

A EURYHALINE OYSTER FROM THE MIDDLE JURASSIC AND THE ORIGIN OF THE TRUE OYSTERS

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ABSTRACT. *Ostrea hebridica* Forbes, 1851 is shown by its morphology to belong to the family Ostreidae, sub-family Ostreinae. Its facies distribution shows that it was euryhaline, as are many members of the Ostreinae but none of the Gryphaeidae, to which all non-plicated Jurassic oysters have previously been referred. *O. hebridica* is closely allied to *O. acuminata* J. Sowerby, the type of *Praeexogyra* Charles and Maubeuge, to which genus it is transferred. Previously it has been placed in *Liostrea* Douvillé. The type species of *Liostrea*, *L. hisingeri* of the Lower Lias, although a gryphaeid, shows some features transitional to the ostreid condition. Consequently the euryhaline oysters (Ostreinae) are diphyletic.

OYSTERS are among the most successful of bivalves, and indeed of invertebrates, in brackish-marine environments of the present day. They have a fossil record in such environments extending at least back to the Cretaceous. In addition, oysters have occurred in fully marine environments since the Triassic. The brackish-water oysters of the present day belong to the family Ostreidae, sub-family Ostreinae of Stenzel (1971); they can be regarded as the 'true oysters'. They are not strongly coiled, nor plicated; characteristically they show high variability of shell shape, much of which is directly phenotypic and arises from their attached mode of life and gregarious habit. They have not received as much attention from palaeontologists as coiled or plicated oyster genera such as *Gryphaea*, *Exogyra*, or *Lopha*; they are not as attractive for studies in functional morphology; they are not good guide fossils in stratigraphy and their apparently chaotic variability has discouraged statistical studies such as those carried out on *Gryphaea* (e.g. Gould 1973). Nevertheless, it is of interest to inquire when the oysters attained euryhalinity, and how this may be reflected in phylogeny—subjects recently discussed by Stenzel (1971).

In Stenzel's classification the sub-family Ostreinae arises in the Cretaceous; the only sub-family of the Ostreidae present in the Jurassic is the Lophinae. These are plicate oysters of tropical origin and distribution and are apparently always stenohaline. The species that we discuss can clearly not be referred to this group. All other Jurassic oysters, including the genera *Liostrea* and *Praeexogyra*, in which *Ostrea hebridica* might be placed, are placed by Stenzel in the family Gryphaeidae. Stenzel considers that all Gryphaeidae were strictly euhaline and stenohaline.

The criteria by which Stenzel distinguishes Ostreidae from Gryphaeidae are primarily concerned with different aspects of the adductor muscle scar, and with shell structure. Those which are potentially applicable to fossils are summarized in text-fig. 1.

In recent years *O. hebridica* Forbes has generally been referred to the genus *Liostrea*. It was Stenzel's conclusion (1971, p. 1103) that *Liostrea* should, on the morphological criteria discussed above, be placed in the Gryphaeidae, and should

therefore presumably be stenohaline, that led us to look closely at *O. hebridica*. We had reason to think this species was euryhaline (Hudson 1963*a, b*). For the present, we shall refer *O. hebridica* to *Ostrea sensu lato*.

MORPHOLOGY OF *OSTREA HEBRIDICA*

The most obvious characteristic of *O. hebridica* is its great variability. The shape variation is well shown in the plates published by Arkell (1934) as part of his excellent description of the species; see also our Plate 14. Arkell also discussed the synonymy of *O. hebridica*, and we accept his conclusion that *O. sowerbyi* Morris and Lycett, 1853 and *O. subrugulosa* Morris and Lycett, 1853 are both junior synonyms of *O. hebridica* Forbes, 1851.

