# THE OSTRACOD GENUS *KRITHE* FROM THE TERTIARY AND QUATERNARY OF THE NORTH ATLANTIC

*by* G. P. COLES, R. C. WHATLEY *and* A. MOGUILEVSKY

ABSTRACT. The ostracod genus *Krithe* is investigated from Cainozoic deep water sediments of the North Atlantic region, mostly from ODP/DSDP cores, although other material is from short cores collected by various NATO vessels, and the geographical and stratigraphical occurrence of the principal species is detailed. The morphological features of the genus are described, and their relative utility in specific discrimination assessed. Of the seventeen species and subspecies described herein, eight have been previously described, five species (*Krithe gobanensis*, *K. regulare*, *K. minima*, *K. aquilonia*, *K. praemorkhoveni*) and two subspecies (*K. morkhoveni lamellalata*, *K. morkhoveni ayressi*) are new, while two are compared to previously described species. In addition, the stratigraphical ranges and distribution of nineteen *nomina nuda* species, too rare to be formally described, are tabulated. A new system, based on the nature of the anterior radial pore canals, is used to erect distinct species groups of the genus and as an aid in species determination. The various carapace biocharacters of the genus are reviewed and evaluated with respect to their taxonomic significance; many are shown to be of little use since they are very conservative within *Krithe* while others, such as size, shape, degree of dimorphism and the nature of the anterior radial pore canals are shown to be of great importance. The stratigraphical ranges of all known *Krithe* species in the North Atlantic are given and the considerable biostratigraphical significance of the genus is demonstrated. The previous use of *Krithe* in palaeoenvironmental reconstruction is discussed and the supposed relationship between vestibulum morphology and oxygen level critically evaluated and shown to be wanting, as is the proposition that there is a determinable relationship between the length of species of the genus and water depth.

THE ostracod genus *Krithe* Brady *et al.* (1874) is an abundant, cosmopolitan taxon with a stratigraphical record of at least 97·5 m.y., extending from the Cenomanian (Shakin 1991) to the Recent. Its diversity over this interval is indicated by the fact that at least 115 species have been described (Kempf 1988). Many new species await description, especially from the deep sea, where it reaches its maximum importance. It has been reported from all studies of bathyal and abyssal faunas, since the voyage of H.M.S. *Challenger* (Brady, 1880) to the present investigation. In most such studies, *Krithe* is both the most numerically abundant genus (sometimes outnumbering all other ostracod taxa combined) and the most specifically diverse genus, where the whole ostracod fauna is considered. *Krithe* also occurs in shallower waters on the continental shelf, where it is dominantly, but not exclusively, cryophilic and is comparatively rare in subtropical waters. Some unusual occurrences in shallow, warmer water environments where the genus is a dominant are known, as in the Middle Miocene Balcomian of SE Australia (Whatley and Downing 1983).

However, the use of *Krithe* is either biostratigraphy or palaeoenvironmental analysis, capitalizing upon its cosmopolitan and eurybathyal distribution, has largely been frustrated by the confused state of its taxonomy. This is a direct result of the smooth carapace of all *Krithe* species and the consequent lack of diagnostic ornamentation, together with an apparently high degree of intraspecific variation, which together give rise to the so called '*Krithe* Problem' (McKenzie *et al.* 1990).

*Krithe*, and to a lesser extent *Parakrithe* van den Bold, have been used extensively in palaeoenvironmental reconstructions, especially in deep water marine settings. This utilization has been made based upon many claims concerning the biology and ecology of *Krithe*, the most

**[Palaeontology, Vol. 37, Part 1, 1994, pp. 71–120, 7 pls.]**

important of which state that there exists an overall relationship between the size (length) of species and water depth and also between the size and shape of the anterior vestibulum and levels of dissolved oxygen. These hypotheses were formulated by Peypouquet (1975, 1977, 1979) and have been considered in some detail and systematically rejected by Whatley and Zhao (1993). The present study provides further evidence of the invalidity of these hypotheses.

Our taxonomic concept of *Krithe* is at considerable variance with that of Peypouquet (1975, 1977, 1979); using the techniques outlined below, we are able to recognize distinct species, using essentially the same taxonomic database as Peypouquet. He recognized many fewer species, most of which comprise a number of ecotypes, some of which varied in size considerably beyond what we would consider possible within contemporary numbers of the same species, notwithstanding differences in their ecology. As a general statement, it would seem that our species would often be equivalent to Peypouquet's ecotypes.

The present authors have studied *Krithe* in detail, many from Cenozoic deep-sea sediments in the North Atlantic, in order to achieve a consistent taxonomy at the species level and to assess the palaeoecological and biostratigraphical utility of the genus as a whole. We also employ the data of a number of other researchers at the University of Wales, Aberystwyth in proposing a morphological scheme for the identification of *Krithe* species.

## MORPHOLOGICAL CHARACTERISTICS OF *KRITHE*

The external and internal morphological features of typical adult *Krithe* species are illustrated in Text-figures 1–2. The smooth carapace of all *Krithe* species, and the consequent absence of much of the information employed in the identification of ornate taxa, necessitates more detailed studies of valve shape and size, as well as internal features only visible in well-preserved material. Nine principal morphological features are considered, with particular emphasis upon their value in specific discrimination.

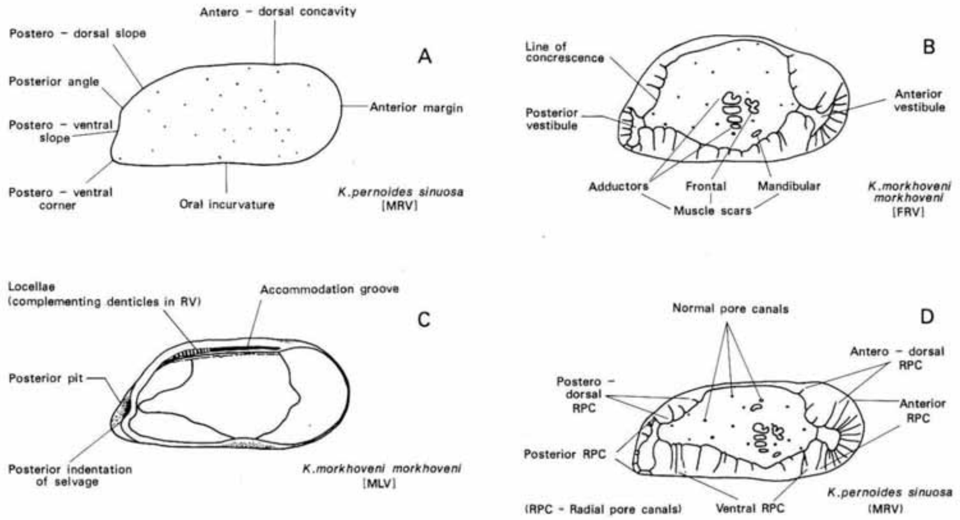
### *Valve shape*

Within certain parameters, this is quite constant within species, and is very useful in specific discrimination once sexual dimorphism is recognized (Text-fig. 1). Males are relatively longer and less high than females, but dimorphism, while often very marked, may be only weakly displayed in some species. The general shape of *Krithe* varies from subovate through subquadrate to subrectangular. The anterior margin is typically broadly rounded or slightly upswept, the posterior margin is truncate, the dorsum is straight to convex and the ventral margin generally has a shallow oral incurvature. However, there are many variations which complicate the basic generic outline. For example, the posterior margin is especially variable; the postero-dorsal corner and posterior angle (if present) vary considerably in their development. The postero-ventral slope makes an angle of 60°–90° with the ventral margin, the stope being less steep in species with a highly tapered posterior margin. The posterior indentation of the selvage is strongest in those valves with a tapered posterior, and is inversely proportional in strength to the increasing angle of the postero-ventral slope.

### *Valve size*

This is often a useful specific character, as there is considerable size variation between species. The smallest species recorded, *Krithe* sp. cf. *K. parvula*, is only 0·43 to 0·46 mm in length, while some male specimens of *K. trinidadensis* exceed 1·50 mm. However, size is also influenced by sexual dimorphism and intraspecific variation. Male valves are usually absolutely and always relatively longer than females. Due to the strong overlap of most species of *Krithe*, one valve (usually the left) is larger than the other.

The degree of intraspecific size variation for each species, based on the maximum dimensions of both valves and both sexes, may be described as being small (< 10 per cent), moderate (10–20 per cent), considerable (20–30 per cent) to extremely large (over 30 per cent). Generally the largest



TEXT-FIG. 1. Main morphological characteristics of the ostracod *Krithe*. A, D, *K. pernoides sinuosus* Ciampo, male right valve. B–C, *K. morkhoveni morkhoveni* van den Bold. B, female right valve. C, male left valve.

species are the most variable in size (up to 50 per cent in the female valves of *K. trinidadensis*). In contrast, the degree of size variation allowed by Peypouquet (1977) between contemporary 'ecotypes' of some of the species he recognized was considerably larger and reached a maximum of 168 per cent within his *Krithe* sp. C. This degree of intraspecific size variation is quite unknown among other Ostracoda and greatly exceeds that allowed by other workers.

### *Normal pore canals* (*NPC*)

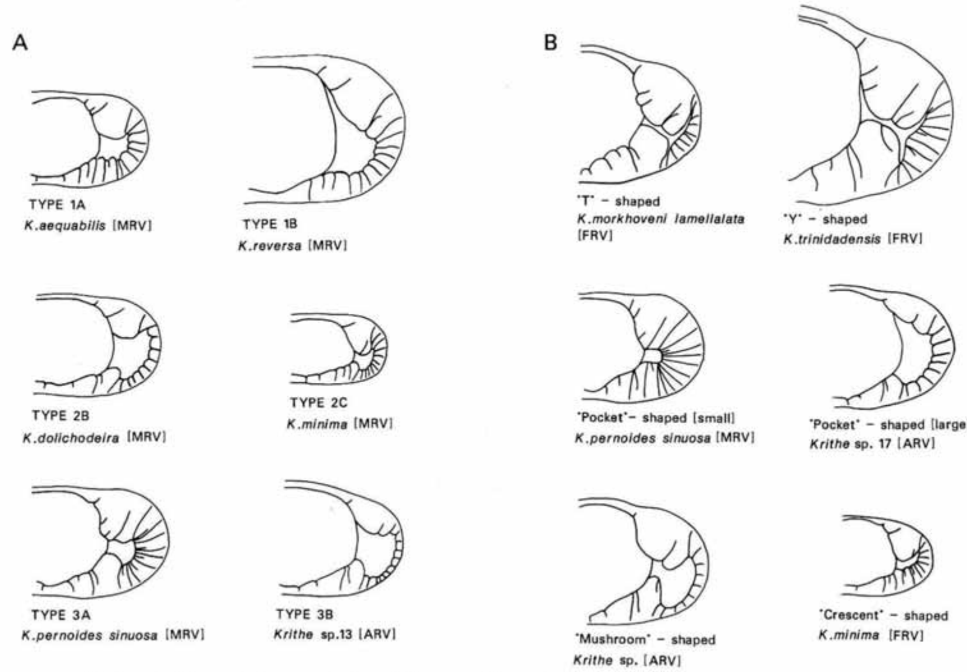
These comprise approximately fourteen to eighteen round canal openings regularly distributed on the surface of each valve. They are very constant in position in all *Krithe* species. They appear to be a conservative character of little use in species discrimination. However, the normal pore canals increase in size in proportion to valve size and, in the larger species, some are of sieve-type.

### *Inner lamella*

The width of the inner lamella and the course of the line of concrescence vary considerably, both between and within species. Species with the widest inner lamellae also have the most irregular lines of concrescence, indented at the base of the radial pore canals and deeply depressed below the adductor muscle scars. In species with narrow inner lamellae, the line of concrescence is usually simple and is only slightly depressed below the adductors. The nature of the inner lamella is generally a useful character in species identification.

### *Anterior vestibulum*

The size and shape of the anterior vestibulum is a very useful specific character, notwithstanding that it is moderately variable within certain species. The anterior vestibulum may be very large, comprising most of the anterior marginal area, or it may be almost absent in some species. The shape of the anterior vestibulum is more constant than its absolute size, and can be described in terms of width of opening, length and width of neck and distal expansion. Four main types of



TEXT-FIG. 2. Morphological characteristics of the anterior end of the *Krithe* valves, A, main types of antero-dorsal radial pore canals (ADRPC). B, main types of anterior vestibule.

anterior vestibule can be distinguished (see Text-fig. 2B). Several intermediate examples occur, but most specimens can be readily assigned to one of the four main types. In general, species with wide inner lamellae have small, constricted anterior vestibulae, while species with narrow inner lamellae have large, expanded anterior vestibulae.

### *Posterior vestibulum*

This is usually much smaller than the anterior vestibulum and is subrectangular in shape. The posterior vestibulum is relatively constant in shape but, since it varies little between species and is frequently obscured by sediment infill, it is not useful as a specific diagnostic character.

### *Radial pore canals*

The number, length and distribution of radial pore canals (both true and false) are very useful in specific discrimination. The length of the radial pore canals (RPC) is directly proportional to the width of the inner lamella. The RPC pattern within a species is remarkably stable, and can be conveniently subdivided into five fields.

*1. Antero-dorsal RPC.* These comprise a maximum of five false canals emergent from the vestibulum deck, dorsal of the first true anterior RPC (ARPC) or in the antero-dorsal fused zone, and can be numbered AD 1–5. AD 1 is short or absent, AD 2 and AD 3 may occur as normal pore canals or may be short or moderately elongate, AD 4 may be absent, short or is frequently the most elongate, and AD 5 is present only where AD 4 is elongate, when it is about half the length of AD 4. Three basic types of antero-dorsal RPC can be recognized.

Type 1: AD 3 elongate, AD 4 absent
  1A: AD 1–2 very short
  1B: AD 1 very short, AD 2 present as a NPC
Type 2: AD 2 elongate
  2A: AD 1, 3–4 very short
  2B: AD 1 short, AD 3–4 absent
  2C: AD 1 short or absent, AD 3 absent, AD 4 short and emergent from the vestibular neck
Type 3: AD 4 elongate
  3A: AD 1–3 short, AD 4 very elongate
  3B: AD 1–3 very short or absent, AD 4 short and emergent from a wide vestibular neck

The principal antero-dorsal radial pore canal types recognized in *Krithe* species from the North Atlantic are illustrated in Text-fig. 2A and have proved more useful in species recognition than the other three types of RPC.

2. *Anterior RPC.* These comprise nine to fourteen true RPC, emergent from the anterior vestibulum. Their length varies in inverse proportion to the size of the anterior vestibulum. Up to eight short false RPC are interspersed between them.

3. *Ventral RPC.* These comprise seven to fifteen false canals, some of which may branch. They are prominent in species with wide ventral inner lamellae.

4. *Postero-dorsal RPC.* These comprise four false canals.

5. *Posterior RPC.* These comprise up to eight short, false canals.

### *Hinge*

The hinge of *Krithe* is essentially adont; the narrow dorsal margin of the smaller right valve is accommodated in a smooth groove in the larger left valve (Text-fig. 1C). It may be straight or arched, depending on the convexity of the dorsal margin. In species with a strongly convex dorsum the hinge groove partly overhung by the dorsal margin. In many species the right valve hinge bar is raised and finely denticulate at the posterior end. There are up to ten minute denticles and complementary locellae in the left valve. The hinge teeth are most prominent in the male valves of large species, producing a pseudodont dentition. Opposite hinge arrangements occur in species with reversed valve overlap, where the right valve is larger than the left. Reversed overlap species are rare and are confined almost exclusively to water depths of 1000 m or more.

The hinge is constant in form within a species, but is only of slight taxonomic use, since the same basic pattern recurs in many different species. The pseudodont dentition of many deep-sea *Krithe* species is almost exactly similar to that of the shallow water, often phytal genus *Parakrithella* Hanai, despite the fact that the pseudodont dentition of the latter genus was used by Hanai to discriminate it from *Krithe*. The similarity of hingement suggests a close relationship between the two genera, notwithstanding their present-day ecological separation.

### *Muscle scars*

The typical central muscle pattern is a straight to slightly arcuate vertical row of four adductors, increasing in size dorsally. The topmost scar is usually reniform or slightly dorsally indented, the second and third scars are smaller, flatter and often biconcave, and the fourth is always smallest and subovate. The frontal scar is usually trilobate, but rarely may be quadrilobate or divided into two scars. The dorsal scars are usually difficult to discern. The size of the muscle scars is generally in direct proportion to valve size, although *K. dolichodeira* has relatively small scars. The pattern of muscle scars is almost as variable within a species as between different species, and hence is of only slight taxonomic value.

In summary, therefore, among the main morphological characteristics of *Krithe* species, valve shape and size, the anterior vestibulum and the antero-dorsal radial pore canals are very useful in specific discrimination; the normal pore canals, the posterior radial pore canals and the muscle scars are of very little use; and the remaining characters are of intermediate value.

## MATERIAL AND METHODS

The principal source of samples for this study is material from ten Deep Sea Drilling Project sites in the North Atlantic from Legs 80, 82 and 94. The studied sites, locations, present day water depths and stratigraphical intervals are detailed in Table 1. This is the same material employed in the studies of Whatley and Coles (1987, 1990) and Coles and Whatley (1989) in which emphasis was placed on ostracod taxa other than *Krithe*.

TABLE 1. The location, present-day water depth (PDWD) and stratigraphical intervals of the studied DSDP sites.

| Site | Latitude | Longitude | PDWD (m) | Stratigraphical interval |
|---|---|---|---|---|
| 549 | 49° 05·28′ N | 13° 05·88′ W | 2515 | U. Palaeocene–U. Oligocene |
| 550 | 48° 30·91′ N | 13° 26·37′ W | 4420 | L. Palaeocene–L. Eocene |
| 558 | 37° 46·20′ N | 37° 20·61′ W | 3754 | L. Oligocene–U. Miocene |
| 563 | 33° 38·50′ N | 43° 46·04′ W | 3786 | M.–U. Miocene |
| 606 | 37° 20·32′ N | 35° 29·99′ W | 3007 | L. Pliocene–Quaternary |
| 607 | 41° 00·07′ N | 32° 57·44′ W | 3427 | U. Miocene–Quaternary |
| 608 | 42° 50·21′ N | 23° 05·25′ W | 3526 | U. Miocene–Quaternary |
| 609 | 49° 52·67′ N | 24° 14·29′ W | 3884 | U. Miocene–Quaternary |
| 610 | 53° 13·30′ N | 18° 53·21′ W | 2417 | U. Miocene–Quaternary |
| 611 | 52° 50·47′ N | 30° 19·58′ W | 3201 | U. Miocene–Quaternary |

A total of 306 samples from twenty-one holes drilled at the above ten sites were analysed and their entire ostracod fauna picked. Over 20000 specimens of *Krithe* were recovered, of which almost 2800 were adult specimens with fully developed internal features.

The internal features of *Krithe* valves were drawn using the Projectina microscope at a standard magnification of × 100. The valves were first cleaned using a brush or fine needle, then placed in a cavity slide and immersed in water. The image was projected onto tracing paper and drawn.

## SYSTEMATIC PALAEONTOLOGY

The following section details the taxonomy, morphology, and biostratigraphical and geographical occurrences of all important *Krithe* species present in the Cainozoic of the North Atlantic Ocean, with notes on their distribution in other regions. It is intended to serve as an example of the way in which the morphological characters outlined above can be used to separate species of this genus.

Type material of all new species is housed in the Palaeontology Collections of the Natural History Museum, London, to which the catalogue numbers prefixed OS refer. Catalogue numbers prefixed GC/NA/ refer to specimens in the Coles Collection, Micropalaeontology Museum, University of Wales, Aberystwyth. In the text, only the numbers of adult specimens are given; there are usually many more juvenile specimens in the collections. The following conventions are employed: F, female; M, male; LV, left valve; RV, right valve; ARPC, anterior radial pore canals; ADRPC, antero-dorsal radial pore canals; PRPC, posterior radial pore canals; NPC, normal pore canals; PDWD, present-day water depth.

Size of species is given as small, medium, large, etc. according to the scale given by Whatley (1970, p. 301). Dimension are given as L, length; and H, height.

Stratigraphical ranges are given by system or subdivision of system and by standard nannofossil zones (NP, Palaeogene; NN, Neogene).

Under the heading *Material and distribution* the number is given of adult specimens of each species which the authors had available for study and the geographical and stratigraphical distribution of the species within the various cores on which the study is based. Additional distributional information, as well as taxonomic comment, is given under *Remarks* with respect to each species.

Class OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PODOCOPINA Sars, 1866
Superfamily CYTHERACEA Baird, 1850
Family KRITHIDAE Mandelstam *in* Bubikyan, 1958
Genus KRITHE Brady *et al.*, 1874

*Discussion*. The species and subspecies of *Krithe* discussed below are arranged according to their ADRPC type.

## ADRPC TYPE 1B

### *Krithe reversa* van den Bold, 1958

Plate 1, figures 1–6; Text-figure 3A–D

| | |
|---|---|
| 1958 | *Krithe reversa* van den Bold, p. 404, pl. 1, figs 4*a*–*g*. |
| 1959 | *Krithe sawanensis* Hanai, p. 302, figs, 3–4; pl. 18, figs 3–7. |
| 1977 | *Krithe* sp. C Peypouquet [*pars*], p. 109, fig. 36 sp. C 34*ei* (*forme* inverse only). |
| 1981 | *Krithe reversa* van den Bold; van den Bold, p. 69, pl. 1, fig. 13*a*–*d*. |
| 1981 | *Krithe reversa* van den Bold; Steineck, p. 362, pl. 2, fig. 12. |
| 1983 | *Krithe* sp. C30 Peypouquet; Benson and Peypouquet, p. 818, pl. 5, figs 4–5. |
| 1990 | *Krithe* sp. 4 Dingle *et al*., p. 282, figs 17D, 18F, 22E. |

*Material and distribution*. Thirty seven adult valves. Holes 549A (U. Miocene), Hole 558 (M.–U. Miocene), Hole 563 (M.–U. Miocene), Hole 606 (U. Pliocene–Quaternary), Hole 606A (L. Pliocene–Quaternary), Hole 607 (L. Pliocene–Quaternary), Hole 608 (L.–U. Pliocene), Hole 609B (U. Pliocene–Quaternary), Hole 610 (U. Pliocene), Hole 611D (L. Pliocene).

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| FLV GC/NA/118 606A–14 L. Pliocene | 1·04 | 0·49 |
| FLV GC/NA/138 606–5 Quaternary | 0·98 | 0·47 |
| FRV GC/NA/51 606A–14 L. Pliocene | 1·03 | 0·46 |
| MLV GC/NA/102 606A–14 L. Pliocene | 0·94 | 0·44 |
| MRV GC/NA/44 606A–14 L. Pliocene | 0·91 | 0·40 |
| FLV GC/NA/39 606A–19 L. Pliocene | 0·95 | 0·50 |
| FLV GC/NA/101 606A–14 L. Pliocene | 0·95 | 0·52 |
| FRV GC/NA/188 606–16 L. Pliocene | 0·97 | 0·56 |
| MLV GC/NA/117 606A–4 Quaternary | 1·12 | 0·48 |
| MRV GC/NA/131 606–11 L. Pliocene | 1·09 | 0·52 |

*Stratigraphical range*. Middle Miocene–Quaternary (NN 6–9, 14–16, 18–21).

*Diagnosis*. A large to very large, thick-shelled, subrectangular species of *Krithe* characterized by reversed valve overlap and strong sexual dimorphism. Female much shorter and relatively higher than the elongate male. Inner lamella quite narrow. Anterior vestibulum very large, 'pocket'-shaped, with wide opening, often extending to antero-dorsal corner of inner margin. Ten or eleven straight to slightly curved ARPC with up to five false ARPC. ADRPC type 1B. RV hinge bar denticulate at posterior end.

*Remarks.* Both adults and juveniles of *K. reversa* are readily identifiable by their reversed valve overlap and characteristic outline. The species occurs consistently from the Middle Miocene to the Recent, but is never the dominant *Krithe* species in any assemblage. The present is the earliest record of this species in the North Atlantic. It is also present in the late Quaternary of the Northeast Atlantic between PDWD 3422 and 4096 m (Porter 1984; material seen by GC), late Quaternary of the Iberian Portal region at PDWD 3700 m (Harpur 1985), Middle Miocene to Pliocene (NN 9–18) of numerous Caribbean localities in Trinidad, Haiti, Venezuela, Jamaica and the Dominican Republic (van den Bold 1958, 1981; Steineck 1981), late Pliocene of Japan (Hanai 1959), latest Pliocene and Quaternary of the Southwest Pacific and eastern Indian Ocean (Downing 1985; Ayress 1988) and the Upper Miocene to Quaternary of the Rio Grande Rise in the South Atlantic (Benson and Peypouquet 1983).

In the Recent it is present in the Atlantic off Florida between 803 and 1080 m (among Cronin's 1983 material seen by GC), the Gulf of Mexico below 1000 m (van Morkhoven, 1972; van den Bold, 1981), South Scotia Sea between 1155 and 3925 m (Coxhill 1985), South Atlantic off Southwestern Africa between 1600 and 2916 m (Dingle *et al.* 1990) and the North Atlantic from 803 to 5726 m (personal observations).

In summary, *K. reversa* appears to have been present throughout the world's oceans from at least the Middle Miocene to the Recent and is usually indicative of water depths in excess of 1000 m. It is absent from the Mediterranean Basin and southern Europe, suggesting that the water depths at the Strait of Gibraltar were never sufficiently deep to permit its migration from the Atlantic.

## ADRPC TYPE 2B

### *Krithe aequabilis* Ciampo, 1986

Plate 1, figures 7–12; Text-figure 3E–K

1980 *Krithe* sp. 3 Ciampo, p. 17, pl. 4, fig. 4 (male).
1986 *Krithe aequabilis* Ciampo, p. 87, pl. 17, figs 1–2.

