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AN ANALYSIS OF CERTAIN TAXONOMIC PROBLEMS IN THE LARGER FORAMINIFERA

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ABSTRACT

Although the major thesis of this discourse is variation in species of larger Foraminifera, two separate, but interrelated problems are discussed. Certain definitions which have been published for genera of camerinids with undivided median chambers are analyzed. The conclusion is that these definitions are not valid because the types of these genera are species whose structures are the same as species upon which other generic names have been based. Variation in *Lepidocyclina* (*Lepidocyclina*) *canellei* Lemoine and R. Douvillé is shown, and four formerly recognized species are considered to be variants of this species. Certain inferences are drawn concerning the possible influence of environment on the variation in the structure of the test of *L.* (*L.*) *canellei.* Illustrations are given of most of the species which are discussed.

INTRODUCTION

In an earlier study (Cole, 1957*a*) *Lepidocyclina* (*Lepidocyclina*) *supera* (Conrad) 1865 was demonstrated to be a synonym of *L.* (*L.*) *mantelli* (Morton), 1833, and *L.* (*L.*) *parvula* Cushman, 1919 was placed in the synonomy of *L.* (*L.*) *giraudi* R. Douvillé, 1907. Although *L.* (*L.*) *mantelli* is considered to be a valid species, proof will be given that *L.* (*L.*) *giraudi* is a synonym of *L.* (*L.*) *canellei* Lemoine and R. Douvillé, 1904.

The conclusion reached is more sweeping than indicated above as several species which have become entrenched in the literature are assigned also to the synonomy of *L.* (*L.*) *canellei.* They are *L.* (*L.*) *asterodisca* Nuttall, *L.* (*L.*) *miraflorensis* Vaughan, and *L.* (*L.*) *waylandvaughani* Cole. These species are invalidated with considerable regret as they have been cited in many publications and certain of these species have been assigned either restricted geographic or stratigraphic ranges.

In the interval since Vaughan (1933, p. 6) wrote "The amount of variation in many species of orbitoids is bewildering," evidence has accumulated to prove the correctness of his observation. Species of larger Foraminifera are variable! Specific names have been given to supposedly recognizable species, but new data have shown that these names have been based upon the variable form and structure of a limited number of specimens rather than upon a complete analysis of the available specimens which should be included in the species.

As many specific names designate a "form" group within a variable species, they do not express a natural relationship. It is entirely possible to

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identify these "form" groups of individuals to which specific names are given. However, the problem arises that another group of specimens may have characteristics which are intermediate between two species. The tendency is to assign another specific name to such specimens, and, finally the literature contains so many specific names that one becomes bewildered.

The difficulties inherent in any classification in which variability in the species is not recognized is compounded by the use of a "form" species as the type of a genus. Several generic names may be given, each of which is supposed to distinguish at the generic level either one species or a group of species from all other species. Yet, these supposedly distinct genera are based upon ecologically or otherwise controlled "form" species which in reality represent only one kind of a variable species. The proliferation of generic names which have been applied to the camerinids with undivided median chambers is an example of the lack of recognition of the variability which occurs in the species of *Camerina*. Although the synonyms of *Camerina* have been discussed (Cole, 1960), additional evidence for the suppression of the superfluous generic names will be given in another section of this discourse.

In the preliminary study of the larger Foraminifera entirely too much emphasis has been placed upon the concepts that the species are limited in time and space by rapid evolution and that a species can be distingushed by relative comparisons with other species.

Lepidocyclina mantelli and *L. supera* were maintained as distinct species because *L. mantelli* was assumed to be restricted to the Marianna limestone, whereas *L. supera* was supposed to be a marker for the Byram marl and related formations. Cole (1957*a*, p. 38) demonstrated that *L. supera* was a synonym of *L. mantelli*. Previous to this he (1953*b*, p. 6) wrote "If these localities represent the lower Oligocene, as it is known in Florida, such species as *Lepidocyclina mantelli* and *Operculinoides dius* might be expected to occur instead of Eocene species." Later, he (1957*a*, p. 34) could state "the *L.* (*L.*) *mantelli* and the *L.* (*Eulepidina*) zones should be combined."

Although the zonation of the American Oligocene proposed by Gravell and Hanna (1938, p. 987) was modified by the recognition that the stratigraphic range of *L.* (*L.*) *mantelli* was more extensive than had been assumed, the appreciation of variability in a species warns of the possible errors which may occur in developing zonation which is based upon "form" species.

