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# Systematics of the American Discocyclinas

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ABSTRACT

Instead of VAUGHAN and COLE's conception of the genera and subgenera of the *Discocyclinidae* (1941), BRÖNNIMANN's subdivision (1945) of these forms into two fundamentally different groups is followed and further developed. The so-called subgenera are all assigned generic rank.

BRÖNNIMANN's groups are recognized as two unrelated families: the *Discocyclinidae* s.s. and the *Orbitoclypeidae*. *Discocyclina* s.s. seems to be restricted to the Eastern Hemisphere; the American forms probably all belong to the *Orbitoclypeidae* and a new generic name, *Neodiscocyclina*, is proposed for them. Another new genus, *Stenocyclina*, is created to separate the group of "*Proporocyclina*" *advena* from *Proporocyclina* s.s.

The family of the *Discocyclinidae* in its restricted sense contains the genera: *Discocyclina*, *Actinocyclina*, *Proporocyclina*, *Athecocyclina* and *Asterophragmina*. That of the *Orbitoclypeidae*: *Orbitoclypeus*, *Neodiscocyclina*, *Stenocyclina*, *Pseudophragmina* and *Asterocyclina*. The genus *Hexagonocyclina* is tentatively placed in the latter group, but its relationship is not yet clear.

In 1940, the Family *Discocyclinidae* was proposed by VAUGHAN and COLE[1]) to include all those forms of Larger Foraminifera with a well defined equatorial layer and lateral tissue in which the equatorial chambers, when properly developed, are rectangular in shape. Each of these chambers is connected by annular and radial stolons with the adjoining chambers in the same and in the adjacent annuli and these stolons were used as a base for the systematics within the family.

The authors recognized two genera: *Discocyclina* and *Pseudophragmina*, each divided into three subgenera. A key to those was given in 1941:

| | |
|---|---|
| Annular stolon proximally situated | genus *Discocyclina* s.l. |
| test circular in plan | |
| without external costae | subgenus *Discocyclina* s.s. |
| with external costae | subgenus *Actinocyclina* |
| test angular in plan | subgenus *Asterocyclina* |
| Annular stolon distally situated | genus *Pseudophragmina* s.l. |
| radial walls complete | subgenus *Proporocyclina* |
| distal part of radial walls degenerate, in places represented by rows of granules | subgenus *Pseudophragmina* s.s. |
| radial walls absent or indistinct | subgenus *Athecocyclina* |

[1]) COLE (1964) recognizes GALLOWAY's priority in naming a "Family *Discocyclinidae*", but there is a wide divergence between the two authors as to the diagnosis of the family and the genera which should be included in it.

Unfortunately, it is only under exceptional conditions of preservation that stolons can be observed and the position of this annular stolon can hardly be of practical use for the determination of the genera. However, as far as the American forms are concerned, there is also a difference in the position and the number of the radial stolons and this finds its expression in a different arrangement of the chambers, which is a much easier criterium:

| | |
|---|---|
| radial walls in subsequent annuli alternating | *Discocyclina* s.l. |
| radial walls in subsequent annuli in alignment | *Pseudophragmina* s.l. |

VAUGHAN (1945, p. 69) has applied this rule of thumb in a worldwide sense, but this leads to difficulties: in *Actinocyclina*[2]) the chambers are as a rule in alignment (BRÖNNIMANN 1945b, 1964) and its place in the genus *Discocyclina* is based exclusively on the proximal position of its annular stolon. Also in America the rule has its exceptions: one or two species of *Discocyclina* s.s. (*D. harrisoni* VAUGHAN, *D.* "*marginata*" [CUSHMAN]) develop aligned radial walls towards the edge.

VAUGHAN and COLE repeat their subdivision in the 4th edition of CUSHMAN's "*Foraminifera*" (1948), adding *Asterophragmina* RAO[3]) as a subgenus of *Pseudophragmina*, and it is also upheld in the Treatise of Invertebrate Paleontology (COLE 1964).

In the meantime, however, many new facts about this interesting group have come to light that make VAUGHAN and COLE's interpretation untenable.

First of all, CAUDRI (1944) came across certain "Discocyclinas" in the Paleocene of Trinidad and Venezuela that do not fit in with any of the above-mentioned genera and subgenera and which were distinguished under the new generic name of *Hexagonocyclina* (= *Bontourina* CAUDRI 1948). They not only have predominantly hexagonal chambers, which in itself would perhaps not be sufficiant reason to separate them from *Discocyclina*, but they are also totally different from any of them in their ontogenetic development: they start out with two symmetric auxiliar chambers on either side of the nucleoconch and four nepionic spirals, a pattern never observed so far in any of the others. VAUGHAN and COLE (in CUSHMAN 1948) ignore this feature and dismiss *Hexagonocyclina* as a synonym of *Discocyclina* s.s., but this is incorrect.

