THE SANNOISIAN AND SOME OTHER UPPER PALAEOGENE OSTRACODA FROM NORTH-WEST EUROPE

by M. C. KEEN

ABSTRACT. 36 species and subspecies of ostracods are described from the Sannoisian of the Isle of Wight, the Paris Basin, and Belgium. Some comparative species are also described from the Headon Beds and Bembridge Limestone of the Isle of Wight and from the Stampian of the Paris Basin and Aquitaine Basin, and from the Sannoisian of Alsace. 3 new genera are described, *Vecticypris*, *Cladarocythere*, and *Hammatocythere*, together with 10 new species and 1 new subspecies. The ostracods support the idea of the Sannoisian as a facies developed at the base of the Rupelian and forming the base of the Oligocene in the Anglo-Paris-Belgian area. 6 distinct ostracod assemblages can be recognised, mainly salinity controlled.

THE Sannoisian was originally defined as the Lower Oligocene stage of the Paris Basin, and as such was equated with the type Lower Oligocene, i.e. the Lattorfian. Denizot (1940) pointed out that the Sannoisian has most of its fauna in common with the overlying Stampian, and recent work has shown that it is merely a brackish-water facies of the traditional Middle Oligocene of the Paris Basin. So it is now used in the sense of a Sannoisian facies (e.g. Cavelier 1964*a*). None the less it is a useful term because the facies is widespread and everywhere precedes the main Rupelian transgression. It is found in England, the Paris Basin, Belgium, the Mainz Basin, Alsace, and the Hesse Basin (text-fig. 1). Because it is a facies it may be diachronous, but the fauna of molluscs, mammals, foraminifers and ostracods, and the flora (especially *Chara*), are very characteristic. The fauna is quite distinct from older ones, but has a lot in common with the Rupelian. The ostracods have been described recently by Keij (1957), Mehrotra (1960), and Margerie (1961). The eastern section, running from Basle to Hesse, contains a closely related fauna described by Stchepinsky (1960, 1963), Triebel (1963), Carbonnel and Ritzkowski (1969), and Malz and Triebel (1970).

STRATIGRAPHY

The type Sannoisian has been comprehensively studied (Girard d'Albissin 1955, 1956; Cavelier 1964*a*, *b*, 1965). The various localities sampled in the Paris Basin during the present work are indicated below. At the base of the succession are the Argile verte de Romainville, divided into the Glaises à Cyrènes and the Marnes vertes (partly stratigraphical and partly geographical). The Bande blanche is developed above these in a region to the north of Paris and consists of a marl with *Chara* and *Lymnaea*. The Upper Sannoisian has the Caillasses d'Orgement at the base, consisting of gypsum bands, clays, and powdery limestones. It is overlain by the Calcaire de Sannois, sandy clays with a thin limestone, and containing *Sinodia suborbicularis* (Goldfuss), *Corbula subpisum* d'Orbigny, and *Pirenella monilifera* (Defrance). Cavelier (1964*a*) showed that

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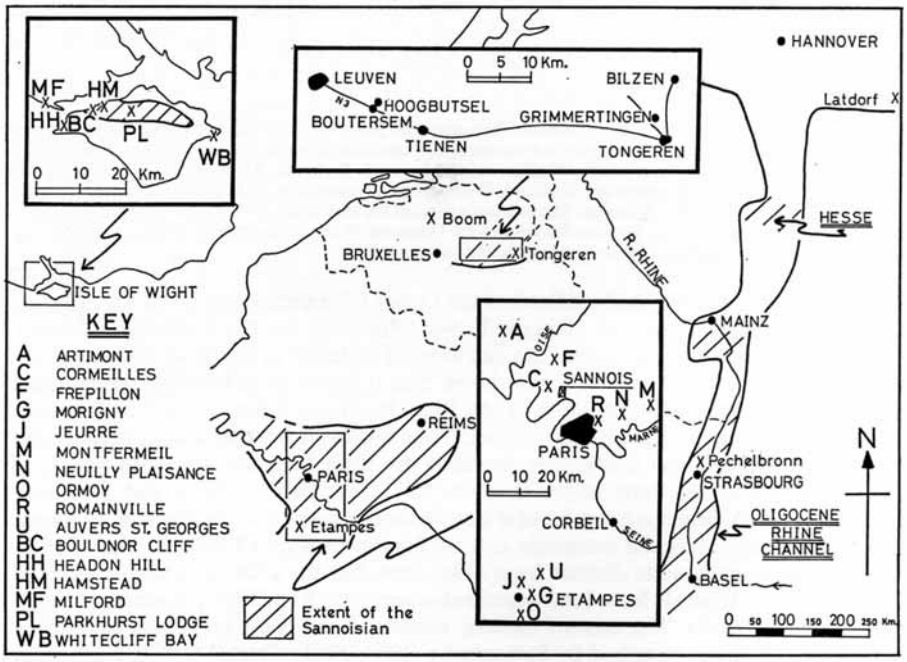
between Cormeilles and Argenteuil, i.e. within the type area of the Sannoisian, the basal Marnes à Huîtres (Rupelian) are synchronous with the summit of the Calcaire de Sannois at Sannois. The continental equivalent of the Calcaire de Sannois is the Calcaire de Brie, which forms the large plateau to the east of Paris from which it takes its name.

In England the Sannoisian facies is taken to be represented by the Hamstead Beds, which outcrop over a large area in the northern half of the Isle of Wight. The Bembridge

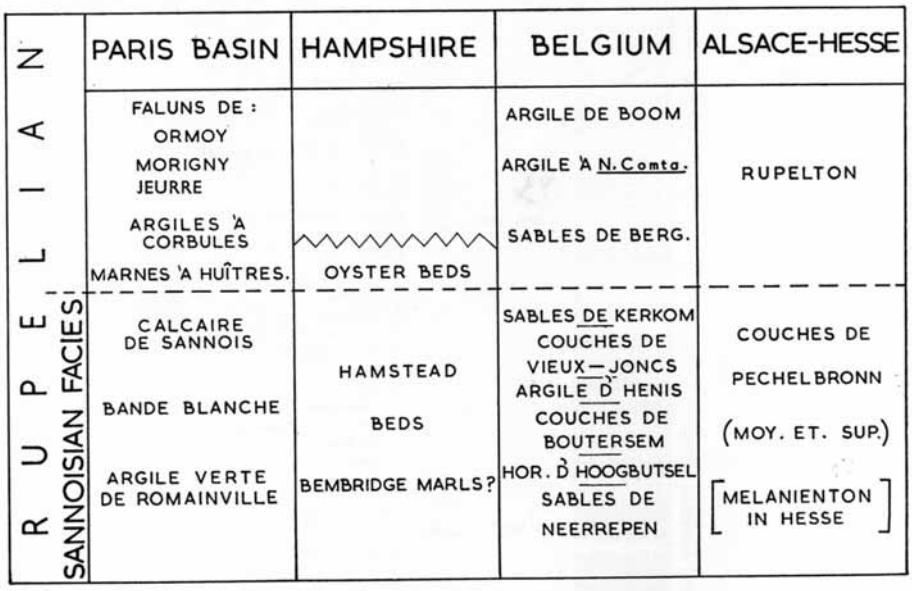


TEXT-FIG. 1. Sannoisian localities mentioned in the text.

Marls may also belong to the Sannoisian, however (see the section on stratigraphical conclusions). The Hamstead Beds are usually divided into an upper and a lower unit following Reid and Strahan (1889), although Forbes (1853) originally divided the series into 4. The outcrops at Bouldnor cliff, the principal locality, form 3 natural units separated from each other by mudflows and landslips, and this appears to have been the case for the last 100 years or so. Furthermore these coincide with 3 different depositional environments: a lower oligohaline–mesohaline unit, a middle freshwater unit, and an upper mesohaline–polyhaline unit. Thus it is proposed to use the terms Lower, Middle, and Upper Hamstead Beds.

The base of the Hamstead Beds is formed by the Black Band, a dark brown carbonaceous shale. Forbes thought that this represented a terrestrial surface with rootlets into the underlying beds; Reid and Strahan utilized it because it was recognizable in

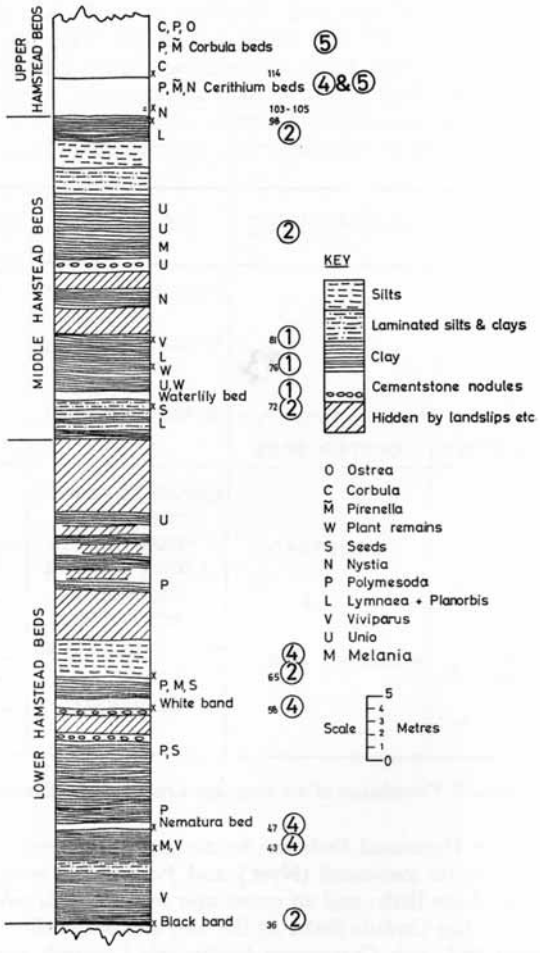
boreholes over a large area of the island. The base of the Middle Hamstead Beds is drawn at the base of a series of bluffs which include the Waterlily Bed, making the Lower Hamstead Beds about 40 m thick. The Middle Hamstead Beds are differentiated from the Lower Hamstead Beds firstly by their separation of outcrop, and secondly by their fauna. The fauna is mainly freshwater, with *Lymnaea*, *Planorbis*, *Unio*, and *Viviparus*, lacking the brackish constituents of the other Hamstead Beds. They are about



TEXT-FIG. 2. Correlation of the Rupelian strata in NW. Europe.

25 m thick. The Upper Hamstead Beds can be divided into 2 units, a lower one with *Pirenella monilifera*, *Nystia duchasteli* (Nyst.) and *Polymesoda convexa* (Brongniart), referred to as the *Cerithium* Beds; and an upper unit with *Corbula subpisum* as an addition, and referred to as the *Corbula* Beds. At the very top of the cliff at Bouldnor small lenticles of an oyster bed with *Crassostrea longirostris* Lamarck were formerly seen. 1 or 2 freshwater horizons were found within the Upper Hamstead Beds, recognized by the ostracods they contained. The Upper Hamstead Beds are about 10 m thick.

The Sannoisian of Belgium is represented by the Upper Tongrian, together with the Sables de Neerrepen. The latter consist of 10 m of fine-grained micaceous sands, usually laminated, sometimes with clay laminae. The Horizon d'Hoogbutsel is only seen at the type locality, a shallow excavation, and is a 10 cm band of dark clay which has yielded vertebrate remains; it overlies the Horizon à bithinies, 30 cm of clay with *Nystia*. The Couches de Boutersem, 3–5 m of sands and marls with *Cerithium* and *Nystia*, form the base of the Upper Tongrian. The succeeding Argile d'Henis is well exposed in the tile pits around Tongeren, where it is about 8 m thick, but rapidly thins northwards.



TEXT-FIG. 3. Section of the Hamstead Beds, Bouldnor Cliff. The small numbers refer to samples mentioned in the text, the large numbers in circles to ostracod assemblages.

It is a green clay, sometimes with carbonaceous beds, and with the molluscs concentrated into certain beds. The fossils are *Sinodia suborbicularis*, *Pirenella monilifera*, and other members of this fauna. The Couches de Vieux-Joncs, or Oude Biezen, are 4–5 m of fossiliferous sands alternating with marly clays, and containing *Polymesoda convexa*, *Pirenella monilifera*, and *Nystia duchasteli*. The top of the Tongrian is formed by the Sables de Kerkom, 15 m of current-bedded sands with local intercalations of clay and

gravel. They are probably of fluviatile origin. The Tongrian is overlain by the Sables de Berg at the base of the Rupelian s.s.

LOCALITIES

1. BOULDNOR CLIFF, ISLE OF WIGHT (Nat. Grid Ref. 392909–404920), (EBC). The details for this locality are illustrated in text-fig. 3.

2. CORMEILLES-EN-PARISIS (PCM). The Carrière Lambert exposes Ludian to Rupelian strata, all of which were sampled. Only the details for the Sannoisian are given here. Glaises à Cyrènes, PCM. 12, 13; Marnes vertes, 14, 15; Bande blanche, 16, 17; samples from the Calcaire de Sannois correspond to the numbered beds (in brackets) of Girard d'Albissin (1955): PCM. 18 (40), 19 (42), 20 (44), 21 (45), 22 (46), 23 (47).

3. MONTFERMEIL, Carriere de Sampin (PMF). The numbers in brackets are those of Girard d'Albissin (1955); Glaises à Cyrènes, PMF. 1 (1), 2 (1), 3 (3), 4 (5); Marnes vertes, 5 (8), 6 (8), 7 (9), 8 (11); Calcaire de Brie, 9 (16), 10 (18), 11 (20).

4. NEUILLY PLAISANCE (PNP). There are several old quarries at this locality; no measurements were made, PNP. 1 came from the Marnes blanches (Ludian), PNP. 2 from the Glaises à Cyrènes, PNP. 3 from the Marnes vertes.

5. ARTIMONT (PAT). The section is very overgrown, but 4–5 m of green clay could be seen with a little digging, from which 3 samples were taken. This locality is of interest, because it formerly exposed fossiliferous Marnes vertes; the ostracods suggest a more saline environment than the normal, almost unfossiliferous Marnes vertes.

6. FREPILLON (PFP). 2 samples were taken from the Marnes blanches; PFP. 3 from the Glaises à Cyrènes; PFP. 4 from an intercalation of Glaises à Cyrènes lithology within the Marnes vertes.

7. BELGIUM. Details of most of these localities can be found in Keij (1957). No detailed collecting was carried out; the localities and horizons sampled are as follows: a roadside cutting just N. of Boutersem (BNP), Sables de Neerrepen; Hoogbutsel (BHG), Horizon d'Hoogbutsel, Couches de Boutersem; Tongeren, claypit N. of the station (BTG), Argile d'Henis, Couches de Vieux-Joncs; Bilzen (BBZ), Argile à *N. comta*; Terhaegen, just E. of Boom (BBM), Argile de Boom.

8. PECHELBRONN. Small brick pit at Pechelbronn; Couches de Pechelbronn supérieur; no detailed measurements taken.

9. OLDER PALAEOGENE BEDS. Comparative species are described from the following: Lower Headon *Unio* Beds, Paddy's Gap, Milford (SZ.278917); uppermost beds of the Upper Headon Beds, Headon Hill (SZ.306860), 1·5 m below the concretionary Osborne Limestone; clays near the top of the Bembridge Limestone, Hamstead Ledge.

10. YOUNGER PALAEOGENE BEDS. Comparative species are described from the Stampian of the Paris Basin (see text-figs. 1, 2; PAG = Auvers-St.-Georges; POM = Ormoy); from the Marnes à Huîtres, St. Cloud (western suburb of Paris); and from Gaas, in the Aquitaine Basin, E. of Biarritz (AGE = Espibos, AGL = Lesbarritz).

SYSTEMATIC DESCRIPTIONS

The classification used is mainly that of the Treatise (ed. Moore 1961), modified by Hazel (1967) for the families Hemicytheridae and Trachyleberididae.

In the descriptions, the heading '*Material*' refers to the total sample examined; the numbers refer to individual specimens deposited at the British Museum (Natural History) (prefixed Io.) or the Geological Survey Museum, Institute of Geological Sciences (prefixed Mik); most of the former are figured specimens.

Abbreviations. L = length, H = height, W = width, N = number, $\bar{x}$ = mean, S = standard deviation, V = variance.

Order PODOCOPIDA Muller 1894
Suborder PLATYCOPINA Sars 1886
Family CYTHERELLIDAE Sars 1886
Genus CYTHERELLA Jones 1849

Type species. Cytherina ovata Roemer.

Diagnosis. Carapace ovate, right valve larger; surface smooth or punctate. Hinge and duplicature simple; 10–12 muscle scars arranged in 2 slightly curved vertical rows.

Discussion. Species of the genus *Cytherella* are notoriously difficult to identify. 2 species are recorded from Sannoisian strata, although none was found in the author's samples. Keij (1957) recorded *C. compressa* (von Munster), but Haskins (1968*a*) stated that some of them are males of *C. muensteri* (Roemer). The species is recorded from Lower Eocene to Miocene, although this probably includes several species. Margerie (1961) listed *C.* aff. *C. gracilis* Lienenklaus from Cormeilles; the species is recorded from the Rupelian and Chattian of Germany and Switzerland.

Genus CYTHERELLOIDEA Alexander 1929

Type species. Cythere (*Cytherella*) *williamsoniana* Jones.

Diagnosis. Similar to *Cytherella*, but with an ornamented surface of ridges.

Discussion. This is sometimes regarded as a subgenus of *Cytherella*, but Ramsay (1968) indicated that all species of *Cytherelloidea* have a basic simple spiral pattern of ornamentation, thus distinguishing it from punctate species of *Cytherella*.

Cytherelloidea jonesiana (Bosquet)

Diagnosis. Species of *Cytherelloidea* with marginal ridge along anterior, ventral, and posterior margins; remainder of surface covered with coarse puncta.

EXPLANATION OF PLATE 45

Figs. 1, 3, 5, 7, 8. *Cytherelloidea jonesiana jonesiana* (Bosquet), ×70. 1, 7, Female carapace, Io. 3661, Falun de Morigny; 1, left view; 7, dorsal view. 3, 8, Left view, female carapace, Io. 3662, Marnes à Huîtres, Cormeilles; 3, left view; 8, dorsal view. 5, Right valve, female, Io. 3663, Falun d'Auvers-St.-Georges.

Figs. 2, 4, 6, 9, 10. *Cytherelloidea jonesiana crassata* subsp. nov., ×70. 2, 10, Male carapace, Io. 3665, Couches de Sannois, Cormeilles: 2, left view; 10, dorsal view. 4, 9, Female carapace, holotype, Io. 3664, Couches de Sannois, Cormeilles; 4, right view; 9, dorsal view. 6, Right view, female carapace, Io. 3666, Marnes à Huîtres, Cormeilles.

Figs. 11, 14, 15. *Ilyocypris boehli* Triebel. 11, 14, Left valve, Io. 3693, Middle Hamstead Beds, Bouldnor Cliff; 11, central muscle scars, ×225 (arrow indicates anterior); 14, internal details, ×60. 15, Left valve, Io. 3692, ×75, Middle Hamstead Beds, Bouldnor Cliff.

Figs. 12, 13. *Ilyocypris cranmorensis* sp. nov., ×70. Lower Hamstead Beds, Bouldnor Cliff. 12, Left valve, holotype, Io. 3694. 13, Right valve, Io. 3695.

Cytherelloidea jonesiana jonesiana (Bosquet)

Plate 45, figs. 1, 3, 5, 7, 8

1852 *Cytherella jonesiana* Bosquet, p. 16, pl. 1, fig. 4.
1895 *Cytherella jonesiana* Bosquet; Lienenklaus, p. 156.
1957 *Cytherella jonesiana* Bosquet; Keij, p. 45, pl. 1, fig. 11.
1963 *Cytherelloidea jonesiana* (Bosquet); Stchepinsky, p. 154.

Type locality and horizon. Jeurre; Falun de Jeurre.

Stratigraphic range and distribution. Marnes à Huîtres; Falun de Jeurre, Jeurre, Auvers-St.-Georges; Falun de Morigny, Morigny; Marnes à Cyrènes, Alsace.

Material. Marnes à Huîtres, Cormeilles, 1 carapace; Auvers-St.-Georges, 8 valves and carapaces; Morigny, 1 valve. Figured specimens, Pl. 45: Io. 3661–3663.

Dimensions. Right valve, female; mean of 2 specimens: *L*, 0·78; *H*, 0·44; *L*/*H*, 1·78; *W*, 0·19.

Diagnosis. Subspecies of *C. jonesiana* in which marginal ridge is poorly developed.

Description. Valves unequal in size, larger right valve with greater height. Sexual dimorphism distinct, males more elongate. Posterior half of dorsal margin of left valve convex, and greatest height of valve is on convexity. Anterior half concave. In right valve, posterior convexity not so prominent. Anterior margin evenly rounded; ventral margin concave; posterior margin has certain 'squareness'. In dorsal view carapace wedge-shaped, tapered towards anterior end, truncated at posterior end.

In left valve wide smooth ridge around anterior, ventral, and posterior margins and particularly prominent at posterior end. Remainder of surface, apart from smooth depression marking site of muscle scars in dorso-median position, coarsely punctate. Smooth marginal ridge poorly developed in right valve, clearly seen at posterior end, absent along venter, and poorly seen at anterior end.

Internal features as for genus.

Discussion. Keij (1957) selected a lectotype, deposited at the Institut Royal des Sciences Naturelles de Belgique, in Brussels.

Cytherelloidea jonesiana crassata subsp. nov.

Plate 45, figs. 2, 4, 6, 9, 10

1896 *Cytherella jonesiana* Bosquet; Lienenklaus, p. 32, pl. 2, figs. 14*a*, *b*.
1956 *Cytherella jonesiana* Bosquet; Oertli, p. 29, pl. 1, figs. 13–17.

Type locality and horizon. Cormeilles-en-Parisis; Couches de Sannois, Bed No. 46 of Girard d'Albissin.

Stratigraphic range and distribution. Couches de Sannois, Cormeilles; basal Marnes à Huîtres, Cormeilles and St. Cloud; these are in the Paris Basin. Blaue Ton of Berne and Basle, Switzerland.

Holotype. Io. 3664, female carapace.

Material. Cormeilles, Bed. No. 46, 13 valves and carapaces; basal Marnes à Huîtres, 1 carapace. St. Cloud, 9 valves and carapaces; Delémont (Switzerland), 6 valves and carapaces. Figured specimens, Pl. 45: Io. 3664–3666.

Dimensions. Female carapaces or right valves from Cormeilles, Bed 46.

	N	$\bar{x}$	*S*	*Range*	*V*
L	10	0·730	0·0200	0·70–0·77	2·7
H	10	0·414	0·0169	0·38–0·43	4·1
L/*H*	10	1·764	0·0364	1·72–1·84	2·1

Holotype, female, Io. 3664: *L*, 0·74; *H*, 0·41; *W*, 0·33.
Male, Io. 3665: *L*, 0·71; *H*, 0·38; *W*, 0·25.
St. Cloud, mean length (7 specimens) of female right valves, 0·761.

Diagnosis. Subspecies of *C. jonesiana* in which marginal ridge is well developed.

Description. Similar to *C. jonesiana jonesiana*, but has very thick, smooth ridge all around anterior, ventral, and posterior margins of both valves. In dorsal view, anterior and posterior parts seen as prominent bulges in outline.

Discussion. The 2 subspecies described above are thought to be stratigraphically significant, i.e. with time the marginal ridge gradually becomes weaker. A second possibility, however, is that the variation in ornamentation is ecologically controlled, i.e. with more marine conditions the ridge gradually becomes weaker. The 1 specimen found at Morigny has lost the marginal ridges almost completely.

Suborder PODOCOPINA Sars 1866
Superfamily CYPRIDACEA Baird 1845
Family CYPRIDIDAE Baird 1845
Genus CYPRIS O. F. Mueller 1776

Type species. Cypris pubera O. F. Mueller.

Diagnosis. Carapace sub-triangular, apex dorsally; anterior higher than posterior. Surface smooth or pitted. Marginal spines at anterior and posterior. Duplicature with well developed selvage.

'*Cypris*' *tenuistriata* Dollfus

Plate 47, fig. 7; text-fig. 4

1877 *Cypris tenuistriata* Dollfus, p. 314, figs. 4*a*, *b*.
1961 *Cypris tenuistriata* Dollfus; Margerie, p. 8, pl. 1, fig. 6; pl. 3, fig. 2.

Type locality and horizon. Romainville; Marnes blanches de Pantin (Ludian).

Stratigraphic range and distribution. Marnes blanches and Bande blanche of the Paris region.

Material. 12 valves from the Bande blanche, Cormeilles, including the figured left valve, Io. 3667 (Pl. 47, fig. 7).

EXPLANATION OF PLATE 46

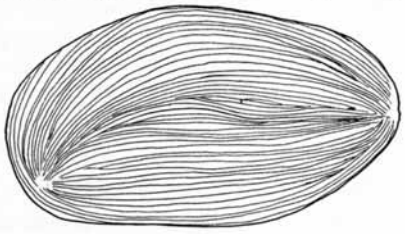
All taken in transmitted light; viewed from outside, except figs. 1, 2, 7.

Figs. 1–4, 6, 7. *Moenocypris forbesi* (Jones). Middle Hamstead Beds, Bouldnor Cliff. 1–3, 6, 7, Left valve, female, Io. 3674; 1, 2, 7, ventral duplicature; 1, ×525; 2, ×125; 7, ×300; positions of figs. 1 and 7 indicated on fig. 2; 3, ×50; 6, Central muscle scars, ×200 (arrow indicates anterior). 4, Right valve, female, Io. 3675, ×60.

Figs. 5, 8–10. *Moenocypris sherborni* sp. nov. Lower Headon Beds, Milford. 5, 10, Holotype, left valve, female, Io. 3676; 5, ×50; 10, central muscle scars, ×200 (arrow indicates anterior). 8, Right valve, female, Io. 3677, ×50. 9, Left valve, female, showing impressions of ovaries, Io. 3678, ×50.

Fig. 11. *Moenocypris reidi* sp. nov. Upper Headon Beds, Headon Hill. Left valve, male, holotype, showing imprint of testes, Io. 3679, ×50.

Discussion. Margerie selected a hypotype from the Bande blanche, Cormeilles-en-Parisis. It is doubtful whether this belongs to the genus *Cypris*; it has the strong selvage and flange groove of the latter, but not the list. Its ornamentation is very distinct, unlike the smooth or punctate *Cypris*, nor does it have the marginal spines or denticles usually developed in the latter. The muscle scars have not been observed. *Zonocypris* Klie has concentric striations, forming complete circuits of the valve, and are not the same as in *C. tenuistriata.* Carbonnel and Ritzkowski (1969) placed their new subspecies *C. tenuistriata straubi* doubtfully in the genus *Cyprinotus.*



TEXT-FIG. 4. '*Cypris*' *tenuistriata* Dollfus, ×75, from the Bande blanche, Cormeilles.

Other similar striated forms are known from the Lymnaean-Mergel (Upper Eocene) to the Hydrobien-Schichten (Upper Aquitainian) of the Rhine Basin (Malz 1962, p. 391, pl. 59, figs. 2, 3*a–c*), Ludian of the Paris Basin, Headon Beds and Bembridge Limestone of the Isle of Wight (Haskins 1968*b*), Lower Oligocene of Hesse (Carbonnel and Ritzkowski 1969), the Upper Miocene of the Rhone Basin (Carbonnel 1969*b*), and from the Pleistocene of Israel (Gerry, pers. comm.). Those from the Ludian of Verzy have a simpler duplicature with a weak selvage; the others have a strong selvage.

