Observations on *Cycloclypeus (Cycloclypeus)* Carpenter and *Cycloclypeus (Katacycloclypeus)* Tan (Foraminiferida)

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Synopsis

Cycloclypeus carpenteri Brady and *C. guembelianus* Brady are redescribed from syntypic material and the former is considered to be a subjective senior synomym of the latter. The type species of *Cycloclypeus, C. mammillatus* Carter, is discussed and the type sample redated as Late Oligocene. It is concluded that this name should be allowed to lapse and that *C. carpenteri* should be declared the type species of the genus. *C.* (*Katacycloclypeus*) *annulatus* Martin is redescribed from syntypic material and compared with other katacycloclypeids occurring in Indonesia, and with the largest-known cycloclypeids from the Futuna Limestone of Fiji. It is considered that only one species of *Katacycloclypeus* can be recognized at present.

Introduction

The genus *Cycloclypeus* has long been recognized as having considerable stratigraphical value in the late Cenozoic owing to the relative ease with which the evolution of the early or juvenile part of the shell (embryonic and nepionic chambers: see Fig. 1) can be traced. Tan (1932) published the first detailed account of its evolutionary history and in so doing established it as a prime example of Haeckel's Law of Recapitulation. Although subsequent authors (Cosijn 1938, Drooger 1955 and MacGillavry 1962) have disputed and, indeed, disproved certain of Tan's conclusions, his main thesis – that after its initial appearance, the genus underwent a progressive shortening of the initial coil (so-called nepionic acceleration) through the reduction of the operculinoid and heterosteginoid stages – has never been questioned.

The purpose of this paper is to clear up some of the taxonomic confusion surrounding the living representatives of the genus and to describe *Katacycloclypeus* from the type section of the Futuna Limestone, Vanua Mbalavu, Fiji, where its association with planktonic foraminifera and *Lepidocyclina* makes it especially important for regional correlation.

The early growth stages of *Cycloclypeus* are illustrated and labelled in Fig. 1, and it is here necessary only to comment briefly on the stolon system and annuli. Stolons are pores which connect the secondary chamberlets through the primary septa. Because the septa are fairly thick, these pores appear as short tubes. As Carpenter (1856) discovered, each secondary chamberlet possesses two stolons on the distal wall, one opening on either side of the proximal end of each secondary septum in the succeeding annulus; Hottinger (1977) has described this arrangement as 'crosswise-oblique', and so far as is known this simple pattern is constant throughout the genus.

The term annulus has been used rather loosely in the past and has been a source of some confusion. Annulate cycloclypeids possess one or more rings of raised shell material between the centre of the test and the periphery (see Fig. 12). The annuli are composed of pillars which may be elevated above the test surface to form granules or pustules. When secondary shell material is laid down between the pustules, the annulus forms a thickened ring which may, or may not, show signs of external granulation. Thin sections, however, invariably show the presence of pillars in the wall. The area between two annuli is relatively depressed, as is the region between the inner annulus and the central boss when this is developed.

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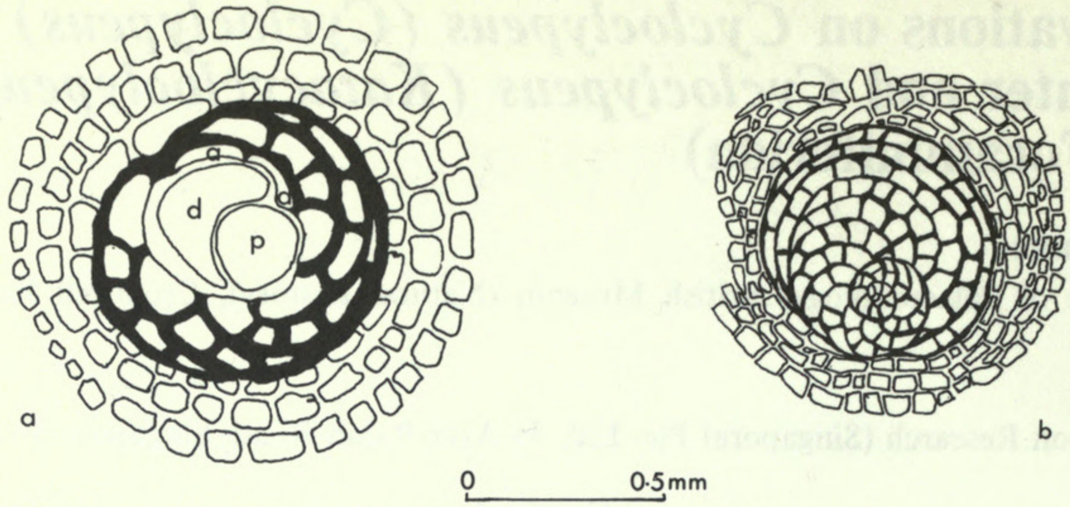


Fig. 1a, b. Early growth stages of megalospheric and microspheric forms of *Cycloclypeus* to illustrate the terminology used in this paper. Fig. a, megalospheric individual of *C.* (*C.*) *posteidae* Tan from the Futuna Limestone, Vanua Mbalavu, Fiji. The embryonic apparatus comprises the protoconch 'p' and deuterconch 'd'. The nepionic stage, outlined in black, includes an ana-nepionic chamber 'a' (in this specimen divided by a single septum but frequently undivided) and 5 nepionic chambers. The neanic stage is represented by the three rings of annular chambers which are divided into chamberlets by numerous secondary septa. Fig. b, microspheric individual of *C.* (*Katacycloclypeus*) *annulatus* Martin. Topotype; ex Martin Collection, Java. P.36377. See Fig. 9 for the internal structure of *C.* (*Cycloclypeus*) *carpenteri* Brady. The embryonic apparatus is invariably minute (c.20 μm) in the microspheric form. It is followed in this specimen by 8 undivided (operculinoid) chambers and at least 17 divided (heterosteginoid) chambers before the first annular chamber appears. As this specimen shows, it can be quite difficult to decide which is the first truly annular chamber.

The difference between *Cycloclypeus* and *Katacycloclypeus* is that the latter always possesses well-developed annuli in both generations, whereas the former usually lacks them. They may, however, be developed (usually feebly) in microspheric forms of *C. carpenteri* (Figs 2a, 4a, 5). The megalospheric forms of *C. eidae* and *C. posteidae* occasionally possess a single prominent annulus.

Acknowledgements

We are grateful to Mr Darwin Kadar (Geological Survey of Indonesia) for helpful information, and to Mr L. O'Herne (Rijksmuseum, Leiden) for kindly answering our numerous enquiries,

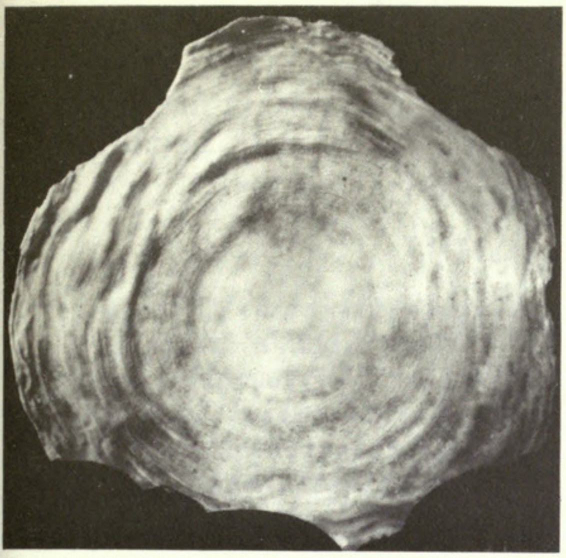
Figs 2a, b, 4a, b. *Cycloclypeus carpenteri* Brady. Microspheric forms (syntypes) from the Sir Edward Belcher Collection. 51.1.20.42, 43. Figs 2a, 4a, ×1. Note presence of incipient annuli towards periphery. Figs 2b, 4b enlargements (c. ×100) of part of shell to show the presence of granules along the primary septa (Fig. 4b) and along and between the septa (Fig. 2b).

