A reconsideration of *Amphistegina lessonii* d'Orbigny, 1826, sensu Brady, 1884 (Foraminifera)

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O'Herne, L. A reconsideration of *Amphistegina lessonii* d'Orbigny, 1826, sensu Brady, 1884 (Foraminifera). — Scripta Geol., 26: 1-53, 3 figs., 20 pls., 3 enclosures, Leiden, September 1974.

At least three of the forms described by Brady (1884) as *Amphistegina lessonii* show specimens with monocular as well as bilocular nucleoconches, probably representing the microspheric and macrospheric generations. Except for the shape of the embryonic apparatus both generations are identical or practically so. Assuming that dimorphism occurs in *Amphistegina*, the above suggests that several species should be distinguished in Brady's *Amphistegina lessonii*. The internal structure of *A. lessonii* is illustrated by photographs and schematic drawings.

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Introduction

Amphistegina lessonii d'Orbigny is probably the most controversial species of the amphistegines. Uncertainty of its taxonomy originates from d'Orbigny's type description (d'Orbigny, 1826) which may refer either to *A. lessonii* or *A. quoii.* D'Orbigny made 6 different species out of *Amphistegina* material from Mauritius, the Sandwich Islands, St. Helena, and the Antilles. In 1903 Fornasini, comparing d'Orbigny's six 'so called species' with Brady's illustrations, reduced this number of species in conformity with the latter's three main forms of *Amphistegina lessonii.* Brady (1884), Formasini (1903), Bagg (1908), Cushman (1910), and Heron-Allen & Earland (1915) extended *A. lessonii* so as to include 2, 3, or more forms which generally occur together.

Hofker (1927) considered the three forms occurring in the Siboga material as due to trimorphism of *Amphistegina radiata* (F. & M.) However, in 1969 Hofker distinguishes in the Pacific: *A. radiata, A. lessonii,* and *A. madagascariensis* and in the Caribbean: *A. radiata* and *A. gibbosa* d'Orbigny, 1839, and has obviously abandoned the conception of trimorphism with regard to *A. radiata.*

Subsequent authors have generally indicated the various 'forms' by the following names: 1) *Amphistegina lessonii* d'Orbigny, 1826, 2) *Amphistegina madagascariensis* d'Orbigny, 1826, 3) *Amphistegina radiata* (Fichtel & Moll, 1798); apparently without agreeing which form either of the names refers to, as is shown by the following examples.

Amphistegina lessonii in Todd (1965, Pl. 11, fig. 4) shows no ventral 'rosette' and in Cushman (1931, Pl. 16, figs. 1, 3) it shows a distinct rosette of secondary lobes on the ventral side.

Amphistegina madagascariensis in Todd (1965, Pl. 2, figs. 1 - 2) shows distinct papillae about the opening, and according to Cushman (1921) and Heron-Allen and Earland (1915) it should, therefore, be referred to *Amphistegina lessonii:* d'Orbigny's type figures of *A. lessonii* and *A. madagascariensis* are practically identical, the latter has more pronounced papillae around the aperture.

Amphistegina radiata in Chapman (1895, Pl. 1, fig. 8) or Graham & Militante (1959, Pl. 16, figs. 12, 13) on the one hand and in Todd (1965, Pl. 13, fig. 1) on the other obviously refer to clearly different forms.

Amphistegina radiata var. *venosa* in Graham & Militante (1959, Pl. 16, fig. 15) is much more similar to *A. lessonii* (of Cushman, 1931) thans to *A. radiata.*

It is remarkable that in the U.S. Professional Papers dealing with foraminifera from Pacific atolls (Todd, 1957; 1966; Todd & Low, 1960; 1970; Todd & Post, 1954), *A. lessonii,* a species which is probably abundant in the Pacific, is nowhere mentioned. According to Todd (1965) 'the only Pacific occurrence of *A. lessonii* is at Kapingamarangi, northeast of New Guinea'. This may be due to taxonomic disagreement.

Generally speaking the various authors distinguish:

1. Rather flattened, lenticular, more or less equilateral, and many-chambered forms without or with little-developed beaded markings about the aperture.
2. Thicker, sometimes dome-shaped, gibbose or plano-convex forms, generally papillose the ventral margin and with less numerous chamber.
3. *Amphistegina radiata,* generally described as being large and with very numerous chambers, may represent a third form.

According to Todd (1965) these forms 'living in mutually exclusive ecologic provinces are clearly distinct without any transitional forms connecting them'. Cushman (1921) is of the same opinion: 'there seem to be no intermediate forms between them'. On the other hand Brady (1884) states that 'wherever *Amphistegina* are abundant all these variations of the typical structure are met with, together with every intermediate condition'. In our samples not a single specimen intermediate between the forms 1 and 2 mentioned above was found. In 1910 Cushman remarks: 'This species (*A. lessonii*) is used at present time to include various forms which may be distinct. Brady notes the fact that various forms occur and Bagg also found them. A study of Recent tropical material should show something definite in regard to these specific or varietal forms'.

Acknowledgements

The author is much indebted to his colleague Mr J. F. de Bock for unravelling and drawing the complex structure of *Amphistegina lessonii* (Pl. 16, fig. 2; Pl. 17, fig. 2; Pl. 18, fig. 3; Pl. 19, fig. 2; Pl. 20, fig. 1 after original drawings by J. F. de Bock). Thanks are due to Messrs B. F. M. Collet, J. Timmers, and T. Velthuyzen for the preparation of photographs (Pl. 1), diagrams and drawings. The excellent scanning electron micrographs were prepared by Messrs H. Kameraat and W. C. Laurijssen of the Geological and Mineralogical Institute in Leiden.

Material

The *Amphistegina*-bearing material studied ranges in age from Oligocene to Recent and originates from the following localities.

Miocene-Pliocene: Java: Tjepu (samples from 3 localities), Lodan (2 loc.); Borneo: Sankulirang Bay area (4 loc.), Tepianbakil (1 loc.), and Gunung Mlendong (1 loc.); Ceram: 1 loc; New Guinea (Irian Barat): Waileh (1 loc.).

Recent: samples from the Admiralty Islands and from the Friendly Islands (Challenger Expedition); Hawaii: North shore Oahu Islands, material from shallow water (1 - 2 fathoms) and beach material; Hoorn Island, Bay of Batavia (Pulau Air-Besar, Teluk Djakarta): beach material; Cuba (20 fathoms); Aruba (37 fathoms).

Besides, many samples of the Java-Madura sections from which the lepidocyclinas (van der Vlerk & Posthuma, 1967) and cycloclypei (O'Herne, 1972) were studied before, proved to be rich in *Amphistegina*. Table 1 gives the sample numbers in stratigraphical order.

About 93% of the samples with *A. lessonii* did also contain *A. quoii*. The samples containing either *A. lessonii* or *A. quoii* were rather small. Larger samples might as yet have shown the simultaneous occurrence of the two species as either is very rare in some cases.

Table 1. Occurrence of *Amphistegina* in samples* from the Java-Madura sections.

Middle Miocene	Bg. 295 Bg. 296 Bg. 297	
	Bg. 312 G. 113 Bg. 316=G.112 G. 5671 G. 5702 Bg. 333	*Amphistegina lessonii* & *A.quoii*
	Ct. 5971 Ct. 2681 Ct. 5968	No *Amphistegina*
Lower Miocene	Ct. 5967a Ct. 5967 Ct. 2679a Ct. 5956 Be. 1145	*A.bikiniensis* and/or older forms cf. *A.lessonii*
	h. 6 h. 7 h. 7a	*A.lessonii* & *A.quoii*
	h. 255a	No *Amphistegina*
	h. 20	Some *A.lessonii* & *A.quoii*
	h. 266	*A.bikiniensis*,*A.lessonii* & *A.quoii*
Oligocene	h. 884 h. 280a,b h. 285 h. 479 h. 481=Be.2200 h. 489 h. 494=Be.2194	*A.bikiniensis* and/or older forms cf. *A.lessonii*

* localities of the samples: Ngimbang (East Java) h. 884; Mlangi (East Java) h. 479, h. 481, h. 489, h. 494, Be. 2200, Be. 2194; Krandji (East Java) h. 255a, h. 266, h. 280, h. 285; Prupuh (East Java) h, 6, h. 7, h. 7a, h. 20; Arosbaja-Kombangan (Madura) Be. 1145; Kombangan (Madura) Bg. 295, Bg. 296, Bg. 297, Bg. 312, Bg. 316, Bg. 333, G. 112, G. 113; Tanah Poteh Olor (Madura) Ct. 2681, Ct. 2679a; Arnih (Madura) Ct. 5971, Ct. 5968, Ct. 5967a, Ct. 5967, Ct. 5956; W. of Batuputih (Madura) G. 5671, G. 5702. (See also van der Vlerk & Postuma, 1967).

Descriptions

A striking distinction which is nowhere stressed, as far as the author is aware, although mentioned by Hofker (1927) and Chapman (1895) is that some forms show relatively short secondary lobes on the ventral side which form a rosette around the umbo (Pl. 1, fig. 1; Pl. 6, fig. 1; Pl. 17, fig. 1). In other forms the ventral side differs from the dorsal mainly by a more complex configuration of the alar prolongations without showing a distinct rosette (Pl. 1, figs. 5 - 11; Pl. 10, fig. 10; Pl. 11, figs. 1 - 2). The shape of the secondary lobes in the first form varies from simple rhomboid to long and curved, sometimes with a complex base near the umbo (Enclosure 3).

In the present study the two forms mentioned above will be referred to as *A. lessonii* (inaequilateral forms with distinct ventral rosette) and *A. quoii* (nearly equilateral forms with superficially more or less similar ventral and dorsal sides) in accordance with Yabe and Hanzawa (1925). Some individuals of a large form with very numerous chambers — referred to below as *A. radiata* — occurred in two of our samples of Recent material. In our older samples from Java two other forms were met with: *A. bikiniensis* and a small form resembling *A. lessonii.*

Amphistegina quoii d'Orbigny, 1826
Pl. 1, figs. 5 - 7; Pls. 7 - 11.

Conform the type description given in Ellis & Messina (1940).

Amphistegina quoii has a rather flattened, bi-convex, nearly equilateral test with bluntly rounded to acute periphery. The chambers are rather numerous, about 16 - 23 in the last whorl of adult specimens. The test is less smooth than that of *A. lessonii.* The umbones are relatively small but prominent, consist of clear shell material and are nearly equal in size on the dorsal and ventral sides. In this paper a distinction is made between *A. quoii* with little developed umbones (form 1) and *A. quoii* with strongly developed umbones (form 2), further referred to as *A. quoii* 1 *and A. quoii* 2. The sutures are nearly straight at first but become strongly angled near the periphery. Between the septa short lines or points of clear shell material occur, especially on the dorsal side. These ornamentations are sometimes strongly developed, giving rise to papillose forms. The alar prolongations on the dorsal side are simple (Pl. 10, fig 1), on the ventral side these prolongations are divided by constrictions and openings into secondary lobes forming a pattern of varying intricacy (Pl. 11, figs. 1 - 2). *A. quoii* is slightly papillose about the aperture. The nucleoconch appeared to be bilocular in most specimens investigated, consisting of a round protoconch and a small crescent-shaped to ovoid deuteroconch (diameter of the protoconch about 30 - 40 μm; Pl. 9, fig. 5; Pl. 10 fig. 1 - 2). One species with a monolocular nucleoconch was found which in other respects proved identical with the specimens with a bilocular nucleoconch (diameter of the protoconch in the monolocular form about 20 μm; Pl. 7, fig. 1).

Amphistegina lessonii d'Orbigny, 1826
Pl. 1, figs. 1 - 4; Pls. 2-6, 16 - 20.

Conform the type description given in Ellis & Messina (1940).

The surface is smooth, often with a porcellaneous lustre. The test is unequally bi-convex, usually less convex on the ventral side, flattened to dome-shaped. It has a large but little prominent umbo of clear shell material on the ventral side, the umbo on the dorsal side is smaller. The sutures on the dorsal side are slightly to strongly sinuous, often with one or two U-shaped re-entrants (cf. *A. bilobata* and *A. trilobata* of d'Orbigny). The secondary lobes on the ventral side are distinct and vary in shape from short rhomboid to long, narrow, and curved (Enclosure 3). The apertural area is generally strongly papillate. The sutures are sometimes depressed. About 12 - 16 chambers occur in the last whorl of adult specimens. The border is acute to carinate, sometimes undulating. About two-third of the specimens examined showed a bilocular nucleoconch consisting of a round protoconch and a kidney-shaped deuteroconch (diameter of the protoconch about 35 - 50 μm; Pl. 2, fig 2; Pl. 3, fig. 1; Pl. 4, figs. 6 - 9). The specimens with a monolocular nucleoconch (Pl. 2, fig. 1; Pl. 3, fig. 2; Pl. 4, figs. 2 - 4; Pl. 5, fig. 1) have a protoconch diameter of about 15 - 20 μm. Forms with a monolocular and those with a bilocular nucleoconch are identical, or nearly so, except for the shape of the embryonic apparatus.

Amphistegina radiata (Fichtel & Moll, 1798)
Pl. 1, figs. 8 - 11; Pls. 12 - 13.

A. radiata is a large form with numerous chambers (24 - 30 or more in the last whorl), radially arranged sutures, almost straight at first and sharply angled near the margin. It resembles *A. quoii* in many respects but has a larger test and more numerous chambers. The nucleoconch, which was predominantly bilocular in the specimens examined, is also similar to the nucleoconch of *A. quoii,* but larger (diameter of the protoconch about 50 - 90 μm; Pl. 12, figs. 1, 2, 5; Pl. 13, figs. 1, 3). One specimen was found with a monolocular nucleoconch (diameter about 20 μm; Pl. 13, fig. 2). Again specimens with monolocular and bilocular nucleoconchs are identical in other external and internal characteristics.

Other species

Amphistegina madagascariensis and *A. radiata* var. *venosa* (Graham & Militante, 1959) are at present considered as varieties of *A. lessonii. A. radiata* var. *palillosa* may be a varietal form of *A. quoii. A. wanneri* may likewise be a variety of *A. quoii* with strongly thickened septa and papillae: forms transitional to *A. quoii* do occur in our sample from Ceram. *A. quoii* generally shows a tendency to form limbate septa and ornamentations.

Amphistegina bikiniensis, which resembles *A. quoii,* occurs together in our samples with a form resembling a small *A. lessonii. A. bikiniensis* is smaller than *A. quoii,* the test is less ornamented and the angle in the dorsal sutures is relatively farther from the margin.

In our samples from Cuba and Aruba only one form, *Amphistegina gibbosa* (Pl. 14; cf. fig. 2, Brady, 1884), occurred. The few specimens examined all showed a bilocular nucleoconch.

Our samples of Recent material from Hawaii predominantly contain a dome-shaped form (cf. Todd, 1965, Pl. 11, fig. 3 = *A. madagascariensis* according to Todd; see also Pl. 1, figs. 12 - 13 and Pl. 15 in the present paper) Todd's *A. madagascariensis* in this case is clearly different from d'Orbigny's type figure and from what is generally understood by this species.

SOME ULTRASTRUCTURES OF THE TEST

The diameters of the pores in the forms examined varies from about 2 - 4 μm. The pores of *A. lessonii* are on an average smaller than the pores of *A. quoii* (compare Pl. 4, fig. 6 and Pl. 9 fig. 3). A Recent, dome-shaped form from Hawaii shows large pores (Pl. 15, fig. 2). The pores are partly covered by what is probably dried up protoplasm. *A. gibbosa* has rather small pores (Pl. 14, fig. 2).