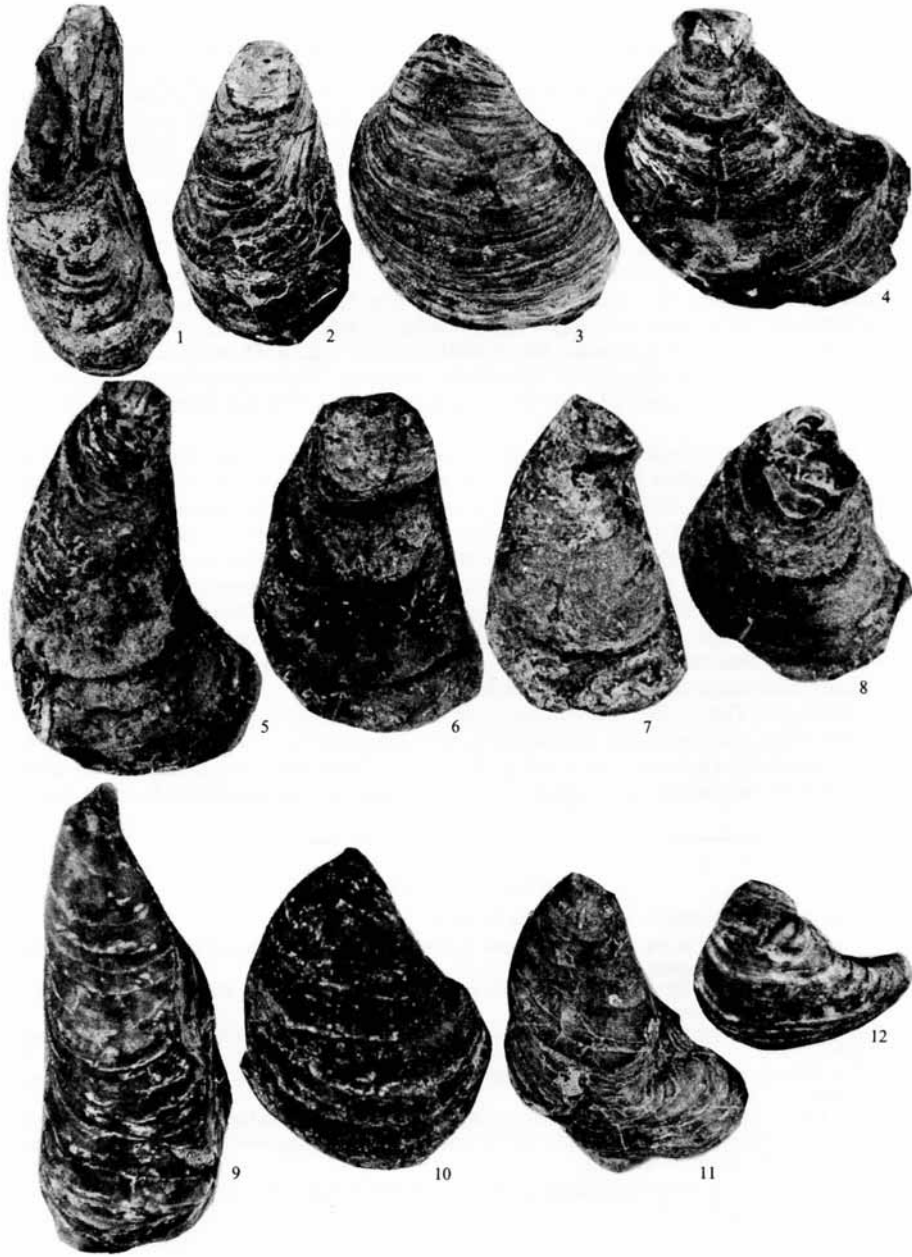
We have applied Stenzel's criteria to *O. hebridica* by considering several large populations independently, in order to take into account variation within and between populations (Table 1). Our observations have established that the species has the following characteristics:

1. The shape of the muscle scar is nearly always crescentic or reniform; occasionally, particularly in thin-shelled individuals, it may be orbicular, although this may be a preservational feature (Pl. 15, fig. 5).
2. The muscle scar is usually positioned nearer to the ventral margin of the valve than to the umbo; occasionally it is more or less central (Pl. 15, fig. 4).
3. The ventral margin of the muscle scar in the left valve is almost invariably not raised.
4. Radial posterior grooves have not been seen on any specimen examined: a shallow sulcus, however, is seen on some specimens from the Fuller's Earth of Langton Herring, Dorset.
5. In the left valve, a shallow to very deep umbonal cavity is present (Pl. 15, fig. 3).
6. Chambers are often present between the shell layers (Pl. 15, fig. 2).
7. A conspicuous outer shell layer (ostracum) of prismatic calcite is present in most specimens (Pl. 15, fig. 1).
8. The attachment area is frequently very large.

All these features are typical of the Ostreidae and suggest that *O. hebridica* should be placed in that family.

EXPLANATION OF PLATE 14

Shape variation in populations of *Praexogyra hebridica* from the Bathonian (Middle Jurassic) of Britain. Figs. 1-4. Lower Ostrea Beds, Duntulm, Trotternish, Isle of Skye (1, 40497; 2, 40495; 3, 45524; 4, 45522), $\times 1.4$. Figs. 5-8. Forest Marble Formation, Wood Eaton Quarry, near Oxford (5, 70511; 6, 70512; 7, 70513; 8, 70514), $\times 1.2$. Figs. 9-12. Fuller's Earth Clay, Langton Herring, Dorset (9, 38042; 10, 38022; 11, 38059; 12, 38020), $\times 1.8$. All specimens in the collection of the Geology Department, University of Leicester.



