Secondary chamberlets in *Cycloclypeus*

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Graphs, showing the relation of the primary chambers to the number of their secondary chamberlets, demonstrate that Tan's nepionic mutants are variable, even in the course of a short period. The evolutionary change of the nepionic mutants is consistent with the evolutionary change of *Cycloclypeus* as a whole.

The number of secondary chamberlets of the first neanic chamber is considered a valuable characteristic for the identification of species.

Reduction of the number of nepionic chambers in the course of time is thought to result from the occurrence of 'transitional nepionic variants'.

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Introduction

The present survey forms, in a way, a continuation of a biometrical investigation of *Cycloclypeus* by Van der Vlerk (1966a). The material examined is the same, i.e. samples of Tertiary outcrops along the north coast of East Java and Madura (see Van der Vlerk, 1966a, 1967). The samples Bg. 295, 296, 297 and Bg. 312, 316, 113 and G. 112 from the Vindobonian of the Kombangan section yielded numerous specimens, especially the finer fractions (< 1 mm) which had not been picked before. The older *Cycloclypeus*-bearing samples of the Java-Madura sections contain too small a number of – rather poorly preserved – specimens to allow a reliable study. As to the earlier species use could be made, however, of the very rich samples from the Aquitanian of Larat (Van der Vlerk, 1966b) and of specimens from the lower Tertiary-f of Sungei Maridan (Balikpapan, Borneo). The Spanish cycloclypei described by Cosijn (1938) were incorporated too.

The stratigraphically younger, well preserved specimens from Kombangan could be studied from micro-radiographs, the older specimens had to be thin-sectioned.

Acknowledgements

The writer is indebted to Prof. Dr. I. M. van der Vlerk for putting at his disposal *Cycloclypeus*-material from the Java-Madura sections and for unpublished data concerning biometrical investigation of the material. Messrs. B. F. M. Collet, J. Timmers, J. J. F. Hofstra and H. Guldemond carefully prepared micro-radiographs, thin sections, figures and plates.

External features

The cycloclypei of the Kombangan section show the strong sculptural variations typical of the *Cycloclypeus carpenteri* group (i.e. Tan's Sectio of *C. carpenteri* Brady, comprising both *C. carpenteri* and *C. guembelianus*). Besides, *Katacycloclypeus* occurs frequently, especially in the younger samples Bg. 295-297. Transitional forms between *Katacycloclypeus* and *C. carpenteri* and between the various forms of *C. carpenteri* are common and constitute, in fact, the bulk of the populations. In the present study *Katacycloclypeus* is not considered a separate subgenus but an advanced form which developed from *C. carpenteri* and which, in the Kombangan population, differs from *C. carpenteri* mainly, if not exclusively, in possessing annuli. A distinction is made between variants with 5-10 and variants with 11-23 nepionic chambers (*sensu* Mac Gillavry, 1965, i.e. including the protoconch and deuteroconch). Notwithstanding the large number of precyclic chambers the latter variants are classified as *C. carpenteri* for reasons outlined below.

In spite of the considerable variation of external features some 'main forms' may be distinguished:

Forms a and a-c; Plates 1, 2 – The pronounced umbo and annuli are typical. These forms resemble *C. martini* Van der Vlerk (Van der Vlerk, 1923; Caudri, 1932, pp. 192-193) but as a rule do not show the long, subdivided, ana-nepionic chamber typical of that species. Some specimens possess a second (a2) or third annulus. Generally, however, the flange is broken off and only the innermost annulus remains (a1). Forms transitional to type c (a-c) are common: umbo and annuli are less pronounced (Pl. 2) and finally the test becomes nearly flat (Form c, Pl. 4).

Form b; Plate 3 – Rare fragments of presumably large, thick-brimmed specimens with irregular knobs and ridges. No perfectly similar form could be found in literature; it bears some resemblance to *C. indopacificus* var. *douvillei* Tan (Tan, 1932, Pl. XXI, figs. 3 and 5). Type b perhaps represents a teratological form.

Form c; Plate 4 – Externally the form resembles specimens illustrated by Tan (1932, Pl. XX, fig. 2) and Douvillé (1916, Plate V, figs. 5 and 6). The test is comparatively flat, sometimes arched or undulating. In the centre the pillars are arranged irregularly and on the flange in more or less concentric rows. A faint annulus may be present (a-c).

Form c1; Plate 5 – Small specimens (maximum diameter ca 2½ mm) often with numerous small pillars, standing closely together in concentric rows, which are distinct on micro-radiographs (Pl. 8, figs. 4 and 11). The pillars may be little developed or even absent. In sculpture this form resembles *C. victoriensis* Crespin and some individuals of *C. eidae* Tan (Tan, 1932, Plate XII, figs. 2 and 3). These species, however, attain a larger diameter. Internally form c 1 is characterized by a comparatively large number of nepionic chambers (11-23). Forms, transitional to form c occur occasionally; the form c1 sometimes shows annuli.

Form d; Plate 6 – Thick, lenticular to subspherical specimens, sometimes with a narrow – regenerated? – flange. This small form possibly represents the umbo of forms a and a-c.

Form e; Plate 7 – Small, probably juvenile specimens which externally resemble type c to some extent. Annuli are not present at this ontogenetic stage but might eventually have developed. The relatively large, 'inflated' embryonic apparatus and the somewhat translucent flange are typical of this form. In contrast to the adult forms from Kombangan (forms a to d) these juvenile specimens are often well preserved.

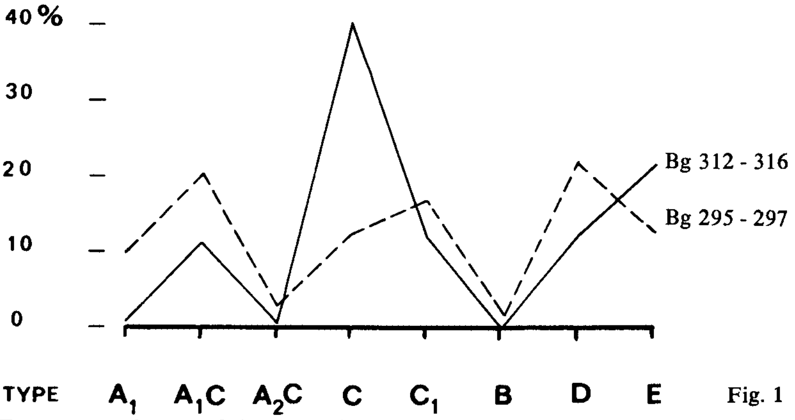

Fig. 1

Fig. 1. Frequency polygons of the *Cycloclypeus* forms of Kombangan.

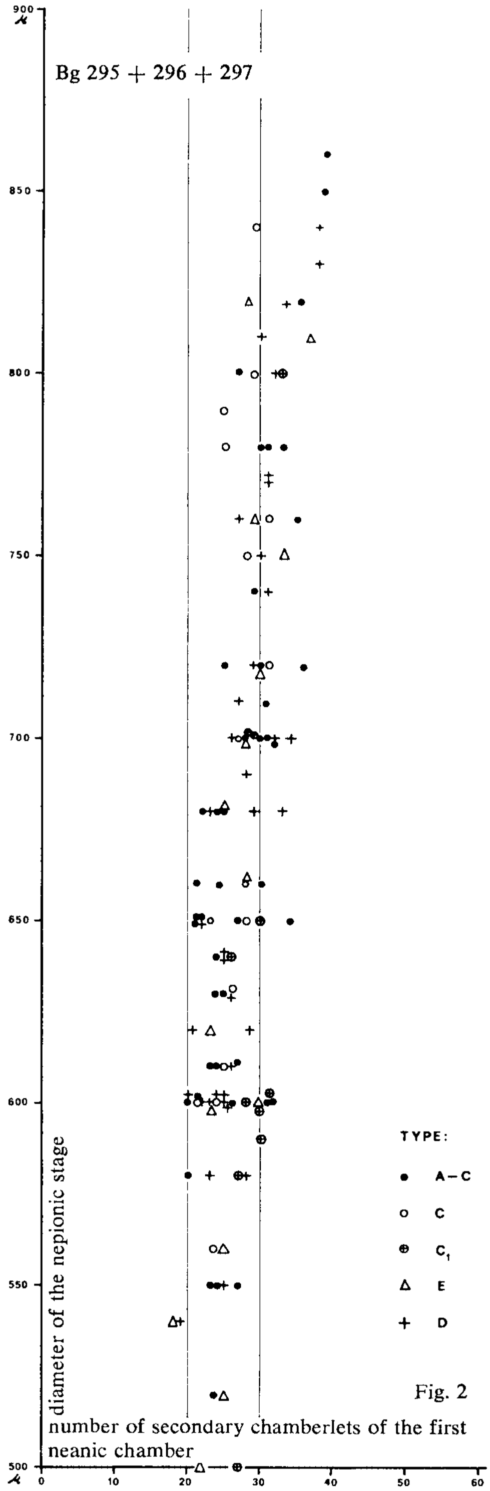

Fig. 2

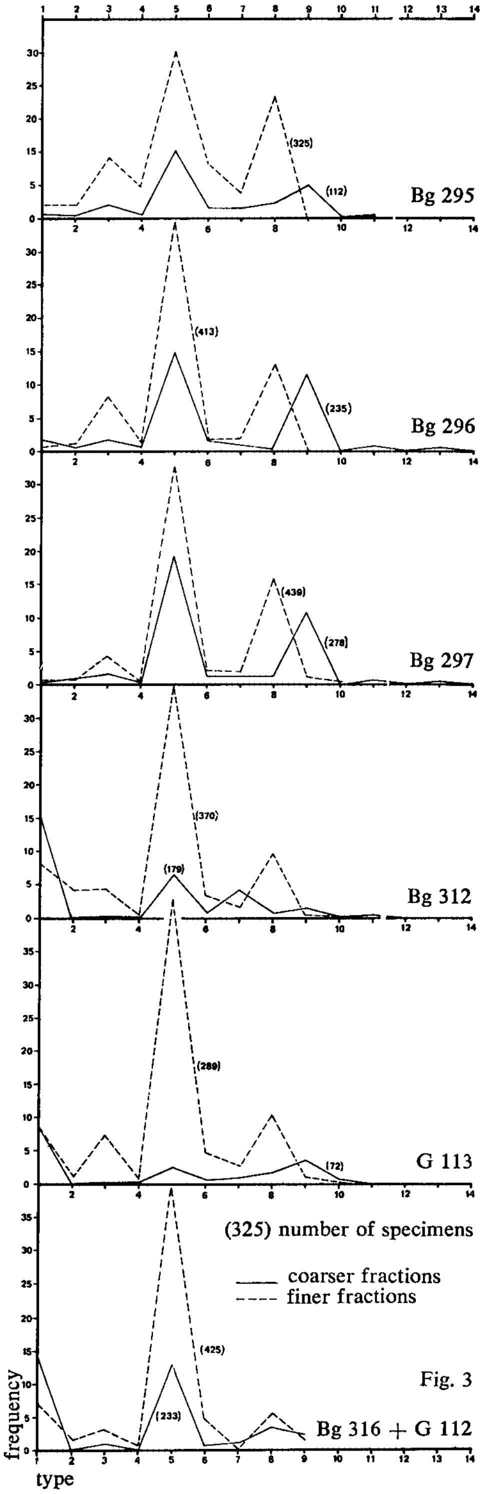

Fig. 3

Fig. 2. Diameter of the nepionic stage plotted against the number of secondary chamberlets of the first neanic chamber, for the Kombangan forms.

Fig. 3. Frequency polygons of the various types distinguished in the Kombangan populations.

Fig. 1 shows the frequency polygons of the above-mentioned forms for the stratigraphically older (Bg. 312-316) and younger samples (Bg 295-297) of Kombangan; the polygons are based on the specimens from the coarser fractions; the percentage of the small forms, i.e. cl, d and e, obviously is larger in the finer fractions.

The younger group of samples shows an increasing percentage of *Katacycloclypeus* (forms a, a-c) and a strong decrease in the percentage of form c. The concurrent increase of d and a (a-c) is in favour of the supposition that d represents the umbo of the latter forms.

Some interrelations of external and internal features

The relation of forms a to e to the mean number of nepionic chambers is represented below; for practical reasons the forms a and a-c have been lumped.

Forms	Mean number of nepionic chambers	Number of specimens counted
a-c	6.21	33
c	7.28	14
cl	ca. 17	25
b	....	few specimens
d	6.30	42
e	6.28	21

Legend fig. 3

				Type
Cycloclypeus s.str.	*communis*-type	abnormal		1
		normal		2
	carpenteri-type	abnormal	3rd chamber normal	3
			3rd chamber long and low	4
		normal	3rd chamber normal	5
			3rd chamber long and low	6
C. cf. *victoriensis*	with distinct pillars			7
	pillars faint or absent			8
Katacycloclypeus	*carpenteri*-type	abnormal	3rd chamber normal	9
			3rd chamber long and low	10
		normal	3rd chamber normal	11
			3rd chamber long and low	12
	communis-type	normal		13
		abnormal		14

The mean values of the forms a-c, d and e agree fairly well with one another, with d and e possibly representing the umbo and the juvenile stages of (mainly) form a-c, respectively. Form c, which has a larger mean value, is presently considered a stratigraphically older form from which form a-c and finally form a evolved by a gradual development of umbo and annuli. Form cl is clearly related to variants with a large number of nepionic chambers (mean value 17).

The relation between the number of secondary chamberlets of the first neanic chamber and the diameter of the nepionic stage is shown in fig. 2 (see also fig. 19). The number of secondary chamberlets, which parameter will be elaborated below, amounts to 20-30 for Kombangan. The various forms show random distribution in the diagram.

Internal features

In his biometrical study Van der Vlerk (1966a) distinguished *Cycloclypeus* s. str. and *Katacycloclypeus* on the one hand and specimens of the *carpenteri*-type (ana-nepionic chamber not subdivided) and *communis*-type (ana-nepionic chamber subdivided) on the other. In the present investigation a more detailed subdivision is pursued (Fig. 3). Before discussing this diagram, some concepts should be dealt with.

ABERRANT FORMS

Individuals with a growth form which clearly deviates from the usual are either not incorporated in the diagrams or represented separately. For convenience' sake specimens are referred to as 'normal' or 'abnormal'. The various growth-anomalies noticed, which are particularly abundant in samples Bg. 312-316, are:

1. An extremely large embryonic apparatus; the diameter of the protoconch may be 600-800 μ and rarely 1100 μ. With this growth-anomaly generally go a small number of nepionic chambers (3-4) and an interrupted first neanic chamber with a typical horn-shape (Pl. 9, figs. 1-5). In the younger samples Bg. 295-297 this kind of deformation is less frequent (Fig. 4, specimens with 3 and 4 nepionic chambers). The development of an irregular embryonic apparatus must be considered 'normal' in the most advanced cycloclypei (Tan, 1932, p. 36); it is only the extremely large embryonic apparatus that renders the form 'abnormal'.
2. Irregularly winding or abruptly narrowing or widening chambers. In narrowing chambers the opposing septa sometimes grow together. This kind of deformation is often attended by relatively small apertural chamberlets.
3. Embryonic chambers which strongly deviate in shape from the usual, i.e. a nearly spherical protoconch and a kidney-shaped deuteroconch.
4. Extremely thick or thin marginal cord and/or primary septa.