---

### EXPLANATION OF PLATE 1

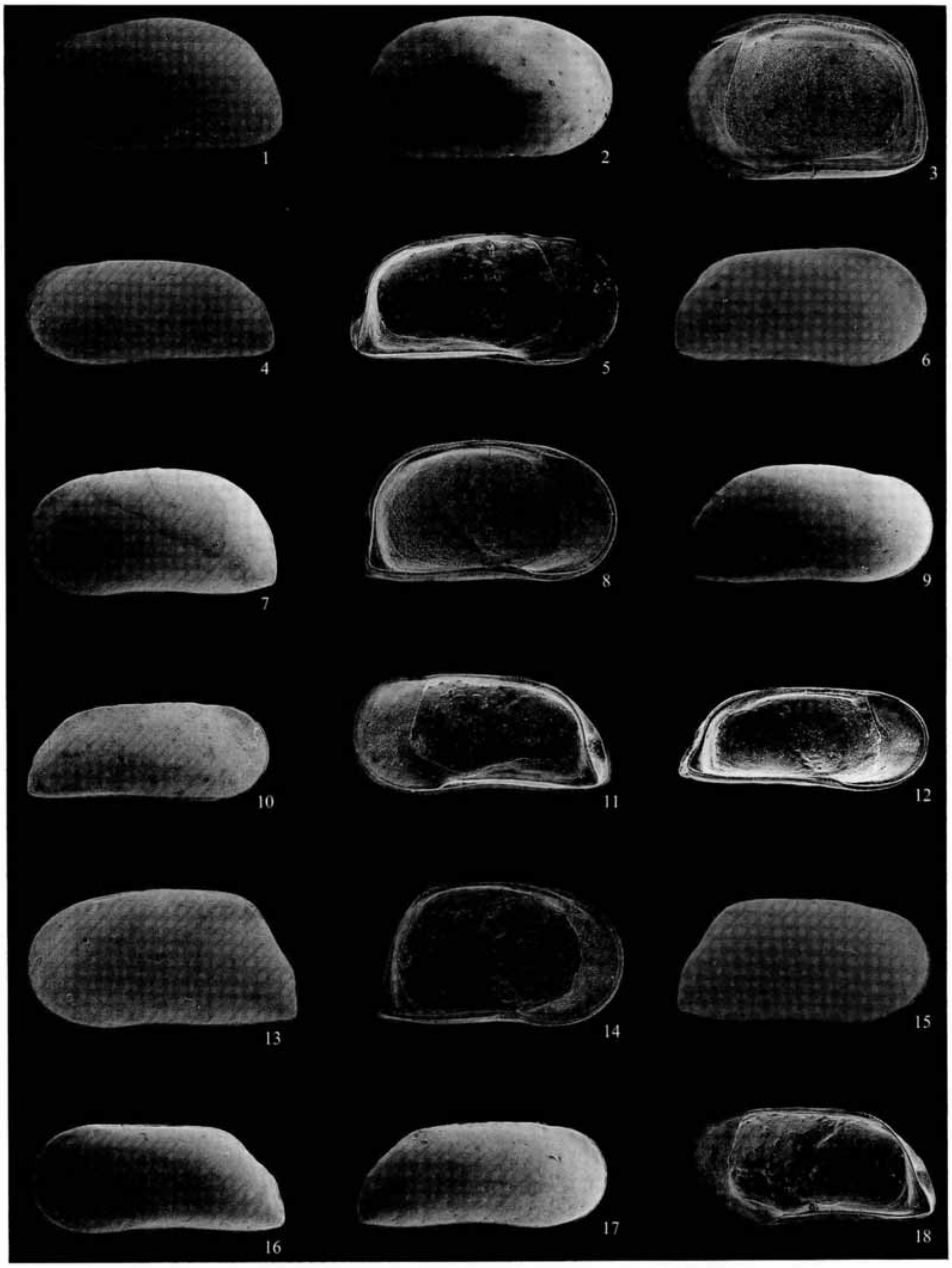
Figs 1–6. *Krithe reversa* (van den Bold). 1, GC/NA/39; DSDP Site 606A, c.c. 19; Early Pliocene; female left valve, external view; ×44. 2–3, GC/NA/188; DSDP Site 607, c.c. 16; Early Pliocene; female right valve, external and internal views; ×43. 4–5, GC/NA/117; DSDP Site 606A, c.c. 4; Quaternary; male left valve, external and internal views; ×37. 6, GC/NA/131; DSDP Site 606, c.c. 11; Late Pliocene; male right valve, external view; ×39.

Figs 7–12. *Krithe aequabilis* Ciampo. 7–8, GC/NA/190; DSDP Site 607, c.c. 18; Early Pliocene; female left valve, external and internal views; ×47. 9, GC/NA/191; DSDP Site 607, c.c. 18; Early Pliocene; female right valve, external view; ×48. 10–11, GC/NA/49; DSDP Site 606A, c.c. 15; Early Pliocene; male right valve, external and internal views; ×50. 12, GC/NA/172; DSDP Site 607, c.c. 10; Late Pliocene; male left valve, internal view; ×46.

Figs 13–18. *Krithe dolichodeira* van den Bold. 13–14, GC/NA/78; DSDP Site 606A, c.c. 13; Late Pliocene; female left valve, external and internal views; ×53. 15, GC/NA/65; DSDP Site 606A, c.c. 9; Late Pliocene; female right valve, external view; ×55. 16, GC/NA/16; DSDP Site 606A, c.c. 3; Quaternary; male left valve, external view; ×47. 17–18, GC/NA/45; DSDP Site 606A, c.c. 3; Quaternary; male right valve, external and internal views; ×47.

All figures are scanning electron micrographs.

PLATE 1



COLES *et al.*, *Krithe*

*Material and distribution.* One hundred and sixty eight adult valves. Hole 549A (M.–U. Eocene), Hole 549A (U. Eocene–U. Oligocene), Hole 558 (L. Oligocene–L. Miocene), Hole 563 (M.–U. Miocene), Hole 606 (Quaternary), Holes 606A and 607 (Pliocene), Hole 608 (Pliocene–Quaternary), Hole 609B (U. Pliocene–Quaternary), Holes 610 and 610C (Quaternary), Hole 610B (U. Pliocene).

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| FLV GC/NA/863 549A 34–1 U. Eocene | 0·66 | 0·31 |
| FLV GC/NA/864 549A 6–5 U. Oligocene | 0·63 | 0·30 |
| FLV GC/NA/865 549A 8–5 U. Oligocene | 0·71 | 0·34 |
| FLV GC/NA/876 549A 8–5 U. Oligocene | 0·62 | 0·29 |
| FLV GC/NA/190 607–18 L. Pliocene | 0·89 | 0·45 |
| FLV GC/NA/71 606A–9 U. Pliocene | 0·88 | 0·44 |
| FRV GC/NA/866 549 6–4 M. Eocene | 0·66 | 0·30 |
| FRV GC/NA/867 549A 6–5 U. Oligocene | 0·64 | 0·28 |
| FRV GC/NA/868 549A 15–1 L. Oligocene | 0·73 | 0·34 |
| FRV GC/NA/869 549A 9–5 U. Oligocene | 0·71 | 0·31 |
| FRV GC/NA/191 607–18 L. Pliocene | 0·87 | 0·42 |
| MLV GC/NA/870 549A 17–1 U. Eocene | 0·76 | 0·31 |
| MLV GC/NA/871 549A 6–5 U. Oligocene | 0·68 | 0·29 |
| MLV GC/NA/172 607–10 U. Pliocene | 0·92 | 0·39 |
| MRV GC/NA/872 549A 9–5 U. Oligocene | 0·78 | 0·30 |
| MRV GC/NA/873 549A 17–1 U. Eocene | 0·75 | 0·30 |
| MRV GC/NA/874 549A 11–5 L. Oligocene | 0·76 | 0·41 |
| MRV GC/NA/875 549A 6–5 U. Oligocene | 0·67 | 0·26 |
| MRV GC/NA/49 606A–15 L. Pliocene | 0·85 | 0·35 |

*Stratigraphical range.* Middle Eocene to Quaternary (NP 16–25; NN 3, 5, 9, 14–21).

*Diagnosis.* A medium to large, sexually dimorphic species of *Krithe*, with ADRPC type 2B. Moderately wide inner lamella with numerous RPC, eleven to twelve long ARPC, anterior vestibulum medium-sized with scalloped margin. Males relatively and absolutely longer than contemporaneous females.

*Remarks.* Ciampo (1986) described *K. aequabilis* from the late Miocene (Tortonian and Messinian) of Italy. This species, recorded under several MS names, is abundant and widespread in the world's oceans. It resembles *K. dolichodeira* van den Bold, 1946, but differs in the expansion of the inner lamella, producing a wider marginal zone. This results in a smaller anterior vestibulum with longer ARPC, and modifies the ADRPC pattern so that the NPC between AD 1 and AD 3 appears as a short AD 2.

Thus, *K. aequabilis* has ADRPC type 1A and *K. dolichodeira* has ADRPC type 2B. However, AD 2 may be absent in some specimens, which are assigned to *K. aequabilis* on the basis of their outline and anterior vestibule form. *K. aequabilis* generally has a more regularly curved posterior than *K. dolichodeira*, although intermediate specimens exist. *K. aequabilis* occurs as two size morphs in the Upper Eocene to Upper Oligocene of Site 549; the larger forms are 10–16% longer than the smaller forms in the same samples. However, the two forms are not treated as distinct subspecies as a near continuous series of intermediate specimens exist. *K. aequabilis* has been recorded from several localities detailed below, but the total distribution is probably under-represented as it may be included within *K. dolichodeira* by other authors. It is also recorded in MS only from the Middle Miocene to Quaternary of the SW Pacific (Smith 1983; Dainty 1984; Downing 1985; Ayress 1988) and Quaternary of the eastern Indian Ocean (Ayress 1988).

This species is also known from the Lower Oligocene of the Bay of Biscay (among the material of Ducasse and Peypouquet 1979, seen by GC), Messinian of Sicily (Ciampo 1980), late Quaternary of the Iberian Portal between PDWD 1200 and 3700 m (Harpur 1985), late Quaternary of the Northeastern Atlantic in cores L4, R3 and R4 between latitude 43° and 61° North and PDWD 2177 and 3422 m (among the material of Porter 1984 seen by GC), Pleistocene and Recent of the Iberian

Portal between PDWD 1285 and 2798 m (Elant 1985), Recent North Atlantic off Mauritania between 3856 and 4000 m (Barkham 1985), Upper Miocene of San Marino and Majorca and Quaternary of the Hebrides Terrace Seamount in the eastern North Atlantic at PDWD 1250 m (personal observations).

In summary, *K. aequabilis* is common in the Middle Eocene to Recent of the North Atlantic, although it is usually less abundant than *K. dolichodeira* and has a narrower depth range (1200 to 4000 m compared with 200 to 5440 m).

### *Krithe dolichodeira* van den Bold, 1946

Plate 1, figures 13–18; Text-figure 3L–Q

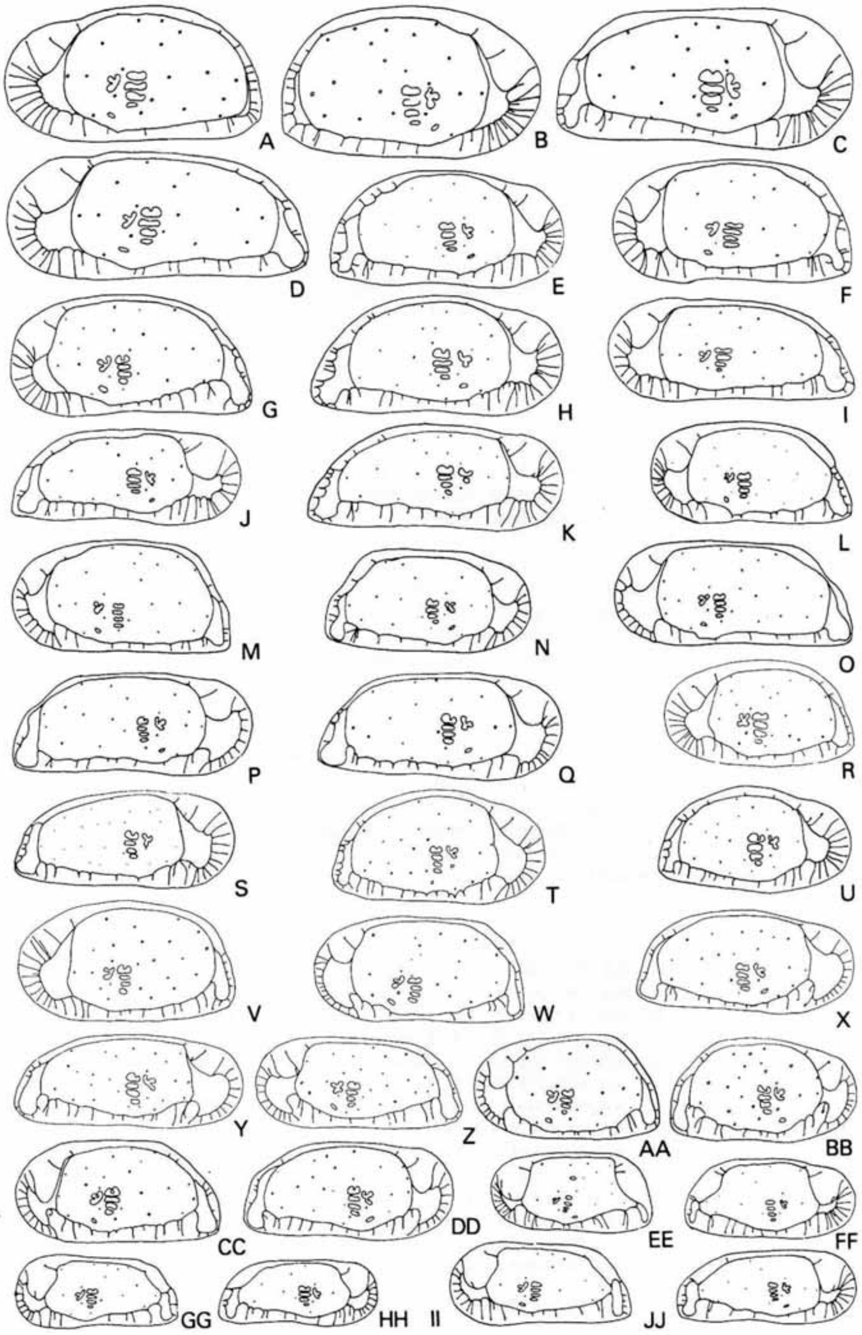
?1880 *Ilyobates compressa* Seguenza, p. 325, pl. 17, figs 30, 30*a* (male).
?1880 *Krithe producta* Brady [*pars*], p. 114, pl. 27, fig. *i* only (female).
1946 *Krithe dolichodeira* van den Bold, p. 75, pl. 4, fig. 14*a*–*b* (male).
1946 *Krithe praetexta* (Sars); van den Bold, p. 75, pl. 4, fig. 16*a*–*b* (female).
1964 *Krithe* cf. *bartonensis* (Jones); Dieci and Russo, p. 78, pl. 15, fig. 15*a*–*b* (female).
1964 *Krithe interrupta* Dieci and Russo, p. 92, pl. 2, fig. 5*a*–*b*; pl. 4, fig. 5*a*–*b* (males).
1964 *Krithe monosteracensis* (Seguenza); Ascoli, pl. 4, fig. 4 (female).
1967 *Krithe oertlii* Dieci and Russo, p. 15, pl. 3, figs 7–8 (male).
1967 *Krithe bartonensis* (Jones); Hulings, p. 644, fig. 5*a* (male).
1968 *Krithe dolichodeira* van den Bold; van den Bold, p. 51, pl. 2, figs 9*a*–*b*, 12*a*–*b*; pl. 10, *fig*. 4*a*–*d*.
1968 *Krithe dolichodeira* van den Bold; Russo, p. 37, pl. 6, figs 2*a*–*b*, 2*d*? (male).
1969 *Krithe producta* Brady; Yassini, p. 82, pl. 22, fig. 4*a* (male).
1972 *Krithe monosteracensis* (Seguenza); Sissingh, p. 84, pl. 4, fig. 7*a*–*b* (female).
1975 *Krithe monosteracensis* (Seguenza); Breman, p. 209, pl. 1, fig. 1*a* (male), 1*b* (female).
1976 *Krithe monosteracensis* (Seguenza); Breman, p. 54, pl. 3, fig. 29.
1977 *Krithe* sp. C Peypouquet [*pars*], p. 109, sp. C13fn, C22fn, C23fn, C24fn, C34en (all female).
1981 *Krithe dolichodeira* van den Bold; van den Bold, p. 66, pl. 1, fig. 12 (male).
1981 *Krithe vandenboldi* Steineck, p. 358, fig. 12, pl. 1, figs 1–4 (male).
1983 *Krithe* sp. C22 Peypouquet; Benson and Peypouquet, p. 818, pl. 5, fig. 2.
1984 *Krithe vandenboldi* Steineck; Steineck *et al.*, p. 1473, fig. 9*j*–*k* (males).
1990 *Krithe spatularis* Dingle *et al.*, p. 272, figs 16D–F, 17B, 18E (males).

*Material and distribution*. Three hundred and eighty adult valves. Hole 549 (L.–U. Eocene), Hole 549A (U. Eocene–U. Oligocene, U. Miocene), Hole 558 (L. Oligocene–U. Miocene), Hole 563 (M. Miocene–U. Miocene), Holes 606, 606A and 607 (Pliocene–Quaternary), Holes 608 and 608A (U. Pliocene–Quaternary), Holes 609 and 609B (L. Pliocene, Quaternary), Hole 610 (Miocene–Quaternary), Hole 610B (U. Pliocene), Hole 610C (Quaternary), Hole 611D (L. Pliocene).

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| FLV GC/NA/853 549 15–1 L. Eocene | 0·60 | 0·29 |
| FLV GC/NA/854 549A 16–1 L. Oligocene | 0·82 | 0·39 |
| FLV GC/NA/78 606A–13 U. Pliocene | 0·80 | 0·42 |
| FLV GC/NA/74 606A–6 Quaternary | 0·81 | 0·40 |
| FRV GC/NA/855 549 15–5 L. Eocene | 0·63 | 0·30 |
| FRV GC/NA/856 558 14–5 L. Miocene | 0·71 | 0·32 |
| FRV GC/NA/857 558 17–5 L. Miocene | 0·73 | 0·33 |
| FRV GC/NA/858 549 15–1 L. Eocene | 0·60 | 0·28 |
| FRV GC/NA/65 606A–9 U. Pliocene | 0·76 | 0·38 |
| MLV GC/NA/859 549 2–1 M. Eocene | 0·70 | 0·30 |
| MLV GC/NA/860 549 H3–3 U. Eocene | 0·71 | 0·33 |
| MLV GC/NA/861 563 10–1 M. Miocene | 0·70 | 0·30 |
| MLV GC/NA/16 606A–3 Quaternary | 0·89 | 0·39 |
| MRV GC/NA/862 549A 8–5 L. Oligocene | 0·71 | 0·30 |
| MRV GC/NA/45 606A–3 Quaternary | 0·89 | 0·38 |

*Stratigraphical range*. Eocene–Quaternary (NP 10–19, 21–25; NN 1–9, 11–21).



TEXT-FIG. 3. For legend see opposite.

*Diagnosis*. A medium to large species of *Krithe* with strongly pronounced sexual dimorphism. Males subrectangular and much longer than females, which are more subquadrate and slightly more inflated posteriorly. Both sexes with dorsal margin almost straight, parallel to ventral margin. Posterior truncate with posterior concavity, strongest in male, Inner lamella narrow, inner margin early parallel with outer margin. Large 'mushroom'-shaped anterior vestibule with wide opening, short neck, frequently extending towards the antero-dorsal corner of the inner margin. ADRPC type 2B; ten to eleven very short, regularly spaced ARPC in fan arrangement.

*Remarks*. This is an abundant, long-ranging species which shows some variation in size and anterior vestibulum shape. There is not a simple increase in size with time, as Upper Eocene and Quaternary specimens may be of similar size, and the largest specimens occur in the Lower Oligocene. Van den Bold (1946) described this species as *K. dolichodeira* from the Miocene of Cuba, but gave poor illustrations. Subsequent authors have, however, used the name *K. dolichodeira* for species clearly conspecific with the present material (e.g. Russo 1968). Other authors have identified this species as *K. monosteracensis* or *K. compressa*, both described by Seguenza (1880) from the Pliocene of Sicily. The present material is not conspecific with *K. monosteracensis* as figured by Seguenza, but is similar in shape to the figures of *K. compressa*. However, as Seguenza's types were destroyed in an earthquake, the identity of these species cannot be confirmed and, therefore, the name *K. compressa* is not used here. *K. dolichodeira* differs from *K. aequabilis* Ciampo, 1986, in the size and shape of the anterior vestibule, RPC pattern and inner lamella. *K. interrupta* Dieci and Russo, 1964, is included within *K. dolichodeira* since it seems to represent an extreme male variant of this species with a very caudate posterior, and also because intermediate specimens occur.

*Krithe producta* Brady 1880 should be considered a *nomen dubium*. The lectotype of Puri and Hulings (1976) is a juvenile valve of indeterminate species and the original illustrations of Brady (1880) embrace some five species, including those with both normal and reversed overlap.

---

TEXT-FIG. 3. A–D. *K. reversa* (van den Bold). A, GC/NA/39; DSDP Site 606A, c.c. 19; Early Pliocene; female left valve. B, GC/NA/188; DSDP Site 607, c.c. 16; Early Pliocene; female right valve. C, GC/NA/131; DSDP Site 606, c.c. 11; Late Pliocene; male right valve. D, GC/NA/117; DSDP Site 606A, c.c. 4; Quaternary; male left valve. E–K. *K. aequabilis* Ciampo. E, GC/NA/191; DSDP Site 607, c.c. 18; Early Pliocene; female right valve. F, GC/NA/190; DSDP Site 607, c.c. 18; Early Pliocene; female left valve. G, GC/NA/865; DSDP Site 549A, c.c. 8–5; late Oligocene; female left valve. H, GC/NA/868; DSDP Site 549A, c.c. 15–1; early Oligocene; female right valve. I, GC/NA/172; DSDP Site 607, c.c. 10; Late Pliocene; male left valve. J, GC/NA/49; DSDP Site 606A, c.c. 15; Early Pliocene; male right valve. K, GC/NA/873; DSDP Site 549A, 17–1; late Eocene; male right valve. L–Q. *K. dolichodeira* van den Bold. L, GC/NA/853; DSDP Site 549, cc. 15–1; early Eocene; female left valve. M, GC/NA/78; DSDP Site 606A, c.c. 13; Early Pliocene; female left valve. N, GC/NA/65; DSDP Site 606A, c.c. 9; Late Pliocene; female right valve. O, GC/NA/16; DSDP Site 606A, c.c. 3; Quaternary; male left valve. P, GC/NA/45; DSDP Site 606A, c.c. 3; Quaternary; male right valve. Q, GC/NA/862; DSDP Site 549A, c.c. 8–5; late Oligocene; male right valve. R–V. *K. gobanensis* sp. nov. R, OS 14015; DSDP Site 548, c.c. 7–4; middle Eocene; female left valve. S, OS 14022, DSDP Site 549A, c.c. 27–1; late Eocene; male right valve. T, OS 14020; DSDP Site 548, c.c. 7–1; middle Eocene; female right valve. U, OS 14021, DSDP Site 549A, c.c. 11–2; early Oligocene; female right valve. V, OS 14016; DSDP Site 548A, c.c. 11–2; early Oligocene; female left valve. W–Z. *K. regulare* sp. nov. W, OS 14002; DSDP Site 548A, c.c. 8–5; late Oligocene; female left valve. X, OS 14010; DSDP Site 549A, c.c. 8–5; late Oligocene; female right valve. Y, OS 14012; DSDP Site 549, c.c. 8–5; late Oligocene; male right valve. Z, OS 14006; DSDP Site 549, c.c. H3–2; late Eocene; male left valve. AA–DD. *Krithe* sp. cf. *K. hiwanneensis* Howe and Law. AA, GC/NA/878; DSDP Site 549A, c.c. 8–5; late Oligocene; female left valve. BB, GC/NA/882; DSDP Site 549A, c.c. 8–5; late Oligocene; female right valve. CC, GC/NA/880; DSDP Site 549A, c.c. 17–1; late Eocene; male left valve. DD, GC/NA/885; DSDP Site 549A, c.c. 8–5; late Oligocene; male right valve. EE–JJ. *K. minima* sp. nov. EE, OS 13954; DSDP Site 606A, c.c. 14; Early Pliocene; female left valve. FF, OS 13955; DSDP Site 606A, c.c. 14; Early Pliocene; female right valve. GG, OS 13958; DSDP Site 606A, c.c. 17; Early Pliocene; male left valve. HH, OS 13959; DSDP Site 606A, c.c. 17; Early Pliocene; male right valve. II, OS 13956; DSDP Site 606A, c.c. 5; Quaternary; male left valve. JJ, OS 13957; DSDP Site 606, c.c. 9; Late Pliocene; male right valve. All projectina drawings; × 50.