HUDSON and PALMER, Jurassic euryhaline oyster

OCCURRENCE AND ECOLOGY OF *OSTREA HEBRIDICA*

O. hebridica is widespread in the Bathonian of the British Isles from the Inner Hebrides (Skye is the type locality) to the Dorset coast (Arkell 1934). It often occurs in rock-forming abundance, making up more or less monotypic shell-beds. Individuals are frequently attached to one another. Although the original relief of an oyster 'reef' is rarely preserved in the British Jurassic, it seems very likely that low reefs comparable to those of *Crassostrea* in Texas today (Stenzel 1971, pp. N1045-1048) were present.

In the Inner Hebrides, *O. hebridica* occurs principally in the Lower Ostrea Beds of the Great Estuarine Series (Hudson 1962, 1963*a, b*; Tan and Hudson 1974). Shape variation is illustrated in Plate 14, figs. 1-4. Elongate forms are common but not as extreme nor as dominant as those in the Fuller's Earth at Langton Herring, Dorset (Arkell 1934; see below); lunate forms similar to the type of *O. sowerbyi* (see Morris and Lycett 1853, Table 1, fig. 3, 3*a*) are also common. Only one definite example of variety *subrugulosa*, with ribs on the left valve (Arkell 1934), has been found (Pl. 15, fig. 6).

In the Lower Ostrea Beds, virtually monotypic shell-limestones and shelly shales are frequent. In other beds interbedded with these, particularly silts and micritic limestones, *O. hebridica* occurs with a variety of other shallow-marine bivalves (*Modiolus*, *Myopholas*, *Corbula*, *Placunopsis*, *Cuspidaria*, etc.). These more diverse assemblages, in which oysters are less dominant and fossils do not compose most of the rock as they do in the shell-beds, may represent soft-bottom assemblages from the sea-floor between patches of densely attached oysters; indeed, in true shales the oysters are almost absent. Other occasional associates of *O. hebridica* in these beds include the brachiopod *Kallirhynchia*, regular echinoids (indeterminate plates and spines), and encrusting tubes of serpulid worms.

The Lower Ostrea Beds cannot, however, be regarded as fully marine. They include, interbedded with the oyster-bearing beds, siltstones with *Unio*, *Viviparus*, *Neomiodon*, and *Euestheria* (but without oysters). No truly stenohaline forms occur even with the oysters: no corals, no cephalopods, no ectoprocts, no brachiopods apart from

EXPLANATION OF PLATE 15

Morphological characteristics of *Praeexogyra hebridica*.

Fig. 1. Well-developed prismatic outer shell layer on right valve of specimen from Waterstein, Isle of Skye (70515). Photomicrograph from thin section, $\times 95$.

Fig. 2. Chambers (now filled with sparry calcite) in left valve of specimen from the Isle of Eigg (J 49718). Photomicrograph from thin section, $\times 10$.

Fig. 3. Umbonal cavity (arrowed) in left valve of specimen with conjoined valves. Langton Herring, Dorset (70516), $\times 3$.

Fig. 4. Interior of right valve, showing ventral position of muscle-scar (arrowed). Wood Eaton, Oxon. (70517), $\times 1.4$.

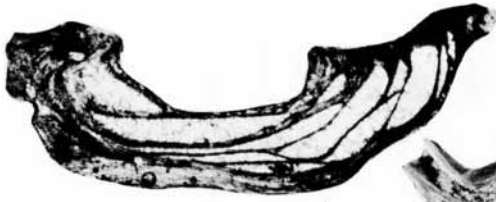
Fig. 5. Interior of right valve, showing reniform adductor muscle scar. Wood Eaton, Oxon. (70518), $\times 1.3$.

Fig. 6. var. *subrugulosa* from Waterstein, Isle of Skye (J 49341), showing characteristic radial riblets on exterior of left valve, $\times 1.2$.

Specimen numbers prefixed J from the Sedgwick Museum, Cambridge; others from the Geology Department, University of Leicester.



1



2



3



4



5



6

HUDSON and PALMER, Jurassic euryhaline oyster

TABLE 1. Variation among populations of *Ostrea hebridica* Forbes, compared to diagnostic criteria for the families Gryphaeidae and Ostreidae. Representative suites of populations examined are in the collections of the Geology Department, University of Leicester, the Sedgwick Museum, Cambridge, and the Oxford University Museum.