The aberrant forms of the samples Bg. 312-316 bring to light the following differences:

Katacycloclypeus	ana-nepionic chamber little or not subdivided; protoconch on an average smaller than in *Cycloclypeus* s. str.; on an average a larger number of nepionic chambers.

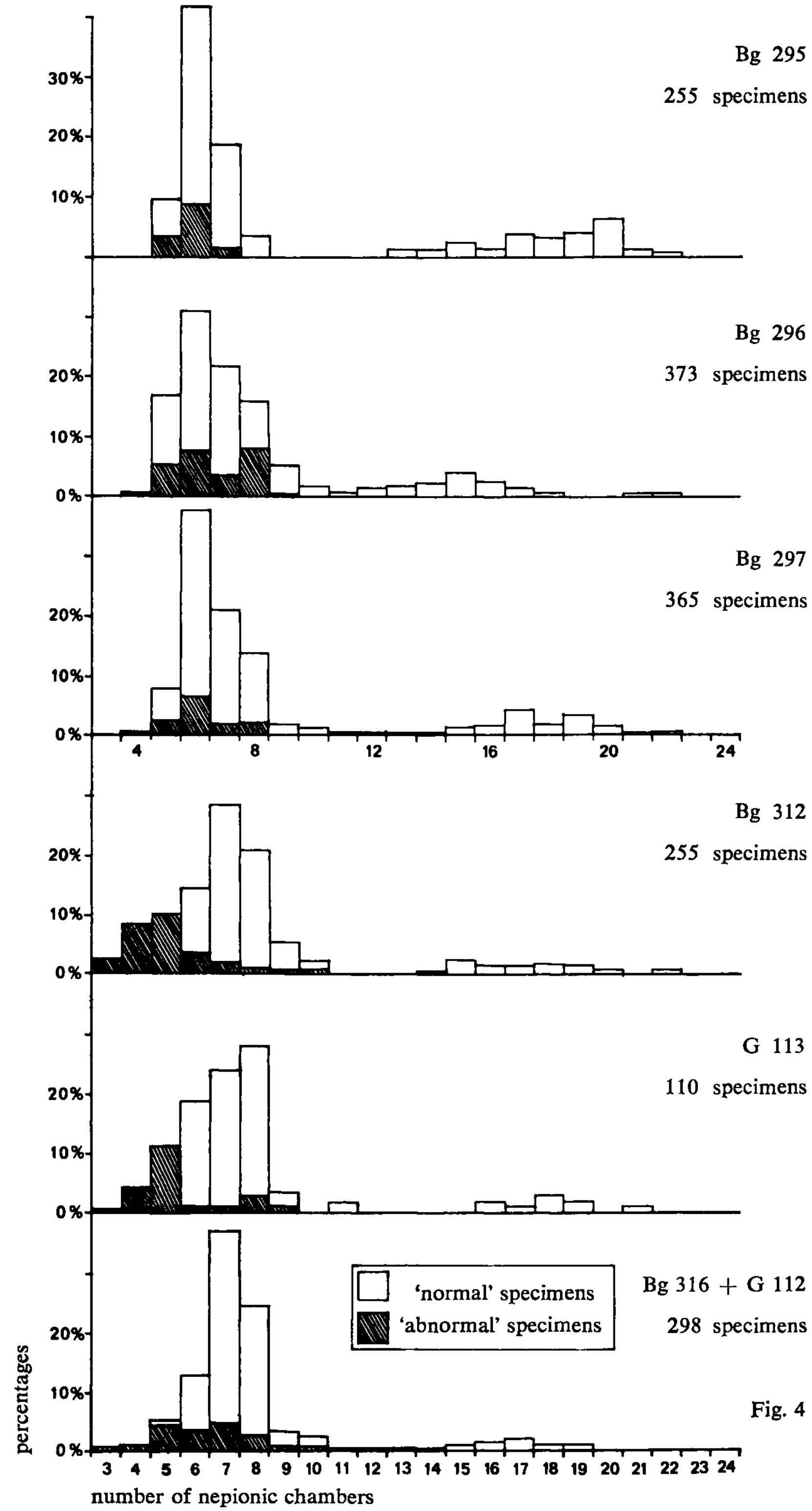

Fig. 4. Histograms of the nepionic variants of Kombangan.

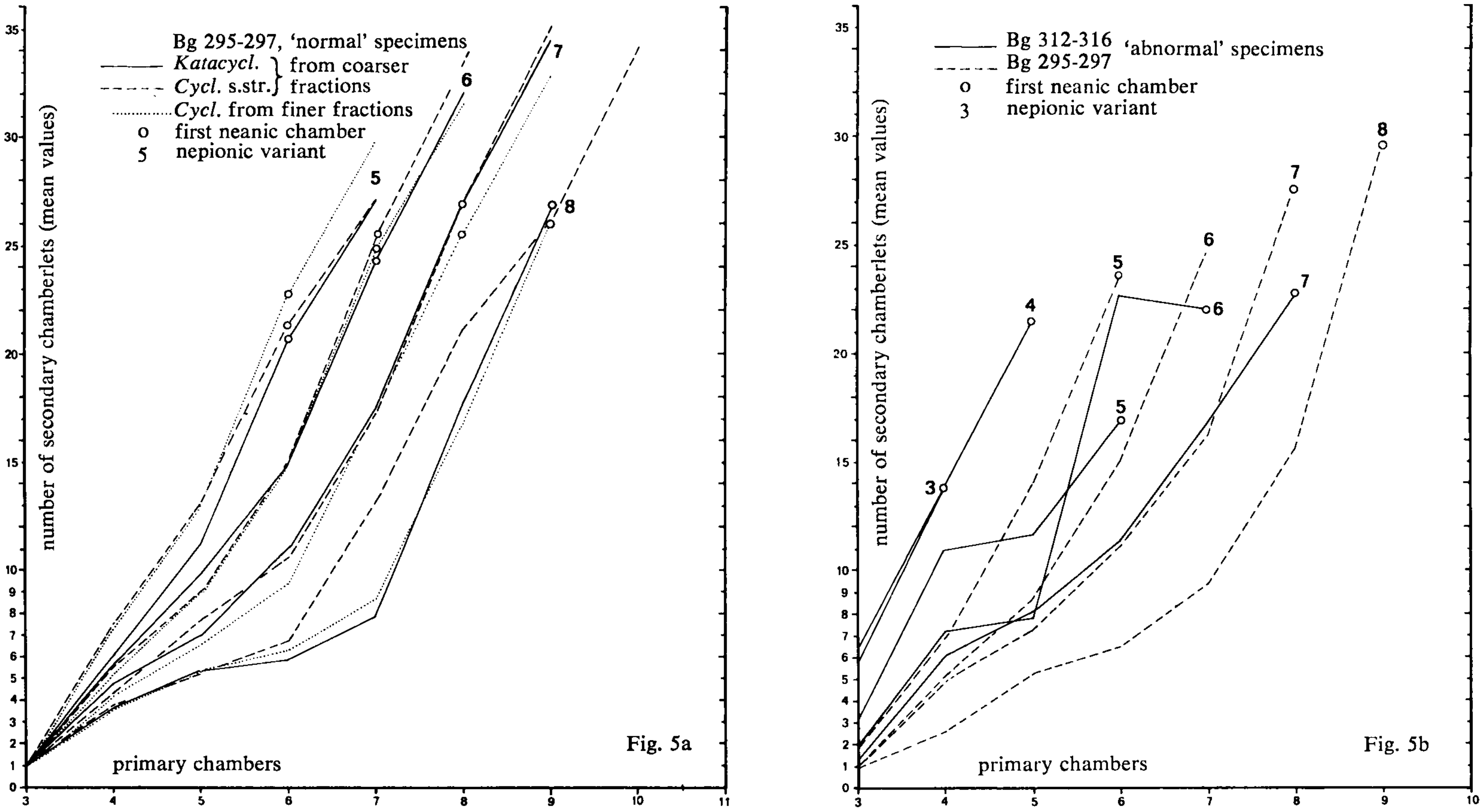

Fig. 5. Primary chambers plotted against their respective numbers of secondary chamberlets, for several forms of Kombangan.

Cycloclypeus s. str.	ana-nepionic chamber often very long and subdivided into numerous chamberlets; protoconch often extremely large; fewer nepionic chambers than in *Katacycloclypeus*.

It is remarkable that the ana-nepionic chamber of *Katacycloclypeus* is generally less subdivided than in *Cycloclypeus* s. str. This is not in agreement with Caudri's (1932) and Martin's (1879-1880) observations, recording a frequently subdivided ana-nepionic chamber in *C. annulatus*. Their observations, however, relate to 'normal' specimens.

The forms mentioned above may indeed be due to growth-anomalies, for the following reasons:
1. They are represented by strongly deviating diagrams (Figs. 4, 5b, 12, 17, 18, 19).
2. The occurrences of the nepionic variants are not in agreement with their stratigraphical positions: specimens with very small numbers of nepionic chambers (3-4) are more frequent in samples Bg. 312-316 than in the younger samples Bg. 295-297 (Fig. 4).
3. Micronodules of pyrite, occurring together with chamosite, are frequently observed in the specimens from samples Bg. 312-316 (Pl. 8, fig. 3). The possibility cannot be excluded that the pyrite was formed *in vivo* (Goni & Parent, 1966) and consequently, that the aberrant forms developed under unfavourable conditions.

THE ANA-NEPIONIC CHAMBER

This chamber is generally not subdivided (*carpenteri*-type). Among individuals with a long subdivided ana-nepionic chamber one may distinguish forms with a 'normal' nucleoconch (cf. *C. communis* and *C. martini*) and forms with an abnormally large nucleoconch (aberrant forms).

A long and low ana-nepionic chamber, which is sometimes subdivided by a growing together of the opposite primary septa, is a rather common occurrence; in other respects this form is as a rule developed normally.

A subdivided ana-nepionic chamber infrequently, if ever, occurs in individuals with 8 or more nepionic chambers. The fewer nepionic chambers there are, the more subdivided the ana-nepionic chamber tends to be (Fig. 5b).

The following may now be noticed (Fig. 3):

The polygons for samples Bg. 295-297 are in conformity with one another and so are on the other hand the polygons for samples Bg. 312-316. The larger individuals from the older samples show a distinctly larger percentage of type 1 and smaller percentages of types 5 and 9 (for an explanation of these types see legend of fig. 3).

The polygon tops for the coarser and finer fraction coincide generally. As likely as not most of the individuals from the finer fractions are juvenile forms, as they agree fairly well both internally and externally with adult forms.

C. cf. *victoriensis* (types 7 and 8) attains a maximum diameter of ca. 2½ mm and is therefore concentrated in the finer fractions. In type 9 the tops for both fractions do not coincide: possibly the juvenile forms have not yet developed annuli and consequently were not recognizable as *Katacycloclypeus*.

The large percentage of juvenile forms probably results from the relative abundance

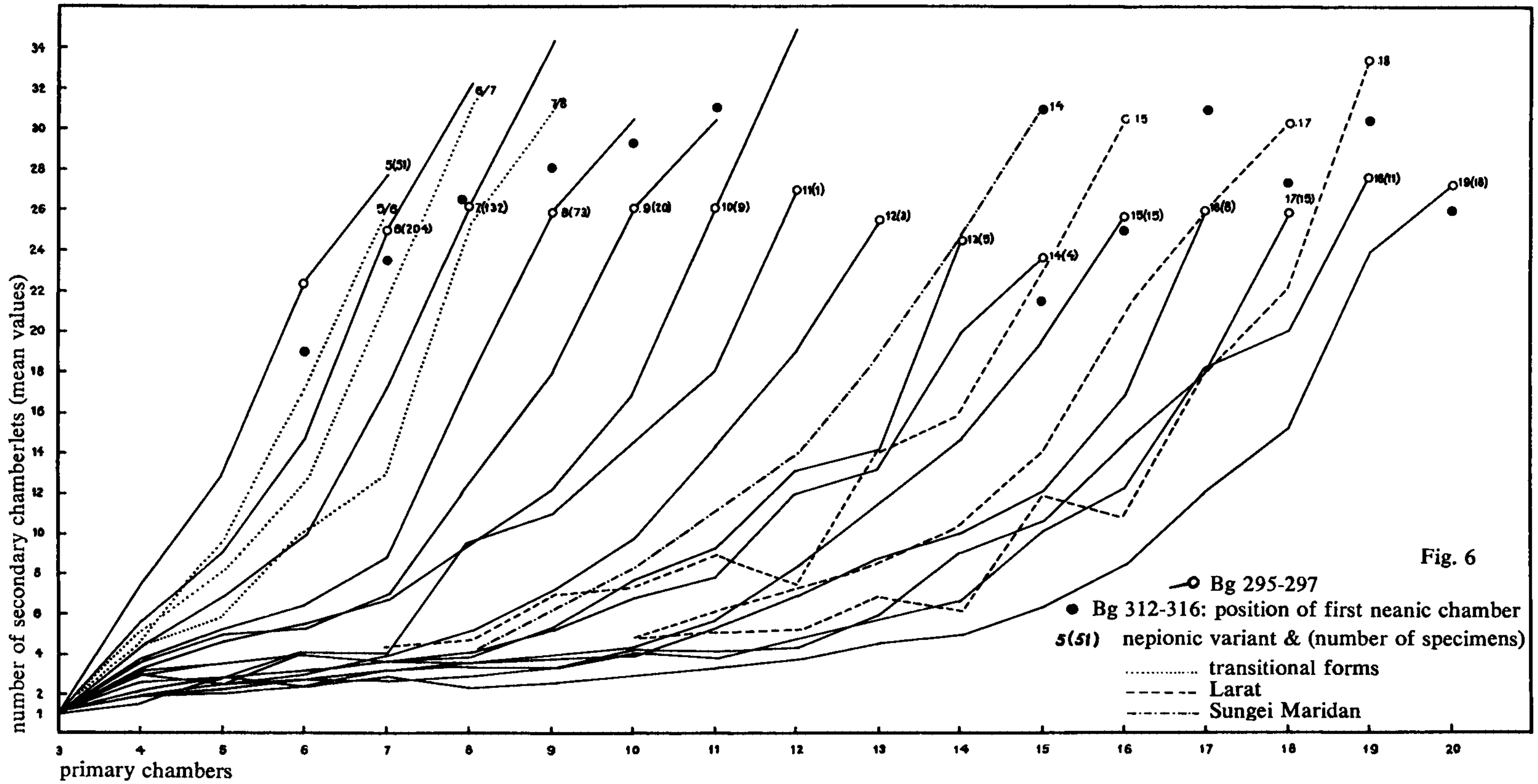

Fig. 6. Primary chambers plotted against their respective numbers of secondary chamberlets, for the nepionic variants of samples Bg. 295-297 (Kombangan).

