

## The genera *Muellerina* Bassiouni, 1965 and *Thaerocythere* Hazel, 1967 from the Neogene of Northwest Europe

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**ABSTRACT** – Twenty one species of the genera *Muellerina* and *Thaerocythere* are considered. Of these, 11 species, including the type species of both genera, have been described previously. Two species are left in open nomenclature due to inadequate numbers but eight are described as new. These species are: *Muellerina latimarginata* (Speyer, 1863), *M. abyssicola* (Sars, 1866), *M. lacunosa* (Jones, 1857), *M. praeabyssicola* Uffenerde, 1981, *M. parvipunctata* Uffenerde, 1981, *Thaerocythere crenulata* (Sars, 1866), *T. hoptonensis* (Brady, Crosskey & Robertson, 1874), *T. mayburyae* Cronin, 1991, *T. oedichilus* (Brady, 1878), *T. trachypora* (Jones, 1857), *T. trapezia* (Brady, 1878), and the new species *M. dolabrata*, *M. metabbyssicola*, *M. orygya*, *M. pliocenica*, *T. biformis*, *T. praecrenulata*, *T. vermiculata*, *T. woutersi* and *T. wittei*. The phyletic relationships of these northwestern European species are considered. *J. Micropalaeontol.* 16(1): 1–18, May, 1997.

### INTRODUCTION

The type material of Jones (1857, 1870), Jones & Sherborn (1887, 1889), Brady, Crosskey & Robertson (1874) and Horne & Kerr (1989), which are presently deposited at the British (Natural History) and Hancock museums, have recently been re-examined. In the light of a recent study by Liebau (1991) and the subsequent re-examination of northwestern European *Muellerina* and *Thaerocythere* species, the present authors have attempted to unravel both the taxonomic and evolutionary problems that presently surround the Plio–Pleistocene species of these genera. The biostratigraphical and ecostratigraphical implications arising from this will be published elsewhere (Wood & Whatley, in press; Wilkinson *et al.*, in press).

### PREVIOUS WORK

The most significant contributions, in the context of the present study, are undoubtedly those of Wouters (1979), Uffenerde (1980–1990), Liebau (1991) and Cronin (1991). The investigation of adductor muscle scar patterns and carapace characteristics of *Muellerina* by Wouters (1979) suggested a tendency towards subdivision within the former and changes in the outline and ornamentation of the valves. He suggested that a gradual change in the composition (grouping *sensu* Wouters, 1979, p. 225) of the muscle scars could be seen through time. However, the evolution of the muellerinids within the southern North Sea basin was justly considered by Uffenerde (1986) to be much more complicated and not just a simple case of muscle scar subdivision or the abatement of reticulation (Uffenerde, 1980, 1986). Investigations into the phylogenetical behaviour of sculptural components (macroreticulation) in Tertiary to Recent trachylebrids and hemicytherids (Liebau, 1977, 1978, 1991) has led to the taxonomical revision of ‘*Quadracythere*-like hemicytherids’ in which Liebau (1991) erected a number of new *Thaerocythere* subgenera and species. Similarly, Cronin (1991) has described a number of new *Muellerina* and *Thaerocythere* species from the Pliocene/Pleistocene of Tjörnes, Iceland.

### LITHOSTRATIGRAPHY, BIOSTRATIGRAPHY AND BIOCHRONOLOGY OF NORTHWESTERN EUROPEAN NEOGENE DEPOSITS

The lithostratigraphical, biostratigraphical and biochronological framework for the British and Dutch Neogene successions have recently been reviewed by Wood *et al.* (1994). In the same paper, a number of new ostracod-based ecozones were erected on the basis of palaeoclimatic-related changes in the generic composition of Upper Miocene and Pliocene ostracod assemblages. The extent of this new ecozonation and previous foraminiferal and palynological biostratigraphical schemes are presented in Figs 1 and 2.

### MATERIAL

Four Dutch Geological Survey boreholes, Altena VI 49E83, Nieuwkuik 45C190, Klundert 43H63 and Cuyck 46A147, comprising comparative sections of the Breda and Oosterhout formations, were examined for ostracods. Figure 3 shows the location of the boreholes in relation to the disposition of major structures within the Netherlands. The sampling intervals and lithologies of Dutch boreholes 43H63 and 46A147 are presented in Fig. 4.

Marine ostracod assemblages from three East Anglian formations were analysed: the Coralline Crag Formation at Sutton Knoll (TM 304440) and Raydon Hall (TM 43265017 – British Geological Survey borehole), the Red Crag Formation at Walton Cliff (TM 26732352), Buckanaye Farm (TM 356424) and Neutral Farm (TM 372811) and the Norwich Crag Formation (Chillesford Sand Member) at Chillesford Church Pit (TM 38285230). The regional disposition of sampled localities and specific sampling horizons are given in Figs 5 and 6.

### SYSTEMATIC DESCRIPTIONS

List of abbreviations: ALV-F = Adult left valve, female; ARV-M = Adult right valve, male; ACp = Adult carapace; A-n =

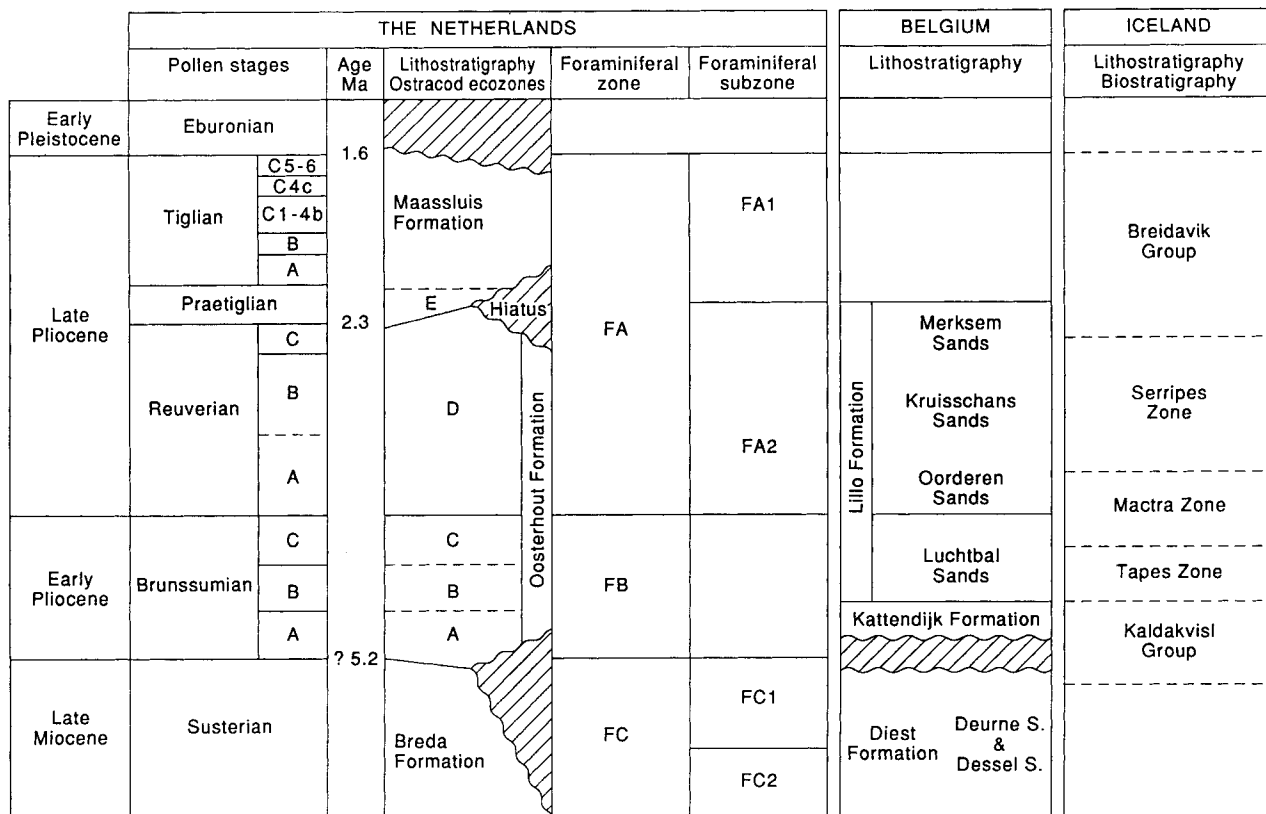


Fig. 1. Lithostratigraphy and biostratigraphy of the Dutch, Belgium and Icelandic Neogene successions (adapted after Wood *et al.*, 1994).

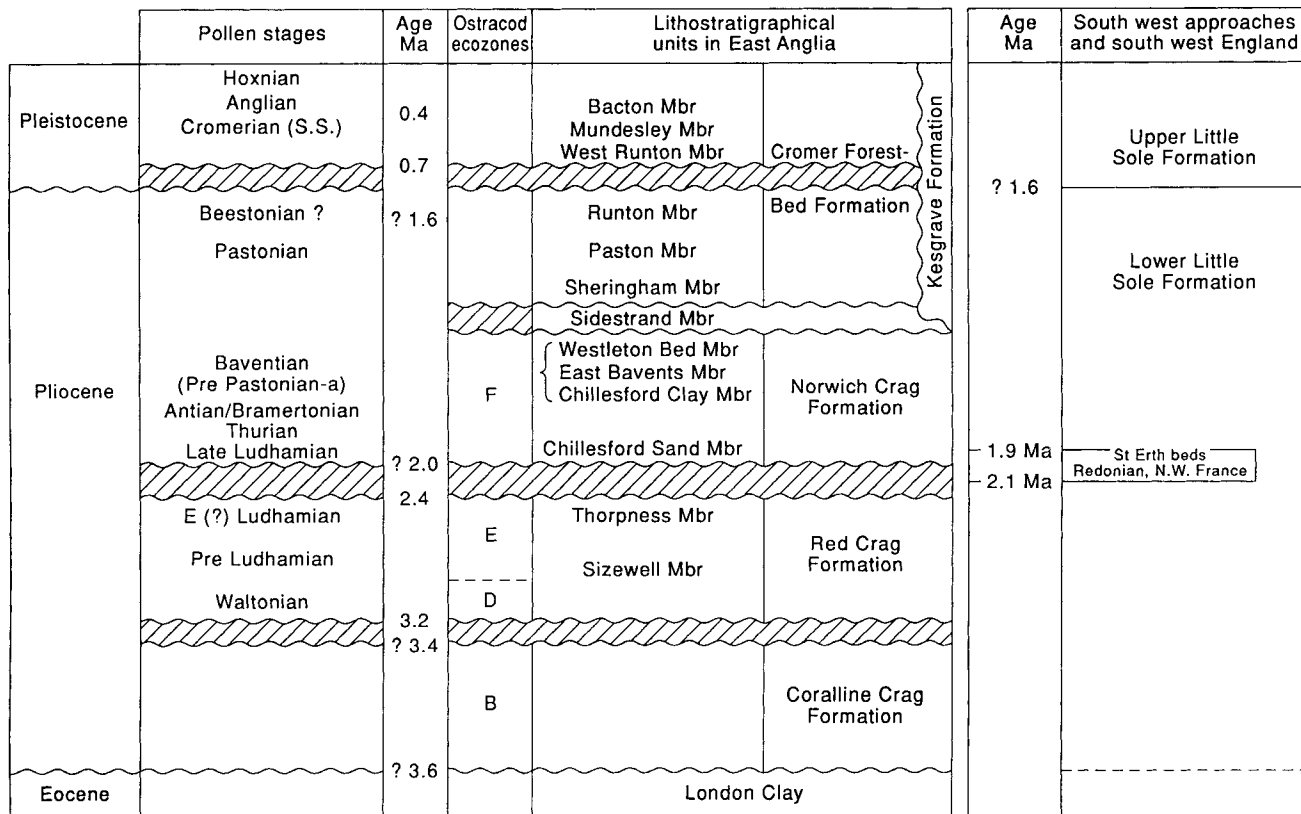


Fig. 2. Lithostratigraphy and biostratigraphy of the East Anglian Pliocene succession (adapted after Wood *et al.*, 1994).

