Neogene to Recent Species of *Krithe* (Crustacea: Ostracoda) from the Tasman Sea and off Southern Australia with Description of Five New Species

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ABSTRACT. The ostracod genus *Krithe* is reported from four grab, two box-core, 62 coretop samples, and Neogene to Quaternary DSDP cores from the abyssal and bathyal regions of the Tasman Sea and off southern Australia. Species identification followed the taxonomic system proposed by Coles *et al.* (1994), in which the anterodorsal radial pore canals are of fundamental importance. A total of 19 species are recognised, five species are described as new: *K. comma*, *K. dilata*, *K. pseudocomma*, *K. prolata*, and *K. triangularis*. Fifteen species are referred to previously described species, and the remaining rare species are left in open nomenclature. Although no living specimens have been recovered, shells of all species have been found in modern sediments and are, therefore, considered to be extant. Overall, the stratigraphic distribution of the species demonstrates an increase in diversity from 3 to 19 species since the Early Miocene, with no extinction. The bathymetric range of most species is wide, though in certain species there are significant differences between the two study regions, such as on the Australian Continental Slope, the relatively much deeper occurrences of *K. triangularis* and *K. marialuisae*, and the absence of *K. dolichodeira* a species found commonly elsewhere. An explanation for such differences is most likely to relate to nutrient, substrate, and oceanographic differences between the two regions.
The benthonic ostracod crustacean genus *Krithe* (Krithidae, Cytheracea, Podocopida) is abundant and widespread in the marine environment, absent only in shallow tropical waters. Despite its wide distribution, it is poorly documented in the Southwest Pacific. Perhaps the most notable study of species from this region is still the pioneering cruise report of the H.M.S. Challenger by Brady (1880). Subsequent studies have avoided identifying *Krithe* to species level, mainly because of the difficulty in classifying taxa with smooth external surfaces which offers few diagnostic characters, and additionally, internal soft-parts are rarely present for study.

Comprehensive studies of *Krithe* are limited mainly to the North Atlantic. The first of these (Peyrouquet, 1975, 1977, 1979), reported considerable intraspecific variation, especially in the anterior vestibulum and carapace size. It was proposed that the anterior vestibulum size of different *Krithe* species is inversely proportional to the dissolved oxygen concentration at the sediment-water interface. That large and small vestibule types are often found in the same sample is dismissed by proponents of the hypothesis as inappropriate sampling: carapaces are an instantaneous record of environmental conditions, and that any one sample may include a number of seasonal morphotypes (Carbonel et al., 1997). In recent years, the earlier claims have been challenged (Whatley & Zhao, 1993; van Harten, 1995, 1996) and the taxonomy has been extensively revised often resulting in further subdivision of previously designated species (Coles et al., 1994). In our view, this alternative, more conservative concept of *Krithe* sets limits to intraspecific variation more consistent with that usually observed in species of other podocopid ostracod genera. Such methods have also been employed in other independent, contemporary studies (e.g., Abate et al., 1993).

Biological data of *Krithe* is lacking, though significant observations on a living species, *Krithe praetexta praetexta*, from the Gullmar Fjord, Sweden, has been made in recent years (McKenzie et al., 1989; Majoran & Agrenius, 1995; Agrenius et al., 1997). Elofson (1941) reported an infaunal mode of life for that species, which has been confirmed by observations on living cultures; the species appears to live >1 cm in the sediment (Majoran & Agrenius, 1995). Careful box-core sampling in water depths up to 1,000 m, off California, has also revealed living specimens (rose bengal stained with intact soft-parts) of several species, present usually 1 cm below the sediment surface (Rathburn, 1998, pers. comm.). Given the similarity in carapace shape, such an infaunal mode of life might occur in all but perhaps the most rotund species of *Krithe*. Investigations into the hypothesis concerning the anterior vestibule size and oxygen content of the ambient seawater, in living populations, has been inconclusive (McKenzie et al., 1989).

The purpose of the present study is twofold: (a) to describe new species of *Krithe* and document the distribution of all species collected during our extensive sampling of deep-sea sediments off New Zealand and southeast Australia. (b) To present the results of direct comparison of our Southwest Pacific material with Atlantic specimens of Coles et al. (1994), applying the anterodorsal radial pore canal (ADRPC) type system proposed by Coles et al. to initially identify the species.

### Material and methods

Material for this study was taken from one grab, 68 coretop, and two box-core samples in the Tasman Sea and Continental Slope regions off southern Australia. Many of the cores also provided us with numerous samples of Quaternary age, dated largely by oxygen isotopic study of the cored sequence. In addition, we have included Pliocene and Pleistocene material from Deep Sea Drilling Project (DSDP) sites of the area, information embodied largely in an unpublished thesis completed during an extensive study programme, co-ordinated by one of us (RCW), investigating deep-sea Ostracoda of the Southwest Pacific (Ayress, 1988; Downing, 1985; Smith, 1983). Undocumented Tertiary material from DSDP sites 592–594 was also made available to us courtesy of Dr K. Swanson (University of Canterbury, New Zealand). Specimens from all nanofossil zones of the Neogene are well preserved and are considered in this study. Poor preservation or undocumented internal carapace features, prevented us from including available Palaeogene data. Table 1 lists details of the site localities (Fig. 1). Ostracod specimens were extracted from the sediment by immersing the samples overnight in a weak 3% solution of hydrogen peroxide and subsequently washing them through a 63 micron mesh sieve. Specimens obtained are disarticulated valves and occasional carapaces. No internal soft-part material was found.

All specimens have been deposited in the micropalaeontological collections of the Geology Department Museum, Australian National University, Canberra. The catalogue numbers are prefixed ANU.

### Systematic palaeontology and comments on species distributions

**Krithidae Mandelstam in Bubikyan, 1958**

**Krithe** Brady, Crosskey & Robertson, 1874

Type species. *Ilyobates praetexta* Sars, 1866

### Discussion

We found invaluable the system of initial identification based on the nature of the anterodorsal radial pore canals (ADRPC types) indicated by Coles et al. (1994), and the following species are ordered according to them. Coles et al. observed that, of the five radial pore canals (RPC’s) in the anterodorsal region, within a species, one particular canal is much longer than the others. The ADRPC types are based on identifying which is the longest canal. Where the 3rd canal (counting away from the dorsal margin) is longest = type 1, the 2nd canal longest = type 2, the 4th canal longest = type 3. See Fig. 2 and Coles et al. (1994, text-figure 1) for additional explanation of terminology.