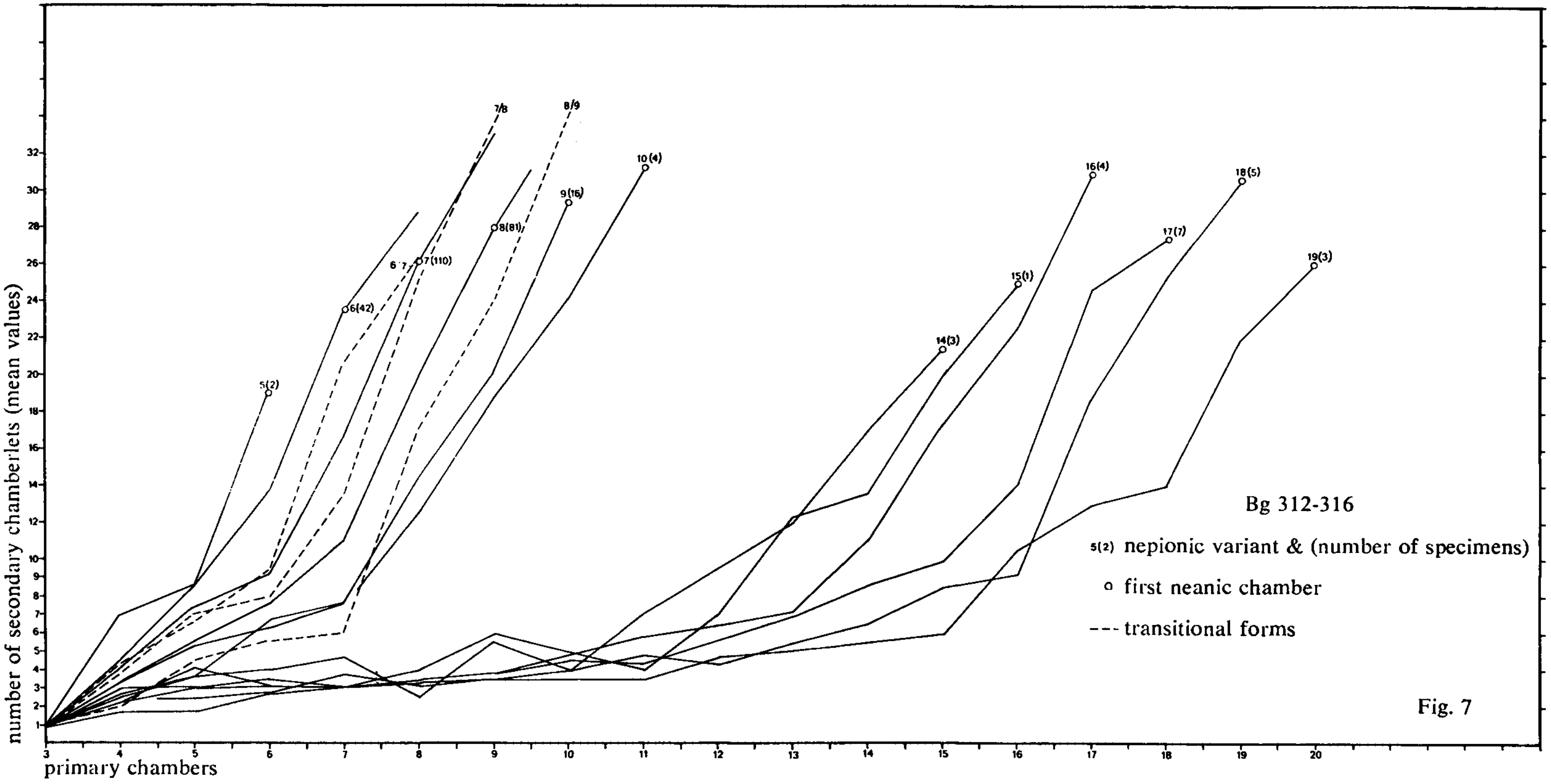

Fig. 7. Primary chambers plotted against their respective numbers of secondary chamberlets, for the nepionic variants of samples Bg. 312-316 (Kombangan).

of individuals in the finer fractions. Selective sedimentation, however, may have played a part too.
The 'normal' *communis*-type (type 2) and the *communis*-type of *Katacycloclypeus* (types 13 and 14) are rare. The types 5 and 8 are predominant.

Increase or decrease of the number of secondary chamberlets?

Van der Vlerk (1966a) concluded that 'from (stratigraphically) old to young there is a gradual increase of the number of secondary chamberlets in the primary chambers 4 and 5, combined'. The obvious next step is to examine the number of secondary chamberlets of the other primary chambers. In this connection it is of importance to define the first neanic chamber.

Several students of *Cycloclypeus* (e.g. Caudri, Cosijn, Tan) have stressed the difficulty of determining the number of nepionic chambers, in certain cases. It will be shown below that this number is not always definable and that transitional forms exist between variants with, for instance, 5 and 6 or 6 and 7 precyclic chambers. For the non-transitional forms it remains essential which chamber should be considered as the first neanic one.

In most cycloclypei, especially the advanced ones (*C. carpenteri, C. guembelianus*), the first cyclic chamber is identifiable by a typical joint shape of the first and last secondary chamberlet of the first neanic chamber (Fig. 22, chamberlets F and L). These chamberlets are generally grown together and the secondary septum in between may be intact or, more often, reduced to half a septum or a short tooth. The double chamberlet, further down referred to as FL-chamberlet, may thus assume various shapes – sometimes long, rectangular or pentagonal – which in most cases are easily recognizable. The prevailing shapes are illustrated: Pl. 8, figs. 9-14, see also other figs. of Pl. 8 and 9, and Tan, 1932, Plate III, figs. 1, 3, 4 and 6. The FL-chamberlet generally covers the outermost secondary chamberlets of the preceding nepionic chamber, much like a key-stone (Pl. 8, fig. 11).

Determining the first neanic chamber by means of the FL-chamberlet is essential as this first cyclic chamber, like most of the other primary ones, may be interrupted and therefore not cyclic at all (Pl. 8, fig. 14, Pl. 9, figs. 1-5). Tan most probably used the criterion of the FL-chamberlet: Tan, 1932, Pl. XV, fig. 1, showing an interrupted first neanic chamber and Pl. XXIII, fig. 4, in which the last nepionic chamber could be regarded as cyclic but lacks the FL-chamberlet, which only appears in the next primary chamber.

In figs. 6 and 7 the successive primary chambers are plotted against their numbers of secondary chamberlets (mean values of all 'normal' individuals) for the populations of samples Bg. 295-297 and Bg. 312-316. It is of little consequence whether the mean value is calculated for *Katacycloclypeus*, *Cycloclypeus* s. str. or 'juvenile forms' apart or together, provided the number of individuals is adequate (Fig. 5a, variants 6 and 7).

The graphs for the successive variants are rather regularly distributed, from the steeply rising curves of the variants with the smaller numbers of nepionic chambers to the less inclined curves of the variants with larger numbers of nepionic chambers. It is apparent that C1s – the number of secondary chamberlets (s) of the first neanic chamber (C1) – is approximately constant, occupying the same level in the diagram, independent of the nepionic variant. The variants with a small number of nepionic chambers reach this level more 'rapidly'.

When comparing fig. 6 with fig. 7, for instance by superposition, it should be taken into account that the two groups of samples differ only little in age and that consequently only a slight evolutionary change may be expected. Allowing for this it would seem that:

1. The increase of the number of secondary chamberlets in the younger group (samples Bg. 295-297) progresses more 'rapidly' for the variants with 5 and 6 nepionic chambers, and generally more 'slowly' for the variants with larger numbers (8?-19) of such chambers. For the variant with 7 nepionic chambers the increase is approximately equal in both groups of samples.
2. The 'level' of the first neanic chamber is on an average somewhat higher in the older group (samples Bg. 312-316).

The curves for the variants represented by only a small number of individuals obviously are not very reliable.

TRANSITIONAL FORMS

Curves for transitional forms are shown in figs. 6 and 7. Morphologically these forms occupy positions between variants with a round number (e.g. 5/6, 6/7 etc.) of nepionic chambers. In the transitional forms the number of nepionic chambers is doubtful and sometimes indeterminable (Pl. 9, figs. 6-11).

The reader may be reminded that the graphs in figs. 6 and 7 represent mean values. If however curves are drawn separately for all individuals, it appears that the clusters of curves for the consecutive nepionic variants overlap. In other words it can be said that an 'advanced' variant 7 coincides with a 'primitive' variant 6 etc. Consequently, the curves of the transitional forms fall between the adjacent curves representing variants with a round number of nepionic chambers.

In the Kombangan samples, transitional forms between the nepionic variants with 5/6, 6/7 and 7/8 nepionic chambers are predominant. Frequency polygons of the transitional forms (Fig. 8) show that the transitions 6/7 and 7/8 prevail in the younger and older samples, respectively.

The above suggests the possibility of a gradually decreasing number of nepionic chambers as a result of the occurrence of the transitional forms; these forms amount to 0.8 and 1.3% of the total populations of the older and younger group of samples, respectively.

It is conceivable (compare Pl. 9, figs. 6-11) that a reduction of the number of nepionic chambers results from an extension and finally fusion of the outermost secondary chamberlets of the last nepionic chamber (cf. Drooger, 1955, p. 432: 'the number of nepionic chambers is dependent on two factors. The first is nepionic acceleration, acting in the course of time on the outermost nepionic chambers and causing a reduction of the number of subdivided chambers...'). Therefore the extended first and last secondary chamberlet of the outermost nepionic chamber and often also of the preceding ones are typical of transitional forms.

In this connection it is worth noting that a nepionic chamber terminates

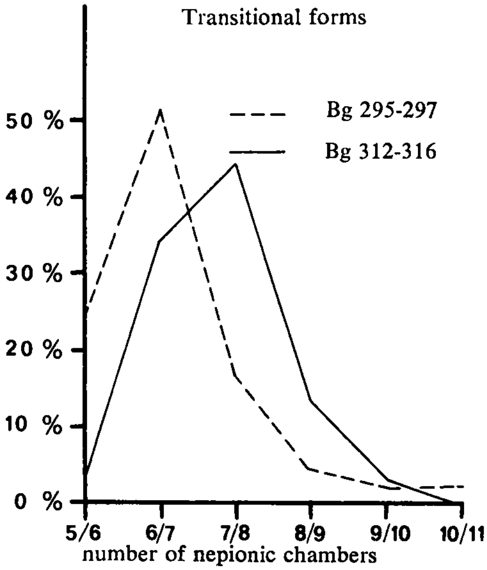

Fig. 8. Frequency polygons of 'transitional nepionic variants' occurring in the Kombangan populations.

either before or beyond the preceding one. The chambers ending beyond the preceding chamber are invariably outer chambers, the number of these chambers varying from 1 to 3 or 4. Part of the marginal cord coincides with the dividing-line between the two kinds of chambers (Pl. 8, figs. 6, 11 and 4 and Tan, 1932, Pl. XIV, figs. 2 and 4).

Curves for *C. eidae* were composed by means of the rich material from Larat (Van der Vlerk, 1966b). For even older forms (*C. koolhoveni, C. oppenoorthi*) Tan's scarce and sometimes indistinct illustrations had to be used (Tan Sin Hok, 1932). The curves for these older forms are represented in an idealized fashion, together with those of Kombangan (Fig. 9). It is evident that the number of secondary chamberlets of the successive nepionic chambers and also of the first neanic chamber – succeeding neanic chambers were not considered – decreases in the course of time, rapidly at first and more gradually afterwards. Evolutionary decrease is particularly striking when the 'levels' of Cls are compared (Fig. 10). The decrease goes hand in hand with the decrease in diameter of the nepionic stage. The approximate dimensions of this stage, as determined from Tan's illustrations are:

C. koolhoveni Tan 1930	5.2 x 3.7 mm
C. oppenoorthi Tan 1930	3.2 x 2.4 mm
C. eidae Tan 1930	1 x 0.8 mm
C. posteidae Tan 1932	0.9 x 0.8 mm
C. carpenteri Brady 1881 and	
C. guembelianus Brady 1881	0.9 x 0.8 to 0.7 x 0.75 mm

These dimensions are approximately equal to the ones mentioned by Tan for the nepionic stages of the microspheric generation (Tan, 1932, p. 107). Likewise, in the same species, Cls is about equal for microspheric and megalospheric forms.

The cycloclypei from Spain investigated by Cosijn (1938) show a more gradual evolutionary decrease (Fig. 10).

In the advanced Indo-Pacific cycloclypei Cls is approximately constant, independent of the nepionic variant; in the earlier species – *C. koolhoveni, C.*

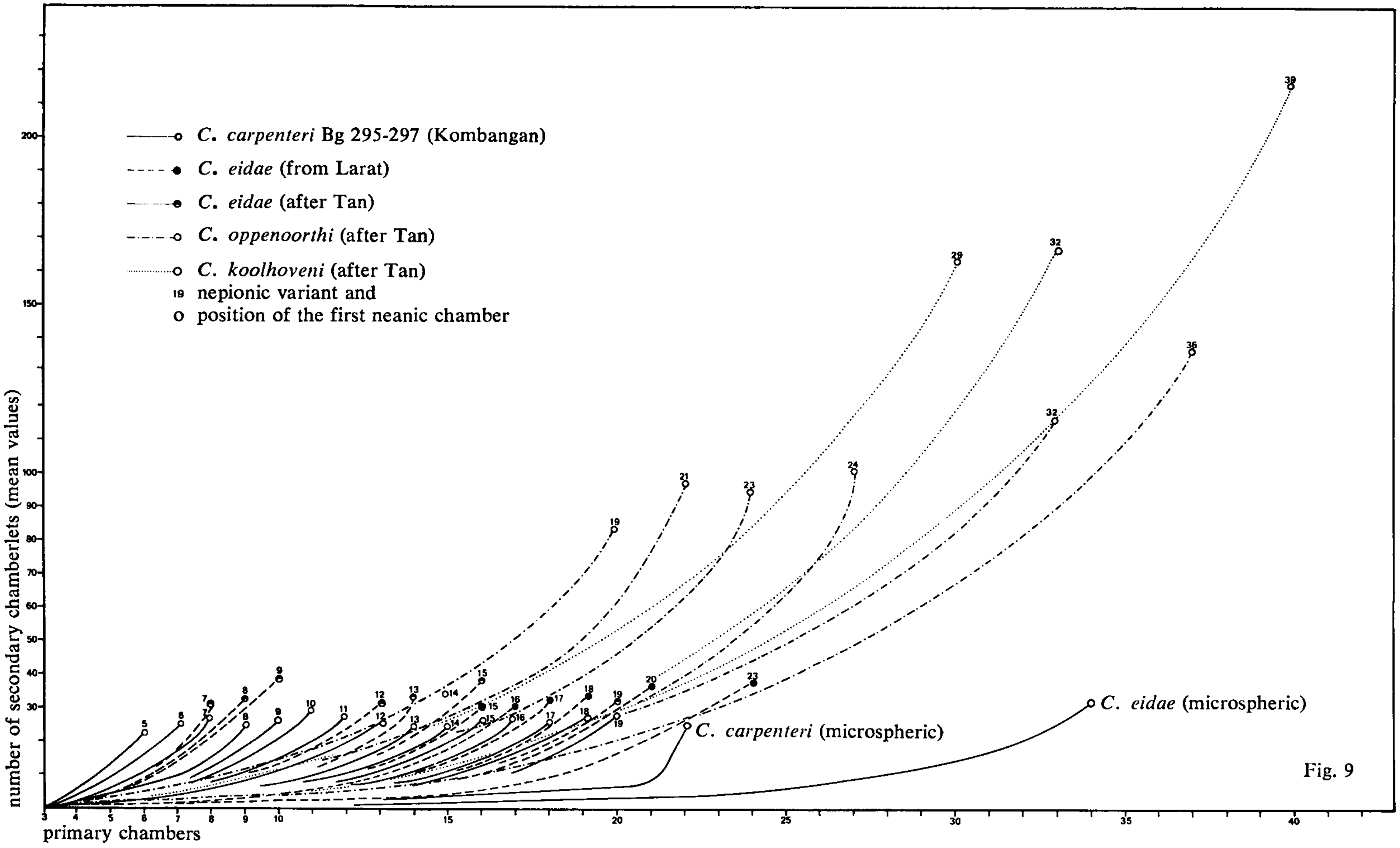

Fig. 9

Fig. 9. Idealized graphs of primary chambers plotted against their respective numbers of secondary chamberlets (Indo-Pacific species).