Genus CYPRIDOPSIS Brady 1868

Type species. Cypris vidua O. F. Mueller.

Diagnosis. Subcircular in shape, convex dorsal margin; surface punctate or smooth. Large anterior vestibule, numerous short and simple radial pore canals. Muscle scars as for Cyprididae. Hinge adont.

Cypridopsis soyeri (Margerie)

Plate 48, figs. 1–3

1961 *Cyclocypris? soyeri* Margerie, p. 11, pl. 1, figs. 1, 2; pl. 3, fig. 3.

Type locality and horizon. Cormeilles-en-Parisis; Bande blanche.

Stratigraphic range and distribution. Bande blanche, Cormeilles, Montfermeil; Middle Hamstead Beds, Bouldnor Cliff.

Material. Cormeilles, 10 valves; Montfermeil, 3 valves; Bouldnor, 20 valves. Figured specimens, Pl. 48: Io. 3668, 3669.

Dimensions. Left valve, Io. 3668: *L*, 0·49; *H*, 0·31
Right valve, Io. 3669: *L*, 0·43; *H*, 0·26

Discussion and additional description. Margerie was unable to describe certain of the internal characters because of the state of preservation of the Paris material; these are well seen in the Bouldnor specimens. There are 4 central muscle scars, with 2 mandibulars. There are some 38 anterior, 31 ventral, and 16 posterior radial pore canals. The antero-ventral angle is finely denticulate. The surface is seen to be punctate in transmitted light.

This is included in the genus *Cypridopsis* rather than *Cyclocypris* because, following van Morkhoven (1963), the normal pores are small and not widened internally, and the ventral vestibule of *Cyclocypris* is lacking. It differs from *Cyprinotus* in that the right valve is not higher than the left along the dorsal margin.

The species shows much variation in shape, both in the Paris Basin and the Bouldnor material (cf. Margerie 1961, pl. 2, fig. 1; pl. 3, fig. 3).

Genus EUCYPRIS Vavra 1891

Type species. Monoculus virens Jurine.

Diagnosis. Subovate, convex dorsal margin; surface smooth, punctate, or striated. Duplicature with large vestibule, short simple radial pore canals, subperipheral selvage. Hinge adont.

Eucypris amygdala (Dollfus)

Plate 48, figs. 8, 10

1877 *Cypris amygdala* Dollfus, p. 314, figs. 2*a–d.*
1961 *Paracandona? amygdala* (Dollfus); Margerie, p. 9, pl. 3, fig. 1.

Type locality and horizon. Romainville; Marnes blanches de Pantin.

Stratigraphic range and distribution. Marnes blanches and Bande blanche of the Paris region.

Material. 17 valves from Cormeilles. Figured specimens, Pl. 48: Io. 3670, 3671.

Dimensions. Left valve, Io. 3670: *L*, 0·87; *H*, 0·52.
Right valve, Io. 3671: *L*, 0·85; H, 0·47.

Discussion. Margerie selected a hypotype from the Bande blanche, Cormeilles. The species as interpreted by Margerie does not completely agree with Dollfus's original description. Dollfus's illustration shows a very convex dorsal margin, more like that of *E. pechelbronnensis* described below. All of the Sannoisian specimens show a very characteristic ornamentation (see Pl. 48), but Dollfus described his species as being smooth, adding that some specimens under high magnification show 'fines perforations'. There is therefore some doubt as to whether the forms from the Bande blanche are really conspecific with those from the Marnes blanches. The problem is unlikely to be solved in the near future because the present-day exposures of the Marnes blanches are unfossiliferous, and Dollfus's specimens are lost. This illustrates the undesirability of choosing a hypotype from a different horizon to that of the original type.

Although the muscle scars have not been seen in the Paris Basin material, they have been in a related species from Bouldnor. For this reason they are placed in the genus *Eucypris*.

EXPLANATION OF PLATE 47

Figs. 1, 4, 5. *Moenocypris sherborni* sp. nov. Lower Headon Beds, Milford. 5, Ventral duplicature, holotype, Io. 3676; 1, ×90; 5, ×550. 4, Ventral duplicature, Io. 3678, ×550.

Figs. 2, 3, 6. *Moenocypris reidi* sp. nov. Upper Headon Beds, Headon Hill, 2, 3, Ventral duplicature, holotype, Io. 3679, 2, ×250; 3, ×500. 6, Female carapace, dorsal view, Io. 3680, ×50.

Fig. 7. '*Cypris*' *tenuistriata* Dollfus. Left valve, Io. 3667, ×50. Bande blanche, Cormeilles.

Fig. 8. *Candona* (*Pseudocandona*) sp. Right valve, Io. 3688, ×75. Middle Hamstead Beds, Bouldnor Cliff.

Eucypris pechelbronnensis Stchepinsky

Plate 48, fig. 9

1960 *Eucypris pechelbronnensis* Stchepinsky, p. 17, pl. 11, figs. 15, 19.
1961 *Paracandona? amygdala* (Dollfus); Margerie, p. 9 (pars.).

Type locality and horizon. Lampertsloch; Couches à *Mytilus*.

Stratigraphic range and distribution. Couches de Pechelbronn moyen (these include the Couches à *Mytilus*) and supérieur of Alsace.

Material. 5 carapaces and 1 valve (Io. 3672) from Pechelbronn.

Dimensions. Right valve, Io. 3672: *L*, 0·98; *H*, 0·54.

Eucypris sp.

Plate 48, fig. 11

Locality and horizon. Bouldnor Cliff; Middle Hamstead Beds.

Material. 1 left valve (Io. 3673) and several fragments.

Dimensions. Left valve, Io. 3673: *L*, 0·93; *H*, 0·53.

Discussion. This differs from *E. amygdala* by its dorsal outline; it is highest at the anterior end, tapering towards the posterior end, and not subquadrate as in the latter. *E. pechelbronnensis* differs in having a symmetrically convex dorsal margin. The ornamentation is similar to these 2 species, i.e. serrated lines or rows of small papillae forming circular patterns on the valve.

The muscle scars are typical of the Cyprididae, and not at all like those of *Paracandona*, which has the usual 6 scars of the Candonidae. The fused duplicature is wider than in typical *Eucypris*, with longer radial pore canals.

The 3 forms described are obviously closely related. There is the possibility that with abundant material the apparently distinct shapes would be seen as merely parts of a highly variable single species.

Genus MOENOCYPRIS Triebel 1959

Type species. Moenocypris francofurtana Triebel.

Diagnosis. Carapace large, elongate; left valve larger; narrowly ovate in dorsal view. No ornamentation. Large anterior vestibule; ventral duplicature with marginal and submarginal radial pore canals and secondary blind marginal canals.

Description. Carapace large, over 1 mm long, elongate. Left valve larger than right. Greatest height near middle. Dorsal margin convex, ventral margin concave, anterior and posterior margins evenly rounded; posterior end usually larger than anterior. In dorsal view, carapace narrowly ovate, with greatest width slightly to posterior of centre. No ornamentation on valve.

Wide anterior vestibule, with narrow zone of concrescence; radial pore canals short, sometimes branched. Duplicature along venter has complex system of pore canals: long radial pore canals which reach margin, and shorter submarginal canals often alternating and branched. Series of blind secondary canals lie along margin, often complexly branched (e.g. Triebel 1959, pl. 3, figs. 9*a*, *b*). Vestibule of varying size present, better

developed in anterior part. Towards posterior end, isolated round spot sometimes present within vestibular area formed by coalescence of 2 lamellae (e.g. Triebel 1959, pl. 2, figs. 5–7). Selvage peripheral.

Central muscle scars in group of 6 with elongate dorsalmost scar, together with 2 mandibular scars. 10 dorsal muscle scars above central field. Hinge of left valve is narrow groove into which margin of right valve fits.

Sexual dimorphism not very apparent in general shape of carapace, but imprints of ovaries and testes often preserved (Pl. 46, figs. 9, 11).

Discussion. The genus has so far been described from the Oligocene of the Mainz Basin, where Triebel (1959, 1963) described 4 species. The ventral isolated round spot only seems to be present in the younger species from the Upper Oligocene and Miocene (i.e. *M. francofurtana* and *M. ingelheimensis* Triebel). Sönmez (1963) erected a subgenus, *Moenocypris* (*Isomoenocypris*), from the Palaeogene of Turkey. This differs from the nominate subgenus in having a markedly convex dorsal margin and only 1 series of ventral pore canals. As the complicated arrangement of the ventral pore canals is the most characteristic feature of the genus, it is perhaps better to regard Sönmez's taxon as a distinct genus. The type species is *M.* (*I.*) *parmiri* Sönmez.

Moenocypris forbesi (Jones)

Plate 46, figs. 1, 2, 3, 4, 6, 7

1856 *Candona forbesii* Jones, p. 157, pl. 7, figs. 22*a*, *b*.
1857 *Candona forbesii* Jones; Jones, p. 18.
1889 *Candona forbesii* Jones; Jones and Sherborn, p. 13.

Type locality and horizon. Near Parkhurst Lodge, Isle of Wight; Middle Hamstead Beds.

Stratigraphic range and distribution. Hamstead Beds, Isle of Wight.

Lectotype. Mik(T)719003, female left valve.

Material. 18 complete valves from the Middle Hamstead Beds (EBC.81) (figured specimens, Pl. 46: Io. 3674, 3675), together with numerous fragments, especially from the Waterlily Bed; 6 valves from the upper Hamstead *Cerithium* Beds.

Dimensions. Mean of 7 left valves: *L*, 1·183; *H*, 0·579; *L*/*H*, 2·046.
Left valve, Io. 3674: *L*, 1·22; *H*, 0·63; *W*, 0·26.
Right valve, Io. 3675: *L*, 1·08; *H*, 0·54.

EXPLANATION OF PLATE 48

Figs. 1–3. *Cypridopsis soyeri* (Margerie). Middle Hamstead Beds, Bouldnor Cliff. 1, Left valve, internal view, Io. 3668, ×128. 2, Right valve, internal view, Io. 3669, ×168. 3, Central muscle scars, Io. 3669, ×230 (arrow indicates anterior).

Figs. 4–7. *Vecticypris jacksoni* gen. et sp. nov. Middle Hamstead Beds, Bouldnor Cliff. 4, 6, 7, Right valve, holotype, Io. 3681; 4, ×70; 6, central muscle scars, ×400 (arrow indicates anterior); 7, anterior duplicature, ×400. 5, Left valve, Io. 3682, ×145.

Figs. 8, 10. *Eucypris amygdala* (Dollfus). Bande blanche, Cormeilles. 8, Left valve, Io. 3670, ×70. 10, Right valve, Io. 3671, ×60.

Fig. 9. *Eucypris pechelbronnensis* Stchepinsky. Right valve, Io. 3672, ×80; Couches de Pechelbronn moyens, Pechelbronn.

Fig. 11. *Eucypris* sp. Left valve, Io. 3673, ×70; Middle Hamstead Beds, Bouldnor Cliff.

Diagnosis. Species of *Moenocypris* with convex dorsal margin; ventral duplicature with 50–55 radial pore canals and small vestibule.

Description. Dorsal margin convex, with greatest height at about mid-point. Anterior end much narrower than posterior, particularly in left valve.

Ventral radial pore canals relatively few, 50–55. Vestibule small. Secondary pore canals have complex branching marginal end, with 1 fairly long branch extending inwards.

Central muscle scars distinct; dorsalmost scar oval; mandibular scars short. 10 dorsal muscle scars.

Discussion. The 3 species described here, *M. forbesi*, *M. sherborni* sp. nov. and *M. reidi* sp. nov., are considered to be parts of a continuous phylogenetical sequence. The shape changes from one where the dorsal margin to the posterior of the highest point is almost straight, to one where it is decidedly convex. The number of ventral radial pore canals, and the size of the vestibular area along the ventral margin, decrease. Within each population all these features show considerable variation, and the individual features probably overlap between species; however, when all features for each individual, but preferably for each population, are considered, 3 distinct groups can be seen. They are described here as stratigraphically arranged species.

Moenocypris sherborni sp. nov.

Plate 46, figs. 5, 8–10; Plate 47, figs. 1, 4, 5

1857 *Candona forbesii* Jones; Jones, p. 18 (pars), pl. 4, figs. 11*a*, *b*.

Type locality and horizon. Paddy's Gap, Milford; Lower Headon *Unio* Beds.

Stratigraphic range and distribution. So far only known at the type locality.

Holotype. Io. 3676, female left valve.

Material. Numerous valves from Milford. (Figured specimens, Pls. 46, 47: Io. 3676–3678.) Also in the British Museum (Natural History), 1 broken valve figured by Jones, I.620.

Dimensions.

Left	*N*	$\bar{x}$	*S*	*Range*	*V*
L	23	1·173	0·0352	1·11–1·25	3·0
H	23	0·567	0·0221	0·53–0·61	3·9
L/*H*	23	2·067	0·0481	1·95–2·13	4·3

Holotype, left valve, female, Io. 3676: *L*, 1·25; *H*, 0·61; *W*, 0·29.
Right valve, female, Io. 3677: *L*, 1·07; *H*, 0·53.

Diagnosis. Species of *Moenocypris* in which posterior part of dorsal margin is almost straight. Ventral duplicature with large vestibular areas and numerous radial pore canals.

Description. Dorsal margin unevenly convex, with highest point near middle. Posterior part of dorsal margin at almost same height as highest point. Margin tapers towards anterior end.

Anterior duplicature has several faint striations. Numerous ventral radial pore canals, *c.* 75. Ventral vestibular areas large, wide, although width varies from specimen to specimen (cf. Pl. 47, figs. 1, 5 with fig. 4). In some specimens, vestibule so wide that

submarginal pore canals extremely short. Some radial pore canals seen to branch. Secondary marginal canals complex, with short branch reaching inwards.

Dorsalmost scar of central group has figure-of-eight shape. Mandibular scars elongate. Imprints of sexual organs clearly seen.

Discussion. The dorsal margin of *M. forbesi* (Jones) is more convex, particularly at the posterior end; the ventral duplicature of the latter is simpler, with fewer radial pore canals and smaller vestibular areas; the dorsalmost of the central muscle scars is less compressed in the middle in *M. forbesi.*

M. olmensis Triebel has similar large vestibular areas, but has a much more convex dorsal margin. *M. ingelheimensis* also has wide vestibular areas, but has the isolated round spot developed, and a more convex posterior part to the dorsal margin.

Moenocypris reidi sp. nov.

Plate 46, fig. 11; Plate 47, figs. 2, 3, 6

1857 *Candona forbesii* Jones, p. 18 (pars), pl. 4, figs. 8, 9.
1968 *Candona forbesii* Jones; Haskins, p. 6, pl. 1, figs. 10, 16.

Type locality and horizon. Headon Hill; Upper Headon Beds.

Stratigraphic range and distribution. Upper Headon Beds: Headon Hill, Whitecliff Bay; Osborne Beds: Cliff End, Whitecliff Bay.

Holotype. Io. 3679, male left valve.

Material. Numerous valves from most of the above localities, but none from Cliff End (reported after Jones 1857). Figured specimens, Pls. 46, 47: Io. 3679, 3680.

Dimensions. Mean of 6 left valves and carapaces: *L*, 1·290; *H*, 0·675; *L*/*H*, 1·965.
Holotype, left valve, Io. 3679: *L*, 1·27; *H*, 0·66; *L*/*H*, 1·92.
Female carapace, Io. 3680: *L*, 1·31; *H*, 0·66; *W*, 0·56.

Diagnosis. Species of *Moenocypris* with convex dorsal margin. Ventral vestibular areas large; 55 ventral radial pore canals.

Description. Dorsal margin more convex than in *M. sherborni*, but posterior part not evenly convex as in *M. forbesi.* Ventral duplicature has *c.* 55 radial pore canals, i.e. same number as *M. forbesi*; vestibular areas, however, almost as large as in *M. sherborni.* Secondary marginal canals not clearly seen, nor muscle scars. Imprints of sexual organs seen.

Discussion. Much of the material is poorly preserved, especially that from the Osborne Beds. The specimens from the type horizon and locality are the largest members of the genus recorded from the Hampshire Basin. The *L*/*H* ratio is smaller than that for *M. forbesi* and *M. sherborni.*

Moenocypris? nuda (Dollfus)

1877 *Cypris nuda* Dollfus, p. 314, figs. 3 *a*, *b*.
1961 *Cryptocandona? nuda* (Dollfus); Margerie, p. 10, pl. 3, fig. 4.

Type locality and horizon. Romainville; Marnes blanches de Pantin.

Stratigraphic range and distribution. Marnes blanches, Bande blanche, and Calcaire de Brie of the Paris region.

Material. 5 incomplete valves from the Bande blanche, Cormeilles; 4 incomplete valves from the Calcaire de Brie, Montfermeil.

Discussion. Margerie selected a hypotype from the Bande blanche, Cormeilles-en-Parisis. This was placed in the genus *Cryptocandona* by Margerie. The muscle scars, however, are clearly typical of the Cyprididae and resemble those of *Moenocypris*. The 2 dorsal angles are sharper than in typical *Moenocypris*. The ventral duplicature could not be seen, so its generic position is still in doubt.

Genus VECTICYPRIS gen. nov.

Type species. Vecticypris jacksoni sp. nov.

Diagnosis. Carapace small, sub-ovate; left valve larger; no ornamentation. Hinge lophodont. Duplicature with strong selvage and flange groove, small anterior vestibule, few radial and normal pore canals. Vertical row of 4 muscle scars.

Description. Only 1 species is referred to genus, so that generic description must be regarded as incomplete. For description see *V. jacksoni.*

Discussion. The lophodont hinge and row of 4 muscle scars distinguish this from such genera as *Cyprinotus*, *Cypridopsis*, *Cyclocypris*, and *Cypria*. These features also place doubt on its assignment to this family. However, its general appearance and occurrence in freshwater sediments suggest this more than any other family.

Vecticypris jacksoni sp. nov.

Plate 48, figs. 4–7; text-fig. 5

Type locality and horizon. Bouldnor Cliff; Middle Hamstead Beds (EBC.76).

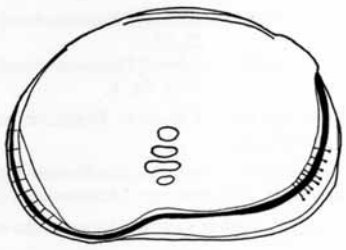
Stratigraphic range and distribution. So far only known from the type locality.

Holotype. Io. 3681, right valve.

Material. 35 valves and carapaces (including Io. 3682–3684).

Dimensions. Holotype, right valve Io. 3681: *L*, 0·39; *H*, 0·27; *W*, 0·17.
Carapace (normal), Io. 3683: *L*, 0·36; *H*, 0·24; *W*, 0·26.
Carapace (inflated), Io. 3684: *L*, 0·38; *H*, 0·26; *W*, 0·31.

Diagnosis and description. Dorsal margin, particularly of right valve, asymmetrically convex, steepest at posterior. Anterior margin obliquely rounded. Ventral margin concave in anterior third. Posterior margin evenly rounded, with tendency towards being straight in right valve. Posterior end higher than anterior; greatest height just to posterior of middle. In dorsal view, carapace inflated, widest at posterior end; 1 carapace extremely inflated at posterior (Io. 3684), but not known whether due to sexual dimorphism.



TEXT-FIG. 5. *Vecticypris jacksoni* gen. et sp. nov., ×150, from the Middle Hamstead Beds, Bouldnor Cliff.

Hinge lophodont. Right valve has 2 simple,

elongate terminal teeth with groove between; anterior tooth longer than posterior. Corresponding elements in left valve, but no true sockets, and 'sockets' seen to be in continuity with 'bar'. Hinge continuous with selvage.

Duplicature narrow at anterior end, with small vestibule and 10 short, simple, radial pore canals. Selvage very strong, particularly prominent in right valve; sub-peripheral at anterior end, but close to inner margin along venter and posterior. Flange strong; wide flange groove along venter and posterior, forming platform in right valve. At posterior end, 8 radial pore canals open into flange groove. About 16 ventral radial pore canals observed. About 30 scattered simple normal pore canals.

Central muscle scars consist of vertical row of 4, central 2 being elongate.

Family CANDONIDAE Kaufmann 1900
Genus CANDONA Baird 1845

Type species. Cypris candida O. F. Mueller 1776.

Diagnosis. Carapace asymmetric with greatest height at posterior; dorsal margin very convex with steep slope to posterior and long, more gentle slope to anterior. Anterior end narrower than posterior. Large anterior vestibule, with numerous short anterior radial pore canals. 6 central muscle scars with characteristic pattern. Hinge adont. Left valve larger. Surface usually smooth in adults, sometimes punctate in larval stages.

Subgenus CANDONA (PSEUDOCANDONA) Kaufmann 1900

Type species. Cypris pubescens Koch 1838.

Diagnosis. Differs from nominate subgenus mainly in soft parts, particularly male antennae. Normal pore canals more densely packed, and larval stages punctate (Triebel 1963, p. 166).

Candona (*Pseudocandona*) *fertilis* Triebel

Diagnosis. $L/H = 1{\cdot}67$. Anterior margin almost evenly rounded; highest point about $\frac{1}{3}$ from posterior.

Candona (*Pseudocandona*) *fertilis fertilis* Triebel

Plate 49, figs. 1, 2, 5, 7, 9

1963 *Candona* (*Pseudocandona*) *fertilis fertilis* Triebel, p. 167, pl. 27, figs. 19–22; pl. 28, figs. 23–29.

1969 *Candona* (*Pseudocandona*) *fertilis fertilis* Triebel; Carbonnel and Ritzkowski, pp. 63–65, pl. 3, fig. 8.

Type locality and horizon. Frankfurt-am-Main; Upper Oligocene Süsswasser Fazies of the Oberen Cyrenenmergel.

Stratigraphic range and distribution. Upper Oligocene of the Mainz Basin; Couches de Pechelbronn supérieur, Pechelbronn; Melanienton, Hesse.

Material. 2 adult valves, 9 larval stage valves. Figured specimens, Pl. 49: Io. 3685–3687.

Discussion. There is a slight difference in the shape of the posterior margin of the specimens from Pechelbronn; the dorsal part of the posterior margin is less curved than in those from the type locality. Comparing Triebel's figures (pl. 27, figs. 19, 21),

there is variation, however, in the shape of the posterior margin amongst the type specimens.

Candona (*Pseudocandona*) sp.

Plate 47, fig. 8

Material. Io. 3688, juvenile right valve.

Discussion. The larval stages of this species are quite commonly found in the Middle Hamstead Beds. 1 penultimate moult stage has been found. As the larval stages of this genus are almost indistinguishable specifically, this particular species cannot be identified until an adult valve has been discovered.

Genus LINEOCYPRIS Zalanyi 1929

Type species. Lineocypris trapezoidea Zalanyi.

Diagnosis. Trapezoidal in shape, left valve larger, straight dorsal margin. Internal features similar to *Candona*.

Lineocypris sp.

Plate 49, figs. 3, 4, 6, 8

Locality and horizon. Lowest Calcaire de Brie, Montfermeil.

Material. 1 broken adult valve, 4 larval valves and carapaces. Figured specimens, Pl. 49: Io. 3689–3690.

Description. Dorsal margin almost straight, with rounded anterior margin and almost straight posterior margin sloping downwards to postero-ventral angle.

Adult has wide anterior vestibule with 45 radial pore canals, in two groups, thin canals extending to margin, and thicker ones, only submarginal, of varying length. Central muscle scars consist of 6 scars typical of Candonidae.

Family ILYOCYPRIDIDAE Kaufmann 1900
Genus ILYOCYPRIS Brady and Norman 1889

Type species. Cypris gibba Ramdohr 1808.

Diagnosis. Dorsal margin straight, greatest height near anterior end, left valve largest. Surface punctate with prominent centro-dorsal depressions, sometimes with tubercule; central muscle scars lie on raised areas which coincide with external depressions; 6 central muscle scars and 2 prominent mandibulars. Marginal spines developed. Anterior vestibule large, list developed, simple radial pore canals.

Ilyocypris boehli Triebel

Plate 45, figs. 11, 14, 15

1889 *Cypris gibba* Jones and Sherborn (*non* Ramdohr), p. 9 (pars).
1928 *Cypris gibba* Böhl (*non* Ramdohr), p. 90 (pars).
1941 *Ilyocypris böhli* Triebel, p. 381, pl. 1, figs. 7 *a*, *b*.
1960 *Ilyocypris* cf. *bradyi* Sars; Stchepinsky, p. 21, pl. 2, figs. 22, 23.
?1963 *Ilyocypris* sp. Stchepinsky, p. 157.
?1963 *Ilyocypris* sp. Triebel, p. 181.

Type locality and horizon. Frankfurt-am-Main (Osthafen); Cyrenenmergel.

Stratigraphic range and distribution. Cyrenenmergel of the Mainz Basin (Upper Oligocene); Couches de Pechelbronn inférieur and Marnes à Cyrènes, Alsace; Bande blanche, Cormeilles and Montfermeil; Argile à *N. comta* of Belgium; Middle Hamstead Beds of England.

Material. 29 valves from the Middle Hamstead Beds (specimens Io. 3691–3693); 20 valves from Cormeilles; 6 valves from Montfermeil; 2 valves from Bilzen.

Dimensions. Right valve, Io. 3691: *L*, 0·84; *H*, 0·43; *L*/*H*, 1·91.

Diagnosis. Species of *Ilyocypris* with spinose central elevation in dorsal depression; small marginal spines sometimes present.

Description. Valves weakly calcified. Sexual dimorphism not observed. Highest point about $\frac{1}{4}$ way from anterior end; dorsal margin almost straight with faint depression $\frac{2}{5}$ way from posterior end. Antero-dorsal angle distinctly straight. Anterior margin evenly rounded; ventral margin concave; posterior margin evenly rounded with fairly sharp postero-dorsal angle. Left valve larger than right.

Surface punctate, with dorsal depressions as for genus. Central elevation of dorsal depressions forms distinct spine in some specimens, whereas in others it is tuberculate. Small spines around anterior, ventral, and posterior margins of some specimens, not along margins, but irregularly dispersed near margins; 60–70 spines, about half at anterior end. Very small denticles also along anterior margin, closely connected with radial pore canals.

Hinge and muscle scars as for genus (Pl. 45, figs. 11, 14). Duplicature has wide vestibule, and list present on latter. Outline of line of concrescence has series of embayments apparently connected with spines on outer surface. Radial pore canals short, simple, widest at base; *c.* 54 anterior, 28 ventral, and 16 posterior radial pore canals, and 50–60 small, normal pore canals.

Discussion. Most of the specimens from England and the Paris Basin have marginal spines, but *I. boehli* as described by Triebel does not have them. However, in shape and in the development of the dorsal depressions it is impossible to differentiate the species. The number of spines varies from specimen to specimen, and their presence is considered to be an infra-specific character.

The specimens from Hamstead were at first considered to be immature or weakly calcified specimens of *I. cranmorensis* sp. nov., described below. However, they are as large or larger in size, although never found together; the duplicature of *I. boehli* is well developed and similar to that described by Wagner (1957) for the type species, and there are more anterior radial pore canals. Therefore, it is certainly an adult form. The difference between these 2 might be ecologically controlled, but if so, it is of a nature so far undescribed for any other ostracod.

EXPLANATION OF PLATE 49

All taken in transmitted light, viewed from outside.

