Eigg; J.48688. Left valve.

Fig. 6. *Mytilus* (*Praemytilus*) *strathairdensis* Anderson and Cox. Mytilus Shales, near Kildonan, Eigg; J.48689. Left valve with nacreous shell preserved.

Fig. 7. *Myopholas acuticostata* (J. de C. Sowerby). Lower Ostrea Beds, Duntulm, Skye; J.48690. Right valve.

Fig. 8. *Pleuromya robusta* (Tate). Lower Ostrea Beds, Lovaig Bay, Waternish, Skye; J.48691. *a*, Right valve. *b*, Anterior view. *c*, Dorsal view.

absence of most of the usual mollusca, especially *Neomiodon*. It is also possible that the lagoons at this time were almost isolated from the open sea, so that even if salinity did increase (for instance during evaporation) marine forms could not enter the area.

h. Mottled Clays

These red beds are almost completely unfossiliferous, and were probably deposited largely above average water-level.

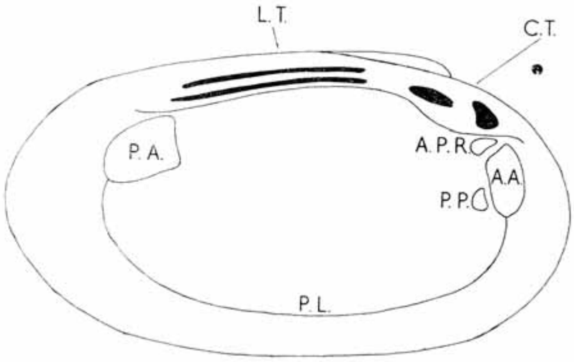
i. The Great Estuarine Series as now defined (Hudson 1962) ends with the Mottled Clays. In Trotternish it is overlain by the Upper Ostrea Beds, with a somewhat reduced marine fauna, and the Belemnite Sands, with a fully marine fauna. These faunas have been listed by Anderson and Cox (1948). They both include *Liostrea hebridica* and *Neomiodon brycei*.

SYSTEMATIC DESCRIPTION

Genus UNIO Retzius, 1788
Unio andersoni sp. nov.

Plate 53, figs. 1, 2; text-fig. 3

Diagnosis. Species of *Unio* with the following generic characters: transversely elongate lamellibranch, with nacreous shell composed of aragonite. In the left valve, two large



TEXT-FIG. 3. *Unio andersoni* sp. nov. Interior of left valve, × 2. Somewhat idealized reconstruction to show Unionid musculature and dentition. L.T., lateral teeth; C.T., cardinal teeth; A.A., anterior adductor muscle impression; A.P.R., anterior pedal retractor; P.P., pedal protractor; P.A., posterior adductor; P.L., pallial line.

cardinal teeth anterior to the umbo, with a socket between them; two long lateral teeth, posterior to the umbo. In the right valve, one large cardinal tooth, sometimes (at least) divided; lateral teeth not seen, but probably one only. Anterior adductor muscle impression deep, anterior to and below the cardinal teeth. Anterior pedal retractor between anterior adductor and cardinal teeth; pedal protractor immediately posterior to anterior adductor. Posterior adductor large, high, shallow. Pallial line simple. External ligament long, posterior to umbo.

Specific characters: shell small for a *Unio*, ovoid, length nearly twice the height, compressed. Umbones depressed, scarcely projecting above hinge-line, situated at the anterior third of the length. Outline smoothly ovate, the ventral margin very gently convex. Inflation smooth, at maximum below the umbo; posterior ridge feebly developed or absent. Shell rather thin for a *Unio*, unornamented except for faint growth-rugae.

Holotype. Sedgwick Museum no. J48684; Lower Ostrea Beds?, Great Estuarine Series (Bathonian), stream 1 mile south of Duntulm Castle, Isle of Skye, Scotland.

Dimensions. Holotype: length 4·5 cm., height 2·5 cm., thickness through both valves (approximate) 1·5 cm. These dimensions are approximately constant for well-preserved, apparently adult, individuals, in the many specimens examined. The maximum length seen was 5·5 cm.

Name after Dr. F. W. Anderson in recognition of his researches on the Great Estuarine Series.

Material. All from the Great Estuarine Series, Middle Jurassic, of the Inner Hebrides.

Locality 1. As for holotype; loose blocks, probably from the Lower Ostrea Beds. The holotype and four other specimens. The holotype is the most complete specimen known. It originally had some shell attached, but was developed as an internal mould to show dentition and musculature. Reversed stereo photographs, used at the suggestion of Dr. C. L. Forbes, enable the mould to be seen as a three-dimensional shell, and greatly help in interpreting the structures.

Locality 2. Reptile Bed, Mytilus Shales, Eigg. My collection, several specimens mostly fragmentary. Geological Survey, Edinburgh: T 2843A, T 2862A, T 2878A (cf. Jackson 1911*a*, pl. 10, fig. 2, neanic form of *U. distortus*), T 2902A, T 2928A–T 2930A.

Locality 3. Unio Bed, Mytilus Shales, Eigg. My collection, fifteen specimens, some with nacreous shell. Geological Survey, Edinburgh: T 2944A–T 2947A. Almost certainly from this bed, from the matrix. T 2944A has part of the ligament preserved.