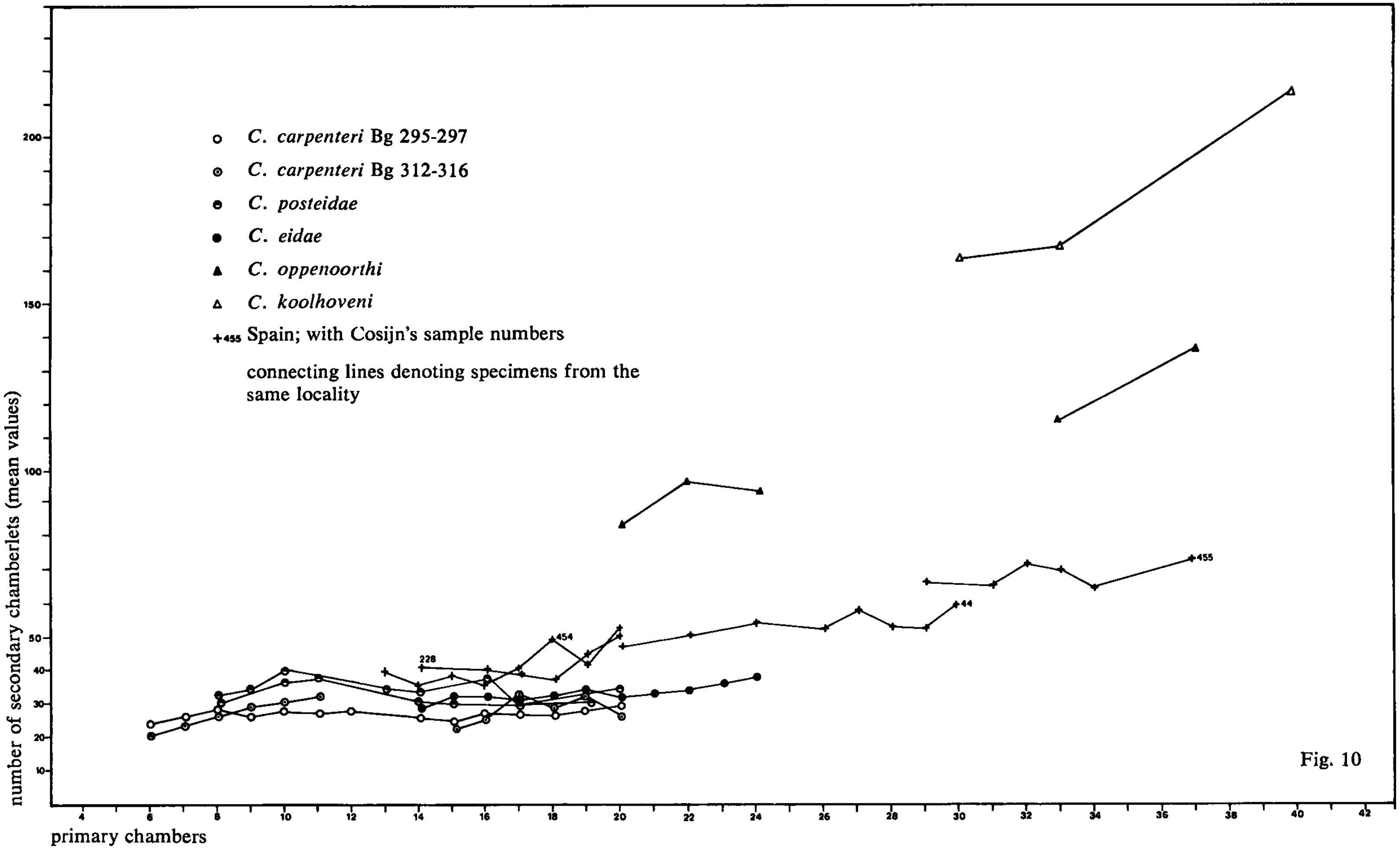

Fig. 10

Fig. 10. First neanic chambers plotted against their respective numbers of secondary chamberlets (Indo-Pacific and Spanish cycloclypei).

oppenoorthi – Cls decreases as the nepionic variant has fewer nepionic chambers (Fig. 9).

The decrease of Cls is plainly shown by specimens with an equal number of nepionic chambers though belonging to different species, e.g. variant 32 (*koolhoveni/oppenoorthi*), variant 19 (*oppenoorthi/eidae*) and variant 18 (*eidae/ carpenteri*): see fig. 9. Variants *carpenteri* 5 and 6 show an evolutionary increase (Figs. 6, 7). The *carpenteri*-variants 5 and 6, and possibly also the variants 3 and 4, seem to form exceptions to the rule of a general decrease.

The above seems to contradict Van der Vlerk's conclusion as to the increase of the number of secondary chamberlets in the 4th and 5th primary chambers. The curves mentioned above (Figs. 6, 7, 9) are obscure with regard to the innermost nepionic chambers. The curves for these innermost chambers (primary chambers 3-7), as composed for the older and younger group of Kombangan, are shown in a separate diagram (Fig. 11). It appears that:

1. The 4th primary chamber shows an evolutionary (?) increase of the number of secondary chamberlets in the variants with 9-10 nepionic chambers or less.
2. The 5th and 6th primary chambers show a similar increase in the variants with

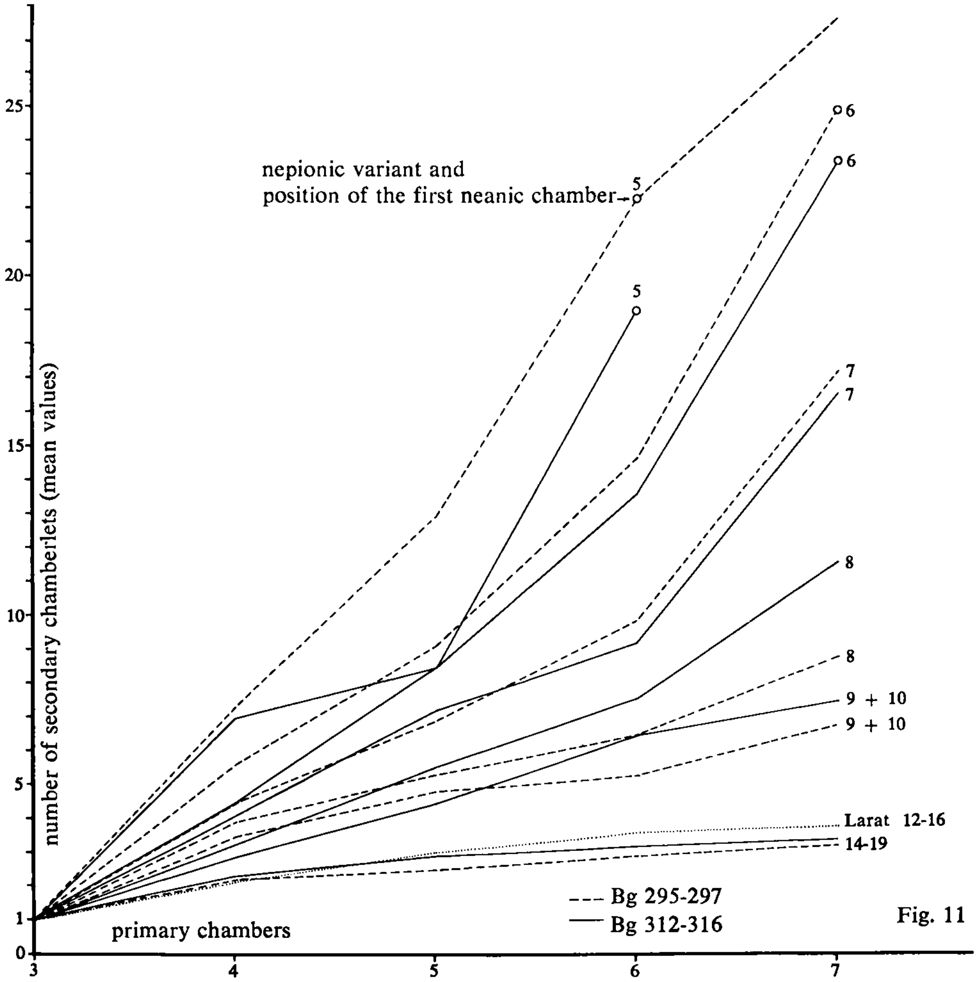

Fig. 11

Fig. 11. Innermost primary chambers plotted against their respective numbers of secondary chamberlets (Kombangan).

5 and 6 nepionic chambers and generally a decrease in the variants having 8 nepionic chambers or more. Again, variant 7 remains more or less constant (compare figs. 6 and 7). It is evident that the number of secondary chamberlets in the 4th and 5th primary chambers, combined, increases. It has to be taken into account, however, that within the same horizon, a *carpenteri*-variant with a large number of nepionic chambers has fewer secondary chamberlets in the primary chambers 4 and 5 than a variant with a smaller number of nepionic chambers (Fig. 20). Stratigraphically older species (Fig. 21, *C. eidae*) are rather indifferent in this respect.

Evolutionary increase of the number of secondary chamberlets in the primary chambers 4 and 5 is slow at first but accelerates in the younger forms, up to the present (Fig. 14). This increase is probably connected with the enlargement of the protoconch. It is likely that C1s is a specific characteristic. Frequency polygons of C1s show the same evolutionary change for all groups represented (Fig. 13; see also scatter diagrams of fig. 19), i.e.:
In the younger group the percentages of individuals with larger C1s-values decrease and the percentages of specimens with smaller C1s-values increase (the curves shift from the right to the left), the mean value of C1s therefore decreases. It is noteworthy that the group of *C.* cf. *victoriensis* shows a similar evolutionary change (Fig. 13b), whereas the histograms of its nepionic variants (Fig. 4) do not reveal a distinct evolutionary change. Very irregular, polymodal polygons result when few individuals are available (Fig. 13f) or 'abnormal' forms (Fig. 13e). The frequency polygon for Larat (Fig. 13a) clearly demonstrates the larger C1s-value of *C. eidae*. The Kombangan variants with 11 or more nepionic chambers (*C.* cf. *victoriensis*) are much more in agreement with *C. carpenteri* than with *C. eidae* (Fig. 13b). The decrease of C1s-averages for the individual samples of Kombangan is shown in fig. 12.

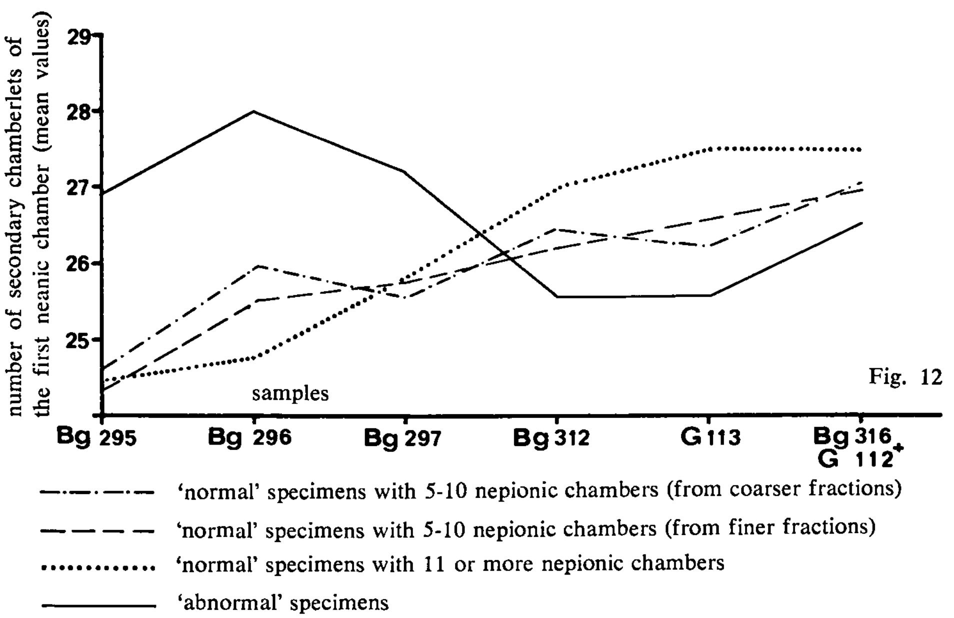

Fig. 12

Fig. 12. Mean numbers of secondary chamberlets of the first neanic chamber (several groups distinguished in the individual Kombangan samples).