Further subdivision of the categories was proposed where canals are short, missing, or present as a normal pore. Since the width of the fused zone can vary, short ADRPC’s may be present as a normal pore close to the inner margin. It follows that in order to recognise natural groupings, normal pore canals (NPC’s) should be considered in ADRPC type recognition where they vary intraspecifically from NPC to RPC, or where they can be shown to be homologous with RPC’s in other species. For example, in *Krithe reversa*, AD 2 (the canal immediately below the dorsal–most anterodorsal radial pore canal) is considered by Coles et al. (1994) to be...
present as a normal pore close to the inner margin. Therefore, the species has ADRPC type 1, rather than type 2, a designation if one was to ignore the normal pore in question.

For this reason, we take great care in illustrating normal pores close to the inner margin. We are less confident that the subdivisional groupings of the ADRPC types can be recognised consistently for the following reasons. (a) The width of the fused zone shows significant variability. (b) NPC’s close to the inner margin can be confused with false RPC’s when the shell is very thick, translucent, or strongly inflated, causing oblique viewing of the canal. (c) Removal of obscuring sediment retained in the narrow zone between the line of concrescence and the inner margin anterodorsally can be difficult.

The following abbreviations are used: A = adult, LV = left valve, RV = right valve, AD = anterodorsal, RPC = radial pore canal, ADRPC = anterodorsal radial pore canal, NPC = normal pore canal.

Key to Southwest Pacific Krithe species

1 Anterodorsal radial pore canal pattern of Type 1 (AD 3 longest) .................................................. 2

— Anterodorsal radial pore canal pattern of Type 2 (AD 2 longest) .................................................. 10

— Anterodorsal radial pore canal pattern of Type 3 (AD 4 longest) .................................................. 14

2 Left valve overlaps right valve ........................................................................................................ 3

— Right valve overlaps left valve ...................................................................................................... K. reversa

3 Large (length usually greater than 1 mm) ......................................................................................... 4

— Medium to small (length usually less than 1 mm) .......................................................................... 5
4  Dorsal margin strongly convex; lateral outline triangular ..................................... *K. triangularis*
   — Lateral outline subrectangular to subrhomboidal ........................................... *K. dolichodeira*
5  Anterior vestibulum semicircular in lateral outline ........................................... 6
   — Anterior vestibulum mushroom or hook-shaped ............................................... 7
6  Medium sized, moderately well inflated ............................................................... *K. antisawanensis*
   — Small, compressed, usually with long, straight RPC’s .................................... *K. compressa*
7  Anterior vestibulum narrow and upward curved .................................................... 8
   — Anterior vestibulum mushroom-shaped ............................................................. 9
8  Anterior vestibulum very narrow; posterodorsal inner lamella
   wide .................................................. *K. minima*
   — Anterior RPC’s often branching; posterodorsal inner lamella
   moderately narrow ............................................................. *K. marialuisae*
9  Carapace moderately well inflated, muscle scars small and
   undivided .................................................. *K. posticiliva*
   — Carapace weakly inflated; muscle scars long, uppermost scar
   subdivided .................................................. *Krithe* sp. 1
10 Carapace small, anterior vestibulum small ......................................................... 11
    — Carapace medium to large sized and subrectangular ...................................... 12
    — Carapace very large and tumid ................................................................. *Krithe* sp. 2
11 Anterior vestibulum bilobed .................................................................................. *K. droogeri*
   — Anterior vestibulum at mid-height and elongate ............................................. *K. perpulchra*
12 Lateral outline subovate; strongly sexually dimorphic; uppermost
   adductor muscle scar a reclined “F” shape ......................................................... *K. prolata*
   — Outline subrectangular; uppermost adductor muscle scar “U”
   shaped .................................................. *K. dilata*
   — Outline subrectangular; uppermost adductor muscle scar
   subdivided .................................................. 13
13 Carapace weakly inflated; males strongly sloped dorsally; anterior
   vestibulum mushroom-shaped ................................................................. *K. comma*
   — Carapace moderately well inflated; sexual dimorphism slight;
   anterior vestibulum strongly downturned ...................................................... *K. pseudocomma*
14 Carapace very small; anterior RPC’s long ......................................................... *K. pernoides sinuosa*
   — Carapace medium to large (length usually less than 1 mm); anterior
   vestibulum mushroom-shaped ................................................................. *K. morkhoveni morkhoveni*
   — Carapace very large (length usually greater than 1 mm); anterior
   vestibulum “T” shaped ................................................................. *K. trinidadensis*
Figure 2. Recognition of the three patterns of anterodorsal radial pore canals (ADRPC types), illustrated by camera lucida drawings of internal valve features. All figures are external views. Anterodorsal radial pore canals or homologous normal pore canals, are numbered 1–4. The three patterns are defined most readily by identifying which of the canals, 1–3 in the anterodorsal region, is the longest. Type 1, canal 3 is longest, shown for example in A, B (K. compressa, expanded vestibule form, female RV, ANU 57036, and male RV, ANU 57038, respectively), C (K. minima, female RV, ANU 57052), D (K. dolichodeira female RV, ANU 57044), E (K. triangularis, expanded vestibule form, male LV, ANU 57011, image inverted for ease of comparison), and F (K. reversa female LV, ANU 57034, image inverted for ease of comparison). Note that canal 2 is usually a normal pore close to canal 1. It occurs as a short radial pore canal where the fused zone is wide, see C (see also K. reversa illustrated by Coles et al., 1994, text-fig. 3D). Canal 4 is always a normal pore. Type 2, canal 2 is longest, and probably homologous to the normal pore close to canal 1 of Type 1 species (the normal pore is absent in Type 2 species); shown for example in G and H (K. comma, male RV, ANU 57023, and expanded vestibulum form of male RV, ANU 57026, respectively). Note that where the fused zone is narrow canal 3 is a normal pore, H, and canal 4 is always a normal pore. Type 3, canal 4 is longest, shown for example in I and J (K. Trinidadensis, expanded vestibulum form, female RV, ANU 57075, and male RV, ANU 57078, respectively). Note that where the fused zone is narrow canals 2 and 3 are normal pores, see I.
**ADRPC TYPE 1**

*Krithe compressa* (Seguenza, 1880)

*Hlyobates compressa* Seguenza, 1880: 325; pl. 17, figs. 30, 30a.