A more serious objection to VAUGHAN and COLE's subdivision has come from the side of BRÖNNIMANN. His study of *Asterocyclina* and *Discocyclina* s.s. from Europe and the Far East (1945a) resulted in the conclusion that these two forms are totally different organisms. *Asterocyclina* is built like the *Orbitoididae:* in its microspheric generation it starts with a simple spiral of tiny subequal chambers and its equatorial chambers are true primary chambers from the beginning (Textfig. 1, 5b, this paper). In *Discocyclina* s.s., on the contrary, the microspheric development resembles that of

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[2]) *Actinocyclina*, which deserves generic rank, has up to now not been found outside Europe and India. Records of its occurrence in the Americas are not confirmed. "*Actinocyclina*" *bainbridgensis* VAUGHAN from Georgia, Alabama and Cuba was re-identified by VAUGHAN himself as *Pseudophragmina bainbridgensis* (1945, p. 68, 85, 86), and the "*Actinocyclina* cf. *asterisca*" of Ecuador (BARKER 1932) is an *Asterocyclina*.

[3]) Subgenerotype: *Pseudophragmina* (*Asterophragmina*) *pagoda* RAO, from the Upper Eocene Yaw shales of Burma. In 1964, COLE again suppresses this form which he considers as a "defective *Asterocyclina*". Actually, it is closely related to *Athecocyclina* (see below).

the *Camerinidae*, in particular that of *Cycloclypeus:* the initial chamber is followed by a planispiral coil of at first sickleshaped and then annular chambers, and the rectangular "equatorial chambers" are formed through radial subdivision of those primary chambers. Morphologically, these "equatorial chambers" are nothing more than secondary chamberlets (compare also GALLOWAY 1933, p. 450) (Textfig. 2–5a, Pl. II).

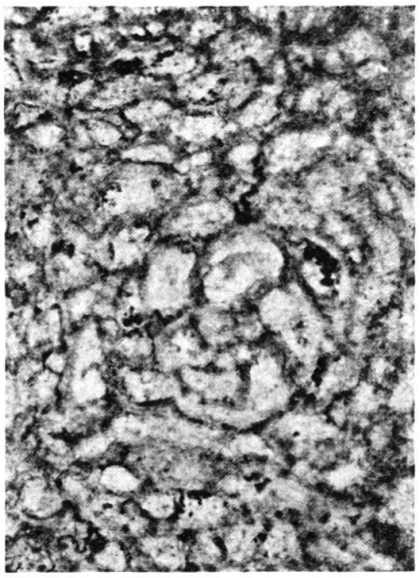

Fig. 1. *Asterocyclina stellaris* (BRUNNER), Ledian, NW Morocco, × 200. After BRÖNNIMANN 1945a, Pl. XXI, Fig. 1.

Fig. 2. *Discocyclina* (*Discocyclina*) *papyracea* (BOUBÉE), Eocene, Kressenberg, Germany, × 160. After BRÖNNIMANN 1945a, Pl. XXI, Fig. 3.

Fig. 3. *Discocyclina* aff. *varians* (KAUFMANN), Upper Eocene, Verona, Italy, × 250. After BRÖNNIMANN 1945a, Textfig. 3.

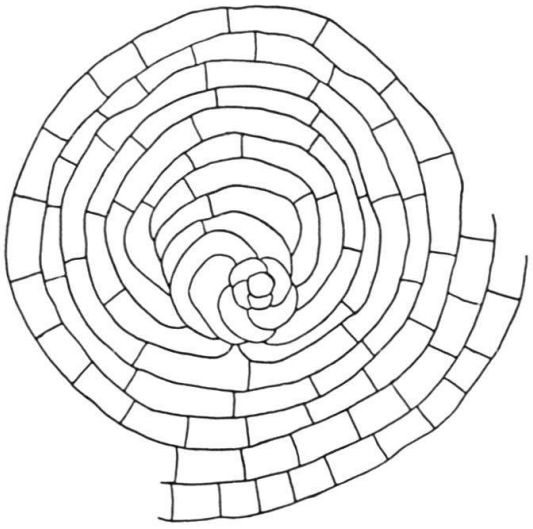

Fig.4. *Discocyclina javana* (VERBEEK), "Eocene", Middle Java, × 270. After TAN SIN HOK 1937, Pl. 1, Fig. 9b.