Fig. 3. *Cycloclypeus posteidae* Tan, ×9. Heavily ornamented form (probably megalospheric) from sample F 181, Futuna Limestone, Vanua Mbalavu, Fiji. For internal details of this species see Fig. 1a.

Figs 5a, b. *Cycloclypeus carpenteri* Brady. Broken microspheric form from the Sir Edward Belcher Collection, Macclesfield Bank, 30 fathoms (=55 m), China Sea. Fig. 5a, ×1; Fig. 5b, enlargement of central area, c. ×4. Note development of annuli in the central area and compare with Figs 12–14 and 16. (1893.8.10.1).

Figs 6a, b. *Cycloclypeus carpenteri* Brady. One of three megalospheric forms in the Sir Edward Belcher Collection. This specimen possesses a multi-embryonic apparatus. Fig. 6a, ×2·8; Fig. 6b, central area (c. ×7) showing well-developed rings of granules on the primary septa and interstitial calcite largely obscuring the ornament over the central boss. 51.1.20.39.

Fig. 7. *Cycloclypeus carpenteri* Brady, ×20. Immature megalospheric form from '210 fathoms (=384 m) off Kandavu, Fiji'. This is Brady's (1881, 1884) unfigured syntype of *C. guembelianus*. Small granules of calcite can be seen on the raised central area. See Fig. 11 for details of internal structure. 1959.5.5.311.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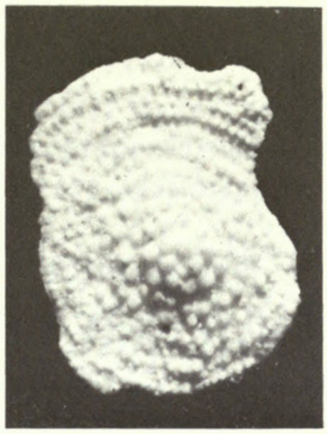
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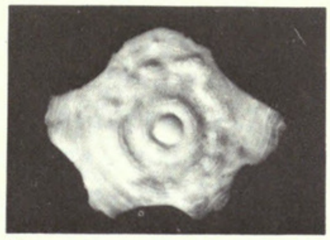
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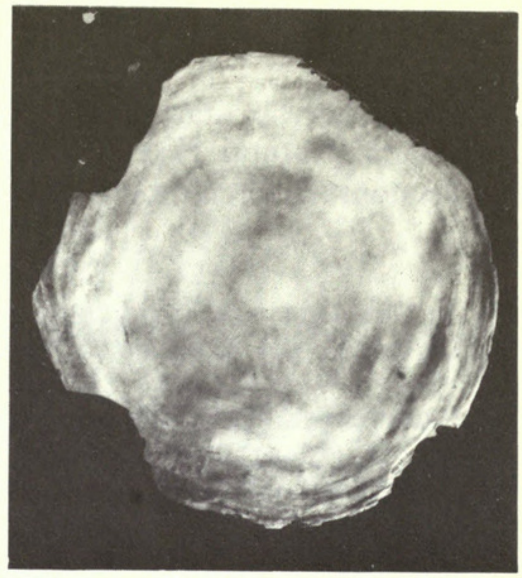
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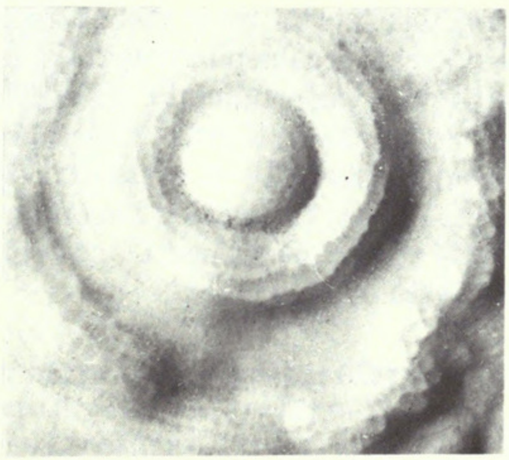
2b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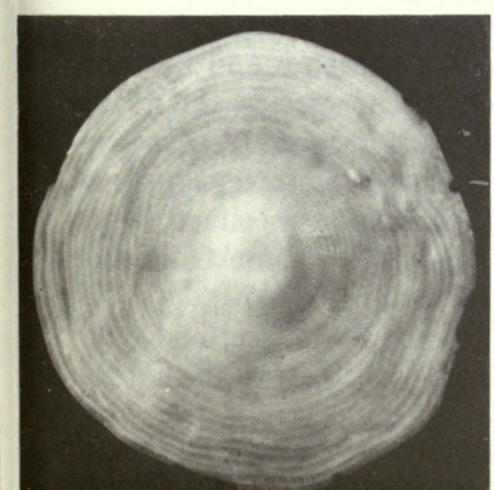
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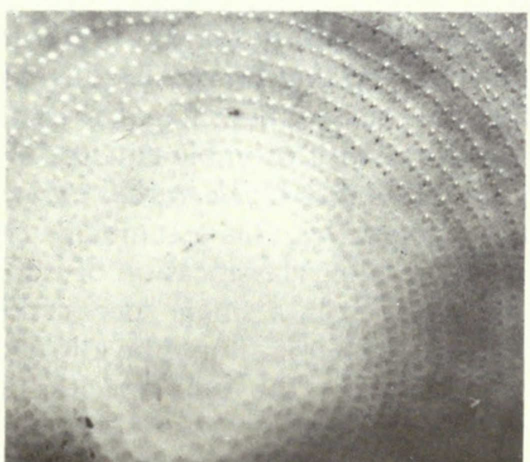
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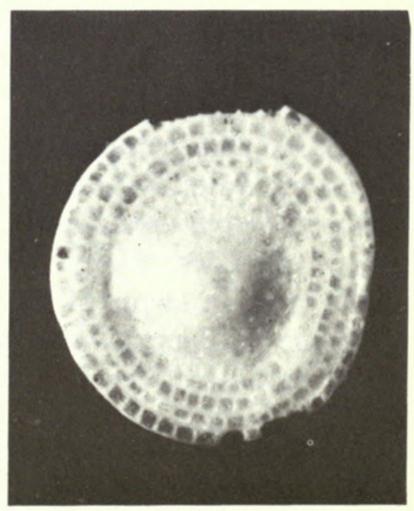
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loaning us comparative material, and allowing us to section one of Dr K. Martin's original rock samples from Java. We also wish to thank Miss Christine Harrison and Mr R. L. Hodgkinson for technical assistance, and Dr J. E. Whittaker for his careful reading of the typescript.

Material

Unless otherwise stated, all specimens figured or referred to herein are preserved in the British Museum (Natural History), and bear register numbers in the Palaeontological or Zoological collections which, although catalogued separately, are curated together.