*Krithe aequabilis* Ciampo, 1986: 87; pl. 3, figs. 1–2;—Coles, Whatley & Moguilevsky, 1994: 78; pl. 1, figs. 7–12; text-fig. 3E–K.

*Krithe compressa* (Seguenza).—Ruggieri, 1991: 60, figs. 5–7.—Abate, Barra, Aiello & Bonaduce, 1993: 354; pl. 5, figs. 1–5; pl. 17, figs. 1, 2.

*Krithe* sp. 5 Whatley & Zhou, 1993: fig. 3.8.

Remarks. We concur with Abate et al. (1993) that *K. compressa* is a senior synonym of *K. aequabilis* Ciampo, 1986. In overall shape it is very similar to *K. marialuisae*. Abate et al. described from the Plio-Pleistocene of Sicily. However, the anterior vestibule of *K. compressa*, although variable in shape, is usually less upturned than it is in *K. marialuisae*, and the radial pore canals do not bifurcate as they do in the latter species. In addition, *K. compressa* can be distinguished from *K. marialuisae* by its weaker inflation. Both species are common in our material.

The width of the anterior fused zone varies somewhat, and the normal pore close to AD 1 sometimes becomes a short AD 2 (Coles et al., 1994). In species which have ADRPC of type 2 there is no normal pore in this position but instead a long RPC is present. For this reason we suggest that the normal pore is homologous to AD 2 in other species. Therefore, to maintain natural relationships of the ADRPC system, we include the normal pore when counting ADRPC’s. Thus, we assign this species to an ADRPC category of type 1B.

Distribution. Occurs widely throughout the study region at water depths from 759 to 3281 m.

Stratigraphical range. Late Miocene (NN 11a) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593.

*Krithe antisawanensis* Ishizaki, 1966


Remarks. This species appears to be identical to *K. reversa* Bold except in having normal overlap (Ishizaki, 1966). Like *K. reversa* there is a normal pore close to AD 1 homologous to AD 2.

Distribution. This is the most widespread species of this study, ranging in depth from 686 to 3403 m.

Stratigraphical range. Middle Miocene (NN 6) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593.

*Krithe dolichodeira* Bold, 1946

*Parakrithe hemideclivata* Ruan in Ruan & Hao, 1988: 272, pl. 45, figs. 12–15.

*Krithe spatularis* Dingle, Lord & Boomr, 1990: 272, figs. 16D–F, 17B, 18E.

*Krithe hemideclivata* (Ruan).—Whatley & Zhou, 1993: fig. 3.9.

Remarks. The characteristic mushroom shaped anterior vestibulum varies in our material, particularly in the width of the neck and dorsally. In this regard, and also in the lateral outline, our material is very close to an Atlantic species illustrated by Coles et al. (1994, text-fig 3AA–DD) as *Krithe* sp. cf. *K. hiwanneensis* (Howe & Law). However, our material is much larger than that species. In size it closely matches those specimens examined by Dingle et al. (1990) (named *K. spatularis*) from off South Africa, and also Quaternary specimens cited by Coles et al. (1994: 81). This is to be expected given the relatively young age of our material.

Distribution. Recorded in our study region at depths from 686 to 3281 m, only in the eastern and northern parts of the Tasman Sea.

Stratigraphical range. Late Miocene (NN 11b) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593. The species is also known to occur much earlier from the Early Eocene zone NP 10 (Coles et al., 1994).

*Krithe marialuisae*

Abate, Barra, Aiello & Bonaduce, 1993

*Krithe dolichodeira* Bold, 1946: 75, pl. 4, figs. 14a,b.—Coles, Whatley & Moguilevsky, 1994: 81; pl. 1, figs. 13–18; text-fig. 3L–Q.

Remarks. The characteristic mushroom shaped anterior vestibulum varies in our material, particularly in the width of the neck and dorsally. In this regard, and also in the lateral outline, our material is very close to an Atlantic species illustrated by Coles et al. (1994, text-fig 3AA–DD) as *Krithe* sp. cf. *K. hiwanneensis* (Howe & Law). However, our material is much larger than that species. In size it closely matches those specimens examined by Dingle et al. (1990) (named *K. spatularis*) from off South Africa, and also Quaternary specimens cited by Coles et al. (1994: 81). This is to be expected given the relatively young age of our material.

Distribution. Recorded in our study region at depths from 686 to 3281 m, only in the eastern and northern parts of the Tasman Sea.

Stratigraphical range. Late Miocene (NN 11b) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593. The species is also known to occur much earlier from the Early Eocene zone NP 10 (Coles et al., 1994).

*Krithe marialuisae*

Abate, Barra, Aiello & Bonaduce, 1993

Figs. 3I, 8G,H

Remarks. The Sicilian material described by Abate et al. (1993) is somewhat smaller (length of holotype 0.58 mm), but in all other respects our material appears to conform to this species. It is similar to *Krithe sphaenoidea* Ruan (in Ruan & Hao, 1988), from the Okinawa Trough. However, judging from the illustrations given, that species appears to have a more convex ventral margin and straighter anterior RPC’s.

Distribution. The species is distributed throughout the study region, ranging in depth from 1066 to 2860 m.

