# MIDDLE JURASSIC (BATHONIAN) OSTRACODA FROM THE INNER HEBRIDES, SCOTLAND

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Pages 1-89: Plates 1-11

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## INTRODUCTION

The ostracod occurrences within the essentially Bathonian Great Estuarine Group should be viewed in the context of the marked faunal change over shown by the Ostracoda during the Bathonian. World-wide some 79% of the Bathonian ostracod species are not found in the preceding Bajocian (Whatley 1988). The Bathonian is seen as a peak of evolutionary activity in the Ostracoda (Whatley & Stephens 1976). Freshwater cyprids, though known from the Triassic, did not dominate in freshwaters until the Bathonian (Whatley 1990). Previously the freshwater realm had been dominated by the Darwinulacea and Limnocytheridae (Whatley 1990). Whatley & Stephens (1976) and Whatley (1988, 1990) noted the adaptive radiation of the Progonocytheridae during the Bathonian. The development of brackish water ostracod faunas also occurred in the Bathonian (Whatley 1990). Many freshwater assemblages have been noted in the Oxfordshire (Bate 1965, 1967; Ware [1978]; Stephens [1980]: Ware & Whatley, 1980, 1983; Ware & Windle, 1981; Jacovides [1982] and Barrington [1986]) and Gloucestershire (Timberlake [1982]) regions, and are of obvious interest with respect to the present study, though the number of species recorded was low. This work, however, contains the largest fresh and brackishwater ostracod fauna yet described from the British Bathonian. This study increases our knowledge of low salinity ostracods in the Bathonian, and for the first time documents ostracods from the Scottish Bathonian. It is strange, however, that the genus Timiriasevia, which is typically found in sediments deposited under similar conditions in the rest of Britain, is absent, and that there are no examples of freshwater cyprids.

## HISTORY OF RESEARCH

#### THE GREAT ESTUARINE GROUP

The first mention in the literature of ostracods from the Great Estuarine Group of the Inner Hebrides was by Tate (1873). In the faunal list for what was then called the "Estuarine Series" cyprids were simply recorded as being present. In his description of the fauna, Hudson (1963a) mentions only that ostracods were present. However, Hudson (1966) in a paper on Hugh Miller's Reptile Bed, recorded Progonocythere and Fuhrbergiella. Kilcnyi (1972) reported Theriosynoecum, Darwinula and Cytheridea? from the Kilmaluag Formation of the Great Estuarine Group. Although the *Theriosynoecum* species was not described, the pattern of its nodes was mentioned in conjunction with work being carried out by Kilenyi on transient and balanced genetic polymorphism. The ostracod genera identified by Kilenyi were also documented in Tan & Hudson (1974). Overall, it is easy to see what prompted Bate (1978, p. 254) to say of the Great Estuarine Group sequence that it ".... is so imperfectly known with respect to its ostracod fauna that it is one area in urgent need of investigation". Andrews [1984] briefly noted the ostracods from the Kilmaluag Formation. He listed Theriosynoecum, Darwinula, Stenestroemia and two indeterminate cytheracean genera. The most recent work on the ostracod fauna is that of Wakefield & Siveter (1989), Wakefield & Athersuch (1990) and Wakefield (1990).

## OTHER BRITISH BATHONIAN WORK

The first published account of Bathonian ostracods from Great Britain was that of T. R. Jones (1884), followed closely by Jones & Sherborn (1888). The works described faunas from the Richmond Borehole in Surrey and from the Fullers Earth, Bath and Bradford Clay, Bradford respectively. The taxonomy of these works was revised by Bate (1969).

It was not until the designation of the genera *Progonocythere* and *Lophocythere* from the Boueti Bed at Langton Herring, Dorset, by P. C. Sylvester-Bradley (1948) that British Bathonian ostracods were studied again. In 1956 Sylvester-Bradley published a study on the evolution, structure and nomenclature of the ostracod hinge. He also designated the genus *Acanthocythere* based upon specimens from Jones & Sherborn (1888).

#### LOCALITIES

The majority of work on British Bathonian ostracods, however, has been undertaken since the 1960s. Bate (1965) described eight freshwater ostracods from the Forest Marble found in the Old Cement Works, Kirtlington, Oxfordshire, including *Theriosynoecum kirtlingtonense* Bate, 1965 and some damaged specimens of what was latter designated as *Darwinula incurva* Bate, 1967. In this latter work Bate described 29 species from 20 genera from the Bathonian Upper Estuarine Series from eastern England. These included *Darwinula incurva*, *Progonocythere levigata* and *Progonocythere kingscliffensis* which occur in the present study.

The revision of the Jones (1884) and Jones & Sherborn (1888) papers by Bate (1969) also included a revision of Lophocythere Sylvester-Bradley, 1948. Ware & Whatley (1980) concluded this revision by raising the subgenus Neurocythere Whatley, 1970 to generic rank and keeping Lophocythere and Terquemula Blaszyk & Malz, 1965 separate. Malz (1975) studied some of the species of Lophocythere from southern Britain including those from the Upper Estuarine Series of the east Midlands and the Forest Marble at the Old Cement Works, Kirtlington, Oxfordshire. Ware & Whatley (1980) described 12 new species from the Old Cement Works at Kirtlington and listed a further 93 species of which Darwinula incurva, Micropneumatocythere falcata and Progoncythere kingscliffensis are dealt with in the present work.

The 'Aberystwyth School' of research, supervised by Prof. R. C. Whatley, has undertaken several studies of British Bathonian ostracod faunas [Ware 1978, Stephens 1980, Jacovides 1982, Timberlake 1982 and Barrington 1986]. Unfortunately these works, though produced as M.Sc. and Ph.D. theses, are only partly published. This is also true of L. M. Sheppard [1981a] who worked on the Ostracoda of southern Britain and northern France. This work mostly covered marine species and, as such, the similarities between this fauna and the present study are small. Sheppard (1981b) did, however, revise the Bathonian ostracod zonation scheme of Bate (1978) from eight to five zones.

## STRATIGRAPHY

The Great Estuarine Group (Harris & Hudson 1980) has been assigned a Bathonian age because of its stratigraphical relationship with the underlying Bajocian Bearreraig Sandstone Formation and the overlying Callovian Staffin Bay Formation (Text-fig. 1). Dating within, and the zoning of, the British Bathonian is usually hampered by the rarity or total absence of ammonites (Torrens 1980). The complete lack of fully marine faunas within the Great Estuarine Group (Hudson 1963a, 1980) means that correlation with other British Bathonian sections has relied upon lithofacies analyses alone. Andrews (1984, 1985) and Andrews & Walton (1990) suggested that the Duntulm Formation has a stratigraphical equivalent in the White/Blisworth Limestone Formation of England, which belongs to the Procerites hodsoni, Morrisiceras (Morrisiceras) morrisi and Tulites (Tulites) subcontractus zones of Cope et al. (1980). On this basis Andrews (1985) correlated the Kilmaluag and Skudiburgh formations with the Forest Marble / Blisworth Clay which belong to the Oppelia (Oxycerites) orbis Zone of Mangold (1984); which is equivalent to the Oppelia (Oxycerites) aspidoides Zone of Cope et al. (1980). Palynological analyses (Bailey, lit. comm. 1989) of samples supplied by the present author have independently confirmed a Bathonian age based upon the presence of the pollen Quadraeculina anellaeformis and the palynomorph Hapsidualax margarethae (Text-fig. 1).

The lithostratigraphical divisions of Harris & Hudson (1980) and the bed numbering of Andrews (1984, 1985) and Andrews & Walton (1990) have been followed in this work. The stratigraphical logs for the Lealt Shale Formation were supplied by J. D. Hudson and can be found in Appendix 1 of Wakefield [1991]. The measured logs from the Isle of Eigg will be published in the 'Small Isles' Memoir of the British Geological Survey (Hudson in press).

#### LOCALITIES

The Great Estuarine Group is geographically limited to the Islands of the Inner Hebrides of Scotland, and in particular Skye, Raasay, Eigg and Muck (Text-fig. 2). However, Trueblood

		Ammonite Zones	Ammonite Subzones	Nor Peter (Cope a and Pa	thants. borough. et. al. 1980 age 1989)	Andrews 1985 Andrews & Walton 1990	Palynomorph Dating by D. Bailey for B. P. Research on samples provided by M. I. Wakefield	N	Aorton 1989	l c	Proposed	
Call	ovian	Macrocephalites herveyi	M. camptus M. terebratus Kepplerites (K.) kepperi	botsbury ibrash Fm.	Fleet Mbr.	Staffin Bay Formation	Top of section not studied	Staffi	Belemnite Sands Member	Staffi	Belemni Sands Membe	te T
		Cyldoniceras (Clydoniceras) discus	C. (C.) discus C. (C.) hollandi	Соп	Berry Mbr.	Skudiburgh & Kilmaluag formations	Kilmaluag Formation	Fm	Upper Ostrea Member	Fm	Upper Ostrea Membe	yr i
	UPPER	Oppelia (Oxycerites) orbis		Blisworth Clay					Skudiburgh & Kilmaluag formations		Skudiburgh & Kilmaluag formations	
		Procerites hodsoni		Bli Lin	sworth nestone	Duntulm	Duntulm Formation		Duntuim		Duntulm	
IAN	Ш	Morrisiceras (Morrisiceras) morrisi		Blisworth Limestone (Kallirhynchia sharpi beds)		Formation		s possible	Formation		ormation	
N O H	IIDDL	Tulites (Tulites) subcontractus						onite zone	Valtos Sandstone Formation	ssible	Valtos Sandston Formation	E GROUI
B A T	N	Procerites progracilis		No attempt Bottom of sec at dating not studied Upper lower	No attem at dating Upper lower		Bottom of section not studied	andard amn	E Lonfearn D L Member	e zones po	Lonfer H Memb	TUARIN
	VER	Aspinctites tenuiplicatus		Estuarine Series		formations		on with sta	び そ Kildonnan Member	d ammonit	Kildon Memb	an er REAT ES
	ΓΟΛ	Zigzagiceras (Zigzagiceras) zigzag	O. (O.) yeovilensis M. (M.) macrescens P. (P.) convergens	••••••	•••••			lo correlati	Elgol	vith standar	Elgol	
		Parkinsonia parkinsonia	P. bomfordi S. truelli P. acris		222			2	Formation	orrelation w	Sandston Formatio	e n
Вај	kian .	Strenoceras (Garantiana) garantiana	S. (G.) tetragona S. (G.) subgaranti S. (P.) dichotoma					Ga	Cullaidh Shale Formation rantiana Clay	° Ž Ga	Cullaidh Sh Formation rantiana Clay	ale n /

TEXT-FIG. 1. Suggested correlation of the Great Estuarine Group with the standard ammonite zones.

## LOCALITIES



TEXT-FIG. 2. Location of Great Estuarine Group (shaded) and of the sections sampled.

& Morton (1991), Trueblood (1992) and Morton (1989, 1992, 1993) use the "Great Estuarine Group" as a sequence stratigraphic unit name within all of the middle Jurassic basins along the western side of the British Isles. As each of these sequences was deposited within a different basin, I consider the Great Estuarine Group to be limited to only the Inner Hebrides.

The sampled localities are listed, where possible, in stratigraphical order. The following information is given for each locality: locality number, geographical location, National Grid Reference and the lithostratigraphical position. Detailed stratigraphical logs with the sampling positions marked are given in the biostratigraphy section. The locations of the sections are shown in Text-fig. 2.

Locality 1. Type section of the Kildonnan Member, Eigg (Harris & Hudson 1980). NM 495,870. Kildonnan Member, Lealt Shale Formation. It appears that the Algal Bed, which marks the lithostratigraphical division between the Kildonnan and Lonfearn members, originally noted at this section, was immediately above a low angle slip plane and has in recent years been eroded away. Less than one metre of section is probably missing from the top of the exposure. The section is exposed in the boulder beach and the amount visible varies as the boulders are moved by storms. Section exposed at low tide.

Locality 2. North West Shore, Eigg. NM 469,904 - 475,908. Kildonnan and Lonfearn members of the Lealt Shale Formation. Only the top of the Kildonnan Member is exposed whilst the probably complete section of the Lonfearn Member is heavily disrupted by numerous thin basalts. Exposure as for locality 1.

Locality 3. Allt na h'Airde Meadhonaich also known as the Shieling Burn, Eigg. NM 497,888. Top of the Lonfearn Member, Lealt Shale Formation and the base of the Valtos Sandstone Formation. The transition between the Lealt Shale and the Valtos Sandstone formations is marked by a series of 10-20cm thick shell hashes with well preserved aragonite from Unio sp. bivalves.

Locality 4. Type section of the Lonfearn Member (Harris & Hudson 1980), Rudha nam Braithairean, also known as Brothers Point, Trotternish, Skye. NG 526,625. Kildonnan and Lonfearn members, Lealt Shale Formation. The basal 10m of the Lonfearn Member was sampled. Thermal metamorphism by a thick (8m) dolerite sill precluded the breakdown of samples into residues from the upper 5m of the sampled section. Kildonnan Member portion of this section exposed at low tides.

Locality 5. North of Elgol, Strathaird, Skye. NG 516,140 - 516,147. Kildonnan and Lonfearn members, Lealt Shale Formation. The rocks have been strongly metamorphosed by the nearby Cuillin Hills Tertiary intrusive complex.

Locality 6. Camas Mor, Muck. NM 406,792. Divisions E and F of the Valtos Sandstone Formation and the lower part of the Duntulm Formation. Low tides are required to expose the lower part of the Duntulm Formation and the Valtos Sandstone Formation.

Locality 7. Type section of the Duntulm Formation (Harris & Hudson 1980). NG 410,739 - 407,734. Upper Valtos Sandstone Formation (not sampled as too strongly metamorphosed by the Duntulm Castle intrusion) and the Duntulm Formation. This section follows on into the Duntulm Formation at Lon Ostatoin (locality 8). Bed 54 of the type section correlates with bed 4 of the Duntulm Formation at Lon Ostatoin. Section exposed at low tides.

Locality 8. Lon Ostatoin, Trotternish, Skye. NG 408,727. Duntulm and Kilmaluag formations. The upper part of the Kilmaluag Formation is exposed in this section (Andrews 1985), which runs upstream from the road bridge. The section at Lon Ostatoin correlates with the Duntulm Formation type section (locality 7); Bed 54 of the type section is the equivalent of Bed 4 of the Duntulm Formation at Lon Ostatoin (Andrews 1984, Andrews & Walton, 1990).

Locality 9. River cliff of the Bay River tributary, Waternish, Skye. NG 270,537. Duntulm Formation. The lowest beds are only a few metres above the top of the Valtos Sandstone Formation (Andrews & Walton 1990).

Locality 10. Laig Gorge, Eigg. NM 473,874. Duntulm and Kilmaluag formations. Only the upper beds of the Duntulm Formation and the lower 6m of the Kilmaluag Formation are exposed; the transition between the two being well exposed. The section is thermally metamorphosed. The upper part of the Kilmaluag Formation is cut out by the upper Cretaceous Laig Gorge Beds of Hudson (1960).

Locality 11. Type section of the Kilmaluag Formation (Harris & Hudson 1980), Kilmaluag Bay, Trotternish, Skye. NG 437,752. Kilmaluag Formation. Exposures are best found between the boat slipway and a prominent dolerite sill. Only exposed at low tides.

Locality 12. Prince Charles's Point, Trotternish, Skye. NG 376,666. Kilmaluag Formation. These beds were placed in the upper part of the formation (Andrews 1985). This foreshore section close to the boat slipway exposes gently dipping sands and shales.

Locality 13. Camas Mor, Muck. NM 405,790. Kilmaluag Formation. This section is separate from the Valtos Sandstone and Duntulm formations and is exposed during low tides at the western side of the bay.

## MATERIAL, TERMINOLOGY AND TECHNIQUES

#### MATERIAL, TERMINOLOGY AND TECHNIQUES

The ostracod material described in this monograph was obtained from samples collected by the author (1988, 1989 and 1990) and by Mrs. K. Invernizzi (1984 and 1985). Prof. J. D. Hudson and Dr. R. G. Clements donated several samples from their own research collections. The type and figured material from this monograph has all been placed in the collections of the Natural History Museum, London; specimens housed in this museum are prefixed with OS or Io. Several specimens are housed in the Senckenberg Museum in Frankfurt, the numbers of which are prefixed with SMF. Populations and residues remain in the author's research collection in the Department of Geology, University of Leicester.

## SAMPLING AND PROCESSING

Individual samples of approximately 1kg each were collected in the field. These were taken from the smallest possible vertical thickness, usually 5-10cm. Shale beds in each section were sampled; in many cases multiple samples were taken. Siltstones, silty-sandstones and occasionally limestones and dolomites were also sampled.

Fresh and brackish water ostracods tend to be more weakly calcified than their marine counterparts and, therefore, the least destructive processing method was employed. Samples were broken into small, 2-3cm sized pieces, half of which were then placed in a plastic container and covered with a 10% solution of  $H_2O_2$  and left overnight. The dissaggregated sediment was wet sieved with 2800  $\mu$ m, 850  $\mu$ m and 125  $\mu$ m sieves. These residues were then dried, weighed and bagged. Residues were picked by hand with an 'OO' sable brush using a Wild M8 binocular microscope.

Specimens were mounted using Balsa Cement and cleaned of any remaining matrix by hand using fine needles and stiff 'Pig-bristle' brushes. After cleaning the specimen could be dismounted by dissolving the Balsa cement in acetone.

As well as using washed residues, the thermal metamorphism of many of the sections by the nearby Tertiary igneous rocks meant that slabs were also examined for ostracods. Many of the bedding laminations, particularly in the Lealt Shale and Kilmaluag formations are covered with ostracods.

Specimens were photographed using a Hitachi S-520 Scanning Electron Microscope (SEM) in the Department of Geology, University of Leicester. All photographs were taken in stereoscopic pairs as described in the instructions to authors for the Stereo-Atlas of Ostracod Shells on 400 ASA Ilford HP5 '120' black and white film.

## **MEASUREMENTS**

Three measurements in microns  $(\mu m)$  are given, maximum valve length, maximum valve height and maximum valve inflation; marginal spines, alar projections and tubercles are not included in these measurements. These measurements are given for each specimen mentioned in the order length, height, inflation. Within the species descriptions relative sizes of specimens are mentioned. These are based upon the following scheme and refer to length:

<400µm	very small
401–500µm	small
501–700µm	medium
701–1000µm	large
>1000µm	very large

Measurements of other features are all given in microns. These measurements were then plotted on an Apple Macintosh LC II using the Cricket Graph (Version 1.3) program in order to differentiate instars and sexual dimorphs graphically. Only those size differences which were confirmed optically were marked on the graphs. Anderson (1964) noted that every time that ostracods moulted they increased in size by a standard amount for each species. This is



TEXT-FIG. 3 Internal morphology of a typical podocopid ostracod, right valve (modified from van Morkhoven 1962).



TEXT-FIG. 4. Nomenclature and orientation of the external lateral surface of an ostracod, left valve (modified after Kesling 1951).

usually around a 20-25% increase in length. This technique was applied to the graphs as a means of checking the divisions marked on by hand. Some authors have used a variation of this technique to determine summer and winter populations (Keen 1972), although this has not been attempted here. Graphs of length against height and length against length:height ratios are given for most species where large enough populations were available for study.

#### TERMINOLOGY

The terminology used in describing ostracod carapaces (Text-figs 3, 4) is that given in the Treatise Part Q by Moore & Pitrat (1961) and in Van Morkhoven (1962). The description of hinge types is given in full. Sylvester-Bradley & Benson (1971) described several new morphological terms as necessitated by the increased resolution brought about by the use of the SEM; these terms are used herein (Text-figs 5, 6).

## ACKNOWLEDGEMENTS

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#### PROCYTHERURA

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## SYSTEMATIC DESCRIPTIONS

Class OSTRACODA Latreille, 1802 Order PODOCOPIDA Müller, 1894 Suborder PODOCOPINA Sars, 1866 Superfamily CYTHERACEA Baird, 1850

Diagnosis. (After Athersuch et al. 1989 and Hartmann & Puri 1974). Carapace smooth to ornamented. Left valve usually larger than right. Hinge merodont, amphidont, lophodont, gongylodont, pentadont and adont. Inner lamella usually broad, often with vestibula. Marginal pore canals few to numerous. Central muscle-scar consists of 3-5 adductor musclescars in a vertical or subvertical row, some of which may be subdivided, and up to three frontal and in addition two mandibular scars. Eye frequently developed, often seen externally as a tubercle. Normal pores simple and sieve type.

#### Family CYTHERURIDAE Müller, 1894

Diagnosis. (After Athersuch et al. 1989, Hartmann & Puri 1974 and Bate 1972). Carapace usually small. Shape variable but usually with a caudal process and often alate or inflated posteroventrally. Valves occasionally smooth, more usually pitted, reticulate or carinate. Inner lamella wide to narrow, inner margin often highly irregular. Anterior and posterior vestibula small or absent. Marginal pore canals few, simple, straight or sinuous and widely spaced. Normal pores simple, without sieve pores. Four adductor muscle-scars in a vertical row; frontal scar ovate, reniform or V-shaped, sometimes subdivided. Hinge lophodont or merodont.

*Remarks.* Bate (1972, text-fig 25) described the hinge of the Cytheruridae as peratodont in which he recognized holoperatodont, hemiperatodont, paraperatodont and artioperatodont hinge types. These terms were not used by Hartmann & Puri (1974) or by Athersuch *et al.* (1989). However, the thickening of the ends of the median bar, an essential component of the peratodont hinge, is mentioned in Athersuch *et al.* (1989). The peratodont hinge is here considered to be a modification of existing hinge types and is described as such.

### Subfamily CYTHERURINAE Müller, 1894

Diagnosis. (After Bate 1972 and Hartmann & Puri 1974). Carapace generally non-alate but usually with a caudal process. Vestibula small or absent.

Remarks. The Cytherurinae differ from the Cytheropterinae Hanai, 1957, in usually having a more strongly defined caudal process.

## Genus PROCYTHERURA Whatley, 1970

Type species. Procytherura tenuicostata Whatley, 1970, pp 323-5, pl. 6, figs. 1-8, text-figs 6a-d; from the Oxfordian of Dorset.

Diagnosis. (Modified after Bate & Coleman 1975). Carapace small with weak anterodorsal eye swelling. Right valve overlapping left along dorsal margin. Valves weakly sulcate dorsomedianly. Lophodont hinge. Muscle-scars consist of an oblique row of four adductor scars with a V- or heart- shaped anterodorsal frontal scar. Marginal pore canals straight. Inner lamella broad with anterior and posterior vestibula.

Remarks. Whatley (1970) considered Procytherura to be ancestral to Cytherura. He described



TEXT-FIG. 5. External surface features of the podocopid ostracod valve. Based on Athersuch et al. (1989). External, left valve, lateral view.



TEXT-FIG. 6. External surface features of the podocopid ostracod valve. Based on Athersuch et al. (1989). Small scale ornamental features.

the hinge of *Procytherura* as being "lophodont, the terminal elements in the right valve being smooth narrow ridges". Bate (1972) described the hinge structure of the Cytheruridae as peratodont and that of *Procytherura* as holoperatodont. The holoperatodont hinge is a modified lophodont hinge with slightly thickened ends to the median bar and is virtually indistinguishable from the lophodont hinge. The hinge of the following species, which was poorly preserved appears to be lophodont.

## **Procytherura**? sp. A Pl. 1, figs 1, 2

*Material.* Eight valves. All from basal 10cm of Bed 3, Lonfearn Member, Lealt Shale Formation, locality 4.

Measurements.

OS 13972 (juvenile? left valve)	400-218-109
OS 13873 (juvenile? right valve)	381-182-100

Description. Valves rhomboidal in shape. Greatest length extends obliquely from below mid-height anteriorly to mid-height posteriorly. Greatest height at anterior cardinal angle. Both anterior and posterior margins are obliquely rounded, with almost straight anterodorsal and posteroventral slopes. Dorsal margin slightly arched and subparallel to ventral margin. Ventral median concavity is overhung by ventrolateral swelling. Weak anterior cardinal angle swelling. Lateral surfaces with first and second order reticulation. Ventral surface with four subparallel ribs.

Hinge appears to be lophodont but is poorly preserved. Other internal details not visible in present material.

Remarks. This species is tentatively placed in Procytherura based on its external morphology and apparent hinge structure, but lack of well preserved internal structures prevents a more confident assignment. The reticulate ornament of Procytherura tenuicostata Whatley, 1970 from the Oxfordian of Dorset differs in having subparallel, arcuate muri. The eye spot in P? sp. A is weakly developed as in P. tenuicostata.