Until this study was undertaken, *L.* (*L.*) *miraflorensis* has been cited as a species restricted to the La Boca marine member of the Panama formation (lower Miocene). If the concept developed in this discourse that *L.* (*L.*) *miraflorensis* is one of the synonyms of *L.* (*L.*) *canellei* is accepted, the supposed unique stratigraphic position of this species as the only American species of *Lepidocyclina* restricted to the lower Miocene will be destroyed.

This is regrettable! However, in the end the problem of stratigraphic correlation may be assisted as other evidence will be sought and a zonation based on the supposed restricted occurrence of *L.* (*L.*) *miraflorensis* will not become entrenched in the literature. Moreover, some of the difficulties in the identification of the species will be eliminated.

Under the influence of superficial appearance species have been defined, and, thereby, supposedly separated from other species by such statements as "Lateral chambers short . . . *L. canellei*"—"Lateral chambers long . . . *L. miraflorensis*" (Cole, 1957*a*, p. 33). On the other hand a plea of convenience is often made in statements such as the following: "These species certainly cannot be separated generically since their specific independence is in question, but one resembles *Operculina* while the other resembles *Assilina*. The latter name is nowadays reserved for Paleocene and Eocene species which form a distinct lineage, so it is convenient to assign both Recent species to *Operculina*" (Smout and Eames, 1960,p.111).

Such statements as those quoted which were selected for illustrative purpose from a multitude of similar expressions must be baffling indeed to anyone attempting taxonomic and stratigraphic research. Are not those of us who are engaged in this kind of research defeating our purpose when we attempt to separate species on preconceived ideas of how much individuals within a species vary, or by a defense of some long established generic or specific name?

Although it has been logical to define species and genera in relative terms when our data were limited, this condition no longer exists with the progress that has been made in the study of larger Foraminifera.

There will be some who object in a serious and conscientious manner that the thesis of this discourse is incorrect, and that the combinations of species proposed is absurd. To some the stellate pattern of *L.* (*L.*) *asterodisca* far overbalances the internal structure of these specimens. Therefore, they will maintain *L.* (*L.*) *asterodisca,* as I have done in the past, is a separate species characterized by its stellate outline.

Others, however, will agree that the internal structure of *L.* (*L.*) *asterodisca* and *L.* (*L.*) *waylandvaughani* is so similar that these two species should be united, the more so because some topotypes of *L.* (*L.*) *waylandvaughani* have an irregular outline (see: Cole, 1928, fig. 1, pl. 35) although these irregular specimens occur infrequently in collections from the vicinity of Tampico.

But, these same persons who accept the identity of *L.* (*L.*) *asterodisca* and *L.* (*L.*) *waylandvaughani* will object to combining these names under *L.* (*L.*) *canellei*. The superficial appearences of the vertical sections of *L.* (*L.*) *waylandvaughani* are indeed different from those of *L.* (*L.*) *canellei* on first inspection. But, detailed study of the illustrations given here and elsewhere should demonstrate that the fundamental internal structures are the same. One is influenced at first by the thinner floors and roofs of the lateral chambers in the so-called typical specimens of *L.* (*L.*) *canellei*. However, as the specimens are studied in detail these thinner floors and roofs become insignificant and the overall structural similarity becomes apparent.

It is more impressive to have a long list of species from a given locality than to have one with few species. There is no objection to this except one begins to believe that identifications can be made with certainty and, therefore, assigns certain species, at least, to restricted geographic or stratigraphic positions. Such may be the case with regard to some species and some genera. It is not implied here that the time tested and well-known species and genera are not restricted geographically and stratigraphically.

But, until species and genera are evaluated rather completely, caution must be used. Above all the natural relationships should be established by a consideration to the limit of our data regarding variability which may occur in individuals because of environmental conditions or because of genetically controlled plasticity.

The specimens used in this study are deposited in the Cole collection at Cornell University and eventually will be transferred to the U. S. National Museum.

LOCALITIES

Cuba

Loc. 1—Northwest of Cienfuegos, one kilometer on Palmira road at Pueblo Grifo, Santa Clara Province (Palmer sta. 336-see: Palmer,

1948, p. 299) ; gift of the late Mrs. D. K. Palmer.

St. Lucia, Windward Islands, West Indies

2—La Titance, Lavoutte (sta. 6138) ; P. H. Martin-Kaye, collector.

Mexico (Tampico Embayment area)

3—Five miles west of La Laja on the road to Ozulama at Bajada de Chichimeca, State of Vera Cruz (Huasteca Petroleum Company no. J 24-1462) ; W. S. Cole, collector.