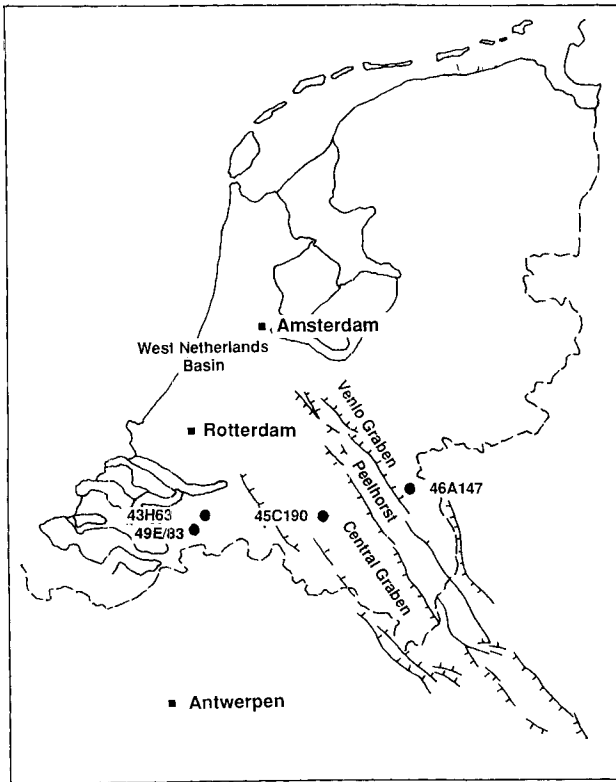


Fig. 3. Location of the four Dutch boreholes under investigation and their relationship to major structural feature (after Wood *et al.*, 1994).

juvenile stage. Type material is either deposited in the Department of Palaeontology, Natural History Museum or the British Geological Survey, for which the catalogue number prefixes are OS and MPK, respectively. Other material is deposited in the Adrian Wood collection in the Micropalaeontology Museum, Institute of Earth Studies, Aberystwyth with catalogue numbers AMW/PL/0 no.

- Class *Ostracoda* Latrielle, 1806
- Order *Podocopida* Müller, 1894
- Suborder *Podocopida* Sars, 1866
- Superfamily *Cytheracea* Baird, 1850
- Family *Hemicytheridae* Puri, 1953
- Subfamily *Hemicytherinae* Puri, 1953
- Genus *Muellerina* Bassiouni, 1965

**Type species.** *Cythere latimarginata* Speyer, 1863.

**Emend. Diagnosis.** Carapace subovate to elongate/subquadrate, with thick, generally smooth, marginal rims imparting a truncated aspect to the end margins in dorsal view. Anterior and posterior margins may be denticulated. Dorsal and ventral margins converging posteriorly. Upper part of posterior margin straight or weakly concave, lower part convex, together forming weak posteroventral caudal process. Dimorphic, males proportionally more elongate, less inflated in dorsal view. Ornament pitted/reticulate with a single concentric row of fossae inside the marginal rim and subcentral tubercle. Maximum length below mid height, greatest height at or just anterior of anterior cardinal angle, maximum width at sub-central tubercle.

Row of four adductor muscle scars, middle two may be subdivided; two frontal scars, ventral scar may be bilobate. Hinge holamphidont with short thick teeth. Narrow anterior and posterior vestibula may be present; marginal pore canals sinuous/straight, simple, 20–30 anteriorly; 10–14 posteriorly.

**Remarks.** The re-examination of adductor muscle scar patterns in *Muellerina*, using a quite separate database of Upper Miocene to Recent species from northwestern Europe, clearly supports the original conclusions of Wouters (1979). Using composite counts for muscle scar groups 1/2 and 3/4 our results confirm the progressive division of median scars from the Miocene to the Recent. The adductor muscle scar pattern of 200 adult specimens, belonging to six species, were analysed from Neogene sites in France, England and The Netherlands. The relative percentage of the three adductor muscle scar groupings, through time, are represented in Fig. 7.

*Muellerina latimarginata* (Speyer, 1863)  
(Pl. 1, fig. 1)

1863 *Cythere latimarginata* Speyer: 22, pl. 3, figs 3a–e.

non 1874 *Cythere latimarginata* Speyer; Brady, Crosskey & Robertson: 163, pl. 16, fig. 6 (= *Cythere abyssicola* G.O. Sars, 1865).

1918 *Cythereis latimarginata* (Speyer); Kuiper: 41, pl. 2, fig. 14.

1965 *Muellerina latimarginata* (Speyer); Bassiouni: 510, pl. 1, figs 2a–c.

1981 *Muellerina latimarginata latimarginata* (Speyer); Uffendorde: 161, pl. 3, figs 7 & 10; pl. 7, fig. 4.

**Diagnosis.** Carapace small, subrectangular, symmetrical about median line. Anterior broadly rounded, posterior somewhat truncated. Surface with moderately large pits/fossae and two delicate ribs. The first parallel to the ventral margins, terminating in a weak posteroventral swelling, the second is angled from the subcentral tubercle towards the posterior cardinal angle. In dorsal view carapace is tapered in front of posterior marginal rim. Ventral frontal muscle scar is often bilobate.

**Material.** East Anglia, 2V; The Netherlands, 3 CP, 11 V.

**Dimensions.**

	Cat. No.	Site	Length	Height
ALV-F	AMW/PL/016	43H/63(175)	0.70	0.31
RV ?A-3	AMW/PL/017	43H/63(176)	0.50	0.18

**Distribution.** Upper Oligocene of North West Germany (Uffendorde, 1981) and Belgium (Kuiper, 1918). Most common in the Miocene of Belgium, Germany and the Netherlands (Wouters, 1979). Rare in the Lower Pliocene of the Netherlands (FB benthonic foraminifera zone, see Doppert, 1975, 1980) and the Coralline Crag Formation of East Anglia, England.

**Remarks.** Jones & Sherborn (1887) described a single specimen of *Muellerina latimarginata* from the Coralline Crag Formation at Sutton Knoll (TM 304 440). It appears, however, that this specimen is now missing from the collections of the Natural History Museum.

*Muellerina abyssicola* (Sars, 1866)  
(Pl. 1, figs 2 & 3)

1866 *Cythereis abyssicola* sp. nov. Sars: 43.

1874 *Cythere latimarginata* Speyer; Brady, Crosskey & Robertson: 163, pl. 16, fig. 6 (non Speyer, 1863).

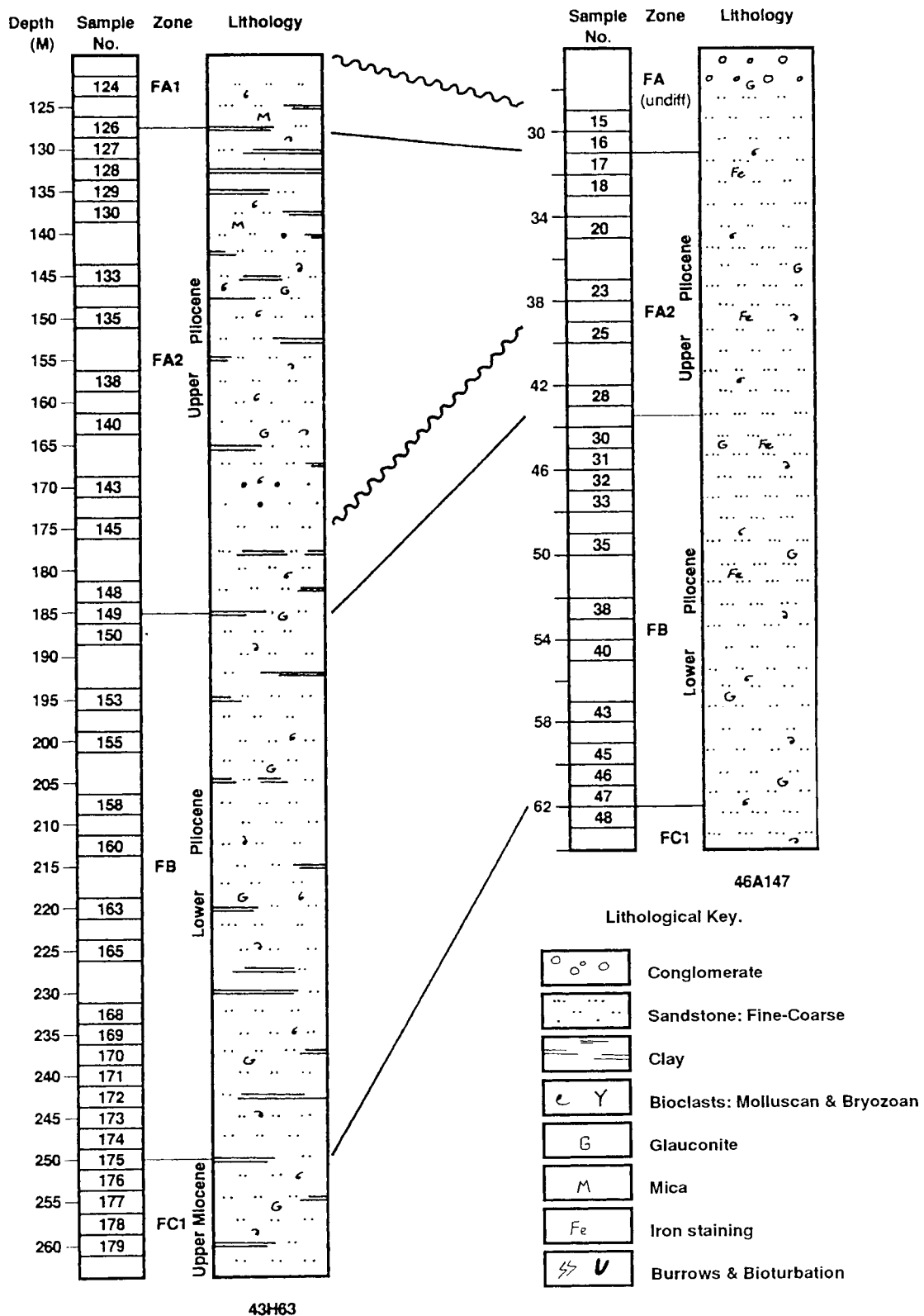


Fig. 4. Lithology and sampled horizons of the Dutch boreholes Klundert 43H63 and Cucyk 46A147.