#### Family PROGONOCYTHERIDAE Sylvester-Bradley, 1948

Diagnosis. (After Bate 1963a). Carapace ovate, rectangular, biconvex in dorsal view. Ventral margin concave and overhung by ventrolateral swelling. Smooth to strongly reticulated. Eye tubercles may be present. Hinge entomodont. Inner lamella of moderate width, vestibulae not developed. Marginal pore canals few, widely spaced and straight. Muscle-scars consist of a subvertical row of four ovate adductor scars, an oval, U-shaped or crescentric frontal scar and an oval mandibular scar which may be subdivided.

Remarks. The Progonocytheridae was divided (Moore & Pitrat 1961) into the Progonocytherinae (entomodont hinge) and the Protocytherinae (antimerodont or hemimerodont hinges). The Protocytherinae are now regarded as either a subfamily of the Trachyleberididae (Kemper 1971), or as a separate family (Bate 1963a, Bate & Coleman 1975). I concur with the latter. The Progonocytheridae thus restricted have an entomodont hinge and an ovate, crescentric or heart shaped frontal scar and straight marginal pore canals while the Protocytheridae have an antimerodont or hemimerodont hinge, and a V-shaped frontal scar and curved marginal pore canals.

#### Genus PROGONOCYTHERE Sylvester-Bradley, 1948

Type species. Progonocythere stilla Sylvester-Bradley, 1948, p 190, pl. 12, figs 1, 2; pl. 13, figs 1, 2, text-figs 1, 2; from the Boueti Bed (Bathonian), Langton Herring, Dorset.

Diagnosis. (Modified after Bate 1963a). Carapace subovate subrectangular, tapers posteriorly. Dorsal margin angled in females. Males more elongate than females. Anterior evenly rounded, posterior less so, both with distinct compressed marginal zones. Carapace has a uniformly biconvex outline in dorsal view. Ventral surface medianly concave and overhung by ventrolateral swelling. Left valve larger than right. Smooth to strongly reticulate. Large sieve pores usually developed. Hinge entomodont. Marginal pore canals short, straight, few in number and widely spaced.

Remarks. Oertli (1963) expressed doubts as to whether Progonocythere juglandica (Jones, 1884) was indeed a member of Progonocythere. Bate (1967) placed P. juglandica within Glyptocythere Brand & Malz, 1962b. The straighter dorsal margin in Progonocythere contrasts with the strongly convex dorsal margin in Glyptocythere. Whatley (1964), discussed the genus in detail and argued against its subdivision based on outline variation. The genus contains a range of outlines from elongate to subrectangular, typified by Progonocythere stilla. I follow Whatley (1964) in not subdividing the genus on these grounds, as the female dimorphs of the former group resemble the latter group, and no other distinguishing characteristics are present on which to base a division.

## Progonocythere milleri sp. nov. Pl. 1, figs 3-16

Name. After Dr. C. Giles Miller in honour of his micropalaeontological work on the Ludlow Bone Bed.

Holotype. OS 13874, female right valve, Pl. 1, figs 13, 14, from top 10cm of Bed 6b, Kildonnan Member, Lealt Shale Formation, locality 1; Paratypes. OS 13875, Pl. 1, figs 6, 7, 9, 10, and OS 13876, Pl. 1, figs 8, 11, 12, 15, 16, from 14cm below top of Bed 6, Kildonnan Member, Lealt Shale Formation, locality 2.

Material. 30 valves and five fragments from the Kildonnan Member, Lealt Shale Formation, localities 1, 2, 4, 5.

Diagnosis. Valves elongate, more so in males than females. Broadly rounded anterior margin with compressed marginal zone. Posterior rounded, triangular, with narrow compressed marginal zone. Dorsal margin almost straight. Right valve distinctly umbonate, only posterior cardinal angle prominent in left valve. Oblique sulcus behind anterior cardinal angle. Weak ventrolateral overhang. Lateral surface micropunctate with large regularly spaced eccentric sieve pores. Ventral and ventrolateral surfaces with seven subparallel ribs. Marginal rib absent only along dorsal margin. 13 straight marginal pore canals anteriorly, 9 posteriorly.

Measurements.

OS 13974 (female right valve)	945-527-225
OS 13875 (male left valve)	891-482-220
OS 13876 (male right valve)	773-436-206

Description. Males more elongate than females (Text-fig. 7). Greatest length through midheight. Greatest height at mid-length. Greatest width in posterior third of valve. Dorsally convex. Anterior broadly rounded with a moderately wide compressed marginal zone. Posterior rounded triangular, compressed marginal zone is narrower than at anterior. Dorsal margin almost straight in right valve, slightly arched in left. Cardinal angles developed in right valve. Only posterior cardinal angle distinct in left valve. Oblique sulcus immediately to the posterior of the anterior cardinal angle. Ventral margin medianly concave and overhung by weakly developed ventrolateral swelling. Prominent marginal rib present along all but the dorsal margin. Micropunctate lateral surface (punctae less than 5  $\mu$ m diameter); ornament lacking above the adductor muscle-scars. Large (15-20  $\mu$ m diameter) eccentric sieve pores evenly spaced over surface. Seven subparallel ribs ventrally and ventrolaterally (less distinct).

Hinge entomodont. Six anterior and 6-7 posterior terminal teeth in right valve. Loculate median groove expanded anteriorly where it is underlain by a thickened lip. Median bar in left valve with five enlarged teeth developed anteriorly the posterior being poorly denticulate. Avestibulate. Inner lamella of moderate width but narrowest posteriorly. 13 straight marginal pore canals anteriorly, nine posteriorly. Muscle-scars consist of a subvertical row of four adductors, frontal scar in line with the top adductor. Mandibular scar was not observed. See Text-fig. 8 for details of internal features.

Remarks. P. milleri is more elongate than Progonocythere kingscliffensis (Bate, 1967) from the Bathonian Upper Estuarine Group of Kings Cliffe, Northamptonshire and Ancaster, Lincolnshire, especially the male. P. milleri differs from Progonocythere levigata Bate, 1967 from the Bathonian Upper Estuarine Series of the Ketton Cement Quarry, Leicestershire in being more prominently micropunctate. The posterodorsal slope is steeper in P. levigata while the females in P. milleri taper more to the posterior.

Progonocythere kingscliffensis (Bate, 1967) Pl. 1, figs 17-21

1967 Galliaecytheridea? kingscliffensis sp. nov. Bate, pp 34-6, pl. 4, figs 6-12; pl. 5, figs 1-8.

Holotype. Io 2316, female carapace (Bate 1967, pl. 4, figs 6,7). Paratypes: Io 2317-27. Designated by Bate (1967) from the Bathonian Upper Estuarine Group of Kings Cliffe, Northamptonshire and Ancaster, Lincolnshire.











TEXT-FIG. 8. Internal morphology of a female right valve of *Progonocythere milleri*. Composite sketch based upon several specimens.

*Diagnosis.* (After Bate 1967). Dimorphic; females inflated, subquadrate with backward sloping dorsal margin and concave posterodorsal margin, producing a short, upturned posterior. Males more elongate. Both sexes with compressed anterior marginal border. Surface finely punctate. Nine anterior and four posterior straight marginal pore canals.

Measurements.

OS 13877 (juvenile? carapace)	600-400-291
OS 13878 (adult? carapace)	627-427-291
OS 13879 (adult? carapace)	709-418-327

Description. Carapace ovate globose in lateral view. Greatest length slightly below midheight. Greatest height at anterior cardinal angle. Dorsal view elongate elliptical with distinct anterior and posterior compressed marginal zones. Greatest width at mid-length. Anterior margin broadly rounded. Compressed marginal zone of moderate width. Posterior smaller in size, rounded triangular in shape with a short, concave, posterodorsal slope and a narrow compressed marginal zone. Dorsal margin arched. Ventral margin overhung by poorly developed ventrolateral swelling in left valve, not visible in right. Left valve overlaps right valve ventrally and around the anterior and posterodorsal margins. Lateral surface evenly covered with punctae and normal pore canals.

Internal details not seen.

Remarks. P. kingscliffensis was erroneously placed in Galliaecytheridea Oertli, 1957 by Bate 1967. As Galliaecytheridea has a merodont hinge G. kingscliffensis is reassigned to Progonocythere. P. kingscliffensis differs from Progonocythere triquetra Bate, 1967 from the Bathonian Upper Estuarine Group of Kings Cliffe, Northamptonshire in having a smaller ventrolateral overhang and appearing more elongate.

Occurrence. The species occurs in the Forest Marble from the Old Cement Works, Kirtlington, Oxfordshire (Ware & Whatley, 1980).

#### **Progonocythere levigata** Bate, 1967 Pl. 2, figs 1-6

1967 Progonocythere levigata sp. nov. Bate, pp 45-6, pl. 10, figs 10-14; pl. 11, figs 1-9.

1978 Progonocythere levigata Bate, 1967; Bate, p. 228, pl. 12, figs 10-12.

1989 Progonocythere levigata Bate, 1967; Wakefield & Siveter, 17-20.

Holotype. Io 2419, female left valve (Bate 1967, pl. 10, figs 11-13). Paratypes: Io 2420-33. Designated by Bate (1967) from the Bathonian Upper Estuarine Group of Ketton Cement Quarry, Leicestershire.

Material. 775 valves and carapaces from the present study. Figured specimens from basal 10cm of Bed 4, Duntulm Formation, locality 9. Other material from the Valtos Sandstone Formation, locality 6; the Duntulm Formation, localities 6, 9-11; the Kilmaluag Formation, localities 10, 11.

Diagnosis. (After Wakefield & Siveter 1989). Species of Progonocythere with subquadrate, elongate, punctate carapace. Puncta contain well developed eccentric sieve pores of two sizes. Small marginal denticles may occur anteriorly at mid-height (four) and posteroventrally (2-3), often on the right valve only. Carapace is umbonate with a convex dorsal margin. Ventrolateral margin is convex.

Measurements.

OS 13373 (female right valve)	872-509
OS 13374 (male carapace)	1018-527
OS 13375 (male right valve)	1073-545
OS 13376 (female carapace)	818-518-200

Description. Female carapace subquadrate, male more elongate (Text-fig. 9). Greatest length in female is slightly below mid-height, through mid-height in male. Greatest height at anterior cardinal angle in female and at mid-length in male. Anterior broadly rounded and marginally compressed. Posterior reduced particularly in female, obtusely rounded and



TEXT-FIG. 9. Size distribution of *Progonocythere levigata* from a single sample taken from Bed 5, Kilmaluag Formation, locality 11. Mean increase in length between instars is approximately 27%.

marginally compressed. Four marginal denticles usually developed at mid-height anteriorly. Pesterodorsal slope with 2-3 marginal denticals. The ventral-most denticle in right value appears one denticle higher anteriorly whilst posteriorly they start below the denticles on the efft value. Dorsal margin convex with a prominent posterior cardinal angle. Ventral margin medianly concave and overhung by ventrolateral swelling. Left value overlaps right value ventrally, dorsally and along the antero- and posterodorsal slopes. Lateral surface with fine puncta of 5  $\mu$ m diameter. Eccentric sieve plates, 15  $\mu$ m and 5  $\mu$ m in diameter, evenly spaced over carapace. Ventral surface with four subparallel ribs.

Hinge entomodont. Left valve with strongly developed terminal locellae and denticulate median bar. Enlarged anterior of median bar with five rounded teeth. Broad accommodation shelf immediately above median bar. Right valve has 6-7 anterior and 6-7 posterior terminal teeth. Occasionally teeth may be dorsally bifid. Posterior terminal teeth increase in size posteriorly. Loculate median groove anteriorly expanded with thickened lower lip. Posterior locellae in median groove are paired. Inner lamella of moderate width. Avestibulate. Marginal pore canals not observed. Muscle-scars consist of a slightly crescentric, subvertical, row of four ovate adductors, a mandibular scar below level of basal adductor and a frontal scar situated lower and nearer to the anterior in the female than in the male (Bate 1967; Wakefield & Siveter 1989).

Remarks. The development of marginal denticles varies both within and between populations. Adults, especially the males, from the Scottish populations are consistently larger than those in England (Wakefield & Siveter 1989). This may be due to more favourable environmental conditions such as food supply or salinity, prevailing for the Scottish populations, although it is not possible to determine the exact cause. It has been observed that ostracods inhabiting cooler waters often grow larger than their warmer water counterparts (R. C. Whatley pers. comm. 1991). The proposed shallow lagoonal environment of the Duntulm and Kilmaluag formations (Andrews [1984], 1985; Andrews & Walton 1990) and evidence of periods of strong desiccation during the deposition of these formations suggests, however, that the waters within the lagoons was probably warm rather than cool, implying that other environmental variables are the cause.

*P. levigata* is similar to *Progonocythere cristata* Bate, 1963a from the Bajocian Kirton Shale, Kirton Cement Quarry, Kirton Lindsey, Lincolnshire, but has a less pronounced ventrolateral overhang. *P. levigata* differs from the type-species *Progonocythere stilla* Sylvester-Bradley, 1948 in tapering less posteriorly (Bate 1967). *P. levigata* is less reduced in height posteriorly than Progonocythere polonica Blaszyk, 1959 from the Bathonian of Ogrodzieniec, Sawiercie, Poland, and Progonocythere acuminata Bate 1965 from the Bajocian deposits of Hundale Point, Cloughton, Yorkshire.

Occurrence. It is also known from the Great Oolite at Shipton on Cherwell Quarry, Oxfordshire [Barrington 1986].

## Genus GLYPTOCYTHERE Brand & Malz, 1962a

Type species. Glyptocythere tuberodentina Brand & Malz, 1962b, pp 433-5, text-fig. 1. See also Brand & Malz 1966, pp 483-6, pl. 52, figs 1-13; pl. 53, figs 14, 15; from the Upper Bajocian of NW Germany.

Diagnosis. (After Brand & Malz 1966). Medium to large oblique trapezoid carapace. Males more elongate than females. Elongate elliptical in dorsal view. Distinct anterior and posterior compressed marginal zones. Dorsal margin arched between the cardinal angles in right valve, straighter in left valve. Ventral margin slightly concave at mid-length and overhung by ventrolateral swelling. Left valve larger than right. Lateral surface with long low oblique ridges; variable in strength of development. Inner lamella of moderate width. 7-12 marginal pore canals anteriorly, 2-5 posteriorly. Entomodont hinge. Muscle-scars consist of a subvertical row of four adductors with rounded frontal and mandibular scars.

*Remarks.* The name *Glyptocythere* first appeared in the literature in Brand & Malz, 1962a, although the generic diagnosis and the erection of a type species were published in a later paper (Brand & Malz 1962b).

Glyptocythere first appears in the Bajocian of Germany (Brand & Malz 1962a & b) and is an important genus throughout the Middle Jurassic within the European province.

## Glyptocythere dextranovacula sp. nov. Pl. 2, figs. 7-12

Name. Latin; dextra, right hand and novacula, sharp knife; with reference to the blade like alar projection present on the right valve only.

Holotype. OS 13764, female right valve, Pl.2, figs 7, 10 - 12, from the basal 5cm of Bed 1, Lonfearn Member, Lealt Shale Formation, locality 2. Paratypes: OS 13765, Pl. 2, fig. 9; OS 13766, Pl. 2, fig. 8; OS 13767 and OS 13769 also from this locality and level. OS 13768 is from 8cm above base of Bed 1, Lonfearn Member, Lealt Shale Formation, locality 4.

Material. 67 valves from the Lonfearn Member, Lealt Shale Formation, localities 2, 4.

Diagnosis. Species of Glyptocythere with a vertical alar projection on the right valve only. Males more elongate than females. Anterior rounded, posterior acute with concave posterodorsal slope, both with broad compressed marginal zones. Dorsal margin straight with prominent cardinal angles. Ventral margin medianly concave, overhung by a well developed ventrolateral alar in right valve only. Slight swelling at anterior cardinal angle with two shallow, oblique sulci immediately to the posterior. Ventral and ventrolateral surfaces with 4-5 ridges. Sieve pores on lateral surfaces. Marginal rib around all margins except for the dorsal margin. Inner lamella narrow. Seven anterior and two posterior straight marginal pore canals.

Measurements.

OS 13764 (female right valve)	655-382-164
OS 13765 (male right valve)	709-382-182
OS 13766 (A-1 right valve)	564-355-145
OS 13767 (A-1 right valve)	555-373-145
OS 13768 (male right valve)	691-391-200
OS 13769 (A-2 left valve)	527-309-118

Description. Medium to large sized species of Glyptocythere. Valves elongate, slightly more so in males than females (Text-fig. 10). Greatest length through mid-height. Greatest height at anterior cardinal angle. Biconvex in dorsal view with well defined anterior and posterior



TEXT-FIG. 10. a) Size dispersion, b) sexual dimorphism of *Glyptocythere* dextranovacula from a single sample taken at the type level, Lonfearn Member, Lealt Shale Formation.

compressed marginal zones. Greatest width at mid-length. Anterior margin well rounded with broad compressed marginal zone. Posterior more acute with concave posterodorsal slope. Dorsal margin almost straight with poorly defined cardinal angles. Ventral margin inclined posteriorly and is medianly concave. Marginal rib around all but dorsal margin, and is closest to the commissure at the extreme posterior. Vertical alar ridge developed in right valve only which is parallel to ventral margin. Lateral surface unornamented but with a slight swelling at the anterior cardinal angle and two shallow oblique sulci immediately posterior of swelling.  $\Im$ ccasionally 4-5 pore conuli develop posterolaterally. Ventral and ventrolateral surfaces with 4-5 subparallel ribs, one of which is enlarged to form a prominent alar projection. Small (10  $\mu$ m diameter) sieve pores evenly spaced over surface.

Hinge entomodont. Six anterior and seven posterior elongate terminal teeth in right valve. Median groove weakly developed but clearly loculate. Anterior third of groove with thickened lower lip. Complementary opposing structures developed in left valve. Avestibulate. Inner lamella narrow. Seven anterior and two posterior straight marginal pore canals. Muscle-scars consist of a vertical row of four ovate adductors, a small round frontal scar lies in front of the second top adductor and a round mandibular scar lies below level of basal adductor.

Remarks. Glyptocythere sutherlandi sp. nov. differs from G. dextranovacula in being larger (Textfig. 11) and lacking the ventral alar ridge on the right valve. The left valves of the two species

are similar but G. dextranovacula lacks the posteroventral square of ridges of G. sutherlandi. G. dextranovacula is easily distinguished from Glyptocythere inversalitera sp. nov. and Glyptocythere shielingensis sp. nov. by its strongly developed alar ridge and by its lack of a reticulate ornament.

## Glyptocythere sutherlandi sp. nov. Pl. 2, figs 13-21

Name. After Dr. S. J. E. Sutherland in recognition of his work on the Chitinozoa of the type Ludlow area.

*Holotype.* OS 13770, male right valve, Pl. 2, figs 14, 15, from basal 5cm of Bed 1, Lonfearn Member, Lealt Shale Formation, locality 2. Paratypes: OS 13771, Pl. 2, fig. 21; OS 13772, Pl. 2, figs 13, 16, 17; OS 13773, Pl. 2, fig. 20; OS 13774 and OS 13775, Pl. 2, figs 18, 19, from same locality and level.

Material. 24 carapaces and 47 valves from the Lonfearn Member, Lealt Shale Formation, localities 2, 4.

Diagnosis. Elongate species of Glyptocythere. Males more elongate than females. Broadly rounded and marginally compressed anterior margin. Triangular posterior, with broad compressed marginal zone. Dorsal margin convex. Ventromedian concavity overhung by ventrolateral swelling. Surface with large eccentric sieve pores. Ventral and ventrolateral surfaces with six subparallel ridges. Posteroventrally situated square of ribs joins ends of three ventral ribs. Finely denticulate marginal rib present along all but the dorsal margin. Weak entomodont hinge. Inner lamella of moderate width. Eight anterior and two posterior marginal pore canals.



TEXT-FIG. 11. Size comparison between *Glyptocythere dextranovacula* and *Glyptocythere sutherlandi*. All specimens from the type level of each species.

## Measurements.

OS 13770 (male right valve)	927-445-224
OS 13771 (female left valve)	872-527-220
OS 13772 (A-1 right valve)	764-418-206
OS 13773 (A-1 male? right valve)	800-400-225
OS 13774 (female left valve)	900-527-225
OS 13775 (female carapace)	818-472-333

Description. Carapace elongate, more so in males than females (Text-fig. 12). Greatest length through mid-height. Greatest height at mid-length. Anterior broadly rounded with moderately wide compressed marginal zone. Posterior triangular, compressed marginal zone broadest at extreme posterior. Dorsal margin convex with rounded but distinct cardinal angles in right valve. Only posterior cardinal angle distinct in left valve. Ventral margin medianly concave and overhung by ventrolateral swelling. Overhang greatest in left valve. Left valve overlaps right valve along the anterior, posterior and ventral margins. Lateral surface with large (20  $\mu$ m diameter), evenly spaced eccentric sieve pores. Ventral and ventrolateral surfaces with six subparallel ribs, posteroventrally three of these ribs are joined together by two sides of a square of ribs. Marginal, finely denticulate rib present along all but the dorsal margin.

Hinge weakly entomodont. Right valve with seven anterior and eight posterior terminal teeth which are elongate and occasionally dorsally bifid. Median groove with 3-4 anterior locellae, which are bifid, underlain by a thickened lower lip. Five paired locellae in posterior of median groove. Left valve with complementary terminal locellae. Median bar with clearly bifid teeth is overlain by a broad accommodation shelf. Avestibulate. Moderately wide inner lamella broadest anteriorly. Striae visible on inner lamella. Eight anterior and two posterior straight marginal pore canals observed as internal and external openings. Some pores appear to have bi- and tripartite external openings. Muscle-scars consist of four adductors in a subvertical row, with a round frontal scar opposite the upper two adductors. The round mandibular scar is less distinct and lies below the level of the basal adductor (Text-fig. 13).

Remarks. The plot of valve length against valve height (Text-fig. 12a) clearly shows the adults and several juvenile stages (A-3 to A-1). It is possible that in this sample (Bed 1, Lonfearn Member, Lealt Shale Formation, locality 2) there are some immature males (A-1). As only six valves plot in this field the findings are inconclusive. Compared with the holotype, paratype OS 13773 shows a slightly reduced height posteriorly. Whatley & Stephens (1977) described precocious sexual dimorphism in the Progonocytheridae, including species of *Glyptocythere*. See also remarks for *G. dextranovacula* sp. nov.

G. sutherlandi differs from Glyptocythere guembeliana (Jones, 1884) from Bathonian strata recovered from the Richmond Borehole, Surrey in its development of a posterior square of ribs and a well developed ventrolateral rib. Glyptocythere oscillum (Jones & Sherborn, 1888) from the Bathonian Blue Fullers Earth Clay, Midford, Somerset, differs in its dorsal margin parallel corrugate ornamentation and in having a much shorter median bar to its hinge line. G. sutherlandi has a more triangular shaped posterior than Glyptocythere polita Bate, 1965 from the Bajocian strata at Hundale Point, Cloughton, North Yorkshire.

## Glyptocythere inversalitera sp. nov. Pl. 3, figs 1-7

Name. Latin; inversa, upside down or back to front and litera, a letter; with reference to the development of an inverted letter 'U' in the reticulum.

*Holotype.* OS 13776, male carapace, Pl. 3, fig. 4, from 35 cm below top of Bed 3g, Kildonnan Member, Lealt Shale Formation, locality 1. Paratypes: OS 13778 and OS 13779, Pl. 3, fig. 5, from same locality and level. OS 13777, Pl. 3, figs 1-3, 6; OS 13780, Pl. 3, fig. 7 and OS 13782 from the top 4cm of Bed 3g, Kildonnan Member, Lealt Shale Formation, locality 1. OS 13781 from 15 cm above base of Bed 4, Kildonnan Member, Lealt Shale Formation,

locality 1. OS 13783 and OS 13784 from Bed 3h, Kildonnan Member, Lealt Shale Formation, locality 1.

*Material*. Seven carapaces and 68 valves from the Kildonnan Member, Lealt Shale Formation, locality 1; three right valves and one carapace contained in slide SMF Xe 14968.

Diagnosis. Carapace subovate. Males more elongate than females (Text-fig. 14). Elongate elliptical in dorsal view with distinct anterior and posterior compressed marginal zones. Anterior view pentagonal. Anterior margin broadly rounded, posterior rounded triangular and smaller. Cardinal angles indistinct. Ventrolateral overhang with a prominent plicate rib along the border. Lateral surface with coarse reticulation and numerous simple and sieve pores. Prominent dorsomedian inverted U-shaped solum within the reticulation. Ventral surface with 3-4 subparallel ribs. Alar projection variably developed on ventral surface of left valve only. Inner lamella of moderate width. 9-11 straight, marginal pore canals anteriorly, 3-4 posteriorly. Measurements.