4—Between kilometer posts 17-18 on the Aguila Petroleum Company's narrow-gauge railroad between Potrero and Tanhuijo, State of Vera Cruz (sta. S. C. M-S 1) ; W. S. Cole, collector (reference: Cole and Gillespie, 1930).

5—Quarry on the Huasteca Petroleum Company's golf course opposite Tampico, State of Tamaulipas; bed of sandy clay overlying massive sandstone (sta. SC 3ABA) ; W. S. Cole, collector (reference: Cole, 1928, p. 221-223, pl. 4).

6—Cut on the Panuco River side of a street below the Palacio Peñal in Tampico (sta. SC 1000) ; W. S. Cole, collector.

7—About 700 feet from the station Andonegui on the electric trolley line between Tampico and Miramar (sta. SC 111) ; W. S. Cole, collector.

8—Arbol Grande near Tampico (sta. SC 1C) ; W. S. Cole, collector (reference: Vaughan, 1933, p. 15, 25, 26).

Panama Canal Zone

9—Low garden islet 0.25 miles northeast of landing at Barro Colorado Island; soft sandy calcareous siltstone (sta. 53) ; S. M. Jones and W. P. Woodring, 1947, collectors (reference: Cole, 1953*b*, p. 6).

CONFUSION IN DEFINING A GENUS

In a review of certain genera of the camerinids Cole (1960, p. 190) wrote" . . . there are only two valid genera of all those that have been proposed for camerinids with undivided chambers. They are *Camerina* and *Miscellanea*." He (Cole, 1960, p. 196) emphasized that ". . . There are no structural differences which may be used to distinguish between *Camerina, Planocamerinoides* (=*Assilina* of authors), *Operculina, Operculinoides, Ranikothalia* and *Paraspiroclypeus*. These genera have been defined in terms of intergradational features which are specific rather than generic differences."

In 1953 Eames (p. 390) had defined *Operculinella* Yabe (1918, p. 126) as follows: " . . . miniature *Nummulites*-like forms of small size, with a very small megalospheric nucleoconch, with little difference in size between the two generations, with or without a tendency to flare in old age." Later, Eames *et al* (1960, p. 448) wrote "*Palaeonummulites* Schubert 1908 (type species *Nummulina pristina* Brady 1874) is regarded as a prior synonym of both *Operculinella* Yabe 1918 and *Operculinoides* Hanzawa 1935." Finally, Smout and Eames (1960, p. 112) stated: ". . . The genus represented by *Operculinella* is, however, an important one."

If the genus *Palaeonummulites* (=*Operculinella* and *Operculinoides*) is to be maintained to include certain species of camerinids with undivided chambers, the species included in this genus should conform to the definition of the genus, and it should be possible to separate this group of species from other groups of species.

The critical criteria given in the definition of *Operculinella* cited are: 1. Miniature *Nummulites*-like forms; 2. The small size of the embryonic chambers; 3. The size relationship between the megalospheric and microspheric generations; and 4. The tendency to develop a flange in the terminal whorl.

These criteria to be valid must stand against data from different species. Four species are chosen for the analysis although others could be added or substituted for those selected. The type species of *Operculinella* is "*Nummulites*" *cumingii* (Carpenter) [=*Camerina venosa* (Fichtel and Moll)]. *Operculinoides* was based on "*Nummulites*" *willcoxi* Heilprin. Therefore, these two species were selected.

The American species "*Operculinella*" *cojimarensis* D. K. Palmer (1934, p. 259) from the Cuban Miocene is one of the species which most nearly resembles the type of *Operculinella,* therefore it was chosen. Finally, *Camerina pengaronensis* (Verbeek) from the Eocene of the Indo-Pacific region was selected as this species has been assigned traditionally to *Nummulites* (=*Camerina*).

The comparison can be made best in tabular form (Table 1) in which the critical statements in the definition of *Palaeonummulites* (=*Operculinella*) are contrasted with data from the selected species. As all the species are "minute *Nummulites*-like forms" this statement is not used in the table.

The species *cojimarensis* does not conform to the definition given of *Palaeonummulites* because the microspheric specimens are at least twice the

Table 1.—Comparison of selected species of camerinids

Statements in definition	Species formerly assigned to:			
	Operculinella		*Operculinoides*	*Camerina*
	venosa[1]	*cojimarensis*[2]	*willcoxi*[3]	*pengaronensis*[4]
Diameter (megalospheric specimens) mm	2.0-4.4	2.7-5.5	2.6-3.9	3.0-4.0
Internal distance across both megalosperic embryonic chambers ... μ	90-130	220	140-270	230-320
Diameter (microspheric specimens) ... mm	3.0	9-12	5.1-6.0	6.0-9.0
Terminal whorl	With or without flange	With or without flange	Without flange	Without flange

[1] After Cole, 1959, p. 362.