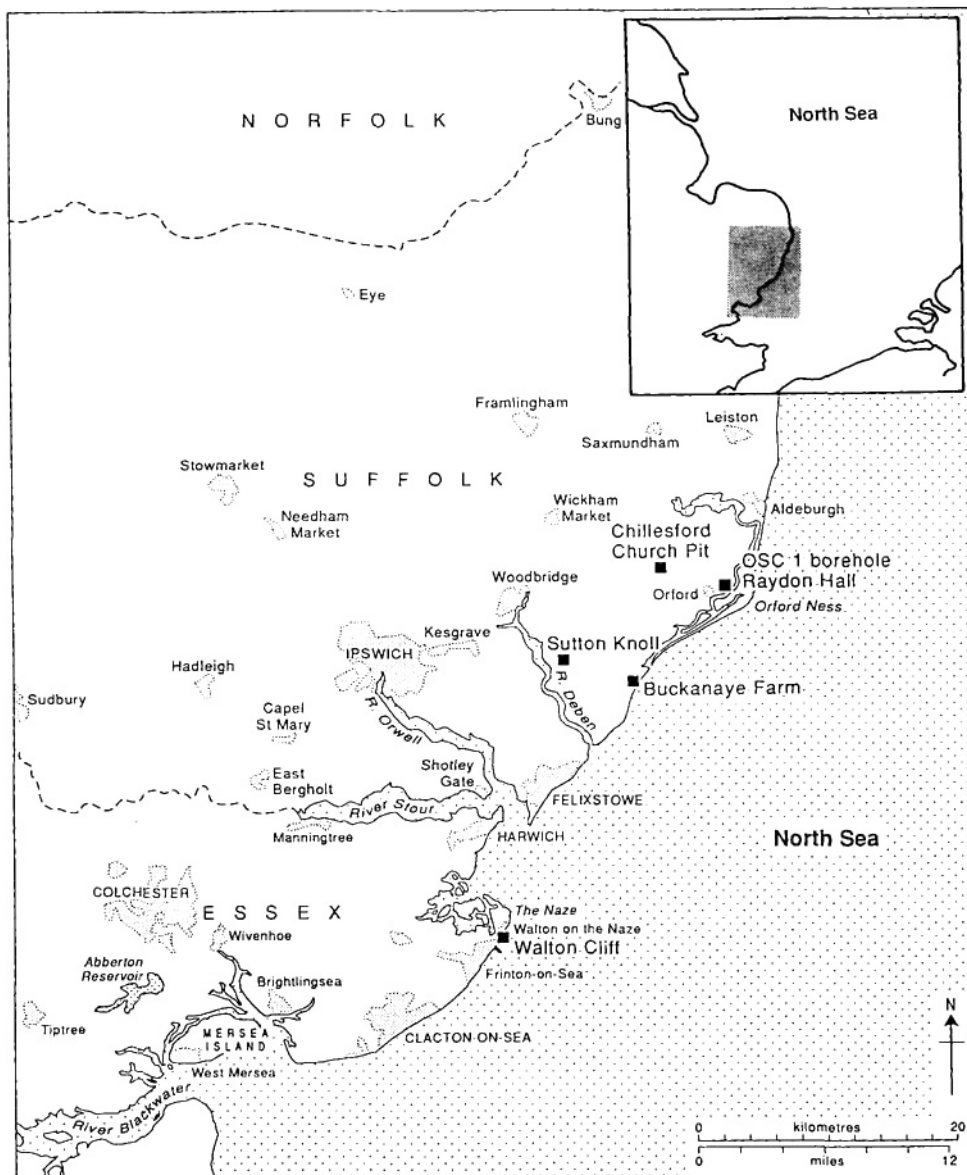


Fig. 5. East Anglian Pliocene sites under investigation.

1965 *Muellerina abyssicola* (Sars); Bassiouni: 510, pl. 1, figs 3–6.  
 1969 *Murrayina latimarginata* (Speyer); Yassini: 84, pl. 24, fig. 5;  
 pl. 39, figs 15 & 16 (*non* Speyer, 1863).

**Diagnosis** (adapted after Athersuch *et al.*, 1989). Carapace subovate; dorsal and ventral margins slightly sinuous, anterior and posterior margins rounded. Marginal rims very broad. Ornament coarsely pitted/reticulated, quadrate fossae inside the marginal rim, and rounded to subquadrate fossae elsewhere.

**Material.** In excess of 2000 specimens.

**Dimensions.**

	Cat. No.	Site	Length	Height
ALV-F	AMW/PL/018	1962,160(8)	0.78	0.45
ARV-M	AMW/PL/019	1962,160(10)	0.76	0.40

**Remarks.** Although both carapace shape and disposition of fossae are quite dissimilar, *M. abyssicola* (Sars) was commonly placed in synonymy with *M. latimarginata* (Speyer) by 19th

century authors. However, comparisons with its proposed Pliocene ancestor *Muellerina metabyssicola* sp. nov. reveal that a number of ornamental features have been retained. These include the posteromedian plication connecting posterodorsal and subcentral tubercles which, although not as salient as in *M. metabyssicola* sp. nov. is very obvious. The mid-dorsally positioned compressed ‘S’ shaped node–ridge–node structure is also retained. In dorsal view, both species are listricly truncated submarginally at the posterior.

**Distribution.** *M. abyssicola* has been recorded from the Pleistocene (Devensian) of southwest Norway (Lord, 1980), Bay of Biscay (Yassini, 1969; Peypouquet, 1971) and the Hoxnian of Denmark and northern Germany (Bassiouni, 1965). Its present distribution on the northeast Atlantic shelf, as recorded by Wood & Whatley (1994), is from the Bay of Biscay north to the Barents Sea.

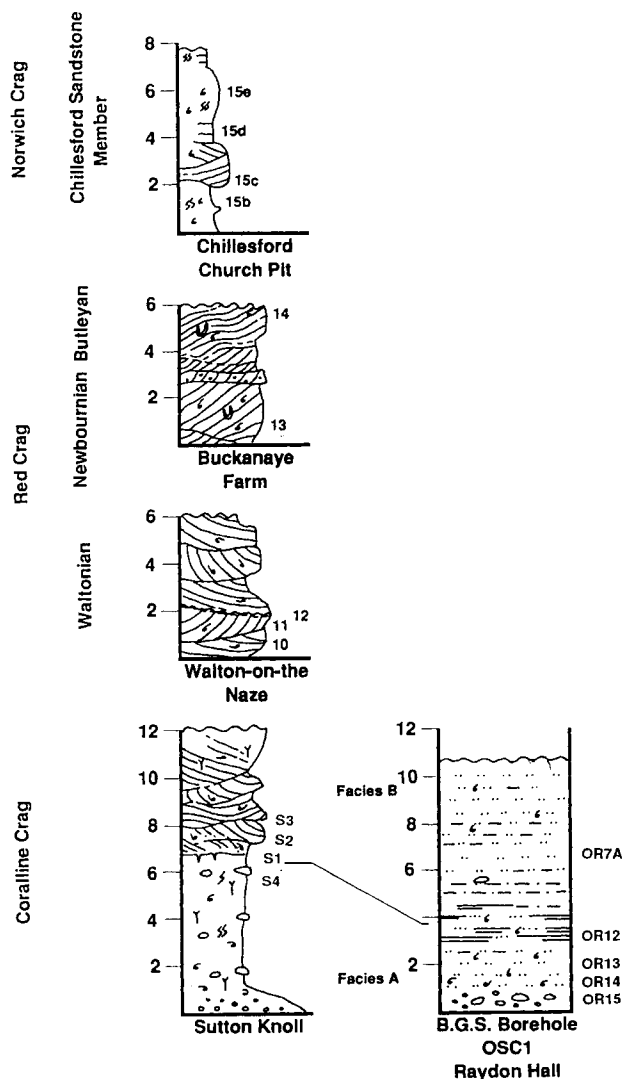


Fig. 6. Lithology and sampled horizons of East Anglian Pliocene sites (adapted after Wood *et al.*, 1992).

***Muellerina lacunosa* (Jones, 1857)**

(Pl. 1, figs 4–6)

- 1857 *Cythere lacunosa* Jones: 31, pl. 3, figs 5a–b  
 1870 *Cythere sublacunosa* Jones; 156 (*nom. nov. pro Cythere lacunosa* Jones, 1857; *non Cytherina lacunosa* Reuss, 1850).  
 1889 *Cythere sublacunosa* Jones & Sherborn; 27.  
 1979 *Muellerina lacunosa* (Jones); Wouters: 228–229, pl. 2, fig. 2b (*non* pl. 2, figs 2a & 2c = *Muellerina orygya* sp. nov.).  
 1980 *Murrayina lacunosa* (Jones); Wilkinson: pl. 2, fig. 14 (*non* pl. 2, fig. 12 = *Muellerina pliocenica* sp. nov.).  
 non 1989 *Muellerina lacunosa* (Jones); Horne & Kerr, pl. 2, fig. d (= *Muellerina pliocenica* sp. nov.).

**Diagnosis.** A species of *Muellerina* with numerous, though rarely coalesced, subcircular fossae set within an undulose network of muri, concentrically arranged around a well developed sub-

central tubercle. Weakly developed posteroventral and postero-dorsal tubercles. Indistinct, plicate, ridge runs from the subcentral tubercle posterodorsally. In dorsal view, convex to straight truncation submarginal to the posterior. Marginal radial pore canals numerous, 14–16 anteriorly, 4–6 posteriorly, straight/sinuus.

**Material.** East Anglia, 19CP, 160V; the Netherlands, 5CP, 115V.  
**Dimensions.**

	Cat. No.	Site	Length	Height
ALV-F	AMW/PL/020	OSC1 OR7a	0.76	0.4
ARV-M	AMW/PL/021	OSC1 OR12	0.89	0.44
ALV-M	AMW/PL/022	OSC1 OR12	0.84	0.45
ARV-F	AMW/PL/023	OSC1 OR15	0.81	0.45

**Distribution.** Pliocene; Kattendijk and Lillo formations, Belgium; FB zone (Doppert, 1980) of the Oosterhout Formation, Holland; Coralline Crag Formation, Waltonian, Butleyan and Newbournian stages of the Red Crag Formation, East Anglia, UK.

**Remarks.** *Muellerina lacunosa* (Jones) bears a strong resemblance to its nominated ancestor *M. parvipunctata* Uffenorde (1981) and also to *Muellerina orygya* sp. nov. However, *M. lacunosa* can be easily distinguished from *M. orygya* sp. nov. as the ornament of the former is constructed from a dense network of large fossae and also comprises two posterior tubercles. *M. parvipunctata* although similar in outline has an ornament dominated by a strong, posteriorly bifurcate, ventromarginal ridge and rather small cellate fossae.

***Muellerina parvipunctata* Uffenorde, 1981**

**Distribution.** Upper Miocene; Reinbekium and Gramium of northwest Germany.

**Remarks.** This species is similar in outline to *M. lacunosa* (see remarks) but appears to be restricted both stratigraphically and geographically to the Upper Miocene of northwest Germany where it can occur with both *M. praeabyssicola* Uffenorde, 1981 and *Muellerina latimarginata* morphotype 1 Uffenorde (1981, p.165).

***Muellerina praeabyssicola* Uffenorde, 1981**

**Distribution.** Upper Miocene of northern Germany.

**Remarks.** The earliest species of the *M. praeabyssicola*–*M. metabysiccola*–*M. abyssicola* lineage, restricted to the Upper Miocene of Germany. *M. praeabyssicola* can be distinguished from *M. metabysiccola* as the latter is compressed and possesses two conspicuous mediodorsal tubercles, however, both possess the shallow ‘S’-shape plication in the dorsomedian region.

***Muellerina dolabrata* sp. nov.**

(Pl. 1, figs 10 & 11)

**Derivation of name.** Latin, *dolabratus* = shaped like an axe. With reference to the ‘axe head’ shape of the carapace in lateral view.

**Diagnosis.** A species characterized by its axe head shaped carapace in lateral view. Almost symmetrical about the median height line. Anterior marginal reticulate with fine radial ridges. Reticulation composed of 15–18 large, circular/subovate, occasionally linked, cellate fossae with normal pores proximal to muri. Additional, scattered normal pores, common. Postero-dorsal and posteroventral tubercles present, the latter more strongly so.

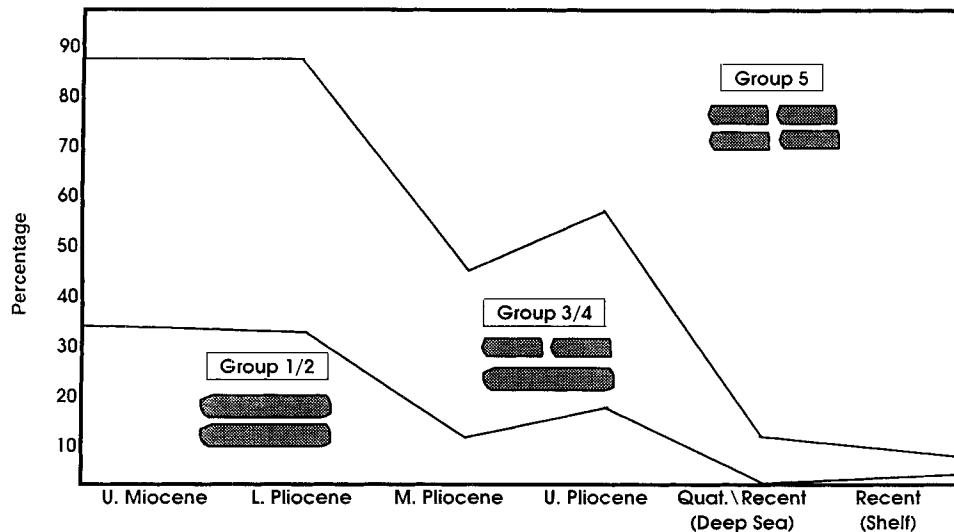


Fig. 7. Percentage variations in muellerinid adductor muscle scar groups (after Wouters, 1979) from the Upper Miocene to Recent of northwestern Europe.