Möbius (1880) states in his description of *A. lessonii:* 'Der durchmesser der Porenkanale beträgt 0.0027 mm. Wo sie dicht beisammen liegen entspringt ein jeder in einem polyedrischen, meistens sechseckigen Grübchen wovon die innere Fläche der Kammern ein bienenwabenähnliches Ansehen erhält'. Möbius' honeycomb-structure is beautifully illustrated by Pl. 4, fig. 1 and Pl. 5, fig. 2 of the present paper. It is not improbable that these extremely delicate structures were in some cases altered during heating in order to split the specimens or by some other external influence (Pl. 4, fig. 10; Pl. 9, fig. 2; Pl. 12, fig. 4). A micrograph of *A. lessonii* from sample Bg. 297 shows sieve plates and pore plugs (Pl. 5, fig. 2).

The configuration of the alar prolongations on the dorsal and ventral sides of *A. lessonii* and *A. quoii* is illustrated by internal casts consisting of chamosite. Specimens infilled with chamosite were rather common in sample Bg. 113. The internal casts could easily be obtained by dissolving the test in HCl (Pl. 6; Pl. 10, fig. 1; Pl. 16, fig. 1; Pl. 17 fig. 1; Pl. 18, figs. 1 - 2; Pl. 20, fig 2).

CRITERIA FOR THE DISTINCTION OF THE SPECIES

The criteria which have generally been used to distinguish the various forms of *A. lessonii* are: size, thickness, equilaterality, number of chambers in the last whorl, prominence and character of the umbones, roundness or acuteness of the periphery, granularity about the opening, curvature of the sutures, and sometimes color. Most of these features, however, appear to be very variable even within one sample. Inaequilaterality of the test, curvature of the sutures, and form of the alar prolongations seem to be rather constant features. The number of chambers is on an average greater in the equilateral than in the inaequilateral forms. Beaded markings about the aperture, although variable, are generally more pronounced in the inaequilateral forms.

Features in relation to time

Frequency of Amphistegina lessonii and A. quoii

Textfig. 1 shows the frequency of *A. lessonii* plotted against time, i.e. the Middle Miocene of Madura (sections of Kombangan and W. of Batuputih which are very rich in *Amphistegina).* There seems to be no relationship between the percentages of *A. quoii* 1 (little developed umbones) and *A. quoii* 2 (strongly developed umbones). The frequency of the three forms fluctuates strongly. *A. quoii* 1 predominates in most and *A. quoii* 1 and 2 combined in all of the samples. In sample G. 5702 *A. lessonii* occurs only in the finest fraction which was not incorporated in the diagram.

Diameter of the test

In the samples Bg. 295 - 297 the observed range is large for all three forms distinguished. The samples G. 5702 - Bg. 312 show a more uniform size; asymmetrical frequency distributions which are skewed to the right in most samples. J-shaped frequency distributions (h6, h7a) may partly result from the exclusion of the finest fraction in preparing the histogram (Enclosure 1). Very irregular frequency distributions in some older samples (h6, h494) are due to small numbers of specimens.

The position of the class or classes with the highest frequencies varies considerably with time; the predominating size in the three forms increases and decreases in an independent fashion without showing a mutual trend. The older forms of *A. lessonii,* and of *A. bikiniensis* (which is possibly ancestral to *A. quoii)* are on an average smaller than the younger and Recent forms.

Diameter in relation to thickness

Correlation is generally poor: individuals of the same diameter differ considerably in thickness. *A. lessonii* is generally, but not always, relatively thicker than *A. quoii* 1 but less thick than *A. quoii* 2 (scatter diagram: Enclosure 2, fig. 3a - f). In a Recent sample from the Flores Sea *A. lessonii* is much flatter than *A. quoii.* Thickness seems, therefore, a poor characteristic for classification. Although some diagrams seem to contradict the supposition, it is probable that *A. quoii 2* — with well developed umbonal plugs — represents the large, adult specimens of *A. quoii* 1, as the two forms are intergrading. Development of the umbones may be dependent on environmental conditions.

In some samples *A. lessonii* occurs mainly in the finer fractions (Bg. 295 - 297), in others the form is represented by the larger individuals (G. 5702, G. 5671) or *A. lessonii* and *A. quoii* are of a size (Bg. 312 - 316). Size is therefore also a poor characteristic. The diagrams do not reveal a particular evolutionary trend.

Diameter in relation to the number of chambers in the last whorl

A. lessonii is characterized by fewer chambers, the number of chambers increases relatively little in relation to size (scatter diagrams: Enclosure 2, fig. 4a - d). As can be seen from enclosure 2 *A. quoii* 2 is not present in all samples which contain *A. quoii* 1.

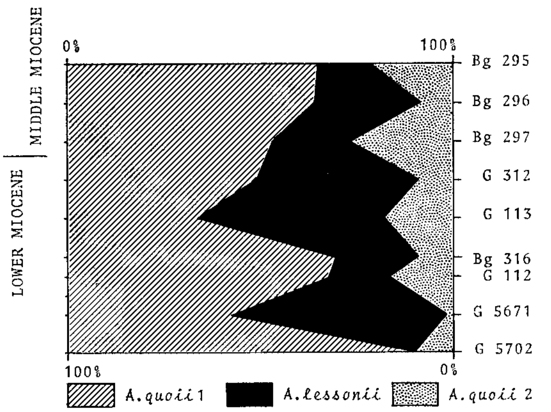


Fig. 1 Percentages of *Amphistegina lessonii, A. quoii* 1 and *A. quoii* 2 in *Amphistegina*-rich samples from part of the Lower and Middle Miocene of Java-Madura.

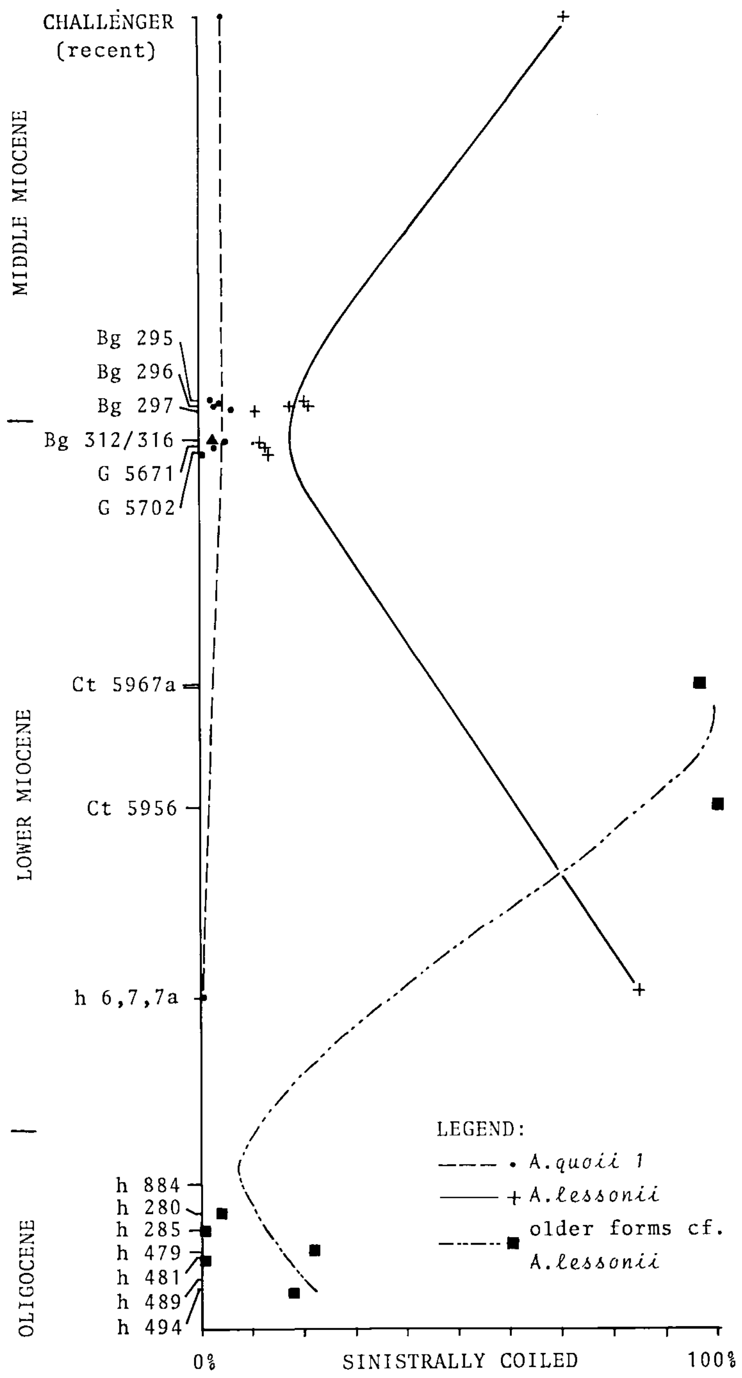


Fig. 2 Percentages of sinistrally coiled *Amphistegina lessonii* and *A. quoi* in the Oligocene to Middle Miocene of Java-Madura and in a Recent sample.

Direction of coiling

The percentage of sinistrally coiled individuals is generally larger in *A. lessonii* than in either *A. quoii* 1 or 2 (textfigs. 2, 3). Taking into consideration the considerable stratigraphical gaps occurring in the succession of *Amphistegina*-bearing material of the Java-Madura sections it appears that *A. lessonii* is predominantly sinistrally coiled in the oldest samples (h. 6, h. 7a). In de Middle Miocene (Bg. 295 - 297) the percentage of sinistrally coiled individuals decreases to about 20% but increases again in the Recent samples from the Flores Sea and the Admiralty Islands (textfig. 3).

External appearance of the test

The secondary lobes on the ventral side of *A. lessonii* are roughly rhomboid in shape in the older forms but become long and curved in the younger and Recent forms, sometimes showing a complex base near the umbo (Enclosure 3). In *A. quoii* of the Madura sections the younger forms are generally more ornamented with limbate sutures and short lines and beads of clear shell material between the sutures, accordingly papillose forms were not found in the older samples from Java and Madura. In *A. lessonii* the sutures on the dorsal side become less sinuous in the youngest forms; in *A. quoii* the backward curve of the sutures is nearer to the margin in the late forms.

Possible reproductive cycle

Specimens with monolocular and bilocular nucleoconchs, probably representing the microspheric and macrospheric generations were found to occur in *A. lessonii* (cf. Brady, Pl. CXI, fig. 5), *A. quoii* (cf. Brady, Pl. CXI, fig. 4), and *A. radiata* (cf. Brady, Pl. CXI, fig. 3). A plausible inference is that bimorphism occurs in these species. However, an important observation made by Chapman (1895) may indicate a more complicated reproductive cycle: 'I especially mention this fact since several examples of the young tests of *A. radiata* have occurred in the peripheral whorls of adult specimens of that species, and are seen in both median and transverse sections of the tests. In all cases those observed consisted of two chambers, and they are exactly comparable in shape with the early specimens of the adult specimens, which, by the way, belong to the megalospheric type of growth.' Apart from the nucleoconch the two generations referred to above proved to be identical, or nearly so, in internal and external chracteristics.

Unless a complicated reproductive cycle is assumed, *Amphistegina lessonii* cannot be extended to include the various forms which generally occur together, as has been done by many of the early authors. At least three and possibly more species are to be distinguished in Brady's *A. lessonii* (Brady's Pl. CXI, fig. 1 may for instance represent another species), each showing considerable variability.

No explanation can as yet be given for the fact that the species generally occur together. Study of living material is urgently needed and may yield interesting results with regard to ecology and reproductive cycle.

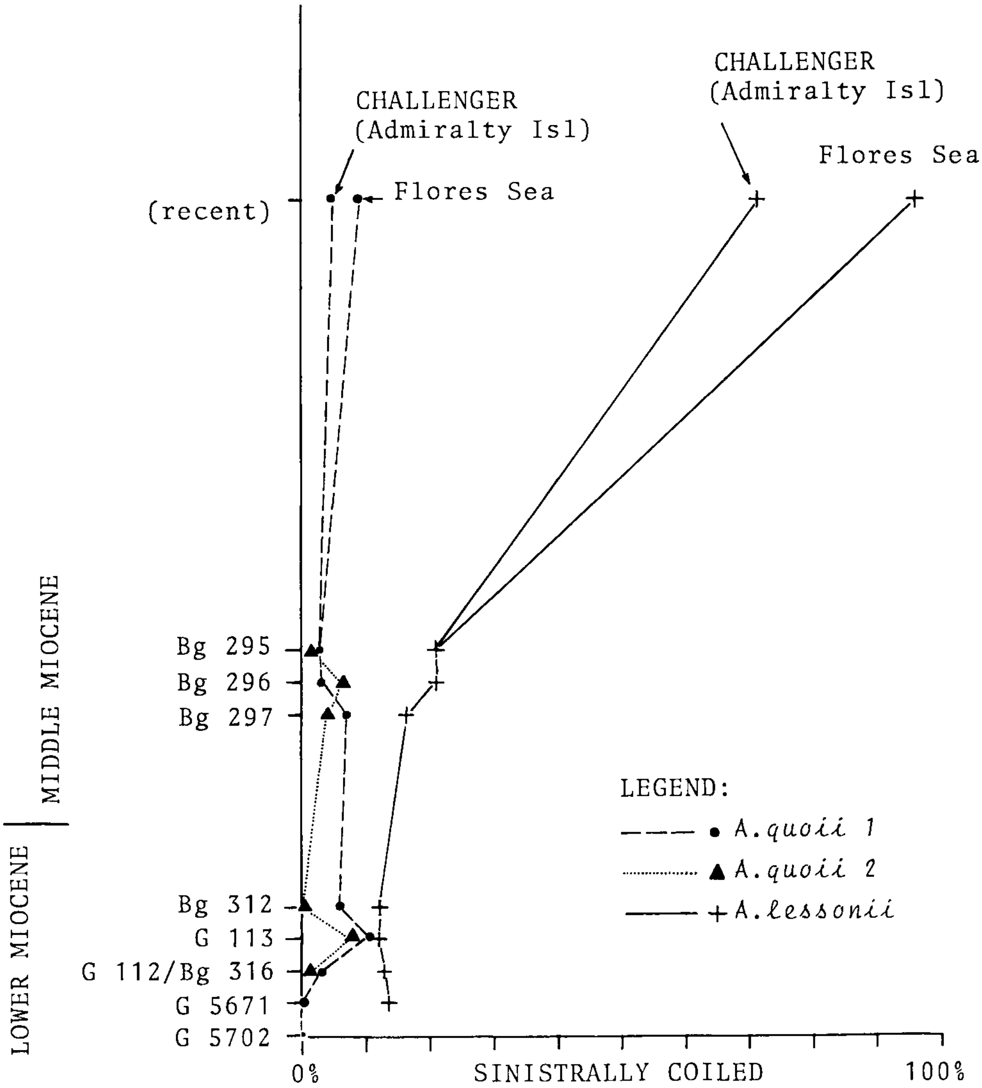


Fig. 3 Percentages of sinistrally coiled *Amphistegina lessonii* and *A. quoii* in part of the Lower and Middle Miocene of Java-Madura and in some Recent samples.

References

Bagg, R. M., 1908. Foraminifera collected near the Hawaiian Islands by the Steamer Albatross in 1902. — U.S. Nat. Mus., Proc., 34, 1603: 113 - 72, pl. 5.

Brady, H. B. 1884. Report on the foraminifera dredged by H. M. S. 'Challenger' during the years 1873-1876. — Rept. Sci. Results Explor. Voyage H. M. S. 'Challenger', Zoology, 49: 1 - 814, pls. 1 - 115.

Chapman, F., 1895. On some foraminifera obtained by the Royal Indian Marine Survey's S. S. 'Investigator' from the Arabian Sea, near the Laccadive Islands. — Zool. Soc. London, Proc., 1895: 4 - 55, pl. 1.