OS 13776 (male carapace)	745-400-273
OS 13777 (female carapace)	673-400-336
OS 13778 (A-1 right valve)	655-364-172
OS 13779 (A-1 left valve)	600-345-143
OS 13780 (A-1 left valve)	636-400-164
OS 13781 (A-1 left valve)	609 <b>-</b> 364-145
OS 13782 (A-2 right valve)	527-309-154
OS 13783 (A-1 right valve)	591-318-164
OS 13784 (A-2 right valve)	527-327-145

Description. Laterally subovate carapace with greatest length at mid-height, and greatest height at anterior cardinal angle. Elongate elliptical in dorsal view with distinct anterior and posterior compressed marginal zones. Greatest width slightly behind mid-length. Anterior view is pentagonal. Anterior margin broadly rounded with a distinct compressed marginal zone. Posterior rounded triangular in shape, smaller and with a poorly developed compressed marginal zone. Posterior compressed marginal zone poorly developed. Right valve dorsal margin slightly convex, cardinal angles barely discernible. Left valve dorsal margin straight, cardinal angles as for right valve. Ventral margin medianly concave, overhung by ventrolateral swelling. In left valve the ventral margin is further obscured by the variable development of an alar projection. This runs at an angle from being close to the ventral commissure posteriorly to being close to the plicate ventrolateral border anteriorly. Left valve overlaps right valve around the ventral, anterior and posterior margins. Lateral surface reticulate, resulting in a chain-like appearance along the ventrolateral border plication. Dorsomedianly an oblique, inverted U-shaped solum is developed. Small, oblique sulcus behind the anterior cardinal angle. This lies immediately behind a margin parallel rib which delineates the slope break of the compressed marginal zone. Anterior marginal zone with two subparallel ribs which are occasionally surmounted by pore conuli. Lateral surface with numerous large (15  $\mu$ m diameter) sieve pores and smaller (5  $\mu$ m diameter) normal pores. Ventral surface with 3-4 subparallel ribs.

Hinge weakly entomodont. Six anterior and six posterior elongate terminal teeth in right valve. Loculate median groove broadest in anterior third where it is underlain by a thickened lower lip. Complementary dentition in left valve with a broad, dorsally elliptical, accommodation shelf above the median bar. Avestibulate. Inner lamella of moderate width. 9-11 straight, marginal pore canals anteriorly, 3-4 posteriorly. Muscle-scars consist of a vertical row of four adductors with round frontal and mandibular scars in front of the upper and basal adductors respectively.

Remarks. G. inversalitera differs from Glyptocythere raasayensis Stevens, 1985, from the Bajocian Garantiana Clay, Isle of Raasay, in being less elongate, in having a broader posterior



b)







TEXT-FIG. 13. Internal lateral view of an A-1 [male?] right value of *Glyptocythere sutherlandi*, based upon specimen OS 13772.



TEXT-FIG. 14. a) Size dispersion, b) sexual dimorphism of *Glyptocythere inversalitera* from a single sample taken at the type level, Kildonnan Member, Lealt Shale Formation. Apparent length increase between A-1 and adults is 16%.

compressed marginal zone and a prominent plicate ventrolateral border. Glyptocythere penni Bate & Mayes, 1977, from the Bathonian Forest Marble of the Old Cement Works, Kirtlington, Oxfordshire, whilst having a pinched out ventrolateral border differs in having two strong median swellings and a small marginal flange at the extreme posterior. Glyptocythere persica (Jones & Sherborn, 1888) from the Bathonian Blue Fullers Earth Clay, Midford, Somerset has an alar projection on the ventrolateral border of only the right valve. While the left valves are not figured in Bate (1969 or 1978) the lack of a keel on the right valve of G. inversalitera immediately differentiates it from G. persica. G. inversalitera differs from Glyptocythere sowerbyi Brand & Malz, 1966 from the Bajocian of Germany in having a less strongly developed ventrolateral overhang. G. sowerbyi has a smoothly arched dorsal margin and the cardinal angles are barely discernible. G. inversalitera has prominent cardinal angles. Glyptocythere rugosa Brand & Malz 1966, from the Bajocian of NW Germany has a coarser reticulation and is more elongate. G. inversalitera does not possess the near vertical ribbing seen in the posterior half of the valves of Glyptocythere concentrica Brand & Malz 1966 also from the Bajocian of NW Germany. See also remarks for G. shielingensis sp. nov.

## Glyptocythere shielingensis sp. nov. Pl. 3, figs 8, 9, 13-15

Name. After the type locality, the Shieling Burn, Isle of Eigg.

Holotype. OS 13785, male right valve, Pl. 3, figs 13, 15, from basal 10cm of Bed 11,



TEXT-FIG. 15. a) Size dispersion, b) sexual dimorphism of *Glyptocythere* shielingensis from a single sample taken at the type level, Lonfearn Member, Lealt Shale Formation.

Lonfearn Member, Lealt Shale Formation, locality 3. Paratypes: OS 13786, OS 13787, Pl. 3, fig. 14; OS 13788 and OS 13789, Pl. 3, figs 8, 9, from same locality and level.

*Material.* 22 carapaces and 20 valves from the type locality and horizon. Preservation generally poor; much material crushed and decalcified.

*Diagnosis*. Carapace subovate. Males more elongate than females. Diamond shaped in dorsal view with distinct anterior and posterior compressed marginal zones. Reticulate with small sieve pores. Prominent ridge on ventrolateral border. Inner lamella of moderate width. Weakly entomodont.

Measurements.

OS 13785 (male right valve)	873-491-227
OS 13786 (A-1 right valve)	709-409-200
OS 13787 (A-3? right valve)	455-273-155
OS 13788 (female carapace)	810-491-391
OS 13789 (A-1 left valve)	673-382-182

Description. Carapace subovate in lateral view, diamond shaped in dorsal view, with distinct anterior and posterior compressed marginal zones. Greatest length slightly below mid-height. Greatest height at mid-length. Greatest width in posterior third of carapace. Males more elongate than females (Text-fig. 15). Anterior margin broadly rounded with a distinct compressed marginal zone. Posterior margin smaller, rounded triangular with a compressed marginal zone. Dorsal margin arched in right valve, straight in left. Cardinal angles poorly

developed. Ventral margin medianly concave and overhung by a ventrolateral swelling. Left valve overlaps right valve around all margins. Lateral surfaces reticulate. Prominent rib on ventrolateral border occasionally becoming subalate anteriorly. Lateral surfaces with small (10  $\mu$ m diameter) sieve pores.

Hinge weakly entomodont. Six anterior and six posterior elongate terminal teeth in right valve. Loculate median groove broadest anteriorly. Complementary dentition in left valve. Avestibulate. Inner lamella of moderate width. At least six anterior and two posterior marginal pore canals. Muscle-scars not preserved in present material.

Remarks. G. shielingensis differs from G. inversalitera sp. nov. in its much weaker development of the ventrolateral border plication and in lacking the dorsomedian inverted U-shaped solum in the reticulum. G. shielingensis differs from G. raasayensis Stevens, 1985 in having a rounded posterior, being more elongate and appearing more ovate in dorsal view. Glyptocythere praecursor Brand & Malz, 1966 from the Bajocian of NW Germany does not have the rounded posterior of G. shielingensis and its reticulation is more pronounced.

#### Genus FRONSLARVATA gen. nov.

*Name.* Latin; *frons*, brow and *larvata*, early stage of growth; alluding to the appearance of a face in the ornament, particularly in the juveniles.

Type species. Fronslarvata chamaeleon sp. nov. from the Kildonnan Member, Lealt Shale Formation, Great Estuarine Group on the Isle of Eigg, locality 1.

Species. Monotypic.

Diagnosis. Carapace subrectangular. Males more elongate than females. Strongly biconvex in dorsal view with distinct anterior and posterior compressed marginal zones. Anterior view appears pentagonal. Anterior broadly rounded, posterior less so. Dorsal margin straight and partially obscured by dorsolateral swellings and a false eye node. Ventral margin subparallel to dorsal margin and partially obscured posteroventrally by ventrolateral border swelling. Lateral surface reticulate, with eccentric sieve pores. Left valve larger than right. Hinge weakly entomodont. Inner lamella of moderate width. 11-12 straight marginal pore canals anteriorly, 4-5 posteriorly. Muscle-scars consist of a subvertical row of four adductors with round frontal and mandibular scars.

Remarks. This genus is similar to Praefuhrbergiella Brand & Malz, 1962a, and rather less so to Fuhrbergiella Brand & Malz, 1962a. This genus has more marginal pore canals than have been observed in Fuhrbergiella or Praefuhrbergiella (H. Malz pers. comm. 1990). The genus closest to Fronslarvata is Tropacythere Gründel, 1973, which has a similar number and arrangement of marginal pore canals and similar lateral swellings. Tropacythere differs in having an ocular sinus and two posterodorsal swellings whilst Fronslarvata has only one.

## Fronslarvata chamaeleon sp. nov. Pl. 3, figs 10-12, 16-20

Name. Latin; chamaeleon, a lizard which changes its appearance; with reference to marked ontogenetic changes.

Holotype. OS 13790, male carapace, Pl. 3, figs 11, 12, from 35cm below top of Bed 3g, Kildonnan Member, Lealt Shale Formation, locality 1. Paratypes: OS 13791, Pl. 3, fig. 10, from same locality and level. OS 13792, Pl. 3, fig. 18 and OS 13793 from top 5cm of Bed 3g, Kildonnan Member, Lealt Shale Formation, locality 1. OS 13794, Pl. 3, figs 16, 17, 19 and OS 13795, Pl. 3, fig. 20 from top 5cm of Bed 5f, Kildonnan Member, Lealt Shale Formation, locality 1.

*Material.* 15 carapaces and 185 valves from the Kildonnan Member, Lealt Shale Formation, localities, 1, 2, 5. One male right valve, two female right valves, three juvenile right valves and four juvenile left valves contained in slide SMF Xe 14967.

Diagnosis. As for genus.

#### LOPHOCYTHERE

#### Measurements.

OS 13790 (male carapace)	955-473-413
OS 13791 (female carapace)	873-500-409
OS 13792 (A-2 left valve)	473-291-145
OS 13793 (A-3 left valve)	364-218- 91
OS 13794 (A-3 right valve)	364-218-123
OS 13795 (A-1 left valve)	636-400-164

Description. Subrectangular carapace tapers slightly to posterior. Males more elongate than females (Text-fig. 16). Strongly biconvex in dorsal view. Compressed marginal zone smaller posteriorly than anteriorly. Anterior view pentagonal. Greatest length slightly above midheight. Greatest height at anterior cardinal angle. Greatest width at posterior cardinal angle. Anterior broadly rounded. Posterior rounded triangular in shape and smaller. Dorsal margin straight, cardinal angles indistinct. Smooth ovate swelling at anterior cardinal angle with short, oblique sulcus immediately to the posterior. No ocular sinus visible internally. Elongate ventrolateral overhang variably developed, extends from mid-length posteriorly. Occasionally a weak rib is developed on the ventrolateral border. Dorsomedian vertical sulcus with vertical ovate swelling immediately to the posterior. Vertical swelling most strongly developed in juveniles, often with a median vertical crenulate rib. Lateral and ventral surfaces reticulate. Ornament is variably developed with secondary reticulation often not being present. Large (20  $\mu$ m diameter) eccentric sieve pores more densely clustered around lateral swellings. Left valve larger than right valve.

Hinge weakly entomodont. Six anterior and seven posterior teeth in right valve. Loculate median groove of same width over entire length. Anteromedian end of median bar slightly thickened. Median bar in left valve when viewed dorsally is arcuate. Anteromedian teeth in median bar slightly longer than posteromedian teeth. Avestibulate. Inner lamella of moderate width. Marginal pore canal openings observed internally and externally these numbered 11-12 anteriorly, 4-5 posteriorly. Muscle-scars consist of a vertical row of four adductors, an elongate frontal scar and a small, round, mandibular scar situated level with top and basal adductors respectively.

*Remarks*. This is one of the most ornamentally variable species of ostracod from the Great Estuarine Group. The juveniles show the strongest development of secondary reticulation and lateral swellings. In the adults secondary reticulation is rarely developed, the ventrolateral swellings are more elongate but less vertically pronounced, while the mid-valve vertical swelling is reduced to a low amplitude ridge.

#### Genus LOPHOCYTHERE Sylvester-Bradley, 1948

Type species. By original designation; Cytheridea ostreata Jones & Sherborn, 1888, p 271, pl. 4, figs 6a-c; from the Yellow Fullers Earth Clay (Bathonian), Midford, Somerset.

Diagnosis. (After Sylvester-Bradley 1948 and Whatley 1970). Progonocytheridae with one or more ridges along the ventrolateral flanks. One ridge becomes rib like anteriorly where it deflects through 90° and extends to the eye node. Anterior broadly rounded, posterior smaller and rounded triangular; both with broad compressed marginal zones. Eye node usually developed. Lateral surfaces usually reticulate. Males more elongate than females. Hinge entomodont. Avestibulate. 6-8 marginal pore canals anteriorly, 3-4 posteriorly.

Remarks. This genus has been subdivided into subgenera based upon ornamental variations. Bate (1969) divided Lophocythere into two groups; the "Bradiana" and "Ostreata" groups. Whatley (1970) designated the subgenus Lophocythere (Neurocythere) which Malz (1975) regarded as the junior synonym of Terquemula Blaszyk & Malz, 1965. Ware & Whatley (1980) now regard Neurocythere as a genus separate from Terquemula. Lophocythere is considered here to include only those forms which possess a prominent ventrolateral ridge which turns through



TEXT-FIG. 16. a) Size dispersion, b) sexual dimorphism of *Fronslarvata chamaeleon* from a single sample taken at the type level, Kildonnan Member, Lealt Shale Formation. Mean increase in length between instar stages is 33%.

 $90^{\circ}$  at the anterior margin from where it runs to the eye node. This would be the "Ostreata" group of Bate (1969).

## Lophocythere sp. A Pl. 3, figs 21-23

*Material.* 32 valves. OS 13808 is from Bed 1; all other specimens from 5cm above base of Bed 8b; all from Lonfearn Member, Lealt Shale Formation, locality 2. Also found in the Lonfearn Member, Lealt Shale Formation, locality 4.

Measurements.

OS 13806 (juvenile right valve)	445-264-120
OS 13807 (juvenile left valve)	564-286-172
OS 13808 (juvenile right valve)	491-255-109

Description. Juvenile valves subtriangular in lateral outline, adults not known. Greatest length at mid-height. Greatest height at anterior cardinal angle. Greatest width at posterior cardinal angle, this is accentuated by the posteriorly enlarged ventrolateral ridge. Anterior margin rounded with broad compressed marginal zone. Posterior is reduced and rounded triangular in shape. Highly concave posterodorsal slope in right valve. Broad compressed posterior marginal zone. Dorsal margin straight with prominent cardinal angles, less so in left valve. Ventral margin inclined to posterior and medianly concave. Ventrolateral overhang

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accentuated by ventrolateral ridge. Prominent ovate eye node at anterior cardinal angle with on oblique post ocular sulcus. Prominent ridge runs from eye node almost to anteroventral margin where it deflects through 90° and runs posteriorly in a ventrolateral position. Posterior of mid-length the ridge becomes more plicate. A second subparallel ridge is situated between the first ridge and the ventral margin and is strongly carinate in some specimens. Both ridges may vary in their intensity of development. Immediately posterior of mid-line is a dome like swelling with a vertical sulcus to the anterior. Lateral surface reticulate. Small (10  $\mu$ m diameter) eccentric sieve pores evenly spaced over lateral surface. Anterior and posterior marginal zones smooth. Ventral surface with 2-3 subparallel ribs.

Antimerodont hinge developed in this juvenile. Muscle-scars consist of a vertical row of four ovate adductors. These lie on a muscle lobe with a sulcus to the anterior. No other internal details seen.

Remarks. L. sp. A resembles the juvenile stage of Lophocythere batei Malz, 1975, from the Bathonian Upper Estuarine Series of Ketton Cement Works, Leicestershire. The uppermost ridge in L. batei is more strongly developed along its whole length, whilst the lower ridge does not display the posterior carinate development of L. sp. A. This is particularly evident in dorsal view where the anterior and posterior marginal zones are smaller in L. batei. Lophocythere interrupta Triebel, 1951, from the Bathonian strata recovered in Borehole 148, N Germany, possesses a mid-dorsal vertically oriented sulcus like L. sp. A, but its anterior compressed marginal zone has a reticulate ornament. L. sp. A differs from the type species Lophocythere pstreata (Jones & Sherborn, 1888) in its lack of reticulate ornament on the prominent 'L shaped ridge and the lack of vertical ridges (Mayes 1975, pl. 2:25:162, fig 3.).

#### Genus ACANTHOCYTHERE Sylvester-Bradley, 1956

Type species. By original designation; Cythere sphaerulata Jones & Sherborn, 1888, p 253, pl. 1, figs 6a-c; from the Bathonian Blue Fullers Earth Clay, Midford, Somerset.

Diagnosis. (Modified after Bate 1963a). Subrectangular carapace. Biconvex in dorsal view. Males more elongate than females. Anterior and posterior well rounded with compressed marginal zones. Dorsal margin straight. Ventrolateral overhang obscures posterodorsal slope. Reticulate, with or without short conjunctive and disjunctive spines. Eye nodes sometimes developed at anterior cardinal angle. Hinge entomodont/lobodont.

Remarks. Acanthocythere differs from Fuhrbergiella Brand & Malz, 1962a in having more marginal pore canals. Fuhrbergiella has no more than eight anteriorly, while Acanthocythere usually has more than ten. Fuhrbergiella does not possess spines and the ventrolateral overhang does not obscure the posterodorsal slope as it does in Acanthocythere.

## Acanthocythere elongata sp. nov. Pl. 4, figs 1-5

Name. Latin; elongata, elongate; alluding to the length of the species.

Holotype. OS 13816, female carapace, Pl. 4, figs 4, 5, from top 5cm of Bed 5f, Kildonnan Member, Lealt Shale Formation, locality 1. Paratypes: OS 13817, Pl. 4, fig. 3 from same locality and level. OS 13818 and OS 13819 from 20cm above base of Bed 3h, Kildonnan Member, Lealt Shale Formation, locality 1. OS 13820, Pl. 4, fig. 2; OS 13821 and OS 13822, Pl. 4, fig. 1, from top 5cm of Bed 2, Kildonnan Member, Lealt Shale Formation, locality 2.

Material. 22 carapaces and 157 valves from the Kildonnan Member, Lealt Shale Formation, localities 1, 2.

Diagnosis. Large to very large Acanthocythere species. Carapace elongate, subrectangular in lateral view. In dorsal view elongate elliptical with compressed anterior and posterior marginal zones. Males more elongate than females. Slight swelling at anterior cardinal angle with oblique sulcus immediately to the posterior. Anterior margin evenly rounded. Posterior rounded triangular. Dorsal margin straight. Ventrolateral overhang obscures posteroventral slope. Left valve larger than right. Lateral surface with weak first and second order reticulation and large eccentric sieve pores. 12-15 marginal pore canals anteriorly, 12 posteriorly.

Measurements.

OS 13816 (female carapace)	891-518-436
OS 13817 (male right valve)	1036-527-264
OS 13818 (male right valve)	1000-509-218
OS 13819 (A-1 carapace)	745-436-324
OS 13820 (A-1 right valve)	691-391-182
OS 13821 (A-1 carapace)	782-455-361
OS 13822 (Adult? left valve)	472-281

Description. Elongate, subrectangular, posteriorly tapering carapace. Males more elongate than females (Text-fig. 17). Greatest length follows an oblique line from the posterior to the anterior, slightly above mid-height in both dimorphs. Greatest height immediately posterior of mid-length in adults and at anterior cardinal angle in juveniles. Dorsal view appears elongate elliptical with broad, compressed anterior marginal zone. Greatest width in posterior third of carapace. Anterior margin broadly rounded with a wide compressed marginal zone. Posterior margin smaller, rounded triangular in shape with a narrow compressed marginal zone. Dorsal margin almost straight, cardinal angles distinct. Anterior cardinal angle surmounted by a slight ovate swelling with a short oblique sulcus immediately to the posterior. Shallow median ventral concavity. Ventral surface overhung from mid-length posteriorly. Left valve overlaps right valve along the ventral, anterior and posterior margins. Lateral surface with weakly developed first and second order reticulation. Numerous large  $(15-20 \ \mu m \ diameter)$  eccentric sieve pores evenly scattered over lateral surfaces. Ventral surface with elongate reticulation giving the appearance of subparallel ribs. Faint rib surmounted by small (5  $\mu$ m diameter) normal pores medianly positioned in the anterior and posterior compressed marginal zones. Marginal rib present around the anterior, posterior and ventral margins only.

Hinge entomodont. Six anterior and seven posterior, elongate and occasionally dorsally thickened and bifid terminal teeth in right valve. Loculate median groove enlarged in anterior third where a thickened lower lip is developed. Complementary structures in left valve with a broad accommodation shelf above the median bar. Avestibulate. Inner lamella moderately wide. 12-15 short, straight marginal pore canals anteriorly, 12 posteriorly. Musclescars consist of four subovate adductors in a subvertical row, a large round frontal scar and a small round mandibular scar situated to the anterior.

Remarks. Acanthocythere aardaensis Basha, 1980, from Bathonian strata near Aarda Ain-Khuneizier, Amman, Jordan, resembles A. elongata in outline but is much smaller and possesses a coarse, triangular patterned reticulate ornament. The type species A. sphaerulata (Jones & Sherborn, 1888) has numerous conjunctive and disjunctive spines. No spines are visible on A. elongata.

## Acanthocythere? sp. A Pl. 4, figs 6-9

Material. Three carapaces and three valves with original shell material and nine internal moulds of carapaces, from the Lonfearn Member, Lealt Shale Formation, localities 3, 4.

Measurements.

OS 1382	23 (cai	rapace)
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OS 13824 (carapace)

964-527-491 855-491-455

Description. Elongate carapace. Subrectangular in lateral view. Greatest length passes obliquely down from posterior to anterior. Greatest height at mid-length. Dorsal view is pear shaped with distinct anterior and posterior compressed marginal zones. Greatest width immediately anterior of posterior cardinal angle. Anterior margin broadly rounded, posterior smaller and triangular in shape. Posterodorsal slope concave. Both margins with broad











TEXT-FIG. 18. Central muscle-scars of *Acanthocythere*? sp. A. Composite sketch based upon two damaged specimens.

compressed marginal zones, though anterior is broader than posterior. Dorsal margin with distinct cardinal angles. Anterior cardinal angle with ovate swelling and oblique sulcus immediately to the posterior. Ventrolateral overhang extends posteriorly from mid-length. Left valve overlaps right valve around the anterior, posterior and ventral margins. Lateral surface reticulate. Numerous small (5-10  $\mu$ m diameter) eccentric sieve pores on lateral surfaces. Ventral surface with elongate reticulation.

Internal moulds suggest an entomodont hinge. Muscle-scars consist of a subvertical row of four adductors. The large round frontal and mandibular scars are level with the upper two adductors and below the level of the basal adductor respectively (Text-fig. 18).

*Remarks.* Because of the general lack of well preserved specimens of A? sp. A it is only tentatively included in the genus. It differs from A. *elongata* sp. nov. in its shape when viewed dorsally, in being more inflated posteriorly (in dorsal aspect) and in a having a wider posterior marginal zone.

#### Family LIMNOCYTHERIDAE Sars, 1925

Diagnosis. (Modified after Moore & Pitrat 1961 and Colin & Danielopol 1978). Valves subequal and weakly to strongly calcified. Sexual dimorphism usually evident; males more elongate and less posteriorly inflated than females. Normal pores numerous. Ornamentation may include the development of primary and secondary reticulation, alar projections, nodes, simple and sieve type pores. Bisulcate. Inner lamella narrow, vestibula when developed are small. Marginal pore canals evenly spaced and straight. Hinge adont or lophodont. Central muscle-scars consist of a subvertical row of four adductors, a reniform frontal scar and an ovate, sometimes divided, mandibular scar.