**Type locality and horizon.** Coralline Crag Formation, BGS borehole OSC1: sample level OR7a, near Orford, Suffolk, East Anglia, UK.

**Material.** East Anglia, 11CP, 15V; the Netherlands, 11CP, 80V.  
**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype ARV-F	MPK9768	OSC1 OR7a	0.67	0.37
Paratype ALV-F	MPK9769	OSC1 OR14	0.65	0.37
Paratype ALV-M	MPK9770	OSC1 OR14	0.63	0.36
Paratype ARV-M	MPK9771	OSC1 OR14	0.62	0.33

**Distribution.** Upper Miocene; FC1 zone and Lower Pliocene FB zone Oosterhout Formation, the Netherlands. Pliocene; Coralline Crag Formation, Sutton Knoll and BGS borehole OSC1, Orford, Suffolk, UK.

**Description.** Carapace subquadrate, dorsal margin convex, ventral sinuous. Anterior margin broadly round, posterior somewhat truncated. In dorsal view the outline is sinuous but truncated in front of the posterior marginal rim. Maximum length well below mid height. Eye tubercles conical, more weakly developed in males. Anterior rim possesses four to seven fine, transverse, arcuate/sinuous riblets. Ornament consists of 15–17 subcircular/ovate cellate fossae, occasionally linked below a sturdy subcentral tubercle. Single, delicate, rib angled from the posteromedian region to the subcentral tubercle. Sensillum pores simple, small, intermural or peripheral on the solum. Avestibulate, inner lamella broad, marginal pore canals simple straight, 24–26 anteriorly, nine posteriorly, 17 orally.

**Remarks.** *M. dolabratus* sp. nov. possessing a number of features common to *M. praeabyssicola* Uffenorde, 1981, i.e. concave dorsal margin with raised anterior cardinal angle, fine anterodorsal carinae, angular/litric truncation of the posterior region and two posterior tubercles.

***Muellerina metabyssicola* sp. nov.**  
(Pl. 1, figs 10 & 11)

**Derivation of name.** Greek; *meta* = between. Pertaining to the intermediate evolutionary stage of this species within the *M.*

*praeabyssicola* Uffenorde–*M. abyssicola* (Sars) lineage.

**Diagnosis.** Carapace elongate, subquadrate/trapeziform. Dorsal margin concave with prominent raised anterior cardinal angle, ventral concave. Litric truncation of posterior in dorsal view. Conspicuous subcentral, posterodorsal and posteroventral tubercles. Two further tubercles positioned in the dorsomedian and posteromedian regions connected by a conspicuous, sinuous, carinate ridge. Second, finer, carina connecting subcentral and posterodorsal tubercles.

**Type locality and horizon.** Coralline Crag Formation, BGS borehole OSC1: OR7a, near Orford, Suffolk, East Anglia, UK.

**Material.** East Anglia, 19V; the Netherlands, 5CP, 14V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype ARV-F	MPK9772	OSC1 OR7a	0.77	0.41
Paratype LV A-1	MPK9773	OSC1 OR15	0.68	0.37

**Distribution.** Lower Pliocene; FB zone, Oosterhout Formation, the Netherlands; mid-Pliocene; Coralline Crag Formation, Orford and Sutton Knoll, East Anglia, UK.

**Description.** Carapace elongate subquadrate/ovate to trapeziform. Dorsal margin of LV concave, raised anterior cardinal angle, RV sinuous. Ventral margin, in both LV and RV, convex. Anterior margin rounded. In dorsal view, posterior litrically truncated. Maximum length just below the mid height. Margin rims broad, rounded in dorsal view. Conspicuous eye tubercle situated just beneath anterior cardinal angle. Coarsely reticulate with rounded/subovate fossae, quadrate submarginally. Fossae and muri suppressed with respect to marginal reticulum. Plicate ventromarginal ridge terminates in the posteroventral region in the form of an alate swelling. Posterodorsal tubercle more weakly developed. Arcuate, ridge, forming an inter-connection between tubercles situated behind mid-point on the dorsal margin and below the anterior cardinal angle. Avestibulate, moderately broad inner lamella, marginal pore canals, straight, numerous; 24 anteriorly, 11 orally and nine posteriorly.

**Remarks.** Although much larger, both the outline of the carapace and the disposition of reticulation of this species are

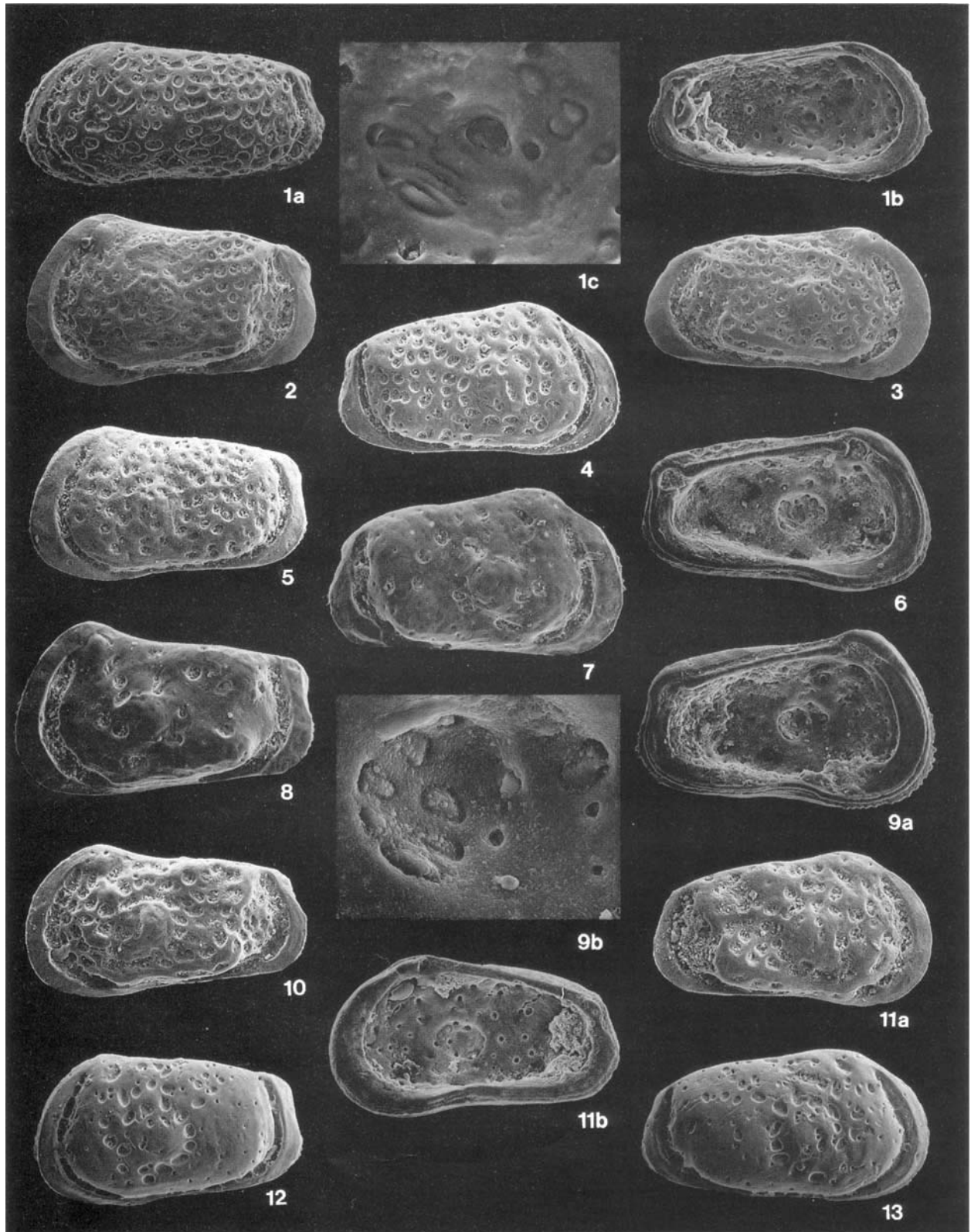


Plate 1



similar to those of *M. praeabyssicola* and *M. abyssicola*. However, the posterior tubercles of *M. praeabyssicola* are greatly inflated and dorsomedian swellings weaker. Although retaining the 'S'-shaped dorsomedian structure in the form of an insubstantial, raised, murus; the ornament of *M. abyssicola* is conservative by comparison.

A fourth species, described by C. A. Maybury (pers. comm.) from the Redonian (Upper Pliocene) of northwest France, may also be a member of the '*abyssicola*' lineage.

***Muellerina orygyma* sp. nov.**

(Pl. 1, figs 12 & 13; Pl. 2, fig. 1)

?1878 *Cythere latimarginata* Speyer; Brady: 389–390, pl. 64, figs 8a–d (*non* Speyer, 1863).

1979 *Muellerina lacunosa* (Jones); Wouters: 228–229, pl. 2, figs 2a and 2c (*non* Jones, 1857) (*non* pl. 2, fig. 2b = *Muellerina lacunosa* (Jones)).

**Derivation of name.** Greek; *orygymus* = moat-like trench. Pertaining to the ring of fossae encircling the raised subcentral tubercle.

**Diagnosis.** A species of *Muellerina* with a well developed pattern of open reticulation characterized by a concentration of fossae anterodorsally and in a chain around the central tubercle. Numerous, small simple pores. Inflated in front of the posterior marginal rim.

**Type locality.** Klundert 43H/63 borehole, 256.50–259 m; FC1 zone, Oosterhout Formation, Upper Miocene, the Netherlands.

**Material.** The Netherlands, 21CP, 361V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype	ALV-F OS14185	43H/63(178)	0.75	0.43
Paratype	ARV-F OS14186	43H/63(178)	0.78	0.42
Paratype	ALV-M OS14187	43H/63(177)	0.75	0.41
Paratype	ARV-M OS14188	43H/63(177)	0.77	0.41

**Distribution.** Upper Miocene (FC zone) and Lower Pliocene (FB zone), Oosterhout Formation, the Netherlands. Pliocene, Kattendijk and Lillo formations at Antwerp (Wouters, 1979), Belgium. Pliocene, Coralline Crag Formation at Sutton Knoll and Orford, Suffolk, UK.

**Description.** Carapace, robust, elongate/subrectangular. Dorsal and ventral margins sinuous. Anterior broadly rounded; posterior somewhat truncated. In dorsal view the outline is inflated with the maximum width behind mid-length. Moderately well developed eye tubercle present just below the anterior cardinal angle. Ornament coarsely pitted/reticulate, fossae inside marginal rim rectangular. Rounded/subovate fossae surround the subcentral tubercle while a discrete cluster occur anterodorsally of this tubercle. Secondary, fine, puncta especially visible in

juveniles. Weak, longitudinal, plicate muri, arising from the subcentral tubercle terminating posterodorsally. Very narrow anterior vestibulum, posterior avestibulate, ventral frontal muscle scar bilobate, inner lamella moderately broad. Marginal pore canals simple, straight/sinuuous, 27 anteriorly, 14 posteriorly and at least four orally.

**Remarks.** *Muellerina orygyma* sp. nov. occurs most commonly in association with *M. lacunosa* (Jones) in the early Pliocene successions of the Netherlands. *Muellerina orygyma* sp. nov. can be distinguished from the latter species by both its swollen mediodorsal region and reduced posterior tubercles, however, it is apparent that intermediate forms also exist between the two end member species; this being especially prevalent within ecozone B, mid Pliocene (Wood *et al.*, 1994).

***Muellerina pliocenica* sp. nov.**

(Pl. 2, figs 2 & 4)

1980 *Murrayina lacunosa* (Jones); Wilkinson: pl. 2, fig. 13 (*non* Jones, 1857).