Cushman, J. A., 1911. A monograph of the Foraminifera of the North Pacific Ocean. — U.S. Nat. Mus., Bull., 71, 4: 1 - 46, pls. 1 - 19.

——, 1921. Foraminifera of the Philippines and adjacent seas. — Ibidem, 100, 4: 1 - 106, pls. 1 - 100.

——, 1924. Samoan Foraminifera. — Carnegie Inst. Washington, Pub. 342: 1 - 75, pls. 1 - 25.

——, 1931. The Foraminifera of the Atlantic Ocean, Part VIII. — U.S. Nat. Mus., Bull., 104: 1 - 179, pls. 1 - 26.

Ellis, B. F. & A. Messina, 1940. Catalogue of Foraminifera, Vol. 1A. — Am. Mus. Nat. Hist., New York.

Fornasini, C., 1903. Le otto pretese specie di '*Amphistegina*' instituite da d'Orbigny nel 1826. — R. Accad. Sci. Ist. Bologna, Rend., n.s., 7: 142 - 145, tav. 2.

Graham, J. J. & J. Militante, 1959. Recent Foraminifera from the Puerto Galera Area, Northern Mindoro, Philippines. — Stanford Univ. Publ., Geol. Sci., 6, 2: 1 - 170, pls. 1 - 19.

Heron-Allen, E. & A. Earland, 1915. The Foraminifera of the Kerimba Archipelago (Portuguese East Africa); Part 2. — Zool. Soc. London, Trans., 20, 17: 543 - 794, pls. 40 - 53.

Hofker, J., 1927. The Foraminifera of the Siboga Expedition; Part 1. — Siboga-Exped. 1899 - 1900, Monogr., Leiden, 4, 1: 1 - 78, pls. 1 - 38.

——, 1969. Studies on the fauna of Curaçao and other Caribbean Islands. — Ed. Nat. wetensch. studiekring Suriname Ned. Antillen, 31, 57: 1 - 158, figs. 1 - 484.

Möbius, K. A., 1880. Foraminifera von Mauritius. In: Möbius, F. Richters & E. von Martens: Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen. — Gutman, Berlin: 65 - 136, Taf. 1 - 14.

O'Herne, L., 1972. Secondary chamberlets in *Cycloclypeus*. — Scripta Geol., 7: 1 - 35, pls. 1 - 9.

Orbigny, A. D. d', 1826. Tableau méthodique de la classe des Céphalopodes. — Ann. Sci. Nat., Paris, 1826, 1, 7: 96 - 314, pls. 10 - 17 (in Atlas).

Todd, R., 1957. Smaller Foraminifera. In: Geology of Saipan, Mariana Islands, Part 3, Paleontology. — U.S. Geol Survey Prof. Paper, 280 - H: 265 - 320, pls. 2, 4, 64 - 93.

——, 1965. The Foraminifera of the tropical Pacific collections of the 'Albatross', 1899-1900. Part. 4: Rotaliform families and planktonic families. — U. S. Natl. Mus. Bull., 161, 4: 1 - 139, pls. 1 - 28.

——, 1966. Smaller Foraminifera from Guam. — U. S. Geol Survey Prof. Paper, 403 - I: 1 - 41, pls. 1 - 19.

Todd, R. & D. Low, 1960. Smaller Foraminifera from Eniwetok drill holes — Ibidem, 260 - X: 799 - 861, pls. 255 - 264.

Todd, R. & D. Low, 1970. Smaller Foraminifera from Midway drill holes. — Ibidem, 680-E: 1 - 49, pls. 1 - 12.

Todd, R. & R. Post, 1954. Smaller Foraminifera from Bikini drill holes. In: Bikini and nearby atolls, Part 4, Paleontology. — Ibidem, 260 - N: 547 - 568, pls. 198 - 203.

Vlerk, I. M. van der & J. A. Postuma, 1967. Oligo-Miocene lepidocyclinas and planktonic Foraminifera from East Java and Madura, Indonesia. — Proc. Kon. Ned. Akad. Wetensch., B, 70, 4: 391 - 398, pl. 1.

Yabe, H. & S. Hanzawa, 1925. A geological problem concerning the raised coral-reefs of the Riukiu Islands and Tawan. — Tohoku Imp. Univ. Sci. Repts., 2, 7: 29 - 57, pls. 5 - 10.

Manuscript received 7 June 1974.

PLATES

PLATE 1

Amphistegina lessonii d'Orbigny, 1826

Middle Miocene, Madura. Specimens from sample RGM 210 007.

1 - 2. Ventral view, 30 x.
3 - 4. Dorsal view, 30 x.

Amphistegina quoii d'Orbigny, 1826

Middle Miocene, Madura. Specimens from sample RGM 210 008.

5 - 6. Ventral view, 30 x.
7. Dorsal view, 30 x.

Amphistegina radiata (Fichtel & Moll, 1798)

Recent, Pacific. Specimens from sample RGM 210 009.

8 - 9. Dorsal view, 15 x.
10 - 11. Ventral view, 15 x.

Amphistegina: dome-shaped form.

Recent, Hawaii. Specimens from sample RGM 210 010.

12. Ventral view, 15 x.
13. Dorsal view, 15 x.

PLATE 1

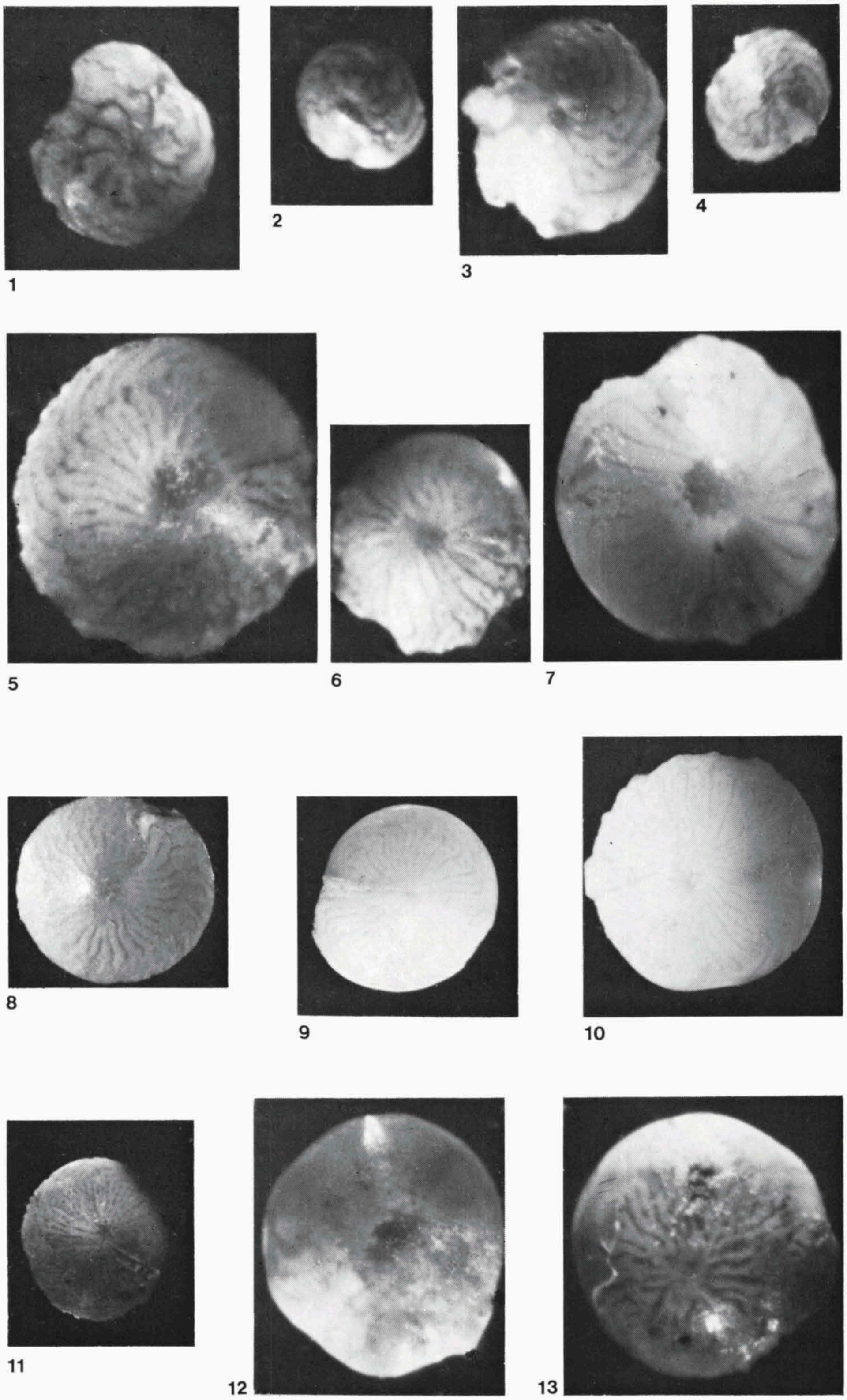


PLATE 2

Amphistegina lessonii d'Orbigny, 1826

Scanning electron micrographs of equatorial sections, 200 x.
Middle Miocene, Madura. Specimens from sample RGM 210 002.

1. Specimen with monolocular nucleoconch.
2. Specimen with bilocular nucleoconch.

PLATE 2

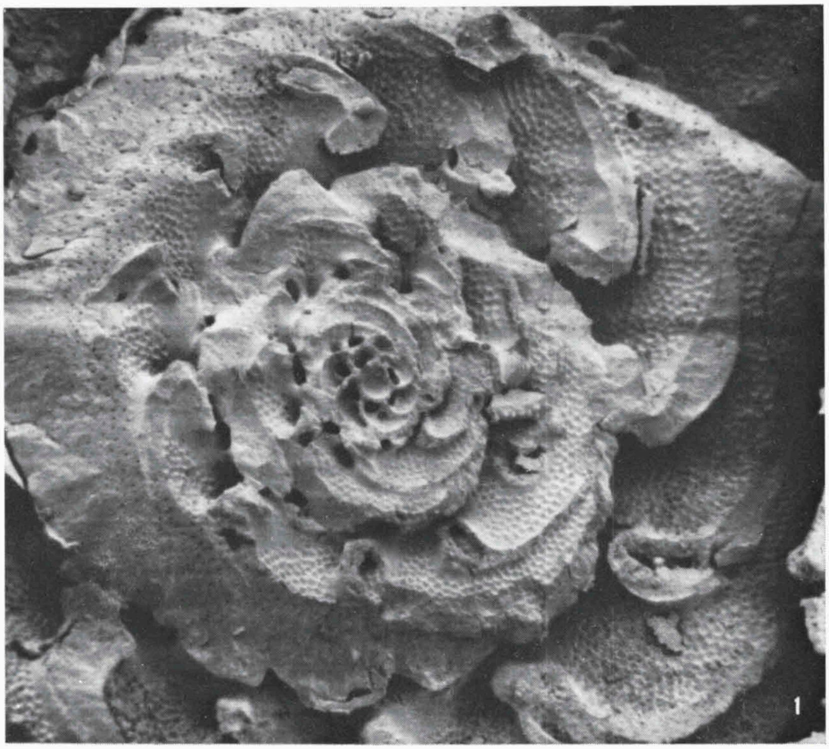


PLATE 3

Amphistegina lessonii d'Orbigny, 1826

Scanning electron micrographs of initial chambers. Middle Miocene, Madura. Specimens from sample RGM 210 002.

1. Bilocular nucleoconch, 500 x.
2. Monolocular nucleoconch, 1000 x.

PLATE 3

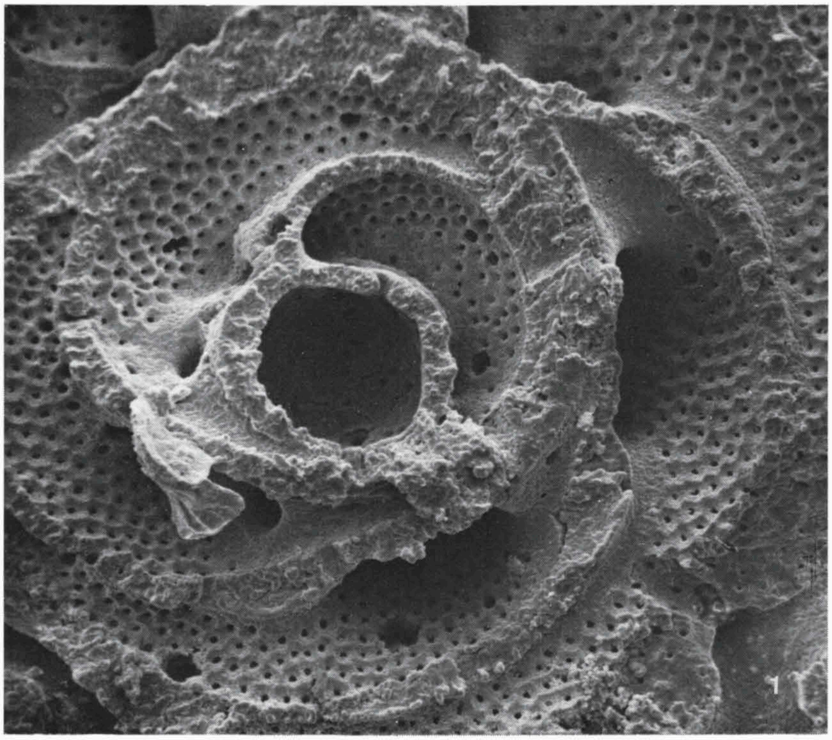


PLATE 4

Amphistegina lessonii d'Orbigny, 1826

Scanning electron micrographs. Specimens from sample RGM 210 002.

1. Internal view of the pore fields showing the cancellate structure, pores, and sieve-plates, 2000 x. Middle Miocene, Madura.

2 - 4. Specimens with a monolocular nucleoconch, 200 x. Middle Miocene, Madura.

6 - 9. Specimens with a bilocular nucleoconch, 200 x. Middle Miocene, Madura.

5. External view of the pores, 5000 x. Recent, Pacific. Specimen lost after micrograph was taken.

10. Internal view of the secondary altered pore fields showing the cancellate structure, pores, and sieve-plates, 5000 x. Recent, Pacific.