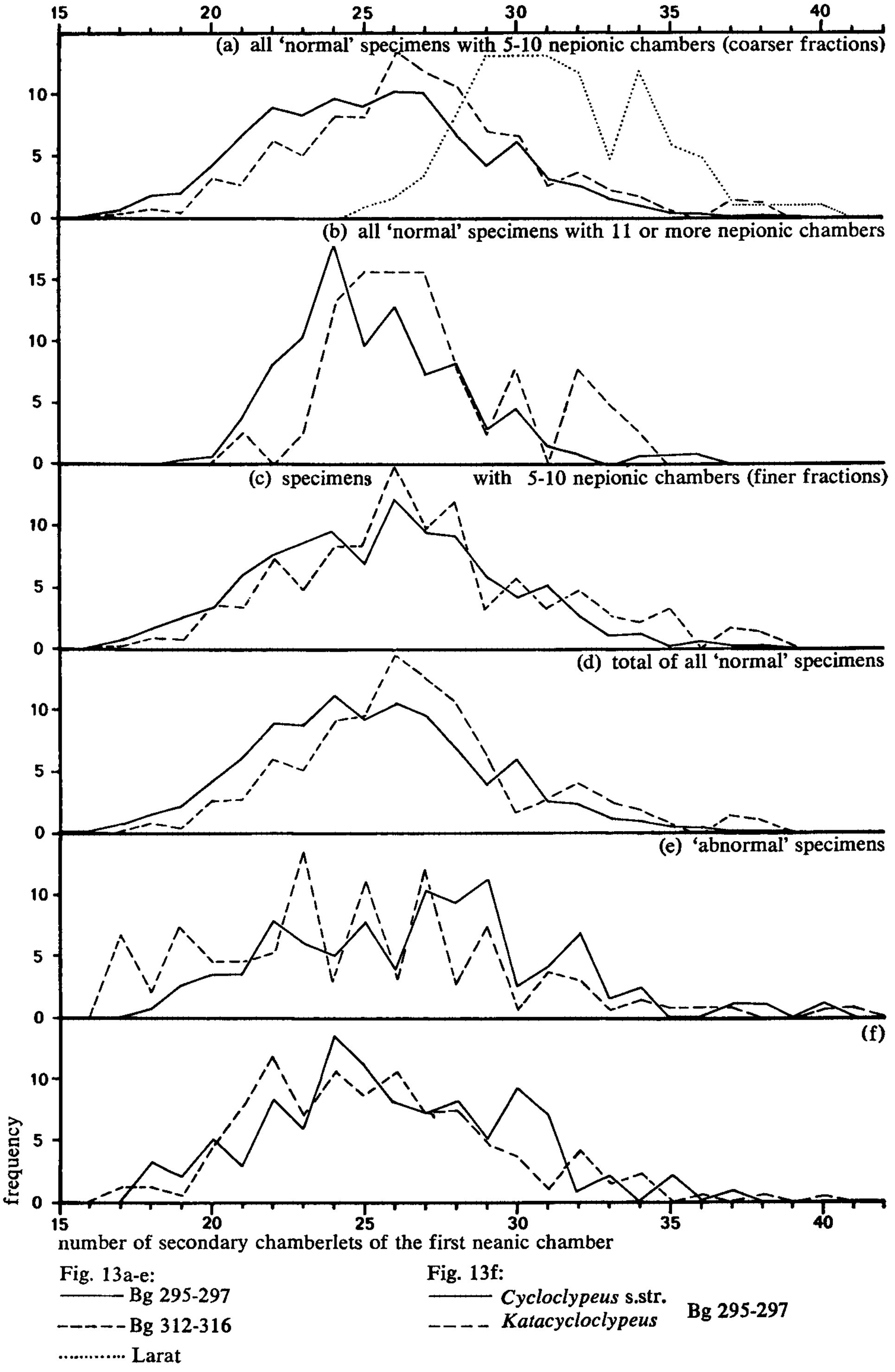

Fig. 13. Frequency polygons of Cls (the number of secondary chamberlets of the first neanic chamber) for the various groups distinguished in the Kombangan populations.

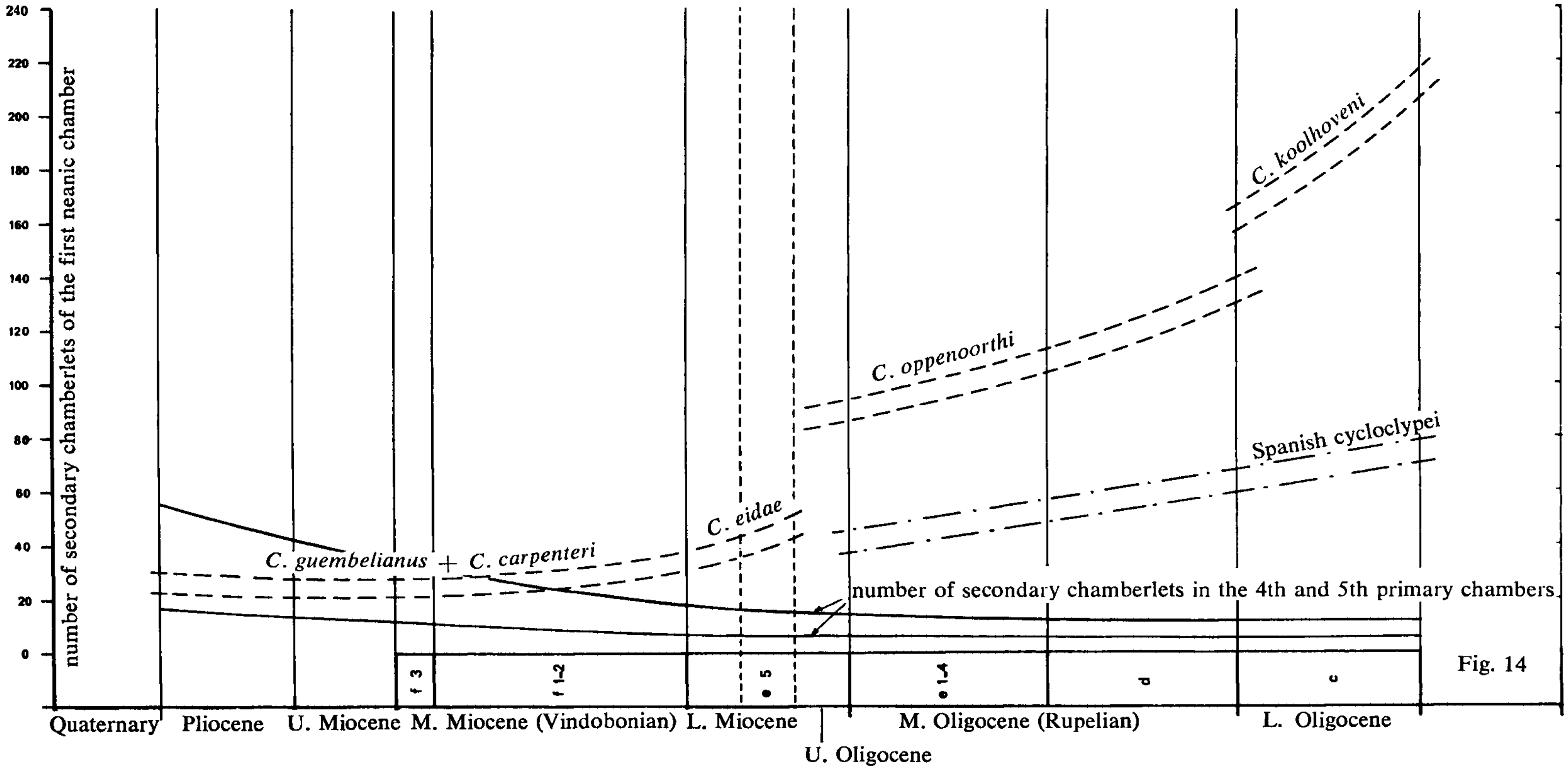

Fig. 14

Fig. 14. Numbers of secondary chamberlets of the first neanic chamber and the number of secondary chamberlets in the 4th and 5th primary chambers, plotted against time.

Decrease in the course of time is represented in a somewhat idealized fashion (Fig. 14). Cls diminishes rapidly at first but would seem to remain constant after Early Miocene time. There are indications, however, that actually a very gradual decrease occurs during this time (Figs. 6 and 7) and possibly even a slight increase after the Pliocene.

Evolutionary trends in *Cycloclypeus*

Two of the trends are well known from literature:

1. The number of nepionic chambers decreases persistently from Early Oligocene time to the present day. This is corroborated by the populations of Kombangan (Fig. 4), at least concerning the variants with 5-10 nepionic chambers; the variants with 11 or more nepionic chambers do not conclusively show a decrease. It is perhaps improbable that the latter variants represent a microspheric generation, using the same arguments as were brought out by Mac Gillavry (1962, p. 441 et seq.) against the existence of a microspheric generation in material from Sg. Tengin as supposed by Drooger (1955). Besides, distinctly microspheric individuals do occur in the Kombangan populations – be it only 3 out of a total number of 3366 specimens investigated – which differ clearly from the variants with 11 or more nepionic chambers. The possibility of the existence of an A2-generation is left open.

The question at issue is whether decrease in the number of nepionic chambers is gradual or saltatory. Tan's polymodal curves, which are especially prominent in the stratigraphically older species, in their totality advocate a saltatory decrease. The frequency-polygon of *C. eidae* from Larat (Fig. 15) is quite different from Tan's (compare Tan, 1932, variation statistics of Sg. Sekuro and Sg. Sumbal). The Larat polygon is not polymodal but shows a skewed frequency distribution. Polymodality occurs when random samples of 18 specimens (compare Tan's 18 specimens from Sg. Sumbal) are taken from the 92 Larat specimens (Fig. 15). Therefore the polymodality of Tan's curves in many cases may be the result of using small samples. Using Tan's data, curves were made (Fig. 16) based on 3 groups of data for 27 specimens each, taken at random from the bulk of data on 125 specimens from Tjiapus-6 (compare Tan's use of 27 specimens from locality Tjiapus-4). In the curves the tops at 24 and 27 nepionic chambers (*sensu* Tan)

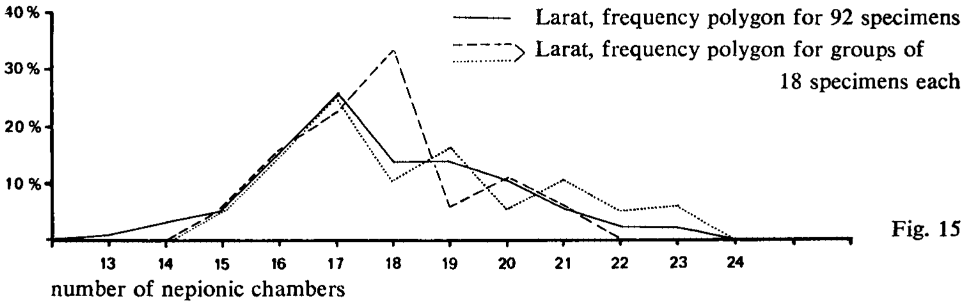

Fig. 15

Fig. 15. Frequency polygons for 92, and 3 random samples of 18, specimens of the nepionic variants from Larat.

Fig. 16

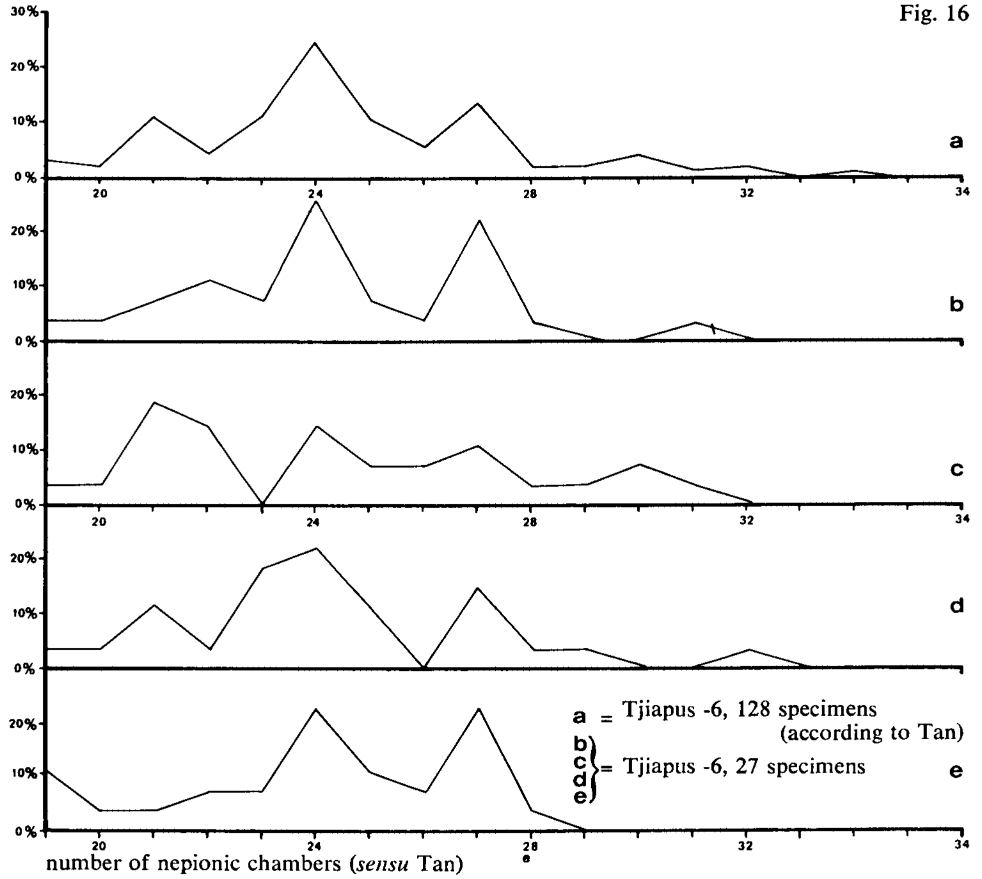

Fig. 16. Frequency polygons of 127, and 3 random samples of 27, specimens of Tan's Tjiapus-6 population.

reappear but the smaller maxima at 21, 30 and 32 nepionic chambers are not always expressed. Admittedly, however, Tan has found polymodality even in the large sample of Tjiapus-6.

It is worth noting that in case of Tan's maxima the percentages for the adjacent elementary species are in many cases also high so that the maxima apparently apply not only to the elementary species, but to groups of variants (Tan, 1932, Table IV).

2. The increase of the diameter of the protoconch during evolution is corroborated by the material from Kombangan (Figs. 17 and 18) as far as *C. carpenteri* is concerned.

Summary

The present study is primarily concerned with evolutionary changes in the number of secondary chamberlets of the primary chambers. These changes may be summarized as follows:

During evolution the number of secondary chamberlets of the successive nepionic chambers and the first neanic chamber (or chambers?) decreases, with the exception of the numbers of chamberlets of the 4th (and sometimes 5th) primary chamber which in the *C. carpenteri*-group generally increase. The decrease is considerable at first but becomes very slight – or may be absent altogether? – in post – Early Miocene time. Conversely, the increase in the 4th and 5th primary chambers is slow in the beginning but accelerates in the stratigraphically younger species, up to the present day (Fig. 14). *C. carpenteri* variants with 5 and 6 nepionic chambers show an evolutionary increase of the number of secondary chamberlets in all primary chambers (Figs. 6, 7 and 11).

The decrease of the number of secondary chamberlets in most of the primary chambers goes hand in hand with the decrease in the diameter of the nepionic stage, whereas the increase in the innermost chambers is probably connected with the increase in the size of the protoconch.

The tangential diameter of the secondary chamberlets is approximately of a size in the various species, so that about 10-12 chamberlets per mm (including the septa) are counted. The radial diameters of the chamberlets are much more variable, even in one and the same individual.

Within one and the same stratigraphical zone (e.g. fig. 6) 'primitive types', with a large number of nepionic chambers, can be distinguished from 'advanced types' with few nepionic chambers. In the advanced forms we see that:

1. The number of secondary chamberlets increases in most nepionic chambers as compared to 'primitive forms' although the total number of secondary chamberlets decreases.
2. The diameter of the nepionic stage and the parameter Cls, decrease in the zones of the older species (*C. koolhoveni, C. oppenoorthi*), as compared to 'primitive' forms, but remain approximately constant in the zone of the stratigraphically younger species (*C. eidae, C. carpenteri*).
3. The number of secondary chamberlets in the 4th and 5th primary chambers, in the *C. carpenteri*-zones, increases (Fig. 20) as does te diameter of the protoconch (Fig. 18).