Stratigraphical range. Middle Miocene (NN 7) to Recent, based on core records of DSDP sites 207, 208, 284, 592 and 593.
Figure 3. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–D, Krithe compressa Seguenza, A, female right valve (ANU 57036), 71GC44, 100 cm, B, female left valve (ANU 57035), SO-36-61, 157 cm, C, male left valve (ANU 57037), 71GC44, 15 cm, Holocene, D, male right valve (ANU 57038), 71GC44, 15 cm, Holocene; E–F, Krithe antisawanensis Ishizaki, E, female right valve (ANU 57040), 67GC03, 274 cm, F, male right valve (ANU 57042), 67GC03, 280 cm; G, H, Krithe dolichodeira Bold, G, female right valve (ANU 57044), SO-36-61, 144.5 cm, H, male right valve (ANU 57046), SO-36-61, 157 cm; I, J, Krithe marialuisae Abate et al., I, female left valve (ANU 57047), 1/86 6GC3, 125 cm, J, male left valve (ANU 57049), SO-36-61, 144.5 cm; K, L, Krithe minima Coles et al., K, male left valve (ANU 57053), SO-36-61, 117 cm, L, female left valve (ANU 57051), SO-36-61, 148.5 cm; M, N, Krithe posticivla Hao, M, female left valve (ANU 57055), 71GC44, 15 cm, N, male left valve (ANU 57057), 71GC26, 15 cm; O, Krithe reversa Bold, female left valve (ANU 57034), 71GC26, 22 cm; P, Q, Krithe sp. 1, P, female? left valve (ANU 57017), 105GC20, coretop, Q, female? right valve (ANU 57018), 105GC20, coretop.
Krithe minima
Coles, Whatley & Moguilevsky, 1994

Figs. 2C, 3K,L, 8I

*Krithe minima* Coles, Whatley & Moguilevsky, 1994: 88; pl. 2, figs. 16–18; pl. 3, figs. 1–5; text-fig. 3EE–JJ.

**Remarks.** The species is distinct by virtue of its relatively small size, very narrow crescentic anterior vestibule, and wide posterodorsal inner lamella. In our material there are two short anterodorsal radial pore canals (AD 1 and AD 2), AD 2 sometimes being present as a normal pore. Thus, the elongate radial pore is AD 3 indicative of ADRPC Type 1A, and IB where AD 2 is a normal pore.

**Distribution.** Found at water depths of 1066 to 3281 m in the Tasman Sea.

**Stratigraphical range.** Early Miocene (NN 1) to Recent, based on core records of DSDP sites 206, 207, 208, 284, 592 and 593. The species is very common throughout the Neogene.

*Krithe posticliva* (Hao in Ruan & Hao, 1988)

Figs. 3M,N, 8K,L

*Parakrithe posticliva* Hao in Ruan & Hao, 1988: 273, pl. 45, figs. 8–11; Ruan, 1989: 121, pl. 22, figs. 14, 15.

**Remarks.** The mushroom-shaped anterior vestibulum of this species is sometimes greatly expanded proximally. *Krithe posticliva* is similar to *Krithe exigua* and *K. marialuisae*, both described from the Plio-Pleistocene of Sicily by Abate et al. (1993). However, *K. posticliva* differs from both species in its more truncate posterior margin and is more elongate.

**Distribution.** The species is rare in our study, found only on the eastern Australian continental slope from 989 to 1989 m.

**Stratigraphical range.** Late Pliocene (NN 16) to Recent, based on core records of DSDP site 593.

*Krithe reversa* Bold, 1958

Figs. 2F, 3O, 8M

For comprehensive pre-1988 synonymy see Coles et al. (1994).

*Krithe reversa* Bold, 1958: 404, pl. 1, figs. 4a–g;–Coles, Whatley & Moguilevsky, 1994: 77; pl. 1, figs. 1–6;–text-fig. 3A–D.

*Krithe tumida* Nohara, Itose & Tabuki, 1988: pl. 2, fig. 1.

*Krithe sawanensis* Hanai, 1959;–Ruan & Hao, 1988: 269; pl. 40, figs. 21–23; pl. 44, figs. 11–17;–Ruan, 1989: 121, pl. 22, fig. 12.–Whatley & Zhao, 1993: figs. 2, 3.–Zhou & Ikeya, 1992: 1108, fig. 3 (uppermost), fig. 7 (lower), figs. 9.1–9.3, figs. 10.1–10.3.

*Krithe* sp. 4 Dingle, Lord & Boomer, 1990: 282, figs. 17D, 18F, 22E.

**Distribution.** This species is not common, but is widely distributed, occurring at almost all sites in our study region. It was found at depths from 850 to 3552 m.

**Stratigraphical range.** Early Pliocene (NN 13) to Recent, based on core records of DSDP sites 206, 208 and 284. The earliest known record of the species is Middle Miocene zone NN 6 (Coles et al., 1994).

*Krithe triangularis* n.sp.

Figs. 2E, 4A–H, 8N,O

*Krithe* sp. 14 Coles, Whatley & Moguilevsky, 1994: text-fig. 6T,U.

**Etymology.** Latin, triangular. Referring to the triangular lateral outline especially of males of this species.

**Type material and dimensions.** Holotype, ANU 57011, male LV, length 1.26 mm, height 0.58 mm. Paratypes: ANU 57012, male RV, length 1.24 mm, height 0.55 mm, core SO-36-61, interval 37 cm; ANU 57013, female LV, length 1.12 mm, height 0.61 mm, core SO-36-61, interval 157 cm; ANU 57014, female RV, length 1.08 mm, height 0.57 mm, core SO-36-61, interval 157 cm; ANU 57015, female LV, length 1.12 mm, height 0.66 mm, core 71GC026, interval 60 cm. All specimens are of Late Pleistocene age.

**Type locality and horizon.** Western flank of Lord Howe Rise, present day water depth 1340 m, Sonne core 36-61, interval 69 cm, Late Pleistocene.

**Diagnosis.** A very large species of *Krithe* with pronounced sexual dimorphism. Males subrectangular to subtriangular in lateral view, with dorsal margin gently convex throughout shell length; females are much shorter and less tapering posteriorly. Inner lamella is narrow posterodorsally, wide posteroventrally with a large posterior vestibulum. The anterior vestibulum is large and mushroom-shaped with variable neck width. ADRPc of type 1B.