PLATE 4

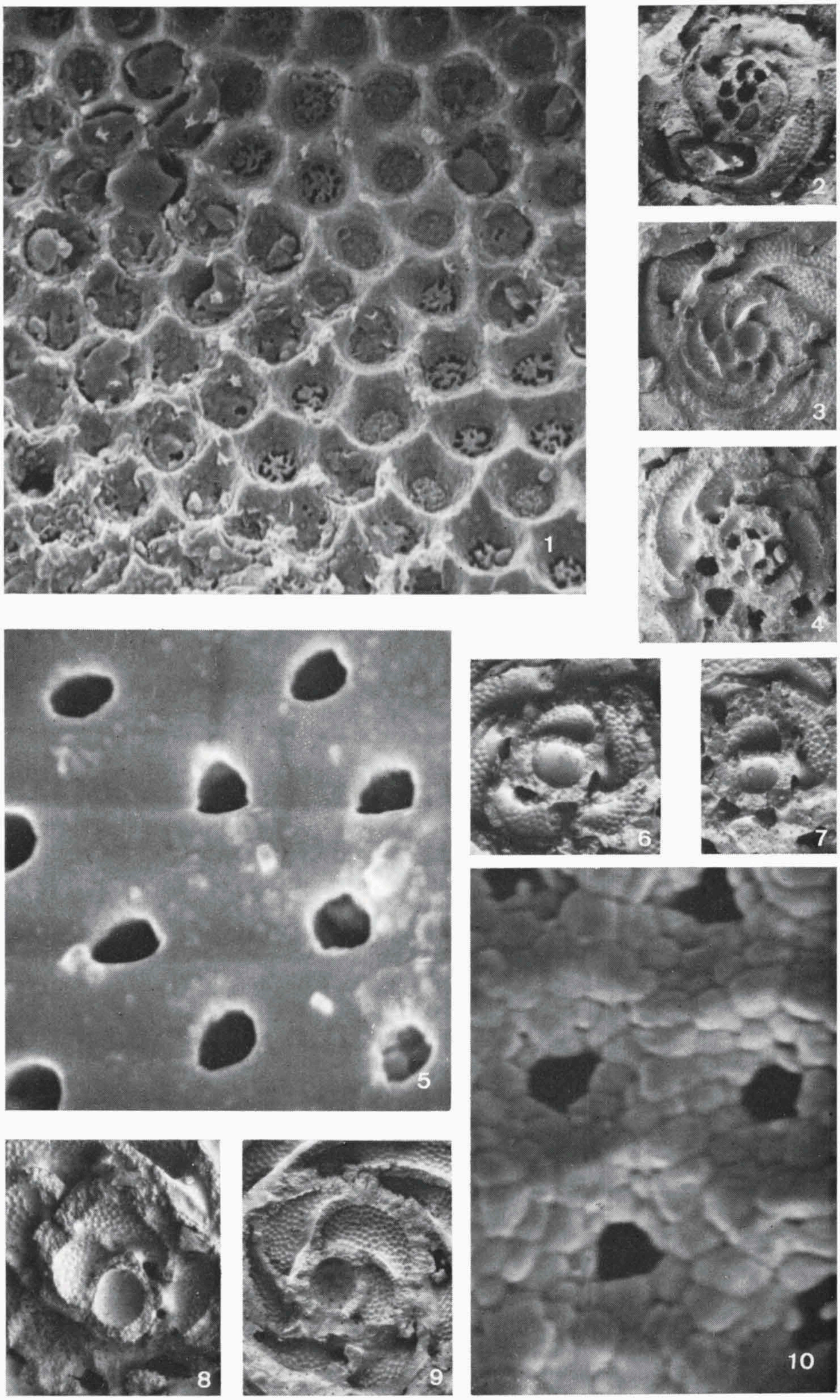


PLATE 5

Amphistegina lessonii d'Orbigny, 1826

Scanning electron micrographs. Middle Miocene, Madura. Specimens from sample RGM 210 002.

1. Equatorial section of a monolocular specimen, 100 x.
2. Internal view of cancellate structure, pores, and sieve-plates, 5000 x.

3 - 4. Specimens with a bilocular nucleoconch, 200 x.

PLATE 5

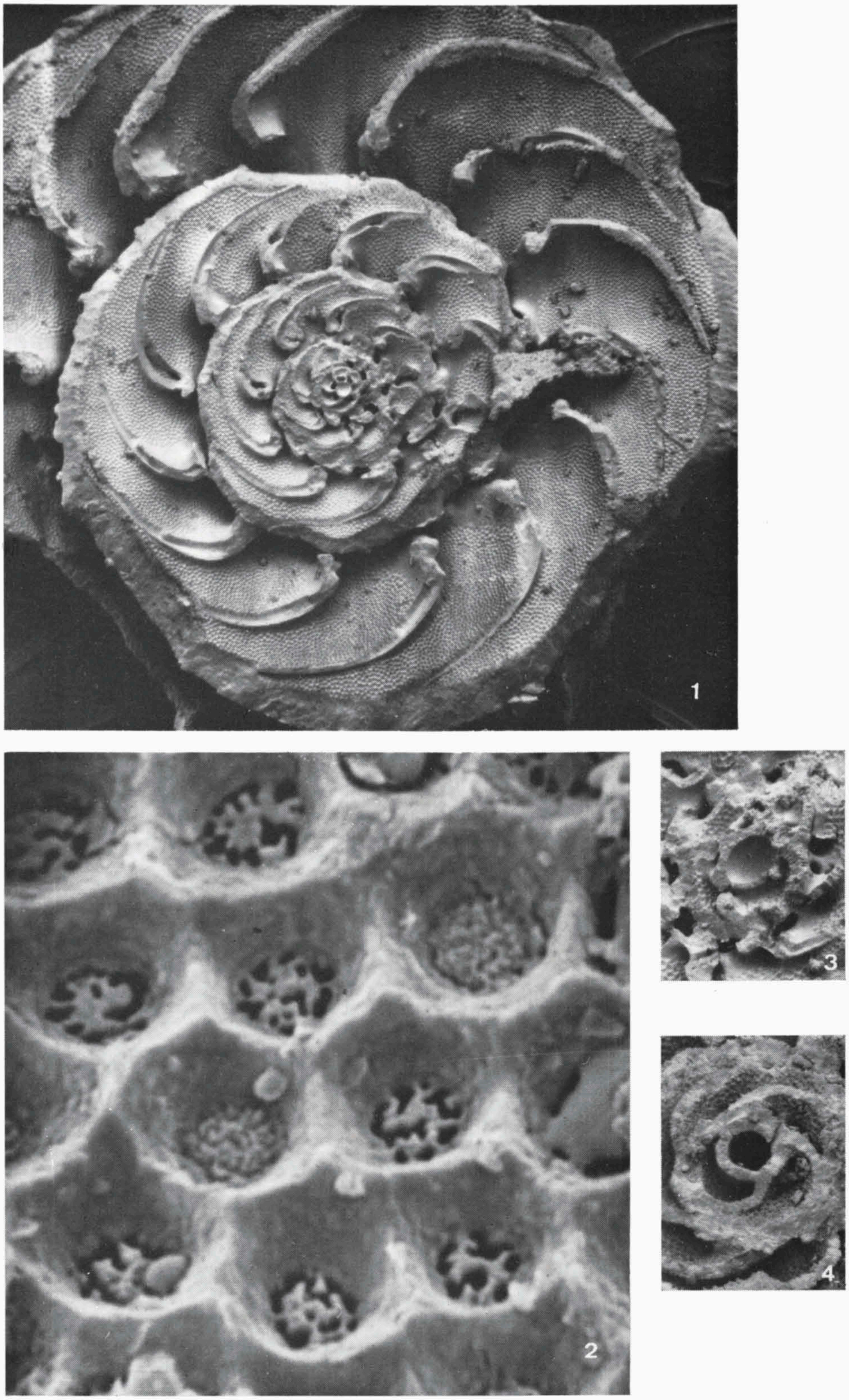


PLATE 6

Amphistegina lessonii d'Orbigny, 1826

Scanning electron micrographs of internal casts consisting of chamosite, 100 x. Middle Miocene, Madura. Specimens from sample RGM 210 003.

1. Ventral view.
2. Dorsal view.
3. Damaged cast showing the large imprints of the papillae about the opening, on the inner side of the ventral lobes.

PLATE 6

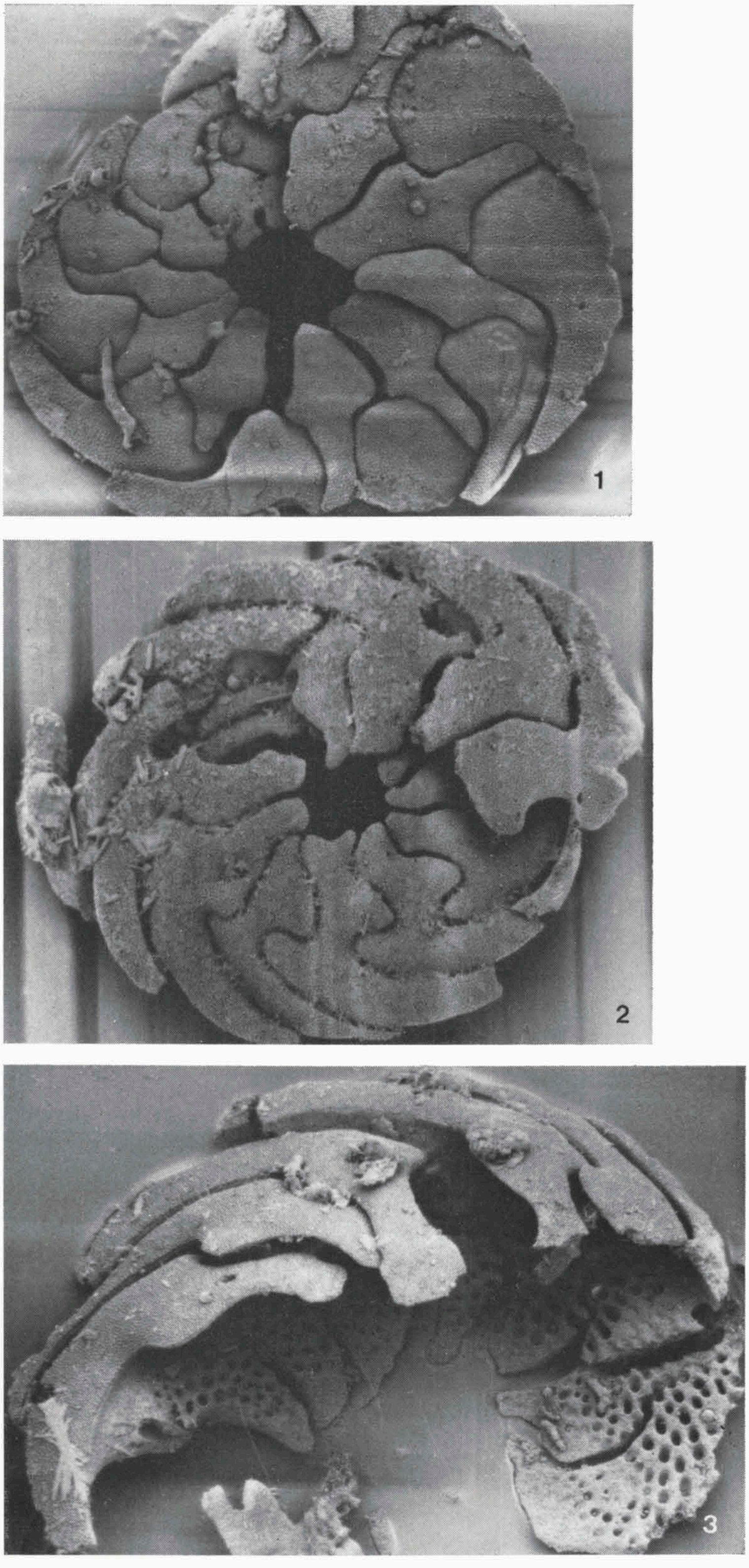


PLATE 7

Amphistegina quoii d'Orbigny, 1826

Scanning electron micrographs of equatorial sections, 500 x. Middle Miocene, Madura. Specimens from sample RGM 210 004.

1. Specimen with monolocular nucleoconch.
2. Specimen with bilocular nucleoconch.

PLATE 7

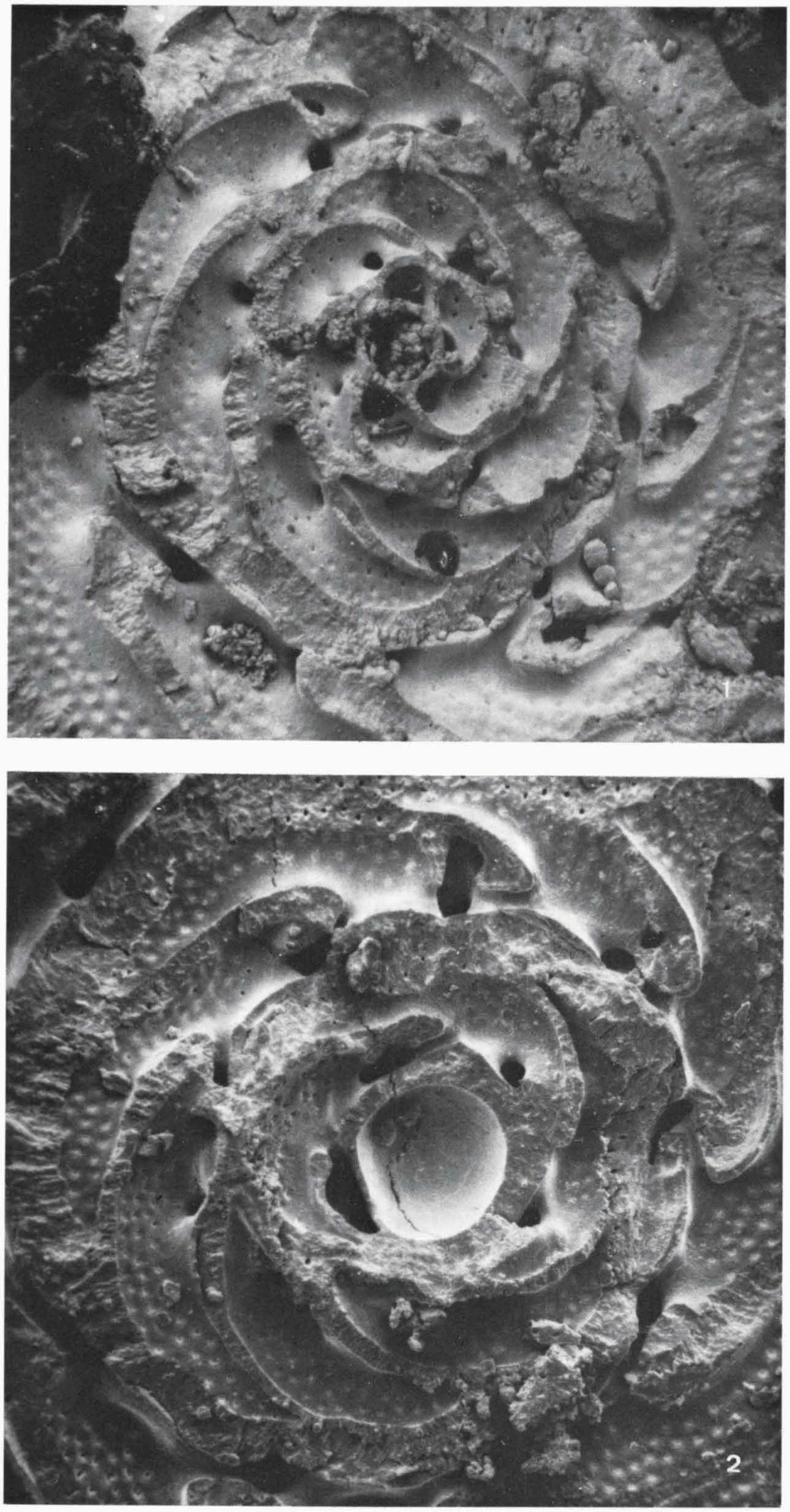


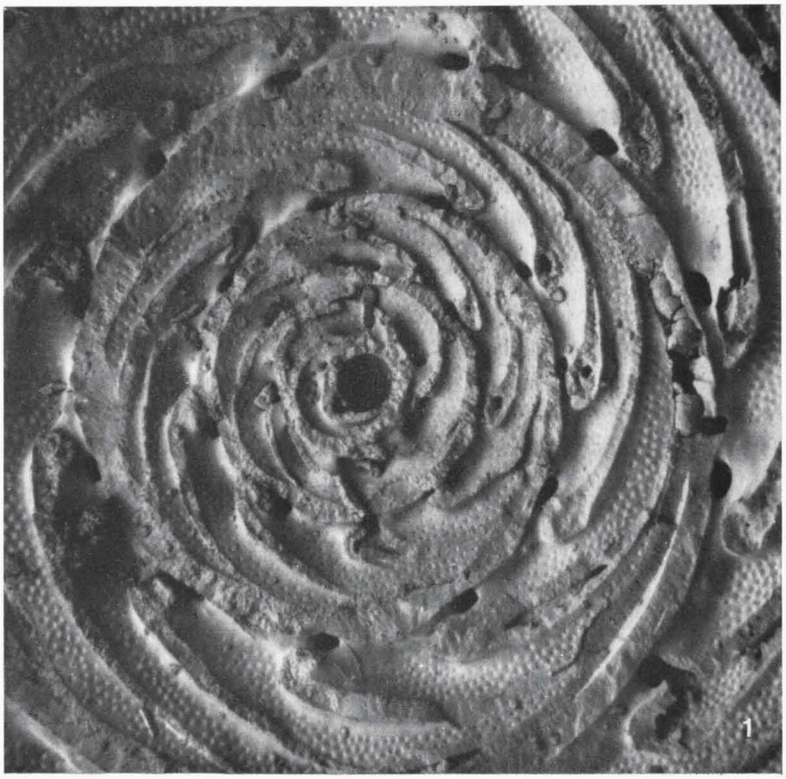
PLATE 8

Amphistegina quoii d'Orbigny, 1826

Scanning electron micrographs. Recent, Pacific.