1989 *Muellerina lacunosa* (Jones); Horne & Kerr: pl. 2, fig. d (*non* Jones, 1857).

1989 *Muellerina* sp. cf. *M. lacunosa* (Jones); Fourniguet *et al.*: pl. 1, fig. 19.

**Derivation of name.** Named for the epoch in which it is most commonly found.

**Diagnosis.** Carapace elongate, subovate. Heavily denticulated, lipped, extension of the anterior margin. Fossae, cellate, irregularly disposed. Posterior dominated by three tubercles situated in the posterodorsal, posteroventral (this swelling continues anteriorly as a strong plicate ridge) and posteromedian fields, interconnected with expanded, undulose, sinuous muri.

**Type locality and horizon.** Klundert 43H/63 borehole, 219–221.5, FB zone, Oosterhout Formation, Pliocene, the Netherlands.

**Material.** East Anglia, 5CP, 11V; the Netherlands, 3CP, 24V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype	ARV-M OS14189	43H/63(163)	0.76	0.32
Paratype	ALV-F OS14190	43H/63(163)	0.70	0.34
Paratype	ALV-M OS14191	43H/63(163)	0.76	0.33
Paratype	ARV-F OS14192	43H/63(170)	0.73	0.32

**Distribution.** Pliocene; FB and FA2 zones, Oosterhout Formation, the Netherlands. Coralline Crag Formation at Orford and Sutton Knoll, East Anglia. Redonian (Upper Pliocene) of the St Erth Beds, Cornwall and northwest France. ?Pliocene/Pleistocene; Knocknasillage Member, Co. Wexford, Ireland.

**Description.** Carapace elongate/subovate, dorsal and ventral margins sinuous. Anterior margin compressed. In dorsal view,

**Explanation of Plate 1**

Figs 1a–c. *Muellerina latimarginata* (Speyer, 1863): fig. 1a, AMW/PL/016 LV-F, ext. lat. (875); fig. 1b, AMW/PL/016, int. lat. (×69); fig. 1c, AMW/PL/019, detail of central muscle scars (×292). Figs 2–3. *Muellerina abyssicola* (Sars, 1866): fig. 2, AMW/RNA/018 LV-F, ext. lat. (×64); fig. 3, AMW/RNA/019 RV-M, ext. lat. (×65). Figs 4–6. *Muellerina lacunosa* (Jones, 1857): fig. 4, AMW/PL/023 RV-F, ext. lat. (×61); fig. 5, AMW/PL/022 LV-M, ext. lat. (×57); fig. 6, AMW/PL/020 LV-F, int. lat. (×66). Figs 7–9. *Muellerina dolabrata* sp. nov.: fig. 7, Holotype MPK9768 RV-F, ext. lat. (×77); fig. 8, Paratype MPK9770 LV-M, ext. lat. (×83); fig. 9a, Paratype MPK9769 LV-F, ext. lat. (×80); fig. 9b, Paratype MPK9769, detail of central muscle scars (×384). Figs 10–11. *Muellerina metabyssicola* sp. nov.: fig. 10, Paratype MPK9773 LVA-1, ext. lat. (×71); fig. 11a, Holotype MPK9772 RV-F, ext. lat. (×63); fig. 11b, Holotype MPK9772, int. lat. (×65). Figs 12–13. *Muellerina orygyma* sp. nov.: fig. 12, Holotype OS14185 LV-F, ext. lat. (×62); fig. 13, Paratype OS14186 RV-F, ext. lat. (×64).

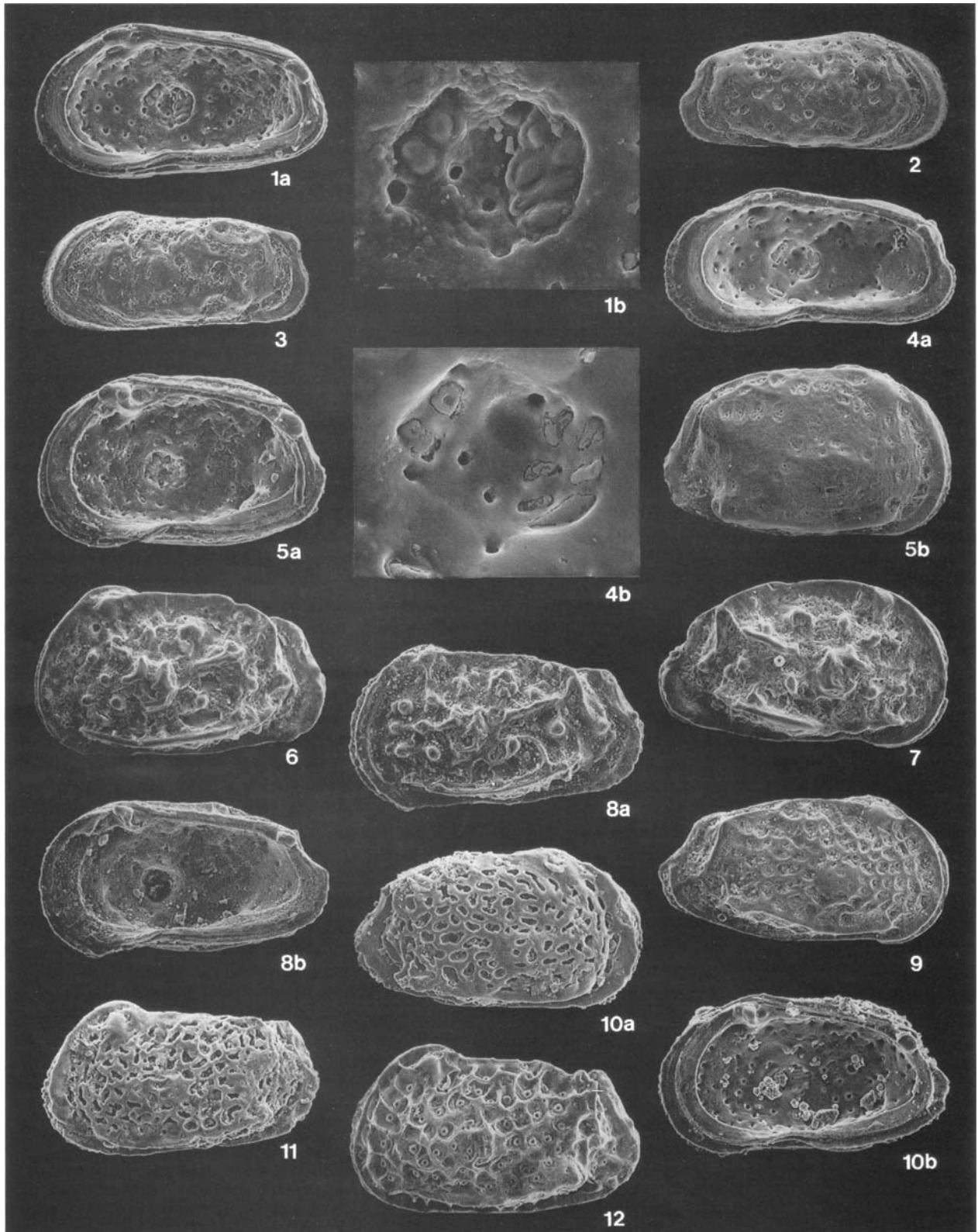


Plate 2

listric truncated in front of posterior margin. Maximum height at or just in front of anterior cardinal angle. Triangular eye tubercle situated in front of the anterior cardinal angle. Anterior margin consists of an outer denticulated lip, broad marginal rim with elongate pits, parallel with margin, occasionally connected to form a sinuous depression. This area is separated from a single concentric row of amorphous fossae by a delicate excavate rib. Posterior margin broad, with five subcircular depressions, lipped, denticulated posteroventrally. Ornament, tuberculate, prominent dorsomedian, posterodorsal and posteroventral swellings. The latter structure tapers anteriorly to form a plicate ridge terminating in the ventromedian field. Dorsal tubercles inter-connected via an excavated rib. Scattered, subcircular, cellate fossae clustered posterodorsally. Sensillum pores common, intramural and simple. Avestibulate, inner lamella moderately broad, marginal pore canals simple, straight; 24 anteriorly, 20 orally and 13 posteriorly.

**Remarks.** As with species of the '*abyssicola*' lineage, *M. pliocenica* sp. nov. possesses a listric truncation of the posterior margin in dorsal view, dorsomedian ridge/bar and posterior tubercles. Aside from *M. latimarginata* (Speyer), which has a range from the Oligocene to mid-Pliocene, this species has the longest recorded range; uppermost Miocene, Holland to Upper Pliocene, St. Erth Beds, Cornwall (c. 2.1–1.8 Ma, Jenkins and Houghton, 1987). It has also been recorded from younger, Pleistocene age, deposits of Co. Wexford although there are indications of reworking (Horne & Kerr, 1989, p. 74).

Family **Thaerocytheridae** Hazel, 1967  
 Subfamily **Thaerocytherinae** Hazel, 1967  
 Genus **Thaerocythere** Hazel, 1967

**Type species:** *Cythereis crenulata* Sars, 1866.

**Emend. Diagnosis.** Carapace elongate subovate/quadrato to trapeziform, thick shelled. Dimorphic, males proportionally more elongate, generally depressed. Ornament coarse to delicate reticulate, usually with prominent sub-central, posteroventral and posterodorsal tubercles, latter extends backwards as a generally robust, submarginal rib approximately two-thirds length of carapace. Moderately wide posterior and anterior marginal rims. Single, reticulate, concentric submarginal furrow commonly developed.

Four adductor muscle scars, middle two somewhat elongate, two frontal scars in oblique row. Hinge strong holamphidont. Avestibulate, marginal pore canals numerous and straight, 25–45 anteriorly, 12–21 posteriorly. Moderately strong anterior selvage.

**Remarks.** Two subgenera *Thaerocythere* (*Thaerocythere*), *T.*

(*Notopleura*) and a questioned third have been erected by Liebau (1991) using sculpture mapping of the mesh (or cell) patterns, pore cones and muscle scars. It is clear from Liebau's work that a number of the Tertiary thaerocytherid species, especially those outside of the European realm, have no or only questionable affiliations with these new subgenera; most notably are *T. sagittata* Liebau, 1991; *T. mayburyae* Cronin, 1991; *T. woutersi* sp. nov.; *T. ruespelensis* (Uffenorde, 1981); *T. schmidtae* (Malkin, 1953) and *T. carolinensis* Hazel, 1977. Without creating a number of new monospecific subgenera, which the present authors feel would only cause additional complications, difficulties in assigning species to the subgenera level cannot be overcome. We have, therefore, refrained from using the new subgenera with respect to this genus.

**Thaerocythere crenulata** (Sars, 1866)  
 (Pl. 2, fig. 5)

1866 *Cythereis crenulata* Sars: 39.

1889 ?*Cythere crenulata* (Sars); Brady & Norman: 158, pl. 15, figs 5 & 6.

1941 *Cythereis (Eucythereis) crenulata* Sars; Elofson: 60.

1967 *Thaerocythere crenulata* (Sars); Hazel: 25, pl. 4, figs 2–5, 8; pl. 9, fig. 4.

1991 *Thaerocythere (Thaerocythere) crenulata* (Sars); Liebau: 149.

**Diagnosis.** Carapace subquadrate in lateral view. Anterior denticulated, broad to obliquely rounded, posterior somewhat truncated. Subdued reticulation, fossae minutely papillate. Short submarginal dorsal rib, both ends terminate in knobs. In dorsal view posterior compressed. Inner margin moderately wide, radial pore canals simple, straight; selvage moderately developed.

**Material.** In excess of 2000 specimens.

**Dimensions.**

	Cat. No.	Site	Length	Height
ALV-M	AMW/PL/001	1962/160(8)	0.74	0.44
ARV-F	AMW/PL/002	1962/160(8)	0.75	0.47

**Distribution.** Recent; Pan Arctic and amphiatlantic species. Commonly encountered on the shelf of the northeast Atlantic between the Bay of Biscay and Greenland (Cronin *et al.*, 1992). Hazel (1968) indicated the presence of late glacial specimens, at depth, between Capes Hatteras and Cod. Holocene; Bay of Biscay (Peypouquet, 1971, 1973).