[2] After D. K. Palmer, 1934, p. 259; specimens illustrated on Plate 28.

[3] After Cole, 1953*c*; 1958*b*, p. 274.

[4] After Cole, 1957*b*, p. 753; Doornink, 1932, p. 283.

size of megalospheric specimens, yet in other respects it is similar to the type species of *Operculinella*. However, some megalospheric specimens do have a diameter greater than any specimens of *"Operculinella" venosa* which I have examined. Therefore, this species may be so large that it can not be considered "miniature."

"Operculinoides" willcoxi, the type species of *Operculinoides* which is stated to be a synonym of *Palaeonummulites,* more nearly resembles *Camerina pengaronensis* than it does *"Operculinella" venosa* or *"O." cojimarensis.*

This brief analysis is indicative of the problems which arise in attempting to group the species of camerinids into genera when the definition of the genus is stated in relative terms. It should be reemphasized that "These genera have been defined in terms of intergradational features which are specific rather than generic differences" (Cole, 1960, p. 196).

From the data available it seems impossible to develop definitions based upon distinctive structures of the test which would serve to separate these four species into readily recognizable genera. Therefore, it would seem reasonable to include them in one genus, a grouping which would emphasize the relationship of the species to each other and which would separate this group of species from all other groups of species whose tests had different structures.

Drooger (1960, p. 312) in reinstating the genus *Ranikothalia* Caudri, 1944, attempted to demonstrate that the test of species which he assigned to this genus did have structures which were different, if only in degree, than those of other species of camerinids. Although this approach is the sound one, it may lead to serious error unless it can be demonstrated that the structures differ sufficiently to be distinctive.

Cole (1953*c*, p. 32; 1960, p. 192) demonstrated that the structure of the test of species assigned to the genus *Ranikothalia* was similar to that of species referred to *Camerina*. Therefore, he placed *Ranikothalia* among other generic names in the synonomy of *Camerina*. Drooger (1960, p. 312) in reinstating *Ranikothalia* wrote (p. 314): "Cole (1953, p. 10) is perfectly right in stating that the difference between *Ranikothalia* and other nummulitic genera is one of degree."

Drooger (1960, p. 314) advanced the argument that ". . . the presence of the coarse canal system, completely open to the exterior both of the marginal cord and through the double row of coarse pores along the sutures . . ." as well as the stratigraphic distribution of the species assigned

to *Ranikothalia* were additional reasons for recognizing this genus.

As Drooger (1960, p. 314) pointed out ". . . such sutural openings, though of much thinner structure, were described and figured already by Carpenter (1862, p. 259, pl. 17) for recent *Operculina* specimens." Barker (1939, p. 309) obtained ". . . Canada-balsam preparations of *Camerina variolaria* (Lamarck) that show excellently developed vertical canals in the bosses of clear shell material in the umbonal area . . ."

Cole (1953*c*, fig. 10, pl. 2) has shown that the marginal cord of *Camerina variolaria* (Lamarck) is as coarse and as completely open to the surface as that of *Camerina planulata* (Lamarck) (Cole, 1960, fig. 4, pl. 23), a species which he (1960, p. 195) decided was the same as "*Nummulites*" *nuttalli* Davies. He placed "*Nummulites*" *nuttalli* in the synonomy of *C. planulata.*

In Europe *C. planulata* occurs in the lower Eocene, whereas *C. variolaria* is found in the upper Eocene. As the structure of *C. variolaria* is so similar to that of *C. planulata,* it would seem reasonable, if the genus *Ranikothalia* is to be maintained, to assign both of these species to that genus.

Another of the arguments for retaining the generic name *Ranikothalia* given by Drooger (1960, p. 314) was ". . .the species are restricted in time (Paleocene—? Early Eocene) and space (southern Asia, Togoland, Caribbean)".

However, it would appear that *C. variolaria* belongs to the same group of species as does *C. planulata.* If this is accepted, the range of this group of species would be Paleocene to upper Eocene at the minimum, thus the argument that *Ranikothalia* is confined to the lowermost Tertiary would be invalidated.