**Description.** Carapace large, strongly sexually dimorphic: in lateral outline males are subtriangular to subrectangular, females rectangular and considerably shorter. Dorsal margin in both sexes is gently convex throughout, except in RV which has a slight concavity at anterior third of length. In males the dorsal margin tapers to an acute posteroventral angle interrupted by a distinct mid-posterior shoulder. In females the posterior is more truncate. Ventral margin usually straight in females, gently to strongly concave in males. Normal overlap. Inner lamella narrow dorsally and mid ventrally, wide elsewhere. Anterior vestibulum is large and mushroom-shaped with variable neck width; dorsal lobe usually more strongly developed than ventral lobe. ARPC’s are short to moderately long. ADRPc of type 1B. AD 1 and 2 are closely adjacent. AD 1, 2 and 4 are normal pores, which are situated, when viewing valve in lateral aspect, usually between line of concrescence and inner margin, or rarely just behind inner margin. Posterior vestibulum is deep with wide neck. Muscle scars large, often with very meandering outlines but are not subdivided.
Figure 4. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–H, *Krithe triangularis* n.sp., A, male left valve (P. Smith M.Sc collection, UC Aberystwyth), 208/3/3, late Pliocene, B, male right valve (P. Smith M.Sc collection, UC Aberystwyth), 208/3/3, late Pliocene, C, male left valve (holotype, ANU 57011), SO-36-61, 69 cm, D, male right valve (ANU 57012), SO-36-61, 37 cm, E, female right valve (ANU 57014), SO-36-61, 157 cm, F, female left valve (ANU 57013), SO-36-61, 157 cm, G, female right valve of carapace (ANU 57015), 71GC26, 60 cm, H, female left valve of carapace (ANU 57015), 71GC26, 60 cm.
Remarks. Males of *K. triangularis* show considerable variation in the degree of posterior acumination. Weakly acuminate forms and females can be confused with *K. antisawanensis*. However, *K. triangularis* can be distinguished easily from that species in its mushroom-shaped anterior vestibulum and larger carapace.

Distribution. Widely distributed particularly in the East Tasman Sea, where it occurs at depths from 1125 to 3281 m. The species is somewhat deeper, ranging no shallower than 1818 m, on the Australian Continental Slope (Table 1).

Stratigraphical range. Early Miocene (NN 1) to Recent, based on core records of DSDP sites 207, 208, 284, 592 and 593. The species is very rare in the Early Miocene.

*Krithe sp. 1*

Figs. 3P,Q, 8P

Description. Carapace very small and weakly inflated. Lateral outline subrectangular; sexes not apparent. Dorsal margin gently convex throughout, except in RV which has a slight concavity at anterior quarter of length. Posterior margin convex dorsally, truncate ventrally with mid-posterior shoulder almost indistinct. Ventral margin is straight. Normal overlap. Inner lamella narrow postero-dorsally moderately wide elsewhere. Anterior vestibulum mushroom-shaped, weakly expanded distally, and with a moderately narrow neck. ARPC's are moderately long. ADRPC of type IB. AD 2 and 4 are normal pores. Posterior vestibulum narrow. Adductor muscle scars large except for the lowermost scar which is much smaller; the uppermost scar is subdivided into two. Frontal scar trefoil, sometimes subdivided.

Remarks. The species is distinct by virtue of its very small size and weak inflation. It is left in open nomenclature due to the paucity of material.

Distribution. Found only at 355 m on the eastern Australian continental slope. A single specimen has also been found in the Early Pleistocene of DSDP site 284.

**ADRPC TYPE 2**

*Krithe droogeri* Keij, 1953

Figs. 5A,B, 8Q

*Krithe droogeri* Keij, 1953: 159, pl. 1, figs 6a,b, 7.–Ruan & Hao, 1988: 269, pl. 44, figs. 1, 2.


Remarks. The species is very distinctive by virtue of its small bilobed anterior vestibulum and branching radial pore canals. There is some variation in lateral outline; the dorsal margin is arched in our specimens, but in the China Sea, specimens illustrated by Ruan & Hao (1988) and Whatley & Zhao (1993) it is straight. Sexual dimorphism may explain these differences. Although we found too few specimens to distinguish the sexes in our material, the convex dorsal margin suggests that they are all female.

Distribution. Found between 1200 and 1989 m on the eastern Australian continental slope.

Stratigraphical range. The species is very rare and found sporadically from the Middle Miocene (NN 6) to Recent. The fossil occurrences are from DSDP cores 206 and 592.

*Krithe perpulchra*

Abate, Barra, Aiello & Bonaduce, 1993

Figs. 5C–E, 8R

*Krithe perpulchra* Abate, Barra, Aiello & Bonaduce, 1993: 364; pl. 3, figs. 6–9; pl. 6, fig. 13.

Remarks. Very few specimens of this species were found and of those only females were well preserved. Although Abate *et al.* (1993) illustrate and describe only males, our specimens clearly show the anteriorly tapering anterior vestibulum characteristic of this species.

Distribution. Found at 759 m, 773 m and, probably transported (single poorly preserved male specimen) at 1321 m off eastern Australia.

Stratigraphical range. Late Pleistocene (NN 21) to Recent, based on numerous piston core records from the Australian Continental Slope. The earliest known occurrence of this species is Pliocene Zone M Pl 4 of Sicily (Abate *et al.*, 1993).

*Krithe prolata n.sp.*

Figs. 5F–I, 8S,T

*Krithe prolata* Guernet, 1993: 348, pl. 1, fig. 10.

Etymology. Latin, elongated. Referring to the elongate shape of this species.

Type material and dimensions. **HOLOTYPE**, ANU 57019, male LV, length 1.21 mm, height 0.52 mm. PARATYPES: ANU 57020, male RV, length 1.12 mm, height 0.50 mm, core 67GC03, interval 56 cm; ANU 57021, female LV, length 0.99 mm, height 0.51 mm, core 67GC03, interval 56 cm; ANU 57022, female RV, length 0.96 mm, height 0.47 mm, core 67GC03, interval 7 cm. All specimens are Late Pleistocene in age.