Systematics

Family **NUMMULITIDAE** de Blainville, 1825

Genus ***CYCLOCLYPEUS*** Carpenter, 1856

Subgenus ***CYCLOCLYPEUS*** Carpenter, 1856

TYPE SPECIES. *Cycloclypeus mammillatus* Carter, 1861a.

Cycloclypeus was originally described from material dredged from 'water of a considerable depth off the coast of Borneo'. Carpenter obtained a number of specimens from the Belcher Collection in the British Museum and prepared some thin sections. He stated, somewhat ambiguously, that they were 'no less than $2\frac{1}{4}''$ (=57 mm) in diameter', and showed, amongst other things, that they had raised centres, pustulate surfaces and numerous complete or incomplete annuli. There are, in fact, three large specimens (57 mm, 50 mm and 48 mm in diameter respectively) in the original collection. We now know that they are all microspheric individuals. Although Carpenter described the microspheric generation, his figures were of one monstrosity (1856 : pl. 30, fig. 3; probably megalospheric) and one normal megalospheric individual (pl. 30, fig. 1) with a diameter of about 14 mm and a large proloculus. Unfortunately, no specific name was erected, the first validly described species being *C. mammillatus* Carter, 1861a, from Takah, south-east Arabia. According to the *Catalogue of Foraminifera* (Ellis & Messina 1940 *et seqq.*) it was said to be of Eocene age although Carter himself (1861a : 83) seemed uncertain. Thus, when Brady (1881 : 67) proposed that Carpenter's specimens should be named *C. carpenteri*, he was already too late to ensure that this became the type species of the genus.

Cycloclypeus (*C.*) *mammillatus* Carter, 1861

1861a *Cycloclypeus mammillatus* Carter : 87.
1861b *Cycloclypeus mammillatus* Carter : 461.

REMARKS. The single unfigured specimen on which this species is based has, unfortunately, been lost. However, the limestone sample whence it came is preserved in this Museum and has now been sectioned. Although Carter believed that he was dealing with an Eocene species, the newly-prepared thin sections reveal that the rock contains *Lepidocyclina* (*Eulepidina*) sp., *L.* (*Nephrolepidina*) sp. indet. (a small primitive form with rhombic equatorial chambers), *Heterostegina* sp. cf. *Heterostegina borneeensis* van der Vlerk and *Cycloclypeus* ex gr. *eidae* Tan (one specimen only). In the absence of any species of *Nummulites*, this assemblage clearly indicates a Late Oligocene age (Te_{1-4} in terms of the East Indies letter classification of the Tertiary; Adams 1970).

Since *C. mammillatus* was described from a single specimen and cannot be redescribed from the original material, we believe that the name should be allowed to fall into disuse, and that the ICZN should declare *C. carpenteri* to be the type species. An appropriate application has, therefore, been submitted to the Commission.

Cycloclypeus (*C.*) *carpenteri* Brady, 1881

Figs 2, 4–11

1856 *Cycloclypeus* Carpenter : 555; pl. 30, figs 1, 3, 4.
1862 *Cycloclypeus* Carpenter : 292; pl. 19, figs 2–7.

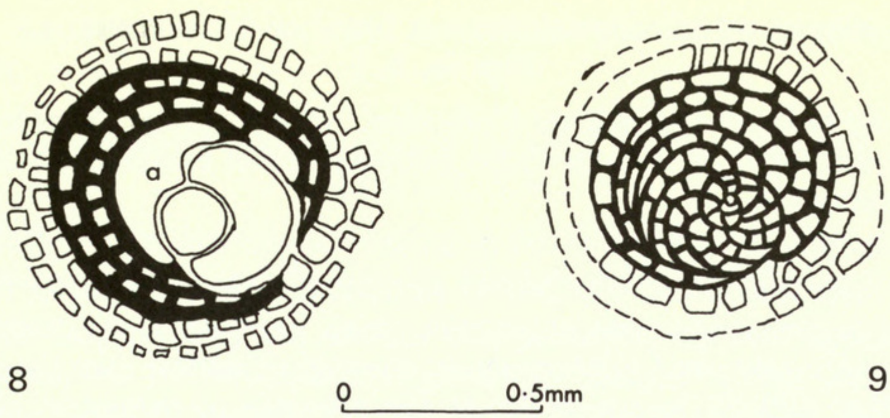
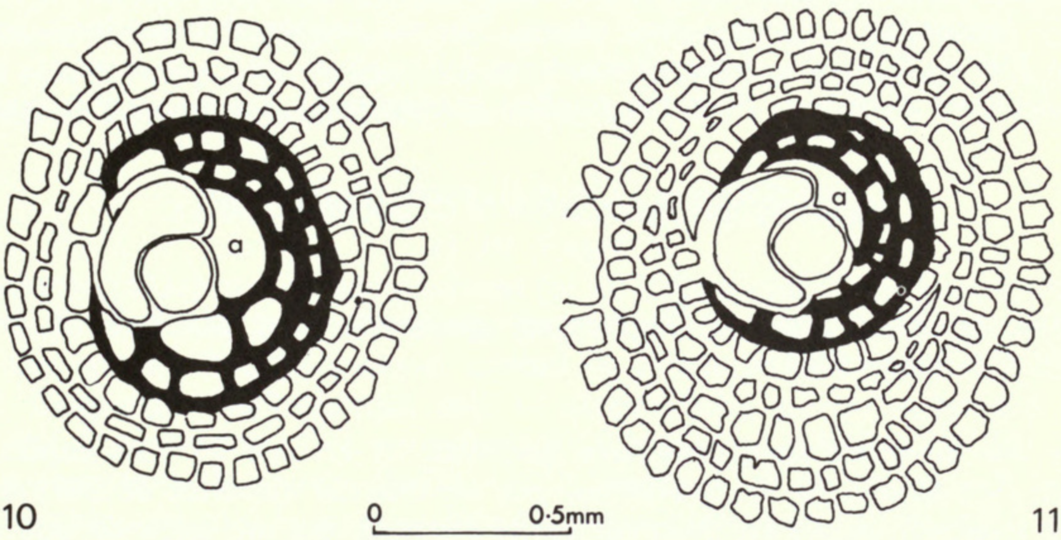


Fig. 8. *C. carpenteri* Brady. Megalospheric individual showing a large subdivided ana-nepionic chamber 'a' and 2 nepionic chambers. The external appearance of this specimen was illustrated by Chapman (1900 : pl. 3, fig. 4). 03.2.5.115.

Fig. 9. *C. carpenteri* Brady. Microspheric individual from Funafuti Atoll showing 4 operculinoid and 14 heterosteginoid chambers making up the nepionic stage. 03.2.4.951–1000 (sq. 49). Cf. the microspheric form of *C.* (*K.*) *annulatus*, Fig. 1b.



Figs 10, 11. Internal structures of the two complete syntypes of *C. guembelianus* Brady. Fig. 10 is the specimen illustrated (external view only) by Brady (1884 : pl. 111, fig. 8 a, b). Both specimens have one undivided ana-nepionic chamber, 'a'. Fig. 10 shows two nepionic chambers and Fig. 11 at least two nepionic chambers, but in this specimen it is difficult to decide at what point the first complete annular chamber begins. Fig. 10, ZF1366; Fig. 11, 1959.5.5.311.