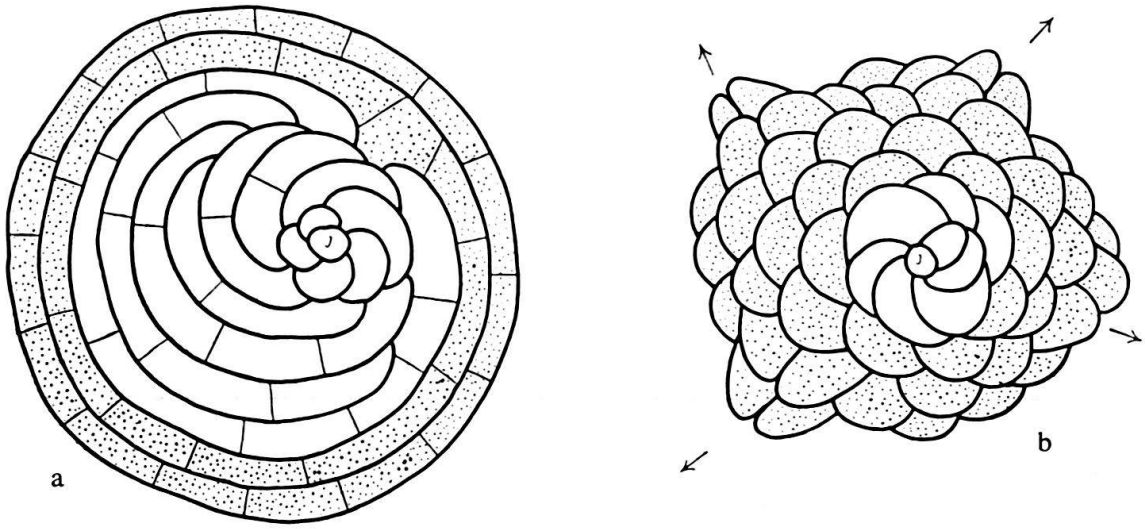


Fig. 5. Schematic comparison of a: *Discocyclina papyracea* (BOUBÉE), and b: *Asterocyclina stellaris* (BRUNNER). White chambers: nepionic stage; grey chambers: beginning of neanic stage. After BRÖNNIMANN 1945a, Textfig. 12.

According to BRÖNNIMANN, the chambers of *Actinocyclina* and *Proporocyclina*, and in principle also the incomplete ones of *Pseudophragmina* s.s. and *Athecocyclina*, develop in the same way as in *Discocyclina*. Interesting is, in this respect, also VAUGHAN's description of *Athecocyclina* (1945, p. 47).

For relatives of *Asterocyclina*, BRÖNNIMANN turns to the genus *Orbitoclypeus* SILVESTRI (= *Exagonocyclina* CHECCHIA-RISPOLI) from the Lower Eocene of Italy and Switzerland, in which the microspheric spiral is also of the simple type and the equatorial layer is formed by primary chambers (Textfig. 6).

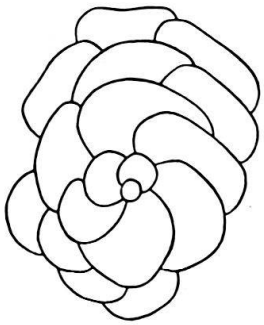

Fig. 6. *Orbitoclypeus himerensis* SILVESTRI, Lower Eocene, Einsiedeln, Switzerland, × 260. After BRÖNNIMANN 1945a, Textfig. 21.

As a result, he divides the family into two different subfamilies:

Family *Discocyclinidae*
Subfamily *Discocyclininae*
Genera: *Discocyclina*
*Actinocyclina*
*Proporocyclina*
*Pseudophragmina*
*Athecocyclina*

Subfamily *Orbitoclypeinae*
Genera: *Orbitoclypeus*
*Asterocyclina*
(note: *Hexagonocyclina* was left out of consideration; at the time of writing his paper, BRÖNNIMANN had not received CAUDRI's publication on the subject.)

In the face of such fundamental differences in the initial development and in the very nature of the equatorial chambers, it is surprising that BRÖNNIMANN left the *Orbitoclypeinae* in the family of the *Discocyclinidae*. Even less understandable is COLE's persistent objection against a subdivision of the family along these lines. In 1964, he counters BRÖNNIMANN's arguments with the observation that, though admittedly some Discocyclinas may have a complicated microspheric nepiont, "the chambers of *Discocyclina* (*Discocyclina*) *anconensis* BARKER are the same as those of typical representatives of the '*Orbitoclypeinae*'" (loc cit., Fig. 586, 1d; this paper: Textfig. 7) and that, therefore, it is impossible to carry through a subdivision on this point.