This species is extremely abundant and widespread from the Eocene to the Recent in the Atlantic, Caribbean and Mediterranean. It is tolerant of a wide depth range, extending from the outer shelf at 200 m to the calcium compensation depth (CCD, maximum recorded depth of species 5440 m), with most records from bathyal and abyssal depths. The following occurrences are noted: Eocene of DSDP Sites 612 and 613 off New Jersey (material of Cronin and Compton-Gooding 1987; seen by GC), Middle Miocene to Pliocene deep water sediments throughout the Caribbean (van den Bold 1977, 1981), Oligocene of Barbados (Steineck *et al.* 1984), Miocene and Pliocene of the Central Equatorial Pacific (Steineck *et al.* 1988), Miocene of Jamaica (Steineck 1981), Middle Miocene to Quaternary of the Rio Grande Rise, South Atlantic (Benson and Peypouquet 1983), Upper Miocene of Italy (Dieci and Russo 1964, 1967; Russo 1968), Pliocene of Crete (Sissingh 1972), Pleistocene of the Western Mediterranean and Iberian Portal region between PDWD 795 and 2798 m (Elant 1985), late Quaternary of the Iberian Portal region between PDWD 1200 and 3700 m (Harpur 1985) and the late Quaternary of the eastern North Atlantic in cores L4, L5, O1, O2, P2, R2, R3, R4, R5 and S3 between latitude 43° and 64°N and PDWD 938 and 4556 m (among the material of Porter 1984 seen by GC).

Occurrences in Recent sediments comprise the Gulf of Mexico between 200 m and 800 m (van den Bold 1981) and 1500 m (personal observations), throughout the North Atlantic between 210 and 5440 m (personal observations; Peypouquet 1977; Davies 1981; Barkham 1985), slope off Florida between 579 and 739 m (among the material of Cronin 1983 seen by GC). Bay of Biscay between 200 and 3900 m (Yassini 1969), Adriatic between 243 and 1200 m (Breman 1975, 1976) and the western Mediterranean and Iberian Portal area from 585 and 2798 m (Elant 1985). Dingle *et al.* (1990) describe this species as *K. spatularis* from the Recent off southwestern Africa between water depths of 392 and 1662 m.

### *Krithe gobanensis* sp. nov.

Plate 2, figures 1–3; Text-figure 3R–V

*Derivation of name.* From the only known occurrence of this species on the Goban Spur.

*Holotype.* Female left valve, OS 14015.

*Type locality and horizon.* DSDP Site 549, Hole 549, Goban Spur, lat. 49° 05·28′ N; long. 13° 05·88′ W; PDWD 2513 m. Core 7, section 4, interval 0·88–0·95 m. Middle Eocene, NP 15. Pale greenish-white nannofossil ooze.

---

EXPLANATION OF PLATE 2

Figs 1–3. *Krithe gobanensis* sp. nov. 1–2, OS 14018; DSDP Site 549A, c.c. 11–2; early Oligocene; female left valve, external and internal views; ×65. 3, OS 14019; DSDP Site S49A, c.c. 11–2; early Oligocene; female right valve, external view; ×65.

Figs 4–9. *Krithe regularae* sp. nov. 4–5, OS 14004; DSDP Site 549A, c.c. 2–5; late Oligocene; female left valve, external and internal views; ×68. 6, OS 14008; DSDP Site 549A, c.c. 8–5; late Oligocene; female right valve, external view; ×68. 6, OS 14008; DSDP Site 549A, c.c. 8–5; late Oligocene; female right valve, external, view; ×66. 7, OS 14007; DSDP Site 549A, c.c. 8–5; late Oligocene; male left valve, external view; ×68. 8–9, OS 140011; DSDP Site 549A, c.c. 8–5; late Oligocene; male right valve, external and internal views; ×66.

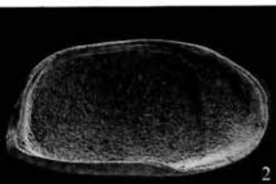
Figs 10–15. *Krithe* sp. cf. *K. hiwanneensis* Howe and Law. 10, GC/NA/878; DSDP Site 549A, c.c. 8–5; late Oligocene; female left valve, external view; ×78. 11–12, GC/NA/882; DSDP Site 549A, c.c. 8–5; late Oligocene; female right valve, external and internal views; ×75. 13–14, GC/NA/881; DSDP Site 549A, c.c. 8–5; late Oligocene; male left valve, external and internal views; ×70. 15, GC/NA/885; DSDP Site 549A, c.c. 8–5; late Oligocene; male right valve, external view; ×68.

Figs 16–18. *Krithe minima* sp. nov. 16, OS 13962; DSDP Site 606A, c.c. 7; Late Pliocene; female left valve, external view; ×66. 17–18, OS 13961; DSDP Site 606A, c.c. 5; Quaternary; female right valve, external and internal views; ×66.

All figures are scanning electron micrographs.

PLATE 2

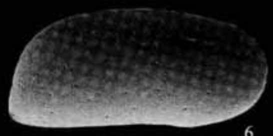

1


2

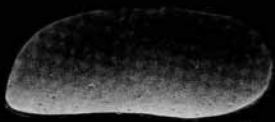

3

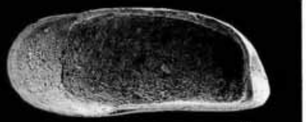

4


5


6


7


8


9


10


11


12


13


14


15


16


17


18

COLES *et al.*, *Krithe*

*Material and distribution.* Ninety eight adult valves. Hole 549 (?U. Palaeocene, M.–U. Eocene), Hole 549A (U. Eocene–U. Oligocene).

| *Dimensions (mm).* | L | H |
|---|---|---|
| Holotype FLV OS 14015 549 7–4 M. Eocene | 0·56 | 0·30 |
| Paratype FLV OS 14016 549A 11–2 L. Oligocene | 0·64 | 0·35 |
| Paratype FLV OS 14017 549 19–3 U. Palaeocene | 0·57 | 0·32 |
| Paratype FLV OS 14018 549A 11–2 L. Oligocene | 0·64 | 0·34 |
| Paratype FRV OS 14019 549A 11–2 L. Oligocene | 0·64 | 0·32 |
| Paratype FRV OS 14020 549 7–1 M. Eocene | 0·57 | 0·30 |
| Paratype FRV OS 14021 549A 11–2 L. Oligocene | 0·62 | 0·32 |
| Paratype MRV OS 14022 549A 27–1 U. Eocene | 0·66 | 0·28 |

*Stratigraphical range.* ?Upper Palaeocene, Middle Eocene to Upper Oligocene (NP 7?, 15–23).

*Diagnosis.* A medium, subovate to elongate-subovate species of *Krithe* with a narrow inner lamella and a larger anterior vestibulum which has a wide opening and is only slightly expanded distally. ADRPC type 2B.

*Description.* Medium, subovate to elongate-subovate and moderately inflated. FLV dorsum slightly convex, broadly rounded anterior, posterior bluntly truncate with steep postero-dorsal slope, ventral margin almost straight. FRV as FLV but dorsum more convex with shallow antero-dorsal concavity. Males as females but much more elongate with straighter dorsum. Normal LV > RV overlap. NPC small and widely scattered. Inner lamella narrow, with simple line of concrescence. Anterior vestibulum large and 'pocket'-shaped with wide opening and very slightly expanded distally. ADRPC type 2B, although a few specimens appear to have type 1A. Eleven simple ARPC in fan arrangement with a few short false canals. Hinge adont. Frontal scar may be quadrifoil.

*Remarks.* This is a common species from the Middle Eocene to the base of the Upper Oligocene of Site 549 to which it is apparently confined, with a single poorly preserved valve occurring in the Upper Palaeocene. Almost all specimens are female; only three male valves were found. It resembles *K. regulare* sp. nov., but that species is more elongate with an almost straight dorsum and a more distally expanded anterior vestibulum.

### *Krithe regulare* sp. nov.

Plate 2, figures 4–9; Text-figure 3w–z

*Derivation of name.* Latin, with reference to the regular, subrectangular outline of this species.

*Holotype.* Female left valve, OS 14002.

*Material and distribution.* One hundred and ninety three adult valves. Hole 549 (L.–U. Eocene), Hole 549A (U. Eocene–U. Oligocene), Hole 558 (L. Oligocene).

*Type locality and horizon.* DSDP Site 549, Hole 549A, Goban Spur, lat. 49° 05·28′ N; long. 13° 05·88′ W, PDWD 2513 m. Core 8, section 5, interval 0·80–0·87 m. Upper Oligocene, NP 24. Creamy white nannofossil ooze.

| *Dimensions (mm).* | L | H |
|---|---|---|
| Holotype FLV OS 14002 549A 8–5 U. Oligocene | 0·62 | 0·30 |
| Paratype FLV OS 14003 549 10–1 L. Eocene | 0·64 | 0·30 |
| Paratype FLV OS 14004 549A 8–5 U. Oligocene | 0·62 | 0·31 |
| Paratype MLV OS 14005 549A 8–5 U. Oligocene | 0·62 | 0·28 |
| Paratype MLV OS 14006 549 H3–2 U. Eocene | 0·61 | 0·27 |
| Paratype MLV OS 14007 549A 8–5 U. Oligocene | 0·62 | 0·28 |
| Paratype FRV OS 14008 549A 8–5 U. Oligocene | 0·64 | 0·29 |

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| Paratype FRV OS 14009 549A 13–2 L. Oligocene | 0·65 | 0·31 |
| Paratype FRV OS 14010 549A 8–5 U. Oligocene | 0·64 | 0·29 |
| Paratype MRV OS 14011 549A 8–5 L. Oligocene | 0·64 | 0·26 |
| Paratype MRV OS 14012 549 5–1 M. Eocene | 0·67 | 0·27 |
| Paratype MRV OS 14013 549A 8–5 L. Oligocene | 0·63 | 0·25 |
| Paratype MRV OS 14014 549A 9–5 L. Oligocene | 0·60 | 0·25 |

*Stratigraphical range*. Lower Eocene to Upper Oligocene (NP 13–25).

*Diagnosis*. A medium, slightly sexually dimorphic, elongate-subrectangular species of *Krithe* with almost parallel, straight dorsal and ventral margins. Posterior bluntly truncate with slight posterior angle. Inner lamella narrow, anterior vestibulum large and 'mushroom'-shaped. ADRPC type 2B.

*Description*. Medium, elongate-subrectangular and slightly inflated carapace. FLV dorsum very slightly convex, broadly rounded anterior, posterior bluntly truncate with steep postero-dorsal slope and no posterior angle; ventral margin almost straight. FRV as FLV but dorsum slightly more convex. Male as female but more elongate and with straighter dorsum. Normal valve overlap. Inner lamella narrow, line of concrescence simple or with slight indentations at the base of the RPC. Anterior vestibulum large and 'mushroom'-shaped with wide opening and expanded distally with rounded margin. ADRPC type 2B. A few specimens have a very short additional ADRPC arising from the base of AD 2. Twelve to fourteen quite short ARPC in fan arrangement, very few false ARPC. Ventral RPC short and well-spaced. Posterior vestibulum large with very short PRPC. Muscle scars relatively small; frontal scar may be subdivided.

*Remarks*. This species is common in the Middle Eocone to Upper Oligocene of Site 549, with two specimens present in the upper Lower Eocene sample 549 10–1. It is most similar to *K. gobanensis* and might be considered to be the male of that species. However, the two species differ in the shape of their anterior vestibula, males and females can be consistently distinguished in *K. regulare* and a few males of *K. gobanensis* are known. The two species also differ in stratigraphical range; *K. regulare* is common in the Upper Oligocene samples 549A 9–5 to 549A 6–5 where *K. gobanensis* is absent. *K. regulare* resembles *K. dolichodeira* in vestibular form and ADRPC pattern, but differs in shape, having a more rounded posterior and much less marked sexual dimorphism.

### *Krithe* sp. cf. *K. hiwanneensis* Howe and Law, 1936

Plate 2, figures 10–15; Text-figure 3AA–DD

?1936 *Krithe hiwanneensis* Howe and Law, p. 72, pl. 5, figs 32–4.

*Material and distribution*. Two hundred and sixteen adult valves. Hole 549 (L.–U. Eocene), Hole 549A (U. Eocene–U. Oligocene), Hole 558 (L. Oligocene–L. Miocene), Hole 563 (M. Miocene).

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| FLV GC/NA/877 549 2–4 M. Eocene | 0·57 | 0·33 |
| FLV GC/NA/878 549A 8–5 U. Oligocene | 0·54 | 0·30 |
| FLV GC/NA/879 558 24–3 U. Oligocene | 0·71 | 0·41 |
| MLV GC/NA/880 549A 17–1 U. Eocene | 0·59 | 0·29 |
| MLV GC/NA/881 549A 8–5 U. Oligocene | 0·60 | 0·29 |
| FRV GC/NA/882 549A 8–5 U. Oligocene | 0·56 | 0·29 |
| FRV GC/NA/883 558 18–5 L. Miocene | 0·54 | 0·28 |
| MRV GC/NA/884 563 10–1 M. Miocene | 0·60 | 0·28 |
| MRV GC/NA/885 549A 8–5 U. Oligocene | 0·62 | 0·28 |
| MRV GC/NA/886 549 13–1 L. Eocene | 0·58 | 0·28 |

*Stratigraphical range*. Lower Eocene to Middle Miocene (NP 11–25; NN 1, 5).

*Diagnosis*. A medium (one FLV is large), subrectangular species of *Krithe* with almost straight, subparallel dorsal and ventral margins. Posterior bluntly truncate with shallow postero-dorsal concavity and almost vertical postero-ventral slope. Inner lamella narrow, subparallel to outer margin. Anterior vestibulum large, 'mushroom'-shaped with narrow neck and may extend up the antero-dorsal inner margin. Eleven to thirteen ARPC short and evenly spaced, ADRPC type 2B. Sexually dimorphic; males relatively and absolutely longer than contemporaneous females.

*Remarks*. This species is common from the Middle Eocene to Upper Oligocene of Site 549, but rare elsewhere, particularly in the Miocene. One late Oligocene female specimen (GC/NA/879) is much larger than typical specimens but is otherwise identical; it may represent a post-maturation moult. The present specimens are very similar to the diagrammatic figures of *K. hiwanneensis* Howe and Law, 1936, from the Oligocene of the North American Gulf Coast. However, they are only compared to *K. hiwanneensis* as the length of the syntype was given as 0·70 mm, longer than all but one of the present specimens, and because specimens of *K. hiwanneensis* illustrated by other authors do not appear to be conspecific. *K.* sp. cf. *K. hiwanneensis* is similar to, and may have evolved from, *K. dolichodeira* in the early Eocene. However, in any given sample, the present species is smaller than *K. dolichodeira*, has a more bluntly truncate posterior, and a more constricted vestibular neck.

## ADRPC TYPE 2C

### *Krithe minima* sp. nov.

Plate 2, figures 16–18; Plate 3, figures 1–5; Text-figure 3EE–JJ

?1977 *Krithe* sp. C11 fn Peypouquet, p. 109, fig. 36 [*pars*].

*Derivation of name*. Latin, with reference to the small size of this species.

*Holotype*. Female left valve, OS 13954.

*Type locality and horizon*. DSDP Site 606, Hole 606A, middle North Atlantic, southwest of the Azores, lat. 37° 20·29′ N; long. 35° 30·02′ W. Core catcher 14, Lower Pliocene, NN 15. White nannofossil ooze.

*Material and distribution*. One hundred and three adult valves. Hole 558 (U. Miocene), Hole 563 (M.–U. Miocene), Holes 606 and 606A (Pliocene–Quaternary), Hole 607 (U. Miocene–Quaternary), Hole 608 (U. Miocene–Pliocene), Holes 608A and 610 (U. Pliocene–Quaternary), Holes 609B and 610C (Quaternary), Hole 611D (L. Pliocene, Quaternary).

---

EXPLANATION OF PLATE 3

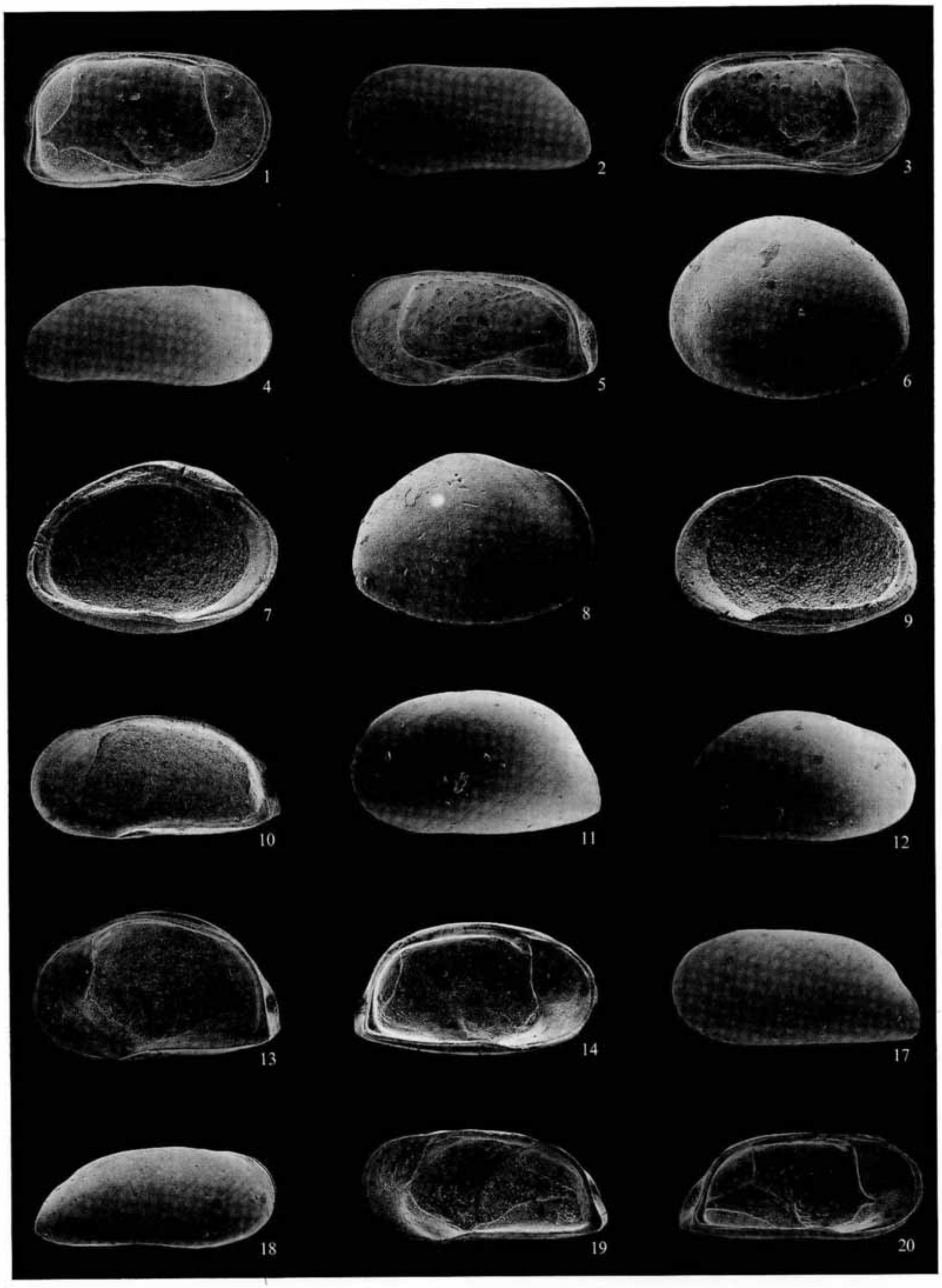
Figs 1–5. *Krithe minima* sp. nov. 1, OS 13962; DSDP Site 606A, c.c. 7; Late Pliocene; female left valve, internal view; × 66. 2–3, OS 13956; DSDP Site 606A, c.c. 5; Quaternary; male left valve, external and internal views; × 65. 4–5, OS 13957; DSDP Site 606, c.c. 9; Late Pliocene; male right valve, external and internal views; × 63.

Figs 6–10. *Krithe crassicaudata* van den Bold. 6–7, GC/NA/958; DSDP Site 549A, c.c. 39–2; late Eocene; juvenile left valve, external and internal views; × 64. 8–9, GC/NA/959; DSDP Site 549A, c.c. 39–2; late Eocene; juvenile right valve, external and internal views; × 68. 10, GC/NA/956; DSDP Site 549A, c.c. 13–2; early Oligocene; male right valve, internal view; × 53.

Figs 11–18. *Krithe morkhoveni morkhoveni* van den Bold. 11, GC/NA/108; DSDP Site 606A, c.c. 14; Early Pliocene; female left valve, external view; × 43. 12–13, GC/NA/114; DSDP Site 606, c.c. 15; Early Pliocene; female right valve, external and internal views; × 46. 14, GC/NA/121; DSDP Site 606A, c.c. 17; Early Pliocene; female left valve, internal view; × 46. 15, GC/NA/118; DSDP Site 606A, c.c. 14; Early Pliocene; male left valve, external view; × 40. 16–17, GC/NA/44; DSDP Site 606A, c.c. 14; Early Pliocene; male right valve, external and internal views; × 46. 18, GC/NA/102; DSDP Site 606A, c.c. 14; Early Pliocene; male left valve, internal view; × 45.

All figures are scanning electron micrographs.

PLATE 3



COLES *et al.*, *Krithe*

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| Holotype FLV OS 13954 606A–14 L. Pliocene | 0·60 | 0·30 |
| Paratype FLV OS 13955 563 10–1 M. Miocene | 0·60 | 0·28 |
| Paratype FLV OS 13956 606A–7 U. Pliocene | 0·64 | 0·31 |
| Paratype MLV OS 13957 606A–5 Quaternary | 0·65 | 0·31 |
| Paratype MLV OS 13958 606A–17 L. Pliocene | 0·60 | 0·28 |
| Paratype FRV OS 13959 606A–14 L. Pliocene | 0·59 | 0·28 |
| Paratype FRV OS 13960 606A–5 Quaternary | 0·64 | 0·30 |
| Paratype MRV OS 13961 606–9 U. Pliocene | 0·67 | 0·28 |
| Paratype MRV OS 13962 606A–17 L. Pliocene | 0·59 | 0·25 |

*Stratigraphical range*. Middle Miocene–Quaternary (NN 5, 9, 11–12, 14–21).

*Diagnosis*. A small, elongate, sexually dimorphic species of *Krithe* with a small, subcrescentic anterior vestibulum and ADRPC type 2C.

*Description*. Small, elongate subrectangular and moderately inflated. Sexually dimorphic; females relatively shorter than males, with a slightly convex, rather than a straight dorsum. Anterior margin broadly rounded, ventral margin with slight oral incurvature, posterior truncate with shallow posterior concavity and steep postero-ventral slope. Thin-shelled, LV slightly overlaps RV. Inner lamella narrow; line of concrescence slightly sinuous and subparallel with outer margin. NPC small and closely spaced. Anterior vestibulum small, subcrescentic, upswept with narrow opening. Eleven short, straight ARPC in fan arrangement. ADRPC type 2C; posterior vestibulum relatively large, with up to five PRPC. Hinge pseudodont, RV hinge bar finely denticulate at posterior end. Central muscle scars small, consisting of a slightly arcuate row of four adductors with topmost scar dorsally indented and trefoil frontal scar.

*Remarks*. *K. minima* is rare in the Middle and Upper Miocene, but is more common in the Pliocene and Quaternary, although it is never a dominant species. It is recorded (mainly in manuscript) from the North Atlantic; the failure of other authors to note it may be due to its small size and inclusion with juvenile specimens of other, larger species. It occurs in the Lower Pliocene of DSDP Site 406 on the Rockall Plateau (among the material of Ducasse and Peypouquet 1979 seen by GC); late Quaternary of the Northeastern Atlantic between latitudes 43° and 68° N and PDWD between 1678 and 4566 m in cores L4, L5, N3, P2, R2, R3, R4, R5, S3, T2 and T3 (among the material of Porter 1984 seen by the authors); late Quaternary of the Iberian Portal between PDWD 1200 and 3700 m (Harpur 1985); Quaternary of the western Mediterranean and Gulf of Cadiz between PDWD 900 and 2798 m (among the material of Elant 1985 seen by GC); Recent Atlantic off Florida at 739 and 472 m among the material of Cronin 1983 seen by GC), the Upper Miocene of San Marino and the Quaternary of the Hebrides Terrace Seamount at 1250 m (personal observations). The single Pacific record is that of Smith (1983) from the late Quaternary of the Challenger Plateau at a PDWD of 1066 m.

*K.* sp. C11 fn of Peypouquet (1977) appears to be the male of *K. minima*, although the length range quoted (0·32–0·38 mm) is much smaller than any known *Krithe* species and is probably an error. In summary, *K. minima* is widespread in the Upper Miocene to Recent of the North Atlantic between 28° and 68° N, with most specimens recorded between 1000 and 3000 m. It is also present in the Quaternary of the Mediterranean at bathyal depths. It is apparently unrecorded from the Caribbean region, although this may be due to its relatively small size which renders it easily overlooked among the juveniles of other species of the genus.

## ADRPC TYPE 3A

(Group *K. trinidadensis* van den Bold, 1958)

*Discussion*. *K. trinidadensis* was described by van den Bold (1958) from Oligocene to Middle Miocene deep water sediments of Trinidad. It is regarded as the typical form of a large group of deep-water *Krithe* species, which are cosmopolitan in distribution but which are especially well documented from the Caribbean, North Atlantic and southern Europe. The species and subspecies of the *K. trinidadensis* group vary greatly in size, the observed length range being 0·50–1·22 mm. There is also considerable variation in length:height ratio, RPC and anterior vestibulum. However, the species and subspecies of the *K. trinidadensis* group are united in sharing the following morphological characteristics:

1. General shape and outline, particularly the convex dorsum, which is strongly influenced by pronounced sexual dimorphism.
2. Marked sexual dimorphism; males are relatively and absolutely more elongate than females in contemporaneous populations, are less inflated posteriorly, have a less strongly convex dorsum, and a more tapered posterior.
3. Wide inner lamella, with a sinuous line of concrescence and curved VRPC.
4. ADRPC type 3A, with AD 1–3 short, AD 4 elongate, AD 5 very short or absent.
5. Normal overlap of valves (LV > RV).