1. Equatorial section of a specimen with a bilocular nucleoconch, 200 x. Specimen from sample RGM 210 004.
2. External view of part of the umbo showing septa and pore-fields, 500 x. Specimen lost after micrograph was taken.

PLATE 8



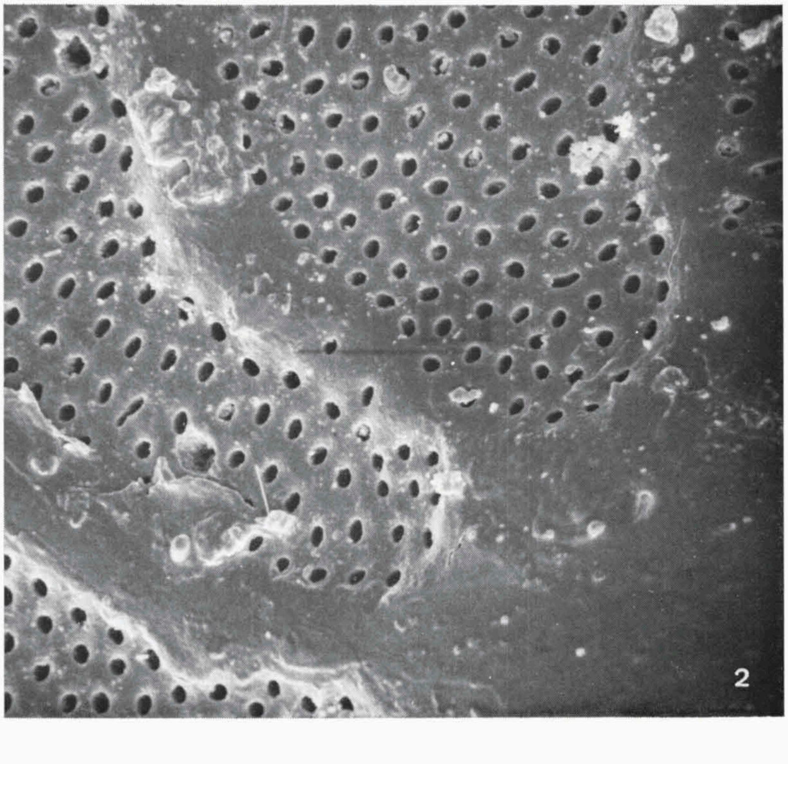


PLATE 9

Amphistegina quoii, d'Orbigny, 1826

Scanning electron micrographs. Specimens from somple RGM 210 004.

1 - 2. Internal view of (secondary altered?) pore-fields, honeycomb structure still distinct in fig. 1, 5000 x. Middle Miocene, Madura.
3. External view of the pores, 5000 x. Recent, Pacific. Specimen lost after micrograph was taken.
4. Internal view of (secondary altered?) pore-fields, 5000 x. Lower Miocene, Java.
5 - 6. Initial chambers of specimens with a bilocular nucleoconch, 5: 1000 x, 6: 500 x. Middle Miocene, Madura.

PLATE 9

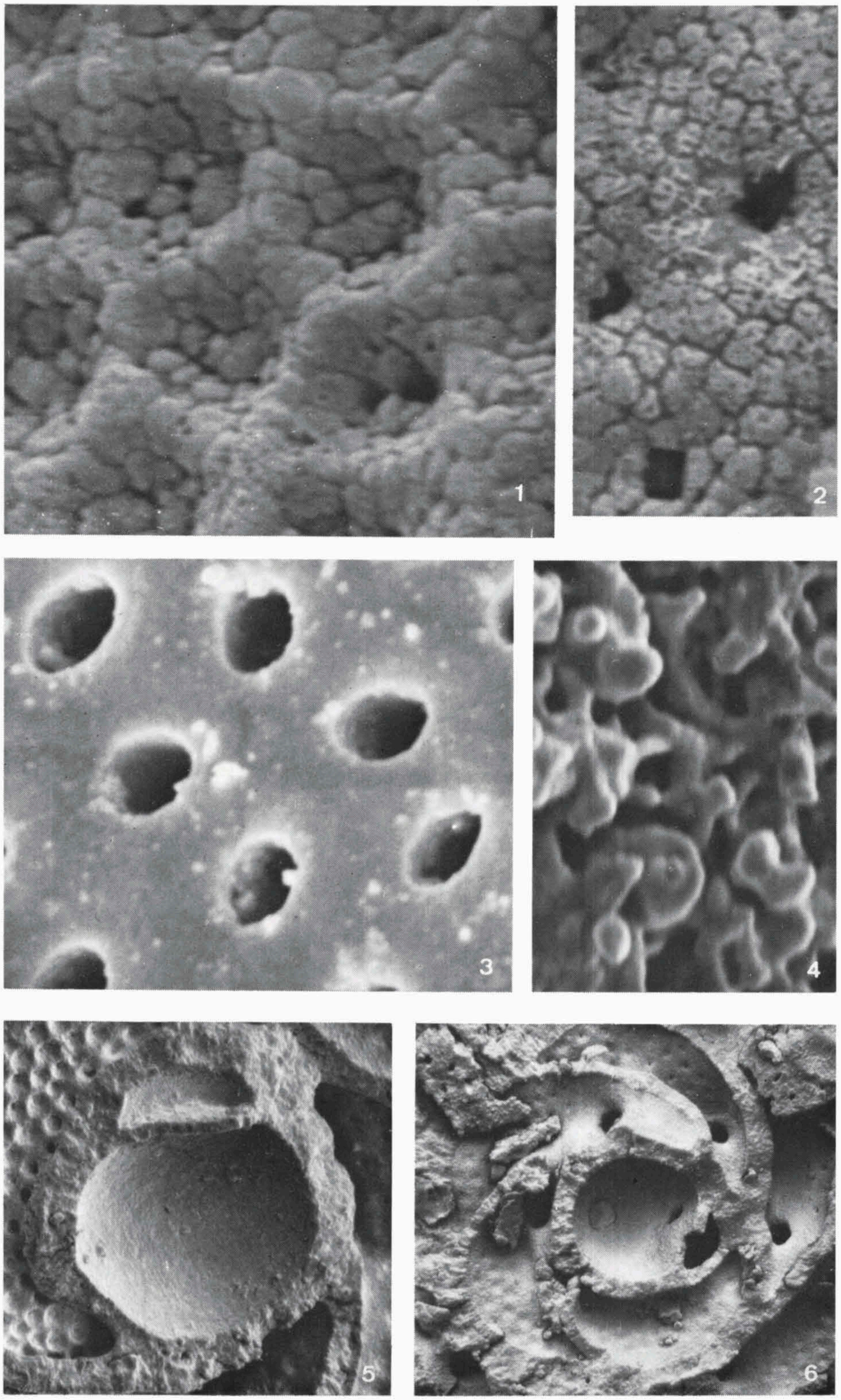


PLATE 10

Amphistegina quoii, d'Orbigny, 1826

Scanning electron micrographs. Middle Miocene, Madura.

1. Internal cast consisting of chamosite, dorsal view, 100 x. Specimen from sample RGM 210 005.

2 - 3. Bilocular nucleoconchs, 1000 x. Specimens from sample RGM 210 004.

PLATE 10

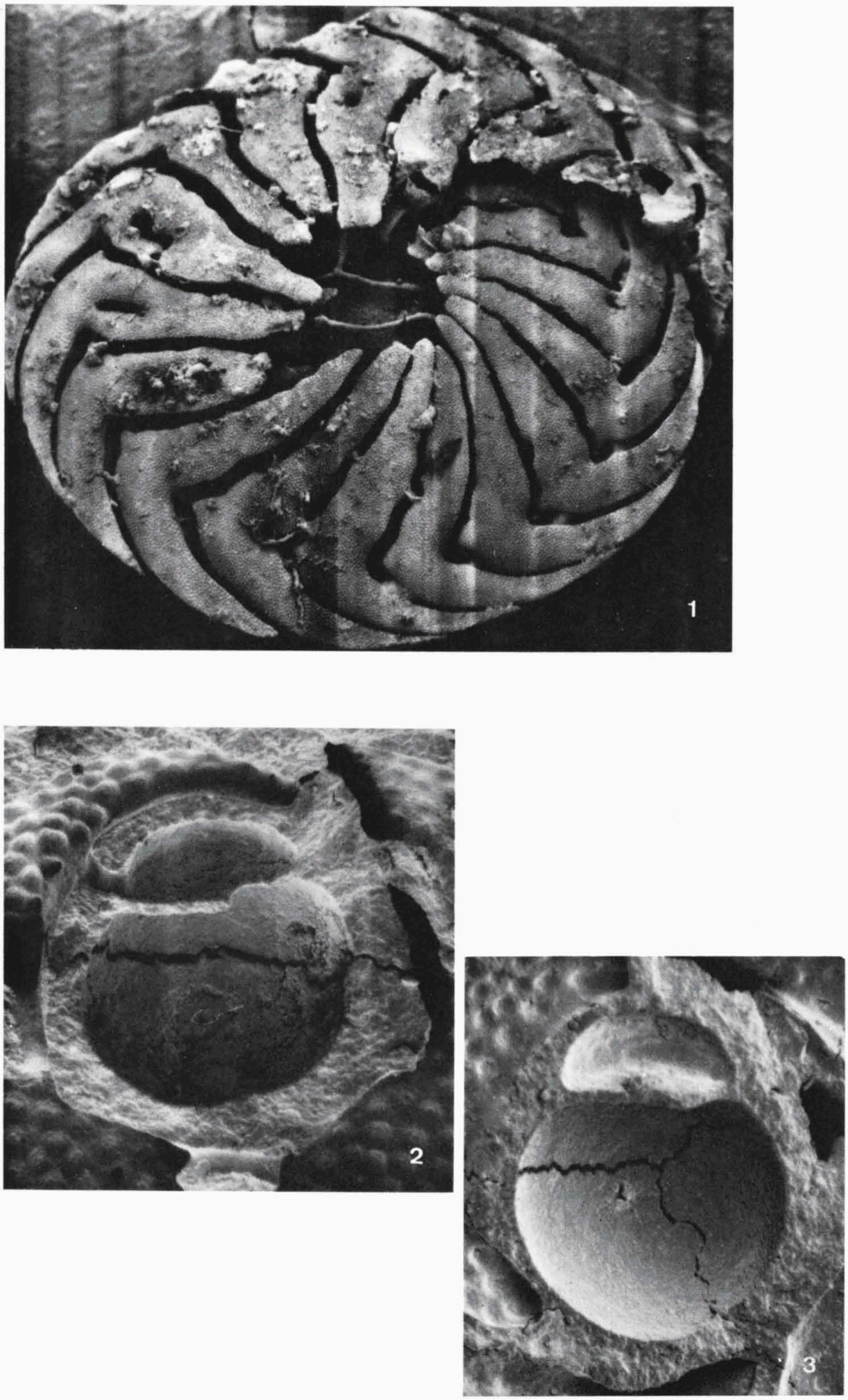


PLATE 11

Amphistegina quoii, d'Orbigny, 1826

Scanning electron micrographs of internal casts consisting of chamosite, ventral views, 200 x. Middle Miocene, Madura. Specimens from sample RGM 210 005.

PLATE 11

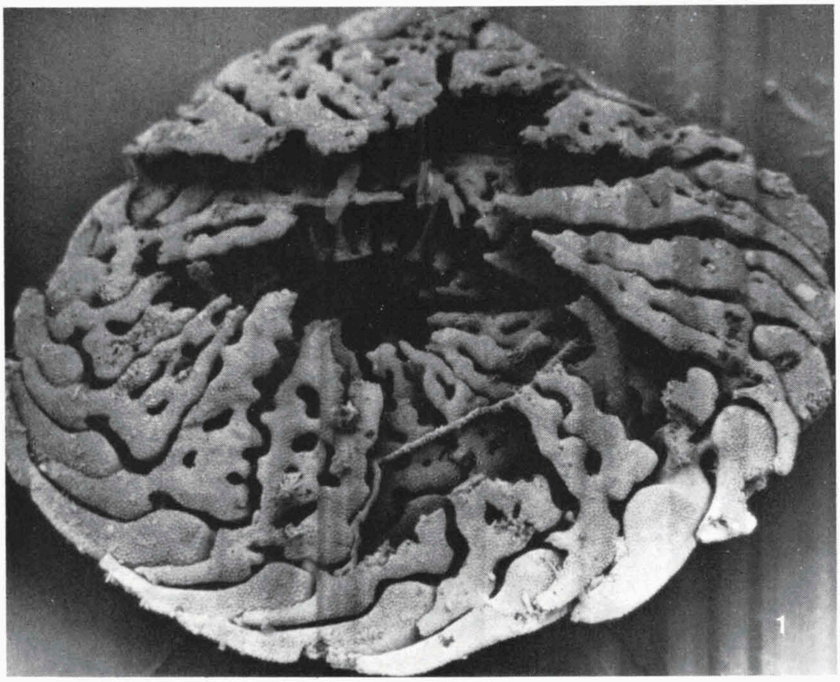


PLATE 12

Amphistegina radiata (Fichtel & Moll, 1798)

Scanning electron micrographs. Recent, Pacific. Specimens from sample RGM 210 001.

1 - 2. Bilocular nucleoconchs, 1: 1000 x, 2: 200 x.
3. External view of the pores, 5000 x. Specimen lost after micrograph was taken.
4. Internal view of secondary altered (?) honeycomb structure, 5000 x.
5. Specimen with a bilocular nucleoconch, 200 x.