Remarks. The Limnocytheridae are supposed to lack sieve type pores (Colin & Danielopol 1978). Whatley & Cholich (1974) demonstrated that limnocytherids possess sieve pore when they described Pampacythere, and Martens (1990) showed that some other limnocytherid genera also have sieve pores. Small sieve pores are also recorded here in Limnocythere incerniculum sp. nov. Limnocythere spinosa sp. nov. Limnocythere sp. A, Theriosynoecum fimbriachela sp. nov. and Theriosynoecum ancasterensis (Bate, 1967). The following limnocytherids, Limnocythere, Ovambocythere, Leucocythere, Gomphocythere, Cytheridella (see Martens, 1990), Gomphodella (DeDeckker, 1981), Stenestroemia (Christensen, 1968) and Theriosynoecum (Wakefield & Athersuch, 1990) are now known to have sieve pores. I do not concur with Kristic (1987) that a separate subfamily of the Limnocytheridae, the Dinarocytherinae, should be recognized on the basis of sieve pores. Colin & Danielopol (1978, 1980) subdivided the Limnocytheridae into the Limnocytherinae and the Timiriaseviinae Mandelstam, 1960. Danielopol (1965) previously divided the family, using soft part morphology, into the Limnocytherinae and the Metacyprinae. As such, the Metacyprinae were considered to be a synonym of the Timiriaseviinae by Colin & Danielopol (1978, 1980).

## Subfamily LIMNOCYTHERINAE Sars, 1925

Diagnosis. (Modified after Colin & Danielopol 1978). Valves subequal, mostly weakly calcified, slender and reniform in shape. Males more elongate than females which are inflated posteriorly. Weakly ornamented. Bisulcate. Sulci vertical. Often nodose and/or alate. Normal pores of simple and/or sieve type. Hinge adont or lophodont. Inner lamella narrow. Marginal pore canals simple and straight. Muscle-scars consist of a subvertical row of four ovate adductors with a reniform frontal scar and an ovate or round mandibular scar.

*Remarks.* Based on morphological differences the subfamily is thought (Colin & Danielopol 1978) to contain 4 groups, characterized by *Limnocythere*, *Leucocythere*, *Gomphocythere*, and *Cytheridella*.

#### Genus LIMNOCYTHERE Brady, 1868

Type species. By original designation; Cythere inopinata Baird, 1843, p 195, figs 1a-e; from the Recent of Whitefield Loch, Dumfries & Galloway, Scotland.

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*Diagnosis.* (Modified after Van Morkhoven 1962 and Delorme 1971). Carapace reniform with medianly concave ventral margin. Males usually more elongate than females. Dorsal margin almost straight. Anterior and posterior well rounded with compressed marginal zones. Bisulcate. Ornament often reticulate. Hollow nodes and alar projections sometimes developed. Avestibulate. Inner lamella narrow to wide. Marginal pore canals few, straight and simple. Lophodont hinge. Muscle-scars consist of a subvertical row of four adductors, a reniform frontal scar and a large round mandibular scar.

Remarks. Van Morkhoven (1962) doubted that Limnocythere ranged older than the Oligocene, and thus only tentatively included Limnocythere fragilis Martin, 1940, from the Upper Jurassic of Germany within the genus. Subsequently the range of Limnocythere has been extended to at least the Middle Jurassic by records of species such as Limnocythere hibernica Athersuch, 1989, and Limnocythere ceratina Ware & Whatley, 1980 (both Bathonian).

### Limnocythere incerniculum sp. nov. Pl. 4, figs 10-19

Name. Latin; incerniculum, a sieve; with reference to the ornament.

*Holotype.* OS 13825, female carapace, Pl. 4, figs 10, 12, from 60cm above base of Bed 7, Kildonnan Member, Lealt Shale Formation, locality 4. Paratypes: OS 13826, Pl.4, fig. 11 and OS 13831, Pl. 4, figs 15, 16, from 30cm above base of Bed 7, Kildonnan Member, Lealt Shale Formation, locality 4. OS 13827 from top 5cm of Bed 5, Kildonnan Member, Lealt Shale Formation, locality 4. OS 13828 from top of Bed 6d, Kildonnan Member, Lealt Shale Formation, locality 1. OS 13829, Pl. 4, fig. 14, from top of Bed 6, Kildonnan Member, Lealt Shale Formation, locality 2. OS 13830, Pl. 4, figs 17-19, from top 5cm of Bed 6b, Kildonnan Member, Lealt Shale Formation, locality 2. OS 13830, Pl. 4, figs 17-19, from top 5cm of Bed 6b, Kildonnan Member, Lealt Shale Formation, locality 1.

*Material*. Several thousand valves and carapaces from the Kildonnan Member, Lealt Shale Formation, localities 1-5. Adult valves are often crushed. Juveniles are usually excellently preserved.

Diagnosis. Very large subrectangular Limnocythere species with strong ventrolateral alae which terminate with a spine. Ventral margin deeply concave. Males more elongate than females. Anterior subcentral sulcus with bordering nodes surmounted by eccentric sieve pores, three anteriorly, two posteriorly. First and second order reticulation variably developed. Inner lamella of moderate width. 10-12 straight marginal pore canals anteriorly, 3-4 posteriorly.

Measurements.

OS 13825 (female carapace)	909-473-382
OS 13826 (male carapace)	1130-582-309
OS 13827 (A-1 carapace)	845-436-332
OS 13828 (A-4 left valve)	341-200- 75
OS 13829 (A-3 right valve)	500-291-117
OS 13830 (A-4 left valve)	464-291-182
OS 13831 (A-4 right valve)	455-291-164

Description. Elongate subrectangular carapace, with males being more elongate than females (Text-fig. 19). Greatest length at mid-height. Greatest height at anterior cardinal angle in juveniles, at posterior cardinal angle in adults. Greatest width median in juveniles and in posterior third of carapace in adults. Dorsal margin straight. Ventral margin with strong median concavity. Dorsal and ventral margins sub-parallel in adults. Juveniles taper posteriorly. Anterior well rounded. Posterior rounded in juveniles, triangular in adults and with a broad posterodorsal marginal flange. Marginally compressed both anteriorly and posteriorly. Lateral surface with variably developed first and second order reticulation. Dorsomedianly sulcate. Vertical median sulcus bordered posteriorly by two and anteriorly by three conical nodes which are surmounted by eccentric sieve pores. Sieve pores scattered



TEXT-FIG. 19. a) Size dispersion, b) sexual dimorphism of *Limnocythere incerniculum* from a single sample taken at the type level, Kildonnan Member, Lealt Shale Formation. Mean increase in length between instar stages is 33%.



TEXT-FIG. 20. Central muscle-scar of a left valve of *Limnocythere incerniculum*. Composite sketch from several specimens.

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Hinge lophodont. Right valve terminal teeth are short and blade-like. In dorsal view, posterior tooth is poorly developed. Accommodation groove is open to the domicilium, as are the left valve terminal locellae. Left valve median bar occasionally with three small anterior fenticles developed. Avestibulate. Marginal pore canals straight, 10-12 anteriorly, 3-4 posteriorly. Muscle-scars consist of four adductor scars in a subvertical row, a reniform frontal car, which in some cases is almost subdivided and a reniform mandibular scar (Text-fig. 20).

Remarks. Ware & Whatley (1980, p. 204) noted that "nearly every species of Limnocythere so far described has a smooth lophodont hinge". Several specimens of L. incerniculum like L. enatina Ware & Whatley, 1980 from the Bathonian Forest Marble at the Old Cement Works, Kirtlington, Oxfordshire have weakly developed denticles at the anterior of the left valve median bar. However, other crenulations noted in L. ceratina were not evident in L. incerniculum. L. ceratina differs from L. incerniculum in being punctate rather than reticulate, and also has a small round eye node. L. fragilis Martin, 1940 from the Upper Jurassic strata recovered from Borehole No. WA11, Hannover, Germany bears a close resemblance to L. incerniculum. The former is more asymmetrically rounded posteriorly and in dorsal view the lateral flanks of L. fragilis are not subparallel but are medianly concave at the position at which the alar projections emanate.

The ornamental variation observed in L. *incerniculum*, in populations from many different borizons and localities, affects the primary muri and the presence of secondary reticulation. This appears to be a primary rather than a preservational effect.

#### Limnocythere spinosa sp. nov. Pl. 4, figs 20-27

Name. Latin; spinosus, spiny; with reference to the outline of the alar projection in dorsal aspect.

Holotype. OS 13832, female left valve, Pl. 4, fig. 20, from 5cm above base of Bed 8b, Lonfearn Member, Lealt Shale Formation, locality 2. Paratypes: OS 13836 and OS 13837, Pl. 4, figs 26, 27, from same locality and level. OS 13833, Pl. 4, fig. 21; OS 13834, Pl. 4, figs 23, 24; OS 13835, Pl. 4, figs 22, 25 and OS 13838 from 20cm above base of Bed 7, Lonfearn Member, Lealt Shale Formation, locality 4.

Material. 46 valves and carapaces from Bed 8, Lonfearn Member, Lealt Shale Formation, locality 2. Several hundred specimens from the Lonfearn Member, Lealt Shale Formation, localities 2, 4, 5.

Diagnosis. Medium to large subrectangular species of Limnocythere. Males more elongate than females. Strong ventrolateral alar projections which terminate posteriorly with a spine. Hemispherical swelling usually developed to the posterior of the alae. Weak median ventral concavity. Anterior margin broadly rounded with a wide compressed zone. Asymmetrically rounded posterior margin with narrow compressed zone. Large subcentral sulcate region. At least eight anterior and two posterior straight marginal pore canals.

Measurements.

OS 13832 (female left valve)	733-455-236
OS 13833 (A-2 left valve)	527-336-146
OS 13834 (A-2 right valve)	445-264- 90
OS 13835 (male left valve)	618-345-182
OS 13836 (A-1 left valve)	636-400-160
OS 13837 (A-2 right valve)	509-309-113
OS 13838 (female left valve)	691-436-164

Description. Subrectangular carapace. Greatest length at mid-height. Males more elongate than females (Text-fig. 21). Greatest height at anterior cardinal angle in both juveniles and adults. Greatest width at mid-length in juveniles and in posterior half of carapace in adults.



TEXT-FIG. 21. a) Size dispersion, b) sexual dimorphism of *Limnocythere spinosa* from a single sample taken at the type level, Lonfearn Member, Lealt Shale Formation. Mean increase in length between supposed A-1 and adults is 21%.



TEXT-FIG. 22. a) Central muscle-scars from a left valve of *Limnocythere spinosa*, OS 13837, b) crosssection of the posterior margin, c) cross-section of the anterior margin. Cross-sections drawn from a female specimen that was deliberately broken so that cross-sections through the margins could be seen.

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Anterior margin broadly rounded with wide compressed region. Posterior margin asymmetrically rounded and with a narrow compressed region. Dorsal margin straight. Ventral margin with broad, shallow median concavity. Dorsal and ventral margins subparallel in all but the smallest instars which taper to the posterior. Left valve overlaps right valve around the posterior and ventral margins. Lateral surface smooth to finely punctate. Ornament distorted above the position of the muscle-scars so that the internal dispositions of the 4 adductor scars are visible. Sieve pores irregularly scattered over lateral surface, often seen on small rounded nodes around dorso-median sulcus. Broad sulcate region subdivided by a central swelling. Strong alar projections developed ventrolaterally. In dorsal aspect they appear strongly curved and with a posterior spine. Both surfaces of alae punctate. Immediately to the posterior of the alae a large hemispherical swelling surmounted by up to four normal pores is usually developed.

Hinge lophodont. Locellae in both valves are open to the domicilium. Muscle-scars arranged in an arcuate subvertical row of four adductors, the frontal scar is reniform, the mandibular scar is large, ovate and underlain by a second smaller round scar (Text-fig. 22). Avestibulate. Inner lamella widest anteriorly. At least eight anterior and two posterior straight marginal pore canals.

Remarks. The ornamental variation observed in L. spinosa may be preservational, as many specimens show calcite overgrowths. L. spinosa and L. incerniculum sp. nov. are similar in their early instar stages. In its later instar and adult development L. incerniculum has a more triangular shaped posterior, is more elongate, is larger and lacks a posterior hemispherical swelling. L. spinosa resembles Limnocythere? sp. of Malz et al., 1985, from Bajocian rocks near Pedra Ghisu, NW Sardinia, but possesses more strongly developed alar projections and is less tapered towards the posterior when viewed dorsally. L? sp. also lacks the swollen posterior node of L. spinosa. Limnocythere sieberi Lutz, 1965, lacks both the alar projections and the posterior node of L. spinosa but has a similar lateral outline.

## Limnocythere melicerion sp. nov. Pl. 5, figs. 1-7

Name. Greek; melikerion, a honeycomb; with reference to the ornament.

Holotype. OS 13839, adult left valve, Pl. 5, figs 4, 7, from 60cm above base of Bed 5, Lonfearn Member, Lealt Shale Formation, locality 4. Paratypes: OS 13840 from 20 cm above base of Bed 7, Lonfearn Member, Lealt Shale Formation, locality 4. OS 13841, Pl. 5, figs 1-3, 5, 6; OS 13842, OS 13843 and OS 13844 from 5cm above base of Bed 8b, Lonfearn Member, Lealt Shale Formation, locality 2.

Material. 11 carapaces and 30 valves from the Lonfearn Member, Lealt Shale Formation, localities 2, 4.

Diagnosis. Elongate species of Limnocythere. Anterior evenly rounded with a wide compressed marginal zone. Posterior asymmetrically rounded with a narrow compressed marginal zone. Ventromedian concavity with short, triangular alar projection immediately above. Wide subcentral dorsal sulcus subdivided by a vertical row of three rounded nodes. Conical node occasionally developed behind the sulcus. Lateral surface with coarse punctation. Prominent anterocentral, semicircular muscle node posteriorly bordered by an arcuate row of fossae. Inner lamella broadest anteriorly. 9-12 straight marginal pore canals anteriorly, 9-10 posteriorly. Sexual dimorphism not evident.

Measurements.

OS 13839 (adult left valve)	891-498-180
OS 13840 (adult left valve)	782-433-145
OS 13841 (juvenile left valve)	600-345-127
OS 13842 (juvenile carapace)	636-327-218
OS 13843 (juvenile right valve)	636-345-109
OS 13844 (adult right valve)	655-400-109
Description. In dorsal view the lateral surfaces appear subparallel in juveniles, whilst in adults the carapace appears pear shaped. Sexual dimorphism not evident. Greatest length runs slightly above mid-height. Greatest height at anterior cardinal angle in juveniles and at posterior cardinal angle in adults. Greatest width median in juveniles and in posterior third of carapace in adults. Anterior evenly rounded with a wide compressed marginal zone. Posterior asymmetrically rounded with a narrow compressed marginal zone. Broad median ventral concavity overlain by a short, triangular alar projection. Dorsal margin straight but with prominent cardinal angles particularly in left valve. Wide subcentral sulcus. This is subdivided by a vertical row of three small rounded, hollow nodes. Hollow conical node occasionally developed immediately to the posterior of sulcus. Immediately below posterior of sulcus lies a semicircular muscle node posteriorly bordered by an arcuate row of fossae. Lateral surface coarsely punctate. Punctae smaller around margins. Lateral surface irregularly scattered with normal pores.

Hinge lophodont. Dorsal profile of terminal teeth appears arcuate, anterior tooth is less pronounced than posterior tooth. Locellae in both valves open to domicilium. In dorsal view the outer lamella forming the terminal locellae/cardinal angles projects over the right valve. Muscle-scars; an arcuate subvertical row of four adductors. Frontal scar paired; a reniform scar with a small round scar immediately to the anterior. Mandibular scar large, circular. Avestibulate. Inner lamella broadest anteriorly. 9-12 straight marginal pore canals anteriorly, 9-10 posteriorly.

*Remarks.* The muscle-scars in one specimen of *L. melicerion* are unusual in that the uppermost adductor scar is subdivided, giving the appearance of 5 adductor scars.

Distinct populations of L. melicerion are found on the isles of Eigg (locality 2) and Skye (locality 4). The latter always has the post-sulcus conical node developed, yet only one specimen from the former population has the node developed. This difference in node development is possibly ecophenotypic, as has been suggested for the modern Cyprideis torosa (see Kilenyi 1972). L. melicerion resembles L. spinosa sp. nov. in lateral view but is clearly differentiated by its well developed punctate ornament, muscle scar node and nodes around the sulcate region.

### Limnocythere? sp. A Pl. 5, figs 8-11

*Material*. One left valve of a presumed juvenile from 35cm above base of Bed 4, Kildonnan Member, Lealt Shale Formation, locality 1.

# Measurements.

OS 13845 (juvenile left valve)

### 764-409-143

Description. Elongate species of Limnocythere? Greatest length at mid-height. Greatest height at anterior cardinal angle. Dorsal margin slightly convex. Distinct cardinal angles rounded. Ventral margin medianly concave. Anterior broadly rounded with narrow compressed marginal zone. Asymmetrically rounded posterior with narrow compressed marginal zone. Weakly bisulcate. Shallow vertical sulcus immediately anterior of mid-length. Second shorter sulcus anterior of first. Blunt alar projections developed ventrolaterally above median concavity. Lateral surfaces with well developed primary reticulation. Primary fossae elongated along ventral surface. Secondary reticulation developed near margins, particularly the anterior and posterior margins. Small (10-15  $\mu$ m long) ovate sieve pores irregularly situated on lateral surfaces. Impression of the four adductor muscle-scars visible in the ornament below the posterior sulcus.

Lophodont hinge. Actual muscle-scars not visible. Avestibulate. Inner lamella broadest anteriorly. No marginal pore canals seen.

Remarks. L? sp. A is tentatively placed in Limnocythere as only a single left valve was available for study.

# Limnocythere? sp. B Pl. 5, figs 12-16

Material. Two valves. OS 13846 from 45cm below the top, and OS 13847 from the top 5cm, Bed 5f, Kildonnan Member, Lealt Shale Formation, locality 1.

Measurements.

OS 13846 (female? right valve)	691-400-189
OS 13847 (male? left valve)	691-309-142

Description. Elongate species of Limnocythere? Laterally appears reniform. Greatest length at mid-height. Greatest height at anterior cardinal angle. Dorsal margin slightly convex. Ventral margin medianly concave. Anterior and posterior well rounded and marginally compressed. Posterodorsal compressed margin much broader forming a distinct flange. Bisulcate. Subvertical sulcus at mid-length with a second shorter, oblique sulcus immediately posterior of anterior cardinal angle. Conical node developed posterocentrally. Short alar projection developed above ventral concavity. Lateral surface with small blunt pustules. Area between pustules is apparently micropunctate.

Lophodont hinge poorly preserved in both specimens. Other internal details not visible. External openings for eleven posterior and at least nine anterior marginal pore canals visible under the SEM.

*Remarks*. L? sp. B is tentatively placed within *Limnocythere* as only two valves were available for study. Based on shape, one specimen may be a male and the other a female.

L? sp. B closely resembles Limnocythere pustulosa Wall, 1960 from Bathonian strata recovered from Tidewater Frontier Crown Well No. 1, Saskatchewan, Canada which differs in having a pustulose anterior marginal rim, larger pustules on the lateral surfaces and a straighter dorsal margin. Note that it is considered that the explanations of the original illustrations of male and female in L. pustulosa were inverted by Wall. L? sp. B differs from all the other Great Estuarine Group species of Limnocythere in having pustulose rather than punctate or reticulate ornament.

# Limnocythere? sp. C Pl. 5, figs 17-19

Material. Three valves from 20cm above base of Bed 7, Lonfearn Member, Lealt Shale Formation, locality 4.

Measurements.

OS 13848 (juvenile ? right valve)	645-364-145
OS 13849 (juvenile ? right valve)	582-327-127
OS 13850 (juvenile ? left valve)	527-327-109

Description. Posteriorly tapering Limnocythere? species. Strongly reniform. Greatest length runs through mid-height. Greatest height at anterior cardinal angle. Greatest width slightly posterior of mid-length. Straight dorsal margin with prominent, rounded cardinal angles. Medianly concave ventral margin. Anterior asymmetrically rounded with a broad compressed marginal zone. Posterior margin asymmetrically rounded. Marginal flange present around posteroventral margin. Alar projection developed above ventral concavity, inclined upwards to posterior margin. Bisulcate. Lateral surface highly punctate. Numerous pore conulae developed. Two rounded nodes immediately behind sulcate region.

Hinge lophodont. Inner margin and line of concrescence coincide. Inner lamella broadest anteriorly. Other internal detail not visible.

*Remarks. L*? sp. C is tentatively placed within *Limnocythere* as only three valves were available for study. *L*? sp. C is found in association with *L. melicerion* sp. nov. from which it is clearly distinguished by its smaller punctae, more numerous pore conulae and its lack of muscle-scar and posterocentral conical nodes. Lack of available material prevents further comparisons.

Occurrence. Bed 7 of the Lonfearn Member, Lealt Shale Formation, locality 4.

# Limnocythere spumida sp. nov. Pl. 5, figs 20-28

Name. Latin; spumidus, foamy or frothy; with reference to the ornament:

Holotype. OS 13851, male right valve, Pl. 5, figs 25, 27, from top 5cm of Bed 5f, Kildonnan Member, Lealt Shale Formation, locality 1. Paratypes: OS 13852, Pl. 5, figs 26, 28, from same locality and level. OS 13853, Pl. 5, figs 22-24, from Bed 3h, Kildonnan Member, Lealt Shale Formation, locality 1.

Material. 21 valves from the Kildonnan Member, Lealt Shale Formation, locality 1.

*Diagnosis.* Valves subovate with straight dorsal margin and medianly concave ventral margin. Males more elongate than females. Cardinal angles prominent in left valve. Large U-shaped sulcus sited in anterior half of dorsal margin. Alar projection. Well developed punctation on all surfaces, including the alae.

Measurements.

OS 13851 (male right valve)	691-364-165
OS 13852 (female right valve)	691-400-165
OS 13853 (juvenile left valve)	636-364-136

Description. Valves subovate in lateral view, with greatest length at mid-height. Greatest height at posterior cardinal angle. Dorsal margin straight in right valve and with prominent cardinal angles in the left. Ventral margin with broad median concavity. Elongate alar projection subparallel to ventral margin. Alar projection starts before and terminates after the ventral concavity. In dorsal view the alar projections appear triangular in well preserved specimens but often appear arcuate in abraded specimens. Alar projection partially obscures ventral concavity. Large, shallow, vertically oriented U-shaped sulcate region sited dorsally, anterior of mid-length. Well developed reticulate/punctate ornament. Finer punctation in the



TEXT-FIG. 23. Comparison of the position and morphology of the alar projection (shaded) in species of Limonocythere (not to scale). References are given, if different from species author then given in brackets. a) Limnocythere hibernica Athersuch, 1989; b) Limnocythere fragilis Martin, 1940; c) Limnocythere mowbrayensis Chapman, 1914 (De Deckker 1981); d) Limnocythere ceratina Ware & Whatley, 1980; e) Limnocythere porphretica DeDekker, 1981 and f) Limnocythere spumida (herein).

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sulcate region and around valve margins. Some of the larger punctae contain several (2-3) smaller punctae. Punctation occurs on both upper and lower surfaces of the alar projections.

Hinge lophodont. Left valve median bar straight and undivided. Locellae in both valves open to domicilium. Muscle-scars consist of a subvertical row of four adductors, reniform frontal scar and large round mandibular scar to the anterior. Avestibulate. Inner lamella is widest anteriorly.

*Remarks.* The alar projection of L. spumida is subparallel to the ventral margin. In many other species of Limnocythere the alar projection is inclined upwards towards the dorsal margin (Text-fig. 23). This character is not deemed to be sufficiently strong to warrant the diagnosis of a new genus.

In more poorly preserved specimens only the primary reticulation is visible. In better preserved specimens many of the larger punctae are seen to contain smaller punctae. The alar projection varies from rounded to more triangular in shape, possibly due to abrasion by transport.

#### Subfamily TIMIRIASEVIINAE Mandelstam, 1960

Diagnosis. (Modified after Hartmann & Puri 1974 and Colin & Danielopol 1978, 1981). Valves ovate in lateral view, rarely slender but often compressed. This is emphasised in the females where the posterior is inflated. Bisulcate. Ornamented; reticulation often in concentric rows producing a concentric costellation; puncta often in small rosette groupings. Nodes and sieve pores often developed. Hinge lophodont. Inner lamella narrow. Vestibula small. Marginal pore canals straight and simple. Muscle-scars consist of a subvertical row of four adductors with a reniform frontal scar and an ovate mandibular scar.

Remarks. The Timiriasiviinae was subdivided by Colin & Danielopol (1978) into the Timiriasevia-Metacypris, the Kovaleskiella-Rosacythere-Frambocythere, the Theriosynoecum and the Afrocythere-Elphidium groups, which were considered to be based upon phylogenetic relationships. As a result of these studies Colin & Danielopol (1978, 1980) concluded that the posterior brood pouch and the sulci of the Timiriaseviinae had been present since the Triassic and that the tuberculation seen in the Theriosynoecum group had appeared in the Bathonian.