In comparing stratigraphically older ('primitive') and younger ('advanced') forms on the one hand with 'primitive' and 'advanced' forms within the same zone on the other, it appears that in both instances 'primitive' and 'advanced' forms show the same differences with respect to the number of nepionic chambers, the diameter of the protoconch, and also – in the *carpenteri-group* – the number of secondary chamberlets in the 4th and 5th primary chambers (Figs. 14 and 20). The number of secondary chamberlets of most nepionic chambers, however, shows a decrease in the first instance and an increase in the other (compare fig. 9, *oppenoorthi* variants 24 and 23 as opposed to variant *eidae* 23).

This discrepancy is due to an evolutionary change of the nepionic 'mutants' which is discernible even over a short period (see Kombangan). Tan's statement: 'For instance *Cycl. oppenoorthi undevingintiseptus* and *Cycl. eidae enneakaidekaseptus* represent one and the same nepionic mutant' (Tan, p. 125) is, therefore, refuted by the present study.

Reduction of the number of nepionic chambers in the course of time is at present thought to result from the occurrence of 'transitional nepionic variants' with outermost nepionic chambers tending to become cyclic.

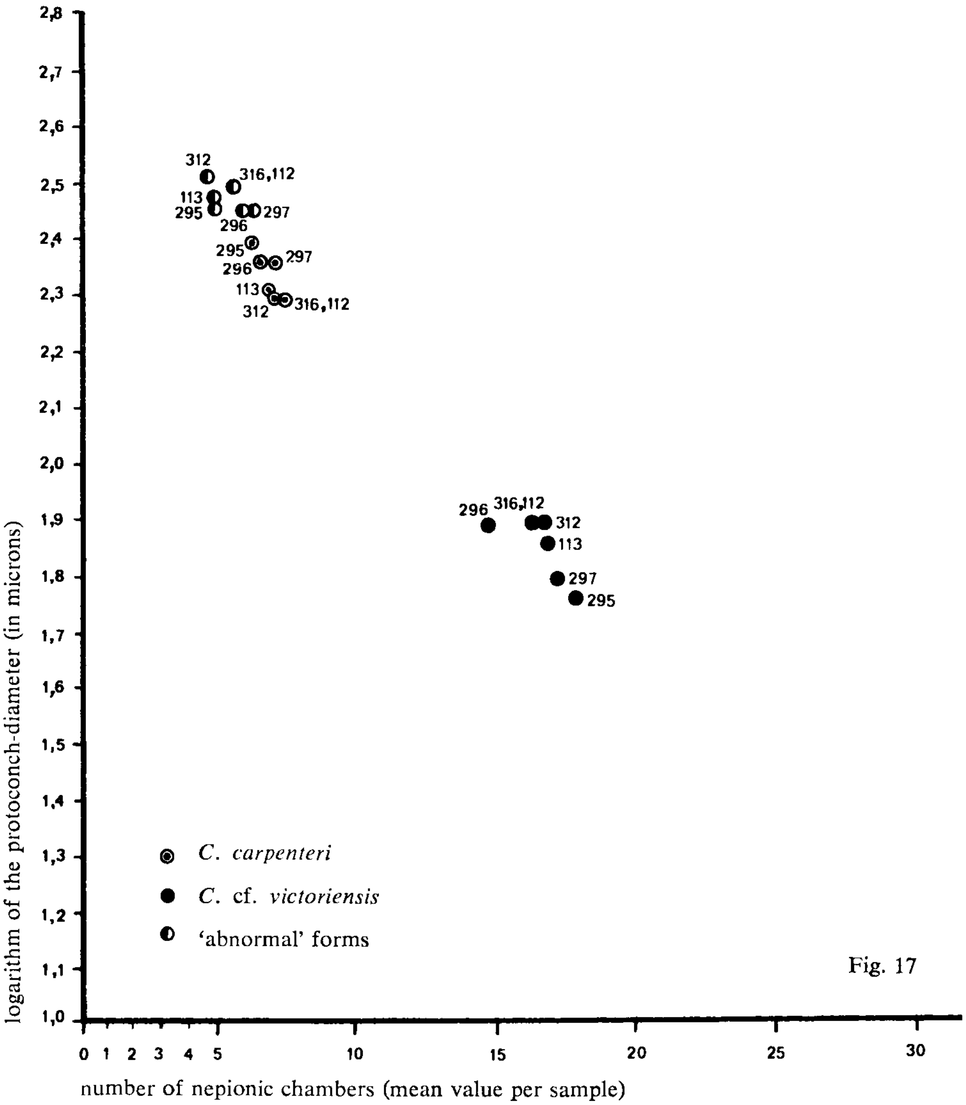

Fig. 17. Number of nepionic chambers (mean value per sample) plotted against the log. of the mean diameter of the protoconch (in microns).

PRACTICAL VALUE OF THE PRESENT INVESTIGATION

The number of secondary chamberlets of the first neanic chamber is thought to be important for the distinction of species. On this characteristic a *koolhoveni-*, an *oppenoorthi-* and an *eidae-*(*posteidae-*) lineage are distinguished. The *carpenteri-*lineage probably developed from the *eidae*-lineage (Figs. 9 and 10).

According to Tan the individuals of *C.* cf. *victoriensis* from Kombangan should probably be assigned to *C. eidae* or *C. posteidae.* The C1s-values render it more probable that *C.* cf. *victoriensis* represents a very primitive form of *C. carpenteri.*

Individuals belonging to different species but having equal numbers of nepionic chambers in most cases are identified by their C1s-values. This may be

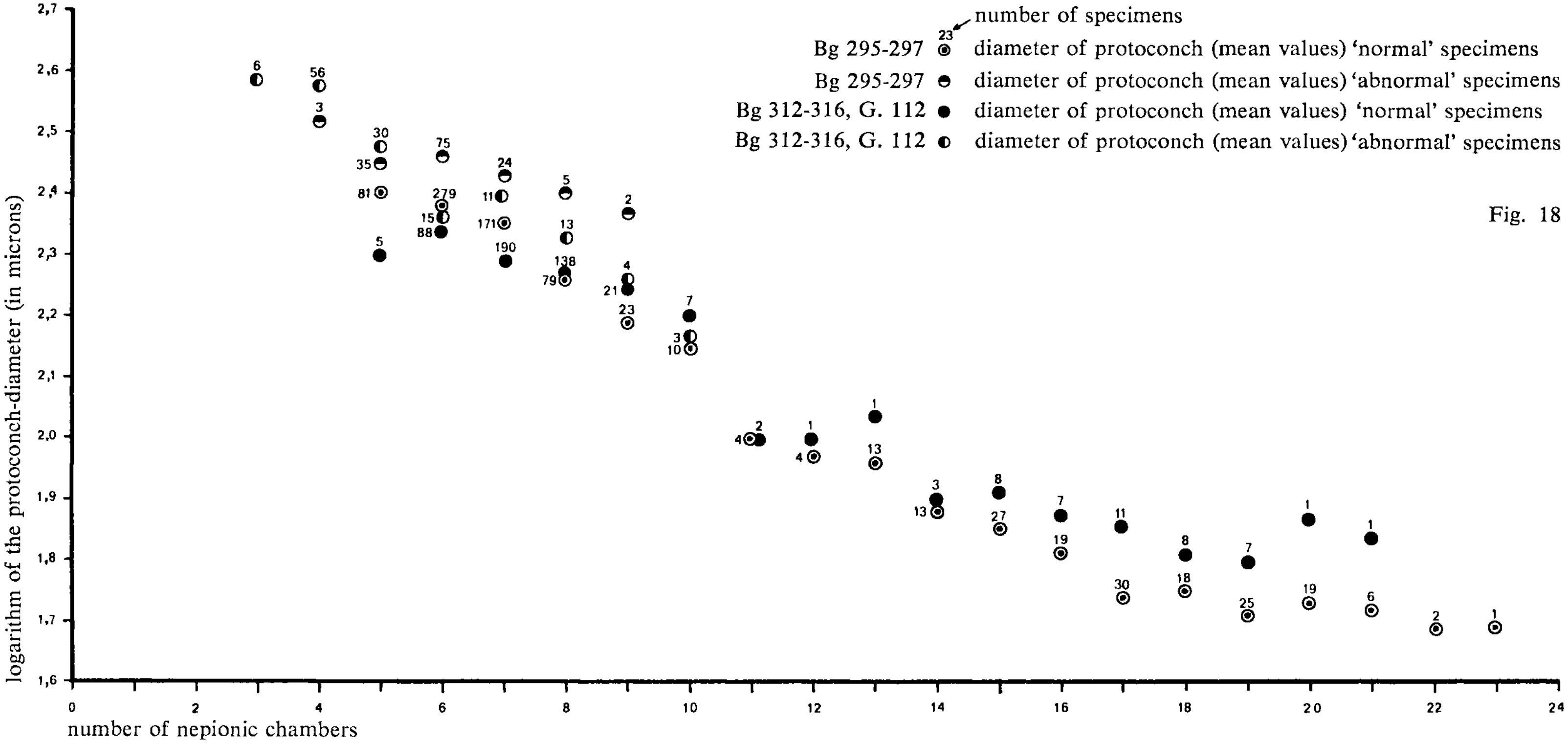

Fig. 18

Fig. 18. Nepionic variants of Kombangan plotted against the log. of the mean diameter of the protoconch (in microns).

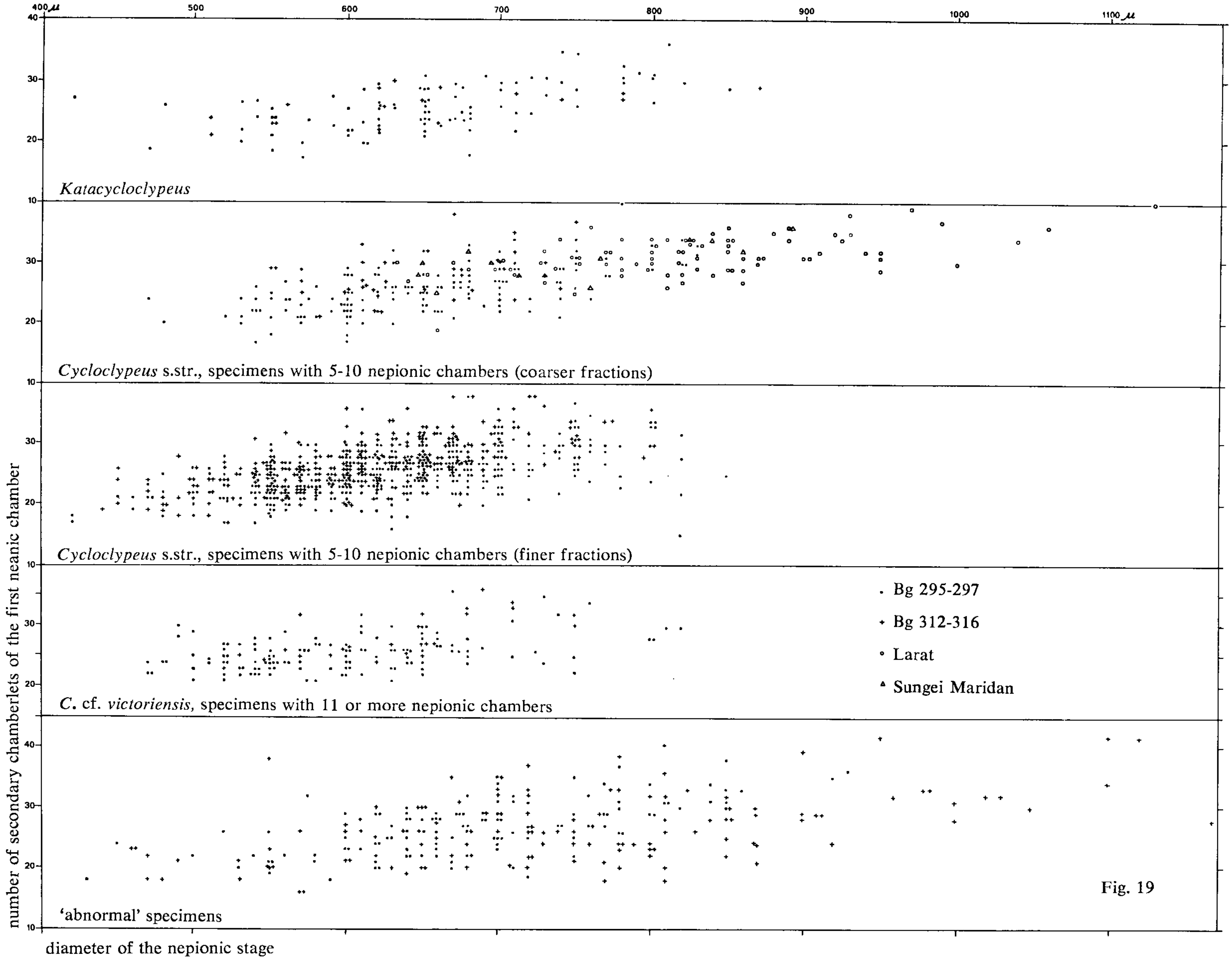

Fig. 19

Fig. 19. Scatter diagrams (diameter nepionic stage/number of secondary chamberlets of first neanic chamber), specimens from Larat and Kombangan.

Fig. 20

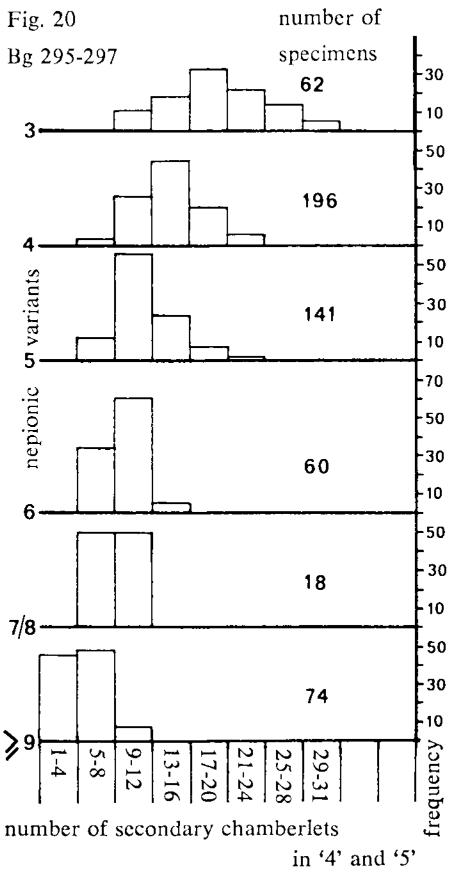

Fig. 20. Histograms of the number of secondary chamberlets in the 4th and 5th primary chambers – combined – for nepionic variants from samples Bg. 295-297 (Kombangan).