Figs. 1, 2, 5, 7, 9. *Candona* (*Pseudocandona*) *fertilis fertilis* Triebel. Couches de Pechelbronn moyen, Pechelbronn. 1, Right valve, larval, Io. 3685, ×95, *L* = 0·50 mm. 2, 7, 9, Left valve, Io. 3686, *L* = 0·78 mm; 2, ×95; 7, central muscle scars, ×450 (arrow indicates anterior); 9, anterior duplicature, ×300. 5, Right valve, Io. 3687, ×95, *L* = 0·75 mm.

Figs. 3, 4, 6, 8. *Lineocypris* sp. Calcaire de Brie, Montfermeil. 3, 6, 8, Broken right valve, Io. 3689, *H* = 0·40 mm; 3, ×90; 6, anterior duplicature, ×260; 8, central muscle scars, ×450 (arrow indicates anterior). 4, Left valve, larval, Io. 3690, ×90, *L* = 0·46 mm.

The species differs from *I. gibba* (Ramdohr) in the lack of tuberculate spines and from *I. bradyi* Sars in shape; the anterior of the latter is markedly asymmetric towards the venter, and the central elevation of the dorsal depressions is much stronger in *I. boehli*, which is also smaller.

Ilyocypris cranmorensis sp. nov.

Plate 45, figs. 12, 13

Type locality and horizon. Bouldnor Cliff; Lower Hamstead Beds (EBC.65).

Stratigraphic range and distribution. So far known only from the type locality.

Holotype. Io. 3694, left valve.

Material. Numerous valves from EBC.65 (Io. 3695–3698).

Dimensions.

	L	*H*	*L*/*H*
Left valve, Io. 3694, holotype	0·74	0·41	1·80
Right valve, Io. 3695	0·69	0·39	1·78

Diagnosis. Species of *Ilyocypris* with weak dorsal depressions; narrow vestibule, long radial pore canals; tapered towards posterior.

Description. Valves strongly calcified. Sexual dimorphism not observed. Left valve larger than right. Greatest height about $\frac{1}{4}$ way from anterior end; dorsal margin slightly convex in posterior part, then depression just to posterior of centre, and anterior part convex, but larger than posterior. Anterior margin evenly rounded; ventral margin concave; posterior margin evenly rounded. Overall impression of tapering towards posterior.

Surface punctate. Dorsal depressions smooth, without tubercules or spines. Some specimens seen to have finely denticulate anterior margin, connected with radial pore canals.

Hinge and muscle scars as for genus. Duplicature of moderate width with narrow vestibule. Selvage peripheral; prominent list on fused part of duplicature. Radial pore canals long, simple, irregularly curved, thicken towards base. 35–40 anterior, 25 ventral, and 22–25 posterior radial pore canals, and *c.* 55 small, simple normal pore canals.

In some valves, imprints of ovaries seen in posterior half, consisting of 3 parallel lines running from position just to posterior of central muscle scars towards postero-ventral angle; 2 other parallel lines run obliquely into these from just below central muscle scars. At postero-ventral angle they curve round parallel to margin and finish near postero-ventral angle. Similar to ovaries of *I. bradyi* illustrated by Müller (1900).

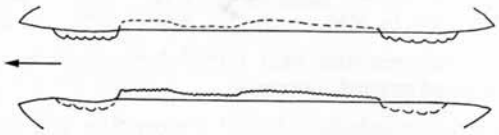
Discussion. The duplicature differs from that of the type species (Wagner 1957) in lacking the large vestibule and the numerous short radial pore canals; the list is on the fused part of the duplicature and not on the vestibule as in other species. It differs from *I. boehli* in the points listed above, and from *I. bradyi* in shape.

Superfamily CYTHERACEA Baird 1850
Family LIMNOCYTHERIDAE Klie 1938
Genus CLADAROCYTHERE gen. nov.

Type species. Limnocythere apostolescui Margerie 1961.

Diagnosis. Valve generally thin, elongate; distinct sexual dimorphism. Surface smooth or reticulate, nodes sometimes developed. Hinge weak, with crenulate terminal elements, median element divided into 3; terminal teeth in right valve, hinge bar in left. Few radial pore canals. 4 adductor muscle scars, 2 frontals, 2 mandibulars.

Description. Carapace elongate, showing pronounced sexual dimorphism; males much more elongate with strong lateral swellings. Left valve larger. 2 swellings, 1 in postero-dorsal position and other antero-ventrally. Surface ornamentation varies within species; some specimens have strong reticulation, others smooth. Strength of reticulation perhaps ecologically controlled (see palaeoecology). Nodes may be developed and seem to have constant distribution; each 'node' consists of mass of smaller ones joined laterally or formed on top of each other. In this respect, resemble those in *Neocyprideis* and *Cyamocytheridea*, rather than *Cyprideis* and *Hemicyprideis*.



TEXT-FIG. 6. The hinge of *Cladarocythere* gen. nov. This exaggerated and schematic drawing should be compared with Plate 50.

Hinge (text-fig. 6) has crenulate terminal elements, posterior being only weakly so. Median element, consisting of bar in left valve, divisible into 3 unequal parts; central part does not project as far as terminal parts. Anterior part, about $\frac{1}{5}$ of hinge bar, always crenulate; other parts smooth or crenulate. Whole of hinge very weakly developed; well-preserved material needed for study.

4 adductor muscle scars and 2 frontals. 1 frontal is 'V' shaped, other small, circular, and lies within 'V', or very close to it. 2 mandibular scars, an elongate scar level with frontal scars and dorsalmost adductor, and second behind it, much closer to the ventral margin.

Radial pore canals few (about 8 at anterior end), simple. Selvage along anterior margin, but sub-peripheral at posterior, where narrow flange groove present; flange

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EXPLANATION OF PLATE 50

Arrows indicate anterior.

Figs. 1–4, 6, 9–12, 14–16. *Cladarocythere apostolescui* (Margerie). Bembridge Limestone, Bouldnor Cliff (EBC.2). 1, Right valve, female, Io. 3709, ×70. 2, Right valve, male, Io. 3710, ×70. 3, Left valve, female, Io. 3707, ×70. 4, 9, 10, 11, 12, Left valve, male, Io. 3708; 4, internal view, ×70; 9, hinge bar, ×200; 10, hinge bar showing tripartite division (note also weakness of hinge), ×140; 11, posterior socket of hinge, ×375; 12, anterior socket of hinge, ×375. 6, 14, 15, 16, Right valve, male, Io. 3706; 6, internal view, ×70 (note the 2 mandibular scars); 14, posterior tooth of hinge, ×400; 15, anterior tooth of hinge, ×400; 16, central muscle scars, ×375.

Figs. 5, 7, 8, 13. *Cladarocythere hantonensis* sp. nov. Upper Headon Beds, Headon Hill. 5, Left valve, female, holotype, Io. 4022, ×70. 7, Right valve, female, Io. 4023, ×70. 8, Right valve, male, Io. 4119, ×70. 13, Central muscle scars, left valve, male, Io. 4092, ×400.

groove and flange along venter. Inner margin and line of concresence coincide. Normal pore canals prominent, small, apparently simple; no sieve-type pore canals seen.

Discussion. 4 closely related species are included in the new genus:

C. apostolescui (Margerie)
C. fragilis (Lienenklaus)
C. fredericensis (Apostolescu)
C. hantonensis sp. nov.

C. fragilis was described from the Cyrenenmergel of the Mainz Basin; *Cytheridea spathacea* Lienenklaus is the male dimorph (Triebel, pers. comm.). These are illustrated in the original description (Lienenklaus 1905) on pl. 4, figs. 22*a–c* (*C. fragilis*), and figs. 23*a*, *b* (*C. spathacea*). *C. fredericensis* was described from thu Letetian V of the Paris Basin and placed in the genus *Perissocytheridea*. A form described by Bate (1965) as *Limnocythere* sp. A from the Bathonian of Oxfordshire may also belong here. Excluding this, however, the range for the genus to date is Middle Eocene–Upper Oligocene.

Cytherissa Sars 1925 differs in its simple lophodont hinge, larger and fewer normal pore canals, small anterior vestibule, and generally larger size. Keij (1957) included *C. fragilis* (identified as *C. spathacea*) in *Cytherissa*. *Limnocythere* Brady 1868 differs in its weak lophodont hinge, presence of marginal denticles and false marginal pore canals, and general lateral outline. *Perissocytheridea* Stephenson 1938 and its possible synonym *Ilyocythere* Klie 1939 differ by their stronger entomodont–merodont hinge, fewer and larger normal pore canals, general lateral outline, and lack of such pronounced sexual dimorphism. All 4 of the above genera have sieve-type normal pore canals, and none seem to have the small circular frontal muscle scar.

Cladarocythere is placed in the Limnocytheridae on account of the hinge, duplicature, radial pore canals, muscle scars, and general shape.

Cladarocythere apostolescui (Margerie)

Plate 50, figs. 1–4, 6, 9–12, 14–16; Plate 56, fig. 13

?1957 *Cytherissa spathacea* Keij (*non* Lienenklaus), p. 73, pl. 2, figs. 19, 20.
1961 *Limnocythere apostolescui* Margerie, p. 12, pl. 1, figs. 7–11; pl. 3, figs. 5, 6.

Type locality and horizon. Cormeilles-en-Parisis; Glaises à Cyrènes.

Stratigraphic range and distribution. France: Glaises à Cyrènes of Cormeilles, Neuilly Plaisance Montfermeil, and Frépillon; Marnes vertes of Cormeilles, and Neuilly Plaisance; Calcaire de Brie of Montfermeil. England: marls below topmost Bembridge Limestone of Hamstead, Thorness Bay, and Whitecliff Bay; Bembridge Oyster Marls of Hamstead. Belgium: Couches de Oude Biezen and Argile à *N. comta* of Bilzen (but see below).

Material. Numerous valves from most of the above localities; 2 valves from the Calcaire de Brie, 1 valve from Bilzen. Figured specimens, Pl. 50: Io. 3706 (also Pl. 56)–3710. Others: Io. 3699–3701.

Dimensions. For the French material see text-fig. 12. Female left valves from Hamstead:

	N	$\bar{x}$	*S*	*Range*	*V*
L	31	0·637	0·0323	0·58–0·73	5·1
H	31	0·326	0·0178	0·30–0·37	5·5
L/*H*	31	1·954	0·0358	1·88–2·03	1·8

Mean of 6 male left valves: *L*, 0·767; *H*, 0·365; *L*/*H*, 2·101.

Diagnosis. Species of *Cladarocythere* with almost straight dorsal margin in female and with female left valve L/H ratio of 1·96; posterior margin of male asymmetrically rounded.

Description. Female left valve rectangular. Dorsal margin of left valve slightly convex with highest point about $\frac{1}{5}$ way from anterior margin, where slight hinge-ear developed. Dorsal swelling overhangs margin in posterior half. Anterior margin evenly rounded. Valve slightly tapered towards posterior in most of French specimens, while English specimens, and few of French, appear more quadrate. In dorsal view, carapace ovate with widest point near centre or slightly to posterior of centre. Right valve similar to left but smaller. English specimens have fringe along posterior part of ventral margin and at postero-ventral angle, giving posterior margin decidedly asymmetrical appearance; only seen in better preserved specimens, and remains of it seen in some of French material. Male has greatest height about $\frac{1}{4}$ way from posterior; dorsal outline shows strong convexity of postero-dorsal swelling, which overhangs margin. Ventral margin has strong concavity in anterior third partly hidden by antero-ventral swelling; posterior part convex. Posterior margin obliquely rounded, with gentle curve into posterior convexity of ventral margin. In dorsal view, widest point to anterior of centre. Ratio of presumed males to females: French specimens, 1:3·5; English, 1:5·0.

In lateral view, valve has 2 large swellings, more exaggerated in males; larger in postero-dorsal position, other in antero-ventral position; tend to merge into each other so that inconspicuous in dorsal view. Nodes on some specimens, especially larval stages, resulting in faint depression on interior of valve. 2 prominent nodes in dorsal and ventral positions about $\frac{2}{5}$ way from posterior; irregular group developed along crest of antero-ventral swelling; another situated in sub-central position. Surface smooth or reticulate; reticulation faint or strong, and tendency for anterior part of valve to become smooth.

Size of specimens shows great range, and separation of moult stages particularly difficult (see palaeoecology section). Shape also shows considerable variation.

Discussion. Differences exist between the English and French specimens. Originally these were interpreted as representing 2 different species, and the English forms were listed (Keen 1968) as *C. bembridgica* Keen MS. After studying the specimens with the aid of the scanning electron microscope, it is now thought that specific separation cannot by justified.

C. fragilis (Lienenklaus) differs in dorsal outline; the female is more strongly convex and the male has a pronounced convexity in the anterior region. The swellings of the male are more subdued in *C. fragilis* and the posterior margin is less asymmetrically rounded. The postero-median hinge element is crenulate.

The specimens described by Keij (1957) from Oude Biezen are similar to *C. apostolescui*, although the postero-dorsal margin is more evenly curved. The few valves are poorly preserved, however, and the 1 specimen obtained from Bilzen is a larval stage. There is therefore some doubt as to the specific determination of the material.

Cladarocythere hantonensis sp. nov.

Plate 50, figs. 5, 7, 8, 13

Type locality and horizon. Headon Hill, Isle of Wight; Upper Headon Beds, the *Theodoxus planulatus* Bed.

Stratigraphic range and distribution. Middle Headon Beds of Headon Hill, Whitecliff Bay, and Milford; Upper Headon Beds of Headon Hill and Whitecliff Bay.

Holotype. Io. 4022, female left valve.

Material. Specimens from the above localities. Figured specimens, Pl. 50: Io. 4022, 4023, 4092, 4119.

Dimensions.

	L	*H*	*L*/*H*
Holotype, female left valve, Io. 4022	0·66	0·36	1·86
Mean of 10 female left valves	0·623	0·332	1·88

Diagnosis: Species of *Cladarocythere* with tapered lateral outline, and *L*/*H* ratio for female left valve of 1·88.

Description. Similar to type species, but differs in following respects. Shape in lateral outline, especially female, has tapered appearance with highest point near anterior margin. Posterior margin asymmetrically rounded and much less quadrate than even French specimens of type species. Median sulcus developed. *L*/*H* ratio, at 1·88, shows less elongate form. Internally, middle 2 adductor muscle scars more elongate than in *C. apostolescui.*

Discussion. This differs from the type species in the points mentioned, and from *C. fragilis* in dorsal outline. *C. fredericensis* also differs in dorsal outline, and appears to be more heavily calcified than the other members of the genus.

Family CYTHERIDEIDAE Sars 1925
Subfamily CYTHERIDEINAE Sars 1925
Genus CYTHERIDEA Bosquet 1852

Type species. Cythere muelleri von Münster 1830.

Diagnosis. Inequivalve, left valve larger; tapered towards posterior, highest point just to anterior of centre; ventral margin almost straight. Anterior and posterior marginal spines present. Hinge of right valve crenulate, 2 terminal sockets, median element with posterior bar and short anterior groove.

Cytheridea pernota Oertli and Keij

Plate 56, fig. 2

1955 *Cytheridea pernota* Oertli and Keij, p. 19, pl. 1, figs. 1–13, text-fig. 2.
1956 *Cytheridea pernota* Oertli and Keij; Oertli, p. 36, pl. 2, figs. 33–38.
1957 *Cytheridea pernota* Oertli and Keij; Keij, p. 56, pl. 3, figs. 22–26; pl. 4, fig. 19.
1960 *Cytheridea pernota* Oertli and Keij; Mehrotra, p. 76 (pars).
1963 *Cytheridea pernota* Oertli and Keij; Stchepinsky, p. 158.

Type locality and horizon. Kleine Spouwen; Argile à *N. comta.*

Stratigraphic range and distribution. Additional localities to those listed by the authors are—Paris Basin: Marnes vertes, Artimont; Couches de Sannois supérieur, Cormeilles; Marnes à Huîtres, Cormeilles, St. Cloud; Falun de Jeurre, Jeurre, Auvers-St.-Georges; Falun de Morigny, Morigny. Isle of Wight: Upper Hamstead Beds, Bouldnor. Alsace: Marnes à Cyrènes.

Thus the total range for this species is now: Belgium, Upper Tongrian–Lower Rupelian; Switzerland, Rupelian–Chattian; France, Sannoisian–Stampian; England, Sannoisian–Stampian.

Material. Bouldnor, 9 valves, Artimont, 1 valve; other Paris Basin localities, numerous valves; Bilzen, 10 valves. Registered specimens: Io. 3712 (Pl. 56), 3711.

Discussion. Amongst the detailed synonymy given by the authors were 3 species recorded by Jones; these are *Cytheridea mulleri* (1857), *C. mulleri* var. *torosa* Jones 1857 and *Cytheridea debilis* Jones 1857. They are queried in Oertli and Keij's synonmy, and can now be eliminated from it. In addition it is thought here that *Cytheridea mulleri* von Münster (Lienenklaus 1895, p. 143) could be added to the synonymy.

Cytheridea? eberti Lienenklaus

1894 *Cytheridea eberti* Lienenklaus, p. 227, pl. 15, figs. 6*a–c*.
1895 *Cytheridea eberti* Lienenklaus; Lienenklaus, p. 145.
1905 *Cytheridea praesulcata* Lienenklaus, p. 39, pl. 3, fig. 17.
1956 *Cytheridea eberti* Lienenklaus; Oertli, p. 38, pl. 2, figs. 51–54.
1957 *Cytheridea praesulcata* Lienenklaus; Keij, pl 57, pl. 3, fig. 16; pl. 4, figs. 3, 4.
1965 '*Cytheridea*' *praesulcata* Lienenklaus; Moyes, p. 34, pl. 4, figs. 5, 6.

Type locality and horizon. Alzey; Cyrenenmergel.

Stratigraphic range and distribution. Germany: Chattian of Mainz and Kassel; Switzerland: Rupelian and Chattian; Paris Basin: Stampian; Belgium: Upper Tongrian–Lower Rupelian; England: Sannoisian; Aquitaine: Lower Miocene.

Material. Marnes à Huîtres, Cormeilles, 4 valves; Auvers-St.-Georges, 20 valves; Upper Hamstead *Cerithium* Beds, Bouldnor, 14 valves; Argile à *N. comta*, Bilzen, 8 valves. Registered specimens: Io. 3713–3715.

Discussion. Oertli (1956) considered *C. eberti* to be synonymous with *C. praesulcata*. Moyes (1965) mentioned that it probably does not belong to the genus *Cytheridea*, having a straighter hinge and a wider anterior marginal zone with more numerous radial pore canals. It also differs in lateral outline, resembling *Clithrocytheridea*. It is thought that Moyes is correct, but a study of topotype material is necessary before any further steps are taken. The Lower Oligocene material studied differs slightly from the Upper Oligocene type, particularly in the outline of the posterior margin.

Genus CYAMOCYTHERIDEA Oertli 1956

Type species. Bairdia punctatella Bosquet 1852.

Diagnosis. Ovate, not normally tapered towards posterior as with *Cytheridea* and *Haplocytheridea*. Well developed anterior vestibule, unlike 2 genera named above or *Hemicyprideis*.

Cyamocytheridea punctatella (Bosquet)
Cyamocytheridea punctatella punctatella (Bosquet)

Plate 56, fig. 16

Type locality and horizon. Jeurre, Falun de Jeurre.

Material. 15 valves from Auvers-St.-Georges including figured right valve, Pl. 56, Io. 3716.

Cyamocytheridea punctatella producta Margerie

Plate 52, fig. 10

1961 *Cyamocytheridea punctatella producta* Margerie, p. 14, pl. 2, fig. 8; pl. 3, figs. 10, 11.

Type locality and horizon. Cormeilles-en-Parisis; Marnes à Huîtres.

Stratigraphic range and distribution. Marnes vertes, Artimont; Couches de Sannois supérieur, Cormeilles; Marnes à Huîtres, Cormeilles, St. Cloud; Upper Hamstead *Corbula* Beds, Bouldnor.

Material. Artimont, 1 valve; Bouldnor, 3 valves. Numerous valves from the other localities. Registered specimens: Io. 3717 (Pl. 52), 3718.

Discussion. This differs from the nominate subspecies in having a more convex dorsal margin, particularly in the left valve.

Genus PONTOCYTHERE Dubowsky 1939

Type species. Pontocythere tchernjawskii Dubowsky 1939.

Diagnosis. Carapace elongate. Hinge of right valve with elongate anterior tooth, shorter median bar, crenulate posterior tooth. Large anterior vestibule.

Pontocythere therwilensis Oertli

1956 *Pontocythere therwilensis* Oertli, p. 57, pl. 6, figs. 152–155.
1963 *Pontocythere therwilensis* Oertli; Stchepinsky, p. 160.

Discussion. This was recorded by Margerie (1961) from the Couches de Sannois supérieur. Amongst the samples examined only 1 specimen of the genus was found, a poorly preserved larval stage, which was not specifically determinable.

The species is recorded from the Cyrenenmergel of Switzerland (Oertli 1956) and the Marnes à Cyrènes of Alsace (Stchepinsky 1963), which are of Chattian and Upper Stampian age respectively.

Genus HEMICYPRIDEIS Malz and Triebel 1970

Diagnosis. Shape ovoid to trapezoid; ornamentation of concentric rows of puncta; 9 nodes may develop; hinge holomerodont, entirely positive in right valve; central muscle scars consist of row of 4 with irregular frontal and elongate adductor; radial pore canals swollen, sometimes branching.

Discussion. The important characters for specific diagnosis are lateral shape (including L/H ratio), and number of anterior and posterior spines.

Hemicyprideis montosa (Jones and Sherborn)

Plate 51, figs. 1–13; Plate 52, figs. 1–3; Plate 56, fig. 5, text-fig. 7

1852 *Cytheridea mulleri* Bosquet (*non* von Münster), p. 39 (pars), pl. 2, figs. 4*a–f*.
1856 *Cythere* (*Cytheridea*) *mulleri* Jones (*non* von Münster), p. 158, pl. 7, fig. 28.
1856 *Cythere* (*Cytheridea*) *mulleri* var. *torosa* Jones, p. 158, pl. 7, fig. 27.
1857 *Cytheridea mulleri* Jones (*non* von Münster), p. 41 (pars).
1857 *Cytheridea mulleri* var. *torosa* Jones, p. 42.
1889 *Cytheridea muelleri* et *torosa* Jones (*non* von Münster); Jones and Sherborn, p. 37.
1889 *Cytheridea montosa* Jones and Sherborn, p. 37, woodcut figs. 4*a*, *b*.
1895 *Cytheridea mülleri* Lienenklaus (*non* von Münster), p. 43 (pars).
1895 *Cytheridea mülleri* var. *torosa* Lienenklaus (*non* Jones), p. 43.
1957 *Haplocytheridea helvetica* Keij (*non* Lienenklaus), p. 62, pl. 3, figs. 27–30.
1960 *Haplocytheridea* cf. *basiliensis* Mehrotra (*non* Oertli), p. 80, pl. 1, figs. 7, 8.
1971 *Hemicyprideis montosa* (Jones and Sherborn); Keen, p. 525, pl. 1, figs. 3, 4.

Type locality and horizon. Median Mills, Isle of Wight; Middle Hamstead Beds.

Stratigraphic range and distribution. Bembridge Marls (?), Lower, Middle, and Upper Hamstead Beds, Isle of Wight; Paris Basin: Glaises à Cyrènes, Marnes Vertes, Bande blanche, Couche de Sannois, Marnes à Huîtres, Falun de Jeurre; Belgium: Sables de Neerrepen, Horizon de Hoogbutsel, Argile d'Henis, Couches d'Henis, Couches d'Oude Biezen, Sables de Berg, Argile à *N. comta*, Argile de Boom.

Holotype. MiK (T) 716001 (Geological Survey and Museum).

Material. Numerous valves and carapaces from the Isle of Wight, Paris Basin, and Belgium. Registered specimens: Io. 3719–3743.

Dimensions. See text-fig. 11 and illustrated specimens. This species shows a great variation in size, ranging from 0·68–0·91 mm for the length of the female left valve; see Keen (1971) for a full discussion of this. The L/H ratio for 69 female left valves from Cormeilles and Bouldnor is $1{\cdot}684 \pm 0{\cdot}0284$; and for 35 male left valves, $1{\cdot}856 \pm 0{\cdot}0243$.

Diagnosis. Species of *Hemicyprideis* in which right valve has 'humped' dorsal margin. Right valve with 18 anterior, 4 posterior spines; left valve with 6 anterior spines.

Description. Sexual dimorphism very pronounced, with more elongate males; ratio of presumed males to females 1:2·3 (167:384 measured specimens). Valves unequal in size and shape. Larger left valve has asymmetrically convex dorsal margin, with greatest height to anterior of centre; anterior slope has tendency to be straight. Anterior margin evenly rounded; ventral margin concave in anterior portion. Posterior margin almost straight, sloping backwards from sharp and distinct postero-dorsal angle. Right valve has more convex dorsal margin, giving females in particular appearance of humped back. Carapace ovate in dorsal view, with almost parallel margins.

3 groups of marginal spines developed along flange: along ventral half of anterior margin, at postero-ventral angle, and along posterior part of ventral margin. Latter generally poorly developed and tend to merge with postero-ventral group. Left valve only has anterior group of spines, 5–8, usually widely spaced, but occurring in irregular ones and twos when larger number present. Right valve has about 18 closely, but irregularly, spaced anterior marginal spines, smaller than those of left valve. Usually only 4 posterior spines and 8 ventral ones; sometimes most posterior of ventral group well developed, and then appear to be 5 posterior spines.

Valve not conspicuously ornamented. Normal adult has several concentric rows of small puncta, with wide, clear spaces between which appear almost ridge-like; 5 rows in anterior and venter; posterior third of valve has 6 rows. Normal pore canals very

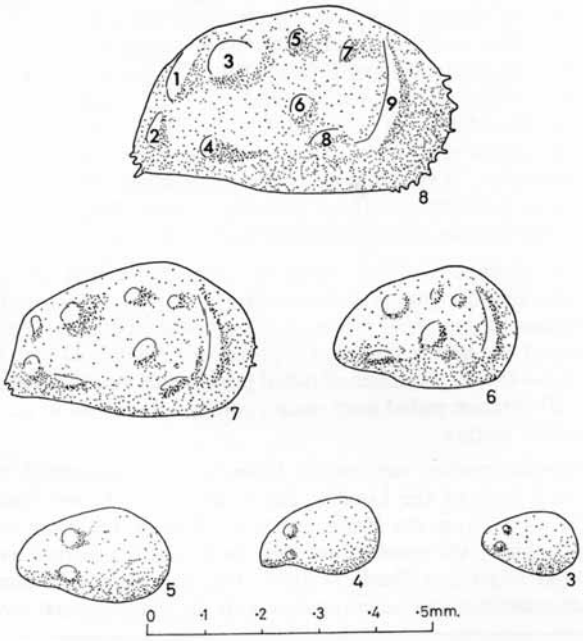
EXPLANATION OF PLATE 51

Arrows indicate anterior. All ×70, except figs. 7, 12.