# Genus THERIOSYNOECUM Branson, 1936

(Synonyms: Morrisonia Branson, 1935 [non Morrisonia Grote, 1874]; Bisulcocypris Pinto & Sanguinetti, 1958; Dryelba Sohn, 1982)

Type species. By original designation; Morrisonia wyomingensis Branson, 1935, p 521, pl. 57, figs 17-21; from the Morrison Formation (Upper Jurassic), Wyoming, USA.

Diagnosis. (Modified after Colin & Danielopol 1981). Carapace expanded posteriorly, compressed anteriorly, appearing pear or heart shaped in dorsal view. Laterally ovate to subrectangular. Females expanded posteriorly. Dorsal and ventral margins subparallel. Anterior and posterior well rounded. Cardinal angles well developed at ends of straight dorsal margin. Bisulcate. Valves divided medianly by a strong sulcus, a second weaker sulcus lies immediately to the anterior. Ornamented; often reticulate or punctate, with or without tubercular development. Generic pore net present (Wakefield & Athersuch, 1990). Marginal pore canals short and straight. Muscle-scars consist of a subvertical row of four adductors, frontal and mandibular scars not always developed.

Remarks. Pinto & Sanguinetti (1958, 1962) and Bate (1965, 1967) considered Bisulcocypris Pinto & Sanguinetti, 1962, to be separate from Theriosynoecum. Colin & Danielopol (1978, 1980) considered Bisulcocypris to be the junior synonym of Theriosynoecum. Sohn (1982) proposed that many of the 44 species of Theriosynoecum then described be placed in his new family Dryelbidae and genus Dryelba. He did not consider Bisulcocypris to belong in the Dryelbidae. Only Theriosynoecum helmdachi Sohn, 1982, Theriosynoecum hemigymnon Helmdach, 1968, and Theriosynoecum wyomingensis (Branson, 1935) were considered to belong in

Theriosynoecum. Sohn (1982) considered that Dryelba differed from Theriosynoecum in its lack of a ventrolateral lobe or alar projection and in the position of two dorsoposterior nodes. Wakefield & Athersuch (1990) noted qualitative differences between Theriosynoecum species in the position of pores/nodes and their proposed "generic pore-net". Limnocytherids in general are known to show wide variation in the development (i.e. presence/absence) of certain morphological features, and in particular nodes and alar projections. Thus I consider Dryelba to be synonymous with Theriosynoecum.

Sohn & Anderson (1964) noted the constancy in position of the nodes of *Theriosynoecum fittoni* throughout its ontogeny. They postulated a genetic control for node position, as did Kilenyi (1972) for material now referred to *Theriosynoecum conopium* Wakefield & Athersuch, 1990, from the Kilmaluag Formation of the Great Estuarine Group. Wakefield & Athersuch (1990; text-figs 6, 7) noted that although the exact positions of pore conuli and nodes varied between *Theriosynoecum* species a generalised pore network for the genus was present (see also Text-fig. 24). The fact that the number of nodes developed, and even the state of the development of the nodes is variable indicates a possible environmental influence such as salinity variations.

In most of the populations studied from the Great Estuarine Group noding is present in a large percentage of individuals at each instar stage up to and including the A-1 instar, whilst being extremely rare in the adults. Kilenyi (1972) observed that juveniles were more likely to be noded than the adults. He suggested that the variations were due to certain advantages which the development of nodes provide, and that these advantages were reduced during ontogeny.

# Theriosynoecum fimbriachela sp. nov. Pl. 6, figs 1-9

Name. Latin; fimbriata, fringed and chela, a claw; with reference to the posterior spines resembling claws.

Holotype. OS 13854, male left valve, Pl. 6, figs 1, 2, from basal 10cm of Bed 11, Lonfcarn



TEXT-FIG. 24. Position of nodes (centred on pores) and pore conuli for species of *Theriosynoecum*: a) *T. fimbriachela*; b) *T. ramocuspis*; c) *T. conopium*; d) *T. sagena* and e) *T.* sp. A. f) Generic standard (Wakefield & Athersuch 1990).

Member, Lealt Shale Formation, locality 3. Paratypes: OS 13858, Pl. 6, fig. 3; OS 13859 from same locality and level. OS 13855, Pl. 6, fig. 7; OS 13856 and OS 13857, Pl. 6, figs 4-6, 8, 9, from 5cm above base of Bed 8b; Lonfearn Member, Lealt Shale Formation, locality 2.

Material. 73 valves and two carapaces from the Lonfearn Member, Lealt Shale Formation, localities 2-4.

Diagnosis. Elongate species of Theriosynoecum. Long slightly convex dorsum. Posterior cardinal angle prominent. Anterior margin compressed. Dorso-central and antero-dorsal sulci coalesce into a deep 'U'-shaped depression. Shell surface strongly reticulate, second order reticulation well developed. Up to six hollow nodes and at least nine pore conulae developed. Four posterior marginal spines usually developed. At least 16 anterior and seven posterior short, straight marginal pore canals.

Measurements.

OS 13854 (male left valve)	1073-582-291
OS 13855 (juvenile left valve)	704-389-160
OS 13856 (juvenile left valve)	800-491-200
OS 13857 (juvenile left valve)	655-364-167
OS 13858 (female carapace)	1109-636-655
OS 13859 (A-1? right valve)	927-527-200

Description. Pear shaped in dorsal view. Females inflated posteriorly. Greatest length at mid-height, greatest height at anterior cardinal angle in juveniles and at posterior cardinal angle in adults. Greatest width in posterior third of valve. Dorsal margin is slightly convex and is sub-parallel to the ventral margin in the adult. Valve tapers posteriorly in juveniles. Anterior asymmetrically rounded, posterior margin almost straight in juvenile - male ontogenetic lineage, rounded in female. Anterior cardinal angle less distinct than posterior cardinal angle. Dorso-central and antero-dorsal sulci coalesce into a deep 'U'-shaped depression. Strongly developed primary reticulation. Secondary reticulation is well developed, particularly in the sulcate and antero-lateral regions. Four short, posteriorly directed spines usually developed on posteroventral margin. Pore net as for the genus. Six hollow nodes generally developed with at least nine pore conulae. Nodes generally absent in adults. Small  $(5 \,\mu m)$  sieve plates present in the sulcate region.

Hinge lophodont. Median bar in left valve is long with a narrow accommodation shelf above. In dorsal view the terminal teeth appear arcuate. Muscle-scars consist of a subvertical row of four adductors. Frontal and mandibular scars not observed. Vestibula small. At least 16 anterior and seven posterior marginal pore canals are visible under transmitted light.

Remarks. Theriosynoecum algarbensis Helmdach & Ramalho, 1976, from the Kimmeridge deposits of the Algarve, Portugal, differs from T. fimbriachela in possessing more posterior marginal spines and a prominent anterior cardinal angle. The lateral surfaces of T. algarbensis also have many more small pore conulae developed. Theriosynoecum isoplektum Krömmelbein & Weber, 1971, from Lower Cretaceous strata recovered from Borehole Ru-1-Ba, Bahia, Brazil, is similar in lateral outline to T. fimbriachela but differs in lacking marginal spines, and in being more inflated when viewed dorsally. T. fimbriachela differs from Theriosynoecum ramocuspis sp. nov. in its lack of spinose cardinal angles, the development of secondary reticulation and in the relative positions of nodes in the pore net (see also remarks for T. ramocuspis sp. nov.).

### Theriosynoecum ramocuspis sp. nov. Pl. 6, figs 10-16

Name. Latin; ramus, antler and cuspis, a point; with reference to the spine on each cardinal angle.

Holotype. OS 13860, female left valve, Pl. 6, figs 13-15, from Bed 42a, Lonfearn Member, Lealt Shale Formation, locality 2. Paratypes: OS 13861, Pl. 6, figs 12, 16; OS 13862, OS 13863, Pl. 6, fig. 11; OS 13864, Pl. 6, fig. 10; and OS 13865 from same locality and level.

*Material.* 111 valves from the Lonfearn Member, Lealt Shale Formation, locality 2 and the Valtos Sandstone Formation, locality 6.

Diagnosis. Elongate species of *Theriosynoecum*. Dorsal margin straight, prominent cardinal angles, each with a single spine. Anterior margin asymmetrically rounded, posterior rounded in female almost straight in male and juveniles. Reticulate. Four adductor muscle-scars reflected in the ornament. Up to six anterior and seven posterior marginal spines, only on left valve. Seven nodes and at least five pore conulae may be developed.

Measurements.

1018-600-255
545-364-155
1036-618-329
982-527-218
455-255- 91
509-327-164

Description. Valves elongate with greatest length at mid-height. Greatest height at anterior cardinal angle in juveniles and at mid-length in adults. Greatest width in posterior third of valve in female and at mid-length in male and juveniles. Anterior asymmetrically rounded, posterior almost straight in males and juveniles but is strongly rounded and inflated in females. Anterior and posterior marginal areas compressed. Posterior compressed margin confluent with postero-ventral marginal flange. Up to seven posteriorly projected spines may be developed on the posteroventral flange, whilst up to six spines are developed around the anterior margin. Spines only developed on the left valve. Dorsal margin straight and subparallel to ventral margin in adults. Well defined cardinal angles, each with a spine; only on the left valve. Both sulci are well developed. They are semi-confluent and form an anterodorsal depression with a positive central region. Lateral surface with well developed reticulation forming an open mesh work. Sola unornamented. Immediately below posterior most sulcus lies an external reflection of the muscle scars in which the four adductors are clearly visible. Ventral surface has four sub-parallel ridges. Seven hollow, conically shaped nodes and at least five pore conulae may be developed.

Hinge lophodont. Median bar in left value is long, straight with a narrow accommodation shelf above it. Locellae simple and open to the domicilium. Muscle-scars consist of a



TEXT-FIG. 25. Size dispersion of *Theriosynoecum ramocupsis* from a single sample taken at the type level, Kilmaluag Formation. Mean increase in length between instar stages is 24%.

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subvertical row of four adductors. Frontal and mandibular scars not observed. Vestibula small. Marginal pore canals not observed.

Remarks. A size dispersion diagram is given in Text-fig. 25. T. ramocuspis differs from all the other Great Estuarine Group species of Theriosynoecum in the development of spinose cardinal angles and in its lack of secondary reticulation. T. fimbriachela sp. nov. does, however, possess similar postero-ventral spines and is considered to be closely related to T. ramocuspis.

Theriosynoecum conopium Wakefield & Athersuch, 1990 Pl. 6, figs 17, 18; Pl. 7, figs 1-10

1990 Theriosynoecum conopium sp. nov. Wakefield & Athersuch, pp. 31-40, pl. 32, figs 1-7; pl. 34. figs 1-8; pl. 36. figs 1-6; pl. 38. figs 1-7.

*Holotype*. OS 13463, male carapace (Wakefield & Athersuch (1990) from the Great Estuarine Group, Inner Hebrides Scotland; pl. 32, figs 1-7). Paratypes: OS 13464-13470 and OS 13478. OS 13467, OS 13469 and OS 13478 from Bed 1, Kilmaluag Formation, locality 11. OS 13468 from bed 7, Duntulm Formation, locality 7. The remainder from top 5cm of Bed 7, Kilmaluag Formation, locality 11.

*Material.* 33 carapaces and nine valves from the type locality and horizon. Several hundred carapaces and valves from the Duntulm and Kilmaluag formations, localities 9 - 12.

Diagnosis. See Wakefield & Athersuch 1990.

Measurements.

OS 13463 (male carapace)	1218-664-545
OS 13464 (female carapace)	1045-618-600
OS 13465 (female carapace)	1082-618-600
OS 13466 (A-1 carapace)	709-418-309
OS 13467 (A-2 right valve)	655-400
OS 13468 (A-1 valves)	909-545
OS 13469 (A-1 right valve)	709-473-185
OS 13470 (female carapace)	1127-673-655
OS 13478 (A-1 right valve)	1200-673

Description. Carapace elongate, bisulcate, anterior and posterior well rounded. Greatest length at mid-height. Greatest height at posterior cardinal angle in adults and at anterior cardinal angle in juveniles. Greatest width at mid-length in juveniles and males but in posterior third of carapace in females. Males and females of similar length (Text-fig. 26). Females with distinctly swollen posterior brood pouch. Dorsal margin slightly convex with a prominent posterior cardinal angle. Ventral margin medianly concave at commissure. Lateral surface strongly reticulate with well developed secondary reticulation. Primary muri often poorly developed or absent in central region of posterior half of carapace. Ventral surface has four sub-parallel ribs. These continue both anteriorly and posteriorly to form a prominent, concentrically parallel and marginally positioned rib pattern. General position of the nodes is that of the genus; up to eight hollow nodes and at least five pore conulae may be developed. Adults only very rarely have nodes. Nodes themselves may be simple cones or castellated. Surface has small (5  $\mu$ m diameter) sieve pores concentrated near sulci.

Hinge lophodont, with strongly developed terminal elements and a median bar with narrow accommodation shelf in left valve. Muscle-scars consist of a subvertical row of four adductors with round frontal and mandibular scars immediately to the anterior. Inner margin and line of concresence almost coincide, vestibule weak. Marginal pore canals not observed.

Remarks. A mean increase in length of 25% between moult stages has been noted in several populations.

The two species closest in morphology to T. conopium are Theriosynoecum anglica (Bate, 1967) and Theriosynoecum ancasterensis (Bate, 1967) from the Bathonian Upper Estuarine Group

at Kings Cliffe, Northamptonshire and Ancaster, Lincolnshire respectively. T. conopium differs from T. anglica in having a more evenly rounded posterior in the female whilst the male is more elongate. T. conopium differs from T. ancasterensis in having a more evenly rounded posterior in the female. The later has a coarser reticulation but lacks the distinctive parallel marginal ridges posteriorly. All three species display variability in the position of pores in the pore net (Wakefield & Athersuch 1990, text-fig. 6).

# Theriosynoecum sagena sp. nov. Pl. 7, figs 11-16

Name. Latin; sagena, a fish net; with reference to the net-like ornament.

Holotype. OS 13866, female left valve, Pl. 7, figs 5, 6, 9, from basal 5cm of Bed 25, Kilmaluag Formation, locality 13. Paratypes: OS 13867, Pl. 7, figs 15, 16; OS 13868, OS 13869 and OS 13870, Pl. 7, fig. 14 from same locality and level.

*Material.* 200 valves from the Kilmaluag Formation, locality 13. Preservation is generally good although the adults are often crushed.

Diagnosis. Elongate ovate species of Theriosynoecum. Male rhomboidal in lateral view, female posteriorly inflated. Dorsal and ventral margins sub-parallel in adults. Ventro-lateral overhang in female. Shell surface punctate in central regions passing into primary and secondary reticulation towards the margins. Disruption of ornament over the central muscle scars. Ventral surface with sub-parallel ribs. Up to five conical nodes and nine pore conulae may be developed.

Measurements.

OS 13866 (female left valve)	964-618-309
OS 13867 (female left valve)	982-582-277
OS 13868 (male left valve)	1000-545-273
OS 13869 (A-1 left valve)	818-509-200
OS 13870 (A-2 right valve)	564-336-164

Description. Juveniles and females elongate ovate, males rhomboidal. Greatest length at mid-height in female and juveniles and in an oblique line running from below mid-height anteriorly to above mid-height posteriorly in male. Greatest height at anterior cardinal angle in juveniles and males and at the posterior cardinal angle in females. Greatest width median for juveniles and in posterior third of valve for adults. Anterior asymmetrically rounded, posterior evenly rounded in female. Male anterior is asymmetrically rounded whilst posterior slopes anteriorly from dorsal to ventral margins. Dorsal margin slightly convex. Carapace tapers slightly to anterior. Ventro-lateral overhang in female not evident in male. Cardinal angles indistinct. Distinct oblique dorso-central sulcus with a reduced second sulcus immediately to the anterior. Lateral surface strongly ornamented with a dislocation of the ornament above the central muscle-scars. Valve centres punctate whilst the primary and secondary reticulation is developed in the marginal regions. Ribs developed on ventral surface. Pore net as for the genus. Up to five hollow, conical nodes and at least nine pore conuli. Adults usually lack nodes though pore conuli are developed.

Hinge lophodont. Median bar in left valve is long and overlain by a narrow accommodation shelf. Muscle-scars consist of a subvertical row of four adductors. These lie immediately below the dorso-central sulcus. Vestibula small. Marginal pore canal openings (15) only noted anteriorly.

Remarks. Males (Text-fig. 27) are much rarer than females. T. sagena differs from Theriosynoecum sp. A. in having finer reticulate ornament and secondary reticulation, fewer marginal pore canals and a less prominent median hinge bar. T. sagena resembles Theriosynoecum difensorum Mandelstam, 1956 from the Barremian, Lower Cretaceous of Tarbagatay, Eastern Transbaikala, Russia in lateral view though the latter does not taper to the anterior. In dorsal view T. difensorum has a more strongly inflated posterior and the compressed anterior marginal zone is broader. The males of Theriosynoecum ilhasensis



TEXT-FIG. 26. a) Size dispersion, b) sexual dimorphism of *Theriosynoecum* conopium from a single sample taken at the type level, Kilmaluag Formation. Modified after Wakefield & Athersuch 1990.



TEXT-FIG. 27. Reconstruction of a male left valve of Theriosynoecum sagena OS 13868.

Krömmelbein & Weber, 1971 from Lower Cretaceous strata recovered from Borehole Ra-1-Ba, Bahia, Brazil are similar in outline to the males of *T. sagena* but are less strongly sulcate and their lateral outline is more rounded posteriorly. The nodes of *Theriosynoecum fittoni* (Mantel, 1844) from the Lower Cretaceous Weald Clay of Punfield Cove, Swanage Bay, Dorset are of a similar conical shape to those of *T. sagena* but their position is different, and in some specimens of *T. fittoni* (see Sylvester-Bradley 1973a, pl. 1:40:218. fig. 2.) the nodes sometimes become castellated. This is a feature which has not been seen in *T. sagena*.

# Theriosynoecum sp. A Pl. 7, figs 17-20

Material. One specimen from top 5cm of Bed 5f, Kildonnan Member, Lealt Shale Formation, locality 1.

Measurements.

OS 13871 (female? left valve)

#### 1072-709-367

Description. Valve ovate in lateral view. Dorsal view appears pear shaped. Evenly rounded anterior and posterior. Greatest length passing through mid-point, greatest height at midlength, greatest width in posterior third of valve. Posterior half of valve inflated. Ventrolateral overhang. Ventral and dorsal margins sub-parallel. Anterior cardinal angle indistinct, posterior cardinal angle rounded and clearly distinct with a prominent flattened area below it. Broad sulcate region lies immediately anterior of mid-length, not visibly sub-divided. Shell surface uniformly reticulate. Prominent node below posterior cardinal angle. Triangular net of pore conulae immediately above mid-height on anterior margin. Crenulate lamella parallel to and immediately inside anterior margin. Marginal pore canal openings visible (using SEM) along this lamella.

Hinge lophodont. Median bar strongly developed, undivided. Muscle-scars not visible. Vestibula small. External openings of marginal pore canals visible; 17 anteriorly and 14 posteriorly.

Remarks. T. sp. A is distinct from Theriosynoecum bathonicum Sylvester-Bradley, 1973b, from the Bathonian Viviparus Marl, Castle Barn Quarry, Sarsden, Oxfordshire, in being more strongly inflated posteriorly. The greatest width in T. bathonicum females is anterior of the posterior cardinal angle but in T. sp. A. (presumed female specimen) it is at the posterior cardinal angle. T. sp. A resembles Theriosynoecum tenuimarginata (Oertli, 1957), from the Bathonian strata of the Vallée de la Creuse, Chateauroux area, Paris Basin, France but is much more inflated posteriorly. The number of anterior marginal pore canals is similar; 15 in T. tenuimarginata and 17 in T. sp. A. However, the crenulate marginal lamella noted in T. sp. A is not visible in T. tenuimarginata. This lamella is visible in T. bathonicum (see Sylvester-Bradley 1973b, pl.1:42:230, figs. 1, 2; pl. 1:42:234, fig. 1).

## Family CYTHERIDEIDAE Sars, 1925

Diagnosis. (After Hartmann & Puri 1974). Carapace ovate, reniform or quadrate. Thick shelled. Carapace smooth or reticulate often with longitudinal ribs and alae. Outer margin smooth or denticulate. Inner lamella of variable width, with or without vestibula. Marginal pores numerous, straight, simple or bifurcating. Normal pores of sieve type. Hinge merodont, adont or lophodont. Four adductor muscle-scars in a vertical row, frontal scar U-, V- or Yshaped.

*Remarks*. Hartmann & Puri (1974) considered the classification of the Cytherideidae to be unclear. They did, however, distinguish the subfamilies, Cytherideinae, Schulerideinae and Cuneocytherinae. The Cuneocytherinae were raised to family status in Athersuch *et al.* (1989, p.119). I do not concur with this.

Subfamily CYTHERIDEINAE Sars, 1925

Diagnosis. As for family.

# Genus MICROPNEUMATOCYTHERE Bate, 1963b

Type species. Micropneumatocythere convexa Bate, 1963b, pp 29-30, pl. 2, figs 12-23; pl. 3, figs 1-15; from the Bajocian (Hyperlioceras discites Zone); Basement beds under the Cave Oolite (Bajocian), Eastfield Quarry, South Cave, North Yorkshire.

Diagnosis. (Modified after Bate 1963b and Bate & Sheppard 1979). Carapace highly biconvex in dorsal view. Ovate in lateral view with short but distinctive posterior caudal process which has a small basal fold; giving a tear-shaped lateral outline. Dorsal margin convex. Ventral margin with small concavity anterior of mid-length, overhung by ventrolateral swelling. Left valve larger than right. Hinge antimerodont. Marginal pore canals few, short, straight and widely spaced. Muscle-scars consist of four adductors with a small rounded frontal scar.

Remarks. Micropneumatocythere was erroneously placed in the Progonocytheridae. On the basis of its antimerodont hinge, its lack of curved marginal pore canals and lack of a U-shaped frontal scar, which precludes its assignment to the Protocytheridea, Micropneumatocythere is reassigned to the Cytherideidae, Cytherideinae. In general morphology Micropneumatocythere resembles other genera from within the Cytherideinae. Bate & Sheppard (1979) stated that the presence of the short posterior caudal process is an essential morphological character of Micropneumatocythere. Micropneumatocythere postrotunda Bate, 1967, lacks a caudal process and is reassigned to Hebatacythere gen. nov.

# Micropneumatocythere falcata Sheppard, 1978 Pl. 8, figs 1-3

1978 Micropneumatocythere falcata sp. nov. Sheppard, pp 97-100.

1979 Micropneumatocythere falcata Sheppard, 1978; Bate & Sheppard, pp 82-3, pl. 1, figs 12-15, 17.

Holotype. OS 9305, female right valve Sheppard 1978, pl. 98, fig. 1). Paratypes: OS 9306-14. From the Bathonian Forest Marble of the Old Cement Works, Kirtlington, Oxfordshire.

Material. Nine valves from the Duntulm Formation, localities 6, 7.

*Diagnosis.* (After Bate & Sheppard 1979). Strongly biconvex in dorsal view. Dorsal outline sickle shaped in female. Anterior broadly rounded, posterior with distinct caudal process at mid-height. Ventral margin medianly concave. Lateral surface micropunctate and with large normal pores. Ventral and ventrolateral surface with six subparallel ribs. Reticulate ornament developed antero- and postero- ventrally.

Measurements.

OS 13796 (juvenile right valve)

455-264-118

Description. Valves tear-shaped in lateral view. Greatest length runs slightly above midheight. Greatest height at mid-length. Anterior margin broadly rounded. Posterior margin with prominent caudal process at mid-height. Posterodorsal slope concave. Dorsal outline sickle shaped in female, less strongly arched in male. Ventral concavity lies directly below anterior cardinal angle. Lateral surface micropunctate. Large number of normal pores on all surfaces. Ventral and ventrolateral surfaces with six subparallel ribs which flow into loose reticulation antero- and posteroventrally.

Hinge antimerodont. Five anterior and at least three posterior terminal teeth in right valve. Median groove subdivided. No vestibula. Inner lamella of moderate width. At least seven short, straight anterior marginal pore canals, posterior canals not seen. Muscle-scars not visible in this material.

Remarks. Sheppard (1978) noted that M. falcata evolved in the late Bathonian from unornamented morphs of M. brendae Sheppard, 1978a from the Bathonian Upper Fullers Earth, Swainswick Borehole, Somerset. This was used to explain why Bate (1978) figured smooth specimens of M. brendae as Micropneumatocythere sp. E which were defined later that year as M. falcata (Sheppard 1978b).