PLATE 12

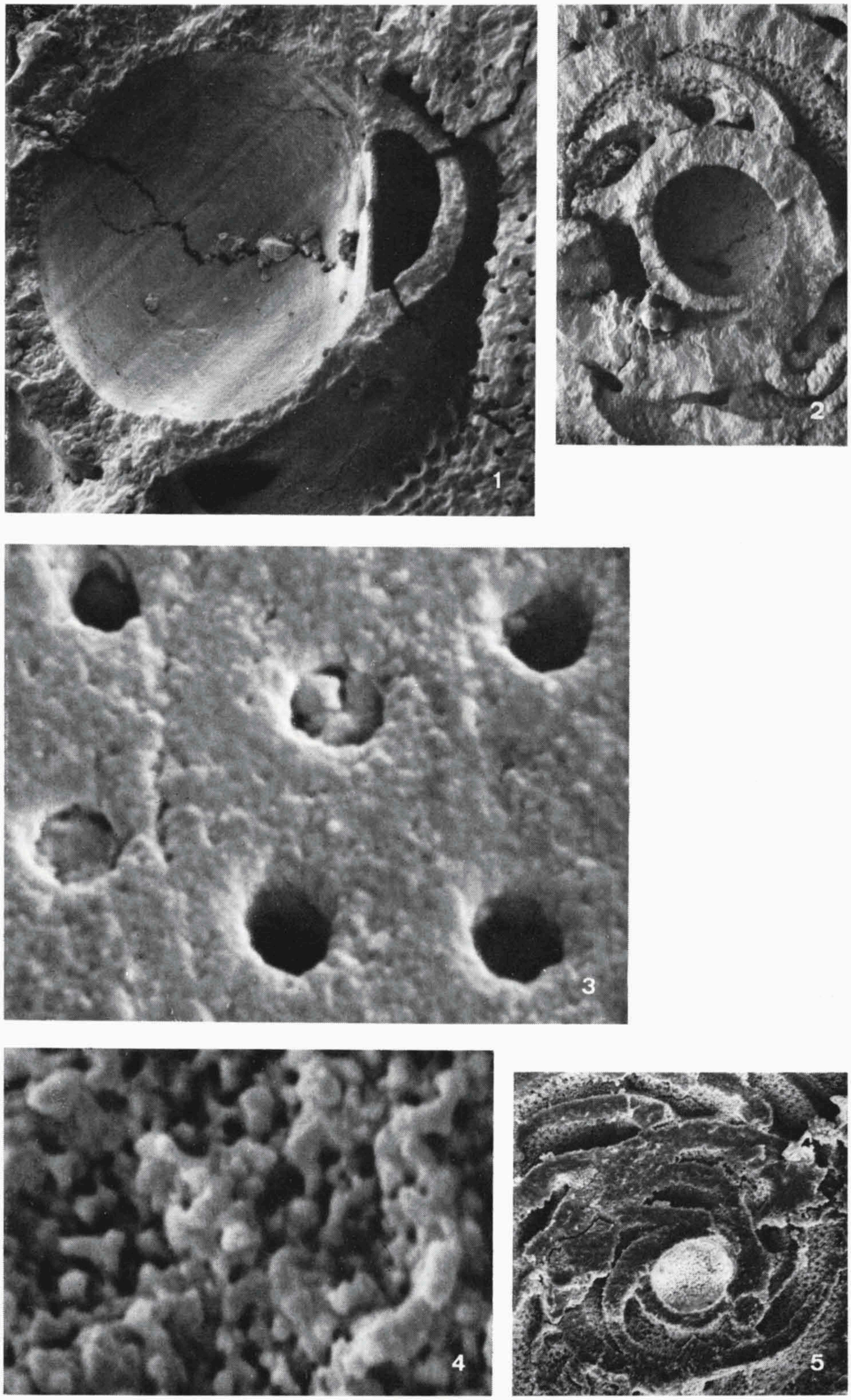


PLATE 13

Amphistegina radiata (Fichtel & Moll, 1798)

Scanning electron micrographs. Recent, Pacific. Specimens from sample RGM 210 001.

1. Equatorial section of a specimen with a bilocular nucleoconch, 100 x.
2. Initial chambers of a specimen with a monolocular nucleoconch, 500 x.
3. Initial chambers of a specimen with a bilocular nucleoconch, 200 x.

PLATE 13

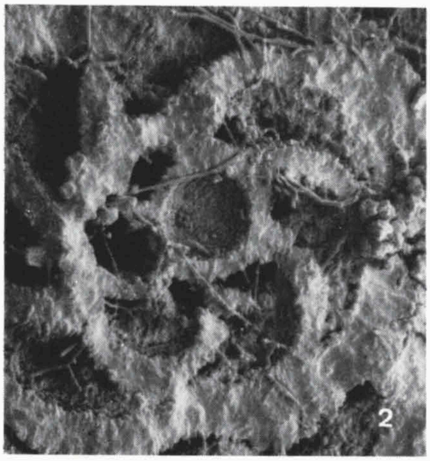


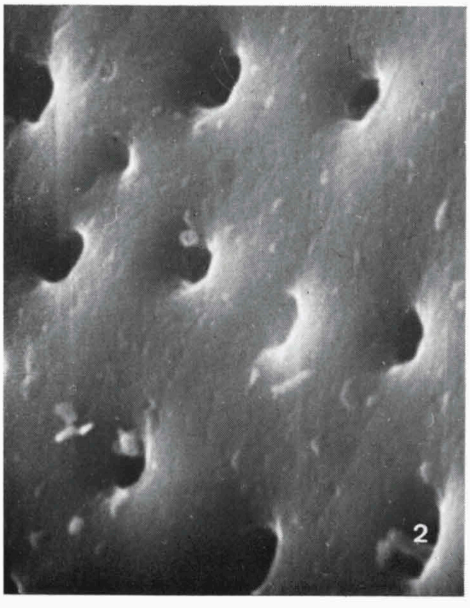
PLATE 14

Amphistegina gibbosa d'Orbigny, 1839

Scanning electron micrographs. Recent, Caribbean. Specimens from sample RGM 210 600.

1. Equatorial section, 200 x.
2. External view of the pores, 500 x. Specimen lost after micrograph was taken.
3. Papillae about the aperture, 200 x. Specimen lost after micrograph was taken.

PLATE 14



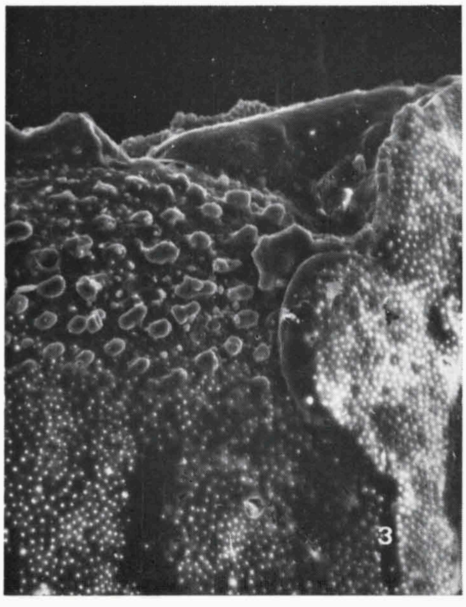


PLATE 15

Amphistegina: dome-shaped form.

Scanning electron micrographs. Recent, Hawaii. Specimens lost after micrograph was taken.

1. Broken specimen showing the nucleoconch, 100 x.
2. External view of the pores, 5000 x.

PLATE 15

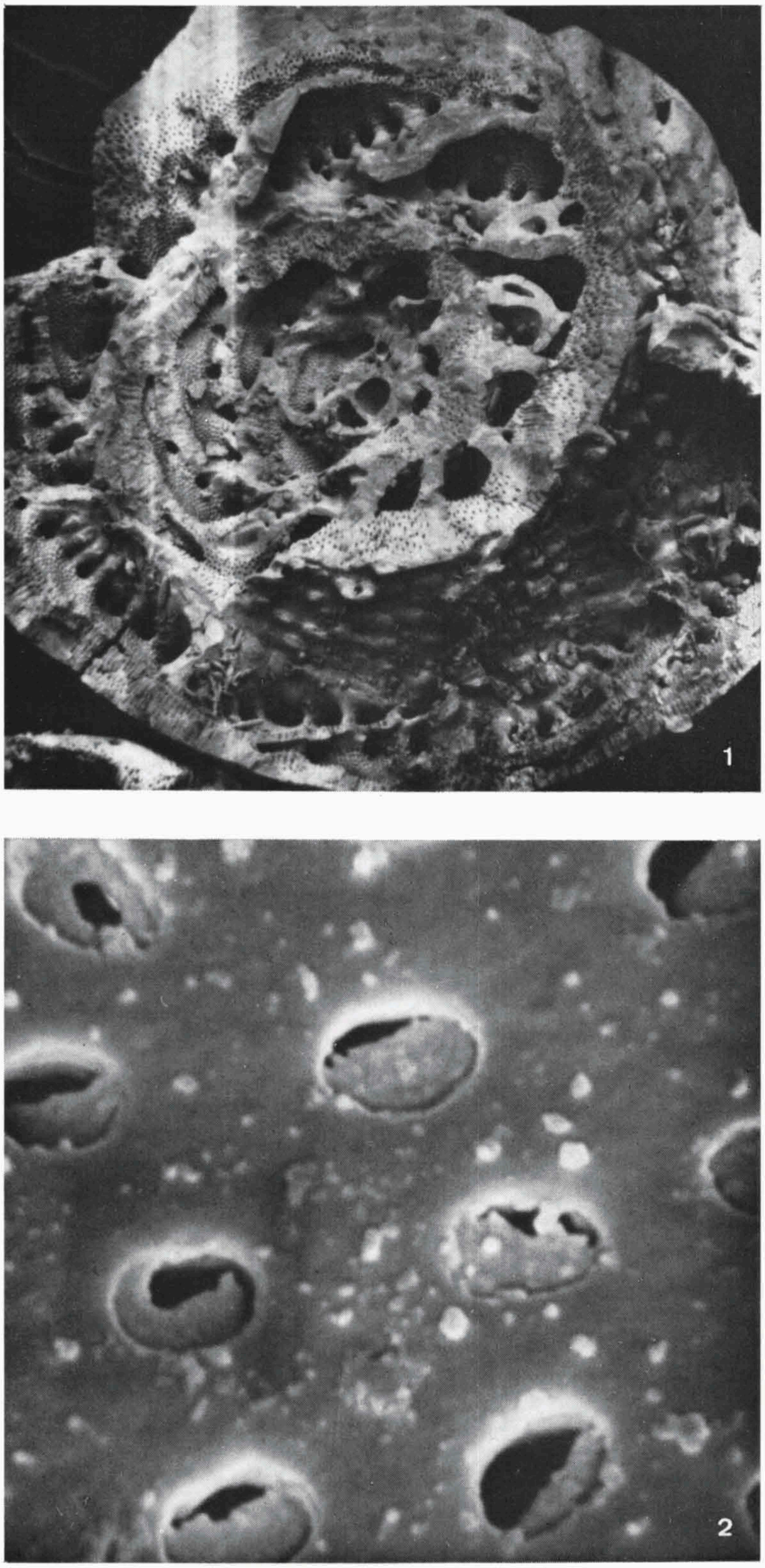


PLATE 16

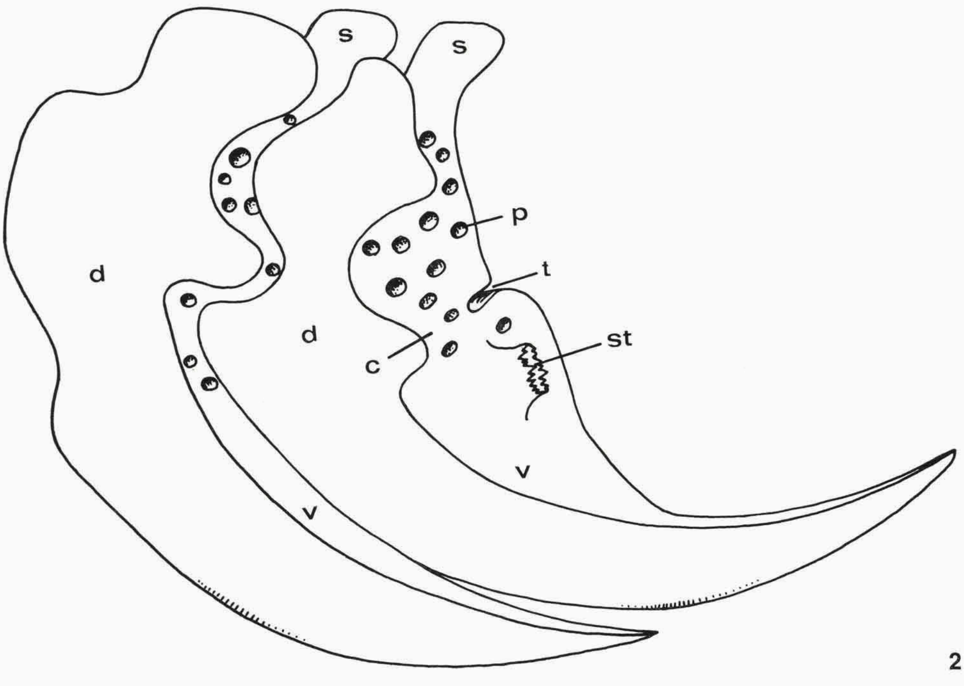
Amphistegina lessonii d'Orbigny

1. Scanning electron micrograph of an internal cast consisting of chamosite, dorsal view, 100 x. Middle Miocene, Madura. Specimen from sample RGM 210 003.
2. Schematic drawing of two instars, dorsal view.

d = dorsal prolongation, v = ventral prolongation, s = secondary lobe of v, st = stolon, c = connection between s and v.

PLATE 16

1



2

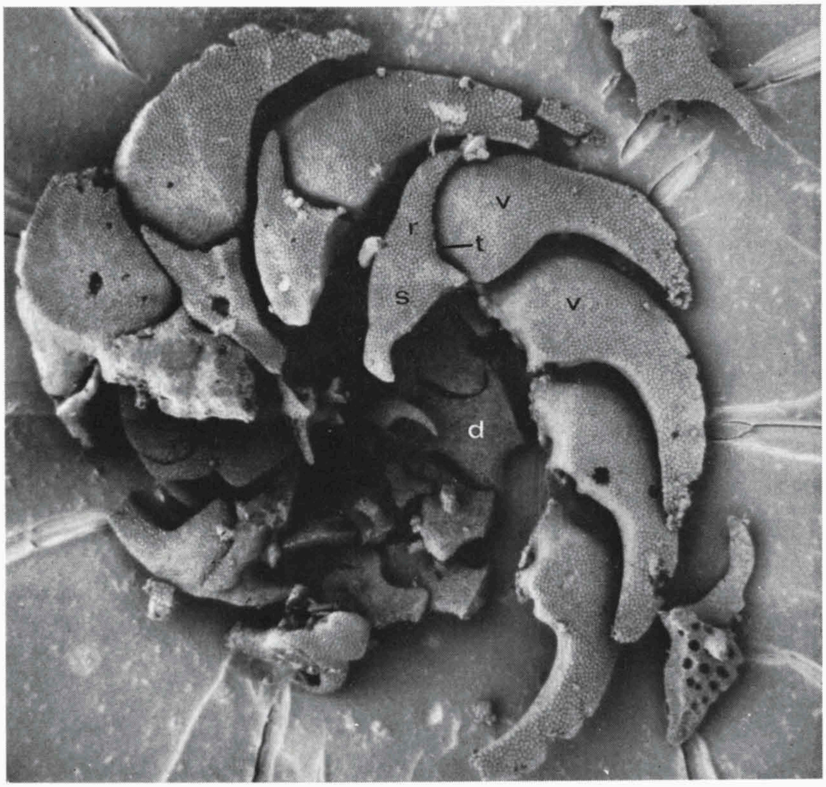
PLATE 17

Amphistegina lessonii d'Orbigny, 1820

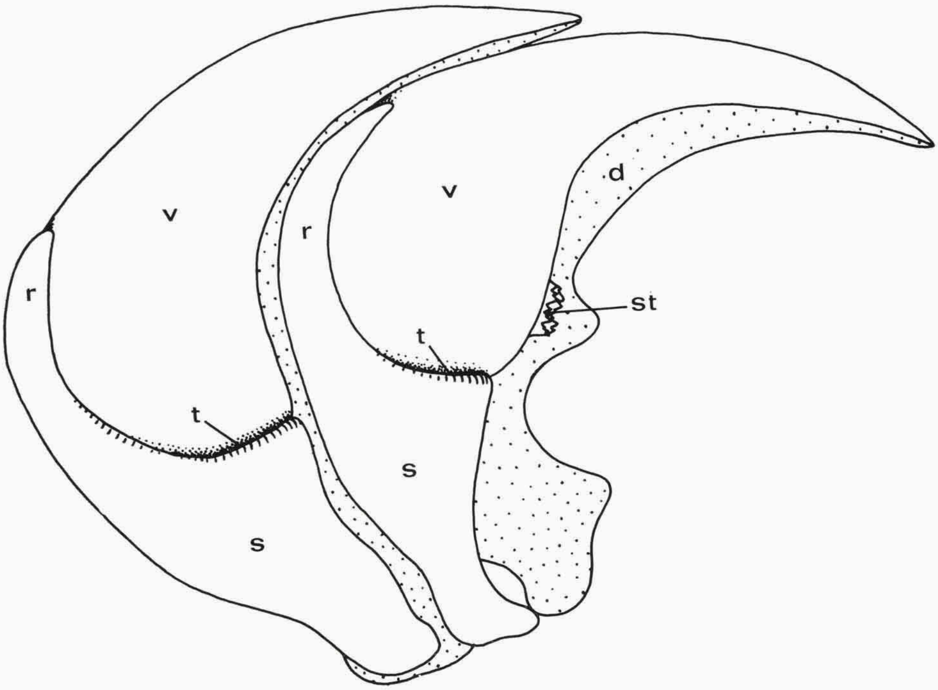
1. Scanning electron micrograph of an internal cast consisting of chamosite, ventral view, 100 x. Middle Miocene, Madura. Specimen from sample RGM 210 003.
2. Schematic drawing of two instars, ventral view:

d= dorsal prolongation, v = ventral prolongation, s = secondary lobe of v, r = retral process of s, t = ridge between s and v (toothplate according to Hofker), st = stolon.