**Remarks.** Only this cryophilic, amphiatlantic type species and *Thaerocythere hoptonensis* (Brady *et al.*, 1874) have been recorded from the Recent. Also see *Thaerocythere praecrenulata* sp. nov for remarks.

#### Explanation of Plate 2

**Fig. 1.** *Muellerina orygya* sp. nov.: **fig. 1a**, Paratype OS14186 RV-F, int. lat. (×65); **fig. 1b**, Paratype OS14186, detail of central muscle cars (×260). **Figs 2–4.** *Muellerina pliocenica* sp. nov.: **fig. 2**, Holotype OS14189 RV-M, ext. lat. (×61); **fig. 3**, Paratype OS14191 LV-M, ext. lat. (×61); **fig. 4a**, Paratype OS14192 RV-F, int. lat. (×69); **fig. 4b**, Paratype OS14192, detail of central muscle scar (×336). **Fig. 5a–b.** *Thaerocythere crenulata* (Sars, 1866): **fig. 5a**, AMW/RNA/002 RV-F, int. lat. (×66); **fig. 5b**, AMW/RNA/002, ext. lat. (×66). **Figs 6–8.** *Thaerocythere hoptonensis* (Brady *et al.*, 1874): **fig. 6**; Holotype 2.04.21 CpLV-F, ext. lat. (×57); **fig. 7**, Holotype 2.04.21 CpRV-F, ext. lat. (×57); **fig. 8a**, AMW/PL/026 LV-M, ext. lat. (×70); **fig. 8b**, AMW/PL/026, int. lat. (×70). **Fig. 9.** *Thaerocythere mayburyae* Cronin, 1991, AMW/PL/004 RV-M, ext. lat. (×66). **Figs 10–11.** *Thaerocythere oedichilus* (Brady, 1878): **fig. 10a**, AMW/PL/007 RV-F, ext. lat. (×70); **fig. 10b**, AMW/PL/007, int. lat. (×70); **fig. 11**, AMW/PL/008 LV-M, ext. lat. (×67). **Fig. 12.** *Thaerocythere trapezia* (Brady, 1878), AMW/PL/011 LV-M, ext. lat. (×63).

*Thaerocythere hoptonensis* (Brady, Crosskey & Robertson, 1874)  
(Pl. 2, figs 6–8)

1874 *Cythere hoptonensis* nov. sp. Brady, Crosskey and Robertson: 168, pl. 14, figs 4–6.

1982 *Quadracythere hoptonensis* (Brady *et al.*); Liebau: 233.

1991 *Thaerocythere (Notopleura) hoptonensis* (Brady *et al.*); Liebau: 153.

1991 *Thaerocythere (Notopleura) lusitanica* n. sp. Liebau; 152–153, pls 80–82; pl. 92, fig. 5.

**Diagnosis.** Elongate, subovate in lateral view; dorsal margin obliquely convex, ventral sinuous. Ornament consists of subovate fossae, marginally subquadrate; radial muri raised with respect to concentric component; pore-conuli common, situated on micropappilate solum where they are proximal to the muri, also present in subconcentric row mid-way between centre and margin (most common above mid-height) where they may be depressed. Well developed anterodorsal and short posterodorsal ridges, latter angled between posterior cardinal angle and subcentral tubercle.

**Dimensions of types.**

	Cat. No	Site	Length	Height
Holotype CpALV-F	2.04.21	Hopton Cliff	0.87	0.48
Holotype CpARV-F	0.89	0.48		
ALV-M	AMW/PL/026	Neutral Farm	0.72	0.40
ARV-M	AMW/PL/027	Neutral Farm	0.72	0.40

**Distribution.** Pliocene; Butleyan stage of the Red Crag Formation, Neutral Farm, Butley (TM 372811) (Lord *et al.*, 1988); Upper Pliocene (Redonian); Pallau II borehole, northwest France (C. A. Maybury, pers. comm.). ?Pleistocene; Hopton Cliff, Norfolk, UK. Recent; Sao Martinho do Porto, Portugal (Liebau, 1991), dredged off Muros, Spain (42.78°N, 9.08°W) (Brady & Norman, 1889) and a single specimen from a depth of 235 m on the northern Moroccan shelf (35.58°N, 6.63°W).

**Remark.** Re-examination of the types revealed that *T. (Notopleura) lusitanica* Liebau, 1991 is in fact a junior synonym of *T. hoptonensis*. Other species considered, by Liebau, 1991 (p. 150), to be members of the subgenus *Thaerocythere (Notopleura)* included *T. transiens* (Moos, 1963) and *T. nodoreticulata* (Bassiuoni, 1962).

*Thaerocythere mayburyae* Cronin, 1991

(Pl. 2, fig. 9)

1889 *Cythere trachypora* Jones: 24, pl. 3, figs 9a & 9b (*non* Jones, 1857).

1989 *Thaerocythere* sp. Horne & Kerr: pl. 2, fig. c.

1991 *Thaerocythere mayburyae* n. sp. Cronin: 777, pl. 10, figs 1–7.

**Diagnosis.** (after Cronin, 1991, p. 777). Carapace thick, subquadrate; surface characterized by well developed anterior marginal ridge, ventral and marginal ridges connected by a short oblique posterodorsal ridge; dorsomedian ridge variably developed. Subcentral tubercle very large, smooth to weakly pitted.

**Material.** East Anglia, 2CP, 9V.

**Dimensions.**

	Cat. No.	Site	Length	Height
LV/A-1	AMW/PL/003	Chillesford	0.70	0.39
ARV-M	AMW/PL/004	Chillesford	0.76	0.40
ALV-F	AMW/PL/005	Chillesford	0.74	0.43

**Distribution.** Pliocene; Chillesford Sand Member, Norwich Crag Formation at Chillesford Church Pit, East Anglia, UK; *Tapes*, *Maetra* and *Serripes* zones, Tjörnes, Iceland. Upper Pliocene (Redonian); St Erth Beds, Cornwall, UK. ?Pliocene/Pleistocene; Knocknasillige Member, County Wexford, Ireland.

**Remarks.** This species has been identified in the Hopton Cliff faunal slide of Brady *et al.* (1874), where it is described as *Cythere macropora* Bosquet (*non* Bosquet, 1852). A cryophilic species which first appeared in the Tapes Zone of Tjörnes (c. 3.40–3.15 Ma, Cronin, 1991). Clearly allied with *Thaerocythere* sp. A from the Coralline Crag Formation of East Anglia (see remarks).

*Thaerocythere oedichilus* (Brady, 1878)

(Pl. 2, figs 10 & 11)

1878 *Cythere oedichilus* nov. sp. Brady: 388, pl. 64, figs 1a–1d.

1967 *Thaerocythere? oedichilus* (Brady); Hazel: 25 and 26.

1991 *Thaerocythere (Thaerocythere) oedichilus* (Brady, 1879 [sic]); Liebau: 158, pl. 90, figs 1–4.

**Diagnosis.** Carapace, robust, subquadrate. Anterior obliquely rounded with broad denticulated marginal rim; posterior, angular, subtruncate. Dorsal margin weakly convex, ventral sinuous, converging posteriorly. Reticulation intricate, labyrinthine network of elongate/ovate cellate fossae. Muri inflated and raised either side of overgrown subcentral tubercle. Subventral ridge with alate posteroventral termination. Simple intermural and conjunctive pores common.

**Material.** East Anglia, 39V; the Netherlands, 22CP, 50V.

**Dimensions.**

	Cat. No.	Site	Length	Height
ALV-F	AMW/PL/006	43H/63(173)	0.68	0.41
ARV-F	AMW/PL/007	43H/63(173)	0.71	0.41
ALV-M	AMW/PL/008	43H/63(170)	0.71	0.39

**Distribution.** ?Miocene; ?Antwerp and Edgam sands, Belgium; FC1 zone, Oosterhout Formation, the Netherlands. Pliocene; Duerne and Lillo formations of Belgium; FB and FA2 zones, Oosterhout Formation; Coralline Crag Formation at Orford and Sutton Knoll, UK; Waltonian stage Red Crag Formation, Walton-on-the-Naze, UK and Butleyan stage Red Crag Formation, Crag Farm, Suffolk, UK.

**Remarks.** On the basis of macroreticulation Liebau (1991) placed this species and both *T. crenulata* and *T. sagittata* Liebau, 1991 within *Thaerocythere (Thaerocythere)* Liebau, 1991. The outline of this species resembles *T. crenulata* in many respects although its ornament is markedly different.

*Thaerocythere trachypora* (Jones, 1857)

(Pl. 3, fig. 1)

1857 *Cythere trachypora* Jones; 36, pl. 3, figs 9f–i.

*non* 1889 *Cythere trachypora* Jones; Jones & Sherborn: 24, pl. 3, figs 9a & 9b (= *T. mayburyae* Cronin, 1991).

1980 *Quadracythere macropora* (Bosquet); Wilkinson: pl. 2, figs 16 & 17 (*non* Bosquet, 1852).

?1981 '*Quadracythere*' *ruspelensis* n. sp. Uffenorde, pl. 7, fig. 21.

1988 *Thaerocythere* sp. Lord, Horne & Robinson; 4.

?1991 *Thaerocythere whatleyi* n. sp. Cronin; 780, pl. 10, figs 11, 12 & 14.

**Diagnosis.** Robust, quadrate, species of *Thaerocythere* with raised anterior cardinal angle in LV, dorsal margin sinuous with

concavity at mid length. Ornament composed of equally well developed radial and concentric arranged muri about solid subcentral tubercle. Muri angled, above mid-height, from posterior cardinal angle to mid height at the anterior margin. Fossae subquadrate, pore-conuli common and central on solum, intermural and conjunctive pores rare.

**Material.** East Anglia, 77CP, 160V; the Netherlands, 3CP, 16V.

**Dimensions.**

	Cat. No.	Site	Length	Height
ACp-F	AMW/PL/009	OSC1/OR12	0.75	0.47
ARV-M	AMW/PL/010	OSC1/OR15	0.75	0.47

**Distribution.** Pliocene; Coralline Crag Formation; Waltonian, Butleyan and Newbournian stages of the Red Crag Formation. FB, FA2 and FA1 (Pleistocene) of the Oosterhout and Maassliu formations, Holland. Oorderen Sands, Belgium (K. Wouters, pers. comm.).

**Remarks.** It appears likely that the rather worn specimens of *T. whatleyi* Cronin, 1991 from the Pliocene of Iceland are synonymous with this species. *T. trachypora* has retained a number of traits common to *T. vermiculata* sp. nov., notably two equally robust, anteromedian, longitudinal ridges and the general structure of both raised and depressed muri in the posterodorsal region.

*Thaerocythere trapezia* (Brady, 1878)

(Pl. 2, fig. 12)

1878 *Cythere trapezia* nov. sp. Brady: 391–392, pl. 66, figs 4a–d.

**Diagnosis.** Carapace sub-trapezoidal in lateral view, anterior obliquely rounded, margin reduced to a fine ridge. Dorsomarginal ridge moderately well developed. Reticulation composed of polygonal/quadrate, elongate quadrate at margins, fossae concentric and radial mural component equally developed. Large pore-conuli, peripheral on caperate solum. Subvertical truncation of reticulation along posterior cardinal angle. Eye tubercle, conical and mounted on murus below anterior cardinal angle.

**Material.** The Netherlands, 1CP, 5V.

**Dimensions.**

	Cat. No.	Site	Length	Height
ALV-M	AMW/PL/011	43H63(153)	0.79	0.47
ARV-M	AMW/PL/012	43H63(153)	0.79	0.43

**Distribution.** Pliocene; FB zone, Oosterhout Formation, the Netherlands; Luchtbal (K. Wouters, pers. comm.) and Oorderen Sands, Lillo Formation, Belgium and Coralline Crag Formation at Orford, Sutton Knoll and Gedgrave (K. Wouters, pers. comm.).