M. falcata is slightly more elongate than Micropneumatocythere quadrata Bate, 1967, from the Bathonian, Upper Estuarine Series of Kings Cliffe, Northamptonshire, and has a larger and

better differentiated caudal process. *Micropneumatocythere tumida* Stephens & Ware, 1980 has a shorter caudal process than *M. falcata* whilst the reticulate ornamentation covers the whole lateral surface and not, as in *M. falcata* only the marginal regions. The tumidity in *M. tumida* is more pronounced than in *M. falcata*, particularly in the male.

Occurrence. This species is also known from the top of the White Limestone and throughout the Bathonian Forest Marble in Oxfordshire, Kent and Dorset (Sheppard 1978, Ware & Whatley, 1980 and Jacovides [1982]).

Micropneumatocythere foveolata sp. nov. Pl. 8, figs 11-13

Name. Latin, fovea, pitted; with reference to the ornament.

Holotype. OS 13797, female carapace, Pl. 8, fig. 11, from basal 5cm of Bed 4, Kilmaluag Formation, locality 11. Paratypes: OS 13798, OS 13799 and OS 13800, Pl. 8, fig. 12 from same locality and level.

Material. 16 carapaces and 10 valves from type locality and horizon.

Diagnosis. Ovate species of Micropneumatocythere. Slight taper to posterior. Males more



TEXT-FIG. 28. a) Size dispersion, b) sexual dimorphism of Micropneumatocythere foveolata from a single sample taken at the type level, Kilmaluag Formation.

elongate than females. Anterior margin evenly rounded. Posterior margin smaller but with a distinct caudal process and concave posterodorsal slope. Dorsal margin arched. Ventrolateral overhang small. Lateral surface strongly reticulate. Small sieve pores evenly scattered over lateral surfaces. Ventral surface with four subparallel ribs. *Measurements*.

OS 13797 (female carapace)	618-364-309
OS 13798 (A-1 carapace)	509-291-200
OS 13799 (male carapace)	673-327-291
OS 13800 (male left valve)	673-327-127

Description. Carapace ovate and slightly posteriorly tapered. Strongly biconvex in dorsal view. Males more elongate than females (Text-fig. 28). Greatest length slightly below midheight. Greatest height slightly anterior of mid-length. Greatest width at mid-length. Anterior margin evenly rounded. Posterior margin smaller but with prominent caudal process at mid-height and a concave posterodorsal slope. Dorsal margin arched in left valve almost straight in right valve. Posterior cardinal angle visible anterior not. Ventrolateral overhang small. Lateral surface usually strongly reticulate. Two small swellings, one lies immediately below position of anterior cardinal angle and the other dorsally at mid-length. Small (5-10  $\mu$ m diameter) sieve pores evenly scattered over lateral surfaces. Ventral surface with four subparallel ribs. Left valve overlaps right around the anterior, posterior and ventral margins.

Hinge antimerodont. Avestibulate. Inner lamella narrow. Material does not allow the observation of marginal pore canals. Muscle-scars consist of a vertical row of four ovate adductors, a round frontal scar and a round mandibular scar, level with top and basal adductors respectively.

Remarks. M. foveolata differs from Micropneumatocythere convexa Bate, 1963b from the Bajocian Basement Beds, Eastfield Quarry, South Cave, North Yorkshire, in being more elongate (particularly the males) and in having a less steep and less strongly arched posteroventral slope. M. foveolata is clearly distinguished from M. falcata Sheppard, 1978 by its well developed reticulate ornament. M. brendae Sheppard, 1978 has a larger caudal process, and Micropneumatocythere subconcentrica (Jones, 1884), from Bathonian strata recovered from the Richmond Borehole, Surrey, has a more weakly developed reticulate ornament and a larger caudal process.

#### Genus HEBATACYTHERE gen. nov.

Name. Latin; hebata, blunted and cythere; with reference to the blunt posterior.

Type species. Hebatacythere hypha sp. nov. from the Kilmaluag Formation, Great Estuarine Group, Isle of Muck, locality 13.

Species. H. hypha, Hebatacythere postrotunda (Bate, 1967).

*Diagnosis.* Valves ovate. Males more elongate than females. Markedly biconvex in dorsal view. Anterior and posterior well rounded. Lateral surfaces reticulate with large sieve pores. Antimerodont hinge. Inner lamella of moderate width. Marginal pore canals short, straight and few in number.

Remarks. This genus was recognized by both Sheppard [1981a] and Dépêche [1984] as being distinct from Pneumatocythere Bate, 1963a and Micropneumatocythere Bate, 1963b.

Hebatacythere resembles Pneumatocythere Bate, 1963a, but lacks the posterior caudal process. Micropneumatocythere Bate, 1963b, also has a caudal process and is smaller. Klieana Martin, 1940, is easily differentiated from Hebatacythere by the presence of ventrolateral alar projections and by its triangular shape when viewed from the anterior.

M. postrotunda Bate, 1967, lacks the typically well developed caudal process of Micropneumatocythere and is therefore reassigned to Hebatacythere.

a)



TEXT-FIG. 29 a) Size dispersion, b) sexual dimorphism of *Hebatacythere* hypha from a single sample taken at the type level, Kilmaluag Formation.

Hebatacythere hypha sp. nov. Pl. 8, figs 4-10

Name. Latin; hypha, a web; with reference to the ornament.

Holotype. OS 13803, female left valve, Pl. 8, figs 4-7, from basal 5cm of Bed 25, Kilmaluag Formation, locality 13. Paratypes: OS 13801, OS 13802, Pl. 8, fig. 9; OS 13804, Pl. 8, fig. 9; and OS 13805, Pl. 8, fig. 10, from same locality and level.

Material. 45 valves from the type locality and horizon.

Diagnosis. Valves ovate. Males more elongate than females. Anterior obliquely rounded with narrow compressed marginal zone. Posterior smaller in female than in male. Dorsal margin almost straight. Median ventral concavity ventrolaterally overhung. Lateral surface with first and second order reticulation. Sieve pores are small round and/or ovate. Ventral surface with four subparallel ribs.

Measurements.

OS 13801 (male right valve)	818-400-173
OS 13802 (male left valve)	818-420-245
OS 13803 (female left valve)	691-400-200
OS 13804 (male right valve)	800-400-218
OS 13805 (female left valve)	736-464-236

#### KLIEANA

Description. Valves ovate and tapering slightly to posterior, with greatest length slightly below mid-height in both dimorphs. Males more elongate than females (Text-fig. 29). Greatest height at anterior cardinal angle in females, posterior cardinal angle in males. Greatest width median. In dorsal view appears strongly convex in shape with a small anterior compressed marginal zone. Anterior obliquely rounded and with narrow compressed marginal zone. Posterior margin subrounded, smaller in female than in male. Dorsal margin almost straight with rounded posterior cardinal angle. Median ventral concavity overhung by ventrolateral swelling. Lateral surface with first and second order reticulation. Small, (10  $\mu$ m diameter) round, and larger, (20  $\mu$ m long) ovate eccentric sieve pores usually found in groups of 2-3. Ventral surface with four subparallel ribs.

Antimerodont hingeline short. Six anterior and six posterior terminal teeth in right valve. Locellate median groove narrow. Complimentary structures in left valve with broad accommodation shelf above median bar. Avestibulate. Inner lamella of moderate width. At least four anterior marginal pore canals observed. Muscle-scars not visible in present material.

Remarks. H. hypha is larger than Hebatacythere postrotunda (Bate, 1967), from the Bathonian Upper Estuarine Group of Kings Cliffe, Northamptonshire, and has more strongly developed ornament.

#### Genus KLIEANA Martin, 1940

Type species. Klieana alata Martin, 1940, pp 322, 3, pl. 5, figs 64-73; pl. 11, figs 158-161; from the "Wealden" of NW Germany.

Diagnosis. (After Martin 1940). Carapace triangular in anterior view. Lateral view subtrapezoid. Male more elongate than female. Ventrolateral alar projections medianly positioned. Anterior and posterior margins rounded with no compressed marginal zones. Dorsal margin convex in left valve almost straight in right valve. Left valve larger than right. Lateral surfaces reticulate. Ventral surface with subparallel ribs. Hinge antimerodont. Narrow inner lamella. Marginal pore canals few and straight.

*Remarks.* The original line drawings of Martin (1940) show differentiation of the teeth in the median bar and as such the dentition may be described as weakly entomodont. A study of specimens of *Klieana levis* Oertli, 1957, originally found in Bathonian rocks near Poitiers, France, obtained by Bate (1967) from the Bathonian Upper Estuarine Group of Leicestershire, revealed well developed eccentric sieve pores and a thickened anterior portion of the lower lip in the right valve suggesting an entomodont morphology (see specimens Io 2520-2). A study of the type material (R.C. Whatley pers. comm. 1993) has confirmed the antimerodont hinge morphology.

As a result of this confusion surrounding the hinge morphology, *Klieana* has often been placed within the Progonocytheridae, Progonocytherinae. Due to the lack of an entomodont hinge *Klieana* is here assigned to the Cytherideidae, Cytherideinae.

#### Klieana williamsi sp. nov. Pl. 8, figs 14-23

Name. After Dr. M. Williams in recognition of his work on Lower Palaeozoic Ostracoda.

*Holotype*. OS 13809, male right valve, Pl. 8, fig. 16, from 20 cm below top of Bed 7, Kilmaluag Formation, locality 11. Paratypes: OS 13810, Pl. 8, figs 18, 19, 22, 23; OS 13811 and OS 13812, from same locality and level. OS 13813, Pl. 8, fig. 21 from basal 10cm of Bed 7, Kilmaluag Formation, locality 11. OS 13814 from Bed 6, Kilmaluag Formation, locality 11. OS 13815, Pl. 8, fig. 20, from 30cm below top of Bed 7, Kilmaluag Formation, locality 11.

Material. 39 carapaces and 59 valves from the Kilmaluag Formation, localities 10, 11.

Diagnosis. Anterior view triangular. Subtrapezoid in lateral view. Males more elongate than females. Anterior margin evenly rounded, posterior more ovate. Dorsal margin straight in right valve, convex in left. Ventral margin with strong median concavity overhung by ventrolateral swelling. Oblique sulcus posterior of anterior cardinal angle. Lateral surface with first and second order reticulation. Sieve pores evenly scattered on surface. Ventral surface with 4-5 subparallel ribs. 5-6 anterior and 2-3 posterior marginal pore canals.

Measurements.

OS 13809 (male right valve)	636-290-164
OS 13810 (female left valve)	636-373-218
OS 13811 (female right valve)	582-309-173
OS 13812 (male right valve)	700-318-200
OS 13813 (female right valve)	655-400-182
OS 13814 (male left valve)	709-345-209
OS 13815 (A-1 male? right valve)	509-245-209

Description. Carapace triangular in anterior view, elongate subtrapezoid in lateral view with males more elongate than females (Text-fig. 30). Greatest length runs obliquely down from posterior in right valve, horizontally and slightly below mid-height in left valve. Greatest height at mid-length. Greatest width at mid-length when viewed dorsally and at ventral margin when viewed anteriorly. Dorsal view strongly biconvex. Anterior margin evenly rounded. Posterior margin smaller in size and more ovate. Dorsal margin convex in male, more so in female. Slight ovate swelling at the anterior cardinal angle with an oblique



TEXT-FIG. 30. a) Size dispersion, b) sexual dimorphism of *Klieana* williamsi from a single sample taken at the type level, Kilmalaug Formation. Mean increase in length between instar stages is 30%.

### ASCIOCYTHERE

sulcus immediately to the posterior. Ventral margin medianly concave and overhung by ventrolateral swelling. Left valve larger than right with greatest overlap along dorsal margin. Lateral surface with first and second order reticulation. This often appears as margin parallel concentric ribs. Small (5-10  $\mu$ m diameter) sieve pores on lateral surfaces. Ventral surface with 4-5 subparallel ribs, of which the 2-3 ribs closest to the ventral margin may anastomose.

Antimerodont hinge. Six anterior and six posterior elongate, occasionally dorsally bifid terminal teeth in right valve. Median groove with weakly developed locellae. Complementary structures in the left valve. Median bar weakly loculate, anterior three teeth slightly enlarged. Avestibulate. Inner lamella narrow. Short straight marginal pore canals number 5-6 anteriorly, 2-3 posteriorly. Muscle-scars not seen.

*Remarks.* The plots of valve length against valve height and valve length against length : height ratio clearly show male, female and three juvenile stages (Text-fig. 30). However, five valves from the A-1 juvenile stage have similar length:height ratios to the males. As with *Glyptocythere sutherlandi* sp. nov., precocious sexual dimorphism may be suspected, though the graphs are, in themselves, inconclusive. When the presumed A-1 males are compared with the fully grown males no difference in shape is observed.

The females of K. williamsi resemble the females of Klieana levis Oertli, 1957, from Bathonian strata near Poitiers, France. They are differentiated by the more strongly developed reticulate ornament and in being slightly more elongate. The males of the two species show marked differences. The posterodorsal slope in K. williamsi is longer and less steeply inclined than in K. levis. The post anterior cardinal angle sulcus is more strongly developed in the K. levis. K. williamsi can be differentiated from Klieana thoracina Anderson, 1971 from Lower Cretaceous rocks in the Montfield No. 3 Borehole, Sussex, by its less projected posterior and its long straight dorsal margin. Klieana? rhaetica Anderson, 1964, from Rheatic rocks recovered from Borehole No. 7 Piere, Saxony, Germany, has a more elongate ventrolateral overhang and when viewed from the anterior is much more inflated than K. williamsi and is smooth rather than reticulate.

### Genus ASCIOCYTHERE Swain, 1952

Type species. By original designation Bythocypris rotundus Vanderpol, 1928, from Lower Cretaceous deposits near Weatherford, Texas, USA.

*Diagnosis*. (After Swain 1952) Carapace subovate. Males more elongate than females. Smooth to ornamented and with normal pores. Vestibulae small when present. Antimerodont. Marginal pore canals numerous.

Remarks. Asciocythere is similar to Mesocytheridea Bate, 1965, which has a strongly developed triangular component to its reticulate ornament that excludes the cardinal angles. Such ornament is lacking in Asciocythere. Asciocythere is distinguished from Praeschuleridea Bate, 1963a, by its antimerodont rather than palaeohemimerodont hinge. Externally Praeschuleridea and Asciocythere are similar in shape though the posterior margin in Praeschuleridea is more pointed when viewed dorsally.

### Asciocythere pactilis sp. nov. Pl. 9, figs 1-5

Name. Latin; pactilis, plaited together or woven; with reference to the appearance of the primary reticulum.

Holotype. OS 13880, male carapace, Pl. 9, figs 1-3, from 60cm above base of Bed 5, Lonfearn Member, Lealt Shale Formation, locality 4. Paratypes: OS 13881, Pl. 9, fig. 5; and OS 13882, Pl. 9, fig. 4, from same locality and level.

Material. 33 carapaces and 18 valves from the type locality.

Diagnosis. Carapace subovate. Males more elongate than females. Anterior view subrounded. Anterior asymmetrically rounded posterior more ovate. Dorsal margin slightly arched. Ventral margin with slight median swelling. Lateral surface with first and second order





TEXT-FIG. 31 a) Size dispersion, b) sexual dimorphism of Asciocythere pactilis from a single sample taken at the type level, Lonfearn Member, Lealt Shale Formation.

reticulation. Ventral surface with 5-6 subparallel ribs. Normal pores evenly spaced over entire surface. Inner lamella narrow. At least 10 anterior and five posterior marginal pore canals. *Measurements*.

OS 13880 (male carapace)	636-336-336
OS 13881 (female carapace)	582-336-338
OS 13882 (female right valve)	527-327-118

Description. Dorsal view appears almond shaped but with slight median swellings. Subround when viewed from anterior. Greatest length through mid-height. Greatest height at mid-length. Males more elongate than females (Text-fig. 31). Greatest width median. Anterior margin asymmetrically rounded, posterior more ovate. Dorsal margin slightly arched and sinuous. Cardinal angles more distinct in left valve. Ventral margin slightly convex, but is not overhung by a ventrolateral swelling. Slight median concavity. Lateral surface with first and second order reticulation. Numerous small (5  $\mu$ m diameter) normal pores evenly placed over entire surface. Ventral surface with 5-6 semi-confluent subparallel ribs. Left valve overlaps right valve around all margins.

Hinge antimerodont; 6-7 anterior and six posterior, elongate, dorsally bifid, terminal teeth in right valve. Median groove finely loculate. Opposing structures present in left valve. Avestibulate. Inner lamella narrow. At least 10 anterior and five posterior marginal pore canal openings observed externally. Muscle-scars consist of a cresentric row of four adductors, frontal scar opposite top adductor and mandibular scar below level of basal adductor.

Remarks. A. pactilis differs from Praeschuleridea quadrata Bate, 1967 from the Bathonian Upper Estuarine Series at Kings Cliffe, Northamptonshire, in having a well developed reticulate ornament, an antimerodont rather than palaeohemimerodont hinge and in being more ovate.

### Subfamily SCHULERIDEINAE Mandelstam, 1959

Diagnosis. (After Hartmann & Puri 1974 and Neale 1982). Cytherideidae with left valve larger than right. Males more elongate than females. Well-developed accommodation groove above the merodont hinge. Inner lamella of moderate width. Large number of marginal pore canals arranged in a fan-like fashion. Muscle-scars consist of a vertical row of four adductors and a large round frontal scar.

*Remarks.* Hartmann & Puri (1974, p. 31) decided to retain the Schulerideinae and Cuneocytherinae, which are only known from the fossil record, separate from the recent Cytherideinae "for merely an organization purpose". See Neale (1982) for a comprehensive review on various aspects of the subfamily.

### Genus PRAESCHULERIDEA Bate, 1963a

Type species. By original designation Cytheridea subtrigona Jones & Sherborn, 1888, p 265, pl. 2, figs 9a-c. Designated by Bate, 1963a, pp 207-9, pl. 12, figs 12-16; pl. 13, figs 1-9; text-fig. 15; from the Bajocian of Lincolnshire.

Diagnosis. (After Bate 1963a). Carapace ovate in lateral outline. Ornamented to smooth. Greatest length at mid-height. Males more elongate than females. Hinge palaeohemimerodont. Radial pore canals arranged in a fan, which curves slightly outwards away from a line drawn through the mid-point; 12-16 anteriorly, 4-6 posteriorly. Muscle-scars; a cresentric row of four adductors a centrally situated frontal scar, often reniform and with a secondary scar in front, but occasionally rounded. Mandibular scar, when seen, in front of and below adductor scars.

*Remarks. Praeschuleridea* differs from *Schuleridea* Swartz & Swain, 1946, in being more ovate in lateral outline, in the number of marginal pore canals (about 30 anteriorly and 10 posteriorly in *Schuleridea*) and in the hinge structure (*Schuleridea* is palaeomerodont).

## Praeschuleridea? sp. A Pl. 9, figs 6-9

Material. One valve from 49cm above base of Bed 1, Lonfearn Member, Lealt Shale Formation, locality 4.

Measurements.

 $\left( \right)$ 

OS 13883 (juvenile right valve) 472-327-127

Description. Valve subovate with triangular dorsum. Greatest length slightly below midheight. Greatest height at mid-length. Dorsal view almond shaped. Greatest width slightly anterior of mid-length. Anterior and posterior margins evenly rounded. Slight anterior compressed marginal zone. Ventral margin almost straight. Lateral surface punctate.

No internal details visible on this specimen.

*Remarks. P*? sp. A is tentatively placed in *Praeschuleridea* as only a single, presumably juvenile, specimen was available for study. *P*? sp. A differs from *P. quadrata* Bate, 1967 from the Bathonian Upper Estuarine Series at Kings Cliffe, Northamptonshire, in being more triangular in lateral outline.

## Family EUCYTHERIDAE Puri, 1954

Diagnosis. (After Athersuch et al. 1989 and Hartmann & Puri 1974). Carapace ovate, reniform or quadrate, anterior broader than posterior. Thick-shelled, punctate or smooth with sieve type normal pores. Lophodont or antimerodont hinge but some carapaces are

almost toothless. Inner lamella broad. Vestibula developed. Few marginal pore canals. Muscle-scars consist of an oblique row of 4 or more adductor scars with a V-shaped frontal scar.

*Remarks*. The Eucytheridae were originally designated as a subfamily of the Cytherideidae. They were raised to family status and separated from the Cytherideidae by Hartmann & Puri in 1974 (p.30).

#### Genus AALENIELLA Plumhoff, 1963

Type species. Aaleniella compressa Plumhoff, 1963, pp 37-9, pl. 7, figs 107-114; from the Aalenian of NW Germany.

Diagnosis. (Modified after Plumhoff 1963). Carapace small. Laterally elongate and posteriorly tapered. Dorsal margin straight. Ventral margin concave. Dorsal view elongate, elliptical, tapers posteriorly. Unornamented. Right valve slightly larger than left which it overlaps dorsally. Ventral margins coincident. Vestibula small. Marginal pore canals simple, straight and widely spaced. Hinge lophodont. Muscle-scars consist of a vertical row of four small adductors, a frontal scar and two mandibular scars.

*Remarks. Aaleniella* was originally described from the Aalenian and has subsequently been recorded from the Toarcian (Bate & Coleman 1975) and the Kimmeridgian (Christensen & Kilenyi 1970). This is the first record from the Bathonian.

#### Aaleniella cuneata sp. nov. Pl. 9, figs 10-16

Name. Latin; cuneatus, wedge shaped; with reference to the lateral outline.

Holotype. OS 13884, adult carapace, Pl. 9, figs 10, 11, 13, from 8cm above base of Bed 1, Lonfearn Member, Lealt Shale Formation, locality 4. Paratypes: OS 13890 from same locality and level. OS 13885, Pl. 9, fig. 16; OS 13886, Pl. 9, figs 14, 15; OS 13887, Pl. 9, fig. 12; OS 13888 and OS 13889 from basal 5cm of Bed 1, Lonfearn Member, Lealt Shale Formation, locality 2.

Material. 31 valves and four carapaces from the Lonfearn Member, Lealt Shale Formation, localities 2, 4.

*Diagnosis.* Posteriorly tapering species of *Aaleniella* in both lateral and dorsal views. Both anterior and posterior asymmetrically rounded. Carapace smooth. Right valve overlaps left valve dorsally between cardinal angles. Hinge lophodont. At least five anterior and three posterior marginal pore canals.

Measurements.

OS 13884 (carapace)	482-273-182
OS 13885 (right valve)	491-273-155
OS 13886 (right valve)	436-245-109
OS 13887 (left valve)	455-264-127
OS 13888 (right valve)	473-273- 91
OS 13889 (right valve)	473-273-127
OS 13890 (carapace)	473-255-200

Description. Elongate carapace which tapers to the posterior in both lateral and dorsal views. Greatest length at mid-height. Greatest height at anterior cardinal angle. Greatest width is anterior of mid-length. Dorsal view biconvex in shape. Anterior and posterior asymmetrically rounded. Dorsal margin straight, though occasionally slightly arched. Cardinal angles weakly developed. Ventral margin concave. Smooth. Right valve overlaps left valve between the cardinal angles. Ventral margins coincident.

Hinge lophodont. Terminal teeth in the right valve are small, peg-like extensions of the inner lamella. Median accommodation groove shallow. Complementary weakly developed median bar in left valve. Vestibula both poorly developed and/or preserved in the present

#### PARACYPRIS

material. Marginal pore canals straight and widely spaced. At least five anterior and three posterior straight marginal pore canals. Muscle-scars consist of a subvertical row of four adductors a reniform frontal scar with two oval mandibular scars.

Remarks. A. cuneata differs from the type species A. compressa Plumhoff, 1963 in being slightly more inflated and less reduced posteriorly in dorsal view, and in being more elongate.

#### Superfamily CYPRIDACEA Baird, 1845

Diagnosis. (After Swain in Moore & Pitrat, 1961). Carapace usually thin-shelled, smooth to weakly ornamented, rarely noded or sulcate. Variable in size and shape. Overlap variable. Eye nodes usually absent. Normal pores simple. Hinge simple, adont or lophodont. Inner lamella always well developed with deep vestibula. Marginal pore canals usually numerous, straight and simple, rarely branching. Muscle-scars variably arranged in a cluster, rarely in vertical rows.

Remarks. This superfamily is today dominated by non-marine forms. Some of its genera such as Pontocypris Sars, 1866, Propontocypris Sylvester-Bradley, 1947, Macrocypris Brady, 1867 and Paracypris Sars, 1866 are marine. These vary from the characteristic appendage morphology of the other cypridaceans (Van Morkhoven 1962; Athersuch et al. 1989, text-fig. 11).