PLATE 17



1



2

PLATE 18

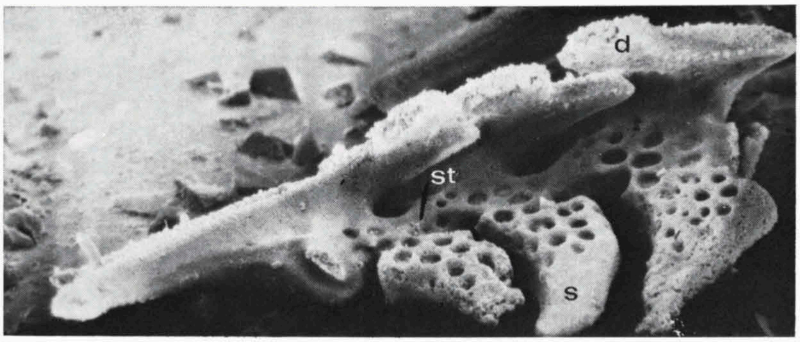
Amphistegina lessonii d'Orbigny, 1826

Scanning electron micrographs, 200 x. Middle Miocene, Madura. Specimens from sample RGM 210 003.

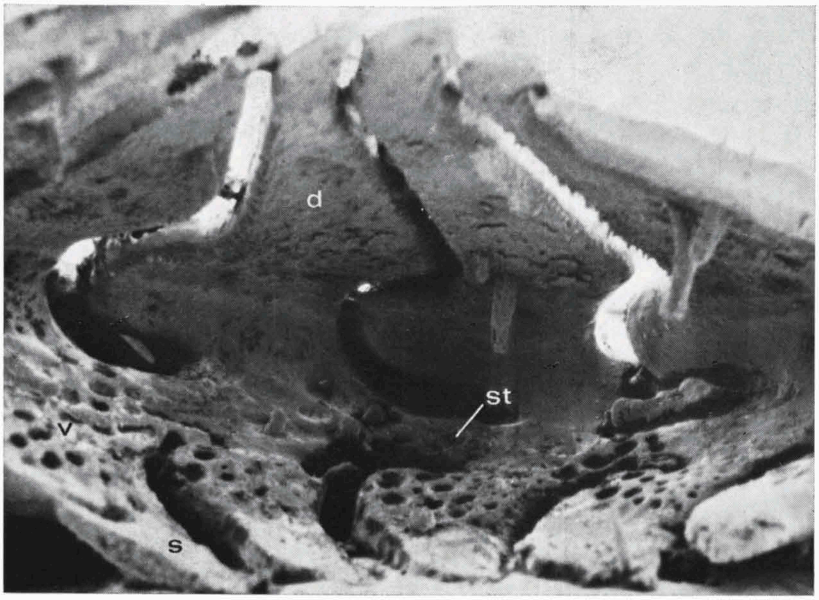
1 - 2. Part of internal casts consisting of chamosite, internal view, approximately equatorial.
3. Schematic drawing of internal equatorial view of two instars.

d = dorsal prolongation, v = ventral prolongation, s = secondary lobe of v, r = retral process of s, st = stolon, t = ridge between s and v (toothplate according to Hofker).

PLATE 18



1



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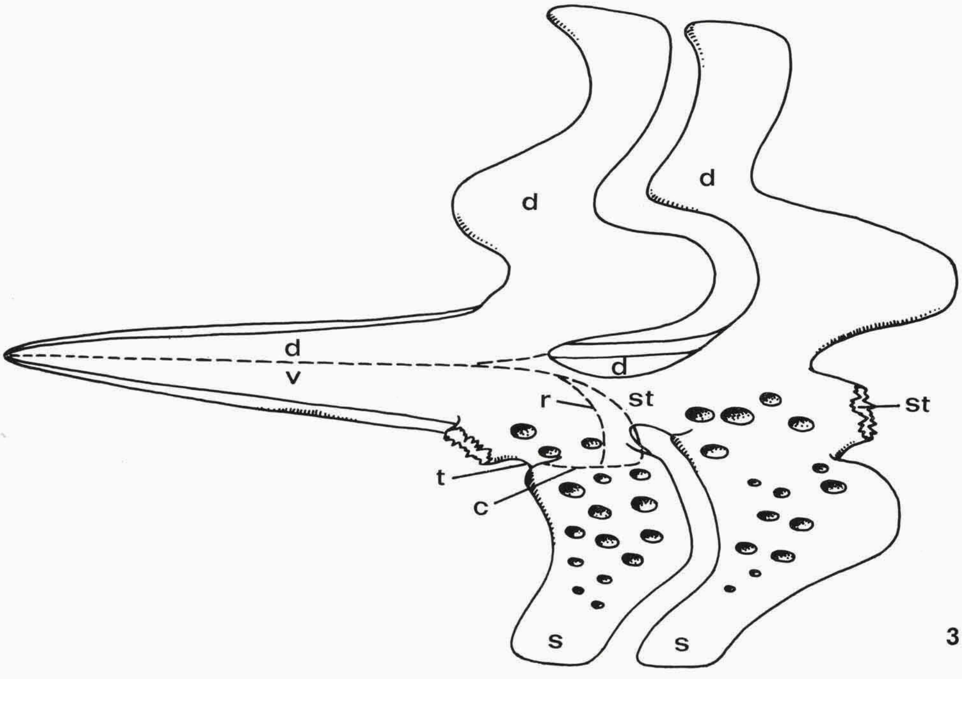


3

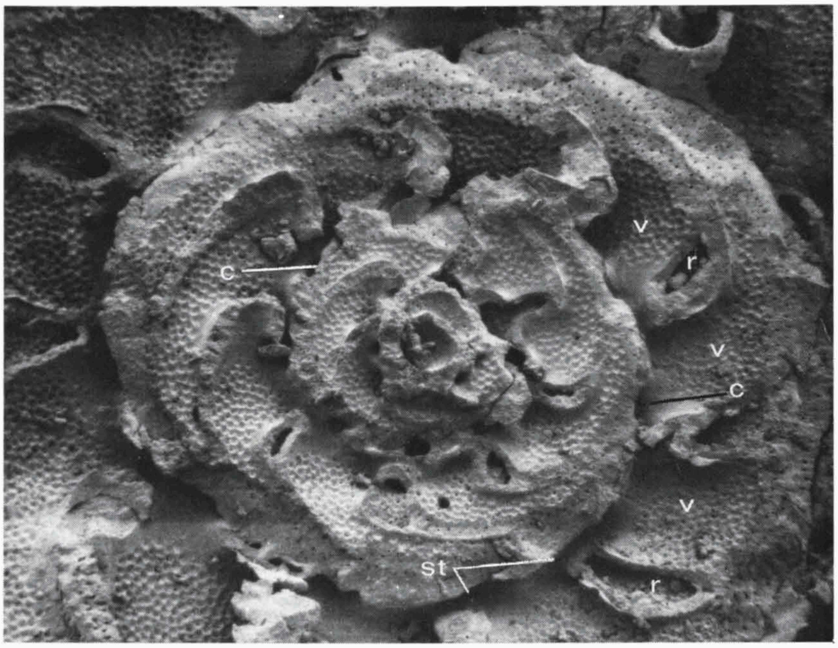
PLATE 19

Amphistegina lessonii d'Orbigny, 1826

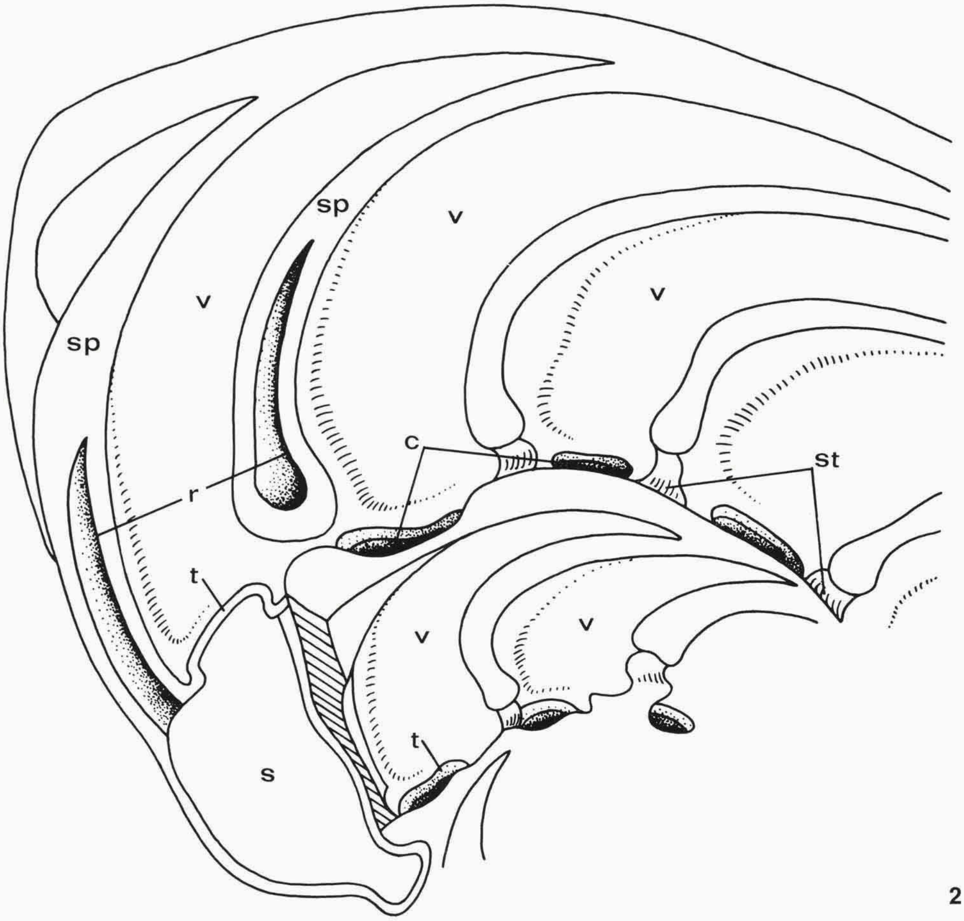
1. Scanning micrograph of an equatorial section, ventral half, 200 x. Middle Miocene, Madura. Specimen from sample RGM 210 003.
2. Schematic drawing of part of an equatorial section, ventral half.

v = ventral prolongation, s = secondary lobe of v, r = retral process of s, st = stolon, sp = septum, c = connection between s and v, t = ridge between s and v (toothplate according to Hofker).

PLATE 19



1



2

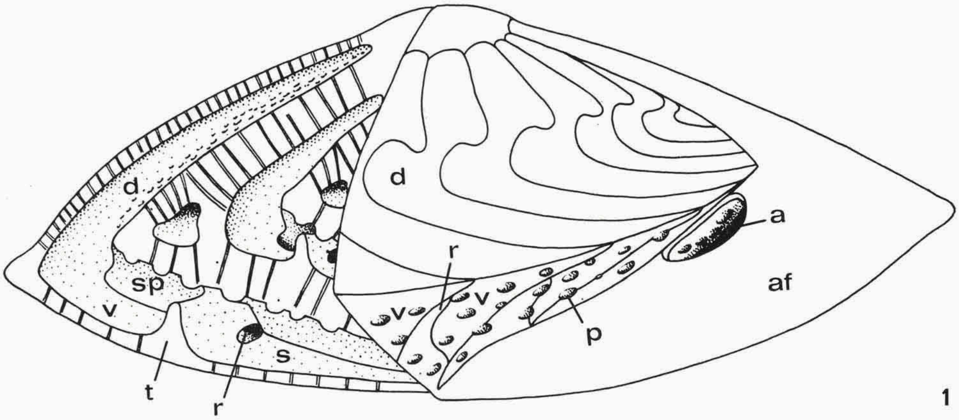
PLATE 20

Amphistegina lessonii d'Orbigny, 1826

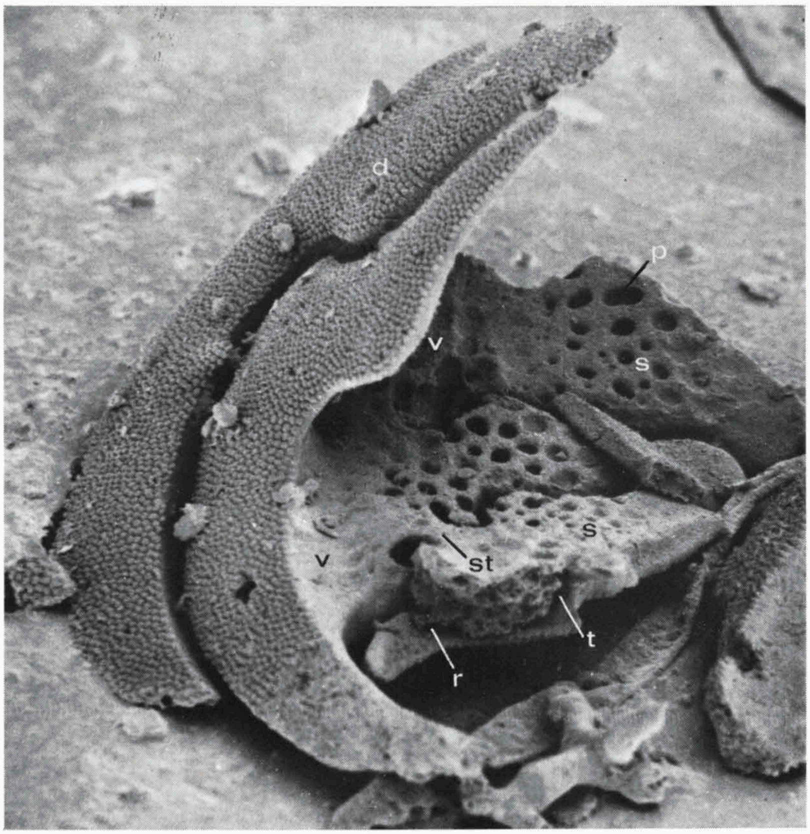
1. Stereogram.
2. Scanning electron micrograph of part of an internal cast consisting of chamosite, 200 x. Middle Miocene, Madura. Specimen from sample RGM 210 003.

d = dorsal prolongation, v = ventral prolongation, s = secondary lobe of v, r = retral process of s, p = papillae, t = ridge between s and v (toothplate according to Hofker).