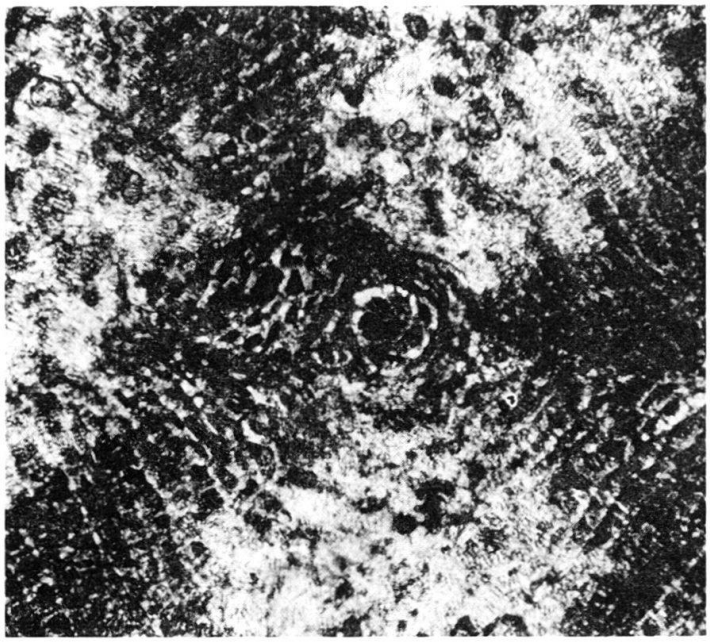

Fig. 7. *Neodiscocyclina anconensis* (BARKER), Middle Eocene, S. 43, Spa, Lower Chalky Mount beds, Barbados, West-Indies, × 100. After VAUGHAN 1945, Pl. 8, Fig. 3.

Actually, the conclusion should be the other way round: that *Discocyclina anconensis* is not a true *Discocyclina* s.s., but a member of the *Orbitoclypeinae*. It is also clear that BRÖNNIMANN's "*Discocyclininae*" and "*Orbitoclypeinae*" are genetically such totally unrelated groups that they can not be united into one natural family. They should be distinguished as the "Family *Discocyclinidae*" and the "Family *Orbitoclypeidae*", and they can only be lumped together for routine purposes as the systematically worthless group of the "Discocycliniformes".

What goes for *Discocyclina anconensis* may well be applicable to the American forms of "*Discocyclina* s.s." in general. The microspheric generation of all the species

I have thus far had the opportunity to study in the extensive material from Trinidad and Barbados (*D. anconensis* BARKER, *D. bullbrooki* VAUGHAN and COLE, *D. grimsdalei* VAUGHAN and COLE, *D. aguerreverei* CAUDRI, *D. fonslacertensis* VAUGHAN, *D. barkeri* VAUGHAN and COLE) start out with a simple rotalid spiral and their equatorial chambers are true primary chambers. At present, we have to place them in the *Orbitoclypeidae*[4]), very close to the genus *Orbitoclypeus* itself (Pl. I, Fig. 1, 2).

There are reasons why, at this stage, they should not be identified with *Orbitoclypeus*. It is true that some of the species (*D. grimsdalei*, *D. anconensis*) resemble *Orbitoclypeus* also in the megalospheric nucleoconch, which in horizontal section appears as a "loose" protoconch entirely surrounded by a much larger circular second chamber (considered by BRÖNNIMANN as more or less diagnostic of *Orbitoclypeus*), but others have a reniform deuteroconch (*D. barkeri*, *D. aguerreverei*, *D. fonslacertensis*, *D. bullbrooki*). Another characteristic of *Orbitoclypeus:* the hexagonal equatorial chambers, shows up occasionally in these American species, especially in *D. barkeri*, but it certainly is not a general feature in any of them. In most cases the circular walls of the annuli tend to be heavier than the radial walls, resulting in a strictly rectangular shape of the chambers. To avoid unwarranted lumping and confusion, it seems better to keep them apart from the Mediterranean form *Orbitoclypeus* under the new generic name of *Neodiscocyclina*. This genus is defined as follows:

*Neodiscocyclina* nov. gen.

Test flat- or inflated-lenticular, clearly differentiated into an equatorial layer and lateral tissue.

Megalospheric nucleoconch two-chambered; deuteroconch either reniform, or circular and enclosing an (in horizontal section) "loose" protoconch.

Microspheric form starting with a simple, rotalid spiral.

Neanic equatorial chambers rectangular, in thinwalled areas tending towards a hexagonal shape.