#### Family PARACYPRIDIDAE Sars, 1923

Diagnosis. (After Hartmann & Puri 1974 and Athersuch et al. 1989). Elongate, laterally compressed carapace. Length more than twice the height. Greatest height in front of mid-length. Strongly calcified, surface smooth or finely ornamented. Few normal pores. Left valve larger than right. Marginal pore canals usually long, branched and numerous. Vestibula well developed.

*Remarks.* The Paracyprididae are distinguished from the Candonindae by their much broader fused zone. The muscle-scars of these two subfamilies are identical. In the past, authors e.g. Bate 1963a, 1963b, 1965, 1967, 1972 have used the family Paracyprididae Sars 1923. This was reduced to subfamily level by Hartmann & Puri (1974) and placed in the family Candonidae. Athersuch *et al.* (1989) comment that the Paracyripdidae have a close affinity with the non-marine Candonidae and Cyclocypridinae than any other marine Cyprid group. They included it in the Candonidae mainly on the basis of the similarities in musclescar patterns. This palacement is considered to be incorrect as the only morphological similarity is the muscle-scars. Therefore the Paracyprididae are retained as a distinct family.

#### Genus PARACYPRIS Sars, 1866

Type species. Paracypris polita Sars, 1866, p. 12; from the Recent of Langesundensfjord and Flekkefjord, Norway.

*Diagnosis.* (After Athersuch *et al.* 1989). Elongate carapace, moderately compressed, trigonal. Well rounded anteriorly, tapering strongly to posterior. Dorsal margin arched, ventral margin concave. Greatest height and width coincident and well in front of mid-length. Surface smooth with few normal pores. Anterior and posterior vestibula relatively large.

*Remarks. Pontonella* Mandelstam, 1956, is similar to *Paracypris* in lateral outline and in muscle-scar arrangement but differs in its lack of branching marginal pore canals. Van Morkhoven (1962) commented that all fossil species of *Paracypris* were probably not congeneric but that they should be conveniently left in *Paracypris* This would be due to the difficulty in subdividing the genus using subtle variation in outline.

# Paracypris? rasilis sp. nov. Pl. 9, figs 17-19

Name. Latin; rasilis, smoothed; with reference to the lack of ornament.

Holotype. OS 13891, adult right valve, Pl. 9, figs 17, 18, from 5cm above base of Bed 4, Kilmaluag Formation, locality 11. Paratype: OS 13892, Pl. 9, fig. 19, from top 5cm of Bed 20, Duntulm Formation, locality 7.

Material. 34 carapaces and 7 valves from the Duntulm Formation, locality 7 and the Kilmaluag Formation, locality 11.

*Diagnosis*. Small to medium sized species of *Paracypris*? with a subreniform carapace. Anterior broadly rounded, posterior short and tapered. Dorsal margin convex, ventral margin concave. Smooth. Left valve overlaps right valve ventromedianly and along the antero- and posterodorsal slopes. Well developed vestibulae.

Measurements.

OS 13891 (right valve)

OS 13892 (carapace)

545-273-109 491-255-182

Description. Carapace subreniform in lateral outline. Greatest length below mid-height. Greatest height and width at anterior cardinal angle. Anterior margin broadly rounded whilst the posterior is short and tapered. Posterodorsal slope steep. The anterodorsal slope is subparallel with the anterior half of the ventral margin. Dorsal margin slightly convex. Anterior cardinal angle visible, posterior cardinal angle less so. Ventral margin medianly concave. Smooth. Left valve larger than right valve which it overlaps ventromedianly and along the antero- and posterodorsal slopes.

Adont hinge consists of a thickened dorsal marginal lip in the right valve which fits into a groove in the left valve. Well developed vestibula. The calcite overgrowths on most valves obscured any marginal pore canals. The muscle-scars were poorly preserved such that only a subvertical row of three adductor scars was visible.

*Remarks.* A size dispersion diagram is given in Text-fig. 32. The poor preservation of the species and the lack of visible branching marginal pore canals results in the questionable assignment to *Paracypris.* However, all the other morphological features are comparable with *Paracypris.* 

*P? rasilis* is similar in outline and shape to *Paracypris bajociana* Bate, 1963a from the Bajocian Kirton Shale, Kirton Cement Quarry, Kirton Lindsey, Lincolnshire but differs in having a much steeper posterodorsal slope. *Paracypris stripta* Ljubimova, 1956b from the Kimmeridge of Izium, Kharkov Region, Ukraine, is slightly shorter and its anterodorsal and anterior half of the ventral margin are not subparallel.

In the present study *P*? rasilis is often found in association with *Progonocythere levigata* Bate, 1967, although only in very small numbers. The only reasonable population is from Bed 20 of the Duntulm Formation, locality 7. This bed is believed to have been formed in a perilittoral freshwater algal marsh facies (Andrews 1986 and Andrews & Walton 1989) onto which the population of ostracods was washed during a storm event. The general lack of A-1 instars (Text-fig. 32) and the presence of only mature carapaces confirm this assumption.

# Paracypris? sp. A Pl. 10, figs 1, 2

*Material.* 20 whole and damaged valves. Figured specimens from 5cm above base of Bed 8b, Lonfearn Member, Lealt Shale Formation, locality 2, remaining specimens from the Lonfearn Member, Lealt Shale Formation, localities 1, 2, 4.

Measurements.

OS 13893 (right valve)	491-255-127
OS 13894 (right valve)	

Description. Subreniform valves with strong dorsal arching. Greatest length below midheight. Greatest height and greatest width at anterior cardinal angle as is greatest width. Tapers posteriorly. Anterior margin rounded. Posterior smaller in size and rounded. Dorsal margin arched, ventral margin concave. Smooth.

Adont hinge consists of a slight ridge in right valve. Left valve with a complementary groove. Well developed vestibula. No marginal pore canals visible. Muscle-scars poorly preserved; consist of an oblique row of three scars with a fourth scar to the posterior (Text-fig. 33).



TEXT-FIG. 32. Size dispersion of *Paracypris? rasilis* from a single sample taken at the type level, Kilmalaug Formation.

*Remarks.* Poor preservation prevents observation of marginal pore canals; thus the species is tentatively assigned to *Paracypris. P*? sp. A is more strongly arched dorsally than *Paracypris*? sp. B. *Paracypris proceras* Blaszyk, 1967 from the Bathonian of the Jaworznik Borehole Czestochowa district, Poland is more acuminate posteriorly and has a more gently inclined posterodorsal slope.

# Paracypris? sp. B Pl. 10, figs 3-7

Material. Five valves from Division F, Valtos Sandstone Formation, locality 6. Measurements.

OS 13895 (right valve) OS 13896 (right valve)

600-291-127
509-263-100

Description. A subrenifirm species of Paracypris? in which the anterior and posterior appear to be almost mirror images. The posterior is slightly more evenly rounded than the anterior. Greatest length slightly below mid-height. Greatest height and width anterior of mid-length. Dorsal margin strongly arched. Ventral margin with slight concavity. Smooth.

Adont hinge poorly developed. Dorsal margin of right valve fits in a groove on the left valve. Vestibula, where preserved, are well developed. Muscle-scars and marginal pore canals not visible.

*Remarks.* The assignment to *Paracypris* is tentative due to the lack of preserved internal features. *P*? sp. B differs from *Paracypris terraefullonicae* (Jones & Sherborn, 1888) from the Bathonian Blue Fullers Earth Clay, Midford, Somerset in being less posteriorly acuminate.



TEXT-FIG. 33. Central muscle-scars from the right valve of *Paracypris*? sp. A, OS 13894.

# Superfamily DARWINULACEA Brady & Norman, 1889

Diagnosis. (After Moore & Pitrat 1961, Hartmann & Puri 1974). Carapace elongate, ovate, subcylindrical and tapering anteriorly. Unornamented. Left valve larger than the right valve but can be reversed. Hinge adont or lophodont. Muscle-scar radially arranged forming a rosette.

Remarks. The superfamily Darwinulacea is defined by the unique rosette type muscle-scar pattern. Van Morkhoven (1962) comments that based upon soft part morphology, Darwinula shows closer affinities to the Cypridacea than any other superfamily. Swain (1961, p. Q253) included only the Darwinulidae within the Darwinulacea. The superfamily has been expanded considerably in recent years to include the Darwinulidae, Suchonellidae Mischina, 1972, Darwinuloididae Molstovkeya, 1979, Panxianidae Wang, 1980, and the Microdarwinulidae Kashevarova & Neustrueva, 1982, (see Sohn 1987 and references therein). The Darwinulidae and the Microdarwinulidae both have Recent and fossil species, while the other families are only known as fossils.

Family DARWINULIDEA Brady & Norman, 1889 Diagnosis. As for the superfamily. Remarks. As for the superfamily.

### Genus DARWINULA Brady & Robertson, 1885

(Synonyms: Polycheles Brady & Robertson, 1870 [non Polycheles Heller, 1862]; Darwinella Brady & Robertson 1872 [non Darwinella Müller, 1865])

Type species. By original designation; Polycheles stevensoni Brady & Robertson, 1870, p 25, pl. 7, figs 1-7; pl. 10, figs 4-14; from the Recent of NW Europe.

Diagnosis. (After Hartmann & Puri 1974). Carapace clongate, subcylindrical. Anterior and posterior rounded. Usually tapers anteriorly. Unornamented externally but with small rounded pimples internally. Sexual dimorphism not evident. Adont hinge.

*Remarks. Darwinula* can be distinguished from *Microdarwinula* Danielopol, 1968, by its adont rather than lophodont hinge. The adductor muscle-scars are situated anterior of the midlength rather than centrally as in *Microdarwinula* which also has a calcified inner lamella and radial pore canals which are not developed in *Darwinula*.

Differentiation between species of *Darwinula* is notoriously difficult, especially in fossil forms, because of the lack of distinctive morphological features in the shell. Valve outline (Text-fig. 34) and the architecture of the muscle-scar varies within fossil groups.

The muscle-scars of *Darwinula* vary between specimens and even between right and left valves on the same specimen (Triebel 1941; Wagner 1957; Pinto & Kotzian 1961; Sohn 1987). These authors felt that the muscle-scar pattern was only of importance at superfamily levels and of no use for differentiating species. It now appears that the variation in muscle-scar patterns can aid the identification of species. The muscle-scar rosette appears to enlarge during ontogeny (see *Darwinula cicatricosa* sp. nov., Text-fig. 35). This may be achieved by simple enlargement of each muscle scar within the rosette or by subdivision of individual scars such that the area covered by that "composite scar" is greater than the undivided scar (see *Darwinula incurva* Bate, 1967, and *D. cicatricosa* sp. nov. Text-fig. 44).

The internal surfaces of the valves of all the *Darwinula* species studied here are ornamented with small rounded pimples. This is probably analogous to the relationship between epidermal cells and reticulation noted by Okada (1981, 1982).

# Darwinula pulmo sp. nov. Pl. 10, figs 8-10

Name. Latin; pulmo, a lung; with reference to the lateral outline.

Holotype. OS 13897, adult left valve, Pl. 10, fig. 8, from Bed 3h, Kildonnan Member, Lealt Shale Formation, locality 1. Paratype: OS 13898, Pl. 10, figs 9, 10; OS 13899 and OS 13900



TEXT-FIG. 34. Comparison of the outlines and the position of the adductor muscle-scar rosette where known (shaded) of the Darwinula species from the Great Estuarine Group (not to scale). a) Darwinula pulmo, b) Darwinula phaselus, c) Darwinula protensa, d) Darwinula incurva, e) Darwinula cicatricosa, f) Darwinula pollex, g) Darwinula sp. A.

from top 3cm of Bed 6d, Kildonnan Member, Lealt Shale Formation, locality 1. OS 13901 is from 1m above base of Bed 3g Kildonnan Member, Lealt Shale Formation, locality 1.

Material. Specimens studied from the Kildonnan Member, Lealt Shale Formation, localities 1, 4, 5. Preservation often fragmentary or in the form of moulds.

Diagnosis. Elongate subcylindrical carapace, tapers anteriorly. Posterior broadly and asymmetrically rounded, anterior appears ovate. Dorsal margin convex. Ventral margin almost straight. Left valve larger than right valve. Adont hinge. Muscle-scars consist of a subcircular rosette of 11 scars.

Measurements.

OS 13897 (adult left valve)	1073-509-200
OS 13898 (juvenile carapace)	673-282-273
OS 13899 (adult left valve)	1091-464-252
OS 13900 (int. mould left valve)	1109-491-234
OS 13901 (int. mould left valve)	fragment

*Remarks.* The muscle-scars of *Darwinula pulmo* are variable (Text-fig. 36). However, as the numbering of the individual scars within each rosette suggests, this variation is based on an initial pattern which holds sway throughout, e.g. scar 10 is of a similar shape in each rosette. The relative positions of each individual scar to the other scars is also constant, see scar one in relationship to scars 10 and 11.

D. pulmo differs from D. incurva Bate, 1967 from the Bathonian Upper Estuarine Series of Kings Cliffe, Northamptonshire and Ancaster, Lincolnshire D. cicatricosa sp. nov. and



TEXT-FIG. 35. Diameter of the adductor muscle-scar rosette of *Darwinula cicatricosa* showing the diameters of the scars from the right and left valves of the same specimen (five specimens each of adults and A-1 instars).

Darwinula pollex sp. nov. in its muscle-scars and its lack of a ventral concavity. Its posterior is also more asymmetrically rounded.

# Darwinula phaselus sp. nov. Pl. 10, figs 11, 12

Name. Latin; phaselus, a kidney bean; with reference to the lateral outline.

Holotype. OS 13902, adult left valve, Pl, 10, fig 11, from 20cm above base of Bed 11, Lonfearn Member, Lealt Shale Formation, locality 4. Paratypes: OS 13903 and OS 13904, Pl. 10, fig. 12, from the same locality and level. OS 13905 from 60cm above base of Bed 5, Lonfearn Member, Lealt Shale Formation, locality 4.

*Material.* Preservation mostly poor with fragmentary and mouldic material dominant. From the Lonfearn Member, Lealt Shale Formation, localities 2-5.

*Diagnosis.* Elongate subcylindrical carapace. Tapers in anterior third of carapace. Dorsal margin arched, ventral margin concave. Left valve larger than right valve. Adont hinge. Muscle-scars composed of nine individual scars in a symmetrical pattern.

Measurements.

OS 13902 (adult left valve)	1072-518-309	
OS 13903 (adult carapace)	982-436-200	
OS 13904 (juvenile right valve)	527-255-164	
OS 13905 (juvenile carapace)	727-345-327	

*Remarks. D. phaselus* is more arcuate in lateral outline than congeneric species from the Great Estuarine Group. Its muscle-scar pattern is the only one found that is symmetrical (Text-fig. 37). A size dispersion diagram from the type level is given in Text-fig. 38.

# Darwinula protensa sp. nov. Pl. 10, figs 13-15

Name. Latin; protensa, extended; with reference to the highly elongate morphology.

Holotype. OS 13906, adult carapace, Pl. 10, fig. 13, from 3cm above base of Bed 3, Division F, Valtos Sandstone Formation, locality 6; Paratype. OS 13907, Pl. 10, figs 14, 15, from top 7cm of Bed 9, Division F, Valtos Sandstone Formation, locality 6.



TEXT-FIG. 36. Comparison of the adductor muscle-scar rosettes of four specimens of *Darwinula pulmo* (not to scale). a) OS 13899; internal mould of left valve; b) OS 13900; internal mould of left valve; c) Internal mould of right valve (specimen lost), line drawing reversed; d) OS 13901; internal mould of left valve.



TEXT-FIG. 37. Adductor muscle-scar rosette of Darwinula phaselus drawn from OS 13902.



TEXT-FIG. 38. Size dispersion of *Darwinula phaselus* from a single sample taken at the type level, Lonfearn Member, Lealt Shale Formation.

*Material.* 40 valves and no carapaces from the Valtos Sandstone Formation, localities 5, 6. Preservation in general is poor.

*Diagnosis.* Elongate, ovate, subcylindrical species of *Darwinula*. Tapers anteriorly. In adults anterior is only slightly smaller than posterior. Left valve larger than right valve. Hinge adont. Internally the anterior margin is constricted. Muscle-scars with 11 segments.

Measurements.

OS 13906 (adult carapace) OS 13907 (left valve mould) 1182-600-382 891-345-218

Remarks. D. protensa is differentiated from congeneric species from the Great Estuarine Group by its more ovate outline and by its muscle-scar architecture (Text-figs 34, 39). Darwinula rotundata Ljubimova, 1956b, from Triassic rocks near Izium, Kharkv region, Ukraine, is differentiated by its more angular posterior and smaller size. D. protensa differs from Darwinula adducta Ljubimova, 1955, from Triassic rocks near Kuibyshev Oblast, Russia, in the presence of a ventral inflexure.

Darwinula incurva Bate, 1967 Pl. 11, figs 1-4, 7

1965 Darwinula sp. A; Bate, p. 751, pl. 109, figs 1-4.

1967 Darwinula incurva sp. nov. Bate, pp. 28, 29, pl. 1, figs 7-12.

1976 Darwinula incurva Bate 1967; W-M Rohr, p. 32, pl. 1, figs 8-10.

1990 Darwinula incurva Bate; Wakefield, pp. 41-44.

Holotype. Io 2259, adult carapace (Bate 1967, pl. 1, figs 10-12). Paratypes: Io 2260-1; from the Bathonian Upper Estuarine Series at Kings Cliffe, Northamptonshire and Ancaster, Lincolnshire.

*Material.* 45 carapaces and 139 valves from the present study. Specimens OS 13460 and OS 13461 from 20cm above base of Bed 21, Duntulm Formation; specimen OS 13459 from the top 5cm of Bed 1, Kilmaluag Formation; specimen OS 13462 from 65cm above base of Bed 5, Kilmaluag Formation; all from locality 10.

Diagnosis. See Wakefield, 1990.

Measurements.

OS 13462 (A-1 carapace)	836-382	
OS 13459 (A-1 right valve)	764-327——	
OS 13460 (A-1 right valve)	836-364-159	
OS 13461 (A-1 left valve)	818-364-165	

Description. Carapace elongate, subcylindrical and tapering anteriorly. In dorsal view carapace appears almond shaped. Broadly rounded posterior. Anterior narrower and rounded. Dorsal margin convex. Ventral margin with concavity anterior of mid-length. Left valve overlaps right valve around all margins. Greatest overlap at ventral concavity.

Hinge adont with simple narrow groove along dorsal margin of left valve. Muscle-scar rosette lies above and immediately to the posterior of the ventral concavity. It is circular in outline and consists of 10-11 primary segments. The basal segment is usually divided asymmetrically. Occasionally other divisions take place in the two segments anterior of the basal segment (Text-fig. 40). This produces an outer triangular sub-segment and an inner sub-segment (Wakefield 1990). The internal of the valves is ornamented with small rounded pimples. This ornamentation is not developed immediately around the muscle-scars.

Remarks. A size dispersion diagram is given in Text-fig. 41. D. incurva is less inflated posteriorly and has a larger ventral overlap than Darwinula tubiformis Ljubimova, 1956a from Lower Cretaceous deposits in the Ukha Region of Mongolia. D. incurva most closely resembles D. cicatricosa sp. nov. but is slightly larger. The only morphological difference is in the shape of the left valve overlap at the ventral concavity (Text-fig. 42). The muscle-scars of the two species are markedly different.

Odcurrence. This species is also known from the Bathonian Upper Estuarine Series of

#### DARWINULA

England at Kings Cliffe, Northamptonshire, Ancaster, Lincolnshire and from the Wychwood Beds at Kirtlington (Bate 1965, 1967). It is known from the Bathonian Forest Marble at the Old Cement Works, Kirtlington, Oxfordshire (Ware & Whatley 1980 and Jacovides [1982]) and the Bathonian at Shipton-on-Cherwell Quarry, Oxfordshire [Stephens 1980 and Barrington 1986]. It has also been reported from Bathonian deposits in southern France (Rohr 1976). Pang & Whatley (1990) reported *D. incurva* from the Middle Jurassic Mawa Formation, Jiyuan County, China. However, until the muscle-scar morphology is confirmed this identification may be considered as questionable based upon the grounds of distribution.

# Darwinula cicatricosa sp. nov. Pl. 11, figs 8-11

Name. Latin; cicatricosa, scarred; with reference to the complex and varied muscle-scars developed in this species.

*Holotype.* OS 13908, adult carapace, Pl. 11, figs 9, 10, from top 5cm of Bed 7, Kilmaluag Formation, locality 12; Paratypes: OS 13909, Pl. 11, fig. 11; OS 13910, OS 13911, Pl. 11, fig. 8; OS 13912, OS 13913, OS 13914, OS 13915, OS 13916 and OS 13917, all from same locality and level.

Material. 176 carapaces and three valves from type locality.

*Diagnosis.* Elongate, subcylindrical, anteriorly tapering *Darwinula*. Slight ventral concavity anterior of mid-length. Ventral and dorsal margins subparallel. Left valve larger than right valve. Hinge adont. Central muscle-scar rosette composed of a variable number of segments, usually 13, with a paired frontal scar and a triangular mandibular scar. Six dorsal scars may be developed.

Measurements.

OS 13908 (adult carapace)	1006-436-344
OS 13909 (adult car. int. mould)	1102-430-327
OS 13910 (A-1 carapace)	855-327-274
OS 13911 (A-1 car. int. mould)	791-309-255
OS 13912 (A-1 car. int. mould)	891-356-270
OS 13913 (adult car. int. mould)	1183-484-369
OS 13914 (A-1 car. int. mould)	941-403-252
OS 13915 (adult car. int. mould)	1183-484-360
OS 13916 (adult car. int. mould)	1156-443-342
OS 13917 (A-2 car. int. mould)	727-297-252

Description. In dorsal view the carapace appears almond shaped. Broadly rounded posterior. Anterior slightly narrower. Dorsal margin broadly convex but posterior half is almost straight. Ventral margin with slight concavity in anterior half. Carapace unornamented externally but with small rounded pimples internally. Left valve larger than right valve which it overlaps around all margins. Greatest overlap at ventral concavity.

Hinge adont, with simple narrow groove along dorsal margin of left valve. Muscle-scar rosette lies immediately anterior of mid-length. It is obliquely ovate in shape and consists of 11-15 segments in the adults. A paired frontal scar and a single triangular mandibular scar lie to the anterior. Dorsally, directly above the rosette, are six elongate dorsal scars.

*Remarks.* A size dispersion diagram of *D. cicatricosa* is given in Text-fig. 43. The presence of frontal, mandibular and dorsal scars differentiates *D. cicatricosa* from the other Great Estuarine Group *Darwinula* species. The rosette itself is variable due to numerous subdivisions of the individual segments. See also remarks for *D. incurva* Bate, 1967.

D. cicatricosa is the first species of Darwinula to be described with frontal and dorsal scars. A mandibular scar has previously been described by Triebel (1941) in the type species D. stevensoni.

# Darwinula pollex sp. nov. Pl. 11, figs 5, 6, 12, 14

Name. Latin; pollex, a thumb; with reference to the lateral outline.

Holotype. OS 13918, adult carapace, Pl. 11, figs 5, 6, from basal 10cm of Bed 7, Duntulm



TEXT-FIG. 39. Darwinula protensa; a) ventral outline of right and left valves; b) cross-section through anterior margin; c) adductor muscle-scar from an internal mould of a left valve. Drawings from several specimens.



TEXT-FIG. 40. Possible development, via segment division, of an 11 segment adductor musclescar rosette from a 10 segment rosette of *Darwinula incurva* (not to scale).

Formation, locality 9; Paratypes. OS 13920 from same locality and level. OS 13919, Pl. 11, figs 12, 14, from top 5cm of Bed 1, Kilmaluag Formation, locality 11.

Material. Five carapaces and 31 valves from the Kilmaluag Formation, locality 11.

Diagnosis. Large species of Darwinula. Tapers strongly in anterior third. Broad but weakly developed ventral concavity. Left valve larger than right valve. Hinge adont. Muscle-scar rosette composed of nine segments each with an outer margin parallel subdivision. Measurements.

OS 13918 (adult carapace)	1145-582-455
OS 13919 (juv. car. int. mould)	855-400-345
OS 13920 (adult right valve)	1218-564-276



TEXT-FIG. 41. Size dispersion of *Darwinula incurva* from a single sample taken from Bed 15, Kilmaluag Formation, locality 11. Mean increase in length between instar stages is 28%.



to scale).