1881 *Cycloclypeus guembeliana* Brady : 66
1881 *Cycloclypeus carpenteri* Brady : 67.
1884 *Cycloclypeus guembelianus* Brady : 751; pl. 111, fig. 8a, b.
1884 *Cycloclypeus carpenteri* Brady : 752.
1895 *Cycloclypeus carpenteri* Brady; Lister : 437, figs 52–54.
1900 *Cycloclypeus carpenteri* Brady; Chapman : 22; pl. 2, figs 6, 7; pl. 3, figs 1–5.
1927 *Cycloclypeus carpenteri* Brady; Hofker : 71; pl. 24, fig. 1; pl. 37, figs 1–10; pl. 38, figs 1–9, 12, 13.
1951 *Cycloclypeus guembelianus* Brady; Hanzawa : 1; pl. 1, figs 1–5; pl. 2, figs 1–7; text-figs 1–10.

Remarks. Early descriptions of this species are confusing because authors have not distinguished between megalospheric and microspheric forms and because Brady's original description of *C. guembelianus* was inaccurate. The following brief descriptions are based upon Brady's syntypes, supplemented, where necessary, by specimens from Chapman's large collection from Funafuti Atoll. They are intended to distinguish clearly between the A and B generations, and between *C. guembelianus* and *C. carpenteri* as originally described.

Megalospheric generation (=A form) of *C. carpenteri* s.s.
Figs 6a, b, 8

MATERIAL. Three syntypes in the Belcher Collection, referred to by Carpenter (1856, 1862). A further 131 specimens, of which 6 have been sectioned, from Funafuti Atoll (Chapman 1900) have also been examined.

DESCRIPTION. The three well-grown syntypes (1 sectioned) range in diameter from 13 to 15 mm. All are ornamented by concentric rings of pustules which, except over the central area, arise from the junctions of the secondary and primary septa; these are broadest over the raised central boss where they are rather difficult to see owing to the presence of secondary shell material. The specimen (Fig. 6a, b) proved on sectioning to be abnormal in that it comprised 3 megalospheric embryonts having proloculus diameters of about 200 μm, 250 μm and 300 μm respectively. There is one other probable megalospheric specimen, one of the two monstrosities mentioned by Carpenter (1856 : 560). This appears to have developed from two megalospheric embryonts which grew their fused tests at right angles.

Chapman's large collection (155 specimens) from Funafuti Atoll contains 131 individuals that are indistinguishable externally from Brady's syntypes except insofar as they include a considerable number of small, immature individuals. Test diameter 1–13 mm (8–13 mm if obvious juveniles are excluded). Ornament is as described above. The six sectioned individuals have proloculi ranging from 190 to 280 μm in internal diameter followed by one ana-nepionic chamber and 1–3 (or ? 4) nepionic chambers. Even the smallest specimens (1–3 mm) are pustulate externally.

Megalospheric generation of *C. guembelianus* s.s.
Figs 7, 10, 11

MATERIAL. Two complete and one fragmentary specimens from 210 fathoms (= 388 m) off Kandavu, Fiji. Challenger Collection.

DESCRIPTION. The complete specimens have diameters of 1·5 and 2·0 mm respectively. In the smaller of the two specimens the proloculus has an internal diameter of 200 μm, and this is followed by a reniform second chamber (diameter 370 μm), one ana-nepionic and two nepionic chambers. Five neanic chambers are present. The second specimen has a proloculus diameter of about 190 μm, a second chamber with a width of 360 μm, one ana-nepionic and at least two nepionic chambers. At least four annular chambers are present. The early neanic chambers are shorter (radially) than wide. Contrary to Brady's second description (1884 : 751) the surface of the test is not smooth except for 'slightly raised lines' marking the annular and radial sutures, but is ornamented by small, irregularly-arranged pustules over the inflated embryonic apparatus. On one specimen the pustules are numerous and heavy.

Five other specimens of *C. guembelianus* in the Heron-Allen & Earland collection (Macassar Straits, 45 fathoms (=82 m)) differ little from Brady's specimens. They range 0·75–3·0 mm in diameter. All have one ana-nepionic and 2–6 nepionic chambers. Proloculus diameter ranges from 120 to 230 μm.

COMMENTARY. Brady (1884) stated that *C. guembelianus* was much smaller than *C. carpenteri*, but failed to realize that he was comparing immature megalospheric individuals with mature microspheric specimens. The discrepancy in size is therefore irrelevant. The only other difference noted by Brady was that the former was smooth and the latter highly pustulate. However, as noted above, the syntypes of *C. guembelianus* are not smooth; in fact they closely resemble the immature specimens of *C. carpenteri* from Funafuti. Young individuals of *C. carpenteri* have very delicate tests in which the large embryonic apparatus projects well above the surface of the equatorial chambers. As growth proceeds, the animal thickens the upper and lower surfaces of the shell with layers of calcite which are laid down around the primary pustules on the central area (Figs 6b, 7).

Later, the central area becomes smooth and domed, the pustules being arranged in concentric rings over the brim.

Microspheric generation (=B form) of *C.* (*C.*) *carpenteri*
Figs 2, 4, 5, 9

MATERIAL. Three fully-grown individuals ranging in diameter from 48 to 57 mm and two broken individuals with diameters of 24 and 28 mm. Sir Edward Belcher Collection.

DESCRIPTION. In the larger forms the surface is ornamented by 4–6 feebly-developed annuli which may form complete or incomplete rings. These sometimes fade into discrete granules (Figs 2b, 4b). The shell surface is otherwise smooth. The internal structure has been described by Carpenter who did not, however, mention the embryonic or nepionic chambers. A section of a juvenile microspheric individual in the Funafuti collection revealed four ana-nepionic chambers and 14 nepionic chambers following a proloculus with an internal diameter of approximately 20 μm. Hofker (1927) described a B form with a proloculus about 30 μm in diameter followed by a coil comprising 10 ana-nepionic and 14 nepionic chambers. Hanzawa (1951) reported a Recent B form (called *C. guembelianus*) with a proloculus diameter of 44 μm and a coil with one ana-nepionic and 15 nepionic chambers. He also described a Pleistocene form with a proloculus diameter of 40 μm, about three ana-nepionic and 18 nepionic chambers. These appear to be the only microspheric forms for which we have internal details. Chapman's (1900) B form from Funafuti was said to have a proloculus diameter of 140 μm but inspection of his illustration (pl. 3, fig. 2) shows that this measurement was incorrect.

Microspheric generation of *C. guembelianus*

Not known.

REMARKS. Cushman (1921) used *C. guembelianus* for all Recent cycloclypeids under the mistaken impression that Brady (1884) had referred the larger (microspheric) individuals in the Belcher collection to this species. But the sentence quoted by Cushman (1921 : 386) actually refers to *C. carpenteri*. Chapman (1900) thought that *C. guembelianus* merely comprised very young specimens of the A generation of *C. carpenteri*; he adduced no evidence for this although we believe that he was intuitively correct. Hofker (1927) 'preferred' to use the name *C. carpenteri* for all living cycloclypeids although he gave no clear reason, and Hanzawa (1951) used *C. guembelianus* for Recent specimens having 2–5 nepionic septa in the A1 and A2 generations regardless of the presence or absence of ornament.

CONCLUSIONS. It is clear from the present observations that *C. carpenteri* and *C. guembelianus* cannot be differentiated either by size or by ornament, and there remains only the possibility that their internal structures might be different. Table 1 compares the principal internal characters of the two 'species'. As the original megalospheric specimens of *C. carpenteri* appear to be abnormal in that they possess multi-embryonic chambers, they are not suitable for comparative purposes; Chapman's material from Funafuti is therefore used instead.