**Remarks.** This species is a close relative of *T. vermiculata* sp. nov., a species restricted to the Miocene of the Netherlands and Belgium. Comparison of the macroreticulation reveals a number of morphological analogues, notably the trapezoidal outline and overall carapace dimensions. *T. vermiculata* sp. nov. is easily distinguish from *T. trapezia* by the presence of two, longitudinal and inflated anteromedian ridges, similar to those developed in *T. trachypora*.

*Thaerocythere biformis* sp. nov.

(Pl. 3, figs 2–5)

**Derivation of name.** Latin; *biformis* = having two forms. Pertaining to the existence of two ecophenotypic variants of this species.

**Diagnosis.** Trapezoidal in lateral view, fossae subovate. Pore-conuli commonly developed with apophysis, peripherally situated on micropapillate solum. Strongly developed submarginal, anteroventral and dorsal ridges, latter reclined 'J'-shaped. Intricate, pinched, mediodorsal nodes present.

**Type locality and horizon.** Klundert 43H63 borehole, 256.50–259 m, Upper Miocene, Oosterhout Formation, the Netherlands.

**Material.** The Netherlands, 5CP, 95V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
<i>Thermophilic forms</i>				
Holotype ARV-F	OS14193	43H/63(178)	0.80	0.47
Paratype ALV-F	OS14194	43H/63(179)	0.81	0.51
Paratype ALV-M	OS14195	43H/63(179)	0.75	0.43
Paratype ARV-M	OS14196	43H/63(178)	0.77	0.43
<i>Cryophilic forms</i>				
Paratype ALV-F	OS14197	43H/63(174)	0.81	0.48
Paratype ARV-F	OS14198	43H/63(174)	0.83	0.47
Paratype ALV-M	OS14199	43H/63(174)	0.82	0.50
Paratype ARV-M	OS14200	43H/63(174)	0.78	0.43

**Distribution.** Upper Miocene (FC1 zone) and Lower Pliocene (FB zone); Oosterhout Formation, the Netherlands. Upper Miocene; Dessel and Duerne sands, Diest Formation, Belgium (K. Wouters, pers. comm.).

**Description.** Heavily calcified, sub-trapezoidal in lateral view. Dorsal margin of RV straight with posterior irregularities, LV arched, ventral margin convex with convexity behind anterior margin. Anterior margin finely denticulated, obliquely rounded with broad angular margin. Posterior denticulated, subtruncated, dorsal region straight or concave, extremity below mid height. Eye tubercle heavily swollen, broadly conical and mounted on submarginal murus. Ornament composed large, irregular, subtriangular/subovate. Radial and concentric murus equally well developed.

Pore-conuli commonly developed, with apophysis, peripheral on micropapillate solum. Robust, submarginal, ridge connecting anterior cardinal angle with posteroventral region, posterior termination inflated, angular and bifurcate. Dorsal margin reinforced with irregular, lateral, ridge forming an inclined 'U' at the posterior cardinal angle. Two 'pinched' nodes developed below dorsal margin in the dorsomedian field.

Inner lamella broad, radial pore canals numerous and straight; 45 anteriorly, 6 orally, 17 posteriorly; selvage broad, well developed.

**Remarks.** Two ecophenotypes of *T. biformis* sp. nov. occur, both forms exhibit an exceptionally high level of reciprocity in the disposition of macroreticulation. The first, and oldest form, is predominantly found in sediments of upper Miocene age (Diest Formation, Belgium, K. Wouters pers comm., and the FC1 Zone, Oosterhout Formation) and is considered by Wood *et al.* (1994) to have existed in a subtropical environment. This thermophilic form is characterized by finely chiselled muri. The second, cryophilic, form is restricted to ecozone A (first phase Lower Pliocene cooling) of the Netherlands and is characterized by a plicate swelling of muri and ridges. The earlier, thermophilic, form of *T. biformis* sp. nov. is similar, in many respects, to *T. gramanni* Liebau, 1991 from the Reinbekium (Middle Miocene) of northern Germany. Both species possess similarities

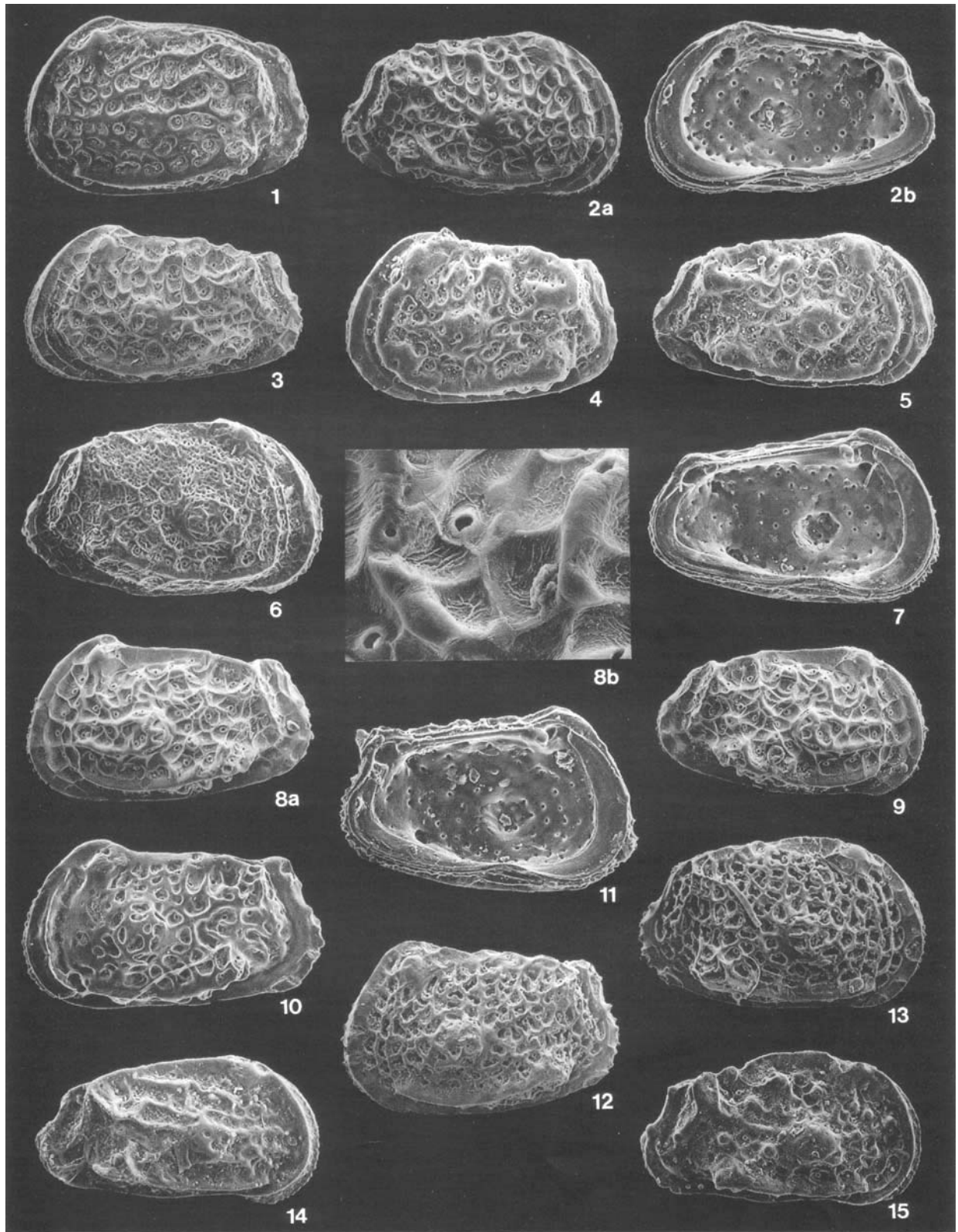


Plate 3

in form of posterior and dorsomedian swellings as well as in the disposition of muri and fossae, however, *T. gramanni* is considerable smaller though proportionally more elongate and lacks the submarginal anterior ridge.

***Thaerocythere praecrenulata* sp. nov.**

(Pl. 3, figs 6 & 7)

**Derivation of name.** Latin; *prae*=before. Pertaining to its possible ancestral links with *T. crenulata* (Sars, 1865).

**Diagnosis.** Carapace subquadrate in lateral view; anterior obliquely rounded, finely denticulated. Ornament composed of a first order polygonal, sub-radial, reticulation with low muri; more elongate parallel to anterior margin. Second order fabric of small sub-triangular/polygonal muri, surrounding commonly marginal pore-conuli.

**Type locality and horizon.** Klundert 43H/63 borehole, 239-241; FB zone. Oosterhout Formation, Upper Miocene, the Netherlands.

**Material.** The Netherlands, 1CP, 3V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype ALV-?F	OS14201	43H/63(171)	0.79	0.50
Paratype ARV-?F	OS14202	43H/63(171)	0.84	0.51
Paratype RVA-1	OS14203	43H/63(171)	0.74	0.42

**Distribution.** Lower Pliocene, FB zone, Oosterhout Formation, the Netherlands.

**Description.** Carapace quadrate; dorsal margin straight to slightly convex, ventral concave with convexity behind anterior margin. Anterior finely denticulated, obliquely rounded with raised cardinal angle in LV; posterior subtruncate with concavity above mid height. Maximum width submarginal to posterior. Small, well defined eye tubercle.

First and second order reticulation, sub-radial disposed, about finely punctate subcentral tubercle. Polygonal, first order fossae with low relief muri, more elongate parallelled to anterior margin. Second order composed of a fine tessellation of sub-triangular/polygonal micro-muri surrounding, commonly peripherally sited, pore-conuli. Muri suppressed or absent at dorsal margin.

Inner lamella moderately wide, avestibulate, marginal radial pore canals, numerous; 12 posteriorly, nine orally and 27 anteriorly, selvage moderately developed.

**Remarks.** Proposed ancestor of *T. crenulata* (Sars, 1866). Size and distribution of primary macroreticulation in both species is clearly analogous, however, the secondary tessellation of the solum in the Pleistocene/Recent species is much simplified, being finely punctate or papillate. Both species are cryophilic, *T.*

*crenulata* is restricted, on the northeast Atlantic shelf, to the European Realm where it attains its acme within the Norwegian Province (*sensu* Wood and Whatley, 1994). *T. praecrenulata* sp. nov. has, as yet, only been found in ecozone A, early Pliocene, of the Netherlands (first phase Pliocene cooling; Wood *et al.*, in 1994), where it occurs in association with other cryophilic species; *Acanthocythereis tuberculatus* (Norman, 1865), *Palmenella limicola* (Norman, 1865), *Elofsonella concinna* (Jones, 1857) and *Neomonoceratina tsurugaskensis* (Tabuki, 1986).

***Thaerocythere vermiculata* sp. nov.**

(Pl. 3, figs 8 & 9)

1878 *Cythere macropora* Bosquet; Brady: 392-392, pl. 66, figs 6a-d (*non* pl. 67, fig. 1a-d = *Thaerocythere woutersi* sp. nov.) (*non* Bosquet, 1852).

**Derivation of name.** Latin; *vermiculata* = worm like. Pertaining to the fine anastomosing secondary microreticulation present on the solum.

**Diagnosis.** Elongate-ovate/subquadrate species of *Thaerocythere* characterized by a well developed dorsal lateral ridge extending from the eye backwards towards termination in front of the posterior margin at its mid-height. Reticulation consists of a network of plicate muri, in which the concentric component may be subdued. Fossae, irregular, polygonal with common pore-conuli; fine secondary reticulation of anastomosing micromuri on caperate sola. Two sub-parallel, longitudinal, swollen muri developed in the anteromedian region, projecting from the subcentral tubercle to the anterior margin.

**Type locality.** Klundert 43H63 borehole, 254-256.50 m, FC1 zone, Upper Miocene, the Netherlands.

**Material.** The Netherlands, 33V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype ALV-M	OS14204	43H/63(177)	0.79	0.46
Paratype ARV-M	OS14205	43H/63(177)	0.79	0.43
Paratype ALV-F	OS14206	43H/63(177)	0.80	0.49
Paratype ARV-F	OS14207	43H/63(177)	0.80	0.52

**Distribution.** Restricted to the FC1 zone (Upper Miocene) and FB, lowest Pliocene (ecozone A) of the Netherlands. Duerne Sand, Upper Miocene, Belgium (K. Wouters, pers. comm.).