Figs. 1–13. *Hemicyprideis montosa* (Jones and Sherborn). 1, Left valve, female, Io. 3730, Glaises à Cyrènes, Cormeilles (PCM.12). 2, Right valve, female, Io. 3728, Glaises à Cyrènes, Montfermeil (PMF.1). 3, Left valve, female, Io. 3724, Upper Hamstead Beds, Bouldnor Cliff (EBC.114). 4, Carapace, female, Io. 3723, dorsal view, Glaises à Cyrènes, Montfermeil (PMF.1). 5, 7, 12, Right valve, female, Io. 3726, Upper Hamstead Beds, Bouldnor Cliff (EBC.114); 5, ×70; 7, posterior tooth of hinge, lateral view from inside, ×250; 12, anterior tooth of hinge, lateral view from inside, ×200. 6, Left valve, male, Io. 3721, Lower Hamstead Beds, Bouldnor Cliff (EBC.47). 8, Left valve, female, Io. 3719, Lower Hamstead Beds, Bouldnor (EBC.47). 9, Right valve, male, Io. 3722, Lower Hamstead Beds, Bouldnor Cliff (EBC.47). 10, Left valve, female, Io. 3729, Horizon d'Hoogbutsel, Hoogbutsel. 11, Right valve, male, Io. 3725, Upper Hamstead Beds, Bouldnor Cliff (EBC.114). 13, Left valve, male, Io. 3727, Upper Hamstead Beds, Bouldnor Cliff (EBC.114).

noticeable, giving surface coarsely pitted appearance, and also arranged with concentric rows of puncta in anterior, ventral, and posterior regions. Faint sulcus at right angles to dorsal margin, in line with central muscle scars.

Tubercles or nodes present on some valves; inside of valve has corresponding depression, but never as deep as tubercle is high, so that thickening of valve also. Nodes have constant position on carapace, although need not all be developed. Text-fig. 7



TEXT-FIG. 7. Moult stages of *Hemicyprideis montosa* (Jones and Sherborn) from the Glaises à Cyrènes, Cormeilles. The nodes are numbered on moult no. 8 as used for descriptive purposes. The adult (no. 9) is not illustrated.

shows position and numbering system adopted. Eighth larval stage shows nodes most clearly. Nodes always best developed on right valve; sometimes carapace has nodose right valve and smooth left. Rarely present on male valves. Nodes 3 and 4 first developed; present on third larval stage, and prominent on fourth and fifth. All except 1 and 2 present on sixth stage, and all except 1 on left valve of seventh. In all these moult stages, 3 and 4 dominant, but in eighth stage, 9, anterior ridge, of equal prominence. In adult, 1 and 2 often merge to form posterior ridge, although all degrees of separation seen. 9 usually dominant feature of valve, although 3 and 4 still prominent. 8 often joined on to 9. In some extreme forms, anterior ridge incorporates 8 and almost joins with 4; specimen chosen by Jones and Sherborn (woodcut figs. 4*a*, *b*) is an example, where

feature is described as 'a thick, rounded, interrupted, and sausage-like ridge nearly surrounding the surface . . .' (p. 37).

Hinge entirely positive in right valve, having 3 elements: elongate, coarsely crenulate anterior tooth; finely crenulate median bar; and elongate coarsely crenulate posterior tooth. Median element is groove in left valve, which deepens towards posterior; at anterior so shallow as to be hardly groove at all. Hinge of seventh and eighth larval stages have, in left valve, anterior and posterior elongate and coarsely crenulate sockets; median element is fine, faintly crenulate bar. In fifth and sixth larval stages, this bar appears smooth. In third and fourth stages not clear whether terminal elements crenulate or not. Adult hinge clearly different from that of larval stages, agreeing with hypothesis of Sandberg (1965*a*), whereby antimerodont hinge (as in moult stages) is more primitive than holomerodont type (as in adult).

Selvage very prominent and sub-peripheral. Flange groove narrow, flange best seen in right valve. 42 anterior, 24 ventral, and 14 posterior radial pore canals, closely spaced, simple; often appear to bifurcate. About 100 simple normal pore canals.

Central and dorsal muscle scars shown in Plate 52, figs. 1, 3.

Larval stages. Larval stages 3–8 recognized (text-fig. 11). Hinge and nodes discussed above. Shape much less elongate in earlier instars, right valve still being more elongate, as in adult. Number of marginal spines increases with maturity; stages 3–5 do not have spines; 6 has 4 anterior spines and 2 posterior; 7 has 5–11 (av. 8) and 3; 8 has 6–17 (av. 12) and 3–4 (av. 3). Number of radial pore canals also increases with maturity; eighth stage has 20 anterior radial pore canals compared with 40 in adult; number not clearly seen in earlier instars.

Discussion. Cytheridea mulleri var. *torosa* Jones was first described by Jones (1857) from the Woolwich Beds of the London Basin, which are Lower Eocene in age. He later included the forms from the Hamstead Beds. Because the 2 are not identical, the name is not applicable to the species here described, and the earliest available name is *Cytheridea montosa* Jones and Sherborn 1889. This is a heavily tuberculate form, but the pattern of the tubercles can be correlated with the more normal development.

EXPLANATION OF PLATE 52

All ×70, except figs. 3, 13.

Figs. 1–3. *Hemicyprideis montosa* (Jones and Sherborn). 1, Right valve, female, internal, Io. 3726, Upper Hamstead Beds, Bouldnor Cliff (EBC.114). 2, Right valve, female, nodose, Io. 3740, Lower Hamstead Beds, Bouldnor Cliff (EBC.58). 3, Left valve, female, central muscle scars, Io. 3719, Lower Hamstead Beds, Bouldnor Cliff (EBC.47), ×200; arrow indicates anterior.

Figs. 4–9. *Hemicyprideis elongata* sp. nov. Upper Hamstead Beds, Bouldnor Cliff (EBC.114), except for Fig. 8. 4, Right valve, female, Io, 3745. 5, Left valve, female, holotype, Io. 3744. 6, Right valve, male, Io. 3748. 7, Left valve, male, Io. 3751. 8, Right valve, female, nodose, Io. 3750, Marnes à Huîtres, St. Cloud. 9, Female carapace, dorsal view, Io. 3747.

Fig. 10. *Cyamocytheridea punctatella* (Bosquet) *producta* Margerie. Left valve, female, Io. 3717, Upper Hamstead Beds, Bouldnor Cliff (EBC.114).

Figs. 11, 12. *Hemicyprideis helvetica* (Lienenklaus). Blaue Ton, Delemont, Switzerland. 11, Left valve, male, nodose, Io. 3753. 12, Left valve, female, Io. 3752.

Fig. 13. *Neocyprideis williamsoniana* (Bosquet). Right valve, moult no. 8, Io. 3810, Upper Hamstead Beds, Bouldnor Cliff (EBC.114), ×80.

Fig. 14. *Hemicyprideis henisensis* (Keij). Left valve, Io. 3705, Upper Tongrian, Kleine Spouwen, $L = 0{\cdot}73$ mm.

The importance of the number of nodes and their position on the carapace is not yet clearly understood in this genus. Sandberg (1965*b*), in his detailed study of *Cyprideis*, stated that the position of the nodes is genetically controlled and that the position is constant within any species. A maximum number of 7 is developed in *Cyprideis*. These may not all be present in any particular species, and individuals may not have their total specific number. The relative position of nodes 3 and 4 in the nomenclature adopted here was given particular importance by Sandberg. Benson (1965, p. 510) mentioned that the position of nodes on *Cyprideis* indicated genetic consistency; Sandberg (1965*a*, p. 511) that node position can be used as a character to determine species of *Cyprideis*; and Pokorny (1965, p. 514) described *Cyprideis* from the Neogene of central Europe with a fairly constant distribution of nodes, believing such forms to be due to definite genetic combinations. It seems, therefore, that in the case of *Cyprideis* the position of the nodes is a constant specific character. *Hemicyprideis* is closely related to *Cyprideis* and possibly the same applies. All the specimens of *H. montosa* which have been examined have a constant distribution of nodes. The difficulty is whether this is a specific or generic character. From the published figures of Malz and Triebel (1970), and the specimens examined here, it would appear to be difficult to use the nodes for separating species. Thus the number and position of nodes is probably a generic character, unlike in *Cyprideis*.

When specimens from the Lower Hamstead Beds are compared with those from the Upper Hamstead Beds, some differences can be seen. The left valves of the latter have their highest point further towards the anterior, and the posterior part of the dorsal margin has a steeper slope, giving rise to a shorter posterior margin and a tapered appearance to the carapace. The specimens from Bilzen show these features to a marked extent. Some Upper Hamstead specimens, but not all, have 3 or 4 larger spines developed along the dorsal part of the anterior margin of the right valve. Nevertheless, it is considered that only 1 species is present. When it is compared with other species, such as *H. henisensis* Keij and *H. elongata* sp. nov., the difference in shape between these species is very sharp and distinct. The number of spines is taken as being a specific character.

H. gilletae (Stchepinsky) (Plate 56, figs. 3, 6) from the Sannoisian of Alsace and the Mainz Basin is very similar to *H. montosa*. The main difference is in the dorsal margin. This is much straighter in *H. gilletae*, with a much more definite highest point. It has the same number of spines. It does not differ from *H. montosa* in shape to the same extent as, for example, *H. henisensis* Keij. It is clearly a very closely related species, possibly even a geographical subspecies.

H. helvetica (Lienenklaus) (Plate 52, figs. 11, 12) is quite different, with 18–22 anterior spines on the left valve, 23–26 on the right, and 6 posterior spines on the right valve (Oertli 1956). *H. basiliensis* Oertli has a similar number of spines as *H. helvetica*.

The specimens from Auvers-St.-George are very worn. Only 1 specimen has been found in the Bembridge Marls; Jones and Sherborn (1889, p. 37) mentioned that it was found in the Bembridge Marls during exploration by the Geological Survey.

Hemicyprideis elongata sp. nov.

Plate 52, figs. 4–9

1961 *Cytheridea pernota* Mehrotra (*non* Oertli and Keij), p. 76 (pars), pl. 1, figs. 5, 6.

Type locality and horizon. Bouldnor Cliff, Isle of Wight; Upper Hamstead *Corbula* Beds.

Stratigraphic range and distribution. Upper Hamstead *Corbula* Beds, Isle of Wight; Paris Basin: Couches de Sannois supérieur, Cormeilles and Marnes à Huîtres, St. Cloud, Cormeilles; Belgium: Argile à *N. comta*, Bilzen, Kleine Spouwen.

Holotype. Io. 3744, female left valve.

Material. Corbula Beds, Bouldnor—43 valves, 1 carapace; Couches de Sannois, Cormeilles—10 valves and carapaces; Marnes à Huîtres, Cormeilles—57 valves and 7 carapaces; Marnes à Huîtres, St. Cloud —26 valves and carapaces (figured female right valve, Pl. 52, Io. 3750); Bilzen—3 carapaces; Kleine Spouwen (Keij Coll., Utrecht)—5 valves. Registered specimens: Io. 3744–3752.

Dimensions.

Holotype, female left valve, Io. 3744: *L*, 0·66; *H*, 0·37.
Female carapace, Io. 3747: *L*, 0·66; *H*, 0·36; *W*, 0·29.
Male carapace, Io. 3746: *L*, 0·73; *H*, 0·39; *W*, 0·32.

		N	$\bar{x}$	*S*	*Range*	*V*
Female left valves	*L*	15	0·664	0·0114	0·64–0·68	1·7
	H	15	0·372	0·0083	0·36–0·39	2·2
	L/*H*	15	1·785	0·0223	1·74–1·86	1·2
Male left valves	*L*	11	0·701	0·0138	0·68–0·73	2·0
	H	11	0·355	0·0099	0·34–0·37	2·8
	L/*H*	11	1·976	0·0315	1·94–2·03	1·6

Comparable means were obtained from PCM. 24:
Female left valves: *L*, 0·652; *L*/*H*, 1·816.
Male left valves: *L*, 0·688; *L*/*H*, 1·989.
N (female) = 16; *N* (male) = 10.

Diagnosis. Species of *Hemicyprideis* with *L*/*H* ratio of 1·785 (female left valve). Left valve with 18 anterior marginal spines; right valve with 21–25 anterior and 6–7 posterior spines.

Description. Sexual dimorphism pronounced, males more elongate; ratio of presumed males to females 1:1·86. In left valve, highest point about $\frac{1}{3}$ length from anterior in female and about $\frac{1}{4}$ in male. Posterior slope of dorsal margin almost straight; shorter anterior part gently convex. Anterior margin evenly rounded; ventral margin slightly concave at posterior. Postero-dorsal angle sharp, and posterior margin almost straight. Right valve has more pronounced posterior concavity in ventral margin, and dorsal margin more convex, with humped appearance. In dorsal view, carapace has almost rectangular outline, with practically parallel sides.

18 anterior marginal spines on left valve; right valve has 21–25 anterior spines and 6–7 posterior spines (more usually 6).

At anterior, 5 low concentric ridges parallel to anterior margin; continuing, more indistinctly, parallel to ventral margin. First 3 from margin are strongest, particularly third, which is sometimes quite swollen. 4 concentric ridges posteriorly. Normal pore canals arranged between these ridges; also fine punctation between more marginal ridges.

7 tubercles on surface of carapace. At posterior, thick tubercle elongated parallel to posterior margin; large round tubercle near centre of dorsal margin and another directly below it, near to and elongated parallel to dorsal margin; 2 small tubercles in sub-central position, often seen as 1 large, indistinct swelling; small tubercle near antero-dorsal angle; swollen ridge parallel to anterior margin completes set.

Internal features very similar to *H. montosa* (Jones and Sherborn). 43 anterior, 25 ventral and 14 posterior radial pore canals.

Discussion. H. helvetica (Lienenklaus) (Plate 52, figs. 11, 12) has a similar number of anterior and posterior spines and a similar nodal distribution. It differs in having a much lower *L*/*H* ratio, particularly in the male. This ratio for the left valve was found to be 1·718 (6 females) and 1·857 (6 males); this compares with 1·785 and 1·976 in *H. elongata. H. basiliensis* Oertli also has a lower *L*/*H* ratio; its dorsal margin is more convex, particularly in the right valve, and the posterior margin is more rounded.

Hemicyprideis henisensis (Keij)

Plate 52, fig. 14

1955 *Haplocytheridea henisensis* Keij (*in* Oertli and Keij), p. 25, pl. 1, figs. 17–22, text-figs. 1–3.
1957 *Haplocytheridea henisensis* Keij; Keij, p. 62, pl. 3, figs. 8–12; pl. 4, figs. 9–11.

Discussion. This species is characterized by its rounded dorsal margin which gives it an ovoid shape in lateral outline. It is recorded by Keij from the Upper Tongrian and, possibly the Rupelian, of Belgium and Dutch Limburg. The type locality is the Henis Clay of Henis; the holotype is deposited at the Geologisch Instituut, Utrecht.

Genus NEOCYPRIDEIS Apostolescu 1956

Type species. Neocyprideis durocortoriensis Apostolescu 1956.

Diagnosis. Carapace ovate; surface smooth or punctate, nodes sometimes developed. Hinge tripartite, all elements crenulate, terminal elements in right valve.

Neocyprideis williamsoniana (Bosquet)

Plate 52, fig. 13

1852 *Cytheridea williamsoniana* Bosquet, p. 43, pl. 2, fig. 6.
1957 *Cyprideis* (*Goerlichia*) *williamsoniana* (Bosquet); Keij, p. 70, pl. 7, figs. 6–8; pl. 18, figs. 18–20.
1960 *Neocyprideis williamsoniana* (Bosquet); Kollman, p. 177, pl. 20, figs. 6, 7.

Discussion. This species is rarely found in Sannoisian rocks, but is recorded by Keij (1957) from the Upper Tongrian and Rupelian of Belgium; it is common in the basal Stampian of the Paris Basin (Marnes à Huîtres) and the Bembridge Oyster Marls in England. 1 specimen was found in the Upper Hamstead Beds (Io. 3810). The closely related *N. colwellensis* (Jones) is found in the Headon Beds of the Hampshire Basin. See also palaeoecological section.

Family HEMICYTHERIDAE Puri 1953
Subfamily CAMPYLOCYTHERINAE Puri 1960
Genus LEGUMINOCYTHEREIS Howe 1936

Type species. Leguminocythereis scarabaeus Howe and Lawy 1936.

Diagnosis. Carapace 'bean'-shaped. Surface reticulate, longitudinal elements usually dominant. Hinge holamphidont.

Leguminocythereis verricula sp. nov.

Plate 54, figs. 5, 9–12; Plate 56, fig. 1

1960 *Leguminocythereis lienenklausi* Mehrotra (*non* Oertli), p. 80, pl. 1, figs. 9, 10.

Type locality and horizon. Cormeilles-en-Parisis; Couches de Sannois, Bed No. 44 of Girard d'Albissin.

Stratigraphic range and distribution. So far only known from the type locality.

Holotype. Io. 3753, male carapace.

Material. 27 valves and carapaces. Figured specimens, Pl. 54: Io. 3754–3756; Pl. 56, Io. 3757.

Dimensions. Female carapace, Io. 3757: *L*, 1·00; *H*, 0·52; *W*, 0·56; *L*/*H*, 1·92.
Male carapace, Io. 3755: *L*, 1·18; *H*, 0·56; *W*, 0·60; *L*/*H*, 2·11.

Diagnosis. Species of *Leguminocythereis* which is tapered towards posterior. Ornamentation of 2 prominent ridges parallel to anterior margin, and 4 concentric ovals of ridges over remainder. Reticulation between the ridges.

Description. Sexual dimorphism distinct, males larger and more elongate. Dorsal margin of left valve slightly convex, with poorly developed anterior hinge ear marking greatest height of valve. Anterior margin evenly rounded. Ventral margin has concavity in anterior third, largely hidden by overhang of slight ventral swelling which gives median portion of ventral margin a strong convex appearance. Dorsal part of posterior margin concave; ventral part slightly rounded with 3 short spines. Right valve more triangular, with straight dorsal margin, which slopes downwards towards posterior; anterior margin has slight concavity in antero-dorsal angle. Carapace ovate in dorsal view.

Reticulate ornamentation with longitudinal elements predominant and forming slight ridges. 2 strong ridges parallel to anterior margin, 1 starts from eye tubercle, which is elongated along it; second starts to anterior of eye tubercle. Small area of double reticulation between these 2 ridges in antero-ventral region, but elsewhere only 1 set of reticulation between them. Lateral surface has 4 concentric ovals of ridges, clearly defined along dorsal, anterior and ventral sides, but merging with reticulation at posterior. Reticulation between ridges.

Hinge of right valve has large pessular anterior tooth and large reniform posterior tooth. Right valve has small conical antero-median tooth, crenulate postero-median bar, and anterior socket with very strong wall. Occular sinus to anterior of anterior hinge element.

EXPLANATION OF PLATE 53

All ×60.

Figs. 1–6, 9–11. *Hammatocythere hebertiana* (Bosquet). 1, 2, Stereo pairs, left valve, female, Io. 3764, Auvers-St.-George. 3, 4, Stereo pairs, right valve, female, Io. 3767, Marnes à Huîtres, Cormeilles (PCM.27). 5, Right valve, female, Io. 3771, Falun de Morigny. 6, Left valve, female, Io. 3772, Upper Hamstead Beds, Bouldnor Cliff (EBC.114). 9, Left valve, male, Io. 3769, Ormoy. 10, Right valve, female, Io. 3765, Couches de Sannois, Cormeilles (PCM.22). 11, Right valve, male, Io. 3770, Ormoy.

Figs. 7, 8. *Hammatocythere trituberculata* (Reuss). Gaas (Espibos), Stampian, southern Aquitaine. 7, Right valve, female, Io. 3777. 8, Left valve, female, Io. 3776.

Fig. 12. *Bradleya dolabra* sp. nov. Left valve, female, holotype, Io. 3758, Glaises à Cyrènes, Montfermeil (PMF.1).

Selvage sub-peripheral, with small flange groove, especially in right valve. 20 anterior, 16 ventral, and 16 posterior radial pore canals, straight, simple. Simple normal pore canal opens into each reticule.

Discussion. The ornamentation is very similar to that of *L. lienenklausi* Oertli, but the shape is different. In lateral view the dorsal and ventral margins are almost parallel in *L. lienenklausi*, which is not the case with *L. verricula*; in dorsal view the latter has much more convex margins than the almost straight margins of Oertli's species.

Specimens of a similar species have been found at Auvers-St.-Georges and Morigny; these are smaller and show much more variation in the strength of the ridges. Some specimens from Auvers-St.-Georges have strong longitudinal ridges with very subordinate reticulation.

Subfamily THAEROCYTHERINAE Hazel 1967
Genus BRADLEYA Hornibrook 1952

Type species. Cythere arata Brady 1880.

Diagnosis. Carapace subquadrate; surface generally reticulate with dorsal and ventral ridges. Hinge hemiamphidont. 2 frontal scars.

Bradleya dolabra sp. nov.

Plate 53, fig. 12; Plate 56, fig. 12

Type locality and horizon. Montfermeil, Carrière du Sampin; Glaises à Cyrènes.

Stratigraphic range and distribution. Glaises à Cyrènes of Montfermeil and Neuilly Plaisance.

Holotype. Io. 3758, female left valve.

Material. Montfermeil, 2 valves and 2 larval stages; Neuilly Plaisance, 1 valve (Io. 3759).

Dimensions.

Left valve, holotype, Io. 3758:	*L*, 0·88; *H*, 0·51; *W*, 0·27; *L*/*H*, 1·73.
Right valve, Io. 3759:	*L*, 0·88; *H*, 0·50; *L*/*H*, 1·76.

Diagnosis. Species of *Bradleya* with 4 prominences. Reticulation strong in some regions, but weak in central area, where prominent punctation developed between reticules.

Description. Sexual dimorphism not recognized. Dorsal margin irregular due to over-reach of dorsal prominence; highest point of valve at strong anterior hinge ear. Anterior margin broadly rounded. Ventral margin has concavity in anterior third, hidden by over-reach of ventral prominence. Posterior margin truncated in both valves, although very small postero-dorsal concavity in right valve; postero-dorsal corner of left valve forms almost right angle. Carapace asymmetrically ovate in dorsal view, widest at posterior end.

Surface has 4 prominences, 1 in dorsal position, another in ventral position; sub-central tubercle is third, and fourth lies between this and postero-dorsal angle. Surface reticulate, strong in antero-ventral, ventral and postero-dorsal regions, but weak in central areas of carapace. Fine punctation between reticules of central region, and more prominent than reticules. Prominent eye tubercle.

About 20 anterior marginal denticles, each bearing radial pore canal. At posterior, 5 small spines, not along margin, but slightly higher on valve.

Hinge of left valve has strong, knob-like antero-median tooth; anterior socket has massive wall; postero-median bar broken, but apparently crenulate. Right valve has large, conical, anterior tooth and pessular posterior tooth; antero-median socket strong. Occular sinus to anterior of anterior hinge element.

Selvage peripheral in left valve and sub-peripheral in right; small flange groove present. About 25 anterior and 10 posterior radial pore canals. Normal pore canals not seen. 4 adductor muscle scars and 2 frontals; another 2 muscle scars seen above dorsal side of muscle scar pit.

2 larval stages seen; stage 8 has similar ornamentation to the adult, with 17 anterior denticles; stage 7 has 4 prominences, but weak reticulation. No anterior denticles present on this last moult stage, but 14 anterior radial pore canals seen. Hinge in both moult stages lophodont.

Discussion. This is a distinct species, both in shape and ornamentation.

Genus HAMMATOCYTHERE gen. nov.

Type species. Cythere hebertiana Bosquet 1852.

Diagnosis. Oblong carapace with 3 ridges: dorsal ridge, median ridge developed irregularly, and strong ventral ridge. Sub-central tubercle well developed with 2 short ridges running from its anterior. Well developed anterior marginal rim. Straight and simple radial pore canals; simple normal pore canals. 4 adductor muscle scars, 2 frontals, 2 mandibulars. Hinge holamphidont. Medium size; sexual dimorphism distinct.

Description. Only 2 species here included in genus and since very similar, detailed description of type species renders detailed generic description unnecessary. Particular features taken to be of generic value are as follows. Presence of 3 ridges; median one short, not always prominent; ventral ridge almost wing-like. Prominent and complicated sub-central tubercle with 2 ridges running from it towards anterior. Well-developed anterior marginal rim with smooth area behind it and parallel to it; and posterior with series of knob-like or blade-like spines.

Discussion. This differs from *Hermanites* Puri in the presence of the median ridge and in having 2 frontal muscle scars instead of a single 'V'-shaped one. *Costa* Neviani has a stronger median ridge which characteristically curves downwards at the posterior weak sub-central tubercle, and lacks the anterior ridges; it also has a 'V'-shaped frontal muscle scar. *Trachyleberidea* Bowen is similar in having 2 frontal muscle scars, but differs in having fewer and larger anterior marginal denticles, the sub-central tubercle is simple, the dorsal and ventral margins converge towards the posterior, and it is much smaller in size (see Haskins 1963). The genus *Bradleya* Hornibrook has in recent years taken the place of *Cythere* Mueller as the depository for Tertiary cytherid ostracods in Europe. *Hammatocythere* differs from it in having a smooth posterior tooth in the right valve instead of the crenulate tooth of *Bradleya*, and *Bradleya* lacks the median ridge, sub-central tubercle, and anterior ridges of *Hammatocythere*.

During the Middle Eocene the cytherid ostracods of western Europe underwent an evolutionary radiation, with many species referred to *Bradleya*, *Hermanites*, *Leguminocythereis*, and *Quadracythere* Hornibrook. Specific, as well as generic, identification is often very difficult, probably a normal situation in such a radiation. *Hammatocythere*

is regarded as being 1 of the branches of this cladogenesis which became diagnostically distinct in the Lower Oligocene. Several species may well be ancestral to it. For example, *Bradleya kaasschieteri* Keij from the Ledian and Bartonian of Belgium and the Netherlands, and *Cythere forbesi* Jones and Sherborn from the Middle Headon Beds of Hampshire. The assignment of older species to the genus will involve difficult taxonomic problems beyond the scope of the present work.

Hammatocythere hebertiana (Bosquet)

Plate 53, figs. 1–6, 9–11; Plate 54, figs. 1–4, 6–8; Plate 56, figs. 4, 7

1852 *Cythere hebertiana* Bosquet, p. 95, pl. 5, fig. 1.
1852 *Cythere reussiana* Bosquet, p. 109, pl. 5, fig. 12.
1895 *Cythere hebertiana* Bosquet; Lienenklaus, p. 142.
1895 *Cythere polytrema* Lienenklaus (*non* Brady), p. 143.
1957 *Hermanites hebertiana* (Bosquet); Keij, p. 109, pl. 13, fig. 4; pl. 18, figs. 1–4 (pars).

Type locality and horizon. Jeurre; Falun de Jeurre.

Stratigraphic range and distribution. Paris Basin: Couches de Sannois; Marnes à Huîtres; Falun de Jeurre, Auvers-St.-Georges and Morigny; Falun d'Ormoy. Belgium: Argile à *N. comta*, Berg and Kleine Spouwen. England: *Corbula* Beds (Upper Hamstead Beds), Bouldnor Cliff.

Lectotype. Coll. Bosquet No. 56, Inst. Roy. Sci. Nat., Brussels.

Material. Auvers-St.-Georges, 28 valves, 2 larval stages; Morigny, 4 valves; Ormoy, 17 valves and carapaces, 23 larval stages; Couches de Sannois of Cormeilles, 8 valves; of St. Cloud, 9 valves; Bouldnor, 5 valves. Registered specimens: Io. 3764–3775, 3807.

Dimensions. Left valves.