Table 1

Species	Proloculus diameter	Deuteroconch diameter	No. of ana-nepionic chambers	No. of nepionic chambers	No. of neanic ch. in 0·75 mm radius
C. guembelianus	190 μm	360 μm	1	2 or more	2 or 3
(syntypes)	200 μm	370 μm	1	2	5
C. carpenteri					
Funafuti (6 specimens)	150–230 μm	220–450 μm	1	1–6	2–5 (or ? 6)

It follows that only one living species of *Cycloclypeus* has been found and that this should be called *C. carpenteri*.

Failure to distinguish an ornate and an inornate living species poses a problem for palaeontologists since MacGillavry (1962), working on Oligocene assemblages from Spain, recognized an inornate lineage which he referred to *C. guembelianus* and an ornate lineage which he called *C. carpenteri*; Cosijn (1938) used a similar terminology. However, neither author studied Recent populations nor did they examine the type specimens of these species.

Subgenus *KATACYCLOCLYPEUS* Tan, 1932

TYPE SPECIES. *Cycloclypeus annulatus* Martin, 1880.

Tan erected *Katacycloclypeus* for cycloclypeids which possess one or more annuli in the megalospheric generation. As originally defined it included the following species: *C.* (*K.*) *annulatus* Martin (3 annuli), *C.* (*K.*) *biplicatus* Tan (2 annuli), *C.* (*K.*) *transiens* Tan (1 annulus and surface pustules) and *C.* (*K.*) *posttransiens* (1 annulus and no surface pustules). *C. martini* van der Vlerk (1923) should also have been included since it was described as having at least one annulus in the megalospheric form.

Unfortunately, the possession of a single annulus in the megalospheric generation is not absolutely diagnostic of *Katacycloclypeus* since certain species of *Cycloclypeus*, e.g. *C. posteidae* Tan, may, or may not, possess an annulus.

Tan believed that he could recognize an evolutionary sequence within *Katacycloclypeus* and planned to describe it in a later paper, which, unfortunately, never appeared. There is, however, sufficient information in his original publication (1932) for us to be able to deduce the main outline of his evolutionary scheme. He stated (1932 : 119) that the most primitive form of the subgenus was *C.* (*K.*) *transiens* and that this evolved from *C.* (*C.*) *eidae*. From his table V it is apparent that his first record of *Katacycloclypeus* (*K.* sp.) was from beds a little younger than those yielding good Te$_5$ (= Aquitanian) assemblages including *Eulepidina*, *Spiroclypeus* and *C. eidae*. *C.* (*K.*) *biplicatus* was reported from slightly younger strata along with 'very seldom' specimens of *C. annulatus*, the latter becoming progressively more numerous until it dominated the katacycloclypeid fauna of supposed Late Vindobonian age. All the strata in which Tan found *Katacycloclypeus* can now be assigned to Tertiary lower *f*, and we may, therefore, conclude that Tan's evolutionary sequence was intended to be *C. eidae* → *C.* (*K.*) *transiens*/*posttransiens* (6–13 heterosteginoid chambers) → *C.* (*K.*) *biplicatus* (unknown number of heterosteginoid chambers) → *C.* (*K.*) *annulatus* (*c.* 3 heterosteginoid chambers in the types; 2–4 in our additional material from Java). It is evident that forms referable to *C.* (*K.*) *annulatus* appeared fairly early in the sequence and came to dominate the faunas later. We may reasonably infer that *C.* (*K.*) *posttransiens* followed *C.* (*K.*) *transiens* in the evolutionary sequence but whether it occurred together with *C.* (*K.*) *biplicatus* is uncertain.

Van der Vlerk (1923) described *C. martini* from strata that are clearly of Tertiary lower *f* age since they contain *Flosculinella bontangensis* (Rutten). He illustrated four specimens, one of which (pl. 2, fig. 4) he regarded as microspheric, although in the light of later knowledge it is seen to be a megalospheric individual with a rather small proloculus (internal diameter 0·37 mm) and about six heterosteginoid chambers. His diagnosis must therefore be amended to include forms with one to six nepionic chambers, in which case it embraces *C.* (*K.*) *annulatus*. However, the latter is supposed to possess three annuli whereas van der Vlerk's species has only one or two. A small piece of the type sample for *C. annulatus*, provided by the Rijksmuseum Leiden, has enabled us to section three broken megalospheric specimens and to show that they possess one ana-nepionic and two to four nepionic chambers (Figs 19, 20).

It is apparent that without a better knowledge of the internal structure and morphological variation of the seven species and varieties of *Katacycloclypeus* so far described, it is impossible to distinguish between them. Since *C.* (*K.*) *annulatus* appears at an early stage in the evolutionary history of the subgenus it seems unlikely that the number of annuli is a feature of major taxonomic significance. This being so, it is proper, for the time being at least, to regard *Katacycloclypeus* as a single evolving monotypic lineage largely confined to the Middle Miocene, and which, in a period of about 4 Ma, reduced the number of nepionic chambers in the megalospheric coil from 6 to 13 (in the most primitive forms) to 0–2 in the most highly evolved forms found in Fiji (see below).

Cole (1975) advocated the abandonment of the subgeneric name *Katacycloclypeus* on three grounds: (1) that the annular inflations were probably ecologically produced growth phenomena, (2) that individuals belonging to the same species could sometimes be assigned to different subgenera and (3) that the use of this subgeneric name could induce a false confidence that any annulate specimens were necessarily of T*f* age. He did not, however, demonstrate that the annuli represent resting stages in growth, and the fact that they are well developed only in certain Miocene species suggests that they are not. Furthermore, the irregular development of annuli in microspheric forms, and in particular the tendency for individual annuli to fade out over part of the test, is inconsistent with the resting stage hypothesis. Whether or not *Katacycloclypeus* is confined to the T*f* stage is irrelevant to the biological validity of the name. Only the fact that individuals of the same species can sometimes be assigned to two subgenera is of substantive importance, and Tan was aware of this when he erected *Katacycloclypeus*. We believe that it will be necessary to examine assemblages rather than isolated individuals in order to determine whether or not this objection is valid, and as yet this has not been done.

Cycloclypeus* (*Katacycloclypeus*) *annulatus Martin, 1880
Figs 12–15, 17–23

1880 *Cycloclypeus annulatus* Martin : 157; pl. 28, fig. 1.
1923 *Cycloclypeus martini* van der Vlerk : 138; pl. 1, figs 1, 2; pl. 2, figs 3, 4.
1932 *Cycloclypeus* (*Katacycloclypeus*) *annulatus* Martin; Tan : 39.
1932 *Cycloclypeus* (*K.*) *annulatus* Martin; Caudri : 190; pl. 1, figs 1–3.
Not 1934 *Cycloclypeus annulatus* Martin; Whipple : 142; pl. 19, fig. 1.
1945 *Cycloclypeus* (*K.*) *annulatus* Martin; Cole : 282; pls 19A, 20G (not H).

The types of *C. annulatus* came from 'Die Kluft des Tji Tarum bei Tjikao, nördlich vom Gunung Parang, West Java'. A small fragment of Martin's original material from the Rijksmuseum Leiden has enabled us to prepare several additional thin sections including three orientated in the equatorial plane (Figs 15, 19, 20). The following descriptions are based on topotypes.