Criteria used for oyster classification in the Treatise (Stenzel 1971)	Populations of <i>O. hebridica</i> Forbes examined by us								
	Gryphaeidae	Ostreidae	Great Estuarine Series, Isle of Skye	Upper Estuarine Series, East Midlands	Haupten Marly Formation, Oxon.	Great Oolite Limestone, Olney, Bedfordshire	Forest Marble Formation, Wood Eaton, Oxon.	Sharp's Hill Formation, Oxon. and Gloucestershire	Upper Fuller's Earth Clay, Langton Herring, Dorset
Shape of adductor muscle scar	Orbicular	Crescentic or reniform	Crescentic or reniform	Orbicular, crescentic, or reniform	Crescentic or reniform	Crescentic	Crescentic	Reniform	Orbicular to reniform
Position of adductor muscle scar	Nearer hinge than opposite margin	Nearly central, or nearer opposite margin than hinge	Nearer opposite margin	Nearer	Central, to nearer opposite margin	Nearer opposite margin	Nearer opposite margin	Central, to nearer opposite margin	Central, to nearer opposite margin
Elevation of ventral portion of adductor muscle scar in L.V.	Raised	Not raised	Not raised	Not raised	Not raised	Sometimes raised	Not raised	Not raised	Not raised
Development of radial posterior groove on exterior of L.V.	Often present	Absent	Absent	Absent	Absent	Absent	Absent	Absent	May be present
Development of umbonal cavity in L.V.	Absent or very shallow	Shallow to deep	Present	Present	Shallow	Shallow to deep	Shallow	Present	Deep
Development of lenticular chambers within shell of L.V.	Absent, except in Exogyrinae	Commonly present	Present in some	Present	Present	Present	Present	Present in some	None seen
Development of prismatic calcite outer shell layer in R.V.	Thin or absent	Thin to conspicuous	Conspicuous	Conspicuous	Conspicuous	Conspicuous	Conspicuous in some specimens	Conspicuous	Present
Salinity tolerance	Euhaline and stenohaline	Sometimes euryhaline	Euryhaline	Probably euryhaline	Probably euryhaline; not fully marine	?Marine	Euryhaline	?Marine	Marine

Kallirhynchia. The bivalve fauna is very low in diversity. In all these features, the faunas contrast with those of the limestones of the contemporary Great Oolite Group of southern England. An inference of a generally brackish-water environment (Hudson 1963a, b) can still be supported. Additional evidence from algal limestones (Hudson 1970) and isotopic studies (Tan and Hudson 1974) indicates hypersalinities at times during deposition of the Lower *Ostrea* Beds, including some of the oyster-bearing strata. Such alternations of conditions are readily understandable in a setting of semi-enclosed lagoons, as in the recent habitat of *Crassostrea virginica* in Texas (e.g. Stenzel 1971, pp. N1038-1039).

In Central England, *O. hebridica* occurs commonly at two levels within the Great Oolite Group. The lower includes the Upper Estuarine Series of the East Midlands and its approximate lateral equivalent in Oxfordshire and Gloucestershire, the Hampen Marly Formation. The upper level includes the Blisworth Clay of the East Midlands, and its lateral equivalent, which extends over the rest of southern England, the Forest Marble Formation.

In the Upper Estuarine Series, *O. hebridica* is extremely common in clays and limestones, interbedded on a scale of a few centimetres with carbonaceous clays that overlie rootlet-beds. The rootlets penetrate the oyster-bearing clays (Aslin, in Sylvester-Bradley and Ford 1968). The associated faunas are, in general, more marine in aspect than those in the Hebrides but, again, fully stenohaline groups are absent. A coastal lagoon environment close to the shore of the Anglo-Belgian landmass, frequently invaded by swamp vegetation, seems indicated. The Hampen Marly Formation of Oxfordshire and Gloucestershire seems to represent the seaward edge of this lagoonal environment. *O. hebridica* commonly forms oyster reefs up to 2 m in thickness (Richardson 1933), and these reefs are interbedded with marls and marly limestones. Nevertheless, the fauna associated with the oysters is principally molluscan, and of low diversity. Stenohaline forms are rare. Passing south-westwards towards the Bath region, however, the Hampen Marly Formation passes into more fully marine limestones in which known stenohaline forms are more common. Significantly, the oyster reefs die out in this region and *O. hebridica*, although still occurring, never approaches the abundance typical of the landward region to the north-east.

In the Blisworth Clay the association of *O. hebridica* with rootlets is again seen. An interesting feature of this region is the occurrence of populations in which the variety *subrugulosa* is common, and locally dominant. The *O. hebridica*/rootlet association also persists across north Oxfordshire, where the Blisworth Clay passes laterally into the Forest Marble Formation. Palmer and Jenkyns (1975) have recently argued, from both faunal and sedimentary evidence, that there was extensive development of brackish lagoons in this region.

Rolled and abraded specimens of *O. hebridica* continue to occur abundantly in the limestones of the Forest Marble Formation over the whole of southern England. Since they are virtually never found in life position, it is difficult to infer their life preferences. They occur with a wide variety of fully marine species, but features suggestive of emergence (mud flakes) and river drainage from land (lignite) are also common.

O. hebridica also occurs relatively rarely in the limestone unit which separates the

two stratigraphic levels referred to above. In the White Limestone Formation of Oxfordshire and Gloucestershire the oyster occurs with marine species in micritic sediments representing marine lagoons with poor water circulation. In the laterally equivalent Great Oolite Limestone of the Midlands the occurrence is similar, and the variety *subrugulosa* is common locally. *Subrugulosa*, therefore, seems to be geographically, rather than stratigraphically, restricted in occurrence.