In any sample or suite of samples of a particular age and locality, the species of this group can be clearly identified. However, these distinctions frequently break down when specimens from a wide temporal and spatial range are considered, due to such phenomena as phylogenetic size variation, size increase with depth and other ecological factors. The species and subspecies which are considered to belong to the *K. trinidadensis* group are listed below. Some species are questionably included, usually due to poor preservation or lack of reliable illustrations of the internal features given by the original or subsequent authors. Some species among the list will be shown later to be junior synonyms e.g. *K. rex*, Dingle *et al.*, 1990. Valid species or subspecies are marked with an asterisk *. Frequently a species is based on only male, female or even juvenile specimens; this is indicated in brackets in each case.

?*K. angusta* Deltel, 1964 (M), **K. aquilona* sp. nov. (M, F), **K. morkhoveni morkhoveni* van den Bold, 1946 (M, F), **K. morkhoveni lamellata* ssp. nov., **K. morkhoveni ayressi* ssp. nov. (M, F), *K. cancuenensis* van den Bold, 1946 (M), *K. cancuenensis ambigua* Pokorny, 1980 (M), *K. citae* Oertli, 1961 (M), ?*K. contracta* Oertli, 1961 (M), **K. crassicaudata* van den Bold, 1946 (M, F), *K. kollmanni* Pokorny, 1980 (M), *K. langhiana* Oertli, 1961 (F), *K. luyensis* Deltel, 1964 (F), ?*K. peypouqueti* Dingle *et al.*, 1990 (juv), **K praemorkhoveni* sp. nov. (M, F), *K. elongata* van den Bold, 1960 (M) (= *K. prolixa* van den Bold, 1966), *K. rex* Dingle *et al.*, 1990 (M, F), **K. trinidadensis* van den Bold, 1958 (M, F), *K. undecemradiata* Ruggieri, 1977 (F), *K.* sp. D Peypouquet, 1977 (F), *K.* sp. E Peypouquet, 1977 (F).

### *Krithe crassicaudata* van den Bold, 1946

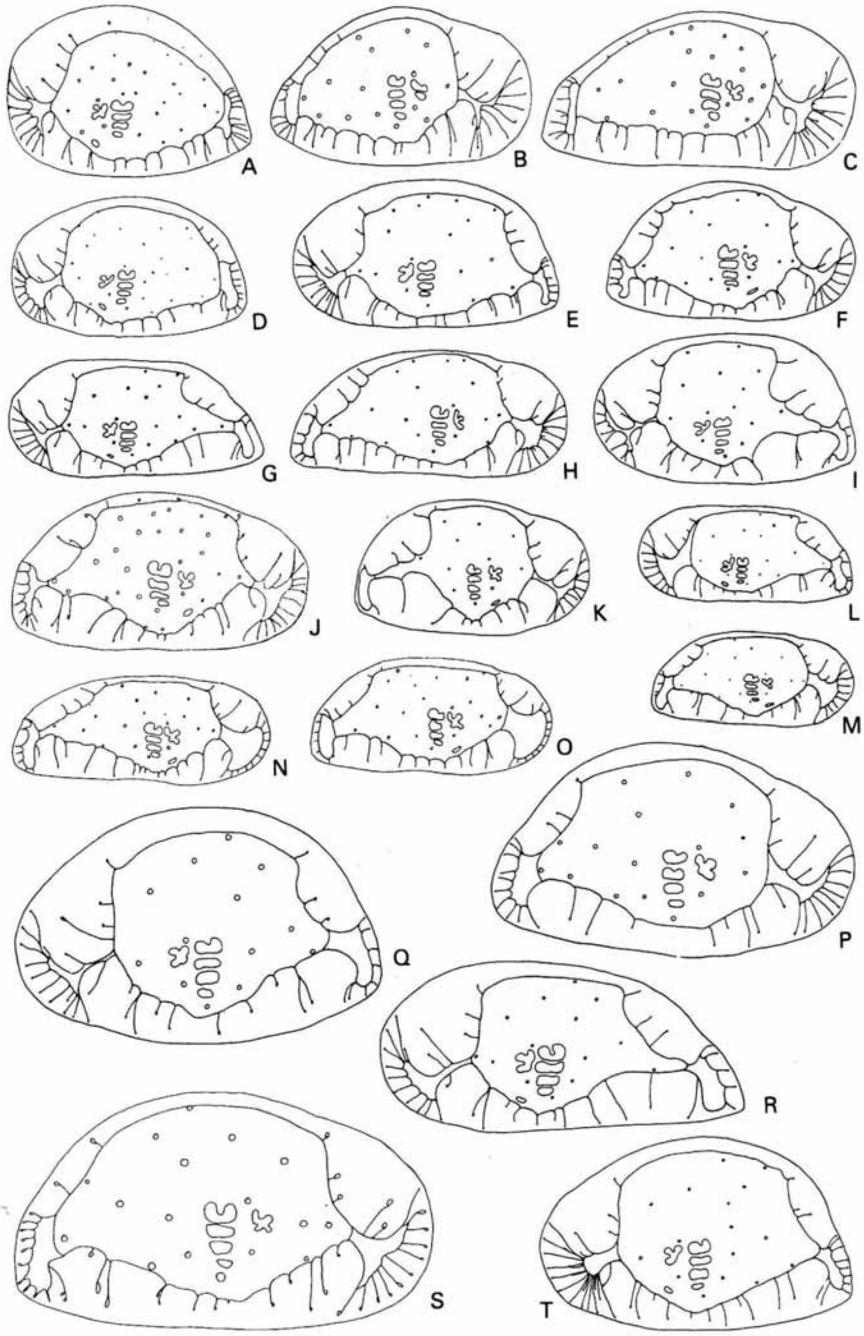
Plate 3, figures 6–10; Text-figure 4A–C

1946 *Krithe crassicaudata* van den Bold, p. 78, pl. 7, fig. 2*a–f*.
1946 *Cytheridea* (?*Dolocytheridea*) *guanjayensis* van den Bold, p. 83, pl. 7, fig. 10*a–d*.
1960 *Krithe crassicaudata* van den Bold; van den Bold, p. 158, pl. 3, fig. 7*a–d*.
1969 *Messinella guanajayensis* (van den Bold); van den Bold, p. 396, pl. 1, fig. 1*a–c*.
?1969 *Messinella jamaicensis* van den Bold, p. 400, pl. 1, figs 1*a–d*, 3*a–b*, 5*a–b*.
1981 *Messinella guanajayensis* (van den Bold); van den Bold, p. 70, pl. 1, fig. 9.
1984 *Messinella guanajayensis* (van den Bold); Steineck *et al.*, p. 1472, fig. 8L.
?1985 *Krithe* sp. 7 Coles, p. 89, pl. 5, figs 23–24; pl. 19, fig. 7.
1987 *Messinella jamaicensis* van den Bold; Whatley and Coles, p. 88, pl. 2, figs 1–2.
1987 *Krithe* sp. Cronin and Compton-Gooding, pl. 6, figs 4, 7.

*Material and distribution*. Forty nine adults and more than 250 juveniles. Hole 549 (M. Eocene), Hole 549A (U. Eocene–L. Oligocene), Hole 558 (L. Oligocene–L. Miocene).

*Dimensions (mm).*

| | L | H |
|---|---|---|
| FLV GC/NA/951 549A 16–2 L. Oligocene | 0·75 | 0·50 |
| FLV GC/NA/952 549A 16–2 L. Oligocene | 0·71 | 0·46 |
| MLV GC/NA/953 549A 13–2 L. Oligocene | 0·80 | 0·44 |
| FRV GC/NA/954 549A 18–1 U. Eocene | 0·76 | 0·45 |
| FRV GC/NA/955 549A 39–2 U. Eocene | 0·77 | 0·46 |



TEXT-FIG. 4. For legend see opposite.

| *Dimensions (mm).* | L | H |
|---|---|---|
| MRV GC/NA/956 549A 13–2 L. Oligocene | 0·80 | 0·44 |
| MRV GC/NA/957 549A 39–2 U. Eocene | 0·91 | 0·45 |
| JLV GC/NA/958 549A 39–2 U. Eocene | 0·66 | 0·46 |
| JRV GC/NA/959 549A 39–2 U. Eocene | 0·62 | 0·40 |

*Stratigraphical range.* Middle Eocene to Lower Miocene (NP 18, 20–23; NN 1, ?2).

*Diagnosis.* A large, thick-shelled *Krithe* species of the *K. trinidadensis* group with a pointed postero-ventral corner. Female subovate, male elongate-subovate, dimorphism not strongly pronounced. Inner lamella wide ventrally with very sinuous line of concrescence, but narrow postero-dorsally. Anterior vestibulum small, 'T' to 'Y'-shaped with indented distal margin; ADRPC long with prominent false ARPC. AD 4 elongate but occasionally short DA 5 short or absent. Posterior margin bluntly truncate with acute indentation. RV hinge bar posteriorly denticulate.

*Remarks.* This species is fairly common in the Upper Eocene to Lower Oligocene of Hole 549A but is rare in Hole 558. The two adult valves from the Lower Miocene of Hole 558 are conspecific with *Krithe* sp. 7 of Coles (1985) from the Upper Miocene and Lower Pliocene of the North Atlantic. These specimens are very similar in shape to *K. crassicaudata* and may be conspecific although they have a narrower inner lamella and branching ARPC.

The original illustrations of this species are very poor but the authors have confirmed the identity of their North Atlantic specimens by examining the type material. This species has been recorded from the Middle Eocene to Oligocene of Barbados (Steineck *et al.* 1984), Middle and Upper Eocene of deep-water deposits in the Caribbean (van den Bold 1960, 1977), Middle Eocene of the NW Atlantic off New Jersey (Cronin and Compton-Gooding 1987) and the Lower Miocene of Jamaica (Steineck 1981).

*K. crassicaudata* probably evolved from *K. praemorkhoveni* in the late Middle Eocene (NP 18), although there is a short gap between the ranges of the two species in Hole 549. *K. crassicaudata* is larger and more angular in outline than *K. praemorkhoveni*, and has a sharper postero-ventral corner. *K. crassicaudata* is thicker-shelled than *K. morkhoveni morkhoveni*, and has a sharper postero-ventral corner and deeper posterior indentation. Both sexes are less elongate than *K. morkhoveni morkhoveni* and sexual dimorphism is less marked. The juveniles of *K. crassicaudata* can be identified by their thick-shell, subovate shape, and in, the last two instar stages, small anterior and posterior hinge teeth. These juveniles were described as a new genus, *Messinella*, by van den Bold (1969). Although van den Bold recognized that his new genus had 'some affinity to the Krithinae' due to the small numbers of false RPC, he considered that the hinge was 'different from anything reported in this subfamily'. From the present material, it is clear that *Messinella* represents

TEXT-FIG. 4. A–C. *K. crassicaudata* van den Bold. A, GC/NA/951; DSDP Site 549A, c.c. 16–2; early Oligocene; female left valve. B, GC/NA/955; DSDP Site 549A, c.c. 39–2; late Eocene; female right valve. C, GC/NA/957; DSDP Site 549A, c.c. 39–2; late Eocene; male right valve. D–H. *K. morkhoveni morkhoveni* van den Bold. D, GC/NA/965; DSDP Site 549A, c.c. 8–5; late Oligocene; female left valve. E, GC/NA/108; DSDP Site 606A, c.c. 14; Early Pliocene; female left valve. F, GC/NA/114; DSDP Site 606A, c.c. 15; Early Pliocene; female right valve. G, GC/NA/102; DSDP Site 606A, c.c. 14; Early Pliocene; male left valve. H, GC/NA/51; DSDP Site 606A, c.c. 14; Early Pliocene; male right valve. I–K. *K. morkhoveni lamellalata* subsp. nov. I, OS 13976; DSDP Site 608, c.c. 15; Quaternary; female left valve. J, OS 13980; DSDP Site 607, c.c. 17; Early Pliocene; female right valve. K, OS 13981; DSDP Site 549A, c.c. 9–5; late Oligocene; female right valve. L–O. *K. morkhoveni ayressi* subsp. nov. L, OS 13963; DSDP Site 606, c.c. 9; Late Pliocene; male left valve. M, OS 13974; DSDP Site 606A, c.c. 6; Quaternary; male right valve. N, OS 13972; DSDP Site 558, c.c. 14–1; Early Miocene; male right valve. O, OS 13986; DSDP Site 558, c.c. 13–5; Middle Miocene; female right valve. P–T. *K. trinidadensis* van den Bold. P, GC/NA/128; DSDP Site 606A, c.c. 13; Late Pliocene; female right valve. Q, GC/NA/127; DSDP Site 606A, c.c. 7; Late Pliocene; female left valve. R, GC/NA/126; DSDP Site 606A, c.c. 14; Early Pliocene; male left valve. S, GC/NA/981; DSDP Site 549A, c.c. 9–5; late Oligocene; female right valve. T, GC/NA/256; DSDP Site 608A, c.c. 13; Early Pliocene; female left valve. All projectina drawings; × 50.

the juveniles of *K. crassicaudata* due to their consistent co-occurrence. The adults resemble the juveniles in shape and in shell thickness, but have a more angular postero-ventral margin. Only the posterior of the RV hinge bar is denticulate; the median hinge denticles of the juveniles are lost in subsequent ontogeny.

We are certain that *M. guanajayensis* from the Oligocene of Cuba and *M. jamaicensis* from the Upper Miocene to Pleistocene of Jamaica are juveniles of *K. crassicaudata*. Although we have not seen Plio-Pleistocene material of *Messinella*, we suspect that this will also prove to be juvenile specimens of *Krithe*. In the light of this, we regard *Messinella* as a junior synonym of *Krithe*.

The youngest confirmed records of *K. crassicaudata* are from the Lower Pliocene (NN 15) of DSDP Sites 609 and 611 from the North Atlantic, recorded as the juveniles of *Krithe* sp. 7 of Coles (1985). Other records of *K. crassicaudata* reported as *Messinella* are as follows: Middle Miocene to Lower Pliocene of the North Atlantic (Whatley and Coles 1987), Middle Miocene to Pliocene of the Caribbean (van den Bold 1977), Lower to Middle Miocene of Jamaica (Steineck 1981) (all as *M. jamaicensis*), and the Upper Eocene to Lower Miocene of the Caribbean (van den Bold 1977), Lower Miocene of Jamaica (Steineck 1981), Middle Eocene to Oligocene of Barbados (Steineck *et al.* 1984), Lower Miocene of Haiti (van den Bold 1981) and Lower Oligocene of the Equatorial Pacific (Steineck *et al.* 1988) (all as *M. guanajayensis*).

### *Krithe morkhoveni morkhoveni* van den Bold, 1960

Plate 3, figures 11–18; Text-figure 4D–H

1958 *Krithe* aff. *K. producta* Brady; van den Bold, p. 18, pl. 2, figs *a*, *c–d* (females).
1960 *Krithe morkhoveni* van den Bold, p. 160, pl. 3, fig. 6 (female).
1960 *Krithe elongata* van den Bold, p. 159, pl. 3, fig. 5*a–c* (males) [junior homonym of *K. elongata* Jones and Kirkby, 1898].
1961 *Krithe langhiana* Oertli, p. 24, pl. 3, figs 24–30 (females).
1961 *Krithe citae* Oertli, p. 25, pl. 3, figs 21–32 only (males).
1961 *Krithe contracta* Oertli; p. 26, pl. 3, figs 35–38 (juveniles).
1964 *Krithe luyensis* Deltel, p. 171, pl. 4, figs 83–85 (females).
1964 *Krithe compressa dertonensis* Ruggieri; Dieci and Russo, p. 79, pl. 15, fig. 7 (male).
1964 *Krithe* cf. *contracta* Oertli; Dieci and Russo, p. 79, pl. 15, fig. 8 (female).
1964 *Xestoleberis subtruncata* Dieci and Russo, p. 85, pl. 2, fig. 13*a–b*; pl. 16, fig. 7 (females).
1966 *Krithe prolixa* van den Bold, p. 180 (males) [new name for *K. elongata*, van den Bold *non* Jones].
1967 *Krithe* aff. *morkhoveni* van den Bold; Ascoli, p. 54, pl. 1, figs 4–6 (females).
1968 *Krithe* aff. *morkhoveni* van den Bold; Russo, p. 39, pl. 6, figs 4*a*, *d* (female); pl. 8, fig. 6; pl. 9, figs 1*a*, *c* (males).
1968 *Krithe trinidadensis* van den Bold; van den Bold, pl. 2, figs 10*a–b* (male), 10*c–d* (female).
1972 *Krithe langhiana* Oertli; Sissingh, p. 171, pl. 4, figs 6*a–b* (female).
1974 *Krithe* aff. *K. bartonensis* (Jones); Leroy and Levinson, p. 24, pl. 11, fig. 4?; pl. 12, fig. 5 (males).
1974 *Krithe undecemradiata* Ruggieri, p. 176, figs 6, 3*a–b* (male); 4*a–b* (female).
1977 *Krithe* sp. D 11fn Peypouquet, p. 113, fig. 37 [*pars*] (female).
1977 *Krithe* sp. D 12fn Peypouquet, p. 113, fig. 37 [*pars*] (female).
1977 *Krithe* sp. D22 Peypouquet, p. 113, fig. 37 [*pars*] (female).
1980 *Krithe cancuensis ambigua* Pokorny, p. 342, figs 8–10; pl. 2, figs 2–3 (males).
1980 *Krithe kollmanni* Pokorny, p. 338, figs 1–3; pl 1, figs 1–3; pl. 2, fig. 1 (females).
1981 *Krithe prolixa* van den Bold; Steineck, p. 359; pl. 1, fig. 13 (males).
1981 *Krithe* sp. 6 Ciampo, p. 67, pl. 6, fig. 3 (female).
1981 *Krithe* sp. 8 Ciampo, p. 67, pl. 6, fig. 4 (female).
1981 *Krithe* sp. 5 Ciampo, p. 67, pl. 6, fig. 7 (male).
1984 *Krithe morkhoveni* van den Bold; Steineck *et al.*, p. 1473, figs *e*, *i* (females).
1984 *Krithe prolixa* van den Bold; Steineck *et al.*, fig. *j* (males).
1985 *Krithe luyensis* Deltel; Ducasse *et al.*, p. 285, pl. 78, figs 11–13 (females).

*Material and distribution*. Three hundred and fifty adult valves. Hole 549 (U. Palaeocene–U. Eocene), Hole 549A (U. Eocene–U. Oligocene, U. Miocene), Hole 558 (L. Oligocene–U. Miocene), Hole 563 (M.–U.

Miocene), Holes 606, 606A, 610 (Pliocene–Quaternary), Holes 607, 608 (U. Miocene–Quaternary), Holes 609B (U. Pliocene–Quaternary), Holes 609, 609C (U. Pliocene), Hole 610E (U. Miocene–L. Pliocene), Hole 611D (Pliocene).

*Dimensions (mm).*

| | L | H |
|---|---|---|
| FLV GC/NA/963 549 H3–2 U. Eocene | 0·83 | 0·47 |
| FLV GC/NA/964 549A 8–5 U. Oligocene | 0·78 | 0·43 |
| FLV GC/NA/965 549A 8–5 U. Oligocene | 0·70 | 0·40 |
| FLV GC/NA/108 606A–14 L. Pliocene | 0·98 | 0·58 |
| FLV GC/NA/121 606A–17 L. Pliocene | 0·91 | 0·54 |
| MLV GC/NA/966 549 15–5 L. Eocene | 0·82 | 0·38 |
| MLV GC/NA/967 549A 8–5 U. Oligocene | 0·87 | 0·43 |
| MLV GC/NA/118 606A–14 L. Pliocene | 1·04 | 0·40 |
| MLV GC/NA/138 606–5 Quaternary | 0·98 | 0·47 |
| MLV GC/NA/102 606A–14 L. Pliocene | 0·94 | 0·44 |
| FRV GC/NA/968 549A 8–5 U. Oligocene | 0·76 | 0·49 |
| FRV GC/NA/969 549 H3–2 U. Eocene | 0·84 | 0·45 |
| FRV GC/NA/970 549A 8–5 U. Oligocene | 0·67 | 0·37 |
| FRV GC/NA/114 606A–15 L. Pliocene | 0·91 | 0·51 |
| MRV GC/NA 971 549A8–5 U. Oligocene | 0·88 | 0·39 |
| MRV GC/NA/51 606A–14 L. Pliocene | 1·03 | 0·40 |
| MRV GC/NA/44 606A–14 L. Pliocene | 0·91 | 0·40 |

*Stratigraphical range.* Upper Palaeocene to Recent.

*Diagnosis.* A medium (females only) to large (females and males), subovate (females) to elongate subrectangular (males) subspecies of *Krithe*. Dorsum convex, most strongly so in females. Greatest height at mid-length (females) or anterior of mid-length (males). Inner lamella moderately wide with sinuous line of concrescence. Anterior vestibulum small, 'mushroom'-shaped. ADRPC type 3A.

*Remarks.* This is an abundant subspecies in the Lower Eocene to Quaternary of the North Atlantic. One specimen from the Upper Palaeocene of Hole 549 is thicker-shelled than the Eocene to Miocene specimens, and may be a post-maturation moult of *K. praemorkhoveni*. There is a considerable degree of variation within this subspecies, as shown by the specimens figured in this study. This variation is expressed in the following features.

1. Size. In this study the length range of this species is 0·67 to 0·87 mm (23 per cent range).
2. Shape. Some variation in the L:H ratio, valve inflation and outline occurs, particularly in the angle of the postero-dorsal slope.
3. Inner lamella. This varies in width, particularly in the posterior region. A few specimens approach the form of *K. morkhoveni lamellalata* subsp. nov.
4. ADRPC pattern. The length and position of the ADRPC is variable; in particular AD 1–3 may be very short where the inner lamella is narrow, AD 4 may arise from the vestibular neck or from the antero-dorsal fused zone and AD 5 may be very short or apparently absent.

*K. morkhoveni morkhoveni* is thought to have evolved from *K. praemorkhoveni*, probably in the early Eocene, by becoming larger, thinner-shelled, and developing a wide inner lamella. *K. trinidadensis* evolved from *K. morkhoveni morkhoveni* in the Middle Eocene of the Atlantic in the area of Hole 549, while the subspecies *K. morkhoveni ayressi* evolved from the nominate subspecies in the Lower Oligocene (see below).

*K. morkhoveni morkhoveni* is a widespread deep-water subspecies, recorded by numerous authors under a variety of names and there have been many errors of identification such as its record as *K. compressa dertonensis* Ruggieri by Dieci and Russo (1964) and as *K. bartonensis* (Jones) by Leroy and Levinson (1974); in both cases the material differed widely from the species to which they were assigned.

In addition to the North Atlantic occurrences cited above, the following are noted: Eocene and Oligocene of Aquitaine (Deltel 1964; Ducasse *et al.* 1985), Eocene and Oligocene of the Bay of Biscay and Eocene of the Rockall Plateau (among the material of Ducasse and Peypouquet 1979 seen by GC), Oligocene of Sicily (Ciampo 1981), Upper Eocene and Lower Oligocene of the Angola Abyssal Plain in the South Atlantic and Upper Eocene of Denmark (GC personal observations), Middle and Upper Miocene of northern Italy (Oertli 1961; Dieci and Russo 1964, 1967; Ascoli 1968), Upper Miocene of Crete (Sissingh 1972), Upper Eocene to Pliocene of the Caribbean region (van den Bold 1977, 1981), Pleistocene of Bologna, Italy (Ruggieri 1974), Pleistocene of the Gulf of Mexico (Leroy and Levinson 1974), Pleistocene of the Iberian Portal at 2798 m (Elant 1985) and at 2421 and 3700 m (Harpur 1985), Pleistocene of the North Atlantic in cores L4, L5, N3, P2, R2, R3, R4, R5, S3 and T3 between 1678 and 4566 m PDWD and lat. 43° to 68° N (among the material of Porter 1984 seen by GC) and Quaternary of the southwestern Pacific (Ayress 1988).

In the Recent this species occurs in the Atlantic off Florida between 739 and 1029 m (among the material of Cronin seen by GC), west of the Iberian Portal at 2798 m (Elant 1985) and in the North Atlantic between 1775 to 5440 m (material of Barkham 1985 and personal observations). It is most abundant below 2000 m and appears to be absent from the present day Mediterranean; indicating that this subspecies is a reliable indicator of deep oceanic waters for post-Eocene time.

### *Krithe morkhoveni lamellalata* subsp. nov.

Plate 4, figures 1–3; Text-figure 4I–K

*Derivation of name.* Latin, with reference to the wide calcified inner lamella of this subspecies.

*Holotype.* Female left valve, OS 13976.

*Type locality and horizon.* DSDP Site 608, Hole 608, mid-North Atlantic, King's Trough, northeast of the Azores. Lat. 42° 0·21′ N; long. 23° 05·25′ W. PDWD 3526 m. Core catcher 5, Quaternary, NN 19. Nannofossil ooze.

*Material and distribution.* One hundred and nineteen adult valves. Hole 549A (U. Eocene–U. Oligocene, U. Miocene), Hole 558 (U. Oligocene, M. Miocene), Hole 607 (L. Pliocene), Hole 608 (U. Miocene–Quaternary), Hole 609 (U. Pliocene), Holes 609B, 610C (Quaternary), Hole 610 (U. Miocene–L. Pliocene), Hole 610D (U. Miocene), Holes 610E, 611D (U. Pliocene).

---

EXPLANATION OF PLATE 4

Figs 1–3. *Krithe morkhoveni lamellalata* subsp. nov. 1, OS 13978; DSDP Site 610E, c.c. 6; Late Miocene; female right valve, external view; × 50. 2–3, OS 13976; DSDP Site 608, c.c. 5; Quaternary; female left valve, external and internal views; × 44.