Megalospheric generation
Figs 15, 19, 20

Description. Test moderately large, ranging in diameter from 4 to 7 mm. Surface ornamented by at least two strongly inflated annuli. Signs of surface granulation visible externally on some specimens but not on others, although thin sections show that pillars are always present in the annuli and over the central part of the test. Embryonic apparatus large. Proloculus subovate, thin-walled, and partly embraced by the larger, thicker-walled, reniform second chamber. One ana-nepionic chamber (divided by a single septum in one specimen) is followed by 2–4 nepionic chambers. Early neanic chamberlets shorter (radially) than wide, but lengthening after the third chamber until radially elongate chambers are dominant after the 5th to 7th annular chamber. Stolon system distinct; canal system not seen.

Dimensions (based on 3 specimens).

Proloculus	228 μm (min)	to	335 μm (max)
Deuteroconch	350 μm (min)	to	480 μm (max)

Remarks. As this material is relatively poorly preserved and shows signs of abrasion and breakage, it is possible that well-preserved specimens would show surface pustules and might possess more than two annuli. These specimens differ from the types in that the second chamber less strongly envelops the proloculus. However, as the types of *C.* (*K.*) *martini* v.d. Vlerk (1923 : pl. 1, fig. 2; pl. 2, figs 3, 4) also show considerable differences, this character is obviously highly variable and requires statistical investigation.

Megalospheric forms from Fiji
Figs 14, 17, 18, 22, 23

MATERIAL. Numerous specimens from samples F 172, F 173b, F 175 and F 181 (Ladd's layers 8, 7, 5 and just below 1 respectively; see Ladd & Hoffmeister 1945 : 36), collected in stratigraphical order through the type section of the Futuna Limestone, Vanua Mbalavu, Fiji. Brown, iron-stained specimens occur in all four samples; white (unstained) individuals in F 132 and F 181. Most specimens somewhat abraded peripherally and therefore smaller than during life.

DESCRIPTION. Test moderately large (4–6 mm in diameter) with one or two prominent annuli; the broad central boss is unornamented, as is the rest of the test including the annuli. Embryonic apparatus very large, the ovate proloculus being strongly embraced by the reniform second chamber. Both chambers are thin-walled. Ana-nepionic chambers absent; nepionic chambers reduced to two or less. When the nepionic chambers are absent (Figs 18, 23), the embryonic apparatus is followed immediately by annular chambers. Early neanic chambers about twice as wide as long near the embryonic apparatus, but after the 4th to 6th chamber becoming slightly longer than wide. Canal system comprises a wide canal in each secondary septum which divides before reaching the primary septa thus producing two parallel smaller canals in the primary septum. Stolon system not observed in any of the sections studied.

DIMENSIONS (based on 10 thin sections).

Proloculus diameter	0·30 mm – 0·80 mm (usually 0·63 mm)
Second chamber	0.59 mm – 1·25 mm (usually 0·90 mm)
Thickness of prolocular wall	10 µm – 20 µm (4 specimens)
Thickness of deuteroconch wall	10 µm – 40 µm (4 specimens)

The smooth external surface and numerous annuli distinguish the megalospheric generation from those of *C. eidae* and *C. posteidae* which are heavily ornamented and much smaller (Tan 1932). Stolon system not visible in the material studied; canal system as in *C. carpenteri*.

Microspheric forms from Fiji
Figs 12, 13, 21

DESCRIPTION (based on 9 specimens from the type section of the Futuna Limestone). Test thin, up to 90 mm in diameter. Small but distinct umbo surrounded by concentric annuli (usually 6–7 in a radius of 20 mm) which are often coarsely pustulate, particularly in the larger specimens. Annuli often incomplete towards the periphery of the test: remainder of shell surface smooth.

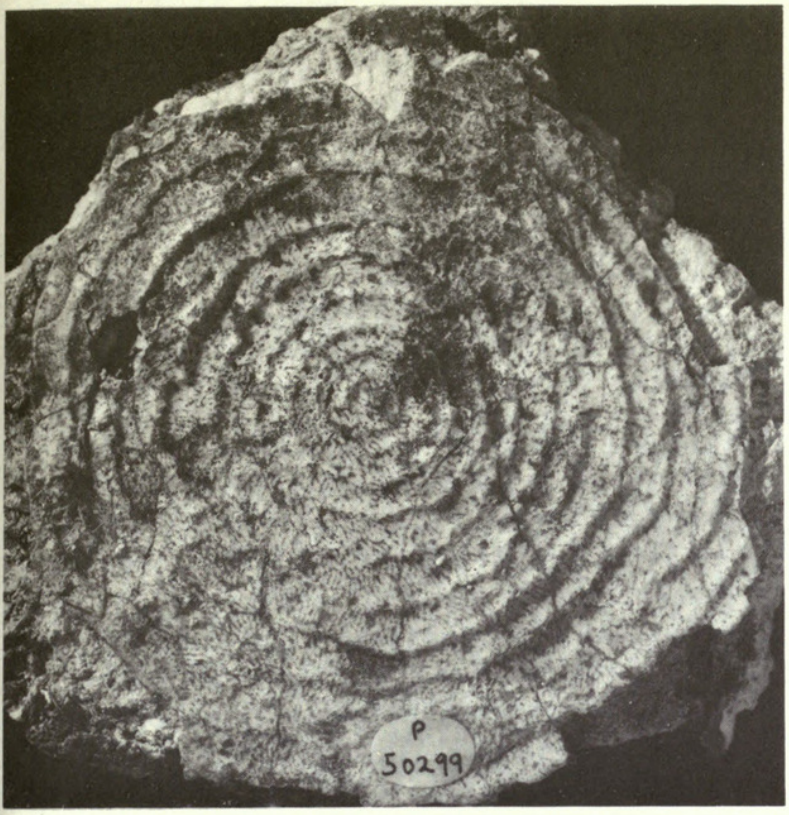
Figs 12, 13. *Cycloclypeus* (*Katacycloclypeus*) *annulatus* Martin, ×1. Microspheric individuals from samples F 180 and F 177, type section, Futuna Limestone, Vanua Mbalavu, Fiji. Note presence of numerous well-developed annuli in both specimens. These tend to be replaced by discrete granules and to fade out towards the periphery in some specimens (see Fig. 13). P.50299 and P.50298.

Fig. 14. *C.* (*K.*) *annulatus* Martin, ×5. Typical broken megalospheric form from Sample F 173b, Vanua Mbalavu, Fiji (cf. Fig. 16). Better-preserved specimens show at least two annuli. Specimen sectioned and registered as P.50466.

Fig. 15. *C.* (*K.*) *annulatus* Martin, c. ×35. Thin section showing the embryonic apparatus and nepionic stage. Topotype from Java. Ex Martin Collection, Leiden. Note undivided ana-nepionic and 4–6 nepionic chambers. P.50464. Test damaged and repaired during life.

Fig. 16. *C.* (*C.*) *posteidae* Tan, ×10. Sample F 181, Futuna Limestone, Vanua Mbalavu, Fiji. Introduced to illustrate that the megalospheric form of *C. posteidae* can closely resemble *C.* (*K.*) *annulatus* externally although they are quite different internally. Compare with Fig. 14; see also Fig. 1a.