		N	$\bar{x}$	S	*Range*	V or V_c
Length,	female					
	PAG	27	0·863	0·0308	0·83–0·91	3·6
	PCM 27	26	0·824	0·0256	0·78–0·88	3·1
	SANN	16	0·877	0·0110	0·86–0·90	1·3
	POM	7	0·840	0·0233	0·81–0·89	2·9
	EBC	5	0·786	0·0253	0·78–0·80	3·3
Height,	female					
	PAG	27	0·490	0·0182	0·45–0·52	3·7
	PCM 27	26	0·467	0·0141	0·45–0·49	3·0
	SANN	16	0·494	0·0070	0·48–0·50	1·4
	POM	7	0·476	0·0050	0·47–0·48	1·1
	EBC	5	0·466	0·0136	0·45–0·48	3·0
L/H,	female					
	PAG	27	1·760	0·0457	1·67–1·87	2·6
	PCM 27	26	1·762	0·0303	1·72–1·83	1·7
	SANN	16	1·778	0·0297	1·72–1·84	1·7
	POM	7	1·766	0·0392	1·72–1·85	2·3
	EBC	5	1·694	0·0364	1·66–1·74	2·2
POM,	male					
	L	10	0·999	0·0243	0·95–1·03	2·4
	H	10	0·521	0·0117	0·50–0·53	2·2
	L/H	10	1·915	0·0301	1·85–1·96	1·6

W, female = 0·41 (PCM 27)
W, male = 0·45 (POM).

Diagnosis. Species of *Hammatocythere* with 2 additional ridges to anterior of sub-central plexus; ventral ridge with swelling at posterior; irregular ornamentation between ridges. Posterior spines knob-like.

Description. Carapace oblong in lateral view with highest point at prominent anterior hinge ear. Sexual dimorphism very pronounced, but males rare (see discussion). Dorsal margin slightly irregular due to over-reach of dorsal ridge; anterior margin evenly rounded. Ventral margin has concavity in anterior third, largely hidden by over-reach of ventral ridge. Posterior margin truncated in left valve, but has postero-dorsal concavity in right. In dorsal view, anterior marginal rim conspicuous and almost symmetrical, with posterior platform; in between, convex outline of carapace interrupted by depression just to posterior of sub-central tubercle. Valves equivalve, although in some carapaces right valve appears slightly longer.

23–25 prominent denticles around anterior margin and anterior part of ventral margin; in dorsal part of anterior margin, replaced by thin fringe. Each denticle bears radial pore canal. Along posterior margin, 5 denticles with another 6 short spines or tubercles on postero-dorsal platform.

Ornamentation of 4 distinct parts: sinuous dorsal ridge; short median ridge; prominent sub-central tubercle; and ventral ridge. Median ridge varies in prominence; in some specimens, particularly those from Marnes à Huîtres, merely strongest of series of postero-dorsal ridges; in others, very strong, and postero-dorsal ridges reduced to rank of reticulation. 4 short ridges run from anterior of sub-central tubercle; central 2 more prominent than others, and of these, lower is longer. Ventral ridge prominent, curving upwards at anterior, but does not join anterior marginal rim. At posterior, swelling, often knob-like in appearance, developed to varying degrees. Reticulation between ventral and median ridges is even in some specimens, and in others broken up into series of lobes and knobs. Between dorsal and median ridges, ornamentation may consist of reticulation, low parallel ridges, or series of lobes and knobs. Anterior marginal rim very strong, in some specimens so large as to completely hide anterior denticles. To posterior of this rim, and parallel to it, wide, smooth area across which sometimes seen faint continuations of 4 ridges from sub-central tubercle. Eye tubercle prominent.

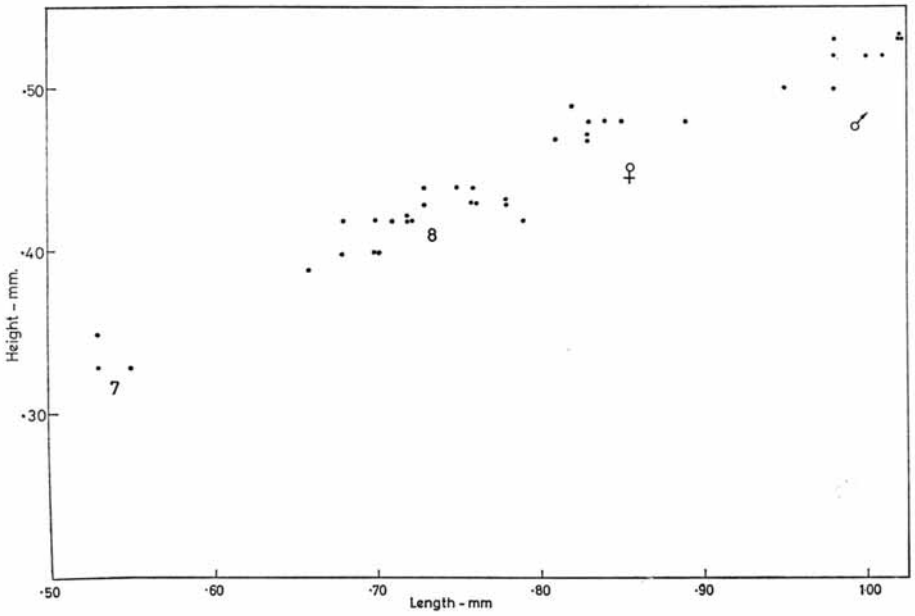
Hinge of left valve has sub-conical antero-median tooth and finely crenulate postero-median hinge bar; anterior socket has very strong wall. In right valve, anterior tooth stirpate, posterior tooth reniform. Prominent occular sinus just to anterior of anterior tooth or socket.

40 anterior and 12 posterior radial pore canals, simple, straight; those which end in anterior denticle are bulbous. No ventral radial pore canals. No vestibule. 45–50 scattered, simple normal pore canals, distribution related to ornamentation. Central muscle scars in a deep pit; 4 adductors along steep posterior edge, 2 frontals on gently-sloping anterior edge. Lower of 2 frontals bilobate. Selvage peripheral in left valve with small ventral flange groove; in right valve, sub-peripheral with small flange along all margins.

Last 3 larval stages recognized; most come from Ormoy. Moult stage 8 shows large size range (text-fig. 8), larger than normally expected. Expected size about 0·70 mm, but specimens range from 0·66–0·79 mm. Large specimens clearly not adults because of weakly developed hinge. Equivalent moult stage of *H. trituberculata* (Reuss), where

female is 0·82 mm in length, is 0·66 mm, while only specimen found at Auvers-St.-Georges is 0·68 mm in length.

Moult stage 8 has 3 ridges well developed, but have ragged appearance; only 2 ridges run from anterior of sub-central tubercle. Anterior marginal rim very strong. 21 anterior denticles and 5 posterior ones, with 9 other spines on postero-ventral platform. Hinge



TEXT-FIG. 8. Size distribution of *Hammatocythere hebertiana* (Bosquet) from Ormoy.

has elements of adult, but only simply developed and with smooth hinge bar and very small antero-median tooth in left valve. Muscle scars similar to those of adult.

Moult stage 7 has ragged ridges as in 8. 12 anterior and 5 posterior denticles. Anterior marginal rim strong. Hinge lophodont. Median ridge absent in moult stage 6, but ridge in position of sub-central tubercle. 7 anterior and 5 posterior denticles. Anterior marginal rim prominent.

Discussion. Keij (1957) selected a lectotype which is deposited at the Institut Royal des Sciences Naturelles de Belgique in Brussels. See also palaeoecological section.

Hammatocythere trituberculata (Reuss)

Plate 53, figs. 7, 8

1869 *Cythere trituberculata* Reuss, p. 485, pl. 6, figs. 6*a*, *b*.
1955*a* *Trachyleberis hebertiana* Keij (*non* Bosquet), p. 127, pl. 16, figs. 5, 6.
1957 *Hermanites hebertiana* Keij (*non* Bosquet), p. 109 (pars).

Type locality and horizon. Gaas; Falun de Gaas (Stampian).

Stratigraphic range and distribution. Stampian of the Aquitaine Basin at Gaas (Espibos, Lesbarritz); Castillon Cambes; Biarritz; Basternes–Gaujacq; Lourquen (the last 3 localities from Deltel 1961).

Material. Espibos—17 valves and carapaces, 6 larval stages; Lesbarritz—7 valves and 4 larval stages; Calcaire de Castillon—1 larval stage. Figured specimens, Pl. 53: Io. 3776–3777.

Dimensions. All females:

Espibos	*N*	$\bar{x}$	*S*	*Range*	*V*
L	18	0·815	0·0214	0·75–0·85	3·0
H	18	0·461	0·0175	0·43–0·48	3·8
L/*H*	18	1·770	0·0362	1·71–1·84	2·0
Lesbarritz					
L	7	0·883	0·0266	0·85–0·92	3·1
H	7	0·509	0·0276	0·48–0·54	5·6
L/*H*	7	1·736	0·0347	1·69–1·79	2·1

$W = 0{\cdot}45$

Diagnosis. Species of *Hammatocythere* with wing-like ventral ridge and weak but even reticulation between ridges. Posterior spines blade-like.

Discussion. This is similar to *H. hebertiana* (Bosquet), but differs in the following respects. The dorsal ridge is much stronger and the median ridge is always prominent. The specimens examined do not show the same variations in morphology. The ventral ridge is more wing-like, is much more regular and does not curve upwards at the anterior end. There are only 2 ridges to the anterior of the sub-central plexus, and no faint continuation of these can be seen across the clear space behind the anterior marginal rim. This clear space is much more prominent. The reticulation is even and more subdued. The spines on the posterior platform are blade-like, not nodose. Internal features are similar, except for the presence of some 7–8 ventral radial pore canals and rather more normal pore canals (56–60).

The specimens from Lesbarritz are larger than those from Espibos.

Family TRACHYLEBERIDIDAE Sylvester-Bradley 1948
Subfamily ECHINOCYTHEREIDINAE Hazel 1967
Genus ECHINOCYTHEREIS Puri 1954

Type species. Cythereis garetti Howe and McGuirt 1935.

Diagnosis. Rounded posterior end; valves different in shape, of about equal length, but left over-reaches right along dorsal margin. Ornament of rounded spines or reticulation. 2 frontal scars. Hinge holamphidont.

EXPLANATION OF PLATE 54

All ×60, except figs. 8, 10.

Figs. 1–4, 6–8. *Hammatocythere hebertiana* (Bosquet). 1–4, Stereo pairs, right valve, female, Io. 3766, Marnes à Huîtres, Cormeilles (PCM.27); 1, 3, internal view; 2, 4, dorsal view. 6–8, left valve, female, Io. 3807, same horizon and locality; 6, 7, stereo pair, internal view; 8, central muscle scars, ×225 (arrow indicates anterior).

Figs. 5, 9–12. *Leguminocythereis verricula* sp. nov. Couches de Sannois, Cormeilles (PCM.20). 5, Female carapace, dorsal view, Io. 3757. 9, Left valve, male, holotype, Io. 3753. 10, Enlargement of part of fig. 9, showing relationship between ornamentation and normal pore canals, ×200. 11, Right valve, male, Io. 3756. 12, Male carapace, dorsal view, Io. 3755.

Echinocythereis? hamsteadensis sp. nov.

Plate 55, figs. 1, 2; Plate 56, figs. 14, 15, 17

Type locality and horizon. Bouldnor Cliff; Upper Hamstead *Cerithium* Beds.

Stratigraphic range and distribution. Cerithium Beds, Bouldnor Cliff; Couches de Sannois, Cormeilles.

Holotype. Io. 3760, left valve.

Material. Bouldnor, 48 valves; Cormeilles, 10 valves and carapaces. Figured specimens, Pl. 55: Io. 3760, 3761; Pl. 56: Io. 3762, 3763.

Dimensions.

Left valve, holotype, Io. 3760: *L*, 0·68; *H*, 0·39; *L/H*, 1·74.
Right valve (EBC.105), Io. 3761: *L*, 0·69; *H*, 0·38; *L/H*, 1·82.
Carapace (PCM.20), Io. 3765: *L*, 0·68; *H*, 0·39; *L/H*, 1·74; *W*, 0·33.

Diagnosis. Species of *Echinocythereis* with posterior and postero-dorsal prominences and ventral ridge. Surface delicately reticulate. Left valve with prominent hinge ear.

Description. Sexual dimorphism not recognized. Dorsal margin of left valve has undulating outline with prominent anterior hinge ear and hump half-way between hinge ear and posterior. Anterior margin broadly rounded. Ventral margin almost straight, with concavity in anterior third. Posterior margin slightly triangular. Right valve has straighter dorsal margin, and stronger concavity in ventral margin. Valves almost equivalve; left valve higher with more prominent hinge ear, but valves of about equal length, with right valve minutely longer. In dorsal view, carapace has uneven outline due to surface ornamentation; at anterior, outline formed by prominent marginal rim; posterior quadrate, and in between outline roughly asymmetrically convex, widest to posterior of centre.

3 prominences on surface, 1 in postero-dorsal area, another in posterior; third is subdued sub-central tubercle. Surface delicately reticulate except for area just behind and parallel to anterior marginal rim. Conspicuous ventral ridge runs almost from anterior marginal rim, in some specimens curving upwards at posterior to form edge of posterior prominence; in other specimens, fades away before joining prominence. Marginal rim has 3 weak, parallel ridges.

Hinge of right valve has pessular, or faintly stirpate, anterior tooth; posterior tooth reniform in plan, tending towards stirpate in dorsal view. In left valve, antero-median tooth small; postero-median bar smooth. Occular sinus to anterior of anterior hinge element.

Selvage strong, sub-peripheral; flange also strong; flange groove narrow. 40 anterior, 22 ventral, and 12 posterior radial pore canals, straight, bulbous, going into small denticles around margins. Numerous simple pore canals near walls of reticulation, but distribution not related to ornamentation. Muscle scars not clearly seen; 2 frontals and apparently 4 adductors, although only 3 clearly seen. 2 central adductors long, thin, dorsalmost very narrow in centre, almost split into 2. Anterior mandibular scar seems to consist of 2 scars touching each other.

Discussion. This is doubtfully included in the genus *Echinocythereis*. The internal features are similar: the muscle scars, particularly the 2 central elongate scars, the 2 frontals and the double anterior mandibular scar; the hinge, with its smooth hinge bar; the duplicature; and the simple pore canals. The over-reach, whereby the valves are of

about equal length, but of differing shapes, is also similar, as is the subdued sub-central tubercle.

The surface ornamentation differs, however, in the presence of the delicate reticulation and absence of spines or tubercles. The ventral ridge and the posterior and dorsal prominences are not usually present in *Echinocythereis*; *E. hamsteadensis* is in this respect similar to *Echinocythereis? ligula* Lienenklaus (after Oertli 1956, p. 81, pl. 11, figs. 285–290) from the Rupelian of Switzerland. Species such as *Echinocythereis hispida* (Speyer) from the Chattian of Germany are reticulate.

The near-splitting of the third adductor muscle scar suggests the Thaerocytherinae, while this together with the general shape suggests the Hemicytheridae.

Subfamily CYTHERETTINAE Triebel 1952
Genus CYTHERETTA Müller 1894

Type species. Ilyobates (?) judaea Brady 1866.

Diagnosis. Inequivalve, left valve largest; ornamentation of longitudinal ridges or rows of pits, or smooth; sinuous inner margin.

Discussion. 2 species have been described from the Couches de Sannois of the Paris Basin (Keen 1972). These are *C. minipunctata* Keen MS, which is related to *C. tenuistriata* Reuss, and *C. buttensis* Keen MS, which is probably ancestral to *C. tenuipunctata* (Bosquet). The latter is represented by 2 subspecies, *C. buttensis buttensis* (Lower Couches de Sannois), and *C. buttensis reticulata* (Middle Couches de Sannois–Marnes à Huîtres).

Family CYTHERURIDAE G. W. Müller 1894
Genus CYTHERURA Sars 1866

Type species. Cythere gibba O. F. Müller 1785.

Diagnosis. Carapace small, elongate, usually with strong caudal process. Surface finely striated or reticulate. Weak eye tubercle. Hinge merodont.

EXPLANATION OF PLATE 55

Figs. 1, 2. *Echinocythereis? hamsteadensis* sp. nov. Upper Hamstead Beds, Bouldnor Cliff (EBC.105), ×70. 1, Left valve, holotype, Io. 3760. 2, Right valve, Io. 3761.

Figs. 3–5. *Microcytherura delphina* sp. nov. Couches de Sannois, Cormeilles (PCM.20), ×125. 3, Right valve, Io. 3785. 4, Carapace, dorsal view, Io. 3784. 5, Carapace, left view, holotype, Io. 3783.

Figs. 6–8. *Eocytheropteron plicatoreticulatum* Margerie. ×60. 6, Right valve, female, Io. 3782, Auvers-St.-Georges. 7, Right valve, female, Io. 3781, Couches de Sannois, Cormeilles (PCM.20). 8, Left valve, male, Io. 3780 (PCM. 20).

Figs. 9, 12. *Cytherura porcina* sp. nov. Couches de Sannois, Cormeilles (PCM.20), ×125. 9, Female carapace, dorsal view, holotype, Io. 3778. 12, Male carapace, dorsal view, Io. 3779.

Figs. 10, 13, 16. *Cytheromorpha zinndorfi* (Lienenklaus). Upper Hamstead Beds, Bouldnor Cliff. 10, Right valve, female, Io. 3789, ×150. 13, Right valve, male, Io. 3790, ×125. 16, Right valve, female, internal view, Io. 3791, ×125.

Figs. 11, 14. *Loxoconcha nystiana* (Bosquet). 11, Left valve, female, Io. 3787, ×75; Sables de Berg, Bilzen; note reticulation. 14, Right valve, female, Io. 3788, ×75; Upper Hamstead Beds, Bouldnor Cliff (EBC.114), smooth form.

Fig. 15. *Loxoconcha delemontensis* Oertli. Left valve, female, Io. 3786, ×125; Couches de Sannois, Cormeilles (PCM.20).

Cytherura porcina sp. nov.

Plate 55, figs. 9, 12; Plate 56, figs. 8–11

Type locality and horizon. Cormeilles-en-Parisis; Couches de Sannois, Bed No. 44 of Girard d'Albissin.

Stratigraphic range and distribution. So far only known from the type locality.

Holotype. Io. 3778, female carapace.

Material. 54 valves and carapaces. Figured specimens, Pls. 55, 56: Io. 3778–3779.

Dimensions.

Female carapace, holotype, Io. 3778: *L*, 0·41; *H*, 0·19; *L*/*H*, 2·16; *W*, 0·15.
Male carapace, Io. 3779: *L*, 0·41; *H*, 0·19; *L*/*H*, 2·16; *W*, 0·15.
Female length ($N = 19$); $\bar{x}$, 0·402; *S*, 0·0158; *range*, 0·37–0·43; *V*, 3·9.
Male length, mean of 9 = 0·419.

Diagnosis. Species of *Cytherura* with 8 ridges, 3 of which are prominent, with small puncta between. Females have prominent, reticulate, postero-ventral prominence.

Description. Sexual dimorphism distinct (see below); valves more or less equal. Dorsal margin gently convex; anterior margin obliquely rounded; ventral margin concave. Prominent caudal process at posterior, approximately evenly placed between dorsal and ventral margins; its ventral side sharply differentiated from posterior outline; its dorsal side slightly concave, curving into dorsal margin. Mean length of caudal process 0·05 mm in female and 0·04 mm in male. In dorsal view, caudal process prominent as narrow addendum to main part of carapace; in females, concavity in posterior part of outline.

Females have distinct depression in ventral part of valve just to posterior of centre. This causes postero-ventral area in front of caudal process to appear as prominence; in males this area almost smooth. Small eye tubercle present. Males also slightly more elongate.

Ornamentation faint. 3 prominent longitudinal ridges run from postero-dorsal position towards centre of anterior margin. Another 5 ventral ridges run parallel to ventral margin. In antero-dorsal region, 2 conspicuous curved ridges join topmost of other ridges; series of irregular ridges covers remainder of dorsal surface. Postero-ventral prominence of female strongly reticulate. Elsewhere, and totally with males, 2 or 3 rows of small puncta between ridges, with very faint reticulation in places. In 1 specimen, coarse reticulation seen over large areas of valve (see below).

No internal details observed.

Discussion. This is similar to *C. gracilis* Lienenklaus described from the Falun de Jeurre. The ridge pattern is almost identical, but is much more weakly developed in *C. porcina*; *C. gracilis* is strongly reticulate and lacks the puncta of *C. porcina*. As mentioned above, 1 specimen from Cormeilles was coarsely reticulate, like *C. gracilis*; however, it differs from the latter, as do all the other specimens, in being more elongate. *C. alata* (Lienenklaus) as illustrated by Oertli (1956) has a similar faint ridge pattern, but this pattern differs markedly in detail; it is less elongated than *C. porcina*.

Genus EOCYTHEROPTERON Alexander 1933

Type species. Cytheropteron bilobatus Alexander 1929.

Diagnosis. Carapace egg-shaped with short caudal process. Prominent ventral swelling. Surface reticulate. Hinge merodont, all elements crenulate.

Eocytheropteron plicatoreticulatum Margerie

Plate 55, figs. 6–8

1852 *Cythere punctatula* Bosquet (*non* Roemer 1840), p. 73 (pars).
?1895 *Cytheropteron bosqueti* Lienenklaus (*non* Speyer), p. 150.
?1895 *Cytheropteron laeve*? Lienenklaus (*non* Brady), p. 152.
1961 *Eocytheropteron plicatoreticulatum* Margerie, p. 16, pl. 2, figs. 1–4; pl. 4, figs. 1, 2.

Type locality and horizon. Cormeilles-en-Parisis; Marnes à Huîtres.

Stratigraphic range and distribution. In the Paris Basin, Couches de Sannois; Marnes à Huîtres; Falun de Jeurre; Falun d'Ormoy.

Material. Couches de Sannois, Cormeilles—17 valves and carapaces; Marnes à Huîtres, Cormeilles —7 valves and carapaces; Auvers St.-Georges—4 valves; Ormoy—1 valve. Figured specimens, Pl. 55, Io. 3780–3782.

Discussion. This is the commonest *Eocytheropteron* found at Auvers-St.-Georges and as such is very probably the same as Lienenklaus's *Cytheropteron bosqueti* (Speyer); the only other large species belonging to *Eocytheropteron* described by Lienenklaus was *Cytheropteron laeve*? Brady, which was probably a worn specimen of the same species. Lienenklaus also described 2 new species, *Cytheropteron ovulum* and *Cytheropteron parisiense*, probably female and male dimorphs respectively; they are much smaller than *E. plicatoreticulatum* (0·50–0·54 mm length, compared with 0·85 mm for Io. 3782) and certainly should not be included in it.

Genus MICROCYTHERURA G. W. Müller 1894

Type species. Microcytherura nigrescens G. W. Müller 1894.

Diagnosis. Carapace small, trapezoidal in shape. Right valve larger than left. Surface weakly striated. Hinge merodont.

EXPLANATION OF PLATE 56

Fig. 1. *Leguminocythereis verricula* sp. nov. Female left valve, Io. 3757, ×60; Couches de Sannois, Cormeilles (PCM.20).

Fig. 2. *Cytheridea pernota* (Oertli and Keij). Female right valve, Io. 3712, ×60; Upper Hamstead Beds, Bouldnor Cliff (EBC.114).

Figs. 3, 6. *Hemicyprideis gilletae* (Stchepinsky). Couches à *Mytilus*, Reimerswiller, Alsace; ×60. 3, Left valve, female, Io. 3742. 6, Right valve, female, Io. 3743.

Figs. 4, 7. *Hammatocythere hebertiana* (Bosquet). 4, Female carapace, Io. 3768, ×60; Marnes à Huîtres, Cormeilles (PCM.27). 7, Male carapace, Io. 3773, ×60; Ormoy.

Fig. 5. *Hemicyprideis montosa* (Jones and Sherborn). Female right value, Io. 3741, ×60; Henis Clay, Bilzen.

Figs. 8–11. *Cytherura porcina* sp. nov. Couches de Sannois, Cormeilles (PCM.20), ×100. 8, 9, Female, holotype, Io. 3778; 8, left view; 9, right view. 10, 11, Male, Io. 3779; 10, left view; 11, right view.

Fig. 12. *Bradleya dolabra* sp. nov. Right valve, Io. 3759, ×60; Glaises à Cyrènes, Neuilly Plaisance (PNP.2).

Fig. 13. *Cladarocythere apostolescui* (Margerie). Female right valve, internal view, Io. 3709, ×70; Bembridge Limestone, Bouldnor Cliff.

Figs. 14, 15, 17. *Echinocythereis hamsteadensis* sp. nov. 14, Carapace, dorsal view, Io. 3763, ×60; Cormeilles, Couches de Sannois (PCM.20). 15, 17, Right valve, Io. 3762, Bouldnor Cliff, Upper Hamstead Beds; 15, hinge, ×105; 17, internal view, ×60.

Fig. 16. *Cyamocytheridea punctatella punctatella* (Bosquet). Right valve, Io. 3716, ×60; Auvers-St.-Georges.

Microcytherura delphina sp. nov.

Plate 55, figs. 3–5

Type locality and horizon. Cormeilles-en-Parisis; Couches de Sannois, Bed No. 44 of Girard d'Albissin.

Stratigraphic range and distribution. So far only known from the type locality.

Holotype. Io. 3783, carapace.

Material. 21 valves and carapaces. Figured specimens, Pl. 55: Io. 3783–3785.

Dimensions. Carapace, holotype, Io. 3783: *L*, 0·39; *H*, 0·20; *L*/*H*, 1·95; *W*, 0·21.
Length ($N = 17$): *x*, 0·374; *S*, 0·0150; *range*, 0·35–0·40; *V*, 4·0.

Diagnosis. Species of *Microcytherura* with small caudal process and weak ornamentation consisting of 3 groups of ridges with puncta between.

Description. Sexual dimorphism not recognized. Carapace sub-trapezoidal. Dorsal margin straight; anterior margin obliquely rounded. Ventral margin slightly concave, hidden by overhang of prominent ventral swelling. Short caudal process at posterior, with long, gentle concave slope up to dorsal margin. Carapace ovate in dorsal view.

Ornamentation very faint, consisting of series of ridges, stronger on ventral swelling, with rows of puncta between. Puncta in double rows on ventral swelling. Ridges in 3 groups; most prominent, group of 5, parallel to ventral margin, but successively cut off by second group of 4 ridges running diagonally across carapace from the postero-dorsal area towards antero-ventral region; third group of 4 ridges on extreme ventral portion of ventral swelling, parallel to curvature of antero-ventral margin and ventral margin, cutting off median group of ridges, then curving round parallel to anterior margin.

Internal features not clearly seen. Hinge of left valve has smooth postero-median hinge-bar, slightly swollen at anterior. Anterior tooth of right valve coarsely crenulate, similar to illustration of *H. fulva* (Brady and Robertson) by Wagner (1957). Selvage peripheral.

Discussion. This is the oldest species of *Microcytherura* so far described and extends its range downwards from the Upper to the Lower Oligocene. By its shape, ornamentation, and hinge, it certainly belongs to the genus. Van Morkhoven (1963) stated that the genus has no caudal process; Wagner (1957) clearly mentioned it in the description of *M. fulva* (Brady and Robertson). The caudal process is not very well developed, however.

Family LOXOCONCHIDAE Sars 1925
Genus LOXOCONCHA Sars 1866

Type species. Cythere impressa Baird 1850.