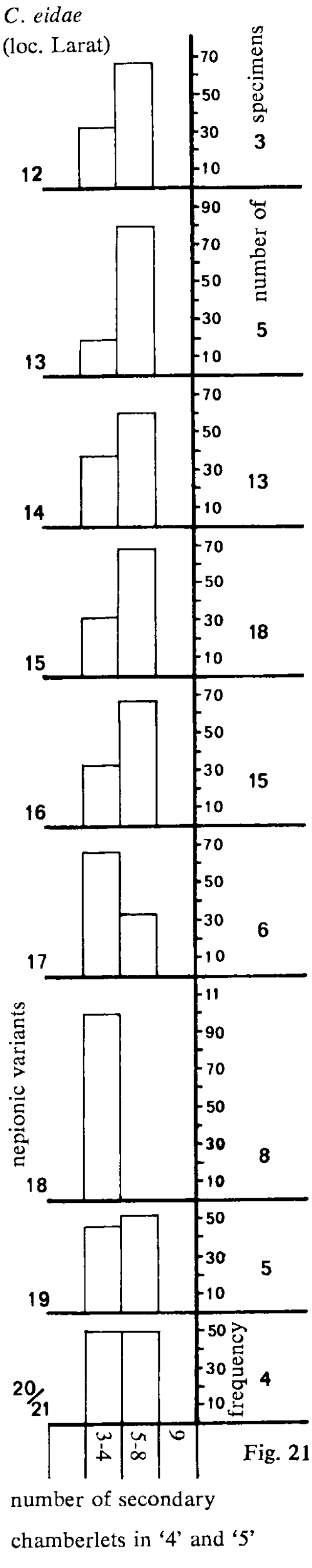

Fig. 21

Fig. 21. Histograms of the number of secondary chamberlets in the 4th and 5th primary chambers – combined – for the nepionic variants from Larat.

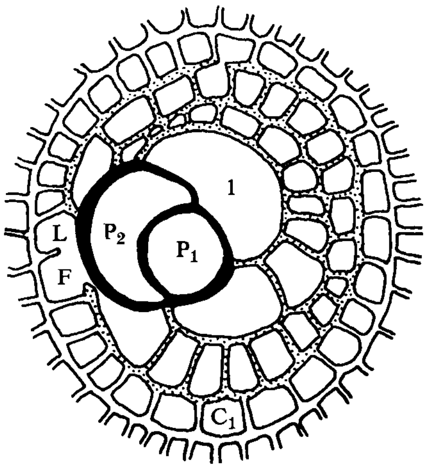

Fig. 22. Centre of *C.* cf. *guembelianus* after Tan.

protoconch – P_1 } black
deuteroconch – P_2 } black

nepionic chambers } dotted
ana-nepionic chamber – 1 } dotted

first neanic chamber – C_1
1st and last chamberlet of C_1 = FL

useful if external features are not available for study. C1s may likewise be useful for the identification of microspheric specimens.

The value of the present study for dating is as yet restricted to a broad age determination based on the various lineages. Fig. 14 may be of use for the stratigraphically older species which show a rapid decrease of the C1s-value. Ages of younger zones may be more easily determined by the curves for the numbers of secondary chamberlets in the 4th and 5th primary chambers. Frequency polygons (Fig. 13) determined for various ages might be even more useful.

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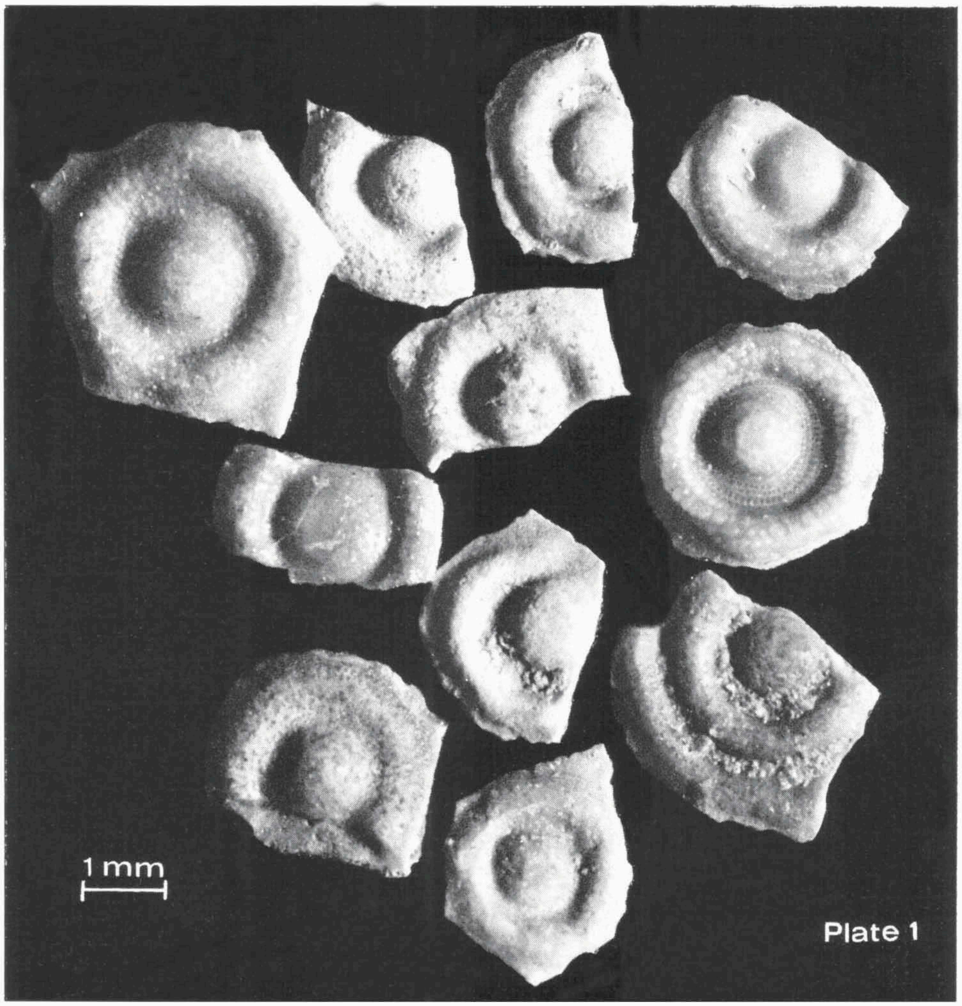
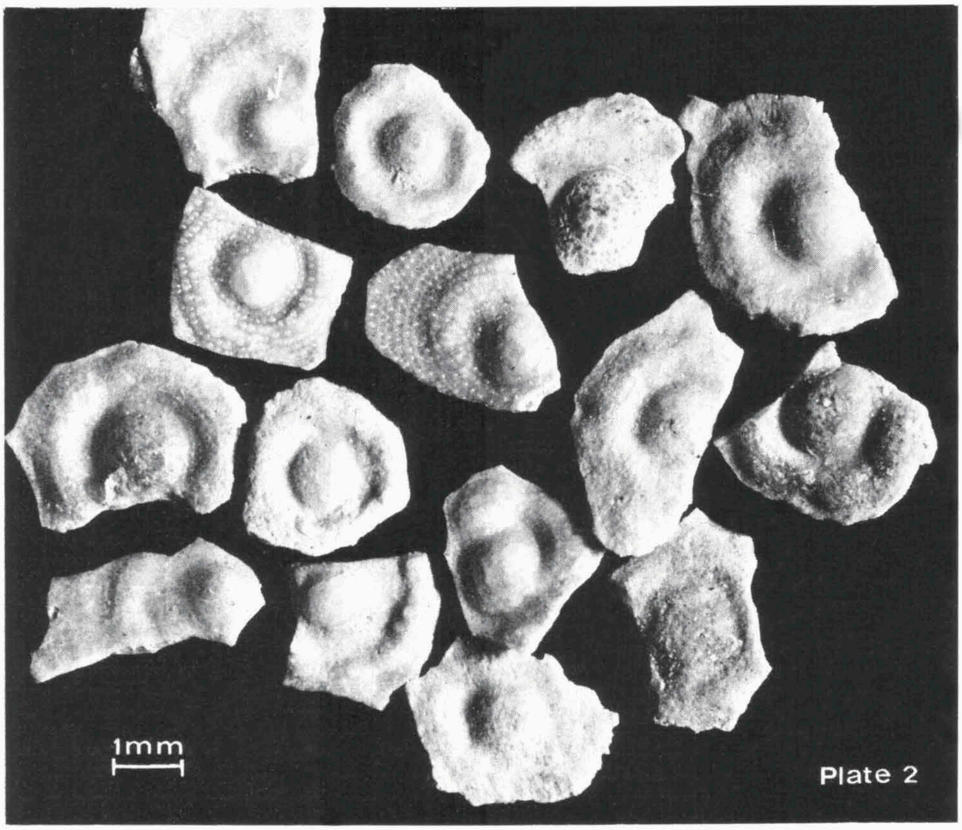
Plates 1-7. The different forms of *Cycloclypeus* from Kombangan

Plate 1. Form a
Plate 2. Form a-c
Plate 3. Form b
Plate 4. Form c
Plate 5. Form c1
Plate 6. Form d
Plate 7. Form e





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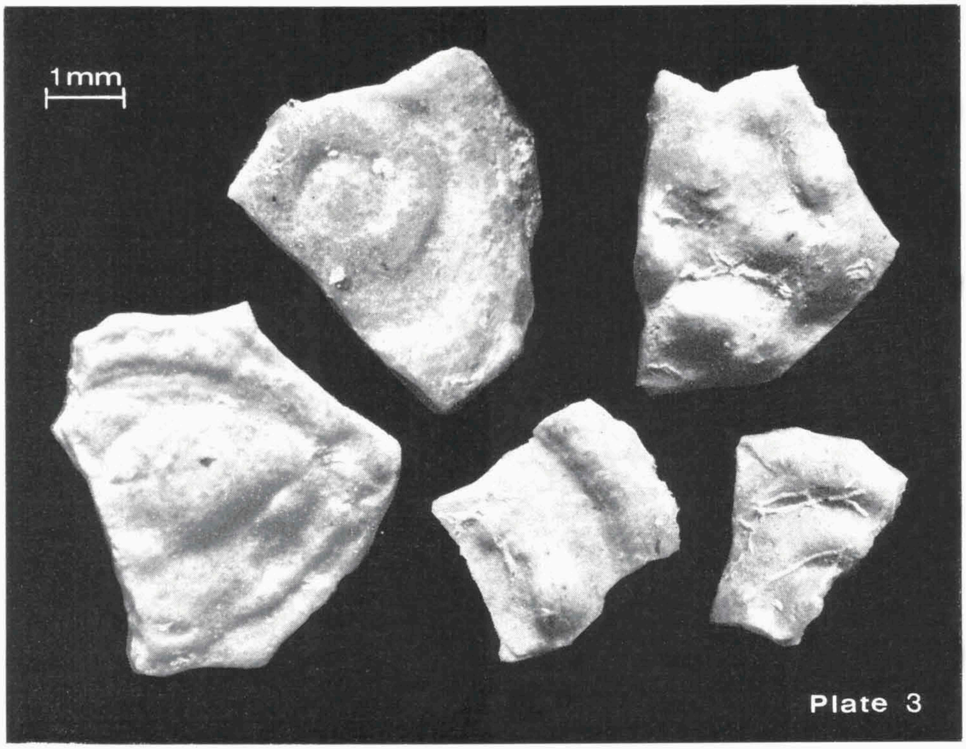

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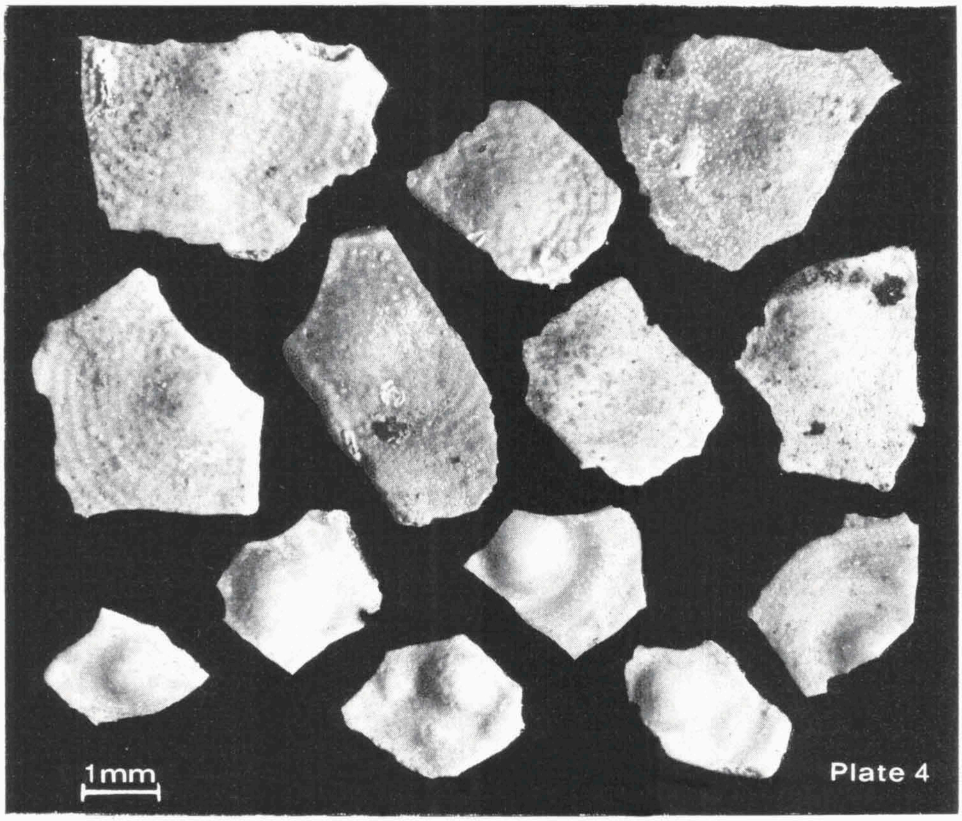

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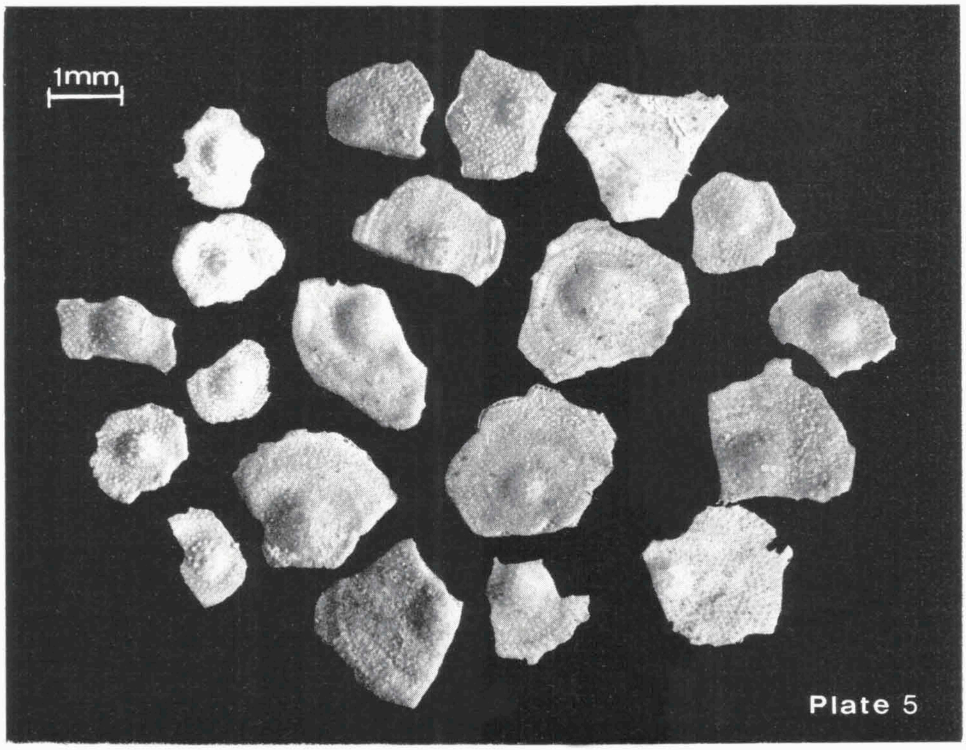