Figs 17, 18. *C.* (*K.*) *annulatus* Martin, ×21 and ×20. Thin sections of megalospheric individuals from sample F 181, Futuna Limestone, Vanua Mbalavu, Fiji. Neither specimen possesses an ana-nepionic chamber; Fig. 17 (P.50462) shows two nepionic chambers and Fig. 18 (P.50463) no nepionic chambers. See also Figs 22, 23.



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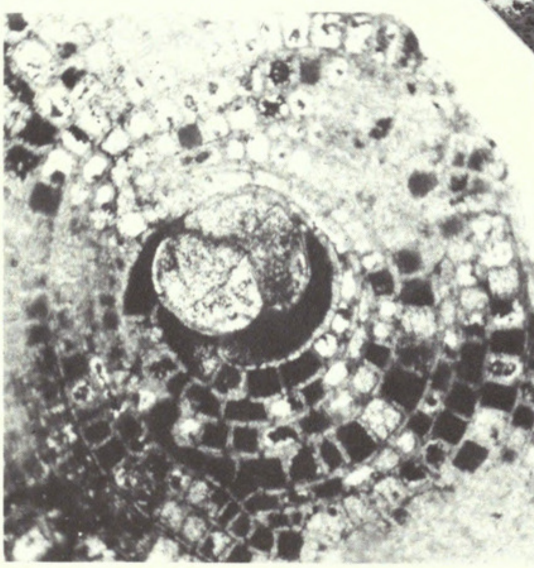

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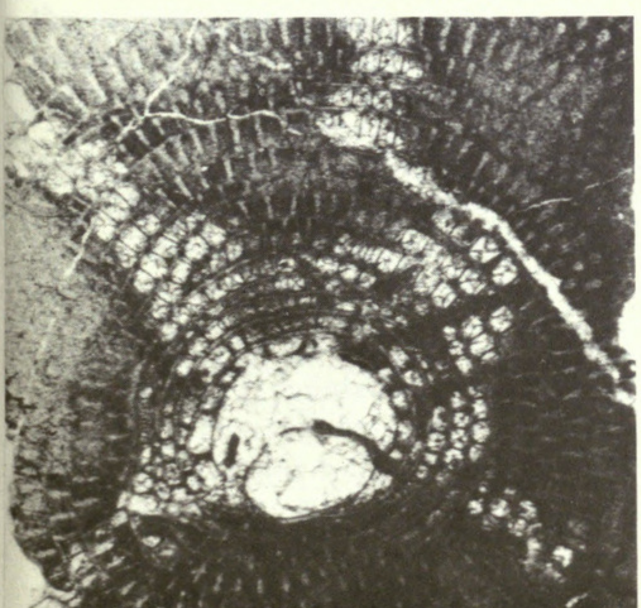

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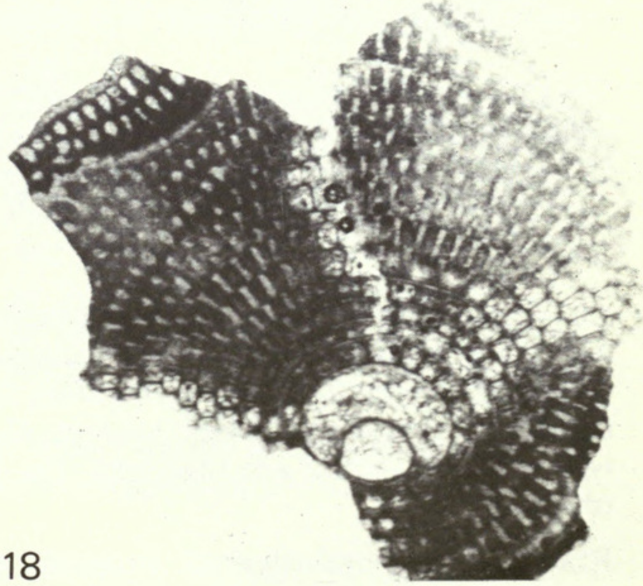

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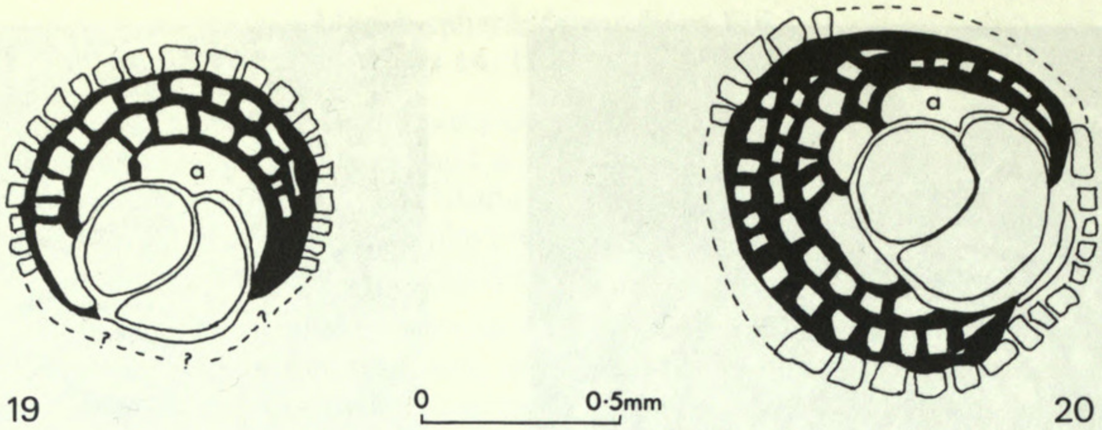
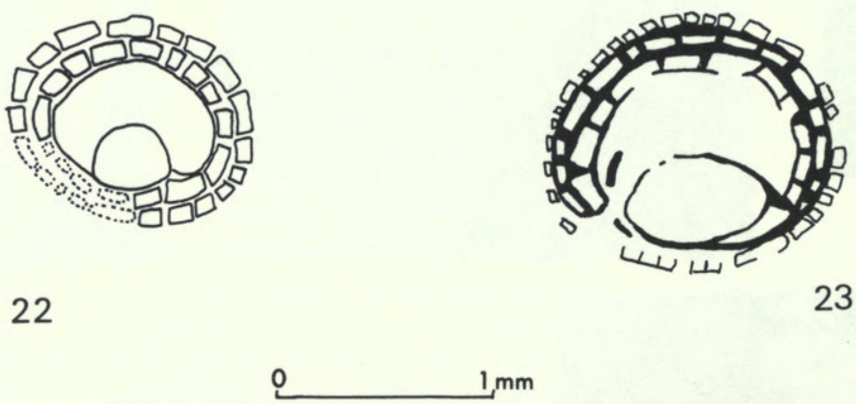


Fig. 19, 20. Internal structure of two topotype specimens of *C.* (*Katacycloclypeus*) *annulatus* Martin. Part of Martin's original material from Java. The first specimen (Fig. 19) shows at least three nepionic chambers including one undivided ana-nepionic chamber. Fig. 20 shows five nepionic chambers. The ana-nepionic chamber is divided by a single septum in this specimen. Fig 19, P.50464; Fig. 20, P.50465.

Fig. 21. *C.* (*K.*) *annulatus* Martin. Microspheric form from the Futuna Limestone, Fiji. The section just misses the proloculus but clearly shows that there are at least six undivided (operculinoid) chambers and about 15 divided (heterosteginoid) chambers in the nepionic stage. P.50298.