Description. In dorsal view appears almond shaped. Broadly rounded posterior, anterior much narrower and rounded. Ventral margin with a broad, shallow concavity. Posterior half of dorsal margin subparallel to ventral margin. Anterior half of dorsal margin slopes steeply towards ventral margin. Carapace unornamented externally but with small rounded pimples internally. Left valve overlaps right valve around all margins but particularly the ventral margin.

Hinge adont. Weakly developed bar in right valve which fits into a simple groove in the left valve. Muscle-scar rosette consists of nine main scars each of which is subdivided (Text-fig. 44). The position of the subdivisions are marginal.

Remarks. A size dispersion diagram of D. pollex from the type level is given in Text-fig. 45. The muscle-scars of D. pollex (Text-fig. 44) are clearly different from any of the other Darwinula species described herein. D. pollex resembles Darwinula magna Rohr, 1976 from Bathonian rocks in southern France, in valve outline but is slightly more elongated. However, the muscle-scar rosette in D. magna is U-shaped rather than circular; the segments form two basally converging, arcuate columns.

# Darwinula sp. A Pl. 11, fig. 13

Material. Only known from the Kilmaluag Formation, locality 13. Mostly damaged valves.



TEXT-FIG. 43. Size dispersion of *Darwinula cicatricosa* from a single sample taken at the type level, Kilmaluag Formation.



TEXT-FIG. 44. Adductor muscle-scar rosette of *Darwinula pollex* drawn from an internal mould of a left valve, OS 13919; note the marginal concentric subdivisions.

Measurements.

OS 13921 (left valve)

782-327-182

Description. Elongate species of Darwinula. Posterior margin broadly rounded, anterior margin appears more ovate. Dorsal margin long and slightly convex. Ventral margin long and with a shallow concavity in the posterior half. Carapace tapers slightly to the anterior. Internal details not seen.

*Remarks.* Due to the poor preservation and the small number of specimens available, it is only possible to say that this appears to be a new species. Usually when *Darwinula* occurs with *Theriosynoecum*, as at Kilmaluag Bay (locality 11), it is more numerous. However, in the Kilmaluag Formation at Camas Mor, Isle of Muck (locality 13), the *Theriosynoecum* species dominate the fauna almost to the exclusion of the *Darwinula* species.



TEXT-FIG. 45. Size dispersion of *Darwinula pollex* from a single sample taken at the type level, Duntulm Formation.

#### OSTRACOD BIOSTRATIGRAPHY OF THE GREAT ESTUARINE GROUP

No ostracods were recorded from either the Cullaidh Shale or Elgol Sandstone formations. The Cullaidh Shale was deposited in a stagnating basin, its dark grey-black shales, though containing articulated fish, contain a sparse macrofauna (Hudson 1962, Harris & Hudson 1979). The Elgol Sandstone Formation was deposited as a series of N-S prograding lagoonal deltas, and is dominated by thick sandstone sequences (Harris 1989).

The Lealt Shale Formation, by comparison, contains the most diverse ostracod fauna from the Great Estuarine Group. Of the 41 species recorded from the Great Estuarine Group 11 occur in the Kildonnan Member, with a further 15 occuring in the Lonfearn Member. Each member has a distinct ostracod fauna, with no species occuring in both members. The Kildonnan Member is dominated by *Darwinula pulmo*, *Limnocythere incerniculum* and *Fronslarvata chamaeleon*, the first being recorded in all of the Kildonnan Member sections sampled (Textfigs 46, 47, 49, 50). *Glyptocythere inversalitera*, *Limnocythere spumida* and *Acanthocythere elongata* are found in the central portions of the section (Text-figs 46, 47, 49, 50).

The Lonfearn Member shows a marked faunal change from the Kildonnan Member. The boundary between the two members is delineated by a stromatolitic algal limestone with pseudomorphs after gypsum, indicating desiccating conditions (Hudson 1970). The base of the section is marked by the incoming of *Glyptocythere sutherlandi*, *Glyptocythere dextranovacula*, *Aaleniella cuneata* and *Lophocythere* sp. A (Text-figs 47, 49). Immediately above this basal level, *Darwinula phaselus*, *Limnocythere spinosa*, *Limnocythere melicerion*, *Theriosynoecum fimbriachela* and *Asciocythere pactilis* appear. *Glyptocythere shielingensis* (Text-figs 48) and *Theriosynoecum ramocuspis* (Text-figs 47, 50) occur in both the Lonfearn Member and the overlying Valtos Sandstone Formation.

The Valtos Sandstone Formation, like the Elgol Sandstone Formation, was deposited as a series of prograding deltas (Harris [1984], 1992). Its ostracod fauna is sparse and appears to be long-ranging, though the number of sections yielding ostracods was low. The section at Camas Mor, Muck contains the most diverse fauna recorded (Text-fig. 51).

The faunal change to the Duntulm Formation is less marked than that observed between the two members of the Lealt Shale formation. *Progonocythere levigata* makes its first appearance in the upper portion (Division F) of the Valtos Sandstone Formation, which is interpreted to have been deposited in a brackish-marine delta top lagoon. The similar brackish-marine conditions of the Duntulm Formation (Hudson 1963a, Andrews [1984],

Andrews & Walton 1990) are dominated by *P. levigata* (Text-figs 51, 52 a, b, 53 a). In many instances, however, the ostracod fauna of the Dutulm Formation is sparse e.g. Text-fig. 52a.

The overlying freshwater lagoonal Kilmaluag Formation (Hudson 1963a, Andrews 1985) is hard to distinguish from the Duntulm Formation using the ostracods. This is probably because the sequence from the delta lagoons of the Valtos Sandstone Formation, through the Duntulm Formation and into the Kilmaluag and Skudiburgh formations, represents an end Bathonian regression in which the Great Estaurine Group was totally cut off from outside influences and ostracod migrations. P. levigata, Theriosynoecum conopium and Darwinula incurva occur in both Duntulm and Kilmaluag formations e.g. Text-fig. 53a. However, like the conchostracan fauna (Chen & Hudson 1991), the ostracod fauna at Camas Mor is quite unlike that of the Kilmaluag Formation elsewhere; Theriosynoecum sagena, Darwinula sp. A and Hebatacythere hypha are unique to this locality (Text-fig. 54b). Andrews [1984] considered the Kilmaluag Formation section on Muck to be equivalent to the 'breccia beds' seen at Glen Scaladal. Ostracods were recorded from Glen Scaladal by Andrews ([1984], 1985), although the material was mostly recorded in thin section work and comparisons are not possible. An interesting feature of the Kilmaluag Formation is that each section contains a different species of Darwinula; locality 10 contains D. incurva (Text-fig. 53a), locality 11 contains Darwinula pollex (Text-fig. 53b), locality 12 contains Darwinula cicatricosa (Text-fig. 54a) while locality 13 contains Darwinula sp. A (Text-fig. 54b). It is not possible to comment on whether they occur in any stratigraphic order.

No ostracods were recorded from the Skudiburgh Formation which was deposited under subaerial conditions (Andrews 1985).

# OSTRACOD CORRELATION OF SECTIONS IN THE GREAT ESTUARINE GROUP

In a broad sense the ostracods from the Great Estuarine Group can easily delineate the lithostratigraphical subdivisions of Harris & Hudson (1980) (Text-fig. 55). The Duntulm and Kilmaluag formations are more difficult to differentiate because of the similarity of some of their species. Two faunal events seem to allow precise bed to bed correlations over the two basins. These are, firstly, towards the top of the Kildonnan Member where P. milleri appears and secondly, at the base of the Lonfearn Member with the appearance of G. sutherlandi, G. dextranovacula, A. cuneata and Lophocythere sp. A. Therefore P. milleri correlates Bed 6b (locality 1) with Bed 6 (locality 2), Bed 9c (locality 4) and Bed 6 (locality 5) all in the Kildonnan Member. The fact that P. milleri appears at the same level over the entire area of exposure of the Kildonnan Member, in both the Inner Hebrides and Sea of the Hebrides basins of Binns et al. (1975), indicates that the event was probably contemporaneous over that area. If the occurrence is purely due to environmental conditions then those influences were present over the entire area. Hudson & Harris (1979) came to the same conclusion to account for the development of the algal limestone at the boundary of the Kildonnan and Lonfearn Members. The palaeoecological significance of the ostracod faunal change over at the Kildonnan/Lonfearn boundary is discussed in Wakefield [1991].

## CORRELATION WITH OTHER BATHONIAN SEQUENCES USING OSTRACODS

Bate (1978) produced an eight-fold ostracod zonal scheme for the Bathonian of Great Britain. He deemed this necessary as, although a complete ammonite zonal scheme did exist (Torrens 1969, Parsons 1974, 1977), ammonites were scarce in many of the British Bathonian rocks (Torrens 1980). These ostracod zones were reduced to five by Sheppard (1981b), who was able to correlate the Bathonian rocks of Dorset and Kent in southern Britain with those of northern France with reasonable success. Provincialism of some of the ostracod fauna was noted, although no details were given. Ostracods have been shown to be controlled strongly by variations in facies (e.g. Ware & Windle 1981, Ware & Whatley 1983 and Whatley 1983). This is not to say that ostracods are of no use at all for stratigraphical correlation (see references in Whatley 1983). The fauna studied by Sheppard [1981a] was essentially marine. None of the low salinity, darwinulid and limnocytherid, ostracod faunas from the Bathonian were recorded. It is not surprising, therefore, that so few faunal links between the Inner Hebrides ostracod fauna and that of southern Britain occur. Only M. falcata (Oxfordshire, Kent and Dorset), P. levigata (Leicestershire and Oxfordshire), D. incurva (Oxfordshire) and P. kingscliffensis (Leicestershire and Oxfordshire) were also reported from the Great Estuarine Group. As such no accurate correlation with the zonal scheme of Sheppard (1981b) is possible. The Great Estuarine Group is entirely non-marine (Hudson 1963a & b, 1966; Andrews [1984], 1985; Andrews & Walton 1990; Tan & Hudson 1974). During the Bathonian southern Britain, though with some documented non-marine ostracod faunas (Bate 1965, 1967; Ware 1978; Stephens 1980 Ware & Whatley 1980, 1983; Ware & Windle 1981; Jacovides 1882; Barrington 1986), has an essentially marine ostracod fauna (see references in Sheppard [1981a]) which may explain the paucity of ostracod correlation's between the regions. The only ostracod available for correlation between the Great Estuarine Group and the ostracod zonation scheme of Bate (1978) and Sheppard (1981b) is the zonal index fossil *M. falcata*. This zone is equivalent to the Clydoniceras (Clydoniceras) discus ammonite zone. M. falcala occurs in the Duntulm Formation which was dated as pre-discus (Procerites hodsoni or older) by Andrews [1984]; Andrews & Walton (1990) and by palynological dating carried out on behalf of the present author by British Petroleum, thus extending its range. The occurrence of P. levigata in the Valtos Sandstone, Duntulm and Kilmaluag formations (dated as hodsoni or older) does comply with the hodsoni dating of *P. levigata* by Bate (1978). While the ostracod zonation of Sheppard (1981b) may be applicable to the more marine settings of southern Britain and much of continental Europe, a greater knowledge of marginal- and non-marine ostracod faunas is required before the scheme can be wholly accepted.

The conchostracan Antronestheria kilmaluagensis Chen & Hudson, 1991, provides a faunal link between the Great Estuarine Group and the offshore Porcupine Basin, SW Ireland. This species occurs widely within the Kilmaluag Formation of the Great Estuarine Group, and was recorded in core material from a British Petroleum well in the northern part of the Porcupine Basin (Chen & Hudson 1991). A structural link via the Slyne and Erris troughs and the Donegal and Malin basins to the Inner Hebrides and Sea of the Hebrides basins existed in the Mesozoic (Trueblood & Morton 1991). A similar sedimentary sequence to that described from the Hebrides basins (Morton 1987; Trueblood & Morton 1991) has also been noted in the Slyne Trough and the North Porcupine Sub-basin (Trueblood & Morton 1991). Though these similar sequences are often termed "Great Estuaire Group" (Trueblood & Morton 1991, Trueblood 1992, Morton 1989, 1992, 1993), in the context of this work the Great Estuarine Group is restricted to the Inner Hebrides. Only Limnocythere hibernica Athersuch, 1989 of the ostracods present in the Porcupine Basin has been described. This species has not been recovered from the Great Estuarine Group. Similar genera are present in both the Porcupine Basin and Great Estuarine Group sediments. These include Darwinula, Theriosynoecum, Limnocythere, Klieana?, Progonocythere and Glyptocythere. Of these the Darwinula species most closely resembles D. incurva Bate, 1967, (J. Athersuch pers. comm. 1991).

Although the above concentrates on links at a specific level there is no disputing the links at a generic level. There are strong faunal links between the ostracod fauna of the Great Estuarine Group and those of the rest of the British Isles, Bate (1965, 1967, 1969), Sheppard [1981a], Ware & Whatley (1980, 1983), Barrington [1986], Jacovides [1982], Stephens [1980], Timberlake [1982]; Europe, Sheppard [1981a], Rohr (1976), Dépêche (1969, [1984]), Brand & Malz (1962b, 1966), Malz (1975), Malz *et al.* (1985), Oertli (1959, 1985); Saudi Arabia, Dépêche *et al.* (1987); Madagascar, Grekoff (1963); China, Pang & Whatley (1990); Russia, Ljubimova (1956b).
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Type Section, N of Kildonnan, Eigg, locality 1.

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Base of section

TEXT-FIG. 48. Ostracod biostratigraphy of the Lonfearn Member, Lealt Shale Formation, Shieling Burn, Eigg, locality 3.



TEXT-FIG. 49. Ostracod biostratigraphy of the Kildonnan and Lonfearn Members, Lealt Shale Formation, Rudha nam Braithairean, Trotternish, Skye, locality 4.



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TEXT-FIG. 51. Ostracod biostratigraphy of the Valtos Sandstone and Duntulm formations, Camas Mor, Muck, locality 6.



End of exposure



TEXT-FIG. 53. Ostracod biostratigraphy of; a) Duntulm and Kilmalaug formations, Laig Gorge, Eigg, locality 10; b) Kilmaluag Bay, Trotternish, Skye, locality 11.

b)



TEXT-FIG. 54. Ostracod biostratigraphy of; a) Kilmalaug Formation, Prince Charles's Point, Trotternish, Skye, locality 12; b) Kilmalaug Formation, Camas Mor, Muck, locality 13.



Base not seen

81



TEXT-FIG. 55. Biostratigraphy of selected species of Ostracoda from the Great Estuarine Group. Correlation with the standard ammonite zones is based upon Text-fig. 1, and is approximate.

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9	dorsal; anterior (stereo-pair), x65; anterior margin (stereo-pair); posterior marginal spines (stereo-pair), x420.	
7	Paratype. Juvenile left valve. OS 13855. External lateral, x65.	

# Theriosynoecum ramocuspis sp. nov.

	Bed 42a, Lonfearn Member, Lealt Shale Formation, loc. 2.
10	Paratype. A-4 left valve. OS 13864. Internal lateral (stereo-pair), x75.
11	Paratype. Male right valve. OS 13863. External lateral (stereo-pair), x45.
12, 16	Paratype. A-3 left valve. OS 13861. External lateral, x75; external ornament over central muscle-scars, x300.
13 - 15	Holotype. Female left valve. OS 13860. External lateral (stereo-pair); ventral; anterior (stereo-pair), x45.

Theriosynoecum conopium Wakefield & Athersuch, 1990	43
Top 5cm, Bed 7, Kilmaluag Formation, loc. 11.	

17

Fig.

Iop 5cm, Bed 7, Kilmaluag Formation, loc. 11. Holotype. Male carapace. OS 13463. Dorsal, x38. Paratype. Female carapace. OS 13464. Ventral, x44. 18



Fig.		Page
	Theriosynoecum conopium Wakefield & Athersuch, 1990	43
	Top 5cm, Bed 7, Kilmaluag Formation, loc. 11.	
1, 3	Holotype. Male carapace. OS 13463. Anterior (stereo-pair); external lateral (stereo-pair), x38.	
2, 4	Paratype. Female carapace. OS 13465. Posterior (stereo-pair); external lateral (stereo-pair), x43.	
5, 6, 9	Paratype. A-1 carapace. OS 13466. External lateral; dorsal, x65; node (stereo-pair), x490.	
	Bed 1, Kilmaluag Formation, loc. 11.	
7	Paratype. A-1 right valve. OS 13478. Internal lateral, x75.	
8, 10	Paratype. A-2 carapace. OS 13467. External lateral, x70; external ornament and sieve pores, x500.	
	Theriosynoecum sagena sp. nov.	44
	Basal 5cm, Bed 25, Kilmaluag Formation, loc. 13.	
11-13	Holotype. Female left valve. OS 13866. External lateral (stereo-pair); ventral (stereo-pair); anterior (stereo-pair), x45.	
14	Paratype. A-2 right valve. OS 13870. External lateral, x75; anterior marginal pore canal openings, x720.	
15, 16	Paratype. Female left valve. OS 13867. External lateral, x45.	
	Theriosynoecum sp. A	46
	Top 5cm, Bed 5f, Kildonnan Member, Lealt Shale Formation, loc. 1.	
17 - 20	Female? left valve. OS 13871. Posterior; external lateral (stereo-pair); dorsal, x40; anterior marginal pore canal openings, x160.	



Fig.		Page
1-3	Micropneumatocythere falcata Sheppard, 1978 Bed 44, Duntulm Formation, loc. 7. Juvenile right valve. OS 13796. Ventral, external lateral, x100; caudal process, x420.	47
11 12 13	Micropneumatocythere foveolata sp. nov. Basal 5cm, Bed 4, Kilmaluag Formation, loc. 11. Holotype. Female left valve. OS 13797. External lateral (stereo-pair), x65. Paratype. Male carapace. OS 13800. External lateral, x65. Female carapace (specimen lost). External lateral, x65.	48
4-7 8 9 10	<ul> <li>Hebatacythere hypha gen. et sp. nov.</li> <li>Basal 5cm, Bed 25, Kilmaluag Formation, loc. 13.</li> <li>Holotype. Female left valve. OS 13803. External lateral (stereo-pair); dorsal; ventral; anterior (stereo-pair), x65.</li> <li>Paratype. Male right valve. OS 13804. External lateral, x65.</li> <li>Paratype. Male left valve. OS 13802. External lateral, x65.</li> <li>Paratype. Female left valve. OS 13805. External lateral, x65.</li> </ul>	50
14, 15, 17	Klieana williamsi sp. nov. Bed 6, Kilmaluag Formation, loc. 11. Paratype. Male left valve. OS 13814. Ventral; dorsal; external lateral, x70.	51
16 18, 19, 22, 23	20cm below top, Bed 7, Kilmaluag Formation, loc. 11. Holotype. Male right valve. OS 13809. External lateral (stereo-pair), x73. Paratype. Female left valve. OS 13810. External lateral; anterior; dorsal; ventral, x70.	
20	30cm below top, Bed 4, Kilmaluag Formation, loc. 11. Paratype. A-1 male? right valve. OS13815. External lateral (stereo-pair), x82.	
21	Basal 10cm, Bed 7, Kilmaluag Formation, loc. 11. Paratype. Female, right valve. OS13813. Internal lateral, x62.	



Fig		.Page
	Asciocythere pactilis sp. nov.	53
1-3	60cm above base, Bed 5, Lonfearn Member, Lealt Shale Formation, loc. 4. Holotype. Male carapace. OS 13880. External lateral (stereo-pair); dorsal (stereo-pair): anterior x65	
4	Paratyne Iuvenile right valve OS 13882 Internal lateral (stereo-nair) x90	
5	Paratype. Female carapace. OS 13881. External lateral (stereo-pair), x65.	
	Praeschuleridea? sp. A	55
	49cm above base Red 1 Lonfearn Member Lealt Shale Formation loc 4	
6-9	Right valve. OS 13883. External lateral (stereo-pair); dorsal; internal lateral; posterior (stereo-pair), x90.	
	Aaleniella cuneata sp. pov	56
	8cm above base Bed 1 Lonfearn Member Lealt Shale Formation loc 4	50
10-11	Holotype Adult carapace OS 13884 External lateral (stereo-pair):	
13	dorsal; posterior (stereo-pair), x85.	
	Basal 5cm, Bed 1, Lonfearn Member, Lealt Shale Formation, loc. 2.	
12	Paratype. Adult right valve. OS 13887. External lateral, x85.	
14, 15	Paratype. Adult right valve. OS 13886. Central muscle-scars, x600; internal lateral (stereo-pair), x85.	
16	Paratype. Adult right valve. OS 13885. External lateral, x85.	
	Paracypris? rasilis sp. nov	57
	5cm above base. Bed 4. Kilmaluag Formation, loc. 11	
17, 18	Holotype. Adult right valve. OS 13891. Internal lateral (stereo-pair), x85; central muscle-scars, x600.	
19	Paratype. Juvenile? carapace. OS 13892. External lateral (stereo-pair), x85.	



Fig.		Page
	Paracypris? sp. A	58
	5cm above base, Bed 8b, Lonfearn Member, Lealt Shale Formation, loc. 2.	
1	Right valve. OS 13893. External lateral (stereo-pair), x85.	
2	Right valve. OS 13894. Central muscle-scars (stereo-pair), x720.	
		<b>60</b>
	Paracypris? sp. B	59
	Top 5cm, Bed 21, Division F, Valtos Sandstone Formation, loc. 6.	
3-5, 7	Right valve. OS 13895. External lateral (stereo-pair); internal lateral;	
	posterior (stereo-pair); ventral, x75.	
6	Right valve. OS 13896. Internal lateral (stereo-pair), x75.	
		60
	Darwinula pulmo sp. nov. Ded 2h Kildemeen Member Leelt Shele Fermation lee 1	02
0	Heloture Adult left value OS 12807 External lateral (starge pair) x45	
0	Holotype. Adult left valve. US 15897. External lateral (stereo-pair), x45.	
	Top 3cm, Bed 6d, Kildonnan Member, Lealt Shale Formation, loc. 1.	
9, 10	Paratype. Juvenile carapace. OS 13898. External lateral (stereo-pair);	
	ventral (stereo-pair), x75.	
	Darwinula phaselus sp. nov.	62
	20cm above base, Bed 11, Lonfearn Member, Lealt Shale Formation, loc. 4.	
11	Holotype. Adult left valve. OS 13902. External lateral (stereo-pair), x45.	
12	Paratype. Juvenile right valve. OS 13904. External lateral, x90.	
	Darwinula protensa sp. nov.	62
	3cm above base, Bed 3, Division F, Valtos Sandstone Formation, loc. 6.	
13	Holotype. Adult carapace. OS 13906. External lateral (stereo-pair), x45.	
	Top 7cm, Bed 9, Division F, Valtos Sandstone Formation, loc. 6.	
14, 15	Paratype. Juvenile left valve, internal mould. OS 13907. Adductor	
	muscle-scar rosette, x420.	


## PLATE 11

Fig.		Page
	Darwinula incurva Bate, 1967	64
	20cm above base, Bed 21, Duntulm Formation, loc. 10.	
1, .	A-1 left valve. OS 13461. External lateral (stereo-pair); ventral	
3, 4	(stereo-pair), x60. A-1 right valve. OS 13460. External lateral (stereo-pair); ventral (stereo-pair), x60.	
	Top 5cm, Bed 1, Kilmaluag Formation, loc. 10.	
7	A-1 right valve, internal mould. OS 13459. Adductor muscle-scar rosette, x395.	
	Darwinula cicatricosa sp. nov.	65
	Top 5cm, Bed 7, Kilmaluag Formation, loc. 12.	
8	Paratype. A-1 carapace, internal mould. OS 13911. Dorsal view of dorsal	
	muscle-scars (stereo-pair), x300.	
9, 10	Holotype. Adult carapace. OS 13908. External lateral (stereo-pair); ventral (stereo-pair), x50.	
11	Paratype. Adult carapace, internal mould. OS 13909. Adductor muscle- scar rosette, x240.	
	Darwinula pollex sp. nov.	66
	Basal 10cm, Bed 7, Duntulm Formation, loc. 9.	
5, 6	Holotype. Adult carapace. OS 13918. External lateral (stereo-pair); dorsal (stereo-pair), x45.	
	Top 5cm, Bed 1, Kilmaluag Formation., loc. 11.	
12, 14	Paratype. Juvenile carapace, internal mould. OS 13919. Adductor muscle-scar rosette, x420; lateral, x60.	
	Darwinula sp. A	67
	Basal 5cm, Bed 25, Kilmaluag Formation, loc. 13.	
13	Left valve. OS 13912. External lateral (stereo-pair), x65.	

## MONOGRAPH OF THE PALAEONTOGRAPHICAL SOCIETY

## WAKEFIELD, Middle Jurassic (Bathonian) Ostracoda

Plate 11