Diagnosis. Carapace shaped like rounded parallelogram. Surface reticulate. Hinge gongylodont. Anterior and posterior vestibules with few straight radial pore canals. Normal pores sieve-type.

Loxoconcha delemontensis Oertli

Plate 55, fig. 15

1896 *Loxoconcha subovata* Lienenklaus (*non* von Münster), p. 28, pl. 2, figs. 9*a*, *b*.
1956 *Loxoconcha delemontensis* Oertli, p. 68, pl. 8, figs. 211–219.
?1957 *Loxoconcha subovata* Keij (*non* von Münster), p. 144, pl. 22, fig. 16.

Type locality and horizon. Birsbett; Rupelian Blaue Tone.

Stratigraphic range and distribution. Switzerland: Rupelian; Paris Basin: Sannoisian, Marnes à Huîtres, Faluns de Jeurre; Belgium: Argiles de Boom.

Material. Numerous valves and carapaces from Bed no. 44 of Girard d'Albissin, Couches de Sannois, Cormeilles, including figured female left valve, Pl. 55, Io. 3786; Auvers-St.-Georges—7 valves.

Discussion. The specimen figured by Keij from the Rupelian of Belgium lacks the prominent ventral swelling of *L. subovata* (von Münster). In size, shape, and ornamentation it is very similar to *L. delemontensis* and is provisionally included in its synonmy.

Loxoconcha nystiana (Bosquet)

Plate 55, figs. 11, 14

1852 *Cythere nystiana* Bosquet, p. 65, pl. 3, fig. 3.
1956 *Loxoconcha nystiana* (Bosquet); Oertli, p. 68, pl. 8, fig. 209.
1957 *Loxoconcha nystiana* (Bosquet); Keij, p. 142, pl. 21, fig. 12; pl. 22, figs. 17–19.

Type locality and horizon. Berg; Argile à *N. comta.*

Stratigraphic range and distribution. Belgium: Argile à *N. comta*; Paris Basin: Couches de Sannois, Cormeilles; England: Upper Hamstead Beds.

Material. Bilzen (argile à *N. comta*)—2 valves (including figured female left valve, Pl. 55, Io. 3787); Bouldnor—8 valves (including figured female right valve, Pl. 55, Io. 3788); Cormeilles—20 valves.

Discussion. In his detailed description of *L. nystiana*, Keij mentioned that the females are dorsally smooth or indistinctly reticulate; the remainder of the surface is reticulate. The extent of the smooth area seems to vary considerably amongst the specimens studied. A few species from Cormeilles are almost entirely smooth, while others have just a small area along the dorsal margin. Most of the Bouldnor specimens are completely smooth, only 1 specimen showing a small ventral area of reticulation. See palaeoecological section.

Genus CYTHEROMORPHA Hirschmann 1909

Type species. Cythere fuscata Brady 1869.

Diagnosis. Carapace small, showing strong sexual dimorphism with very elongate male; surface ornament of pits, reticulation, and ridges; internal details similar to *Loxoconcha.*

Cytheromorpha zinndorfi (Lienenklaus)

Plate 55, figs. 10, 13, 16

1905 *Limnicythere zinndorfi* Lienenklaus, p. 58, pl. 4, figs. 32*a*, *b*, and figs. 33*a*, *b*.
?1917 *Cythereis strangenbergensis* Klähn, p. 66, pl. 12, figs. 5*a–c*, 8, 9, 10*a–c*.
1952 *Cytheromorpha zinndorfi* (Lienenklaus); Straub, p. 501, pl. c, figs. 57–61.
1956 *Cytheromorpha zinndorfi* (Lienenklaus); Oertli, p. 72, pl. 9, figs. 244–252.
1957 *Cytheromorpha zinndorfi* (Lienenklaus); Keij, p. 89, pl. 16, figs. 8, 9.
1960 *Cytheromorpha* cf. *zinndorfi* (Lienenklaus); Stchepinsky, p. 26, pl. 1, figs. 10, 11.
1963 *Cytheromorpha zinndorfi* (Lienenklaus); Triebel, p. 212, figs. 28, 29.
1963 *Cytheromorpha zinndorfi* (Lienenklaus); Stchepinsky, p. 160.
?1964 *Cytheromorpha zinndorfi* (Lienenklaus); Sonmez-Gokcen, p. 54, pl. 2, figs. 5*a*, *b*, 6.

Type locality and horizon. Offenbach-am-Main; Chattian.

Stratigraphic range and distribution. Germany: Schleichsand and Cyrenenmergel of Frankfurt and the Mainz Basin; Switzerland: Blaue Tone and Chattian; Paris Basin: Bande Blanche Inférieur, Montfermeil; Couches de Sannois Supérieur, Cormeilles; Marnes à Huîtres, Cormeilles, St. Cloud; Alsace: Couches de Pechelbronn moyen; Zone Salifère moyen; Couches à *Mytilus*; Marnes à Cyrènes; Belgium: Upper Tongrian of Kleine Spouwen; England: Upper Hamstead Beds; Turkey: (?), Oligocene of Catalca (near Istanbul).

Material. Numerous specimens from Bouldnor Cliff (including figured specimens, Pl. 55, Io. 3789–3791), Cormeilles and St. Cloud; 2 valves from Montfermeil.

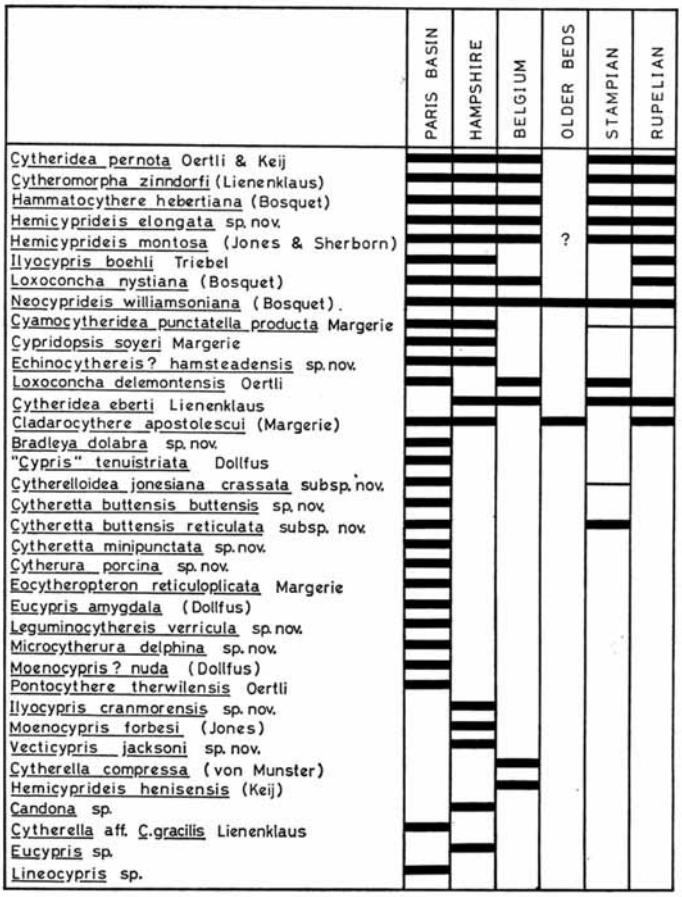
Discussion. The diagnostic features of this species are the irregular short median ridge, the longer ventral ridge, the reticulation and the two posterior prominences (see Plate 55, figs. 10, 13). In the Isle of Wight *C. zinndorfi* is only found in the Upper Hamstead Beds and topmost Middle Hamstead Beds. A related species is found in the Bembridge Marls and the Osborne Beds. The latter is almost certainly the species described by Jones (1856) as *Cytherideis unisulcata* sp. nov.

STRATIGRAPHICAL CONCLUSIONS

This study of the Sannoisian ostracods was carried out with the aim of establishing whether or not they would be useful for correlation, and if so, whether they had anything to add to the controversy over the Eocene–Oligocene boundary.

Since the mid-fifties there has been a lively debate concerning the position of the base of the Oligocene in France, Belgium, and Germany. The traditional concept of Lattorfian (= Sannoisian = Tongrian) as the basal Oligocene stage was first challenged by Krutzch and Lotsch (1957, 1964), who were supported by several Russian authors (e.g. Korobkov 1964). These maintained that the Lattorfian was really Upper Eocene in age and that the type horizon could be correlated with nummulite-bearing sediments in northern Germany, Poland, and Russia. The large Lattorfian molluscan fauna was compared with the Rupelian and Tongrian by Glibert and Heinzelin (1954), Cox (*in* Eames *et al.* 1962), and Curry (1966), but with the Eocene by Korobkov (1964). Most of these relied on the original faunal lists of von Koenen (1893). Cavelier (1964*c*) established a convincing case for correlating the Hamstead Beds with the Sannoisian of the Paris Basin, and placed the base of the Oligocene at the base of the Sannoisian (1964*a*,*b*). This left the Headon Beds in a pre-Sannoisian and pre-Oligocene stage; traditionally they have been correlated with the Lattorfian. This appeared to confirm an Eocene age for the Lattorfian. An examination of the Foraminifera of Belgium led Batjes (1958) to conclude that the Lower Tongrian might be of Upper Eocene age, and the Upper Tongrian of Oligocene age. This led to the concept of Lattorfian (= Headon Beds = Lower Tongrian = Upper Eocene) overlain by Sannoisian (= Upper Tongrian = facies of the Rupelian = Oligocene).

The principal difficulty is that while we can examine the stratotypes of both the Tongrian and Sannoisian, the Lattorfian type section is an inaccessible flooded mine in the German Democratic Republic. The extensive molluscan fauna monographed by von Koenen unfortunately contains a mixed group of Middle and Upper Eocene species, besides the Oligocene ones (Korobkov 1964; Curry 1966), so that the validity of a Lattorfian fauna is thrown into doubt. Furthermore, Cox and Korobkov used the same faunal lists of Lattorfian molluscs and arrived at opposite conclusions.



TEXT-FIG. 9. The stratigraphical distribution of Sannoisian ostracods.

Curry (1966) extracted some planktonic foraminifers from the interior of molluscs which were collected at Lattorf in the last century and are now in the collections of the British Museum (Natural History). Banner and Blow identified them as being essentially the same as those from the Rupelian Boom Clay of Belgium. Examination of nannoplankton by Martini and Ritzkowski (1968, 1969) indicated that the Lattorf Sands and Grimmertingen Sands (Lower Tongrian) are time equivalents, but younger than the Headon Beds of Hampshire. Cavelier (1969) also queried the Lattorfian age of the Headon Beds, and if they are in fact older than the Lattorf Sands, i.e. Upper Eocene in age, we would have a return to the concept of Lattorfian = Sannoisian = Tongrian, which defines the base of the Oligocene.

The ostracods have proved to be extremely useful for correlation within the Anglo–Paris–Belgian area. The Upper Hamstead Beds contain the youngest Palaeogene fauna found in the Hampshire Basin. 10 species of polyhaline–marine ostracods are present. 2 of these are recorded from lower beds, *Hemicyprideis montosa* from the Lower and Middle Hamstead Beds and more doubtfully from the Bembridge Marls, and *Neocyprideis williamsoniana* from the Bembridge Limestone and Oyster Marls; the remaining 8 are known only from this horizon in Britain. The fauna is completely different from that of the Marine Middle Headon Beds (Keen 1968). All 10 species are present in the Sannoisian of the Paris Basin; 7 are recorded from the Stampian, but none is known in older beds in the Paris Basin. 7 of the species are also found in the Upper Tongrian Beds of Belgium, but not in lower horizons. The Belgian Sannoisian has yielded 11 polyhaline–marine species, of which 8 are known in the Paris Basin. Taking the whole ostracod fauna, 33 species and subspecies are recorded, together with 3 in open nomenclature; 27 are recorded from the Paris Basin, 15 from Hampshire, and 13 from Belgium. 7 species are present in all 3 countries; 14 species, together with 2 which are subspecifically distinct, are found in the overlying Rupelian, while only 2 are definitely present in older rocks, i.e. *N. williamsoniana* and *Cladarocythere apostolescui* in the Bembridge Beds.

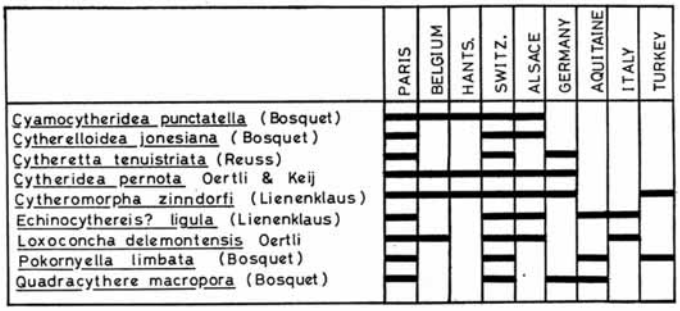
The discussion so far has been concerned with taxonomy at the species level. It is difficult to use genera because most of these range throughout the Tertiary, and many are still living at the present day. Nevertheless, *Hemicyprideis*, *Ilyocypris*, and *Microcytherura* appear for the first time in western Europe, as well as the newly described genera *Hammatocythere* and *Vecticypris*. *Hammatocythere* has probable ancestors in the area, however.

About half of the Sannoisian species can be related to local Upper Eocene species. The other half have no known ancestors in the area. This great break between the Sannoisian ostracod fauna and older faunas is the most conspicuous in the Palaeogene. The Headon Beds, for example, have many species in common with older horizons (Keen 1968). The difference cannot be explained by ecological differences because similar environments had existed in immediately preceding periods. Such a great faunal break can only be explained by the arrival of a new fauna which rapidly colonized the entire area, together with the more rapid evolution of indigenous species. Both events were perhaps connected with the spread of lagoonal conditions which just preceded the main Rupelian transgression.

Thus in the Anglo–Paris–Belgian area the Sannoisian has an ostracod fauna which differs considerably from that of older beds, but is closely related to that of the overlying Rupelian. In fact, apart from the freshwater and brackish ostracods it can hardly be separated from the latter. This strongly supports Cavelier (1964*a*,*b*) in placing the base of the Oligocene at the base of the Sannoisian, and regarding the latter as a facies developed at the base of the Rupelian stage. The next problem is to decide how the Lattorfian fits into this scheme.

The Lattorf ostracod fauna has been described by Moos (1968), who recorded 37 species and subspecies, some obtained from material from von Koenen's shells. 28 of these are indigenous, and of the remaining 9, 2 are thought to be present in the Middle Headon Beds (Keen 1968); 4 in the Melanienton, and 2 of these 4 also in the Sannoisian of Alsace; and 4 in Miocene strata. Its closest link is thus with the Melanienton, bearing

in mind that the latter has only yielded 12 named marine ostracods (Moos 1969). Carbonnel and Ritzkowski (1969) have also described 12 freshwater ostracods from the Melanienton, 2 of which are found in the Sannoisian of Alsace. One of the most striking features of the Melanienton fauna is the absence of *Hemicyprideis*. The latter is abundant in the Sannoisian of the Mainz Basin (Malz and Triebel 1970) and Alsace. The Alsace Sannoisian fauna is rather poor (Stchepinsky 1960), with 7 named freshwater ostracods and 5 polyhaline–marine; 2 of the latter are species of *Hemicyprideis* and the other 3 are present in the Melanienton. The Melanienton also has *Cytheridea pernota* in common with the Rupelian of Alsace. Altogether, correlation between these different regions of the eastern sector is unsatisfactory. There is a tenuous link between Lattorf and Alsace via the Melanienton of Hesse.



TEXT-FIG. 10. The geographical distribution of some characteristic Sannoisian–Rupelian ostracods.

When this region is compared with the Sannoisian of the Anglo–Paris–Belgian area, only 2 species are found in common: *C. pernota* and *Cytheromorpha zinndorfi*; a third, *Cypris tenuistriata straubi* (Carbonnel and Ritzkowski) is only subspecifically distinct. The Alsatian *Hemicyprideis gilletae* is closely related to *H. montosa*, and *Eucypris pechelbronnensis* to *E. amygdala*. If the whole Sannoisian–Rupelian fauna is compared, correlation is much better. 8 out of the 19 species of Alsace are found in the Paris Basin, 4 of them also in Belgium.

Thus once again it is seen that the Sannoisian can hardly be separated from the Rupelian except by the freshwater and brackish fauna. Nor can the Sannoisian be correlated with any detail outside the Anglo–Paris–Belgian area, except by the occurrence of similar facies at a similar stratigraphical level. When the whole Sannoisian–Rupelian fauna of the Anglo–Paris–Belgian area is considered, it is found to be part of a widespread fauna occurring over large parts of Europe (text-fig. 10). Thus the ostracods would appear to offer a more reliable means of correlation most than fossil groups for this part of the stratigraphical column.

In conclusion, the evidence of the ostracods favours drawing the base of the Oligocene at the base of the Sannoisian in the Paris Basin, and between the Bembridge Oyster Marls and the Lower Hamstead Beds in the Hampshire Basin (Keen 1968). The ostracod fauna of the Lower Tongrian of Belgium is poorly known, but the evidence seems to

favour drawing the base at the base of the Sables de Neerreppen. The Lattorfian is probably the time equivalent of the Sannoisian, as indicated by the Melanienton fauna. Until the exact position of the Lattorfian is established within the Anglo–Paris–Belgian area, it is considered desirable to retain the term Sannoisian as a facies developed at the base of the Rupelian, rather than use the term Lattorfian.

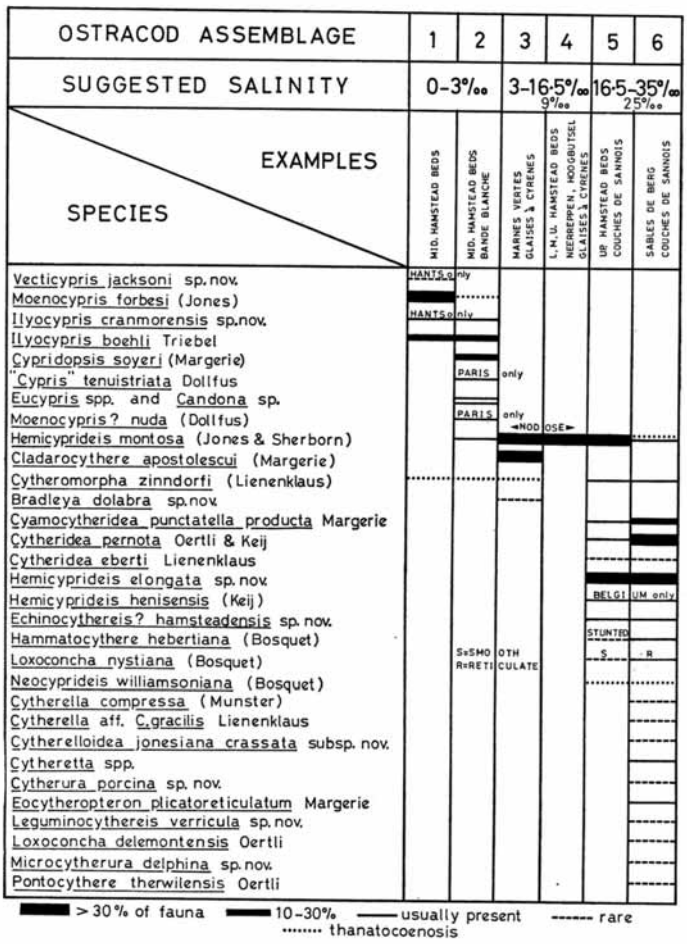
PALAEOECOLOGY

Ostracod assemblages and the Sannoisian environment

6 ostracod assemblages can be recognized from the Sannoisian strata of the Anglo–Paris–Belgian area, shown in text-fig. 11. 3 of these are characterized by the typical Sannoisian ostracod *H. montosa*. The palaeoecology of this species is dealt with in detail in Keen (1972). Salinity was probably the principal controlling factor; the suggested salinities are based on comparisons with Recent ostracods, necessarily on the generic level because no Sannoisian species are still living. The main works consulted are Kruit (1955), Swain (1955), Wagner (1957), Curtis (1960), van Morkhoven (1962, 1963), Puri (1968) and Kilenyi (1969). Supporting evidence can be obtained from the associated molluscan faunas. The palaeoecology of the ostracods from Cormeilles-en-Parisis has been partly dealt with by Margerie (1961) and Oertli (1967). The assemblages listed are believed to represent biocoenoses (as the term is generally applied to the study of ostracods). This simply implies that the ostracods found in a sample can be divided into two parts: those which lived in the environment represented by the sample at the time and place of its formation, and those which did not, although both parts need not be present in every sample. The latter are referred to as the thanatocoenosis. The biocoenosis content can be recognized by the presence of larval stages, carapaces, males and females, equal numbers and size range of left and right valves, and the presence of common associates. The absence of any of these criteria does not necessarily rule out a biocoenosis, however.

Assemblages 1 and 2 represent a freshwater environment. The first is characterized by the extinct genus *Moenocypris*, the second by *Cypridopsis* and *Candona* (*Pseudocandona*). These 2 distinct freshwater assemblages can also be recognized in the Headon Beds. Assemblage 1 is found in shales and clays, often rich in aquatic plant remains, and with molluscs such as *Viviparus* and *Unio*. This would seem to indicate still, or very gently flowing water, with much material in suspension, and probably with a cover of aquatic plants such as water-lilies. Assemblage 2 is found in limestones and calcareous clays associated with *Lymnaea*, *Planorbis*, and abundant *Chara*. This probably indicates clear, slowly-flowing but well-circulated water. These 2 systems were quite separate because gradations from one assemblage to the other are very rare.

Assemblages 3 and 4 are taken to represent a mesohaline environment. *Hemicyprideis* is related to the modern *Cyprideis*, which Sandberg (1965*b*) has shown to have its greatest development in mesohaline conditions, although ranging from freshwater to hypersaline. Kruit (1955) found that *C. torosa* occurred so abundantly in the mesohaline and hypersaline environments of the Rhone delta as to exclude all other ostracods. Bate (1971) observed a similar situation with *Cyprideis* in the hypersaline lagoons of Abu Dhabi. There is a possibility therefore that Assemblage 4 sometimes represents a hypersaline environment. It is associated with gypsum in the Paris Basin, although



TEXT-FIG. 11. Sannoisian ostracod assemblages.

modern ideas (Fontes 1968) do not indicate hypersaline conditions for its formation in the Paris Basin. *H. montosa* has been regarded as a euryhaline ostracod, occurring more commonly in mesohaline salinites (Keen 1971). *Cladarocythere* is found with a brackish water assemblage of molluscs and ostracods from the Lutetian to the Chattian. It is never found with true freshwater associates, nor with marine ones. The general rarity of *C. apostolescui* in the Glaises à Cyrènes and its greater abundance in the beds transitional to the Marnes vertes probably indicates a preference for a lower mesohaline salinity. Thus Assemblage 3 is regarded as inhabiting waters with a salinity of 3–9‰, and Assemblage 4, 9–16‰.

The polyhaline ostracods have been divided into 2 groups, represented by Assemblages 5 and 6. Comparing these with Recent ostracods, Assemblage 5 includes those with a fairly wide salinity tolerance, while Assemblage 6 consists of those genera restricted to marine or very slightly brackish waters. Thus *Cytheretta* and *Cytherelloidea* have never been recorded from salinities less than 30‰. The 2 assemblages contain much in common and presumably graded into each other. It is noticeable that Assemblage 6 is not developed at Bouldnor Cliff.

The Sannoisian facies can be seen to represent several environments. Assemblages 1 and 2 indicate freshwater lakes and rivers, while Assemblages 3–6 probably indicate lagoonal conditions. Comparing them with the Texan bays and lagoons (Ladd *et al.* 1957), Assemblages 3 and 4 could represent closed lagoons, i.e. no sea connection, and Assemblages 5 and 6 open lagoons, i.e. some connection with the sea, where Assemblage 6 is near such connections. The Belgian and Hampshire successions probably represent tropical, well forested, low lying coastal regions. The Paris Basin area show signs of being a centre of internal drainage in semi-arid surroundings, an environment also developed during the Oligocene in Alsace.

Infraspecific variation

Loxoconcha nystiana shows a large amount of variation in the strength and development of reticulation. Specimens from the Upper Hamstead Beds (Assemblage 5) are almost smooth (Pl. 55, fig. 14), those from the Argile à *N. comta* (Assemblage 6) mainly reticulate, while the Couches de Sannois (Assemblages 5 and 6) yield both. Sandberg (1965*a*) mentioned that the Recent *Cytheromorpha paracasteana* (Swain) is weakly reticulate in low salinities and strongly reticulate in marine salinities. A similar relationship between salinity and ornamentation has been demonstrated by Carbonnel (1969*a*, and also discussion, pp. 254–256) for the Upper Miocene species *Elofsonella amberii* Carbonnel. It seems likely that the development of reticulation in *L. nystiana* is also related to salinity, the most reticulate forms occurring in Assemblage 6 with near marine salinities.

C. apostolescui also shows a variation in reticulation, but in this case the extreme forms are found within a single sample. It is difficult to correlate this with environmental factors such as salinity or pH.

H. hebertiana shows a considerable amount of variation in calcification. The specimens from the Upper Hamstead Beds and the Falun d'Ormoy have a 'ragged' appearance, particularly of the ridges. Those from the Hamstead Beds are also weakly calcified and shorter than normal. This is taken to be a case of stunting, with the individuals living near the limit of their salinity tolerance.

In common with other Cytheridinae, *H. montosa* develops nodes. It has been postulated (Keen 1971) that a 'peak' of nodosity for this species occurred with salinities of about 10‰. Specimens from freshwater and polyhaline–marine assemblages are virtually always smooth.

The distribution of the males of Hammatocythere hebertiana

The distribution of the males of this species is puzzling. Apart from Ormoy, they are very rare; only 1 male compared with 74 females was found. Yet at Ormoy 60% of the adults are males. The presence of larval stages (text-fig. 8) indicates that we are

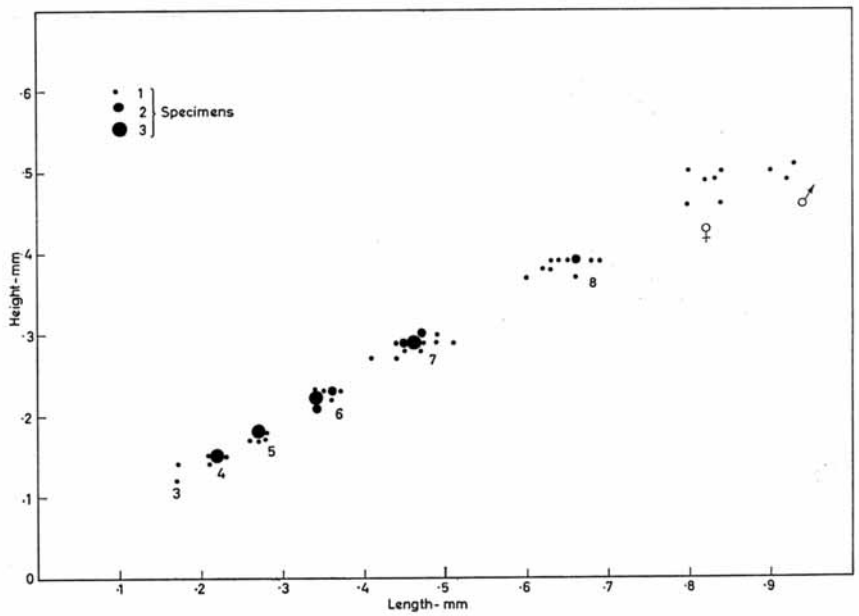
dealing with a biocoenosis, although Ormoy has only yielded 5 species of ostracods. 90% of the fauna consist of *H. hebertiana*; in the other localities it only constitutes 2–3% of the much richer faunas. No males were found of the related *H. trituberculata*. Thus the norm for the species, and perhaps for the genus, is for the presence of very infrequent males, so rare in fact that it might be assumed that reproduction was parthenogenetic. Bearing this in mind, it would seem that the abundance of males at Ormoy was controlled by some environmental factor. The Faluns d'Ormoy were deposited in slightly brackish interdunal lagoons (Alimen 1936).