Figs 22, 23. *C.* (*K.*) *annulatus* Martin. Embryonic apparatus of megalospheric individuals from the Futuna Limestone, Fiji, illustrated in Figs 17, 18. Note absence of nepionic chambers in Figs 18, 22. Figs 17, 23, P.50462; Figs 18, 22, P.50463.

The small proloculus and second chamber are followed by a coil comprising at least 8 ana-nepionic chambers and about 16 nepionic chambers. The first nepionic chamber is divided by a single septum. Early neanic chamberlets slightly shorter than wide but becoming longer than wide after the 7th or 8th chamber: towards the margin they are very elongate (2–3 times longer than wide). Stolon system not observed. The primary septa contain two canals, the secondary septa only one.

REMARKS. The cycloclypeids from the Futuna Limestone of Fiji are the largest calcareous foraminifera known. Our specimens (up to 90 mm in diameter) are considerably larger than the types of *C.* (*K.*) *annulatus* from Java, and even bigger individuals have been observed in the field: Cole (1945) measured specimens up to 100 mm in diameter from the type section, while Ladd & Hoffmeister (1945 : 36) mentioned specimens of up to 6 inches (=152 mm) in diameter. The embryonic apparatus in the megalospheric form is also much larger than in the types of *C.* (*K.*) *annulatus* while the reduction of the ana-nepionic and nepionic chambers provides a further striking difference. However, these characters could merely reflect the fact that the proloculus itself is so much larger, in which case they are not of fundamental importance. Proloculus size is, however, a very poor taxonomic character in foraminifera and should be used only with caution.

The most important feature of the Futuna Limestone specimens is that some of them have reduced the nepionic spire completely. No further evolution of this character is possible, and it may be significant that having reached this stage, the species (and subgenus) became extinct.

ASSOCIATED FAUNA. *Cycloclypeus* (*C.*) *posteidae hexasepta* Tan, *C.* cf. *C.* (*C.*) *posteidae dodekaseptus* Tan and *C.* cf. *C.* (*C.*) *eidae heneikaseptus* Tan; the last two are remarkable in that they possess very small proluculi – smaller than those of the microspheric generations as described by Tan – and yet in all other characters closely resemble the megalospheric forms. *Lepidocyclina rutteni* van der Vlerk and *L. martini* (Schlumberger) are also present.

Planktonic foraminifera include more than 25 species, but the association of *Globigerina nepenthes* Todd *picassiana* Perconig, *Globigerinoides bollii* Blow, *Gs. subquadratus* Brönnimann, *Gs. parkerae* Bermudez, *Globigerinita glutinata* (Egger), *Gt. glutinata juvenalis* (Bolli), *Globorotalia* (*Turborotalia*) *siakensis* (LeRoy), *Gr.* (*T.*) *continuosa* Blow and *Gr.* (*Gr.*) *cultrata* (d'Orbigny) *limbata* (Fornasini) establishes the age as N13/14 (probably N14) in terms of Blow's (1969) zonation. The reduction of the nepionic coil to 0–2 chambers in *C.* (*K.*) *annulatus* supports this late Middle Miocene age.

Evolution

Tan (1932), in an elaborate and rather difficult paper, described an evolutionary series in *Cycloclypeus* beginning with *C. koolhoveni* Tan (21–38 nepionic chambers in the A form) in the Oligocene and ending with the Recent *C. carpenteri* (1–6 nepionic chambers: this paper). His numerous subspecies have not stood the test of time, most specialists preferring to recognize five or six main species. However, Cosijn (1938) and MacGillavry (1962) concluded that *C. carpenteri* evolved directly from *C. eidae* in the Miocene, thus eliminating the need to recognize *C. posteidae* and the *C. indopacificus* Tan group. They did not, however, study the living representatives of the genus on which this species is based, but assumed that the presence of a short nepionic coil in a few Miocene specimens proved their point. Notwithstanding this, all authors are agreed that the early Oligocene cycloclypeids had a long initial coil comprising some 21–38 chambers in the megalospheric form, and that this was eventually reduced to 2 or 3 nepionic chambers, a process known as nepionic acceleration. The greater part of this shortening had already taken place by Middle Miocene times.

The subgenus *Katacycloclypeus* has been little studied since 1932, presumably because authors thought of it as comprising a different evolutionary lineage, the presence of annuli having been regarded (for no very good reason) as a character of fundamental taxonomic importance. If reduction of the ana-nepionic and nepionic chambers in *Cycloclypeus* is accepted as an indication of the grade of evolution, then *C.* (*K.*) *annulatus* s.l. is not only the largest, but also the most highly evolved member of the genus, notwithstanding the fact that it is extinct and that more 'primitive' members live on today. If the history of this subgenus has any predictive value, *C. carpenteri* must now be on the verge of extinction and will disappear when it loses its initial coil.

We believe that Tan (1932) and MacGillavry (1962) were justified in regarding species of *Katacycloclypeus* as representing a separate lineage from those species of *Cycloclypeus* which led eventually to *C. carpenteri.*

Drooger (1955) studied numerous specimens of *Cycloclypeus* s.s. from samples of early *f* age from Borneo, and concluded that the number of nepionic chambers depended on two factors, nepionic acceleration and the size of the proloculus. He thought that the former acted to reduce the number of heterosteginoid chambers, and the latter to decrease the number of operculinoid chambers in the microspheric generation, and, above a certain size, the number of heterosteginoid chambers in both generations.

Conclusions

The foregoing evidence permits us to draw the following conclusions.

1. The range of the genus *Cycloclypeus* is Early or Middle Oligocene to Recent, *C. mammillatus* Carter having been shown to be from strata of Late Oligocene age and not from the Eocene as originally stated.

2. *C. carpenteri* Brady is a subjective senior synonym of *C. guembelianus* Brady, and there is no evidence to suggest that more than one species is alive today.

3. *C. carpenteri* should be declared the type species of *Cycloclypeus*, and *C. mammillatus* Carter, which was described from a single unfigured specimen, should be allowed to fall into disuse.

4. It is not possible to recognize more than one species of *Katacycloclypeus* at present. So far as can be ascertained, neither surface ornament nor number of annuli are of great taxonomic significance, and it will not be possible to use the embryonic apparatus and nepionic coil satisfactorily until an adequate number of specimens from well-dated horizons throughout its complete range have been collected and investigated statistically. It might then be possible to recognize a primitive group with some 6–13 nepionic chambers (perhaps *C.* (*K.*) *transiens*), an intermediate group with 2–5 nepionic chambers (*C.* (*K.*) *annulatus*) and an advanced group with 0–2 nepionic chambers (*C.* (*K.*) *martini*). This cannot, however, be done at present and it is therefore best to refer them all to *C.* (*K.*) *annulatus*.

5. It is currently convenient to regard *Katacycloclypeus* as a subgenus of *Cycloclypeus*, but for biostratigraphical rather than biological reasons. It is not possible to state that the mere possession of annuli is a character of diagnostic importance at generic level although it has some significance at species level, at least in the megalospheric form.

6. All published references to *Katacycloclypeus* from strata which are not clearly of Tertiary e_5 or f_{1-2} age should be treated with caution. The subgenus can be recognized only from properly orientated thin sections or from matrix-free megalospheric individuals. In random thin sections of limestone it can easily be confused with *Cycloclypeus* (*Cycloclypeus*).

7. The presence or absence of surface ornament (granules or pustules) can only be regarded as significant after vertical sections have been examined, since secondary (organic) calcification often obscures the primary ornament.

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