PLATE 20



1



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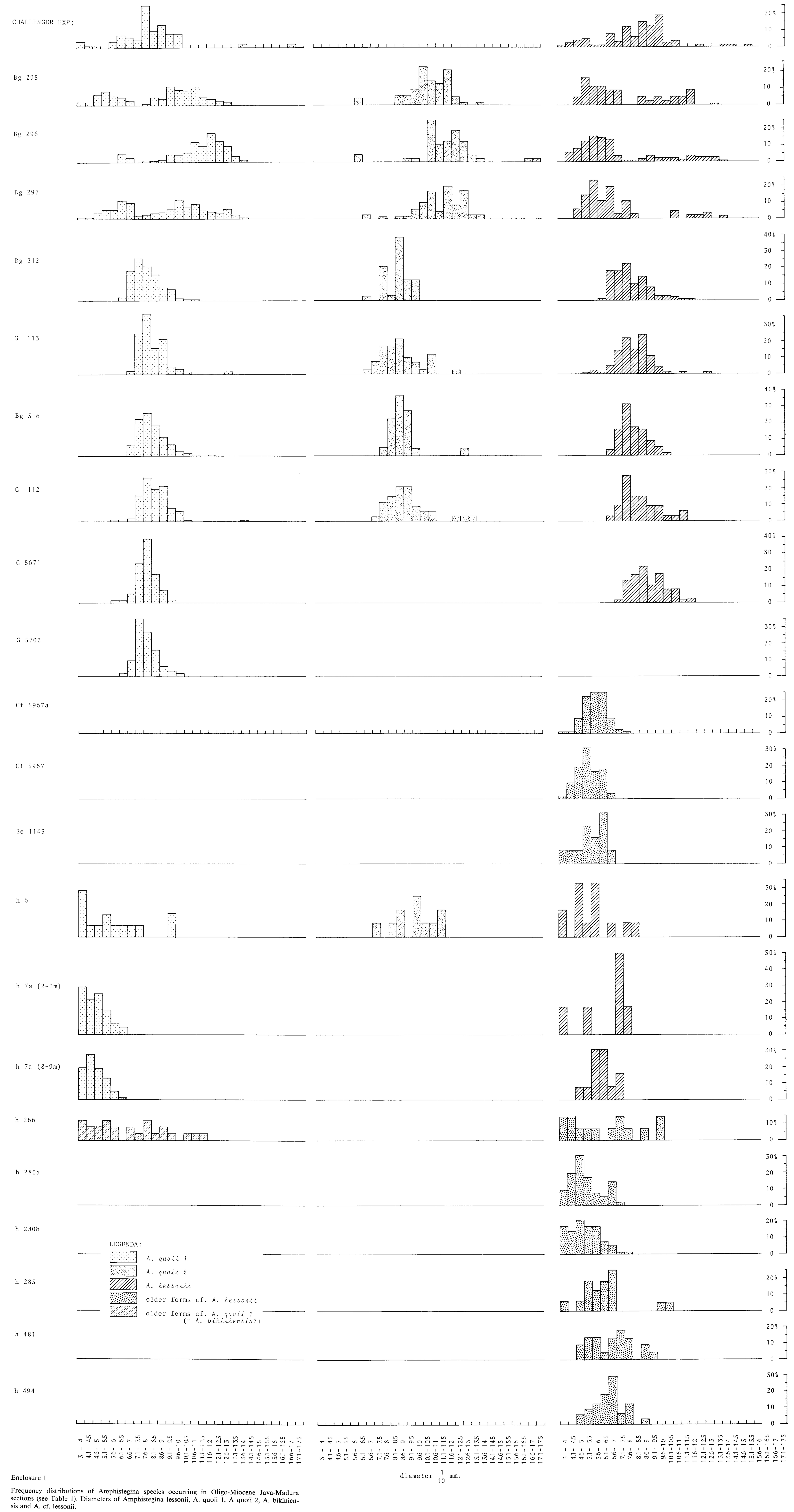
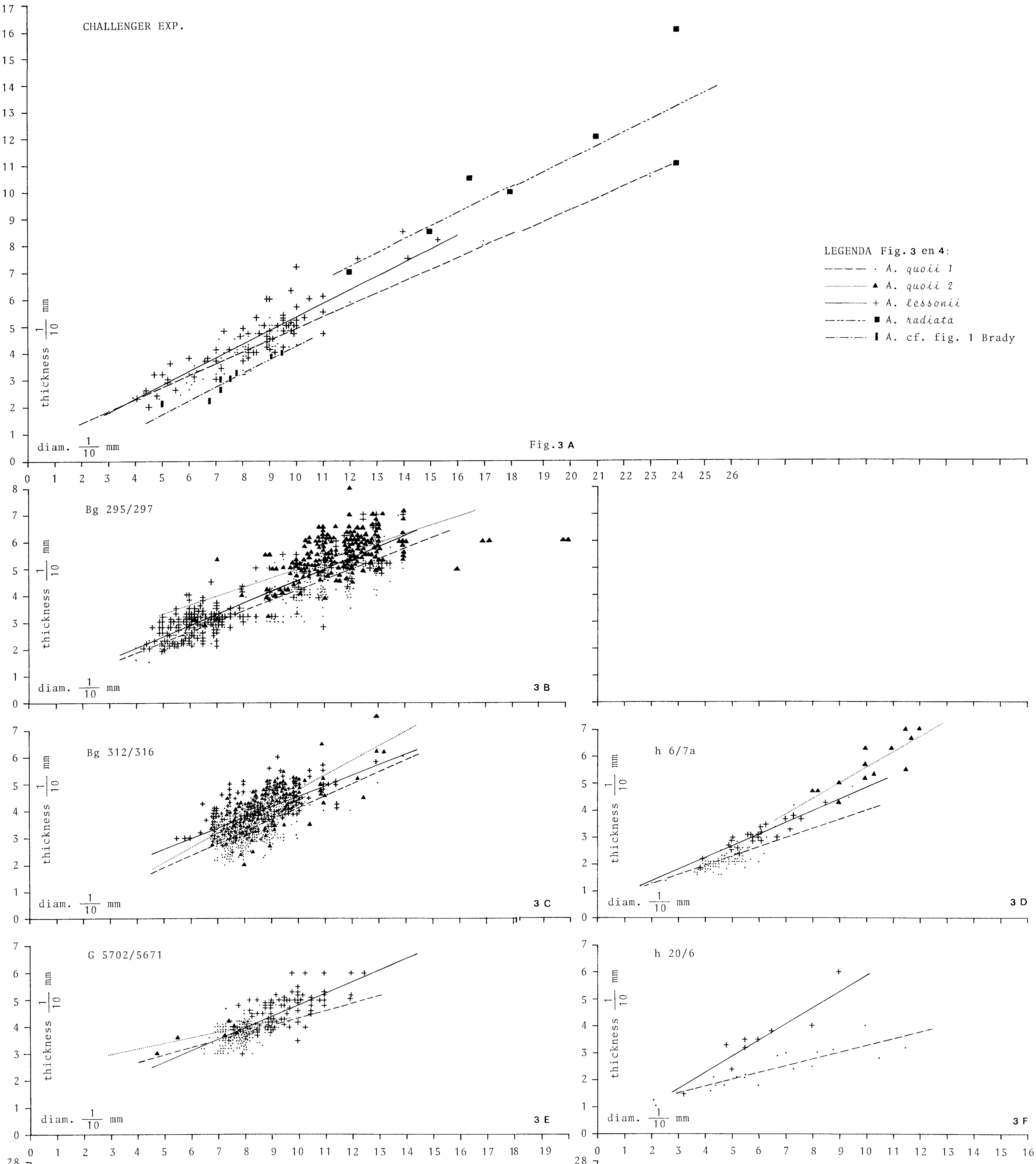
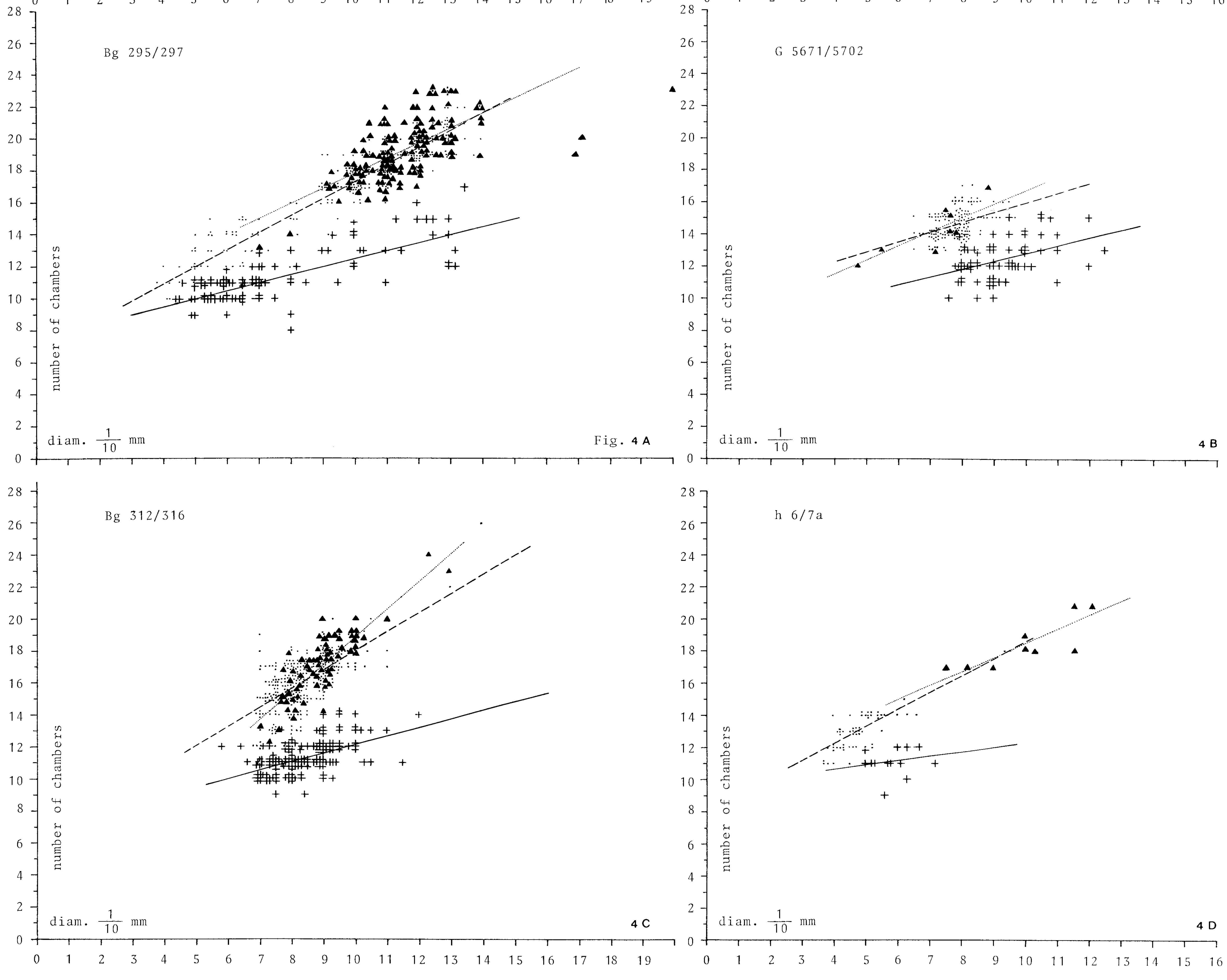


Enclosure 1

Frequency distributions of Amphistegina species occurring in Oligo-Miocene Java-Madura sections (see Table 1). Diameters of Amphistegina lessonii, A. quoii 1, A quoii 2, A. bikiniensis and A. cf. lessonii.

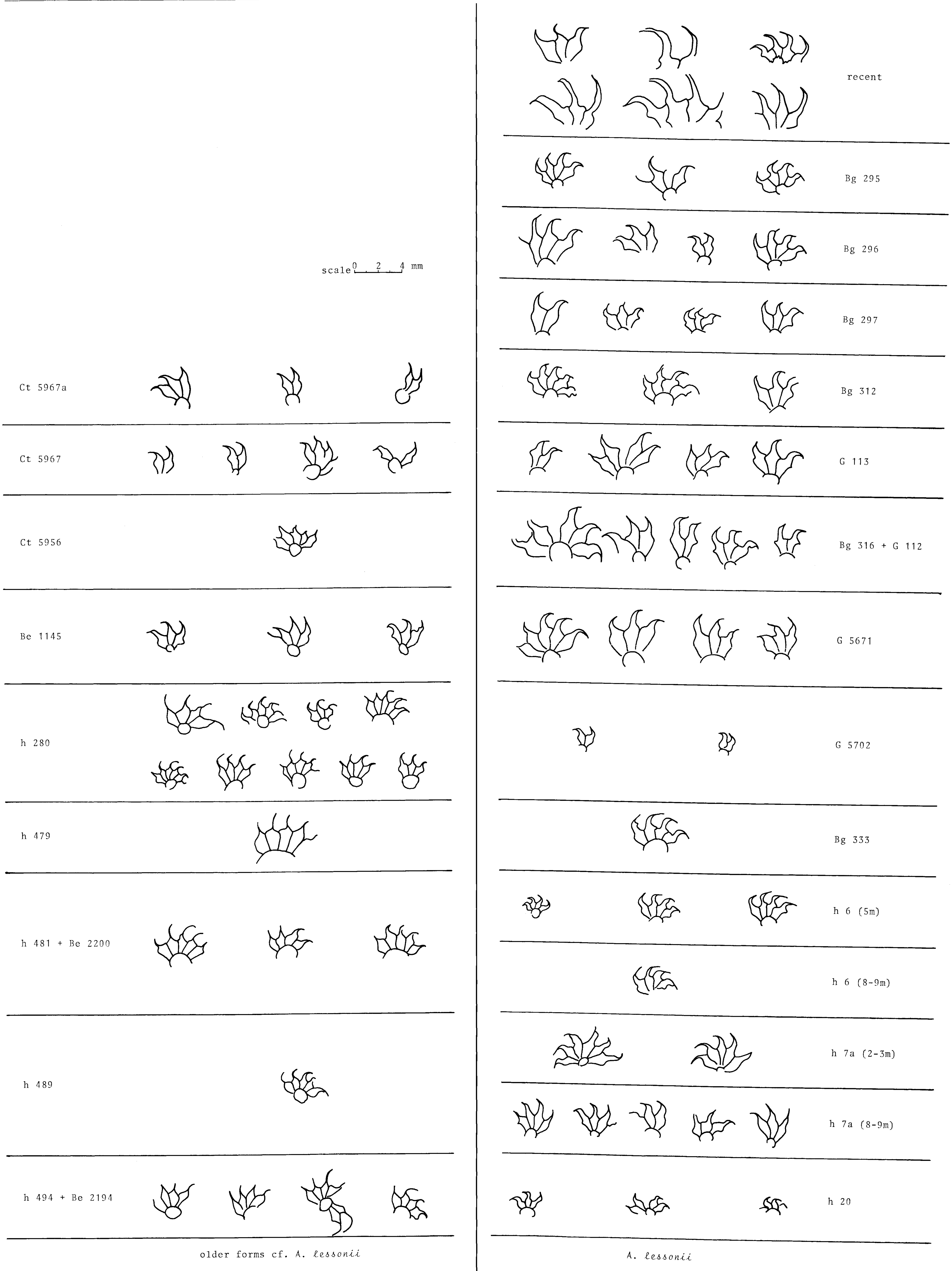




Enclosure 2

Fig. 3A-3F: scatter diagrams, thickness relative to diameter. Samples of various ages from Java-Madura (see Table 1) and a recent sample from the Admiralty Islands.

Fig. 4A-4D: scatter diagrams, number of chambers in the last whorl relative to diameter. Samples of various ages from Java-Madura.



Enclosure 3

Shape of the secondary lobes on the ventral side of Amphistegina lessonii during the Oligo-Miocene of Java-Madura (see Table 1) and in a recent form (Admiralty Islands).