It has often been speculated that male ostracods inhabit a different area or environment from the females, and one migrates to the other during the breeding season. The only recorded instance, however, is that of *Philomedes* where the males are planktonic and the females benthonic; the females rise to the surface for mating and then return to the sea floor (Sylvester-Bradley 1969). Van Morkhoven (1962) mentioned the case of *Erpetocypris reptens* (Baird) which apparently reproduces sexually in North Africa, but parthenogenetically in Western Europe. Hulings (1969) found that males of *Parasterope pollex* Kornicker were only present in his samples from Hadley Harbour, Massachusetts, for about 8 weeks during the year; this was interpreted as indicating a short life span, rather than the effects of migration. Pokorny (1965, p. 477), in a discussion on Bohemian Cretaceous ostracods, postulated that a parthenogenetic mode of reproduction may have been advantageous in a stable environment; presumably the reverse would also be true. Thus there are a variety of possible explanations for the distribution of the males of *H. hebertiana*. The males may have been present for only a short period, either because of migration or short life span, and this season has been 'captured' at Ormoy. This fails to explain the absence of males in other samples, perhaps as 'thanatocoenosis' members in the more strict sense of the word, and seems very unlikely because implying very rapid sedimentation (the sample represents about 6 inches in thickness of the rock). Perhaps the males inhabited the environment represented by Ormoy, and the females one represented by the Couches de Sannois, in which case the females migrated to the males. This would explain the presence of females, although they should be much more abundant by comparison with other ostracods, and there are no known examples of this amongst Recent ostracods. Finally, the environment at Ormoy may have favoured sexual reproduction, with the presence of males; again, no Recent ostracod so far described shows this, and females should be more abundant. The exact explanation is therefore difficult to determine. It seems fairly certain that the environment is the cause of this particular distribution. Salinity cannot have been the controlling factor, because polyhaline to marine samples from the Couches de Sannois, and Bouldnor Cliff contain no males. It seems unlikely that there could have been any great change in temperature, and there is no evidence for extremes of pH or Eh in the Sannoisian samples or the Faluns d'Ormoy. Food supply may be the answer, but there is no way of proving this. Perhaps the answer lies in the periodic drying up of the lagoons, which led to isolated populations where sexual reproduction was advantageous.

Moult stages

When the height and length of ostracod moult stages are plotted on graphs, 2 types of pattern are found. The classical distribution shows discrete groups representing individual moult stages; this type is seen in the case of *H. montosa* (text-fig. 12) and

H. hebertiana (text-fig. 8). The second distribution pattern shows continuous gradation with no clearly marked groupings, as seen in *C. apostolescui* (text-fig. 13). The second type is rarely mentioned in the literature, perhaps because deviations from the norm, i.e. the classical pattern, were considered to be due to abnormal sampling. It is commonly met with, however, and may even be the more normal, particularly amongst freshwater ostracods.



TEXT-FIG. 12. Size distribution of the moult stages of *Hemicyprideis montosa* (Jones and Sherborn) from the Glaises à Cyrènes, Cormeilles.

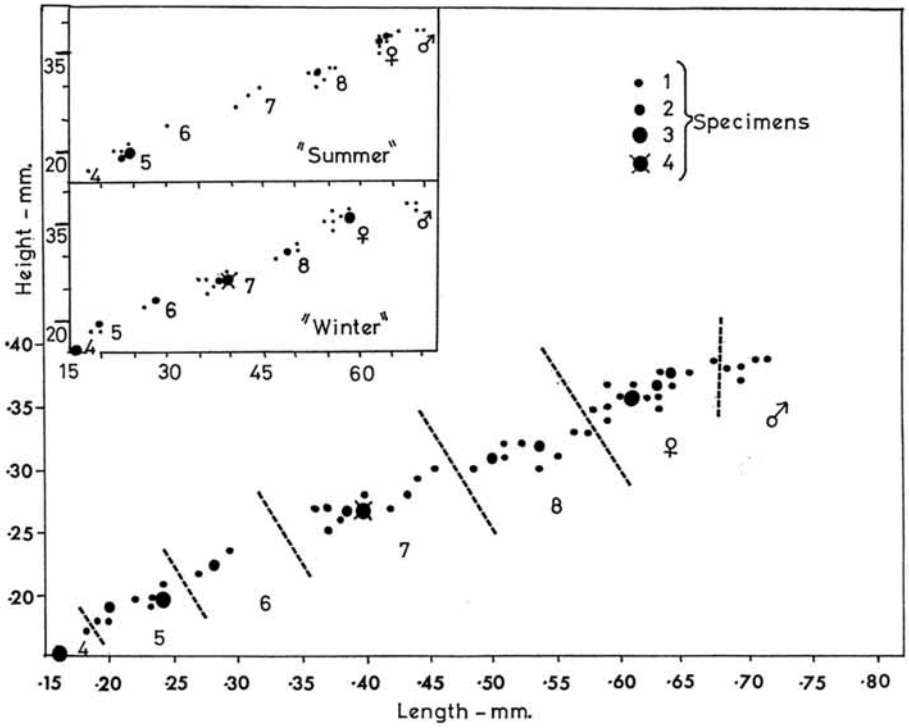
Van Morkhoven (1962) mentioned that most ostracods probably breed throughout the year. Recent work does not seem to support this. Hulings (1969), for example, studied *Parasterope pollex*, which has only 1 breeding season, although larval forms are present throughout the year, and shows clear moult stage groupings. Szczechura (1971), however, found that *Cyprinotus* (*Heterocypris*) *incongruens* Ramdohr had 2 breeding seasons, with different sized moult stages according to the time of year. This leads to a continuous gradation between instars.

Perhaps therefore the 2 types of graph can be explained by these 2 breeding patterns. The classical distribution would indicate 1 breeding season per year, the other more than 1. It is relatively easy to try out different numbers of distribution present by using Anderson's table (1964), i.e. 2, 3, 4, etc. breeding periods. In the case of *C. apostolescui* 2 periods give the clearest results, so it is possible to separate the moult stages into 'summer' and 'winter' groupings (text-fig. 13). Bearing in mind the tropical conditions of

Sannoisian times, 'rainy season' and 'dry season' may be better terms. This is of course only intended as a possible interpretation; the main graph is still the reference.

Predators

Ostracods from Assemblages 5 and 6 sometimes have circular holes, assumed to represent the borings of carnivorous gastropods. The holes are neat, circular, and conical



TEXT-FIG. 13. Size distribution of the moult stages of *Cladarocythere apostolescui* (Margerie) from the Marnes vertes, Cormeilles. The inset is an interpretation of the distribution of moult stages as representing 2 distinct breeding seasons.

in shape. This probably indicates that the predator was a member of the Naticacea (Taylor 1970), 2 species of which are present, *Natica achatensis* Koninck and *N. crassatina* Desh. The ostracods which have been bored are *C. pernota* (in some samples as many as 1 in 6), *H. montosa*, and *C. buttensis*. The holes are small, between 0·1 and 0·2 mm diameter, generally present in the dorsal part of the valve, but showing no preference to left or right valve, or anterior or posterior. This is presumably related to the living position of the ostracod. Unlike Reyment (1963), no examples of unsuccessful borings were observed. The predators were presumably young individuals, and it

is of interest to note Kaesler's observation (1969, p. 244) that ostracods form the food of young oyster drills. Presumably the predators moved on to larger prey as they themselves grew larger.

Hemicyprideis *and* Neocyprideis

The relationship between these 2 genera is interesting. Both have been regarded as ancestral to *Cyprideis*, and to have occupied a similar environmental niche. It seems likely, therefore, that they were direct competitors. They rarely occur together, and then only as isolated individuals within a population of the other. Stratigraphically, *Neocyprideis* is the older, first appearing in the Palaeocene. It is very abundant in the Headon Beds and Bembridge Beds in England, and the Lutetian and basal Stampian of the Paris Basin. A phylogenetic series *N. durocortoriensis* → *N. apostolescui* → *N. colwellensis* → *N. williamsoniana* can be seen in the Anglo–Paris–Belgian area, so *Neocyprideis* can be regarded as the typical brackish water cytheridinid ostracod of the area. *Hemicyprideis* appeared in the Sannoisian and occupied the environment previously held by *Neocyprideis*. It probably migrated into the area from central Europe. *Neocyprideis* regained its niche in the lower Stampian of the Paris Basin and Belgium, but *Hemicyprideis* continued into the Miocene in the Mainz Basin, Switzerland, Austria, and probably also in eastern Europe. *Hemicyprideis* appeared to have been a true euryhaline ostracod, unlike *Neocyprideis*, which was probably restricted to a mesohaline–polyhaline environment, never being present in freshwater. Perhaps this is the reason *Hemicyprideis* held the stage during Sannoisian times, but with the disappearance of the Sannoisian environment lost its advantage.

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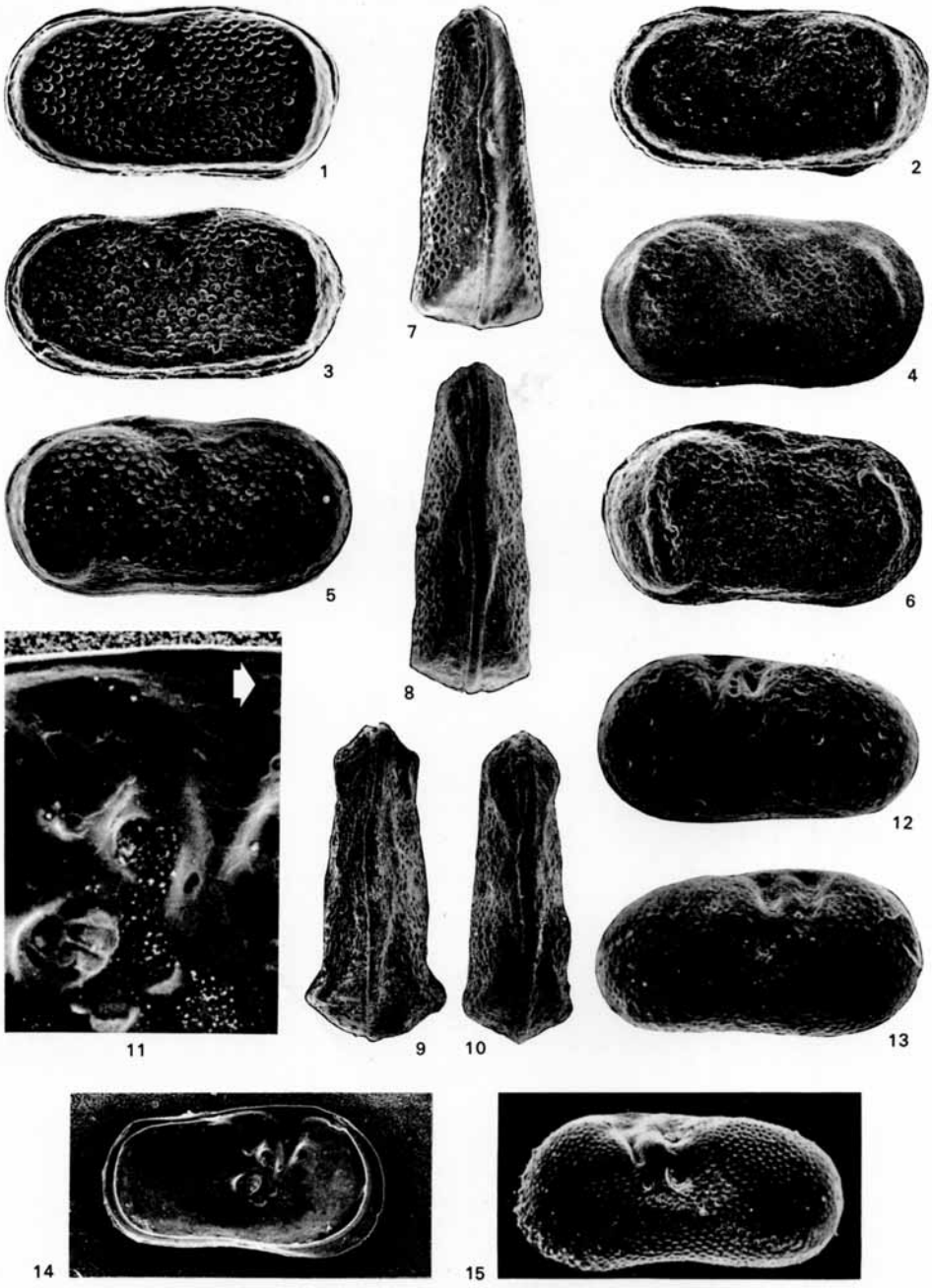

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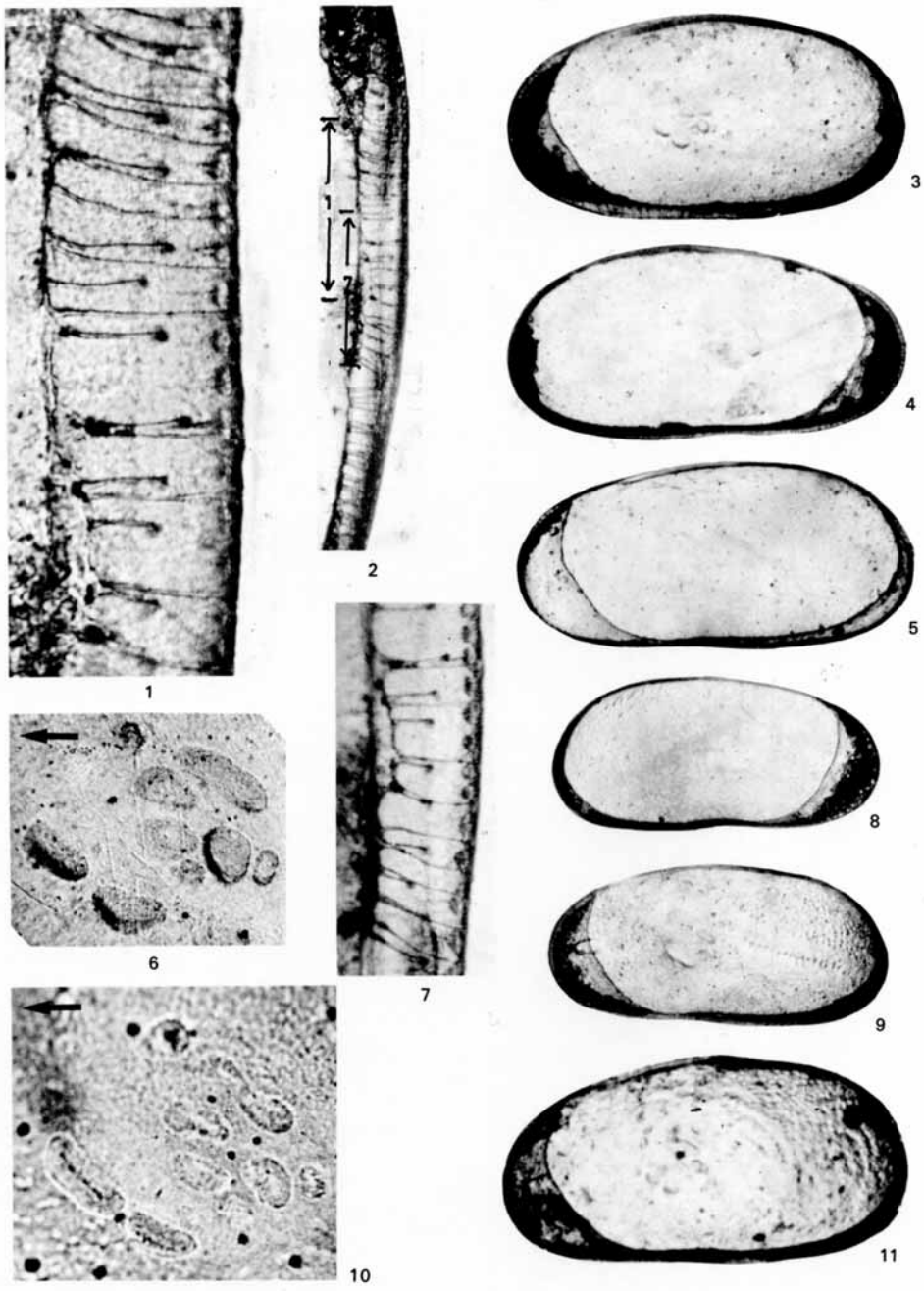

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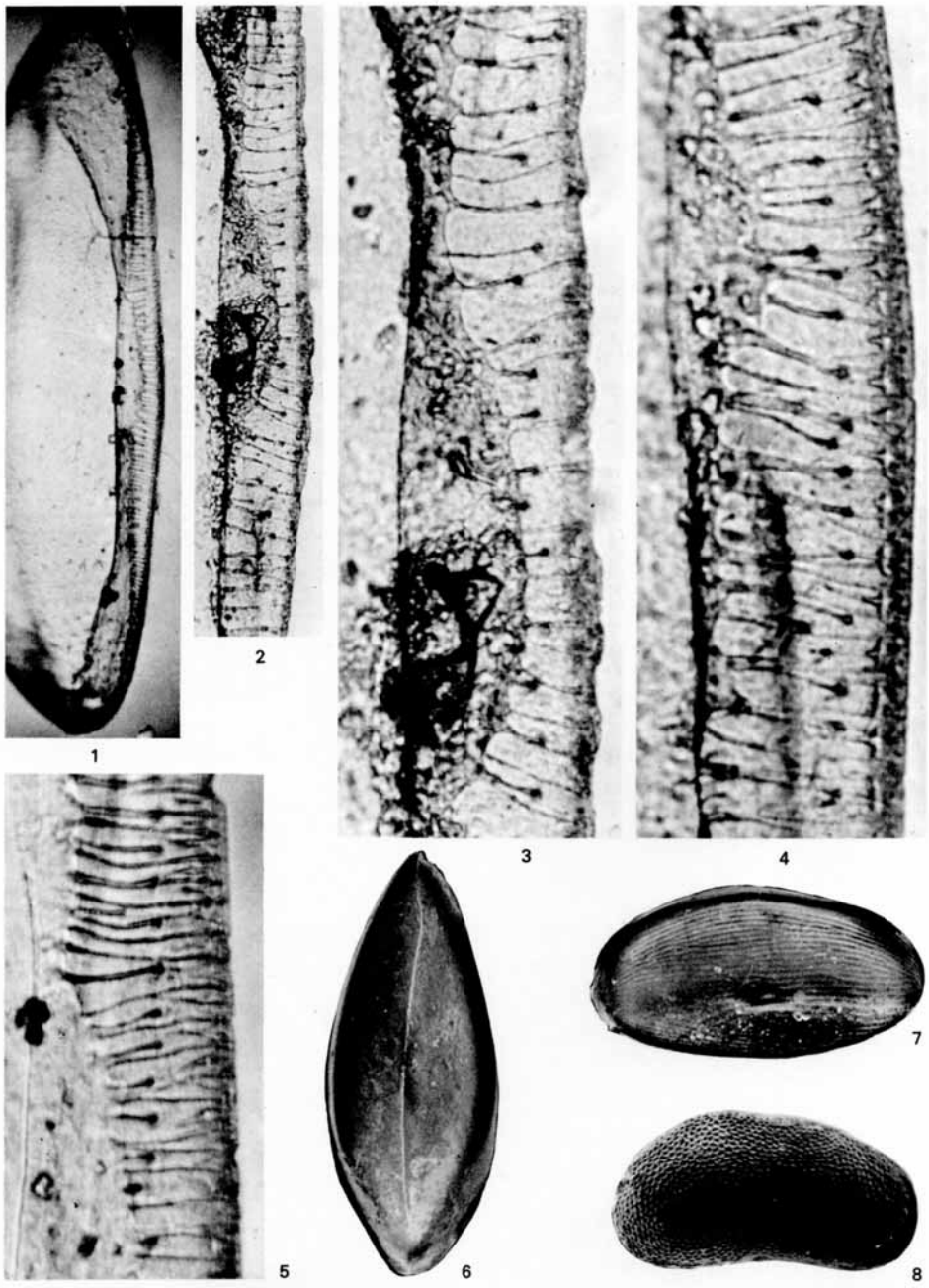

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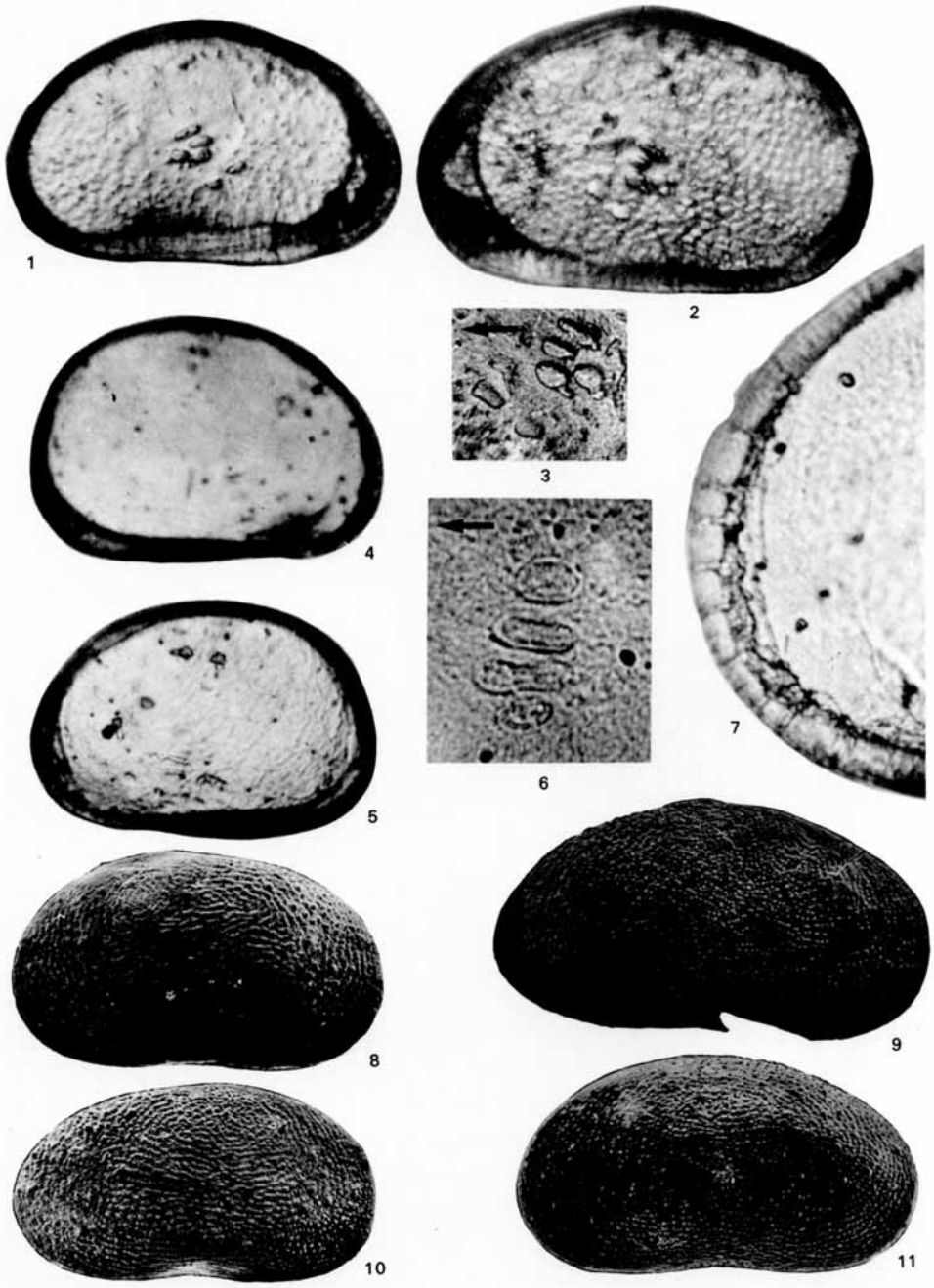

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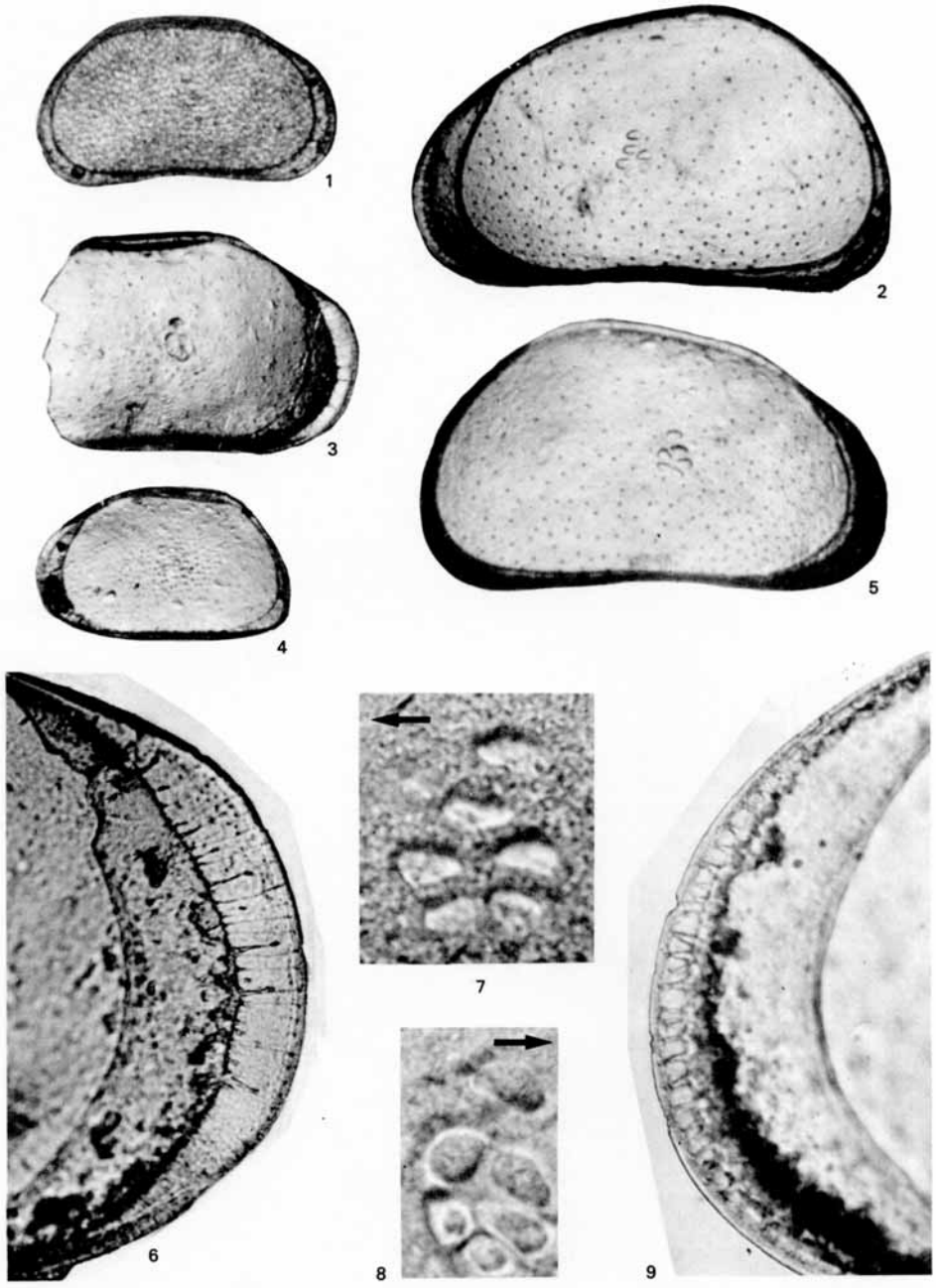