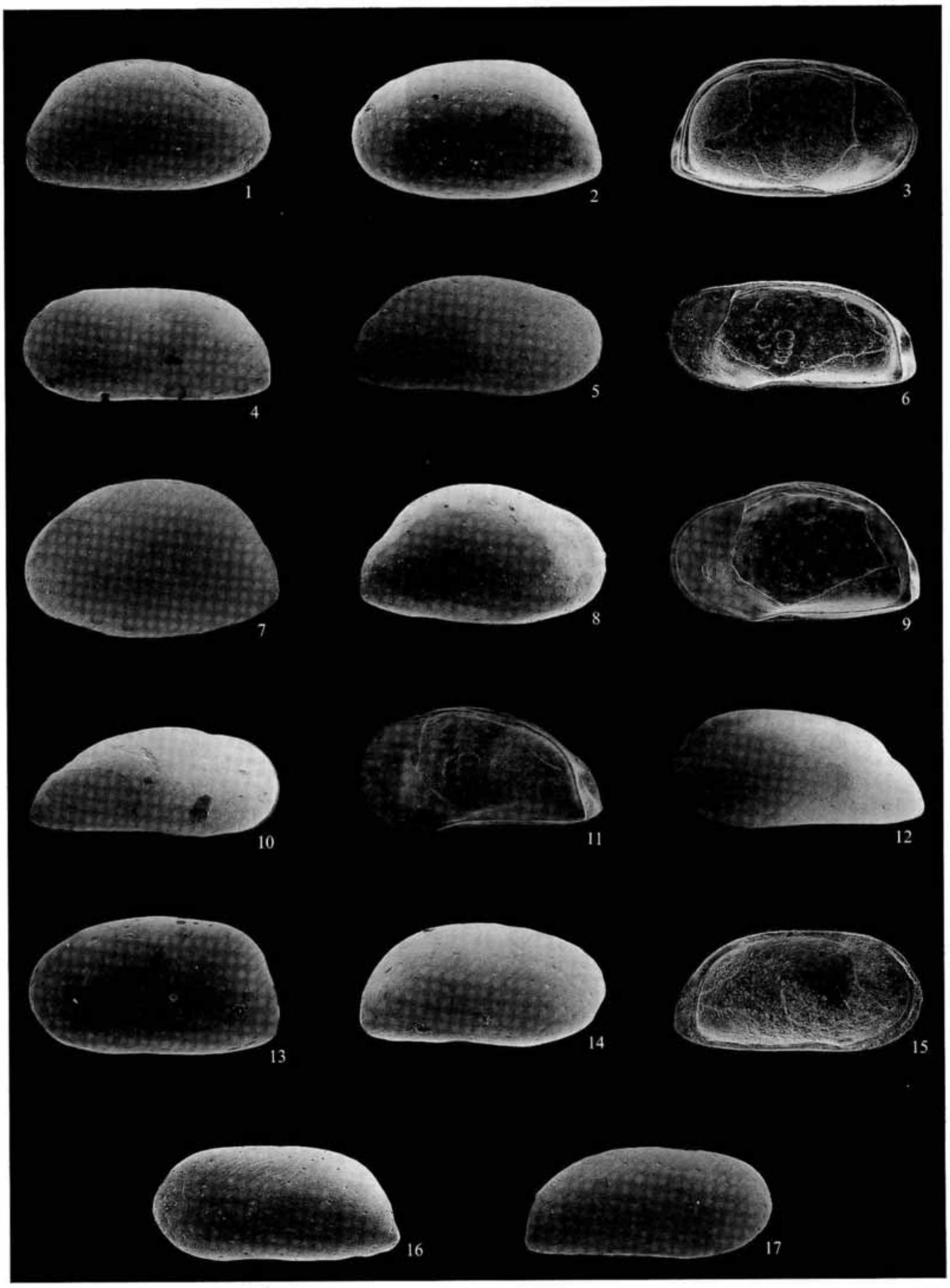
Figs 4–6. *Krithe morkhoveni ayressi* subsp. nov. 4, OS 13963; DSDP Site 606, c.c. 9; Late Pliocene; male left valve, external view; × 53. 5, OS 13969; DSDP Site 558, c.c. 24–3; late Oligocene; female right valve, external view; × 60. 6, OS 13973; DSDP Site 608, c.c. 5; Quaternary; male left valve, internal view; × 50.

Figs 7–12. *Krithe trinidadensis* van den Bold. 7, GC/NA/127; DSDP Site 606A, c.c. 7; Late Pliocene; female left valve, external view; × 31. 8–9, GC/NA/128; DSDP Site 606A, c.c. 13; Late Pliocene; female right valve, external and internal views; × 31. 10–11, GC/NA/124; DSDP Site 606A, c.c. 14; Early Pliocene; male right valve, external and internal views; × 33. 12, GC/NA/126; DSDP Site 606A, c.c. 14; Early Pliocene; male left valve, external view; × 31.

Figs 13–17. *Krithe aquilonia* sp. nov. 13–15, OS 13996; DSDP Site 610, c.c. 5; Quaternary; female left valve, external and internal views; × 66. 16, OS 13999; DSDP Site 610E, c.c. 3; Late Miocene; male left valve, external view; × 62. 17, OS 14000; DSDP Site 608, c.c. 11; Late Pliocene; male right valve, external view; × 62.

All figures are scanning electron micrographs.

PLATE 4



COLES *et al.*, *Krithe*

| *Dimensions* (*mm*). | L | H |
|---|---|---|
| Holotype FLV OS 13976 608–5 Quaternary | 0·97 | 0·56 |
| Paratype FLV OS 13977 608–7 U. Pliocene | 0·90 | 0·53 |
| Paratype FLV OS 13979 610E–5 U. Miocene | 0·96 | 0·50 |
| Paratype FRV OS 13981 549A 9–5 U. Oligocene | 0·88 | 0·46 |
| Paratype FRV OS 13980 607–17 L. Pliocene | 0·87 | 0·50 |
| Paratype FRV OS 13978 610–4 Quaternary | 0·93 | 0·50 |
| Paratype MLV OS 13982 549A 5–5 U. Miocene | 0·94 | 0·47 |
| Paratype MRV OS 13983 549A 5–5 U. Miocene | 0·92 | 0·43 |

*Stratigraphical range*. Upper Eocene to Upper Oligocene, Middle Miocene to Quaternary (NP 20–5; NN 5, 9, 11–13, 15–19). The subspecies probably also occurs in the Recent of the North Atlantic.

*Diagnosis*. A large, strongly inflated subspecies of *Krithe* expressing moderate sexual dimorphism. Outline very similar to that of *K. morkhoveni morkhoveni* but rather more elongate-subovate. Inner lamella very wide, much wider than in *K. morkhoveni morkhoveni*, especially so posteriorly, with a highly sinuous line of concrescence, deeply depressed below adductors. Anterior vestibulum small, elongate 'mushroom' to 'Y'-shaped, with very narrow opening, long narrow neck and branching distally. Other features as for *K. morkhoveni morkhoveni*.

*Remarks*. *K. morkhoveni lamellalata* differs from the nominative subspecies in its much wider inner lamella, more sinuous line of concrescence and more elongate-subovate outline. In the present material, *K. morkhoveni lamellalata* is common only in the Oligocene and Upper Miocene of Hole 549A. It also occurs in the Pleistocene of the North Atlantic in core L4 at 3422 m and lat. 43° N (among the material of Porter 1984 seen by GC) and west of the Iberian Portal at 2421 m (along the material of Harpur 1985 seen by GC).

### *Krithe morkhoveni ayressi* subsp. nov.

Plate 4, figures 4–6; Text-figure 4L–O

*Derivation of name*. Named for Dr Michael Ayress, in recognition of his work on *Krithe* and other deep-sea Ostracoda from the Indo-Pacific.

*Holotype*. Male left valve OS 13963.

*Type locality and horizon*. DSDP Site 606, Hole 606, mid-North Atlantic, S.W. of the Azores. Lat. 37° 20·32′ N, long. 35° 29·99′ W. PDWD 3007 m. Core catcher 9, Upper Pliocene, NN 18. Nannofossil ooze.

*Material and distribution*. One hundred and thirty six adult valves. Hole 558 (L. Oligocene–U. Miocene), Holes 606, 606A (U. Pliocene–Quaternary), Hole 608 (U. Miocene, U. Pliocene–Quaternary, Hole 607 (Pliocene–Quaternary), Holes 610E, 611D (L. Pliocene), Holes 609A, 609B, 610 (Quaternary).

| *Dimensions* (*mm*). | L | H |
|---|---|---|
| Holotype MLV OS 13963 606–9 U. Pliocene | 0·79 | 0·36 |
| Paratype FLV OS 13964 558 10–1 M. Miocene | 0·72 | 0·39 |
| Paratype FLV OS 13965 558 14–5 L. Miocene | 0·74 | 0·36 |
| Paratype FLV OS 13966 588 22–1 U. Oligocene | 0·75 | 0·39 |
| Paratype MLV OS 13973 608–5 Quaternary | 0·84 | 0·40 |
| Paratype FRV OS 13967 558 16–1 L. Miocene | 0·71 | 0·36 |
| Paratype FRV OS 13968 558 13–5 M. Miocene | 0·71 | 0·33 |
| Paratype FRV OS 13969 558 24–3 U. Oligocene | 0·70 | 0·34 |
| Paratype MRV OS 13970 558 24–3 U. Oligocene | 0·81 | 0·33 |
| Paratype MRV OS 13971 558 25–5 U. Oligocene | 0·84 | 0·31 |
| Paratype MRV OS 13972 558 14–1 L. Miocene | 0·76 | 0·31 |

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| Paratype MRV OS 13974 606A–6 Quaternary | 0·75 | 0·35 |
| Paratype MRV OS 13976 607–18 L. Pliocene | 0·79 | 0·35 |

*Stratigraphical range*. Lower Oligocene to Quaternary (NP 21?, 22–25; NN 2, 5, 8?, 11–12, 15–21) in the present study. The species is extant.

*Diagnosis*. A medium to large, subrectangular, elongate subspecies of *Krithe* with slight sexual dimorphism. Straight (male) to slightly convex (female) dorsal margin; posterior bluntly truncate with very steep postero-ventral slope. Inner lamella moderately wide; anterior vestibulum large, 'mushroom'-shaped. RV with secondary accommodation groove.

*Remarks*. This taxon is considered to be a subspecies of *K. morkhoveni* because of its close morphological similarity to the nominative subspecies. However, *K. morkhoveni ayressi* is smaller than *K. morkhoveni morkhoveni* and is more elongate with a less tapered posterior in the males. Sexual dimorphism is less marked than in *K. morkhoveni morkhoveni*; the females of *K. morkhoveni ayressi* are elongate-subovate, and are relatively lower and less inflated. In other features such as ADRPC pattern and inner lamella, the two subspecies are indistinguishable.

In the present material, *K. morkhoveni ayressi* is only common in the Oligocene of Hole 558, but occurs persistently if rarely in the Miocene to Quaternary of the North Atlantic. It probably evolved from *K. morkhoveni morkhoveni* in the Lower Oligocene. This subspecies has also been found in the Recent of the Gulf of Mexico at a depth of 1500 m (personal observations), although these specimens have a smaller anterior vestibulum.

### *Krithe trinidadensis* van den Bold, 1958

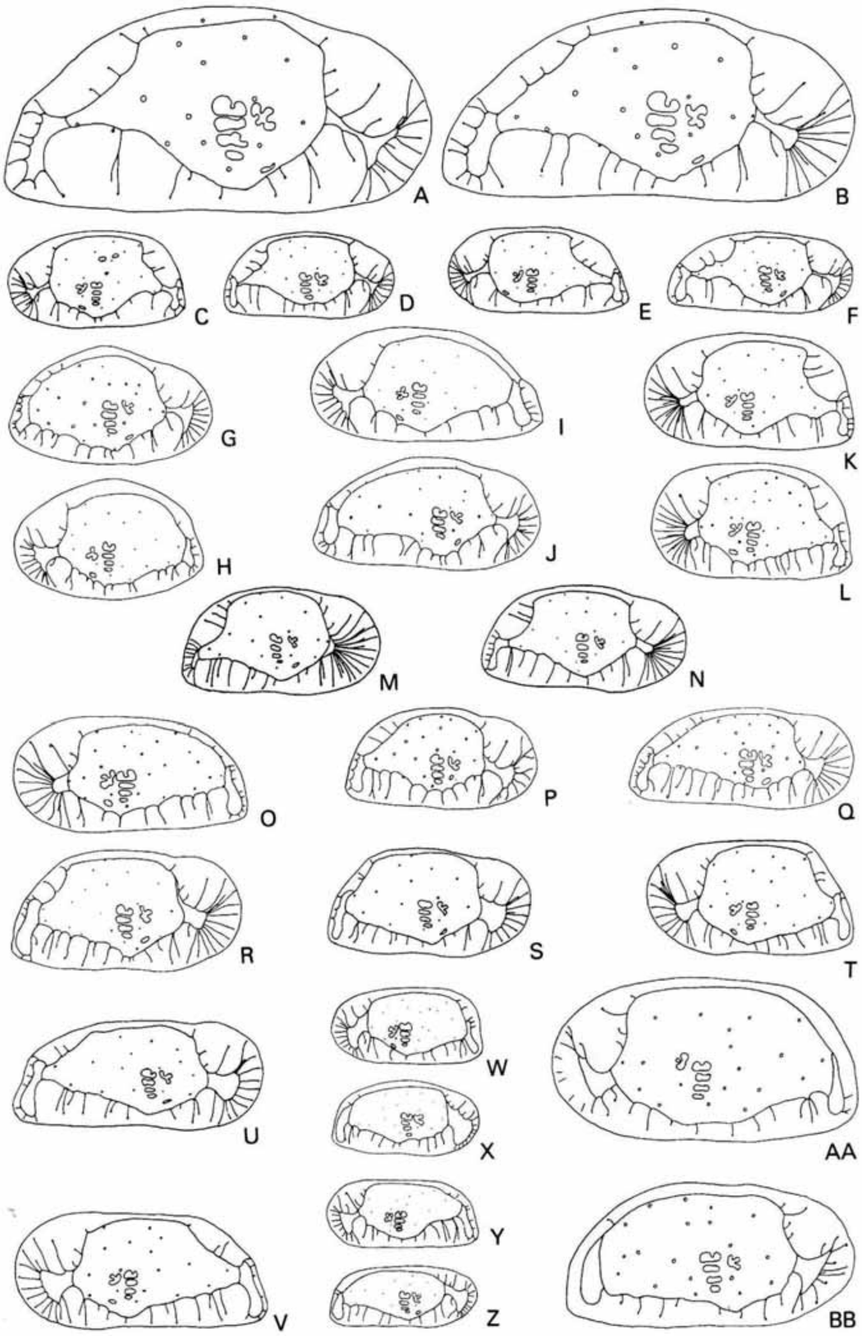
Plate 4, figures 7–12; Text-figure 4P–T, Text-figure 5A–B

1958 *Krithe trinidadensis* van den Bold, p. 398, pl. 1, figs 3*a*, 6*e* (males); 3*c*–*d*, *f* (females).
1969 *Krithe producta* Brady; Yassini, pl. 22, fig. 4 (female).
1977 *Krithe* sp. D21 en Peypouquet, p. 113, fig. 37 [*pars*] (female).
?1977 *Krithe* sp. D22 en Peypouquet, p. 113, fig. 37 [*pars*].
1981 *Krithe* sp. 1 Ciampo, p. 67, pl. 6, fig. 5 (male).
?1990 *Krithe peypouqueti* Dingle *et al*., p. 279, figs 17L–M, 18L, 21E–F, 22A (juveniles).
1990 *Krithe rex* Dingle *et al*., p. 276, figs 17G–H, 18H, 21A–D (males and females).

*Material and distribution*. Three hundred and thirty nine adult valves. Hole 549 (M.–U. Eocene), Hole 549A (U. Eocene–U. Oligocene, U. Miocene), Hole 558 (L. Oligocene–U. Miocene), Hole 563 (M. Miocene–U. Miocene), Holes 606, 609B (U. Pliocene–Quaternary), Holes 606A, 608, 608A (Pliocene–Quaternary), Hole 607 (U. Miocene–Quaternary), Holes 609, 609A, 610C (Quaternary), Holes 610, 610D (U. Miocene), Hole 610B (U. Pliocene), Hole 610E (U. Miocene–L. Pliocene), Hole 611D (L. Pliocene, Quaternary).

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| FLV GC/NA/979 549 2–4 M. Eocene | 0·98 | 0·60 |
| FLV GC/NA/983 549 H3–2 U. Eocene | 0·87 | 0·58 |
| FLV GC/NA/127 606A–7 U. Pliocene | 1·36 | 0·89 |
| FLV GC/NA/161 607–6 Quaternary | 1·34 | 0·86 |
| FLV GC/NA/256 608A–13 U. Pliocene | 1·15 | 0·73 |
| FLV GC/NA/148 606–1 Quaternary | 1·32 | 0·82 |
| MLV GC/NA/980 549 5–1 M. Eocene | 1·10 | 0·56 |
| MLV GC/NA/126 606A–14 L. Pliocene | 1·36 | 0·55 |
| MLV GC/NA/159 607–6 Quaternary | 1·57 | 0·78 |
| FRV GC/NA/984 549A 16–1 L. Oligocene | 1·09 | 0·61 |
| FRV GC/NA/981 549A 9–5 U. Oligocene | 1·22 | 0·70 |
| FRV GC/NA/146 606–4 Quaternary | 1·37 | 0·80 |
| FRV GC/NA/128 606A–13 U. Pliocene | 1·34 | 0·80 |



TEXT-FIG. 5. For legend see opposite.

| *Dimensions* (*mm*). | L | H |
|---|---|---|
| FRV GC/NA/162 607–6 Quaternary | 1·27 | 0·74 |
| MRV GC/NA/982 549 H3–2 U. Eocene | 0·99 | 0·45 |
| MRV GC/NA/124 606A–14 L. Pliocene | 1·26 | 0·57 |
| MRV GC/NA/160 607–6 Quaternary | 1·52 | 0·70 |
| MRV GC/NA/130 606A–5 Quaternary | 1·58 | 0·76 |

*Stratigraphical range*. Middle Eocene to Quaternary (NP 16–25; NN 1, 3–21) in the present study, also extends to the present day.

*Diagnosis*. A very large, thick-shelled species of *Krithe* with strong sexual dimorphism. Female subovate and very tumid; male elongate to very elongate, subtriangular and less strongly inflated than female. Inner lamella broad; anterior vestibulum 'T' or 'Y'-shaped to small 'pocket'-shaped. ADRPC type 3A. Hinge strong, LV with arched, deep accommodation groove. Central muscle scars large, increasing in size dorsally; most dorsal adductor reniform to 'U'-shaped, trefoil frontal scar.

*Remarks*. *K. trinidadensis* was described by van den Bold (1958) from the Oligocene and Miocene of Trinidad. It is very similar in shape, inner lamella and ADRPC pattern to its probable ancestor, *K. morkhoveni morkhoveni*, but is always much larger and more inflated; the A-1 juveniles of *K. trinidadensis* are approximately equal in size to the adult females of *K. morkhoveni morkhoveni*.

The anterior vestibulum ranges from a large 'T' to 'Y' shape to a small 'pocket' shape and, while most specimens have either small or large vestibula, the present material includes specimens with an anterior vestibulum intermediate in form between the two types (e.g. GC/NA/980). There are few published records or illustrations of this species, probably because it has been included within *K. morkhoveni* and other species. In addition to the occurrences in the present study material, the following are noted: Upper Oligocene of Sicily (Ciampo 1981), Upper Miocene to Quaternary of the Rockall Plateau (among the material of Ducasse and Peypouquet 1979 seen by GC), Pleistocene of the Iberian Portal at 2798 m (Elant 1985) and at 2414 and 3700 m (Harpur 1985) and Pleistocene of the North Atlantic in cores L4, P2, R2, R3, R4 and R5 between 1678 and 3422 m and lat. 43° to 61° N (material of Porter 1984 seen by GC). In the Recent it ranges in the North Atlantic from 1320 to 5440 m (Davies 1981; Barkham 1985; GC, RCW, personal observations), and also occurs at 1080 m off Florida (material of Cronin 1983 seen by GC) at 1500 m in the Gulf of Mexico

TEXT-FIG. 5. A–B. *K. trinidadensis* van den Bold. A, GC/NA/130; DSDP Site 606A, c.c. 5; Quaternary; male right valve. B, GC/NA/160; DSDP Site 607, c.c. 6; Quaternary; male right valve. C–F. *K. aquilonia* sp. nov. C, OS 13996; DSDP Site 610, c.c. 5; Quaternary; female left valve. D, OS 13998; DSDP Site 608, c.c. 5; Quaternary; female right valve. E, OS 13999; DSDP Site 620E, c.c. 3; Late Miocene; male left valve. F, OS 14000; DSDP Site 608, c.c. 11; Late Pliocene; male right valve. G–J. *Krithe praemorkhoveni* sp. nov. G, OS 13984; DSDP Site 549, c.c. 16–3; late Palaeocene; female right valve. H, OS 13985; DSDP Site 549, c.c. 14–4; early Eocene; female left valve. I, OS 13988; DSDP Site 549, c.c. 8–1; middle Eocene; male left valve. J, OS 13993; DSDP Site 549, c.c. 16–3; late Palaeocene; male right valve. K–Q. *K. pernoides pernoides* (Bornemann). K, GC/NA/310; DSDP Site 611D, c.c. 12; Late Pliocene; female left valve. L, GC/NA/844; DSDP Site 549A, c.c. 8–5; late Oligocene; female left valve. M, GC/NA/171; DSDP Site 607, c.c. 10; Late Pliocene; female right valve. N, GC/NA/311; DSDP Site 611D, c.c. 12; Late Pliocene; female right valve. O, GC/NA/849; DSDP Site 549A, c.c. 8–5; late Oligocene; male left valve. P, GC/NA/846; DSDP Site 549, c.c. 2–1; middle Eocene; female right valve. Q, GC/NA/850; DSDP Site 5409A, c.c. 8–5; late Oligocene; male right valve. R–V. *K. pernoides sinuosa* Ciampo. R, GC/NA/852; DSDP Site 563, c.c. 10–1; Middle Miocene; female right valve. S, GC/NA/35; DSDP Site 606A, c.c. 5; Quaternary; female right valve. T, GC/NA/180; DSDP Site 607, c.c. 13; Late Pliocene; female left valve. U, GC/NA/156; DSDP Site 607, c.c. 5; Quaternary; male right valve. V, GC/NA/155; DSDP Site 607, c.c. 5; Quaternary; male left valve. W–Z. *Krithe* sp. cf. *parvula* Deltel. W, GC/NA/926; DSDP Site 549, c.c. 11–1; early Eocene; female left valve. X, GC/NA/928; DSDP Site 549, c.c. 8–4; middle Eocene; female right valve. Y, GC/NA/932; DSDP Site 549, c.c. 16–3; Late Pliocene; male left valve. Z, GC/NA/931; DSDP Site 549, c.c. 11–1; early Eocene; male right valve. AA–BB. *Krithe* sp. 1. AA, GC/NA/892; DSDP Site 549, c.c. 19–3; Late Pliocene; female? left valve. BB, GC/NA/893; DSDP Site 549, c.c. 19–3; Late Pliocene; female? right valve. All projectina drawings; × 50.

(GC personal observations) and in the Bay of Biscay at bathyal and abyssal depths down to 3950 m (Yassini 1969, as *K. producta* Brady). It has been described as a new species, *K. rex*, by Dingle *et al.* (1990) from the South Atlantic off southwestern Africa at a depth of 2916 m, while another of their species, *K. peypouqueti*, recorded at 2916 m and 4736 m in the same area probably represents the juveniles of this species.

### *Krithe aquilonia* sp. nov.

Plate 4, figures 13–17; Text-figure 5C–F

*Derivation of name*. Latin, with reference to the northerly distribution of this species.

*Holotype*. Female left valve OS 13996.

*Type locality and horizon*. DSDP Site 610, Hole 610, eastern North Atlantic, west of the Rockall Trough on the Feni Drift. Lat. 53° 13·30′ N, long. 18° 53·21′ W. PDWD 2417 m. Core catcher 5, Quaternary, NN 19. Nannofossil ooze.

*Material and distribution*. Fifty three adult valves. Hole 558 (L. Miocene), Holes 607, 609, 611D (L. Pliocene), Hole 608 (Pliocene–Quaternary), Holes 608A, 610B (U. Pliocene), Hole 609B (U. Pliocene–Quaternary), Hole 610 (U. Miocene, Quaternary), Hole 610C (Quaternary), Hole 610D (U. Miocene), Hole 610E (U. Miocene–L. Pliocene).

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| Holotype FLV OS 13996 610–5 Quaternary | 0·65 | 0·36 |
| Paratype FLV OS 13997 08–11 U. Pliocene | 0·63 | 0·33 |
| Paratype FRV OS 13998 608–5 Quaternary | 0·63 | 0·31 |
| Paratype MLV OS 13999 610E–3 U. Miocene | 0·67 | 0·31 |
| Paratype MRV OS 14000 608–11 U. Pliocene | 0·67 | 0·30 |
| Paratype MRV OS 14001 558 14–1 L. Miocene | 0·62 | 0·28 |

*Stratigraphical range*. Miocene–Quaternary (NN 1, 4, 5, 10–21) in the present study. It almost certainly also occurs in the Recent.

*Diagnosis*. A small, subrectangular, elongate species of *Krithe* with moderate sexual dimorphism. Females relatively higher and more inflated than elongate males. Both sexes with gently (LV) to quite strongly convex (RV) dorsum, and bluntly truncate posterior. Inner lamella wide, anterior vestibule small 'T' to 'mushroom'-shape. ADRPC type 3A.