In the Fuller's Earth Clay of Langton Herring on the Dorset coast is one of the best-known occurrences of *O. hebridica* (described by Arkell 1934, 1947). The surrounding bed is a marine clay, although the oyster bed itself is almost monotypic. The bed varies in thickness from 1 to 4 m over a distance of 1.6 km; the same horizon may, however, be present at Watton Cliff, Bridport, 20 km away (Arkell 1947, pp. 16-17). The population is dominated by the variety *elongata* Dutertre (see Arkell 1934) and is somewhat distinct from the others we have studied (Table 1). Growth rugae tend to be more regularly developed. The oysters are heavily encrusted with adherent Foraminifera, a feature only infrequently observed on those from the Great Estuarine Series or the Great Oolite. This probably indicates a higher and more stable salinity, and the elongation may be explained as a phenotypic response to a muddy bottom. It is proposed that this occurrence represents an offshore, sub-tidal marine environment, while the other populations we studied came from more or less enclosed marginal bays and lagoons.

There is therefore strong evidence that *O. hebridica* was a euryhaline species. This is in contrast to Stenzel's view of the ecological preferences of the Gryphaeidae as 'strictly euhaline and stenohaline' (Stenzel 1971, p. N1097). Furthermore, *O. hebridica* individuals frequently grew attached one to another and formed oyster reefs. Again, this is contrary to Stenzel's view of the Gryphaeidae (p. N1097). We feel that these characteristics, taken together with the strong morphological evidence considered above, necessitate placing *O. hebridica* in the Ostreidae. If accepted, the conclusions so far drawn establish our main point, that euryhaline Ostreidae existed in the Middle Jurassic. There are, however, some taxonomic and phylogenetic consequences that need exploring.

GENERIC AFFINITY OF *OSTREA HEBRIDICA*

O. hebridica (as *O. sowerbyi* Morris and Lycett; see above) was one of the original species included in the genus *Liostrea* Douvillé, 1904 by its founder. According to the 'form genus' concept discussed, and deplored, by Stenzel (1971, pp. N1066-1067), *Liostrea* has been widely used since as a name for almost all 'flat' and not strongly ribbed oysters from the Jurassic, including *O. hebridica*. If, however, one is to attempt to disentangle the phylogeny, it is necessary to inquire whether these oysters are a single stock and, as a first step, to examine the type species of *Liostrea*. This is *O. sublamellosa* Dunker, 1846. According to Stenzel (1971) the following species are synonymous: *O. hisingeri* Nilsson, 1832; *O. irregularis* Munster, 1833; *O. anomala* Terquem, 1855; *O. liassica* Strickland, 1876; ?*O. bristovi* Richardson (ex. Etheridge MS.), 1905. Thus the correct name for the type species is *L. hisingeri*. It is widespread in the Lias and Rhaetic of Europe, and its characteristics caused Stenzel (1971, p. N1103) to place the genus firmly in the Gryphaeinae. We discuss *L. hisingeri* below.

Charles and Maubeuge (1953) included *O. sowerbyi* and *O. subrugulosa* in *Praeexogyra*, their new sub-genus of the cupped oyster *Catinula*. They were evidently unaware of Arkell's (1934) demonstration that *O. sowerbyi* and *O. subrugulosa* are synonyms of *O. hebridica*. Furthermore, they placed *O. sowerbyi* and *O. subrugulosa* as members of different lineages in their phylogeny. The type species of *Praeexogyra* is *O. acuminata* J. Sowerby, and our concept of the taxon must be based on that species. *Praeexogyra* was raised to generic rank in Stenzel (1971), and placed in the Gryphaeidae.

All authors are agreed that *O. acuminata* and *O. hebridica* are closely related. When the species occur together, as in the Sharp's Hill Beds and Stonefield Slate (Great Oolite Group) of the Cotswolds (Arkell 1934), they are far from easy to separate. Arkell denied their intergradation, but Sylvester-Bradley (pers. comm.) and the present authors are inclined to uphold it. However, this is unimportant in the present context, because Arkell (1934, p. 31) clearly thought that *O. acuminata* gave rise to *O. hebridica*, but at an earlier horizon; *O. acuminata* characterizes the Upper Bajocian in Eastern France, but ranges into the lower parts of the Bathonian, which is the type horizon. Pugaczewska (1971, pl. XI) figures examples of *O. acuminata* from Poland, some of which approach *O. hebridica* in shape. If one accepts that *Praeexogyra* has generic status, then *O. hebridica* must belong to it. We accept this generic status, but believe on the evidence presented in this paper that *Praeexogyra* Charles and Maubeuge, 1953 should be transferred to the family Ostreidae, sub-family Ostreinae.