Generotype: *Discocyclina anconensis* BARKER, as presented by VAUGHAN in 1945 (Pl. 8, Fig. 1, 2 and 3)

Material used for this discussion: Spa, Scotland District (Parish of St. Joseph), Barbados, West-Indies; level: lower Chalky Mount Member of the Upper Scotland Formation, Middle Eocene

The phylogenetic relationship of *Asterocyclina* (generally accepted by now as a genus in its own rights) to either *Orbitoclypeus* or *Neodiscocyclina* is still vague. There are indications that, in the Americas, *Asterocyclina* has more or less directly developed from *Neodiscocyclina barkeri*, but this should not be rashly applied to the *Asterocyclinas* from other parts of the world (see footnote 4). There remains a possibility

[4]) We have no pertinent data on the initial coil of *Orbitoclypeus*, but chances are that it is planispiral (see BRÖNNIMANN 1938, p. 603, and 1945, p. 608). If this should be the case, it may be a reason to deny the American "Discocyclinas" a place in the true *Orbitoclypeidae*.

The same may apply to *Asterocyclina*. It has been stated for the microspheric *Asterocyclina* of Morocco that their nepiont is planispiral (BRÖNNIMANN 1938, p. 303 and 306), whereas my own observation on specimens of the Trinidadian species *Asterocyclina asterisca* (GUPPY) suggests a rotalid pattern, the same as in those "Discocyclinas".

that stellate forms were produced along parallel lines from the *Orbitoclypeidae* in the Eastern and the Western Hemispheres.

My observations on the microspheric nepiont of *Proporocyclina* (*P. tobleri* VAUGHAN and COLE, *P. flintensis* [CUSHMAN]) and *Athecocyclina* (*A. soldadensis* VAUGHAN and COLE, *A. soldadensis* var. *calebardensis* VAUGHAN) confirm BRÖNNIMANN's suggestion that these two genera belong to the *Discocyclinidae*. Plate I, Figure 4 of the present paper shows the B-form of *Proporocyclina flintensis* and good illustrations of *P. tobleri* were given by VAUGHAN and COLE (1941, Pl. 22, Fig. 4) and by COLE (1959, Pl. 32, Fig. 11–12). VAUGHAN (1945, p. 46, Pl. 18) describes the initial stage of *Athecocyclina* as "flabelliform". Also RAO's *Asterophragmina* finds its place in this group.

Data on the other species of "*Pseudophragmina*" s.l. are scanty and generalization is risky. But at least one of them: *Pseudophragmina* s.s. *bainbridgensis* VAUGHAN, appears to have a simple spiral (Pl. I, Fig. 3, this paper) and HOFKER (1932) describes the microspheric nepiont of "*Orthophragmina*" *advena* CUSHMAN as a planorbuline spiral. This latter form, and the whole group of similar organisms of which it is the type species, has been placed by VAUGHAN (1945) in the subgenus *Proporocyclina* and by BUTTERLIN (1967) in *Pseudophragmina* s.s. The present writer, however, feels that, both for morphological and phylogenetic reasons, they should be distinguished as a separate genus, for which she proposes the name of *Stenocyclina*.

The diagnosis of *Stenocyclina*, based on published data and on new observations on *S. cloptoni* (VAUGHAN) from California (Las Llajas Formation; see VAUGHAN 1945, p. 99) runs as follows:

*Stenocyclina*, nov. gen.

Test circular, flat, with or without a central knob which sometimes shows a depression in the center. Surface smooth or evenly covered with tiny granulations.

Chambers clearly differentiated in an equatorial layer and lateral tissue.

Megalospheric nucleoconch consisting of two chambers; deuteroconch either circular in horizontal section, entirely surrounding but touching the protoconch, or reniform and only partially embracing this first chamber (twin or multichambred nucleoconchs rather frequent in *S. cloptoni*).

Microspheric form starting with a simple planorbuline spiral.

Neanic equatorial chambers very small, squarish, arranged in numerous very narrow annuli (hence the name). Radial walls generally in alignment in subsequent rings, often complete but mostly disintegrated into granules (which phenomenon may be chiefly due to secondary alterations during fossilization!). At least in *S. cloptoni*, annular stolons seem to be present both at the proximal and the distal end of the chambers, and radial stolons form an uninterrupted system across all the annuli.

Equatorial layer in vertical section very thin, only slightly increasing in height towards the edge. Numerous layers of very low lateral chambers.