In the Geological Survey, Edinburgh, are some small *Unios* from the Brora Estuarine Series which may be conspecific with *U. andersoni* (R and S 3564–7). None of them shows musculature or dentition. A small *Unio* from Brora was referred to *U. distortus* by Jackson (1911*a*, p. 120).

Discussion. The shell characters are undoubtedly those of a Unionid (text-fig. 3) and compare closely with those of modern *Unio* (e.g. Cox 1961, p. 329). The species appears to be more closely related to *Unio* than to *Margaritifera*, from the list of shell characters given by Mongin (1961, p. 341).

The only described Middle Jurassic *Unios* from Britain are from the Yorkshire 'Estuarine' Series. In internal characters my species agrees with *U. kendalli* Jackson (1911*b*) from the Lower Estuarine Series (Bajocian), but in shape of shell and lack of ornament it more closely resembles *U. distortus* Bean (Jackson 1911*a*) from the Upper Estuarine Series (Bathonian?). The internal characters of *U. distortus* are unfortunately not accurately known, and it is also about twice as large as my species. Jackson (1911*a*) referred it tentatively to *Margaritana* (= *Margaritifera*).

Various genera, or subgenera, of *Unio*, have been proposed for Mesozoic Unionids from North America and Japan; Dr. L. R. Cox kindly sent me a list of these. The only one which at all resembles my specimens is *Rhabdotophorus* Russell 1935, from the Cretaceous of Alberta. The internal structures, size, and outline are similar, but it has costae on the post-umbonal slope which my species lacks. The geological horizon and locality are also very different. Until a comprehensive review of Mesozoic Unionacea is undertaken it seems best to leave the species in *Unio sensu lato*.

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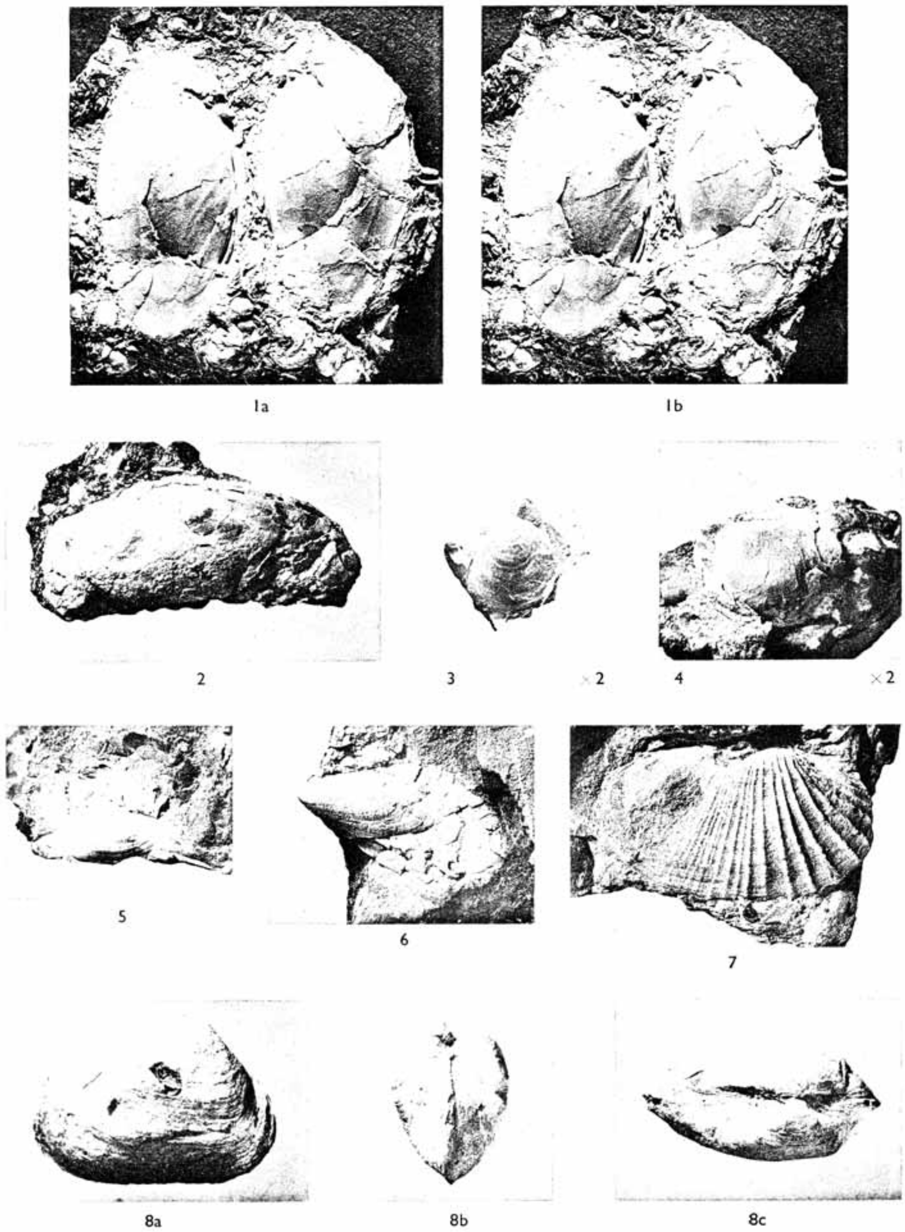

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