*Description*. Small, elongate, subrectangular and strongly inflated, especially so in female. FLV dorsal margin regularly convex, continuously curved with broadly rounded anterior; ventral margin with very shallow oval incurvature at mid-length; posterior bluntly truncate, very steep postero-ventral slope at about 85° to the ventral margin. FRV as FLV but with a very slight antero-dorsal concavity. Male similar, but more elongate and dorsal margin straighter, especially so in MLV. In both sexes, selvage narrow, slight posterior indentation and shallow posterior pit; moderately thin-shelled. LV overlaps RV and overreaches RV along dorsal margin. NPC small, regularly distributed. Inner lamella wide, deeply depressed below adductors. Anterior vestibule small, 'T' to 'mushroom'-shaped, with narrow opening and long, narrow neck. Ten to eleven short, straight ARPC in fan arrangement; ADRPC type 3A; three to four short to moderately elongate PDRPC. Posterior vestibule similar in size to anterior vestibule, elongate subrectangular, with up to five very short PRPC. Hinge pseudodont; RV with slightly arched hinge bar which is raised posteriorly and bears up to six tiny denticles, complementing posteriorly locellate groove in LV. Central muscle scars relatively large, consisting of a slightly arcuate row of four adductors, the topmost is reniform and the middle scars are biconcave. Trefoil frontal scar and ovate mandibular scar.

*Remarks*. *K. aquilonia* is distinctly smaller than *K. morkhoveni ayressi*, which may be its ancestor. This species is also recorded from the Upper Miocene of the Rockall Trough (among the material of Ducasse and Peypouquet 1979 seen by GC) and in the Pleistocene of the North Atlantic between lat. 43° and 61° N and PDWD 938 to 4566 m in cores L4, L5, O1, P2, R2 and R3 of Porter (1984). *K. aquilonia* is only known from the Miocene to Quaternary of the North Atlantic between lat. 37° and 61° N, with no records from other oceans.

### *Krithe praemorkhoveni* sp. nov.

Plate 5, figures 1–6; Text-figure 5G–J

*Derivation of name.* Latin, referring to the ancestral relationship of this species to *K. morkhoveni.*

*Holotype.* Female right valve OS 13984.

*Type locality and horizon.* DSDP Site 549, Hole 549, Goban Spur. Lat. 49° 05·28′ N, long. 13° 05·88′ W; PDWD 2513 m. Core 16, section 3, interval 0·41–0·48 m. Upper Palaeocene, NP 9. Olive-grey nannofossil chalk.

*Material and distribution.* One hundred and ninety five adult valves. Hole 549 (U. Palaeocene–M. Eocene), Hole 550 (L. Palaeocene–L. Eocene).

| *Dimensions (mm).* | L | H |
|---|---|---|
| Holotype FRV OD 13984 549 16–3 U. Palaeocene | 0·58 | 0·34 |
| Paratype FLV OS 13985 549 14–4 L. Eocene | 0·54 | 0·35 |
| Paratype FLV OS 13986 54915–5 L. Eocene | 0·59 | 0·37 |
| Paratype MLV OS 13987 549 11–1 L. Eocene | 0·64 | 0·34 |
| Paratype MLV OS 13988 549 8–1 M. Eocene | 0·68 | 0·33 |
| Paratype MLV OS 13989 549 13–4 L. Eocene | 0·60 | 0·33 |
| Paratype FRV OS 13990 549 11–1 L. Eocene | 0·57 | 0·34 |
| Paratype FRV OS 13991 549 9–2 M. Eocene | 0·71 | 0·41 |
| Paratype FRV OS 13992 549 15–5 L. Eocene | 0·59 | 0·36 |
| Paratype MRV OS 13993 549 16–3 U. Palaeocene | 0·66 | 0·32 |
| Paratype MRV OS 13994 549 11–1 L. Eocene | 0·62 | 0·30 |
| Paratype MRV OS 13995 549 15–5 L. Eocene | 0·66 | 0·34 |

*Stratigraphical range.* Lower Palaeocene to Middle Eocene (NP 3–4, 6–16) in the present study.

*Diagnosis.* A medium, thick-shelled, strongly sexually dimorphic species of *Krithe* belonging to the *K. trinidadensis* group, similar to *K. morkhoveni* van den Bold, but smaller, more robust and with a narrower inner lamella.

*Description.* Medium-sized, thick-shelled and moderately inflated. Females subovate, males subovate to elongate-subrectangular. FLV dorsum strongly convex, anterior broadly rounded, posterior bluntly truncate, ventral margin convex. FRV as FLV but dorsum more convex, with shallow antero-dorsal concavity and slightly convex ventral margin. Males similar but more elongate, with less convex dorsum; ventral margin may be concave. Normal LV > RV overlap, NPC relatively large. Inner lamella moderate width with sinuous line of concrescence. Anterior vestibulum small, 'mushroom' to 'T'-shaped, with eleven to twelve ARPC. ADRPC type 3A; AD 1–3 very short, AD 4 elongate and arises from the vestibular neck. Hinge adont; frontal scar may be quadrifoil.

*Remarks.* This is the most abundant *Krithe* species in the Palaeocene and Lower Eocene of Holes 549 and 550, but does not occur above the Middle Eocene (NP 16). It is the ancestor of *K. morkhoveni morkhoveni*, from which it differs in being smaller (length range 0·54 to 0·71 mm) and thicker-shelled.

The Lower Eocene species *K. kollmanni* Pokorny, 1980, and *K. cancuenensis ambigua* Pokorny, 1980, from deep-water *Globigerina* marls in the former Czechoslovakia, probably represent the female and male, respectively of the present species. However, the early Oligocene holotypes of both species are larger and thinner-shelled and are included within *K. morkhoveni morkhoveni.*

### ADRPC TYPE 3A
(Other species not assigned to *K. trinidadensis* Group)

### *Krithe pernoides pernoides* (Bornemann, 1855)

Plate 5, figures 7–12; Text-figure 5K–Q

?1855 *Bairdia pernoides* Bornemann, p. 358, pl. 20, fig. 7*a–c*
1918 *Krithe pernoides* (Bornemann); Kuiper, p. 36, pl. 1, figs 12*a*, *c*? only.
1957 *Krithe pernoides* (Bornemann); Keij, p. 86, pl. 6, fig. 11*a–b*.
1962 *Krithe pernoides* (Bornemann); Bassiouni, p. 22, pl. 9, figs 1–3.
1969 *Krithe pernoides* (Bornemann); Schremeta, p. 90, pl. 7, figs 8–10.
1969 *Krithe pernoides* (Bornemann); Pietrzeniuk, p. 24, pl. 5, fig. 11?; pl. 15, figs 13, 14?

*Material and distribution*. Two hundred and ninety five adult valves. Hole 549 (M.–U. Eocene), Hole 549A (U. Eocene–U. Oligocene), Hole 558 (L. Oligocene–M. Miocene), Hole 607 (U. Pliocene–Quaternary), Hole 608A (Quaternary).

*Dimensions (mm)*.

| | L | H |
|---|---|---|
| FLV GC/NA/843 549A 16–2 L. Oligocene | 0·59 | 0·33 |
| FLV GC/NA/844 549A 8–5 U. Oligocene | 0·59 | 0·34 |
| FLV GC/NA/884 549A 8–5 U. Oligocene | 0·59 | 0·34 |
| FLV GC/NA/255 608A–3 Quaternary | 0·73 | 0·43 |
| FRV GC/NA/845 549A 8–5 U. Oligocene | 0·58 | 0·30 |
| FRV GC/NA/846 549 2–1 M. Eocene | 0·57 | 0·29 |
| FRV GC/NA/171 607–10 U. Pliocene | 0·73 | 0·40 |
| MLV GC/NA/847 549 5–1 M. Eocene | 0·64 | 0·29 |
| MLV GC/NA/848 549A 16–1 L. Oligocene | 0·81 | 0·39 |
| MLV GC/NA/849 549A 8–5 U. Oligocene | 0·70 | 0·34 |
| MRV GC/NA/850 549A 8–5 U. Oligocene | 0·67 | 0·29 |
| FLV GC/NA/310 611D–12 L. Pliocene | 0·78 | 0·43 |
| FRV GC/NA/311 611D–12 L. Pliocene | 0·75 | 0·38 |

*Stratigraphical range*. Middle Eocene to Middle Miocene, Upper Pliocene to Quaternary (NP 15–25; NN 4–5, 18–19).

*Diagnosis*. A medium (female) or medium to large (male) subspecies of *Krithe* with an elongate, subrectangular carapace, subparallel dorsal and ventral margins, wide inner lamella, long RPC, and ADRPC type 3A. Posterior convex, with no posterior concavity and no marked posterior angle.

---

### EXPLANATION OF PLATE 5

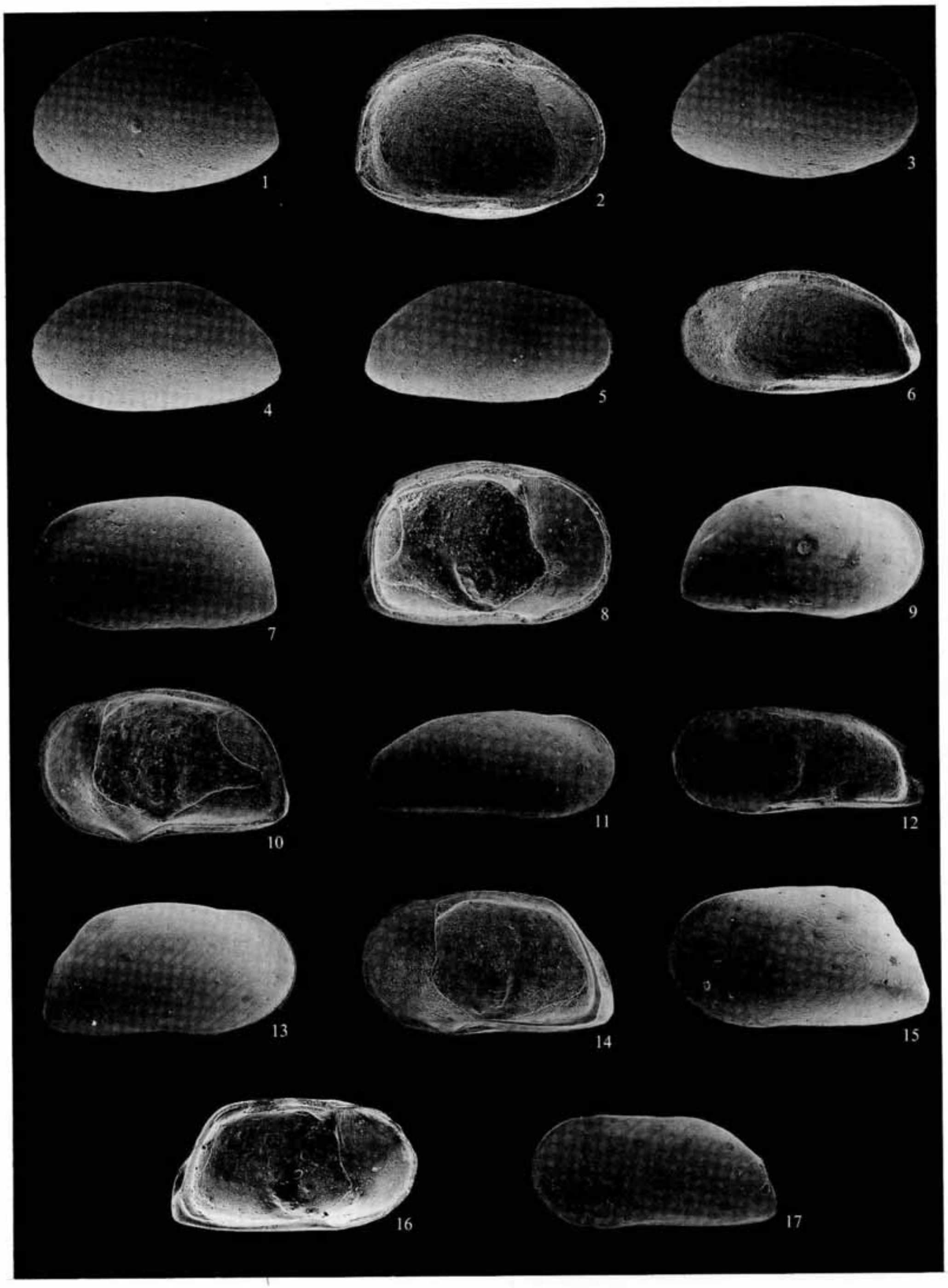
Figs 1–6. *Krithe praemorkhoveni* sp. nov. 1–2, OS 13986; DSDP Site S49, c.c. 15–5; early Eocene; female left valve, external and internal views; × 71. 3, OS 13992; DSDP Site S49, c.c. 15–5; early Eocene; female right valve, external view; × 71. 4, OS 13989; DSDP Site S49, c.c. 13–4; early Eocene; male left valve, external view; × 70. 5–6, OS 13995; DSDP Site S49, c.c. 15–5; early Eocene; male right valve, external and internal views; × 64.

Figs 7–12. *Krithe pernoides pernoides* (Bornemann). 7, GC/NA/884; DSDP Site S49A, c.c. 8–5; late Oligocene; female left valve, external view; × 71. 8, GC/NA/255; DSDP Site 608A, c.c. 3; Quaternary; female left valve, internal view; × 57. 9–10, GC/NA/171; DSDP Site 607, c.c. 10; Late Pliocene; female right valve, external and internal views; × 57. 11–12, GC/NA/850; DSDP Site 549A, c.c. 8–5; late Oligocene; male right valve, external and internal views; × 63.

Figs 13–17. *Krithe pernoides sinuosa* Ciampo. 13–14, GC/NA/35; DSDP Site 606A, c.c. 5; Quaternary; female right valve, external and internal views; × 56. 15–16, GC/NA/180; DSDP Site 607, c.c. 13; Late Pliocene; female left valve, external and internal views; × 54. 17, GC/NA/155; DSDP Site 607, c.c. 5; Quaternary; male left valve, external view; × 45.

All figures are scanning electron micrographs.

PLATE 5



COLES *et al.*, *Krithe*

*Remarks.* This abundant, widely distributed subspecies is especially common in the Oligocene of Hole 549A, but is rare or absent in Miocene to Quaternary sediments. Considerable size variation occurs in this subspecies; there is a general but not consistent increase in size from the Middle Eocene to the Oligocene. *K. pernoides pernoides* differs from its descendant, *K. pernoides sinuosa* Ciampo, 1986 in having a regularly convex posterior margin, while in the latter it is more angular with a marked posterior angle and posterior concavity. *K. pernoides pernoides* may have branching ARPC and a 'Y'-shaped anterior vestibulum, which are not present in *K. pernoides sinuosa.*

The original figures of Bornemann (1855) are poor and only the exterior of the carapace was illustrated. The identification of the present specimens with *K. pernoides* (Bornemann) is based on the records of subsequent authors who illustrated the internal features.

The known occurrences of this species are as follows: Upper Eocene of Denmark, eastern Germany (Pietrzeniuk 1969) and the Ukraine (Schremeta 1969); Oligocene of Denmark, Netherlands (Kuiper 1918), Hermsdorf near Berlin, Germany (Bornemann 1855), Belgium (Keij 1957), northern Germany (Uffenorde 1981); Miocene of northwestern Germany (Bassiouni 1962; Uffenorde 1981); Upper Pliocene to Quaternary of the North Atlantic (Coles 1985) and late Quaternary of the Atlantic west of the Iberian Portal at 2414 and 2421 m (Harpur 1985).

In summary, this species is common in deep-water Middle Eocene to Oligocene sediments in the North Atlantic, but is rarer in the Miocene to Quaternary of the same area. In the Upper Eocene to Miocene interval of Europe it occurs in shallower (outer shelf?) warmer waters from the evidence of the associated fauna, and is frequently associated with such long-ranging and eurybathic species as *Henryhowella asperrima* (Reuss).

### *Krithe pernoides sinuosa* Ciampo, 1986

Plate 5, figures 13–17; Text-figure 5R–V

| | |
|---|---|
| 1962 | *Krithe pernoides* (Bornemann); Ruggieri, p. 17, pl. 1, figs 12–13. |
| 1976 | *Krithe pernoides* (Bornemann); Breman; p. 55, pl. 3, fig. 28. |

---

### EXPLANATION OF PLATE 6

Figs 1–3. *Krithe pernoides sinuosa* Ciampo. 1, GC/NA/155; DSDP Site 607, c.c. 5; Quaternary; male left valve, internal view; × 45. 2–3, GC/NA/156; DSDP Site 607, c.c. 5; Quaternary; male right valve, external and internal views; × 45.

Figs 4–6. *Krithe* sp. cf. *K. parvula* Deltel. 4–5, GC/NA/927; DSDP Site S49, c.c. 8–4; middle Eocene; female left valve, external and internal views; × 95. 6, GC/NA/929; DSDP Site 549, c.c. 8–4; middle Eocene; female right valve, external view; × 93.

Figs 7–9. *Krithe* sp. 7. 7, GC/NA/900; DSDP Site 549A, c.c. 5–5; Late Miocene; female left valve, external view; × 54. 8, GC/NA/903; DSDP Site 549A, c.c. 5–5; Late Miocene; male right valve, external view; × 47. 9, GC/NA/901; DSDP Site 549A, c.c. 5–5; Late Miocene; female right valve, internal view; × 55.

Figs 10–12. *Krithe* sp. 8. 10, GC/NA/269; DSDP Site 610E, c.c. 7; Late Miocene; female left valve, external view; × 70. 11–12, GC/NA/270; DSDP Site 610E, c.c. 7; Late Miocene; female right valve, external and internal views; × 70.

Figs 13–14. *Krithe* sp. 9. GC/NA/210; DSDP Site 607, c.c. 24; Early Pliocene; female left valve, external and internal views; × 52.

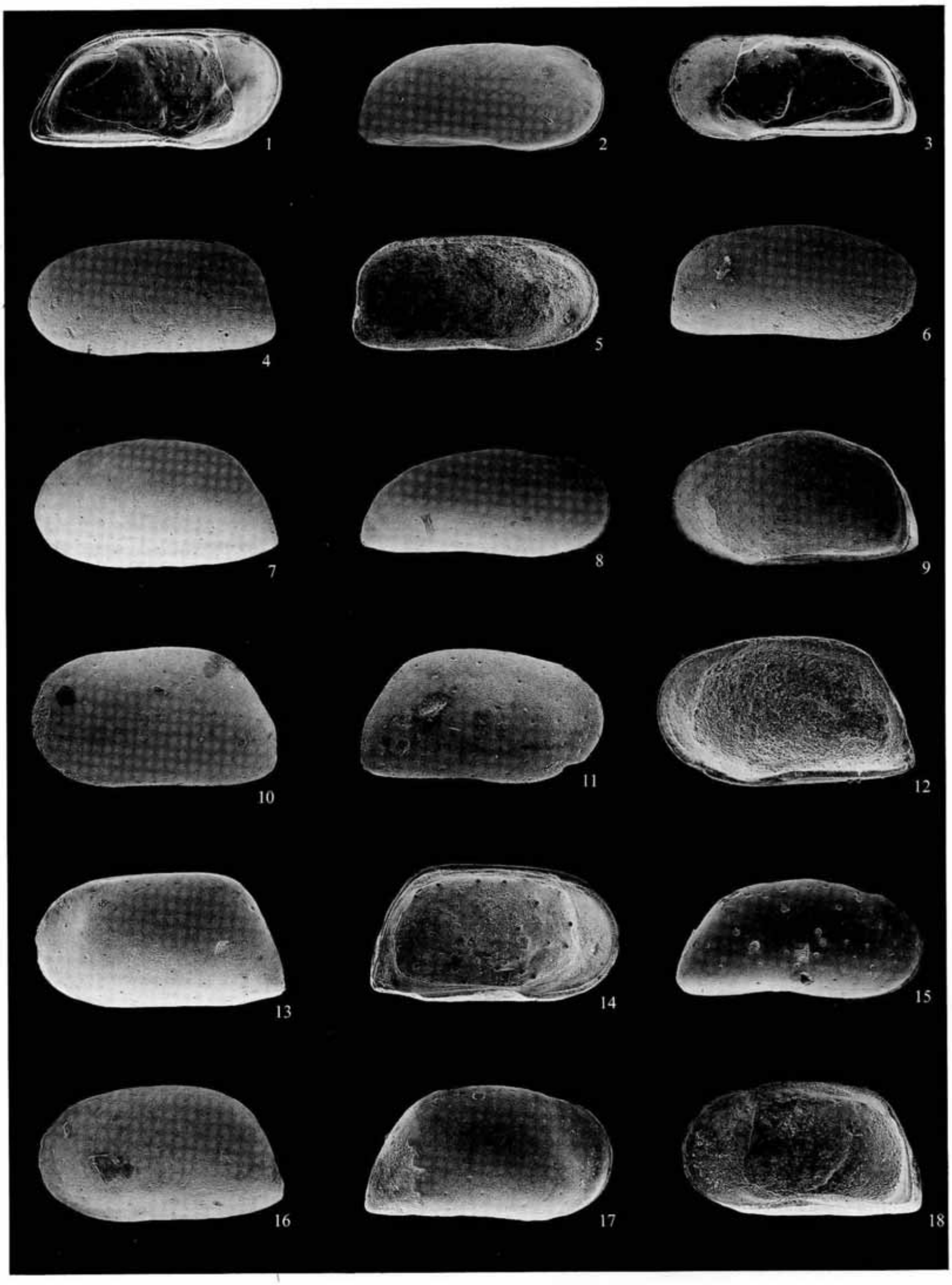
Fig. 15. *Krithe* sp. 10. GC/NA/42; DSDP Site 606A, c.c. 19; Early Pliocene; female? right valve, external view; × 52.

Fig. 16. *Krithe* sp. 11. GC/NA/206; DSDP Site 611D, c.c. 9; Early Pliocene; female left valve, external view; × 66.

Figs 17–18. *Krithe* sp. 12. GC/NA/266; DSDP Site 609B, c.c. 29; Early Pliocene; female right valve, external and internal views; × 60.

All figures are scanning electron micrographs.

PLATE 6



COLES *et al.*, *Krithe*

1977 *Krithe* sp. A Peypouquet, p. 104, fig. 34 (not sp. A24?).
1985 *Krithe producta* Brady; Guillaume *et al.*, pl. 106, fig. 5.
1986 *Krithe sinuosa* Ciampo, p. 87, pl. 17, figs 3, 5.

*Material and distribution.* One hundred and eight adult valves. Hole 549A (U. Miocene). Hole 550 (U. Miocene), Hole 558 (L.?–U. Miocene), Hole 563 (M.–U. Miocene), Holes 606, 606A, 607, 609, 610 (Pliocene–Quaternary), Hole 608 (U. Miocene–Quaternary), Holes 608A, 609B (U. Pliocene–Quaternary), Holes 609A, 610C (Quaternary), Hole 610B (U. Pliocene), Hole 611D (L. Pliocene, Quaternary).

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| FLV GC/NA/180 607–13 U. Pliocene | 0·77 | 0·43 |
| FLV GC/NA/36 606–1 U. Pliocene | 0·74 | 0·40 |
| MLV GC/NA/155 607–5 Quaternary | 0·94 | 0·44 |
| MLV GC/NA/851 558 17–5 L. Miocene | 0·80 | 0·36 |
| FRV GC/NA/852 563 10–1 M. Miocene | 0·69 | 0·35 |
| FRV GC/NA/35 606A–5 Quaternary | 0·75 | 0·40 |
| MRV GC/NA/156 607–5 Quaternary | 0·92 | 0·41 |

*Stratigraphical range.* Middle or possibly Lower Miocene to Quaternary (NN 1?, 5–7, 9–12, 14–21) in the present study. The species also occurs in the Recent.

*Diagnosis.* A medium (female) to large (male), subrectangular and moderately inflated subspecies of *Krithe* with strong sexual dimorphism. Females moderately high, males elongate to very elongate. Both sexes with straight to slightly convex dorsal margin; posterior bluntly truncate with distinct angle between shallow posterior concavity and steep postero-ventral slope. Anterior vestibulum small to medium sized, 'pocket'-shaped. ADRPC type 3A. VRPC long, slightly curved; some are branched.

*Remarks. Krithe sinuosa* was described from the Upper Miocene of Italy by Ciampo, but is here considered to be a subspecies of *K. pernoides* Bornemann, evolving from the nominative subspecies in the Early to Mid-Miocene. *K. pernoides sinuosa* seems to be an ecological subspecies of *K. pernoides*, with the former dominating at abyssal depths, although the latter has been recorded down to a PDWD of 3526 m at Site 608.

---

## EXPLANATION OF PLATE 7

Figs 1–3. *Krithe* sp. 13. 1–2, GC/NA/260; DSDP Site 609B, c.c. 2; Quaternary; female left valve, external and internal views; × 50. 3, GC/NA/227; DSDP Site 608, c.c. 5; Quaternary; female right valve, external view; × 50.

Figs 4–6. *Krithe* sp. 14. 4, GC/NA/312; DSDP Site 611D, c.c. 12; Late Pliocene; female left valve, external view; × 38. 5–6, GC/NA/170; DSDP Site 607, c.c. 10; Late Pliocene; female right valve, external and internal views; × 39.

Figs 7–9. *Krithe* sp. 15. 7, GC/NA/293; DSDP Site 610, c.c. 5; Quaternary; male left valve, external view; × 58. 8–9, GC/NA/294; DSDP Site 610, c.c. 5; Quaternary; male right valve, external and internal views; × 59.

Figs 10–11. *Krithe* sp. 16. GC/NA/262; DSDP Site 609B, c.c. 9; Quaternary; female? right valve, external and internal views; × 45.

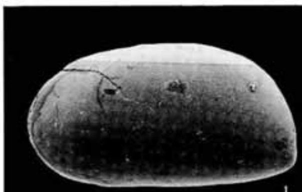
Figs 12–13. *Krithe* sp. 17. GC/NA/52; DSDP Site 606A, c.c. 4; Quaternary; female? right valve, external and internal views; × 47.

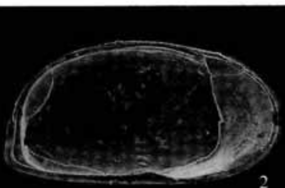
Figs 14–15. *Krithe* sp. 18. GC/NA/166; DSDP Site 607, c.c. 6; Quaternary; male? right valve, external and internal views; × 49.