Generotype: *Orthophragmina advena* CUSHMAN

Type locality of type species: Cane River, Natchitoches, Louisiana

Type level of type species: Cane River Formation, Claiborne Group, Middle Eocene

*Stenocyclina* is very closely related to the late Eocene genus *Pseudophragmina* s. s.; it may even be nothing but a subgenus of it. But the latter is characterized by very broad annuli of extremely elongated narrow chambers and thus presents a totally different overall picture. It is improbable that *Pseudophragmina* has developed from *Stenocyclina* as the end-product of a phylogenetic line, as (unlike *Proporocyclina*) *Stenocyclina* does not show a tendency to grow more elongated chambers with advancing geological time: *S. perkinsi* (VAUGHAN), also from the Upper Eocene, has the narrowest rings of them all.

It should be pointed out that the planorbuline nepiont of the B-form in Stenocyclina has so far only been observed in *S. advena* itself. Of the 45 topotype specimens studied by HOFKER, four proved to be microspheric. I have not been that lucky with my material of *S. cloptoni:* over sixty specimens have been sectioned and all have turned out to be megalospheric. But it is unlikely that within this group, which in other respects shows so little variation, there should be more than one type of microspheric nepiont. Without much hesitation, *Stenocyclina* (as well as *Pseudophragmina* s. s.) is, therefore, assigned to the *Orbitoclypeidae*.

The systematical place of *Hexagonocyclina* remains obscure. Its quadriserial nepiont resembles that of certain "*Orbitoididae*", but it does not fit into any of the phylogenetic lines within that heterogeneous group and its delicate texture corresponds more with the *Discocycliniformes*, especially (because of its hexagonal chambers) with *Orbitoclypeus*. In a sense, it might be looked upon as an "ancestral" form of *Neodiscocyclina*, in the same way in which an advanced *Polylepidina* is related to the *Nephrolepidinas* and *Eulepidinas* in the *Lepidocyclinidae*. But so far we have no data on the microspheric development of *Hexagonocyclina* and it is only tentatively included in the *Orbitoclypeidae*.

The question whether or not the *Orbitoclypeidae* should be further subdivided on the exact growth plan of their microspheric spiral (rotalid or planispiral; see footnote 4) needs further study. At the moment, the following relationships within the *Discocycliniformes* are suggested:

Group "*Discocycliniformes*" (of no systematical value)

Family *Discocyclinidae*

genera: *Discocyclina* s. s.
*Actinocyclina*
*Proporocyclina*
*Athecocyclina*
*Asterophragmina*

Family *Orbitoclypeidae*

genera: *Orbitoclypeus*
*Neodiscocyclina*
*Stenocyclina*
*Pseudophragmina* s. s.
*Asterocyclina*
? *Hexagonocyclina*

Further consolidation of this scheme is expected from continued study of the microspheric form of all the "Discocycliniformes" the world over.

If, for the sake of simplicity or from conventionalism, we go on using in literature the general name of "*Discocyclina*" for the American forms, it must be done with the understanding that they (and also the Asterocyclinas) probably all belong to phylogenetic lines that are different from the Old World, lines with their own rate of evolutionary acceleration and their own stratigraphic limits, and that no long-ranged correlations should be attempted on the occurrence of these forms in the Eastern Hemisphere and in the Americas.

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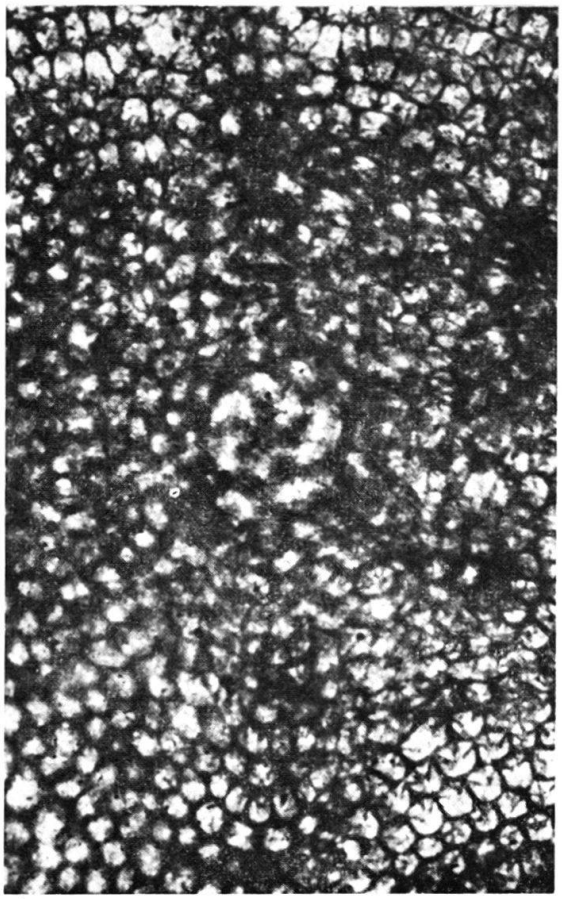
## Plate I

Fig. 1 — *Neodiscocyclina bullbrooki* (VAUGHAN and COLE), Eocene (reworked from the upper Lower or the basal Middle Eocene), K 3878, Soldado Rock off Trinidad, West Indies, × 120.