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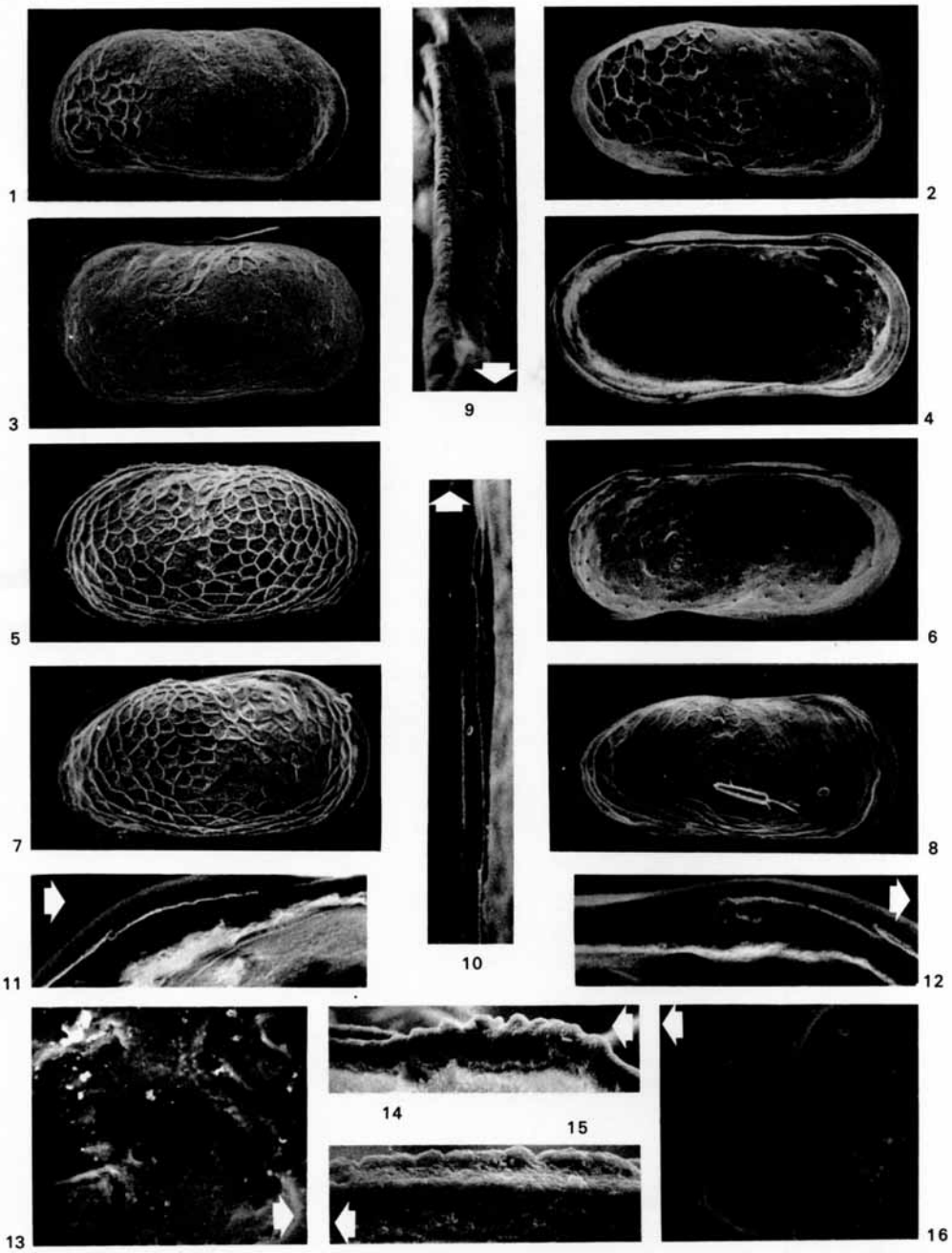

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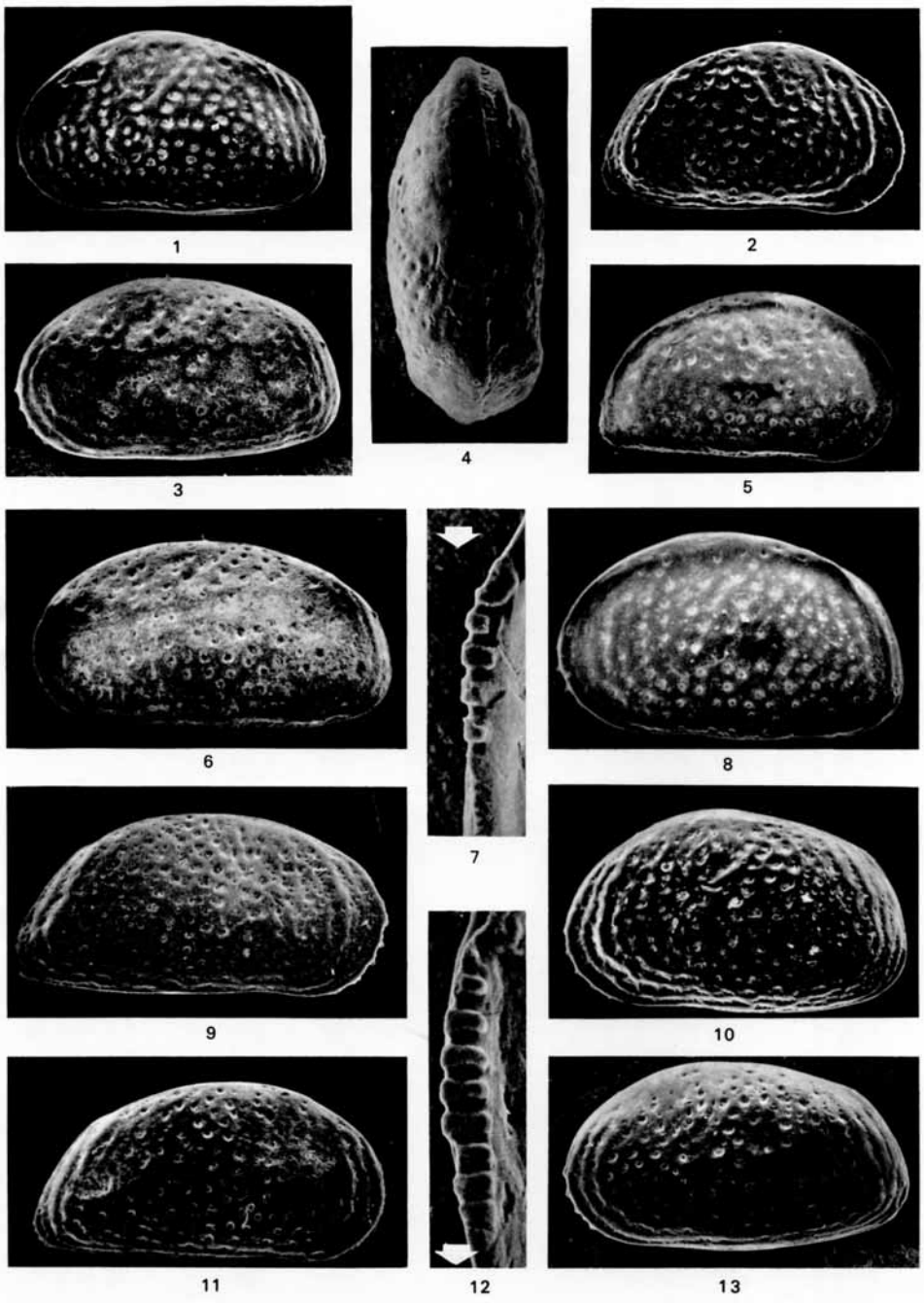

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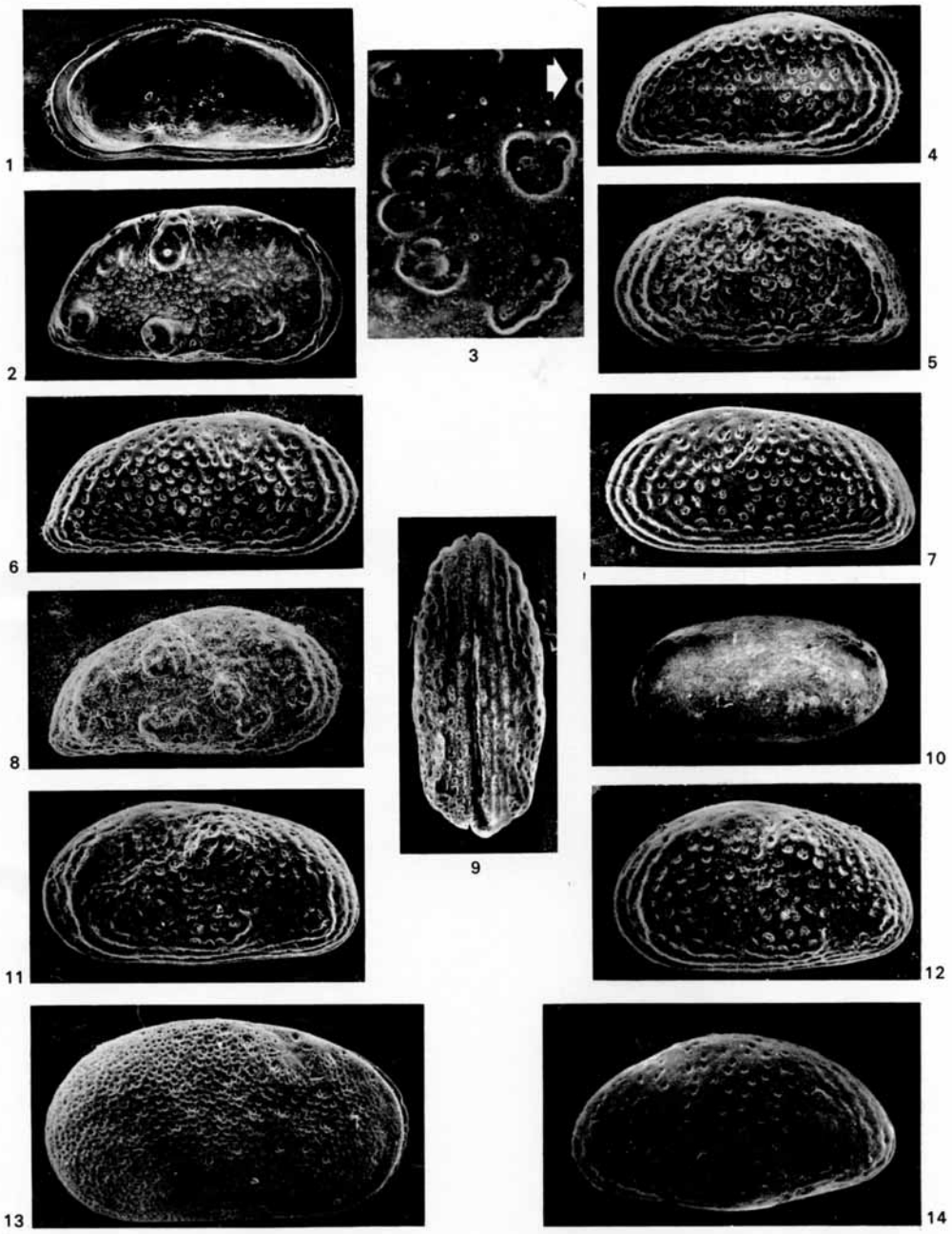

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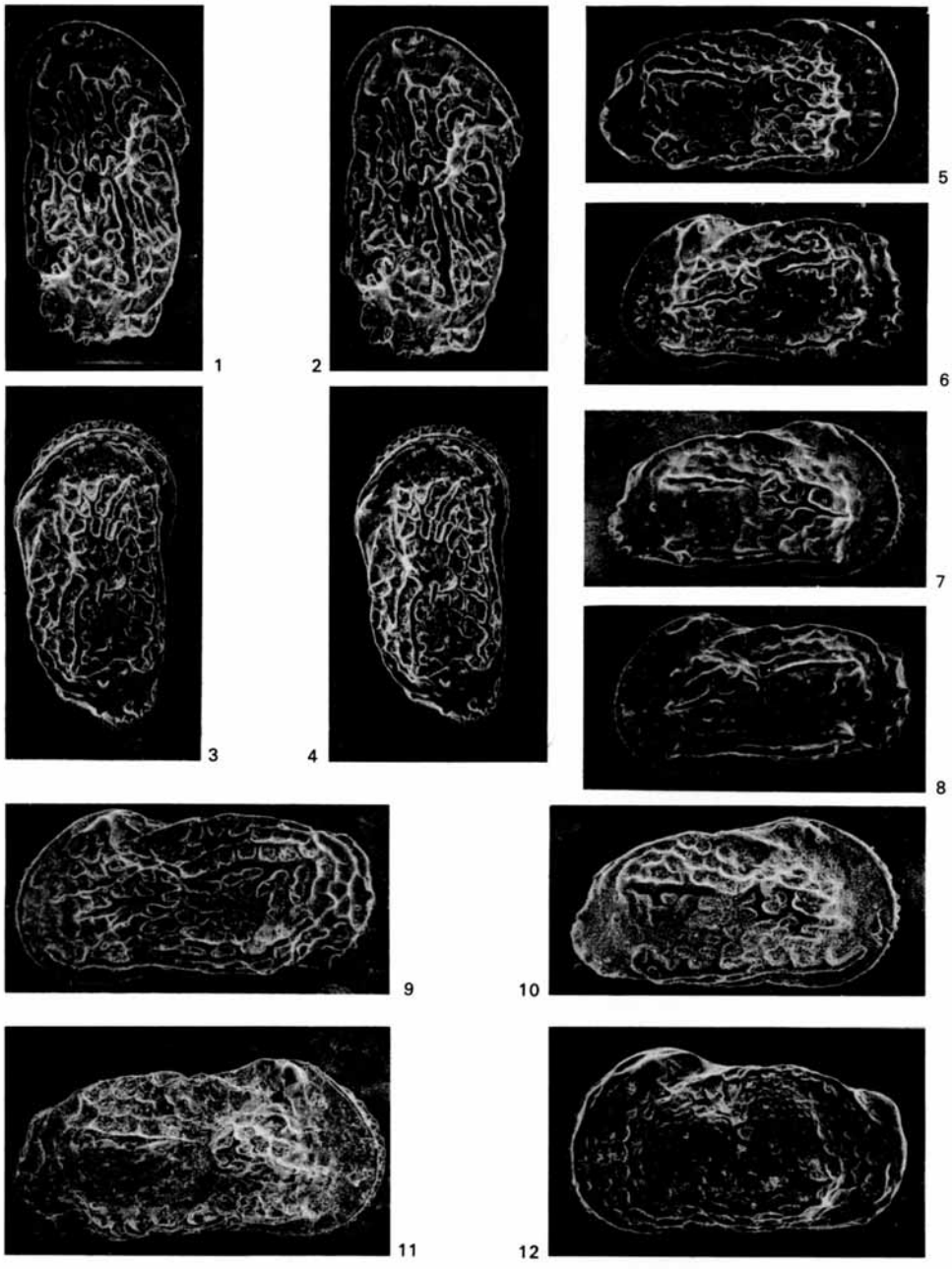

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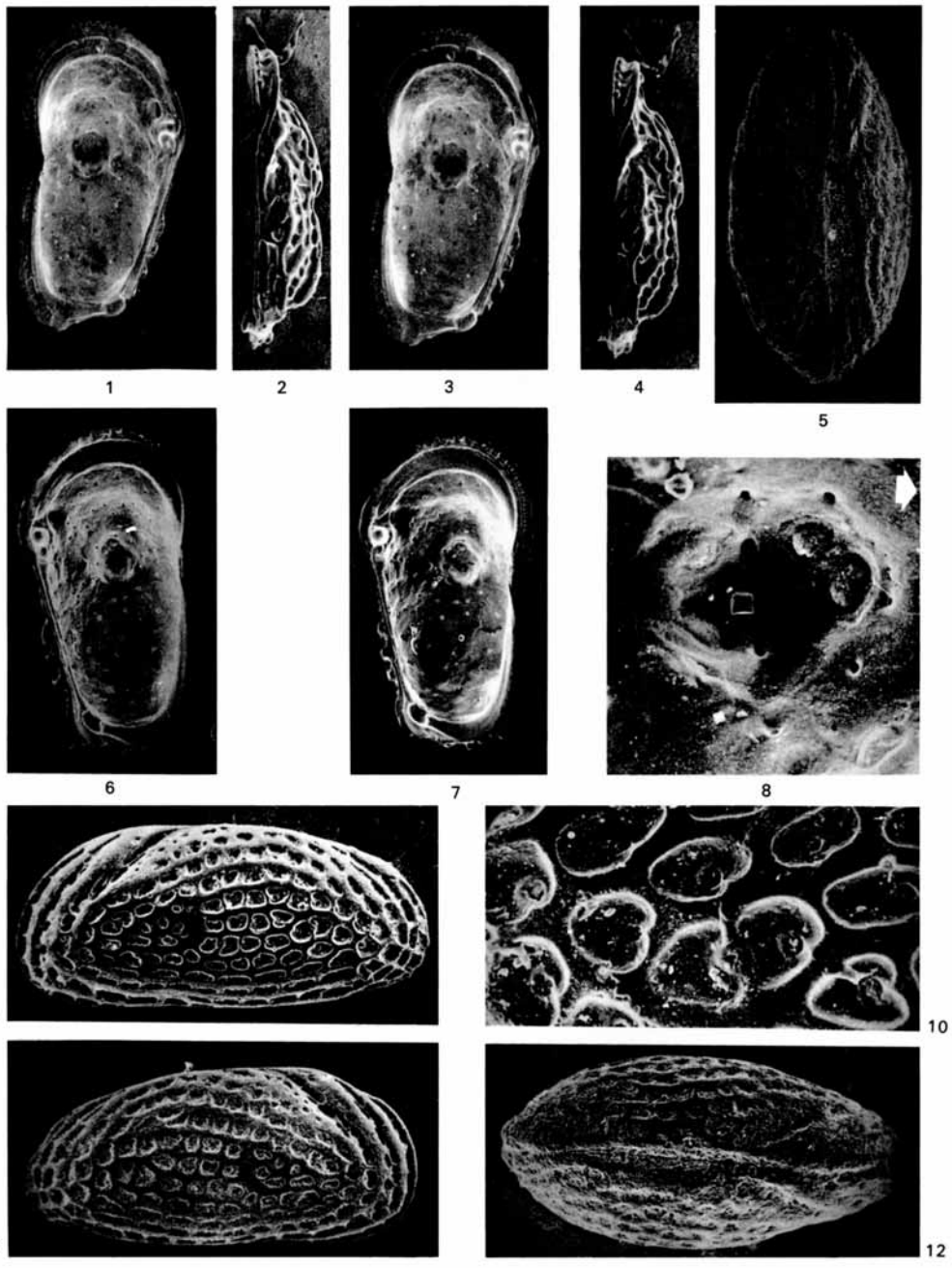

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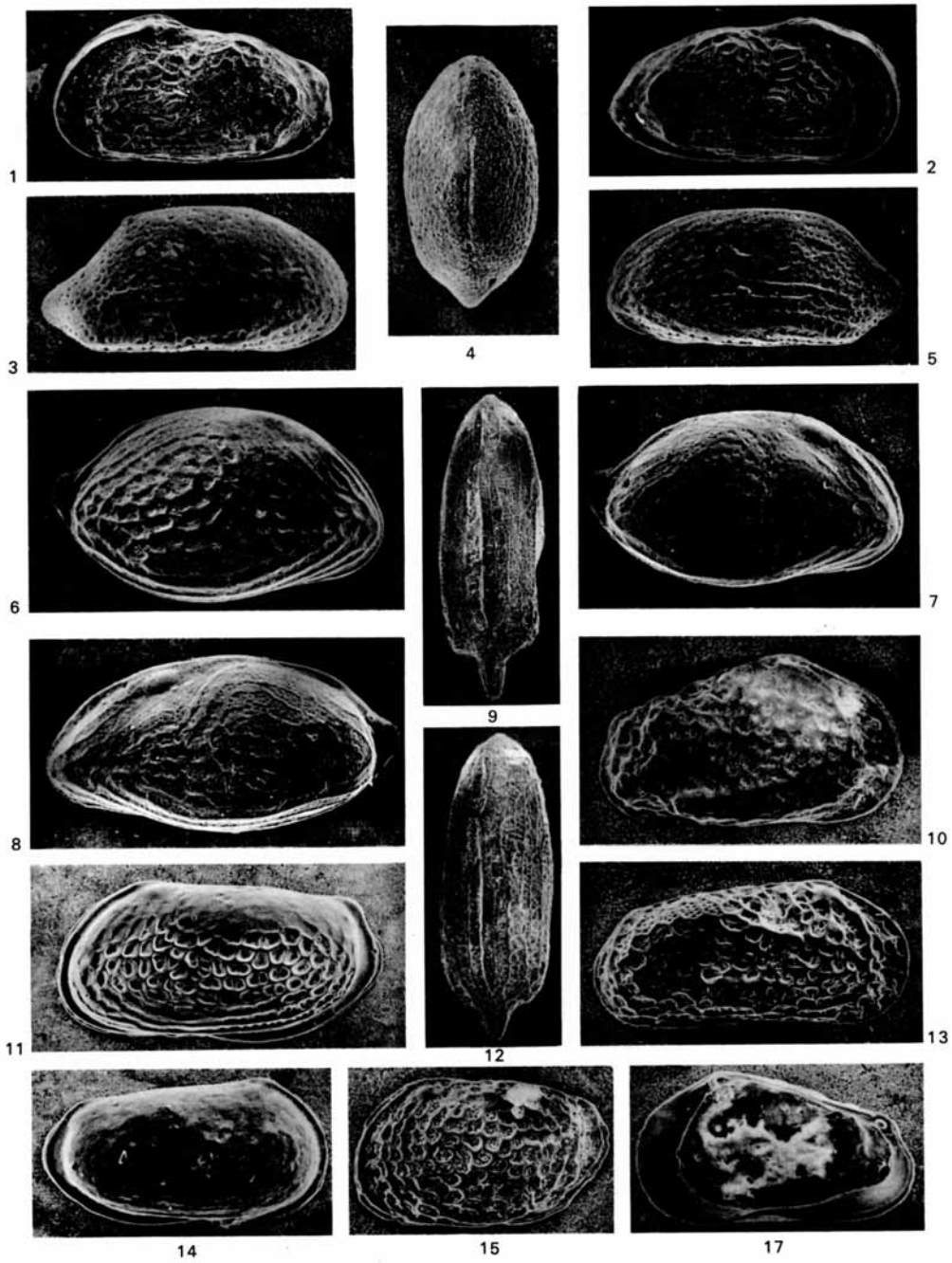

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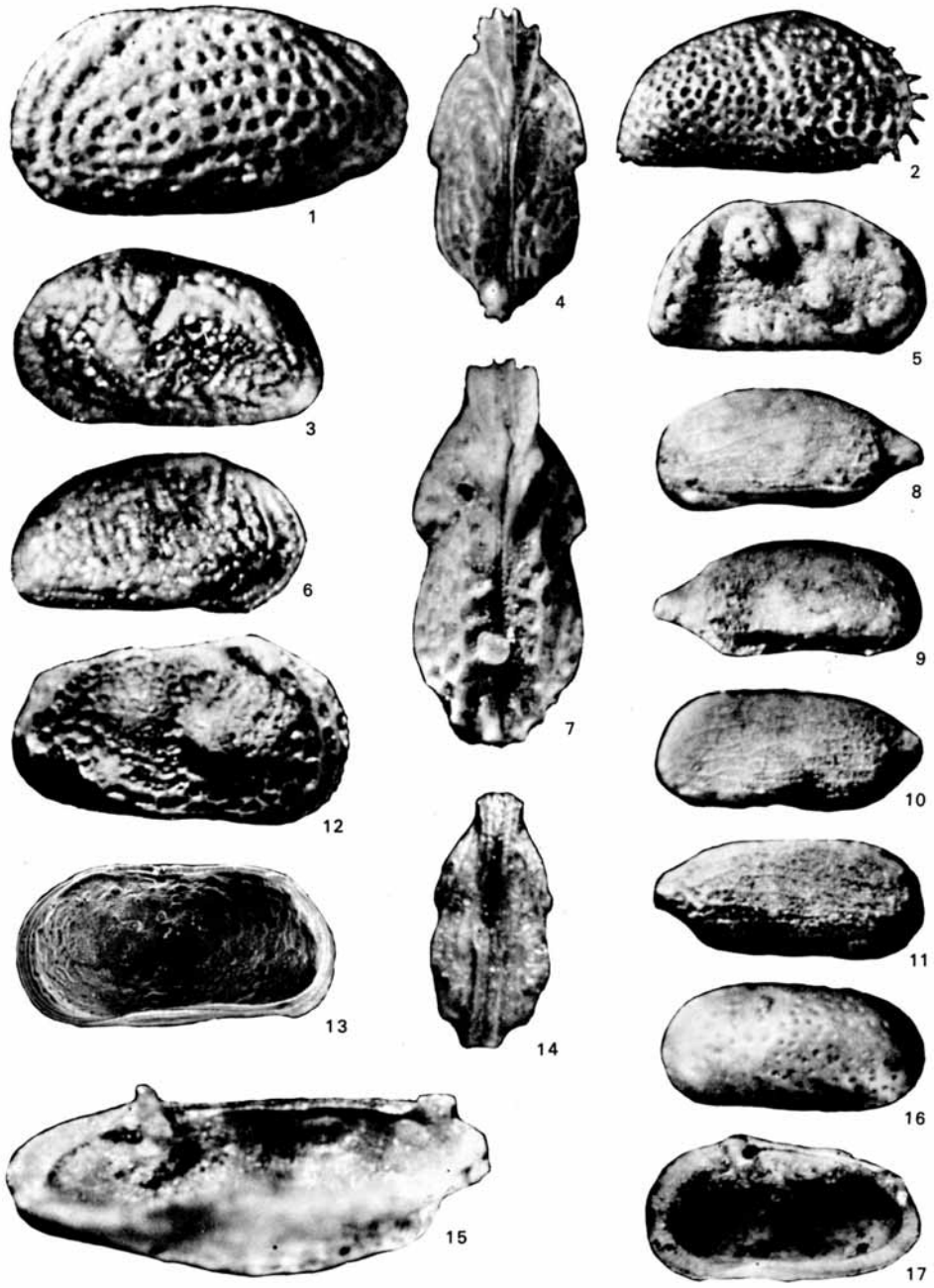

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