**Description.** Carapace subquadrate/elongate subovate, dorsal margin straight to weakly convex, cardinal angle in LV raised. Anterior denticulated, obliquely rounded; posterior subtruncate to ovate in LV, RV subtruncate. Surface strongly reticulate, irregular polygonal fossae with carinate and plicate muri, concentric component subdued. Secondary reticulation present on sola of the fossae in the form of anastomosing micropapillae.

**Explanation of Plate 3.**

Fig. 1. *Thaerocythere trachypora* (Jones, 1857): fig. 1, AMW/PL/009 CpLV-F, ext. lat. (×65). Figs 2-5. *Thaerocythere bififormis* sp. nov. (figs 2-3 thermophilic form): fig. 2a, Holotype OS14193 RV-F, ext. lat. (×61); fig. 2b, Holotype OS14193, int. lat. (×63); fig. 3, Paratype OS14195 LV-M, ext. lat. (×64); (figs 4-5 cryophilic form): fig. 4, Paratype OS14197 LV-F, ext. lat. (×57); fig. 5, Paratype OS14200 RV-M, ext. lat. (×63). Figs 6-7. *Thaerocythere praecrenulata* sp. nov.: fig. 6, Paratype OS14202 RV-?F, ext. lat. (×61); fig. 7, Holotype OS14201 LV-?F, int. lat. (×64). Figs 8-9. *Thaerocythere vermiculata* sp. nov.: fig. 8a, Holotype OS14204 LV-M, ext. lat. (×63); fig. 8b, Holotype OS14204, detail of microreticulation (×323); fig. 9, Paratype OS14205 RV-M, ext. lat. (×60). Figs 10-11. *Thaerocythere wittei* sp. nov.: fig. 10, Paratype OS14209 LV-M, ext. lat. (×60); fig. 11, Holotype OS14208 LV-F, int. lat. (×63). Figs 12-13. *Thaerocythere woutersi* sp. nov.: fig. 12, Holotype OS14212 LV-F, ext. lat. (×61); fig. 13, Paratype OS14215 RV-M, ext. lat. (×64). Fig. 14. *Thaerocythere* sp. A, AMW/PL/013 RV-M, ext. lat. (×63). Fig. 15. *Thaerocythere* sp. B, AMW/PL/024 RV-F, ext. lat. (×65). AMW/PL/024 RV-F, ext. lat. (×65).

Pore-conuli peripheral on solum, with apophysis; rare, simple disconjunctive pores. Eye tubercle mounted on, carinate, murus which projects backwards in an arcuate curve towards termination at mid height of posterior margin. Subventral ridge terminates posteriorly in swollen bifurcation. Two sub-parallel, plicate, muri extend from a masked subcentral tubercle, forward towards the anterior margin.

Inner lamella moderately wide, marginal radial pore canals straight/sinuuous; 35 anteriorly, 6+ orally and 18 posteriorly. Anterior selvage.

**Remarks.** This species was original described by K. Wouters (pers. comm.) from the Duerne Sands Member of Belgium. Its morphological affinities with the younger mid-Pliocene species, *T. trachypora* are unquestionable (see remarks).

*Thaerocythere wittei* sp. nov.

(Pl. 3, fig. 10)

1991 *Thaerocythere* (*Thaerocythere*) sp. LA58 Liebau: 158, pl. 90, fig. 5.

**Derivation of name.** In recognition of the enormous help given by Dr Leendert Witte of the Royal Dutch Geological Survey in supplying both samples and information for this study and also of his important work on West African Ostracoda.

**Diagnosis.** Carapace elongate rectangular with sub-parallel dorsal and ventral margins. Marked concavity of posterodorsal margin resulting in a sub-triangular posterior extremity. Surface pitted with moderately large, deep, subcircular to slit-like cellate fossae, coalescing posteriorly, radially disposed about high subcentral tubercle.

**Type locality and horizon.** Klundert 43H/63 borehole, 239-241.5, FB zone, Oosterhout Formation, Pliocene, the Netherlands.

**Material.** East Anglia, 1CP, 28V; the Netherlands, 3CP, 24V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype	ARV-F OS14208	43H/63(171)	0.92	0.48
Paratype	ALV-M OS14209	43H/63(171)	0.87	0.48
Paratype	LV A-2 OS14210	43H/63(174)	0.71	0.38
Paratype	RV A-3 OS14211	43H/63(158)	0.53	0.30

**Distribution.** Upper Miocene to Upper Pliocene (FC-FA2 zones); Oosterhout Formation, the Netherlands. Mid to Upper Pliocene Coralline Crag Formation, Orford, UK; Waltonian and Butleyan stages of the Red Crag Formation at Walton-on-the-Naze and Neutral Farm, UK. Upper Pliocene and ?earliest Pleistocene, Belgium (Liebau, 1991, p. 158).

**Description.** Carapace heavily calcified, subrectangular in lateral view. Dorsal margin concave in LV with moderately raised anterior cardinal angle, RV straight; ventral sinuous to slightly convex in LV, sinuous in RV. Anterior obliquely rounded with numerous, webbed, marginal denticles. Posterior angular/sub-triangular. Surface pitted with moderately large, deep, slit-like to subcircular cellate fossae, coalescing posteriorly. Pore-conuli peripheral on solum, rarer disconjunctive, simple, normal pores. Posterodorsal tubercle forms a forward reclined 'U'. Inner lamella moderately broad, radial pore canals numerous, straight and evenly spaced; 29 anteriorly, 4+ orally, 18 posteriorly, selvage well developed.

**Remarks.** This species was placed with *T. oedichilus* (Brady, 1878) in the subgenus *Thaerocythere* (*Thaerocythere*) by Liebau (1991). Although, both species possess heavily cellated fossae,

subdued reticulation on the dorsal margin and a sub-triangular posterior the overall structure of their ornament is very different.

*Thaerocythere woutersi* sp. nov.

(Pl. 3, fig. 11-13)

1878 *Cythere macropora* Bosquet; Brady: 392-392, pl. 67, figs 1a-d (non pl. 66, figs 6a-d=*T. vermiculata* sp. nov.) (non Bosquet, 1852).

?1990 '*Quadracythere*' sp. Uffenorde; pl. 1, fig. 10.

**Derivation of name.** In honour of Dr K. Wouters for his contribution to the study of Neogene Ostracoda from Belgium.

**Diagnosis.** Quadrate species of *Thaerocythere* characterized by a serrated dorsal margin and finely sculptures reticulation comprising a basket-like ponticulate tegman bearing disconjunctive normal pores and ingrowing spines edging fossae. Pore-conuli common and proximal to muri.

**Type locality and horizon.** Klundert 43H63 borehole, 239-241.50 m, Lower Pliocene, Oosterhout Formation, the Netherlands.

**Material.** The Netherlands, 8CP, 110V.

**Dimensions of types.**

	Cat. No.	Site	Length	Height
Holotype	ALV-F OS14212	43H/63(171)	0.82	0.50
Paratype	ARV-F OS14213	43H/63(177)	0.82	0.48
Paratype	ALV-F OS14214	43H/63(171)	0.79	0.50
Paratype	ARV-M OS14215	43H/63(171)	0.78	0.48
Paratype	Cp-F OS14216	43H/63(171)	0.78	0.51

**Distribution.** Upper Miocene and Lower Pliocene (ecozone A) of the Netherlands. Middle and Upper Miocene, ?Brecham and Diest formations, Belgium (Brady, 1878). Upper Miocene, *parvipunctata* superzone (Uffenorde, 1990, p.372), Wusterheide, northern Germany.

**Description.** Thick shelled, sub-trapezoidal in lateral view. Dorsal margin serrated, LV broadly concave, RV straight or slight convex. Ventral margin broadly convex. Anterior margin obliquely rounded with very fine radial muri, posterior truncate. Conspicuous eye tubercle mounted on reticulate tegman. Carapace intricate, reticulate with fine subquadrate/ovate 'basket-like' sculpture with both radial and concentric components comprising ponticulate tegmina bearing disconjunctive normal pores and minute, ingrowing, spines edging fossae. Pore-conuli common, proximal to muri. Dorsolateral ridge terminates posteriorly in angular, wedge shaped, swelling. Weakly projecting posterodorsal structure of cellate, cross-weaved, ribs.

Inner lamella broad, radial pore canals, numerous; especially in anteroventral quadrant, anterior 28, orally 3+, posterior 15. Selvage broad, well developed.

**Remarks.** Its outline in lateral view is similar to that of another Upper Miocene species *T. nodoreticulata* (Bassiouni, 1962). Both species are characterized by a serrated dorsal margin, however, *T. woutersi* sp. nov. is both longer and possess a rather distinctive ornament, whereas in *T. nodoreticulata* the celation of the fossae is complete.

*Thaerocythere* sp. A

(Pl. 3, fig. 14)

**Diagnosis.** Elongate ovate in lateral view. Well developed anterodorsal marginal ridge terminating posteriorly at mid-height on the sub-margin; this peripheral structure is connected



to the subcentral tubercle via a ridge attached to the posterior cardinal angle. Muri within the dorsomedian field parallel this obliquely angled ridge.

**Distribution.** Coralline Crag Formation at Sutton Knoll and Orford, UK.

**Type locality and horizon.** Sutton Knoll, sample S3, Coralline Crag Formation, Pliocene, East Anglia, UK.

**Material.** East Anglia, 7V.

**Dimensions.**

	Cat. No.	Site	Length	Height
ARV	AMW/PL/013	Sutton Knoll (S4)	0.78	0.38
RV ?A-1	AMW/PL/014	Sutton Knoll (S3)	0.70	0.38
LV A-1	AMW/PL/015	Sutton Knoll (S3)	0.61	0.36

**Remarks.** This species has a number of morphological affinities with *T. mayburyae* Cronin, 1991 and may be a possible evolutionary precursor. Both species possess a marginal ridge, eyes mounted on reticulation and similar carapace proportions, however, in *T. sp. A* the dorsomarginal ridge is strongly developed and overhangs this periphery along most its length, muri heavily calcified.

*Thaerocythere* sp. B

(Pl. 3 fig. 15)

1989 *Quadracythere* sp. 1 Maybury MS; Fourniguet *et al.*: pl. 2, fig. 13.

?1991 *Hermanites* sp. B Cronin; pl. 8, fig. 3.

**Diagnosis.** Carapace elongate subovate in lateral view; anterior obliquely rounded and minutely denticulated. Dorsal convex, ventral sinuous. Reticulation characterized by a radial pattern of muri and fossae about a robust subcentral tubercle. Prominent anterodorsal ridge. Inclined Y-structure of ridges and pore-conuli developed posterodorsally, ventrolateral ridge terminates posteriorly in a bifurcate structure of nodes. Seven pore-conuli arranged subconcentric mid-way between centre and margin in the dorsomedian and anterior fields. Two further pore-conuli located below mid height, behind subcentral tubercle.

**Material.** East Anglia, 4V.

**Dimensions.**

	Cat. No.	Site	Length	Height
ARV-F	AMW/PL/024	OSC1/OR12	0.75	0.39
ARV-M	AMW/PL/025	OSC1/OR12	0.74	0.37

**Distribution.** Pliocene; Coralline Crag Formation, Orford, Suffolk, UK; ?*Maetra* Zone, Tjörnes Iceland (Cronin, 1991).

**Remarks.** In lateral view *T. sp. B* is clearly allied with *T. hoptonensis* (Brady *et al.*, 1874) as both possess a very well developed, marginal, anterodorsal ridge; convex dorsal margin and pore-conuli in the dorsal field. However, *T. hoptonensis* differs in possessing muri with a subdued concentric component, being less elongate and lacking the complex, posterodorsal structure. *T. vermiculata* sp. nov. also possess a strong dorsolateral ridge but unlike *T. sp. B* it possesses two characteristic sub-parallel, plicate, muri in the anteromedian region.

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