MORPHOLOGY OF *LIOSTREA HISINGERI*

O. hebridica, however, remains very similar in general morphology, including range of shape variation, to the type species of *Liostrea*, *L. hisingeri* of the Lower Lias. It is, in fact, much more similar to 'typical' *L. hisingeri* in shape than it is to 'typical' *O. acuminata*. Is it possible that all three species are closely related, or that *L. hisingeri* was an Ostreid, not a Gryphaeid? Were these Liassic oysters euryhaline?

Stenzel (1971, p. N1103) claims that 'orbicular muscle adductor imprint, radial posterior sulcus on left valve, lack of chomata, and absence of umbonal cavity place the genus (*Liostrea*) firmly in the Gryphaeinae'. However, our examination of collections from the Lower Lias at various British localities suggest that its morphological characteristics are somewhat more variable and equivocal (cf. text-fig. 1).

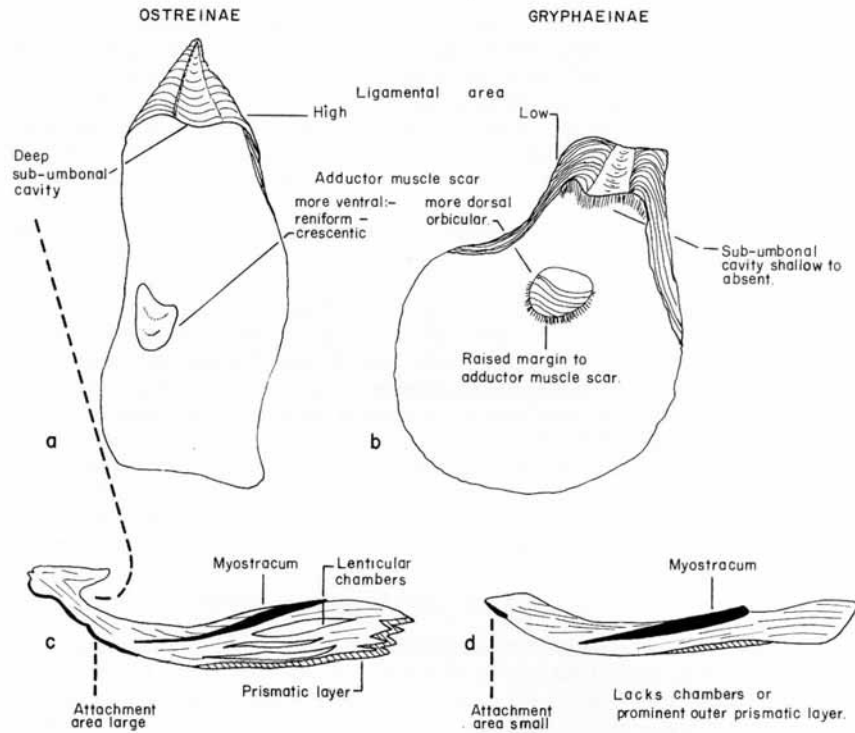
Shape and position of muscle scars. Mainly orbicular; ventral portion of scar in left valve sometimes raised; usually positioned nearer hinge than opposite margin, but position varies.

Radial posterior groove. Not present on any of the material seen by the authors, although present in the material of *L. sublamellosa* seen in Paris by Stenzel.

Umbonal cavity in left valve. Small or absent.

Shell structure. Some chambers; thin prismatic layer sometimes seen.

The general shape and ecological occurrence (reviewed below) of *L. hisingeri* are consistent with Ostreid affinity, as are, more equivocally, the occasional presence of chambers and a prismatic shell layer. On the other hand, the muscle scars, absence



TEXT-FIG. 1. Distinguishing shell-features of left valves of generalized members of the Ostreinae (a, c) and Gryphaeinae (b, d), reconstructed from data in Stenzel (1971). a, b, shell interiors; c, d, dorso-ventral sections.

of umbonal cavity, and occasional presence of a radial posterior groove point to Gryphaeid affinity.

Stenzel (1971, p. N1096) gives particular weight to shell structure in classification. It is therefore unfortunate from our point of view that Siewert's (1972) recent study of oyster-shell structure includes neither *L. hisingeri* nor *O. hebridica*. It is clear from his list of species that Siewert has a broad concept of the genus *Liostrea* including species referred to *Deltoideum* and to *Praeexogyra* by Stenzel. Our own observations suggest that *L. hisingeri* is more Gryphaeid, *O. hebridica* more Ostreid, in shell structure, but both are variable and the situation is not clear cut.

We discuss aspects of the ecology of *L. hisingeri* below but, basing our taxonomic conclusions on morphological evidence, it seems safest at present to keep *O. hebridica* generically separate from *L. hisingeri*. The unwelcome conclusion is thus that the correct name for *O. hebridica* is currently *Praeexogyra hebridica* (Forbes, 1851). The two species are consequently in different families of the superfamily Ostreacea.