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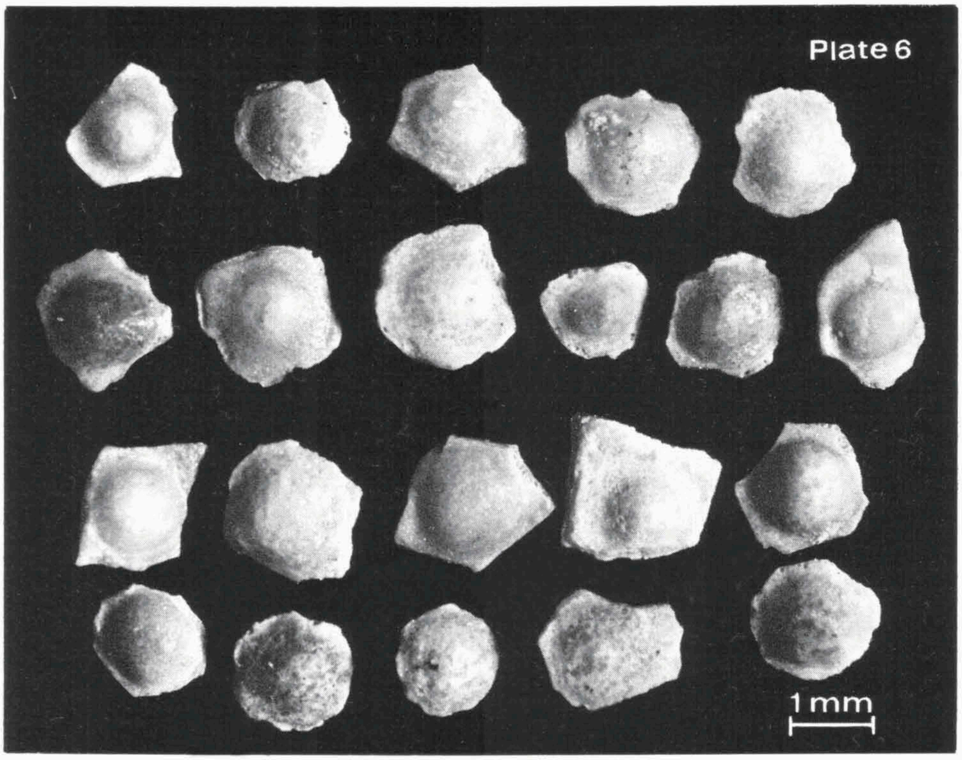
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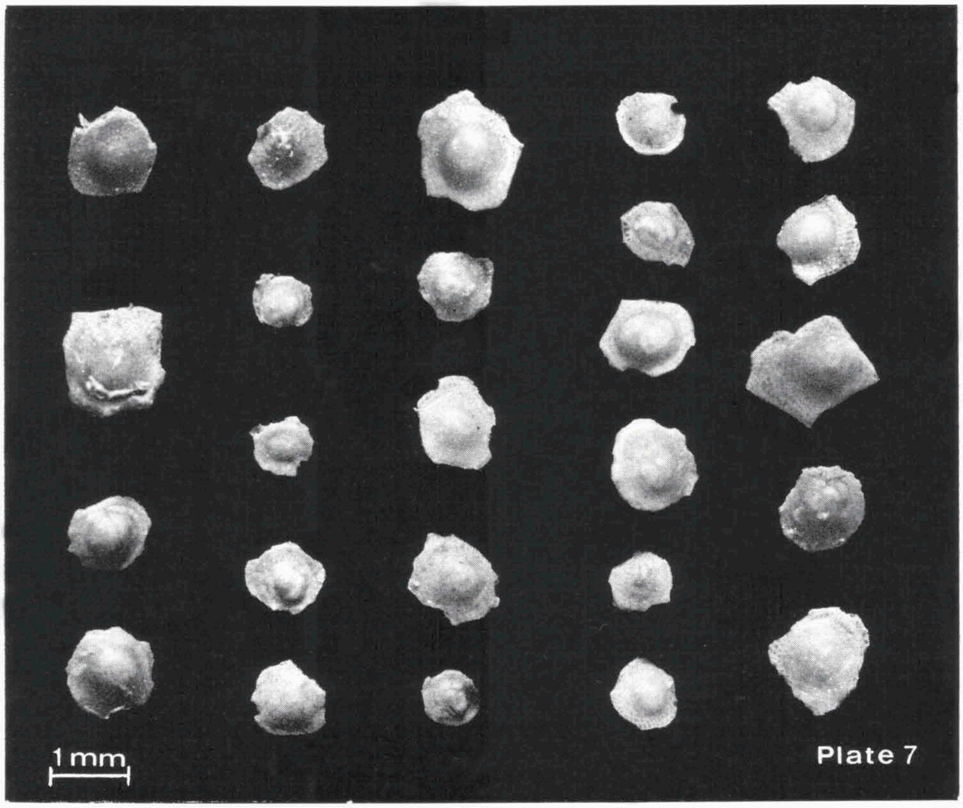

Plate 7

Plate 8

All figs. x 80.

Fig. 1. Interrupted first neanic chamber, FL-chamberlet indicated by a tooth

Fig. 2 Irregular septa, 5th, 6th and 7th primary chambers possibly consisting of an apertural chamberlet only

Fig. 3 Chamberlets with micronodules of pyrite

Fig. 4 *C.* cf. *victoriensis:* well developed pillars, first neanic chamber interrupted but defined by FL-chamberlet

Fig. 5 Irregular septa, FL-chamberlet indistinguishable

Fig. 6 FL-chamberlet irregular

Fig. 7 FL-chamberlet determining first neanic chamber in a damaged specimen

Fig. 8 FL-chamberlet irregular

Fig. 9 FL-chamberlet long, almost rectangular

Fig. 10 FL-chamberlet long, with little developed tooth

Fig. 11 *C.* cf. *victoriensis:* FL-chamberlet pentagonal, well developed pillars

Fig. 12 FL-chamberlet long, partly visible

Fig. 13 FL-chamberlet long

Fig. 14 FL-chamberlet in irregular and interrupted first neanic chamber

Plate 9

Figs. 1-6 and 8-10 x 50, figs 7 and 11 x 80

Figs. 6-11: Transitional forms

Figs. 1-5: 'Abnormal forms', protoconch large, horn-shaped interrupted first neanic chamber which in some specimens is defined by the FL-chamberlet (more or less pentagonal in figs. 5, 6 and possibly consisting of 2 fused chamberlets in figs. 1 and 3)

Fig. 6 Last nepionic chamber nearly cyclic

Fig. 7 Irregular septa, FL-chamberlet indistinguishable, first neanic chamber indeterminable

Fig. 8 Do., FL-chamberlet not developed

Fig. 9 Outermost nepionic chamber almost cyclic

Fig. 10 Do.

Fig. 11 Position of FL-chamberlet uncertain, long chamberlet probably formed by fusion of the outermost chamberlets of the last nepionic chamber

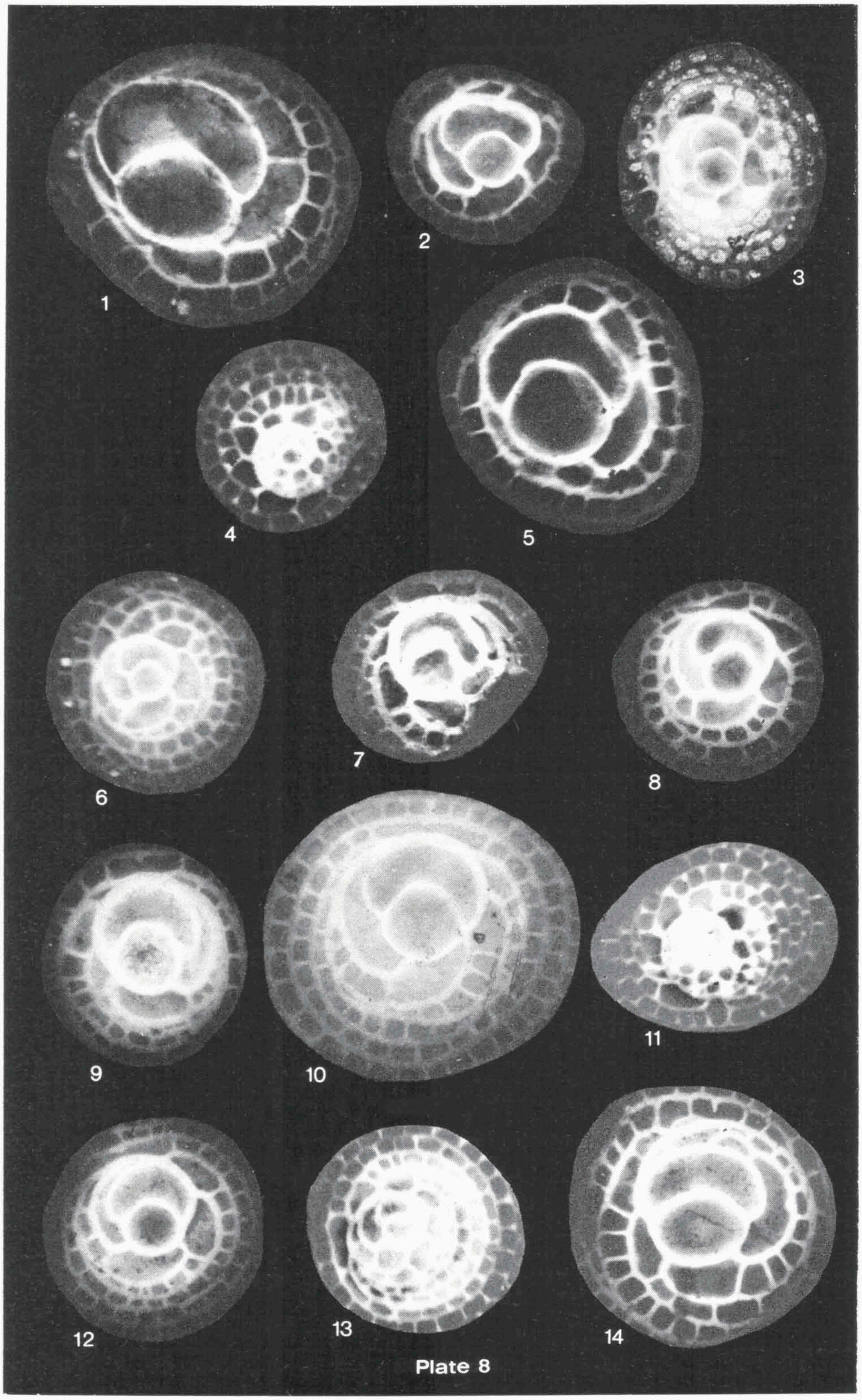

Plate 8

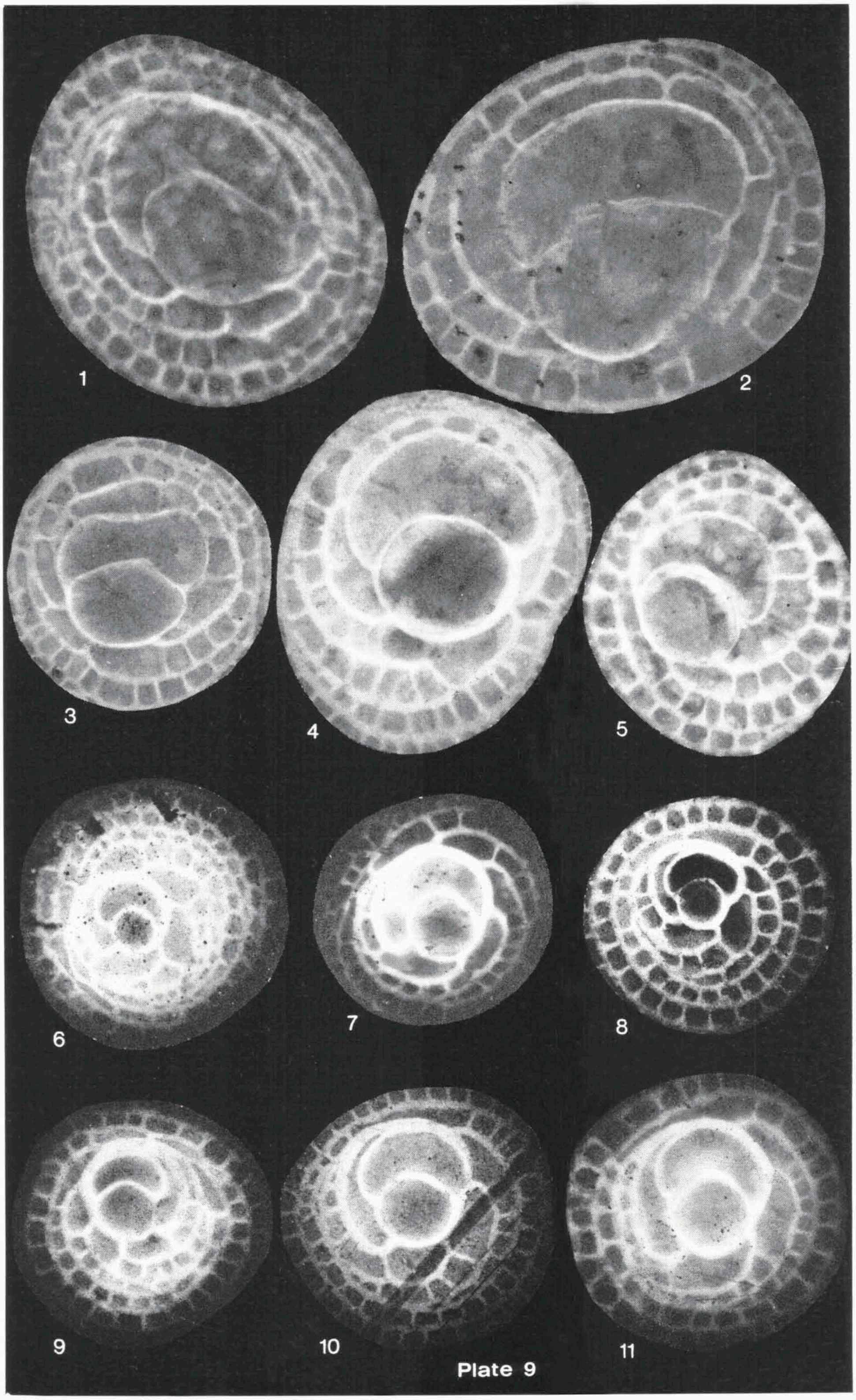

Plate 9