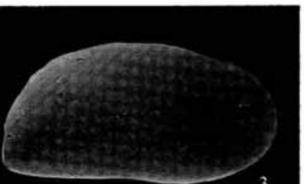
Figs 16–17. *Krithe* sp. 19. GC/NA/54; DSDP Site 606A, c.c. 2; Quaternary; female? right valve, external and internal views; × 46.

All figures are scanning electron micrographs.

PLATE 7

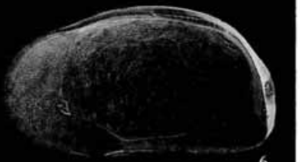

1


2


3

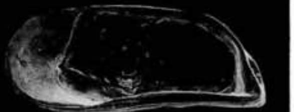

4

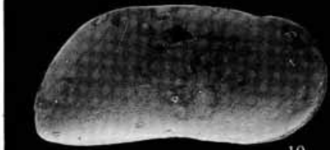

5


6


7

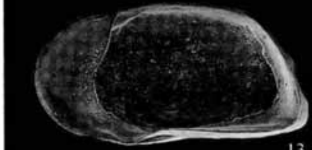

8

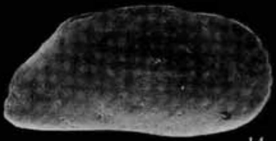

9


10

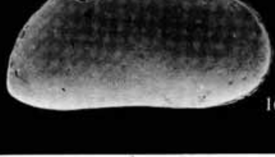

11

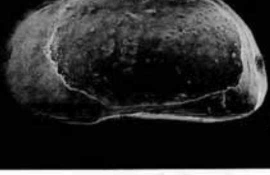

12


13

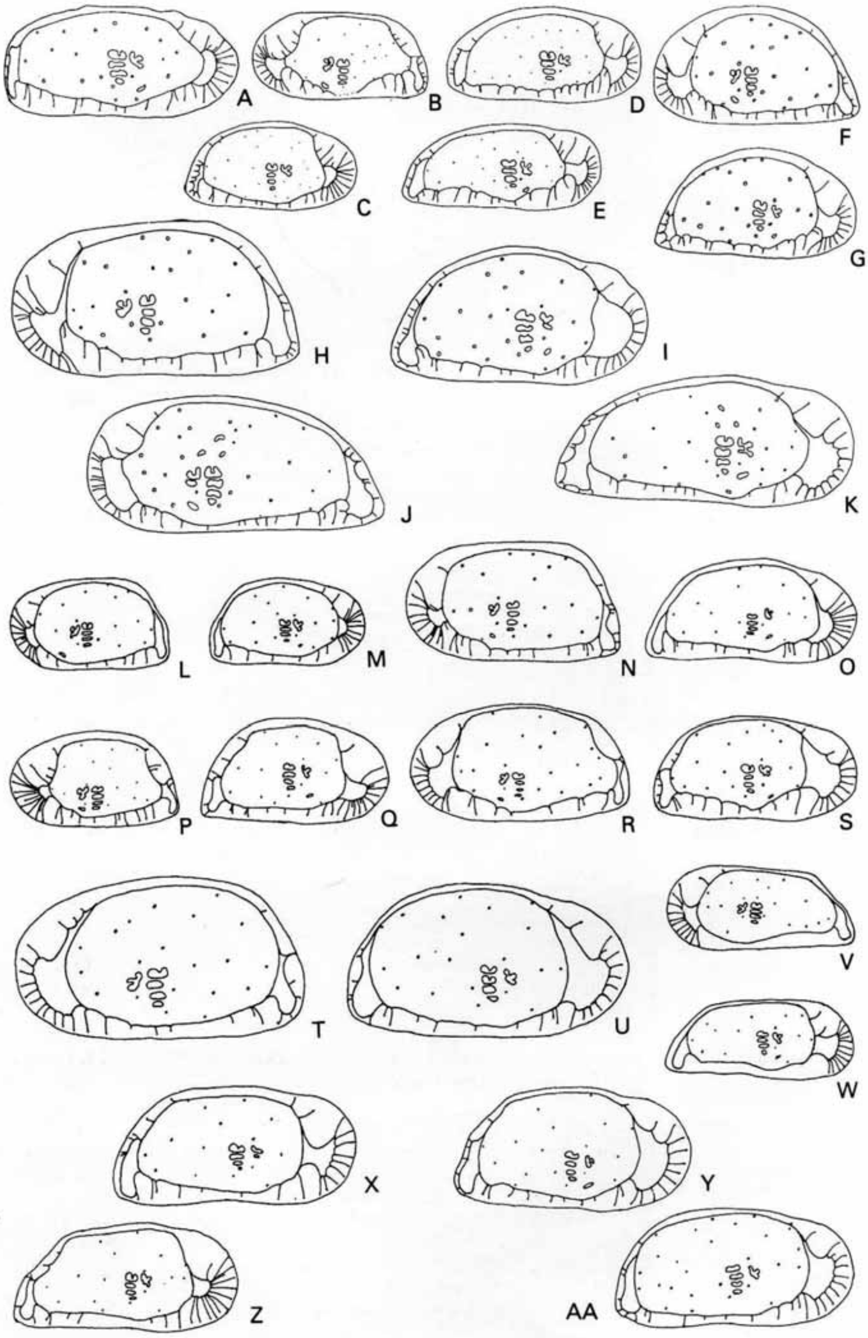

14


15


16


17

COLES *et al.*, *Krithe*



TEXT-FIG. 6. For legend see opposite.

In the present material, *K. pernoides sinuosa* is common in Middle Miocene to Quaternary sediments in the North Atlantic. A single MLV occurred in the Lower Miocene with an abnormally large anterior vestibulum, but is otherwise very similar to typical *K. pernoides sinuosa*.

In addition to the occurrences cited above, the following are noted: Upper Miocene of Sicily (Ruggieri 1962) and DSDP Site 403 on the Rockall Plateau (material of Ducasse and Peypouquet 1979 seen by GC), Pliocene of DSDP Site 613 off New Jersey (among the material of Cronin and Compton-Gooding 1987 seen by GC), late Quaternary of the northeastern Atlantic in cores L4, L5, P2, R3, R4, T2 and T3 between PDWD 1678 and 4566 m and lat. 43° and 68° N (among the material of Porter 1984 seen by GC and RCW), late Quaternary of the North Atlantic west of the Iberian Portal between 453 and 3700 m (Harpur 1985) and Quaternary of the western Mediterranean, Gulf of Cadiz and Cape St Vincent between 795 and 2798 m (Elant 1985).

In the Recent it occurs in the Adriatic between 175 and 302 m (Breman 1976), the Atlantic around the Iberian Portal and the western Mediterranean between 585 and 2798 m (Elant 1985), Atlantic off northwest Africa between 997 and 1250 m (Barkham 1985), Porcupine Sea Bight between 1320 and 1942 m (Symonds pers. comm.), Atlantic off Florida between 185 and 739 m (material of Cronin 1983 seen by GC), Gulf of Benin and Atlantic off the Ivory Coast (Peypouquet 1977), deep-water Bay of Biscay (Guillaume *et al.* 1985), off south Norway between 300 and 630 m, Gulf of Mexico at 1500 m and North Atlantic at 5383 and 5440 m (GC personal observations).

In summary, *K. pernoides sinuosa* is common in the North Atlantic from the Middle Miocene to the Recent with a maximum depth range of 185 to 5440 m and ranging from lat. 5° N to at least 68° N. It has, however, not been recorded from the Caribbean, or the Indian or Pacific oceans.

### *Krithe* sp. cf. *K. parvula* Deltel, 1963

Plate 6, figures 4–6; Text-figure 5w–z

1964 *Krithe parvula* Deltel, p. 172, pl. 4, figs 86–89.
?1985 *Krithe parvula* Deltel; Ducasse *et al.*, pl. 78, fig. 14.

*Material and distribution*. Sixty eight adult valves. Hole 549 (U. Palaeocene–M. Eocene) (NP 9–15).

TEXT-FIG. 6. A, *Krithe* sp. 2. GC/NA/891; DSDP Site 549, c.c. 19–3; late Palaeocene; adult right valve. B–C. *Krithe* sp. 3. B, GC/NA/934; DSDP Site 550, c.c. 33–3; early Eocene; male? left valve. C, GC/NA/935; DSDP Site 550, c.c. 30–3; early Eocene; female? right valve. D–E. *Krithe* sp. 5. D, GC/NA/932; DSDP Site 549, c.c. 4–1; middle Eocene; female right valve. E, GC/NA/932; DSDP Site 549, c.c. 4–1; middle Eocene; male right valve. F–G. *Krithe* sp. 4. F, GC/NA/889; DSDP Site 550, c.c. 30–3; early Eocene; female left valve. G, GC/NA/890; DSDP Site 550, c.c. 30–3; early Eocene; female right valve. H, *Krithe* sp. 6. GC/NA/887; DSDP Site 549A, c.c. 9–5; late Oligocene; female left valve. I–K. *Krithe* sp. 7. I, GC/NA/896; DSDP Site 549A, c.c. 5–5; Late Miocene; female right valve. J, GC/NA/897; DSDP Site 549A, c.c. 5–5; Late Miocene; male left valve. K, GC/NA/898; DSDP Site 549A, c.c. 5–5; Late Miocene; male right valve. L–M. *Krithe* sp. 8. L, GC/NA/269; DSDP Site 610E, c.c. 7; Late Miocene; female left valve. M, GC/NA/270; DSDP Site 610E, c.c. 7; Late Miocene; female right valve. N, *Krithe* sp. 9. GC/NA/210; DSDP Site 607, c.c. 24; Early Pliocene; female left valve. O, *Krithe* sp. 10. GC/NA/42; DSDP Site 606A, c.c. 19; Early Pliocene; female? right valve. P, *Krithe* sp. 11. GC/NA/206; DSDP Site 611D, c.c. 9; Early Pliocene; female left valve. Q, *Krithe* sp. 12. GC/NA/266; DSDP Site 609B, c.c. 29; Early Pliocene; female right valve. R–S. *Krithe* sp. 13. R, GC/NA/260; DSDP Site 609B, c.c. 2; Quaternary; female left valve. S, GC/NA/227; DSDP Site 608, c.c. 5; Quaternary; female right valve. T–U. *Krithe* sp. 14. T, GC/NA/312; DSDP Site 611D, c.c. 12; Late Pliocene; female left valve. U, GC/NA/170; DSDP Site 607, c.c. 10; Late Pliocene; female right valve. V–W. *Krithe* sp. 15. V, GC/NA/293; DSDP Site 610, c.c. 5; Quaternary; male left valve. W, GC/NA/294; DSDP Site 610, c.c. 5; Quaternary; male right valve. X, *Krithe* sp. 16. GC/NA/262; DSDP Site 609B, c.c. 9; Quaternary; female? right valve. Y, *Krithe* sp. 17. GC/NA/52; DSDP Site 606A, c.c. 4; Quaternary; female? right valve. Z, *Krithe* sp. 18. GC/NA/166; DSDP Site 607, c.c. 6; Quaternary; male? right valve. AA, *Krithe* sp. 19. GC/NA/54; DSDP Site 606A, c.c. 2; Quaternary; female? right valve. All projectina drawings; × 50.

*Dimensions* (*mm*).

| | L | H |
|---|---|---|
| FLV GC/NA/925 549 11–1 U. Eocene | 0·44 | 0·22 |
| FLV GC/NA/926 549 11–1 U. Eocene | 0·44 | 0·22 |
| FLV GC/NA/927 549 8–4 M. Eocene | 0·44 | 0·22 |
| MLV GC/NA/932 549 16–3 U. Palaeocene | 0·46 | 0·20 |
| FRV GC/NA/928 549 8–4 M. Eocene | 0·43 | 0·21 |
| FRV GC/NA/929 549 8–4 M. Eocene | 0·45 | 0·21 |
| FRV GC/NA/930 549 11–1 L. Eocene | 0·44 | 0·21 |
| MRV GC/NA/931 549 11–1 L. Eocene | 0·44 | 0·18 |

*Diagnosis*. A small, elongate, subrectangular (male and FLV) to elongate subovate (FRV) species of *Krithe* with almost straight, subparallel dorsal and ventral margins. Anterior vestibulum moderately large, 'mushroom'-shaped with a narrow neck and directed postero-ventrally. Inner lamella wide, with sinuous line of concrescence and long RPC; ADRPC type 3A with AD 1, 2, 3 and 5 short to moderately long and elongate AD4. Sexual dimorphism slight; males relatively but not absolutely longer than females.

*Remarks*. This small, distinctive species is common only in the Lower Eocene of Hole 549 and disappears in the lower Middle Eocene (NP 15). *K. parvula* Deltel, 1964, described from the Middle and Upper Eocene of Aquitaine, is very similar in shape and external features to the present specimens. However, as Deltel did not illustrate the internal features, and her specimens are slightly larger (L = 0·52 mm), the present material is only compared to *K. parvula*.

### *Nomina nuda* species

*Discussion*. In addition to the seventeen species and subspecies detailed above, there are numerous quite distinctive *Krithe* species present in the Cenozoic of the North Atlantic (Pls 6–7; Text-figs 5–6). However, these are all too rare to be described formally; none of the species is represented by more than seven adult specimens and many are known from only one or two individuals. The stratigraphical ranges of nineteen *nomina nuda* species are given below, together with their occurrence.

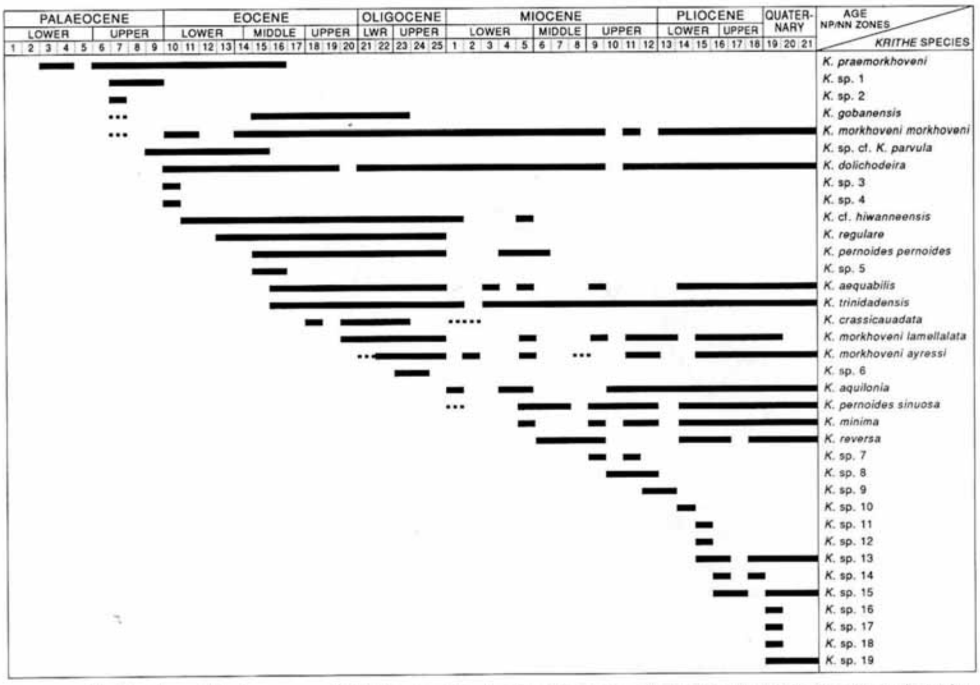
| Species | Location | Stratigraphical position |
|---|---|---|
| *Krithe* sp. 1 | DSDP Hole 549 | U. Palaeocene, NP7–9 |
| *Krithe* sp. 2 | DSDP Hole 549 | U. Palaeocene, NP 7 |
| *Krithe* sp. 3 | DSDP Hole 550 | L. Eocene, NP 10 |
| *Krithe* sp. 4 | DSDP Hole 550 | L. Eocene, NP 10 |
| *Krithe* sp. 5 | DSDP Hole 549 | M. Eocene, NP 15–16 |
| *Krithe* sp. 6 | DSDP Hole 549A | U. Oligocene, NP 23–24 |
| *Krithe* sp. 7 | DSDP Hole 549A | U. Miocene, NN 9, 11 |
| *Krithe* sp. 8 | DSDP Hole 610 | U. Miocene, NN 11 |
| | DSDP Hole 610E | U. Miocene, NN 10, 12 |
| *Krithe* sp. 9 | DSDP Hole 607 | L. Pliocene, NN 13–14 |
| *Krithe* sp. 10 | DSDP Hole 606A | L. Pliocene, NN 14 |
| *Krithe* sp. 11 | DSDP Hole 607 | L. Pliocene, NN 15 |
| *Krithe* sp. 12 | DSDP Hole 609B | L. Pliocene, NN 15 |
| *Krithe* sp. 13 | DSDP Hole 607 | Quaternary, NN 19 |
| | DSDP Hole 608 | L. Pliocene, Quaternary, NN 15, 18–19 |
| | DSDP Hole 609B | Quaternary, NN 19 |
| | DSDP Hole 610 | U. Pliocene, NN 16 |
| *Krithe* sp. 14 | DSDP Hole 607 | U. Pliocene, NN 16 |
| | DSDP Hole 611D | U. Pliocene, NN 18 |
| *Krithe* sp. 15 | DSDP Hole 609C | U. Pliocene, NN 16–17 |
| | DSDP Hole 609A | Quaternary, NN 20–21 |
| | DSDP Hole 610 | Quaternary, NN 19 |
| | DSDP Hole 610C | Quaternary, NN 21 |

| Species | Location | Stratigraphical position |
|---|---|---|
| *Krithe* sp. 16 | DSDP Hole 609B | Quaternary, NN 19 |
| *Krithe* sp. 17 | DSDP Hole 606A | Quaternary, NN 19 |
| *Krithe* sp. 18 | DSDP Hole 607 | Quaternary, NN 19 |
| *Krithe* sp. 19 | DSDP Hole 606A | Quaternary, NN 19–21 |

## BIOSTRATIGRAPHY

Several authors have attempted to utilize *Krithe* in Cainozoic biostratigraphy, though usually in conjunction with other genera. The work of van den Bold (1977) in the Caribbean region and the South Atlantic is especially notable, while others have recognized some stratigraphically useful species in the Mediterranean, e.g. Ascoli (1968), Sissingh (1972), and Ciampo (1980, 1986). However, there has been relatively little work in the North Atlantic, mostly limited to the studies of Ducasse and Peypouquet (1979) in the upper Cainozoic of the eastern North Atlantic and that of Peypouquet (1977, 1979) with reference to Pleistocene glacial cycles. More recent biostratigraphical utilization of the genus, among other North Atlantic deep water taxa, are by Whatley and Coles (1991) and Whatley (1993).

The neglect of *Krithe* in biostratigraphical studies from deep-water sediments, despite its high abundance and diversity, is undoubtedly a consequence of the formidable problems of consistent species discrimination within the genus. Nevertheless, the careful discrimination of species throughout the Cainozoic of the North Atlantic in the present study has revealed the stratigraphical utility of several common species, The stratigraphical ranges of the seventeen described species of *Krithe* considered in this study are shown in Text-figure 7 to the level of the calcareous nannofossil



TEXT-FIG 7. Stratigraphical ranges of *Krithe* species in the Cenozoic of the North Atlantic, plotted against chronostratigraphy and calcareous plankton biozones.

NP and NN zones of Martini (1971). Also included are the stratigraphical ranges of the nineteen *nomina nuda* species listed above. This diagram clearly illustrates the importance of the genus as a biostratigraphical marker in the Tertiary of the North Atlantic. The consistency of new appearances in the succession bears impressive witness to the rapidity of evolution in this taxon in the deep sea.

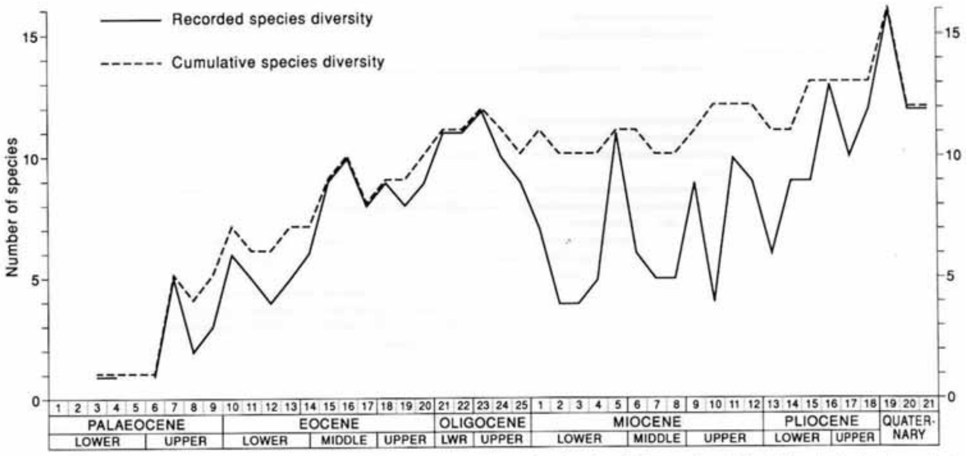
Certain species are entirely (*K. praemorkhoveni*, *K. gobanensis*, *K. regulare*, *K.* cf. *parvula*) or mostly (*K. crassicaudata*, *K.* cf. *hiwanneensis*, *K. pernoides pernoides*) confined to the Palaeogene, while others are confined to the Miocene to Quaternary interval (*K. reversa*, *K. minima*, *K. aquilonia*, *K. pernoides sinuosa*); the remainder span the boundary (*K. aequabilis*, *K. dolichodeira*, *K. morkhoveni* – all subspecies, and *K. trinidadensis*).

The most important first appearances for stratigraphical purposes are of *K. reversa* (NN 6, Middle Miocene), *K. minima* (NN 5, Middle Miocene), *K. aquilonia* (NN 1, Lower Miocene) and *K. pernoides sinuosa* (NN 5, Middle Miocene), while the most notable last occurrences are *K. gobanensis* (NP 23, Upper Oligocene), *K. regulare* (NP 25, Upper Oligocene), *K. crassicaudata* (NP 23, Upper Oligocene) and *K. praemorkhoveni* (NP 16, Upper Eocene).

The data in Text-figure 7 and the stratigraphical range chart for all North Atlantic Cainozoic benthonic Ostracoda given in Whatley and Coles (1991, fig. 4), indicate that this group in this environment has considerable potential as biostratigraphical markers. This information is augmented by that of Whatley (1993, table 1) who further extolled the virtues of benthonic ostracods as biostratigraphical indices in deep-sea environments in the Pacific and Indian Oceans, as well as the Atlantic.

## DIVERSITY AND PALAEOCEANOGRAPHY

The number of *Krithe* species present in each NP and NN zone in the North Atlantic may be used to show diversity trends in the taxon through the Cainozoic. The results are shown in Text-figure 8. Both recorded (which indicates the actual presence of a species in a given zone) and cumulative (which discounts the effect of temporary 'Lazarus' absences within the overall stratigraphical range of a species) have been calculated to enable comparison with Whatley and



TEXT-FIG. 8. Recorded and cumulative *Krithe* species diversity in the Cainozoic of the North Atlantic, plotted against chronostratigraphy and calcareous plankton biozones.

Coles (1991, table 1 and fig. 2) which show the diversity trends of the entire North Atlantic Cainozoic deep-water ostracod fauna.

From Text-figure 8 it is evident that *Krithe* steadily increased in both recorded and cumulative diversity from low levels in the Palaeocene to a peak in the late Oligocene (NP 23 zone). Subsequently, recorded *Krithe* species diversity plummeted in the early Miocene only to rise in an irregular series of peaks through the Neogene to a Cainozoic maximum in the Quaternary (NN 19 zone). However, the cumulative species diversity pattern shows no dramatic late Oligocene–early Miocene diversity and records a much more gradual rise in diversity through the Neogene to the same Quaternary maximum. It is this later pattern, by eliminating the effects of unequal sampling and taphonomy, that probably most closely reflects the true diversity of *Krithe* in the study area, although it certainly masks an environmental perturbation which was responsible for the temporary disappearance of a considerable number of species at this time. A similar diversity decline for the entire ostracod fauna of the Atlantic deep water is shown in Whatley and Coles (1991, fig. 2) who suggest that this early and mid-Miocene phenomenon was probably brought about by more sluggish circulation patterns in the North Atlantic consequent upon the closure of the Iberian Portal and effective isolation of the Tethys (Whatley and Coles 1987). The global temperature decrease of some 7–8 °C brought about by the expansion of the Antarctic Ice Cap (Stanley 1987) and the spillage of cold North Polar bottom waters into the North Atlantic over the subsided Greenland–Iceland–Faroes–Scotland Ridge, produced the equivalent of modern North Atlantic Deep Water (Schnikter 1980) and in this medium this characteristic fauna has evolved.

The essential features of *Krithe* diversity thus show strong similarities with the diversity pattern of the entire ostracode fauna demonstrated by Whatley and Coles (1991, fig. 2), namely the steep diversity increase through the Palaeogene to a late Oligocene peak, considerable reduction in diversity in the early Miocene and a stable to gradual diversity rise through the Miocene and Pliocene to a peak in the Quaternary. The mid-Pliocene warming interlude seems to be reflected in a diversity peak in *Krithe* followed by a late Pliocene decline. This is in turn succeeded by an early Quaternary peak which is the highest diversity for the Cainozoic for this taxon.

## ECOLOGY AND PALAEOECOLOGY

All species of *Krithe* are blind and smooth-shelled with elongate subcylindrical carapaces being the dominant shape-type. They are thus well adapted to an infaunal mode of life as burrowers in soft sediment substrates, principally fine sands, muds, and deep-water *Globigerina* and nannofossil oozes. *Krithe* is cosmopolitan, but is confined to fully marine waters with salinities greater than 35 parts per thousand. The very wide depth range of *Krithe* was first noted by Brady (1880) in the Challenger report, who recorded species from depths of 15 to 1825 fathoms (27–3340 m).