ECOLOGY OF *LIOSTREA HISINGERI*

Our conclusion that *L. hisingeri* may be morphologically intermediate between Gryphaeidae and Ostreidae suggests that its ecological preferences, particularly as regards salinity tolerances, should be investigated. We have not made detailed studies of the conditions of deposition of the beds concerned, but some information is available in the older literature summarized by Arkell (1933) and in works by Hallam (e.g. Hallam 1971).

L. hisingeri is common in the Rhaetic Beds of Dorset, Somerset, and Gloucestershire, principally associated with *Dimyodon intusstriatus*, *Modiolus langportensis*, *Lima valoniensis*, *Cardinia* sp., and *Protocardia* sp. These bivalves may occur in great abundance, whereas known stenohaline groups such as corals, ectoprocts, brachiopods, cephalopods, and echinoderms are either absent or occur only locally. Indicators of shallow water or near-by land, such as mammal, insect, and plant remains, algal limestones (Hamilton 1961), and desiccation cracks, are also found.

A similar situation is seen in the 'pre-*planorbis* beds' of the Lias of South-West England, Yorkshire, Northern Ireland, and Western Scotland. Again, *Liostrea hisingeri* and a small number of other bivalve species occur to the exclusion of stenohaline forms. Such low diversity/high abundance faunas are characteristic of reduced or highly variable salinity, and strongly suggest that *L. hisingeri* was a successful euryhaline species which thrived in the marginal environments associated with the Rhaetic-Liassic transgression in England. As the transgression continued, stenohaline *Gryphaea* almost completely replaced *L. hisingeri*; the typical *Gryphaea* beds of the Lias are also replete with ammonites, belemnites, and echinoderms. A similar picture of the ecology of *L. hisingeri* in the Lias of western Portugal is drawn by Hallam (1971).

EVOLUTION OF EURYHALINITY IN THE OYSTERS

We here present a discussion of the acquisition of euryhalinity in the oyster stock that led to the modern Ostreinae, and thus of the phylogeny of Mesozoic oysters. This is necessarily speculative, because we have not made the required detailed studies of all the oyster species potentially involved; in particular, the bewildering variety of flat oysters in the Lower Lias require further study. The belief that they all belong to one species may well not be correct, and their relationship with the contemporaneous *Gryphaea* species is still far from clear. What we present is one plausible interpretation of the evidence we have discussed.

We believe that *Praeexogyra hebridica* was a fully developed ostreid, and that the group of *L. hisingeri* includes its ancestors. Thus this evolution also represents the evolution of the Ostreidae from the Gryphaeidae. This process began in the Upper Trias/Lower Lias of north-west Europe, and was complete by the Middle Jurassic.

It is possible that many of the ostreid characters shown by *L. hisingeri*, and more strongly by *P. hebridica*, can be explained as adaptations to the marginal marine, highly variable conditions in which these species lived. These include not only the salinity changes which we have stressed so far, but also fluctuations in temperature, current activity, turbidity (associated with river discharge and storms), and temporary

subaerial exposure; none of these are experienced to the same extent, if at all, by fully subtidal animals. These effects combine to exert strong selection pressure for 'opportunism', to allow the next generation to be produced quickly before drastic environmental change should wipe out the population, and for various devices to protect the animal from environmental fluctuations.

Changes from a primitive gryphaeid to an ostreid could have helped in the following ways:

1. The young oysters remained attached longer, or throughout life, developing a larger attachment area and becoming less susceptible to current activity. Thus they had no need of the coiled and thickened left valves characteristic of *Gryphaea*. (Whether this represents an evolution of *Liostraea* from *Gryphaea*, as Stenzel believes, or divergent evolution from a common ancestor, is at present uncertain.)

2. The greater importance of cemented attachment meant that suitable attachment sites were more important; thus the reef-forming habit, in which spat-fall and growth were encouraged by a stable framework of adults and dead individuals, developed. The reef-forming habit also allows synchrony of gamete release, as seen in some Recent Ostreinae, which maximizes the chance of fertilization.

3. The oysters developed means of sealing themselves more efficiently from a temporarily unfavourable environment. This included the development of a fringe of flexible conchiolin scales around the edge of the right valve (Stenzel 1971, p. N977). In Recent oysters these scales merge at their proximal ends with the calcite prisms of the outer shell layer, which is well developed in such species. By analogy, fossil Ostreidae, with better-developed prismatic layers than the Gryphaeidae, were more efficient at sealing themselves. The presence of well-developed conchiolin scales in *P. hebridica* may also be inferred from the fact that the margin of the right valve frequently lies inside that of the left valve (Douvill  1920).