Fig. 2 — *Neodiscocyclina barkeri* (VAUGHAN and COLE), Paleocene, K 2951, Soldado Rock off Trinidad, West Indies, × 120.

Fig. 3 — *Pseudophragmina bainbridgensis* VAUGHAN, Upper Eocene, St. 46, Point Bontour, Trinidad, West Indies, × 80.

Fig. 4 — *Proporocyclina flintensis* (CUSHMAN), Upper Eocene, K 3677, Soldado Rock off Trinidad, West Indies, × 80.



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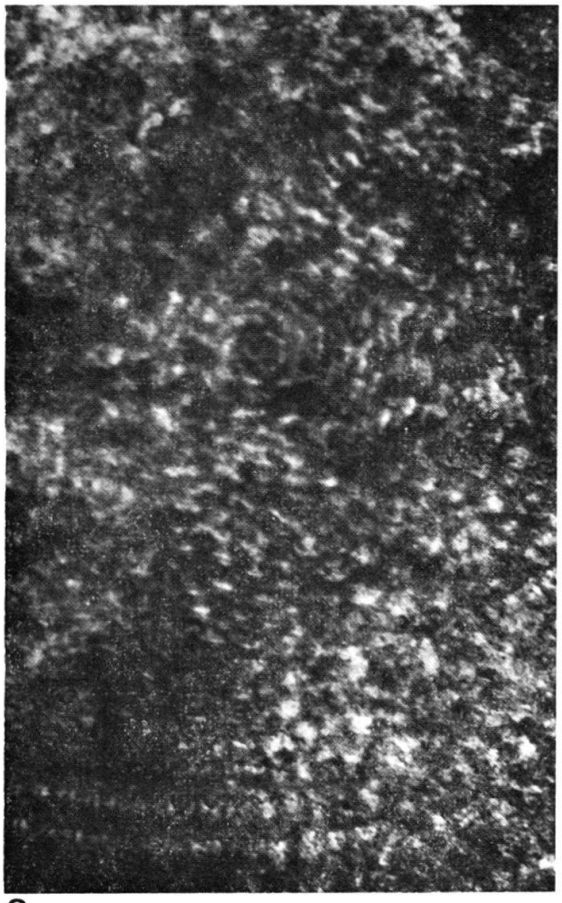

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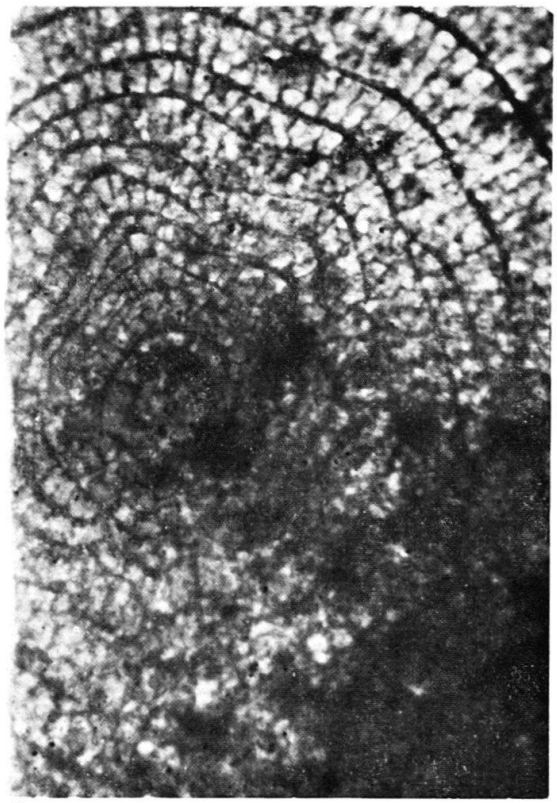