Type locality and horizon. Continental slope off southeastern Australia, present day water depth 1476 m, AGSO core 67GC03, interval 7 cm, Holocene.
Figure 5. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A, B, Krithe droogeri Keij, A, female left valve (ANU 57059), 71GC44, 15 cm, Holocene, B, female right valve (ANU 57060), 71GC44, 15 cm, Holocene; C–E, Krithe perpulchra Abate et al., C, male right valve (ANU 57063), 71GC44, 160 cm, D, female left valve (ANU 57061), 5/91 40Pc10A, coretop, E, female right valve (ANU 57062), 5/91 40Pc10A, coretop; F–I, Krithe prolata n.sp., F, female right valve (ANU 57022), 67GC03, 7 cm, G, female left valve (ANU 57021), H, male left valve (holotype, ANU 57019), 67GC03, 7 cm, I, male right valve (ANU 57020), 67GC03, 56 cm; J–M, Krithe comma n.sp., J, male right valve (holotype, ANU 57023), SO-36-61, 12 cm, K, female left valve (ANU 57025), GR5/4, 6 cm, Holocene, L, male left valve (ANU 57024), SO-36-61, 12 cm, M, female right valve (ANU 57026), GR5/4, 6 cm, Holocene.
Diagnosis. A very large species of Krithe with pronounced sexual dimorphism. Males elongate subrectangular in lateral view, females much shorter. In both sexes dorsal margin is weakly convex, almost straight in LV. Posterior margin steeply inclined with shallow indentation. Inner lamella narrow posterodorsally. Anterior vestibulum moderately large and subtriangular. ADRPC of type 2B. Dorsal adductor scar is narrow with an anterior and a medial dorsally directed lobes.

Description. Carapace large, strongly sexually dimorphic: in lateral outline males elongate subrectangular, females subrectangular and considerably shorter. Dorsal margin in both sexes gently convex throughout, except in RV which has a very slight concavity at anterior quarter of length. Anterior margin strongly convex; posterior margin truncate and steeply inclined. Ventral margin straight or weakly concave. Normal valve overlap. Inner lamella narrow dorsally and mid ventrally, moderately wide elsewhere. Anterior vestibulum subtriangular in lateral aspect and weakly upturned distally. ARPC’s short to moderately long. ADRPC of type 2B. AD 1 often a short false RPC or a normal pore. AD 2 and 4 are normal pores. Posterior vestibulum moderately deep with wide neck. Muscle scars large, outline of the upper adductor is a reclined “F” shape.

Remarks. The species can be confused with K. antisawawensis which differs mainly in its ADRPC type. The shape of the adductor muscle scars also serves to readily distinguish the species. A similarly elongate species from the Miocene of the Exmouth Plateau, Indian Ocean, is illustrated by Guernet (1993, pl. 1, fig. 10) and may be conspecific; internal features were not given.

Distribution. Krithe prolata occurs rarely on the eastern Australian continental slope from 1270 to 1989 m.

Stratigraphical range. Late Pleistocene (NN 21) to Recent, based on piston core records from the Australian Continental Slope.

Krithe comma n.sp.

Figs. 2G,H, 5J–M, 8U,V

Etymology. Latin, mark of punctuation. Referring to the lateral outline of this species resembling a comma.

Type material and dimensions. Holotype, ANU 57023, male RV, length 1.12 mm, height 0.48 mm. Paratypes: ANU 57024, male LV, length 1.13 mm, height 0.52 mm, core SO-36-61, interval 12 cm; ANU 57025, female LV, length 1.03 mm, height 0.53 mm, core GR 5/4, interval 6–8 cm; ANU 57026, male RV, length 1.05 mm, height 0.45 mm, core GR 5/4, interval 6–8 cm. In age specimens from SO-36-61 are latest Pleistocene; those from GR 5/4 are Holocene.

Type locality and horizon. Western flank of Lord Howe Rise, present day water depth 1340 m, Sonne core 36-61, interval 12–13 cm, latest Pleistocene.

Krithe dilata n.sp.

Figs. 6A–D, 8W,X

Etymology. Latin, dilate. Referring to the considerable expansion of the anterior vestibulum often displayed in this species.

Type material and dimensions. Holotype, ANU 57031, female RV, length 1.00 mm, height 0.51 mm. Paratypes: ANU 57032, female LV, length 0.99 mm, height 0.56 mm, core 71GC044, interval 1.00–1.01 m; ANU 57033, female RV, length 0.92 mm, height 0.49 mm, core 71GC044.
Figure 6. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–D, Krithe dilata n.sp., A, male left valve (ANU 57016), 105GC20, coretop, B, female right valve (ANU 57033), 71GC44, 100 cm, C, female left valve (ANU 57032), 71GC44, 100 cm, D, female right valve (holotype, ANU 57031), 71GC44, 100 cm; E–H, Krithe pseudocomma n.sp., E, male left valve (holotype, ANU 57027), GR5/4, 6 cm, Holocene, F, male right valve (ANU 57028), GR5/4, 2 cm, Holocene, G, female left valve (ANU 57029), GR5/4, 2 cm, Holocene, H, female right valve (ANU 57030), GR5/4, 4 cm, Holocene; I, J, Krithe sp. 2, I, female left valve (ANU 57064), TL8758, coretop, J, female right valve (ANU 57065), 12/87 12GC9, 65 cm.
interval 1.00–1.01 m; ANU 57016, length 0.91 mm, height 0.45 mm, coretop 105GC20. Specimens from 71GC044 are late Pleistocene in age.

**Type locality and horizon.** Tasman Sea, off eastern Australia present day water depth 1321 m, AGSO core 71GC044, interval 1.00–1.01 m, latest Pleistocene.

**Diagnosis.** A large, subrectangular species of *Krithe* with weak sexual dimorphism. Males lower than females. Posterior margin very truncate with a very shallow posterior indentation. Inner lamella narrow postero-dorsally. Anterior vestibulum mushroom-shaped, often with extremely wide proximal expansion. ADRPC of type 2B; AD 1 is usually a normal pore sometimes a short RPC, AD 3 and 4 are normal pores.

**Description.** Carapace moderately large and rectangular. Dorsal and ventral margins are straight and subparallel. Anterior margin regularly convex; posterior margin rounded dorsally, truncate ventrally with no median shoulder and only weakly indented. Normal valve overlap. Inner lamella narrow postero-dorsally and mid ventrally, moderately wide elsewhere. Anterior vestibulum large and mushroom-shaped with variable neck width, usually wide. ARPC’s are short. ADRPC of type 2B. AD 1 is usually a normal pore sometimes a short RPC. AD 3 and 4 are normal pores. Posterior vestibulum is very narrow but often expanded proximally. Muscle scars large, undivided.