Development of a highly mobile pallial curtain, as described in Recent ostreids by Yonge (1936) and Nelson (1938) may also have occurred at this stage under a similar selection pressure. We cannot, however, make inferences about this property from hard parts alone.

4. The longer time spent with both valves closed produced greater demands on the catch muscle. As Stenzel (1971, p. N1058) points out, ventral shift of the muscle would improve the leverage (and see 6 below). It would also improve the efficiency of the quick muscle, which would be particularly important in a near-shore environment with more suspended inorganic matter, leading to the necessity for frequent expulsion of pseudo-faeces. These points have also been stressed by Yonge (1936) and Nelson (1938).

5. The change in cross-section shape of the adductor muscle to crescentic or reniform increases its surface area/volume ratio. With the heart tucked well into the dorsal concavity of the muscle, improved oxygenation in response to the increased demands on both components of this organ would be a likely result.

6. In Recent non-incubatory Ostreidae, the presence of an umbonal cavity correlates with presence of a promyal passage (Stenzel 1971, p. N1127). This suggests that *P. hebridica* also contained this structure. Nelson (1938) saw the evolutionary development of the promyal passage, resulting in more efficient removal of sediment

from the exhalant chamber, as being a specific adaptation to living in more turbid water, such as is found in marginal marine conditions. Such an opinion supports those which we have stated above. However, living Gryphaeidae all have a promyal passage, and Stenzel considers it a characteristic of the family. This being so, we prefer to regard the presence of the promyal passage in *P. hebridica* (and in Recent non-incubatory ostreids) as being a characteristic inherited from gryphaeid ancestors (discussed further below). We think it is less likely to be one of the specific adaptations developed in response to pressures associated with marginal marine environments, as are the other characteristics discussed above.

PHYLOGENY OF OYSTERS

Our conclusion, although based on a detailed study of only one species, has consequences for the phylogeny of Mesozoic oysters proposed by Stenzel (1971). According to his views, oysters are diphyletic: *Lopha* arises in the Triassic in the Tethyan realm and *Gryphaea* in the Boreal realm; *Liostrea* is an early offshoot of *Gryphaea*; all Ostreidae are descended from *Lopha*; the Ostreinae (true oysters) do not arise until the Cretaceous; *Liostrea* and other non-coiled genera of the Gryphaeidae die out at the end of the Jurassic.

In the phylogeny published by Siewert (1972), *Liostrea* (including *Praeexogyra*) also dies out at the end of the Jurassic. Thus, in both these phylogenies, the origin of the modern 'flat' oysters coincides with the extinction of the morphologically similar 'flat' oysters of the Jurassic, but the two groups are supposedly not related. In Pugaczewska (1971, fig. 3), *Liostrea* (including *Praeexogyra*) is shown persisting to the end of the Cretaceous, but again the modern oysters are derived from *Lopha* (= *Alectryonia*) during the Cretaceous.

Our finding that the *Praeexogyra* belongs to the Ostreidae thus means that the Ostreidae (*sensu* Stenzel) are diphyletic. It also raises the possibility that some, at least, of the Cretaceous to Recent true oysters (Ostreinae) may be descended from the Gryphaeidae via *Liostrea* and *Praeexogyra*, and not from *Lopha* as hitherto believed. This proposal can only be tested by a close examination of the Cretaceous oysters, which we have not attempted. However, a likely descendant of *P. hebridica* is *O. distorta* Sowerby of the middle Purbeck Beds of southern England, now generally dated as basal Cretaceous. Its morphology is poorly known, but in general shape and inferred ecology it is similar to *P. hebridica*. The Lower Cretaceous species, referred to *Ostrea* and figured by Pugaczewska (1975, Pl. XIV) from Poland, are also at least as similar to Jurassic *Liostrea* and *Praeexogyra* as to later *Ostrea*, and could be Gryphaeid descendants.

An independent speculative argument about which modern oysters may be derived from Gryphaeidae, and which from Lophinae, may be stated as follows. Hudson (1963b, p. 332) pointed out that *P. hebridica* is closer in morphology and inferred ecology to *Crassostrea* than to *Ostrea*, among living oysters. *Crassostrea* has a promyal passage, is non-incubatory, and is predominantly estuarine in distribution; *Ostrea* lacks a promyal passage, is incubatory, and is more stenohaline. As discussed above, the left valves of many *P. hebridica* exhibit a deep umbonal cavity. According to Stenzel (1971, pp. N1127, 1138) this correlates with the presence of a promyal passage

in living members of the Ostreidae. The few living Gryphaeidae (Pycnodonteinae) also have a promyal passage, as does *Crassostrea*, but *Ostrea* and *Lopha* lack this feature. It is possible that Stenzel's informal group of genera centred on *Crassostrea* comprises Gryphaeid descendants, and that genera like *Ostrea* are descendants of *Lopha*.

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