In shallow waters, *Krithe* is mainly cryophilic and confined to low-energy, soft sediment substrates, although a few warm-water species have been recorded (Whatley and Downing 1984). It is in the deep sea, at bathyal (1000–2000 m) and abyssal (> 2000 m) depths, where it is both abundant and diverse that *Krithe* is most significant. All records of deep-sea ostracod faunas include *Krithe*, which is normally the dominant genus below 1000 m. Indeed, *Krithe* frequently outnumbers all other ostracode species combined when the total number of valves is considered. This is demonstrated in Table 2, which details the composition of the Cainozoic deep-water North Atlantic ostracod fauna in terms of the percentage of individuals belonging to each genus for each age. The ten genera which comprise an average of 5 per cent of the individuals in any one age are shown, together with the percentage of total individuals in the other fifty-nine genera. These figures are calculated from sixty-six samples containing 100 or more specimens, comprising twenty-six from Hole 549, twenty-five from Hole 549A, one from Hole 550, eight from Hole 558 and six from Hole 563. Also included are thirty-three samples from the DSDP Leg 94 study of Whatley and Coles (1987) which contained 100 or more specimens.

From Table 2, it can be seen that *Krithe* comprises a mean of some 50 per cent (range 45 to 55 per cent) of Eocene and Oligocene faunas, and becomes progressively more dominant during the

TABLE 2. The percentage generic composition of the deep water North Atlantic fauna by age. The ten genera which comprise 5 per cent or more of the individuals in any age are shown, with the percentage of total individuals in the remaining fifty nine genera. (@ = genus absent; × = genus is present but comprises < 1 per cent of the fauna in that age.) Ages are early (E), middle (M) and late (L) divisions of the Palaeocene (Pa), Eocene (E), Oligocene (O), Miocene (M) and Pliocene (P) epochs, and of the Quaternary (Q) Period.

| Age | LPa | EE | ME | LE | EO | LO | EM | MM | LM | EP | LP | EQ | LQ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. studied samples | 2 | 13 | 10 | 11 | 9 | 10 | 3 | 3 | 5 | 10 | 11 | 9 | 3 |
| *Argilloecia* | 7 | 5 | 15 | 11 | 9 | 10 | 4 | 1 | 1 | 4 | 4 | 3 | 5 |
| *Bairdia/Bairdoppilata* | 3 | 4 | 6 | 6 | 4 | 2 | 1 | 1 | 2 | 1 | × | × | × |
| *Cytherella* | 2 | 14 | 7 | 9 | 6 | 3 | × | 5 | 1 | 1 | × | × | × |
| *Cytheropteron* | @ | 1 | 1 | × | 1 | 2 | 1 | 1 | 1 | 2 | 4 | 5 | 4 |
| *Henryhowella* | @ | @ | 1 | 3 | 4 | 4 | 9 | 9 | 9 | 6 | 5 | 5 | 2 |
| *Krithe* | 69 | 55 | 46 | 49 | 51 | 48 | 45 | 52 | 60 | 64 | 68 | 67 | 67 |
| *Parakrithe* | @ | @ | 1 | 4 | 4 | 6 | 6 | 9 | 2 | 1 | 2 | × | × |
| *Poseidonamicus* | @ | @ | @ | @ | 1 | 5 | 4 | 3 | 11 | 8 | 6 | 6 | 10 |
| *Trachyleberidea* | 6 | 9 | 5 | 2 | 1 | 1 | @ | @ | @ | @ | @ | × | × |
| *Xestoleberis* | 1 | 1 | 2 | 3 | 3 | 2 | 5 | 1 | 1 | 1 | × | × | × |
| Others (59 genera) | 12 | 11 | 16 | 13 | 16 | 17 | 25 | 18 | 12 | 12 | 11 | 14 | 12 |

Miocene, to comprise on average, some two-thirds (64 to 68 per cent) of Pliocene and Quaternary faunas. This may be due to the greater palaeodepth of the Pliocene and Quaternary samples, relative to those from the Eocene and Oligocene. *Argilloecia* or *Cytherella* are usually the second most dominant genera in Palaeogene samples while *Poseidonamicus* is the next most abundant genus in terms of individuals from the upper Miocene to the Quaternary.

A major palaeoecological application of *Krithe* in recent years has been based upon the supposed relationship of anterior vestibular form with depth and the level of dissolved oxygen in sea water (Peypouquet 1975, 1977). It is argued that in high levels of dissolved oxygen (> 0·4 ml), species of *Krithe* with small vestibula and wide inner lamellae would predominate while in waters where oxygen levels were low (< 0·4 ml), vestibula would be large with narrow inner lamellae. It is further suggested that as a consequence of this relationship, past oxygen levels could be determined from the size of the anterior vestibulum and inner lamella, leading to the reconstruction of past oceanic oxygen levels. An attempt has been made to apply this to Cainozoic palaeoenvironments in the Atlantic (Peypouquet 1977, 1979) and to the study of Cretaceous–Tertiary boundary events in Tunisia (Peypouquet 1983).

In an attempt to investigate the validity of this hypothesis, the present-day water depth range of eleven species or subspecies which occur in the Quaternary and Recent of the North Atlantic have been calculated (see the taxonomic section for further details), and compared with their size and anterior vestibulum and ADRPC type, shown in Table 3.

Table 3 shows that those species with the broadest depth distribution are *K. dolichodeira* and *K. pernoides sinuosa* with large and small anterior vestibula respectively. Although species with small vestibula predominate at abyssal depths, the deepest known *Krithe* species in this study is *K. reversa* at 5726 m, which has a large 'pocket'-shaped anterior vestibulum. Therefore, the data from the present study cannot support the correlation of vestibular size with depth and, consequently, oxygen levels as proposed by Peypouquet (1977, 1979).

In addition, there is no obvious link between ADRPC type and water depth, with all three main types being present at abyssal depths. However, most species with ADRPC type 3A except the *K. pernoides* (i.e. the *K. trinidadensis* group) are confined to depths below 1000 m. These findings confirm those of Whatley and Zhao (1993) and Zhao and Whatley (1993) that there is no relationship between the size and shape of the anterior vestibulum, and depth or oxygen concentration. These authors also were able to discount the assertion by Peypouquet (1977, 1979)

TABLE 3. The present-day water depth range, anterior vestibulum type and antero-dorsal radial pore canal type. of the eleven *Krithe* species and subspecies present in the Quaternary and Recent of the North Atlantic.

| Species/subspecies | PDWD range | Vestibule type | ADRPC type |
|---|---|---|---|
| *K. reversa* | 803–5726 m* | Large 'pocket' | 1B |
| *K. aequabilis* | 1200–4000 m | Large 'pocket' | 2B |
| *K. dolichodeira* | 200–5440 m | Large 'mushroom' | 2B |
| *K. minima* | 739–4566 m* | Small crescentic | 2C |
| *K. mork. morkhoveni* | 739–5440 m* | Small 'mushroom' | 3A |
| *K. mork. lamellalata* | 2421–3422 m | Small 'mush.'/'Y' | 3A |
| *K. mork. ayressi* | 1500–3884 m | Large 'mushroom' | 3A |
| *K. trinidadensis* | 1080–5440 m | Small 'pock.'/'Y' | 3A |
| *K. aquilonia* | 938–4566 m | Small 'mush.'/'Y' | 3A |
| *K. per. pernoides* | 2414–3526 m | Small 'pocket' | 3A |
| *K. per. sinuosa* | 175–5440 m | Small 'pocket' | 3A |

* Almost all records are from water depths in excess of 1000 m.

that the overall size of species of *Krithe* increases with depth; this is confirmed by the size distribution with depth of the taxa considered in the present paper.

*Acknowledgements.* The authors thank their colleagues (Michael Ayress, Simon Barkham, Howard Davies, Sian Downing, Chris Harlow, Will Harpur and Christine Porter) at Aberystwyth for access to their research material and numerous valuable discussions. In particular, Chris Harlow is acknowledged for his part in the original formulation of the antero-dorsal radial core canal classificatory scheme for *Krithe*. Ian Gully and David Griffiths are thanked for their skills in draughtmanship and photography respectively. Graham Coles wishes to acknowledge the NERC studentship which made this study possible. Officers of DSDP/ODP are thanked for sending the various samples upon which much of this work is based.

## REFERENCES

ASCOLI, P. 1964. Preliminary ecological study on Ostracoda from bottom cores of the Adriatic Sea. *Pubblicazioni della Stazione Zoologica di Napoli*, **33**, 213–246.

—— 1968. Preliminary report on the Ostracoda of the type Tortonian. *Giornale di Geologia*, **35** (2), 31–54.

AYRESS, M. A. 1988. Late Pliocene to Quaternary Deep-Sea Ostracoda from the eastern Indian and southwestern Pacific Oceans. Unpublished Ph.D. thesis, University of Wales, Aberystwyth.

BAIRD, W. 1850. *The natural history of the British Entomostraca*. Ray Society of London, London, 364 pp.

BARKHAM, S. T. 1985. Recent Ostracoda from off the N.W. African coast. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

BASSIOUNI, M. A. A. 1962. Ostracoden aus dem Mittelmiozän in N.W. Deutschland. *Romeriana*, **3**, 1–123.

BENSON, R. H. and PEYPOUQUET, J.-P. 1983. The upper and mid-bathyal Cenozoic ostracode faunas of the Rio Grande Rise found on Leg 72 Deep Sea Drilling Project. *Initial Reports of the Deep Sea Drilling Project*, **72**, 805–818.

BOLD, W. A. VAN DEN 1946. Contribution to the study of Ostracoda with special reference to the Tertiary and Cretaceous microfauna of the Caribbean region. Dissertation, Utrecht University. Debussy, Amsterdam.

—— 1958. Ostracoda of the Brasso Formation of Trinidad. *Micropaleontology*, **4**, 391–418.

—— 1960. Eocene and Oligocene Ostracoda of Trinidad. *Micropaleontology*, **6**, 145–196.

—— 1966. Ostracoda of the Pozon Section, Falcon, Venezuela. *Journal of Paleontology*, **40**, 175–185.

—— 1968. Ostracoda of the Yague group (Neogene of the northern Dominican Republic). *Bulletin of American Paleontology*, **54**, 239–266.

—— 1969. *Messinella*, a new genus of Ostracoda in the Caribbean Cenozoic. *Micropaleontology*, **15**, 397–400.

—— 1977. Cenozoic marine Ostracoda of the South Atlantic. 495–519. *In* SWAIN, F. M. (ed.). *Stratigraphic micropaleontology of Atlantic Basin and borderlands*. Elsevier, Amsterdam.

BOLD, W. A. VEN DEN 1981. Distribution of Ostracoda in the Neogene of central Haiti. *Bulletin of American Paleontology*, **79**, 7–136.

BORNEMANN, J. G. 1855. Die mikroskopische Fauna des Septarienthones von Hermsdorf bei Berlin. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **7**, 1–167.

BRADY, G. S., CROSSKEY, H. W. and ROBERTSON, D. 1874. The Post-Tertiary Entomostraca. *Monograph of the Palaeontographical Society*, **28** (127), i–v + 1–232.

BREMAN, E. 1975. Ostracoda in a bottom core from the deep south-eastern basin of the Adriatic Sea. *Koninklijke Nederlandse Akademie van Wettenschappen, Series B*, **78**, 198–218.

—— 1976. *The distribution of ostracodes in the bottom sediments of the Adriatic Sea.* Vrije Universiteit Amsterdam, 165 pp.

BREMAN, G. S. 1880. Report on the Ostracoda dredged by H.M.S. Challenger during the years 1873–1876. *Report of the Scientific Results, Voyage of H.M.S. Challenger, Zoology*, **1**, 1–184.

BUBIKYAN, S. A. 1958. [Ostracods of the Paleogene deposits of the Erivan Basin.] *Izvestiya Akademii Nuak armyanskoi, Erevan, SSR (series Geology–Geography)*, **11**, 3–16. [In Russian.]

CIAMPO, G. 1980. Ostracodi Miocenici (Tortoniano–Messiniano) della regione di Ragusa (Sicilia). *Bolletino della Società Paleontologica Italiana*, **19**, 5–20.

—— 1981. Ostracoda fossili (Oligocene superiore–Serravalliano) del Monte Cammarata (Sicilia centro–occidentale) e del Ragusano (Sicilia sud–orientale). *Bolletino della Società Paleontologica Italiana*, **20**, 53–72.

—— 1986. Ostracodi del limite Tortoniano/Messiniano in alcune sezioni italiane. *Bolletino della Società Paleontologica Italiana*, **24**, 29–110.

COLES, G. P. 1985. Upper Miocene, Pliocene and Quaternary *Krithe* and *Parakrithe* from DSDP Leg 94, N. Atlantic. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

—— and WHATLEY, R. C. 1989. New Palaeocene to Miocene genera and species of Ostracoda from DSDP Sites in the North Atlantic. *Revista Española de Micropaleontologia*, **21**, 81–124.

COXILL, D. J. 1985. Deep water Recent Ostracoda from the South Atlantic around South Georgia, South Sandwich Islands and the Antarctic Peninsula and the littoral ostracods of the Falkland Islands. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

CRONIN, T. M. 1983. Bathyal ostracodes from the Florida–Hatteras Slope, the Straits of Florida and the Blake Plateau. *Marine Micropaleontology*, **8**, 89–119.

—— and COMPTON-GOODING, E. E. 1987. Cenozoic Ostracoda from DSDP Leg 95 off New Jersey (Sites 612 and 613). *Initial Reports of the Deep Sea Drilling Project*, **95**, 439–451.

DAINTY, E. J. 1984. Pleistocene Ostracoda from four DSDP Sites of the South-West Pacific. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

DAVIES, H. C. 1981. The areal and depth distribution of N.E. Atlantic Ostracods. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

DELTEL, B. 1964. Nouveaux ostracodes de l'Eocène et de l'Oligocène de l'Aquitaine méridionale. *Actes de la Société Linnéenne de Bordeaux*, **100**, 127–221.

DIECI, G. 1967. Riesame di alcune specie di ostracodi Tortoniani dell'Appennino settentrionale. *Bolletino della Società Paleontologica Italiana*, **6**, 3–17.

—— and RUSSO, A. 1964. Ostracodi Tortoniani dell'Appennino settentrionale (Tortona, Montegibbio, Castelvetro). *Bolletino della Società Paleontologica Italiana*, **3**, 38–88.

DINGLE, R. V., LORD, A. R. and BOOMER, I. D. 1990. Deep-water Quaternary Ostracoda from the continental margin off south-western Africa (SE Atlantic Ocean). *Annals of the South African Museum*, **99**, 245–366.

DOWNING, S. E. 1985. The taxonomy, palaeoecology, biostratigraphy and evolution of Pliocene Ostracoda from the W. Pacific. Unpublished Ph.D. thesis, University of Wales, Aberystwyth.

DUCASSE, O., GUERNET, C. and TAMBAREAU, Y. 1985. Paléogène. 257–311. *In* OERTLI, H. J. (ed.). Atlas des ostracodes de France. *Bulletin du Centre de Recherches Exploration et Production, Elf-Aquitaine*, **9**, 1–396.

—— and PEYPOUQUET, J.-P. 1979. Cenozoic ostracodes: their importance for bathymetry, hydrology and biogeography. 343–363. *In* MONTADERT, L. and ROBERTS, D. G. (eds). *Initial Reports of the Deep Sea Drilling Project*, **48**. US Government Printing Office, Washington.

ELANT, M.-O. 1985. Les ostracodes et les relations hydrologiques Atlantique–Méditerranée du dernier glaciaire à l'actuel. Thesis, Université de Bordeaux no. 2065.

GUILLAUME, M.-C., PEYPOUQUET, J.-P. and TETART, J. 1985. Quaternaire et Actuel. 337–377. *In* OERTLI, H. J. (ed.). Atlas des Ostracodes de France. *Bulletin du Centre de Recherches Exploration et Production, Elf-Aquitaine*, **9**, 1–396.

HANAI, T. 1959. Studies on the Ostracoda of Japan. Part 4. Family Cytherideidae Sars, 1925. *Journal of the Faculty of Science, Tokyo University*, **2**, 291–308.

HARPUR, W. K. 1985. Late Quaternary deep-sea Ostracoda from the extra-Iberian Portal region. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

HOWE, H. V. and LAW, J. 1936. Louisiana Vicksburg Oligocene Ostracoda. *Louisiana Geological Survey Bulletin*, **7**, 1–96.

HULINGS, N. C. 1967. Marine Ostracoda from the Western North Atlantic Ocean between Cape Hatteras, North Carolina, and Jupiter Inlet, Florida. *Bulletin of Marine Science*, **17**, 629–659.

JONES, T. R. and KIRKBY, J. W. 1989. On Carboniferous Ostracoda from Ireland. *Scientific Transactions of the Royal Dublin Society, Series 2*, **6**, 173–200.

KEIJ, A. J. 1957. Eocene and Oligocene Ostracoda of Belgium. *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique*, **136**, 1–210.

KEMPF, E. K. 1988. Index and bibliography of marine Ostracoda. 1, Index A. *Geologisches Institut der Universität zu Köln Sonderveröffentlichungen*, **50**, 1–762.

KUIPER, W. N. 1918. Oligocäne und Miocäne Ostracoden aus den Niederlanden. *Proefschrift Gebroeders Hoitsema, Gröningen*, 1–91.

LATREILLE, P. A. 1806. *Genera crustaceorum et insectorum*. Koenig, Paris.

LEROY, D. O. and LEVINSON, S. A. 1974. A deep-water Pleistocene micro-fossil assemblage from a well in the northern Gulf of Mexico. *Micropaleontology*, **20**, 1–37.

MARTINI, E. 1971. Standard Tertiary and Quaternary calcareous nannoplankton zonation. *Proceedings of the 2nd Planktonic Conference, Rome*, **2**, 739–785.

McKENZIE, K. G., MAJORAN, S., EMAMI, V. and REYMENT, R. A. 1989. The *Krithe* problem – first test of Peypouquet's hypothesis, with a redescription of *Krithe praetexta praetexta* (Crustacea, Ostracoda). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **74**, 343–354.

MORKHOVEN, F. P. C. M. VAN 1972. Bathymetry of Recent marine Ostracoda in the North-West Gulf of Mexico. *Transactions of the Gulf-Coast Association of Geological Societies*, **22**, 241–252.

MÜLLER, G. W. 1894. Die Ostracoden des Golfes von Neapel und der angrezenden Meeres-Abschnitte. *Fauna und Flora des Golfes von Neapel*, **21**, 1–404.

OERTLI, H. J. 1961. Ostracodes du Langhien-type. *Rivista Italiana di Paleontologia*, **67**, 17–44.

PEYPOUQUET, J.-P. 1975. Les variations des caractères morphologiques internes chez les ostracodes des genres *Krithe* et *Parakrithe*: relation possible avec le teneur en $O_2$ dissous dans l'eau. *Bulletin de l'Institut de Géologie du Bassin Aquitaine*, **17**, 81–88.

—— 1977. *Les ostracodes et la connaissance des paléomilieux profonds. Application au Cénozoïque de l'Atlantique Nord-Oriental*, Université de Bordeaux, 433 pp.

—— 1979. Ostracodes et paléoenvironnements. Méthodologie et application aux domaines profonds du Cénozoïque. *Bulletin, Bureau du Recherches Géologiques et Minières, 2ème série*, **4**, 3–79.

—— 1983. *Krithe* and *Parakrithe* in the Kef Section (Northeast Tunisia) around the Cretaceous–Tertiary boundary: palaeoecological implications. 510–519. *In* MADDOCKS, R. F. (ed.). *Applications of Ostracoda*. Department of Geosciences, University of Houston, 677 pp.

PIETRZENIUK, E. 1969. Taxonomische und biostratigraphische Untersuchungen an Ostracoden des Eozan 5 im Norden der Deutschen Demokratischen Republik. *Paläontologische Abhandlungen*, **4**, 1–162.

POKORNY, V. 1980. The genus *Krithe* (Ostracoda, Crustacea) in Palaeogene deep-sea deposits in the Zdanice Unit, Moravia, Czechoslovakia. *Casopsis pro Mineralogii a Geologii*, **25**, 338–349.

PORTER, C. 1984. Late Quaternary Ostracoda from the N.E. Atlantic. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

PURI, H. S. and HULINGS, N. C. 1976. Designation of lectotypes of some ostracodes from the Challenger Expedition. *Bulletin of the British Museum (Natural History), Zoological Series*, **29**, 251–314.

RUGGIERI, G. 1962. Gli ostracodi marini del Tortoniano (Miocene medi superiore) di Enna, nella Sicilia centrale. *Paleontologia italiana Memorie*, **2**, 1–68.

—— 1974. Revisione della ostracofauna marina Quaternaria di Imola (Bologna). *Revista Española de Micropaleontología*, **6**, 419–446.

RUSSO, A. 1968. Ostracodi Tortoniani di Montebaranzone (Appennino settentrionale Modenese). *Bolletino della Società Paleontologica Italiana*, **7**, 6–56.

SARS, G. O. 1866. Oversigt af Norges marine ostracodes. *Förhandlinger i Videnskabsselskabet i Kristiania*, **7**, 1–130.

SCHNITKER, D. 1980. Global palaeoceanography and its deep-water linkage to the Antarctic glaciation. *Earth Sciences Reviews*, **16**, 1–20.

SCHREMETA, V. 1969. *The Paleogene ostracods of the Ukraine*. Isdatel Lvov University, 274 pp.

SEGUENZA, G. 1880. Le Formazioni Terziarie nella provincia di Reggio (Calabria). *Memorie della R. Accademia dei Lincei. Classe di scienze fisiche e naturali*, **6**, 1–443.

SHAKIN, A. 1991. Cenomanian/Turonian ostracods from Gelel Nezzarat, southwestern Sinai, Egypt, with observations on $\delta$13C values and the Cenomanian/Turonian boundary. *Journal of Micropalaeontology*, **10**, 133–149.

SISSINGH, W. 1972. Late Cenozoic Ostracoda of the south Aegean Island Arc. *Utrecht Micropaleontological Bulletins*, **6**, 1–187.

SMITH, P. D. 1983. Quaternary deep sea Ostracoda from the Southwest Pacific. Unpublished M.Sc. thesis, University of Wales, Aberystwyth.

STEINECK, P. L. 1981. Upper Eocene to Middle Miocene ostracode faunas and paleo-oceanography of the North Coastal Belt, Jamaica, West Indies. *Marine Micropaleontology*, **6**, 339–366.

—— BREEN, M., NEVINS, N. and O'HARA, P. 1984. Middle Eocene and Oligocene deep-sea Ostracoda from the Oceanic Formation, Barbados. *Journal of Paleontology*, **58**, 1463–1496.

—— DEHLER, D., HOOSE, E. and McCALLA, D. 1988. Oligocene to Quaternary ostracodes of the Central Equatorial Pacific (Leg 85, DSDP–IOPD). 597–617. *In* HANAI, T., IKEYA, N. and ISHIZAKI, K. (eds). *Evolutionary biology of Ostracoda. Its fundamentals and applications*. Kodansha–Elsevier, Amsterdam, 1361 pp.

UFFENORDE, H. 1981. Ostracoden aus dem Oberoligozän und Miozän des unteren Elbe-gebeites (Niedersachsen und Hamburg, NW Deutsches Tertiarbecken). *Paläontologisches Abhandlungen*, *A*, **172**, 103–198.

WHATLEY, R. C. 1970. Scottish Callovian and Oxfordian Ostracoda. *Bulletin of the British Museum* (*Natural History*), *Geological Series*, **19**, 300–358.

—— 1993. Ostracoda as biostratigraphical indices in Cainozoic deep-sea sequences. *High Resolution Stratigraphy*, **70**, 155–167.

—— and COLES, G. P. 1987. The Late Miocene to Quaternary. Ostracoda of Leg 94, Deep Sea Drilling Project. *Revista Española de Micropaleontología*, **19**, 33–97.

—— —— 1990. Global change and the biostratigraphy of North Atlantic Cainozoic deep water Ostracoda. *Journal of Micropalaeontology*, **9**, 119–132.

—— and DOWNING, S. E. 1983. Middle Miocene Ostracoda from Victoria, Australia. *Journal of Micropalaeontology*, **2**, 83–104.

—— and ZHAO QUANHONG 1993. The *Krithe* problem; a case history of the distribution of *Krithe* and *Parakrithe* (Crustacea, Ostracoda) in the South China Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **103**, 281–297.

YASSINI, I. 1969. Ecologie des associations d'ostracodes du Bassin d'Arcachon et du littoral Atlantique. Application à l'interprétation de quelques populations du Tertiaire Aquitaine. *Bulletin de l'Institut de Géologie du Bassin d'Aquitaine*, **7**, 1–288.

ZHAO QUANHONG and WHATLEY, R. C. 1993. [The ostracod genera *Krithe* and *Parakrithe* in the South China Sea: implications for palaeoceanography.] 141–156. *In* YE ZHIZHENG and WANG PINXIAN (eds). *Contributions to late Quaternary paleoceanography of the South China Sea*. Qingdao Ocean University Press, Beijing, 329 pp. [In Chinese with English abstract.]

G. P. COLES

R. C. WHATLEY

A. MOGUILEVSKY

Micropalaeontology Research Group
Institute of Earth Studies
University of Wales
Aberystwyth, Dyfed SY23 3DB, UK

Typescript received 16 January 1993
Revised typescript received 1 July 1993

*Editorial note*. It is the policy in *Palaeontology* to use the International Union of Geological Sciences chronostratigraphical nomenclature. The authors of this paper are opposed to the spelling 'Cenozoic' given in the IUGS scheme, and prefer the etymologically more correct 'Cainozoic'. In view of the strength of feeling they expressed on this matter, the Editorial Board has used 'Cainozoic' in this paper.