**Remarks.** The species is most similar to *K. comma* n.sp. and *K. pseudocomma* n.sp. It differs from these species, however, in its more symmetrical and greatly expanded anterior vestibulum, and its undivided adductor scars. The Atlantic Palaeogene species *Krithe regulare* Coles et al., 1994, is also very similar, despite the considerable difference in geographical locality and stratigraphical range. Morphologically, *K. dilata* differs in size, having a more rounded posterior and much less marked sexual dimorphism.

**Distribution.** A relatively shallow occurring species recorded in this study between 355 to 1321 m on the eastern Australian continental slope.

**Stratigraphical range.** Early Miocene (NN 14) to Recent, based on core records of DSDP sites 207, 284, 592 and 593.

*Krithe pseudocomma* n.sp.

Figs. 6E–H, 8Y,Z

**Etymology.** Latin, referring to the close resemblance of this species to *Krithe comma* n.sp.

**Type material and dimensions.** HOLOTYPE, ANU 57027, male LV, length 0.88 mm, height 0.44 mm. PARATYPES: ANU 57028, male RV, length 0.86 mm, height 0.40 mm, core GR 5/4, interval 2–4 cm; ANU 57029, female LV, length 0.90 mm, height 0.52 mm, core GR 5/4, interval 2–4 cm; ANU 57030, female RV, length 0.86 mm, height 0.45 mm, core GR 5/4, interval 4–6 cm; All specimens are Holocene in age.

**Type locality and horizon.** Challenger Plateau, present day water depth 686 m, GRAINZ core 5/4, interval 2–4 cm, Holocene.

**Diagnosis.** A large, subrectangular species of *Krithe* with weak sexual dimorphism. Males lower than females. Posterior margin very truncate with a very shallow posterior indentation. Inner lamella wide postero-dorsally. Anterior vestibulum crescentic, with distinct ventral distal expansion. ADRPC of type 2B; AD 3 and 4 are normal pores. The uppermost adductor scar is subdivided.

**Description.** Carapace large, strongly inflated, weakly sexually dimorphic, males lower than females. Dorsal margin straight to slightly convex and parallel with ventral margin, which is very slightly concave. Posterior margin truncate with shallow indentation. Normal overlap. Inner lamella moderately wide. Anterior vestibulum hook-shaped with variable neck width, strongly distally expanded ventrally. ARPC’s are moderately long. ADRPC of type 2B. AD 1 is a short RPC or normal pore, AD 3 and AD 4 are normal pores. Posterior vestibulum is narrow. Muscle scars large, the upper adductor is subdivided.

**Remarks.** Internal carapace features of this species are similar to those of *K. comma* n.sp. as are certain aspects of its external morphology. However, there is a slight difference in ADRPC pattern: *K. pseudocomma* has an ADRPC of type 2B since AD 3 and AD 4 are always normal pores, whereas in *K. comma* AD 3 is usually a short RPC and, therefore, has an ADRPC of type 2A. Moreover, *K. pseudocomma* differs significantly from *K. comma* in its more cylindrical shape and its ventral distally expanded anterior vestibulum.

**Distribution.** Occurs only on the Lord Howe Rise and Challenger Plateau, ranging in depth from 686 to 1389 m.

**Stratigraphical range.** Early Miocene (NN 1) to Recent, based on core records of DSDP sites 207, 284, 592 and 593.

*Krithe* sp. 2

Figs. 6I, J, 8AA

**Description.** Female carapace extremely large, well inflated and heavily calcified. Dorsal margin is strongly convex; ventral margin less so. Anterior margin strongly convex, weakly concave dorsally. Posterior margin very truncate with weak posterior indentation. Normal valve overlap. Inner lamella is wide anteriorly and posteriorly, moderately wide ventrally. Anterior vestibulum narrow and mushroom shaped. ARPC’s are moderately long. ADRPC of type 2B. AD 2 is very long and very close to the dorsal margin. Posterior vestibulum very narrow. Muscle scars large and not subdivided.
Figure 6. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–D, *Krithe dilata* n.sp., A, male left valve (ANU 57016), 105GC20, coretop, B, female right valve (ANU 57033), 71GC44, 100 cm, C, female left valve (ANU 57032), 71GC44, 100 cm, D, female right valve (holotype, ANU 57031), 71GC44, 100 cm; E–H, *Krithe pseudocomma* n.sp., E, male left valve (holotype, ANU 57027), GR5/4, 6 cm, Holocene, F, male right valve (ANU 57028), GR5/4, 2 cm, Holocene, G, female left valve (ANU 57029), GR5/4, 2 cm, Holocene, H, female right valve (ANU 57030), GR5/4, 4 cm, Holocene; I, J, *Krithe* sp. 2, I, female left valve (ANU 57064), TL8758, coretop, J, female right valve (ANU 57065), 12/87 12GC9, 65 cm.
Remarks. Only a few poorly preserved, probably female, specimens were found. In overall morphology they resemble *K. trinidadensis* but the ADRPC pattern is very different.

Distribution. Found at 1545 to 3281 m on the flanks and plateau of the Lord Howe Rise.

Stratigraphical range. Early Miocene (NN 1) to Recent, based on core records of DSDP sites 208.

**ADRPC TYPE 3**

*Krithe morkhoveni morkhoveni* Bold, 1960

Figs. 7A–C, 8DD,EE

For comprehensive pre-1988 synonymy see Coles et al. (1994).

*Krithe morkhoveni* Bold, 1960: 160; pl. 3, fig. 6.
*Krithe* sp. 11 Whatley & Zhao, 1993: fig. 3.11.
*Krithe undecimradiata* Ruggieri; Abate, Barra, Aiello & Bonaduce, 1993: 364; pl. 5, figs. 1–3.
*Krithe morkhoveni morkhoveni* Bold; Coles, Whatley & Moguilevsky, 1994: 94; pl. 3, figs. 11–18, text-fig. 4D–H.

Remarks. This species is significantly smaller (see Fig. 9) than the very similar species *K. trinidadensis*.