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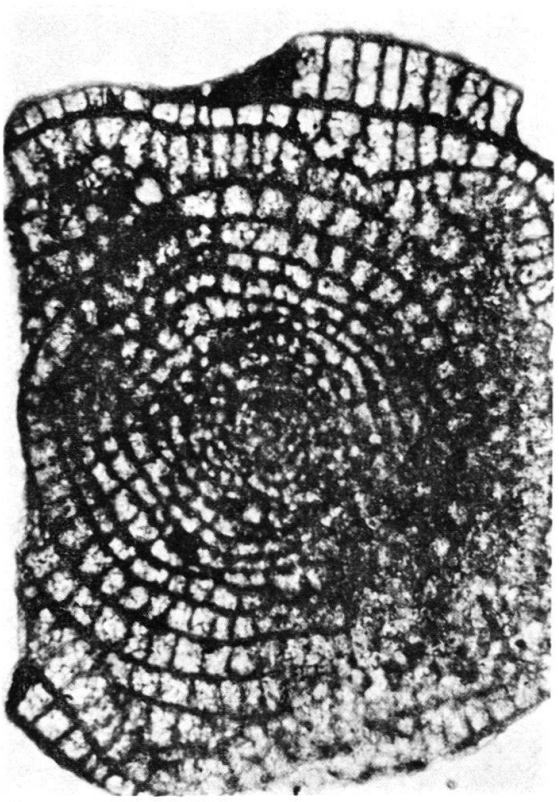

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## Plate II

*Discocyclina archiaci* SCHLUMBERGER, microspheric generation. Shell split along equatorial plane.

Material from Tuilerie de Gan, near Pau, Southern France. Lower Eocene.

Stereoscan photographs. Tilting angle 13°, 10 KV

Fig. 1 Equatorial plane showing first spiral growth stages presenting secondary subdivisions of chambers and first annular chambers. × 250

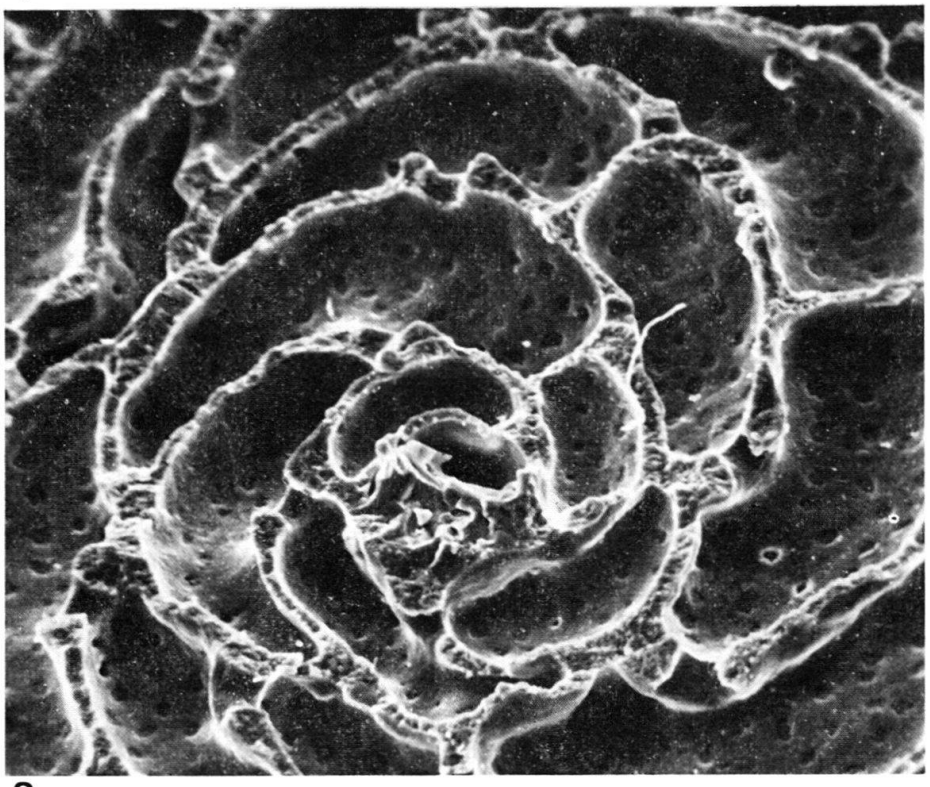
Fig. 2 Detail of fig. 1, × 1000. The proloculus is not entirely open as the fracture does not follow exactly the equatorial plane. The first five main chambers have one aperture at the base of the apertural face. The sixth chamber shows two apertures and is followed by a seventh chamber divided correspondingly by a secondary septum.

C: chamber of median layer (main chamber).

S: main septum of chamber, SS: secondary septum, dividing chamber into chamberlets.

Photographs and explanation provided by L. HOTTINGER, Basel.

1

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