Distribution. A species common on the Continental Slope of Australia, recorded from 804 to 3552 m, but almost absent elsewhere in the Tasman Sea being found only at one site at 1125 m on the Challenger Plateau.

Stratigraphical range. Early Pliocene (NN 14) to Recent, based on core records of DSDP sites 206 and piston cores on the Australian Continental Slope. The subspecies is known from the Early Miocene elsewhere (Coles et al., 1994).

**Krithe trinidadensis** Bold, 1958

Figs. 2I,J, 7H–L, 8FF,GG

For comprehensive synonymy see Coles et al. (1994).

*Krithe trinidadensis* Bold, 1958: 398; pl. 1, figs. 3a, 3c,d, 3f, 6e–f; Coles, Whatley & Moguilevsky, 1994: 99; pl. 4, figs. 7–12; text-fig. 4P–T, text-fig. 5A,B.

Remarks. The large size of this species (see Fig. 9) readily serves to distinguish it from the smaller, but otherwise very similar species, *K. morkhoveni morkhoveni* Bold.

Distribution. In coretop material we found this species only on the Continental Slope off Tasmania at a depth range of 1476 to 2346 m. Elsewhere in our study region it has been recorded rarely only as fossil in DSDP site 206, 3196 m in the New Caledonian Basin.

Stratigraphical range. Late Pliocene (NN 16) to Recent, based on core records of DSDP site 206. *Krithe trinidadensis* is known to occur from the Middle Eocene zone NP 16 (Coles et al., 1994).

Discussion

Table 1 shows the depth distribution of all the species found in the two study regions, the East Tasman Sea (including the New Caledonia Basin, Lord Howe Rise and Challenger Plateau) and the Continental Slope off southern and eastern Australia. As in other parts of the world oceans greatest diversity occurs beyond 1,000 m in the bathyal and abyssal environment. In both our study areas some 15 species occur, or have occurred in the past. Not all of them, however, are common to both regions. Five species are absent from the Australian Continental Slope. They include *K. comma*, *K. pseudocomma*, *Krithe* sp. 2, these being confined to the plateau or flanks of the Lord Howe Rise; and *K. dolichodeira* and *K. minima*, which are geographically and bathymetrically widespread species, common, for example in the North Atlantic (Coles et al., 1994). The absence from the slope regions of Australia of these two, otherwise cosmopolitan species, is perplexing. Three species, *K. posticliva*, *K. pernoides sinuosa*, and *K. trinidadensis* appear to have diminished their range, since they are recorded in modern sediments off Australia, but only in ancient sediments in the East Tasman Sea. Four other species, *K. dilata*, *K. perpulchra*, *K. prolata* and *Krithe* sp. 1, are restricted entirely to the Australian Continental Slope. Vertical range distribution of ubiquitous species likely relates to variations of vertical watermass structure and substrate type. The relatively steep-sided Australian Continental Slope offers only narrow areas of uniform watermass, and generally unstable, terrigenous rich
Figure 7. Camera lucida drawings of internal valve features. All figures are external views. All specimens are of late Pleistocene age unless otherwise indicated. A–C, Krithe morkhoveni morkhoveni Bold, A, female right valve (ANU 57067), 9/86 Pc7, 84 cm, B, female left valve (ANU 57066), 67GC03, 25 cm, C, male right valve (ANU 57069), 67GC03, 107 cm; D–G, Krithe pernoides sinuosa Ciampo, D, female left valve (ANU 57070), 71GC44, 45 cm, E, female right valve (ANU 57071), 71GC44, 45 cm, F, male right valve (ANU 57073), 71GC44, 45 cm, G, male left valve (ANU 57072), 112GC9, coretop; H–L, Krithe trinidadensis Bold, H, female left valve (ANU 57074), 67GC03, 25 cm, I, female right valve, form with large anterior vestibulum (ANU 57075), 67GC03, 280 cm, J, male right valve (ANU 57078), 67GC03, 25 cm, K, female right valve (ANU 57076), 67GC03, 177 cm, L, male left valve (ANU 57077), 67GC03, 137 cm.
sediment regimes. Whereas the plateau regions of the eastern Tasman Sea are relatively stable, carbonate rich areas. These factors must have a profound influence upon the distribution of any benthonic living community.

Table 2 shows the stratigraphic ranges of all the species documented here. The success of the genus is striking, with a radiation throughout the Neogene from three species in the Early Miocene, to 19 by the Late Pleistocene. By comparison with the North Atlantic (Coles et al., 1994), this diversity trend appears to be a global one. Of the seven species shared with the North Atlantic none appear at the same time in each ocean. Only two species, *K. minima* and *K. triangularis*, have earlier occurrences in the Southwest Pacific and, therefore, have probably evolved there. The Late Miocene to Late Pliocene saw the invasion of the Pacific of most of the Atlantic shared species. Further work is needed on Palaeogene occurrences in the Pacific to make further definite comparisons here concerning migration patterns and inter-oceanic correlation. It is clear, however, that the Pacific fauna consists of a mix of immigrant and endemic species. There exist species, characterised by ADRPC Type 2A (*K. comma*, and *K. pseudocomma*), that have remained in the Southwest Pacific region throughout their long, at least Miocene to Recent, range.

**Figure 9.** Size variation in adult *Krithe morkhoveni morkhoveni* and *Krithe trinidadensis*.

**Acknowledgments.** Michael Ayress would like to thank sincerely G. Coles for useful and constructive discussion during our comparisons of Pacific and Atlantic material while completing our doctoral theses at the University of Wales, Aberystwyth. Initial progress of this study capitalised upon the efforts of Coles in his unique persistence to resolve “the Krithe Problem”, and his comprehensive literature searches in this endeavour. He is also thanked for reading and commenting on an early version of this paper. Kerry Swanson is heartily thanked for the loan of some Tasman Sea material included herein. Michael Ayress is extremely grateful to the Australian Conservancy Council for the financial support of this project of the Australian Biological Resources Study.

**References**


Table 1. Bathymetric distribution of *Krithe* species and location details of sites considered in this report. ● = present; ○ = Lazarus occurrences; + = fossil occurrence only.

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