If criteria, such as the size of the embryonic chambers, the number of nepionic chambers, the total size of the test, the size relationships of the megalospheric and micospheric specimens and similar relationships were to be applied to the species of the genus *Cycloclypeus,* this genus would have to be split into several genera. In so doing a subjectively derived, artificial set of generic names would result which would destroy the unity given by one generic name. Moreover, many species would have to be assigned arbitrarily to one or the other of the genera defined in such artificial and relative terms.

Two subgenera of the genus *Cycloclypeus* have been proposed, but these subgenera have been defined as possessing different structures than

those of *Cycloclypeus* (*Cycloclypeus*). *Radiocycloclypeus* was based upon stellate specimens and *Katacycloclypeus* was defined as possessing concentric, annular, thickened rings upon the surface of the test.

It may be questioned, however, whether these structures are of sufficient magnitude to warrant subgeneric rank as the internal structure of these specimens is identicial to that of specimens assigned to the subgenus *Cycloclypeus*. These superficial modifications could be considered to be specific characteristics rather than subgeneric ones.

Tan (1932, p. 71) in discussing *Cycloclypeus* (*Cycloclypeus*) *indopacificus* stated "These annuli appear to be either rows of large pillars (Pl. XX, fig. 6) or irregular folds (vide Douvillé's fig. 6 on Pl. V) which never attain the same regularity and continuity as with *Katacycl. annulatus*."

In studies (unpublished) which I have made of *Cycloclypeus* collected on Guam, I had difficulty in attempting to separate certain specimens on the presence or absence of the annular folds into subgenera and had to rely on thin sections by which *Cycloclypeus annulatus* could be recognized readily and distinguished from other species. As *Cycloclypeus annulatus* is a typical representative of the subgenus *Katacycloclypeus*, the presence or absence of the annular folds should be so constant that specimens could be identified subgenerically without the difficulties encountered.

Cole (1960, p. 198) suggested that in genera, such as *Camerina* and *Cycloclypeus*, the phylogenetic relationships are best expressed by indicating lineages within the genera rather than attempting to use either subgeneric or different generic names for species which differ in degree, but not in fundamental structure, from other species. If this suggestion is followed, a natural, but flexible, classification results, and the confusion entailed by arbitrarily assigning species to genera which have been defined in relative terms is eliminated.

Stratigraphic correlation based upon species is not only more accurate but also less liable to error than that based upon generic ranges. Although it is accepted that genera have longer stratigraphic ranges than do species, it is not appreciated by many stratigraphers that certain of the so-called index genera are recognized by subjectively determined definitions. Therefore, a certain supposedly stratigraphically restricted genus may have a longer range in geologic time than implied because species which should be included in this genus are assigned to another genus.

It is easier to recognize species such as *Camerina catenula* (Cushman and Jarvis) (Cole, 1958*b*, p. 270) than to decide to which genus this

species should be referred if multiple generic names for camerinids with undivided median chambers are maintained. This species has been assigned by competent authorities to *Miscellanea, Operculinoides, Pellatispirella,* and *Camerina.* It is remarkable that specimens of this species of the kind illustrated by Cole and Herrick (1953, figs. 6, 15, 16, pl. 4 among others) have not been assigned by someone to *Operculina.* If this had happened, *C. catenula* would have been assigned at one time or another to three genera which are synonyms of *Camerina* as well as to two genera which are not synonyms of *Camerina.*

VARIATION IN A SPECIES OF CAMERINA

Although variation in species of *Camerina* has been discussed recently by Cole (1961: see also papers listed in this reference on p. 123, 124) additional illustrations are given of *Camerina dia* (Cole and Ponton) on Plate 29 as individuals of this species vary greatly especially as viewed in transverse section.

The specimen illustrated by figure 4, Plate 29 is compressed, whereas the specimen illustrated by figure 5, Plate 29 is inflated. If only these two specimens were available, it is easy to understand how they could be assumed to represent two distinct species. However, the specimen illustrated by figure 2, Plate 29, is intermediate between the other two specimens.

If time had been available, it would have been possible to prepare a series of illustrations which would form a completely integrated series. However, the evidence as presented here and elsewhere seems to substantiate the synonomy given for this species (Cole, 1958*b*, p. 270).

VARIATION IN *LEPIDOCYCLINA CANELLEI* LEMOINE AND R. DOUVILLÉ

THE SPECIFIC NAMES

Lepidocyclina (*Lepidocyclina*) *canellei* Lemoine and R. Douvillé (1904, p. 20) was described from specimens collected at Peña Blanca, Panama Canal Zone. This locality on the Rió Chagres was submerged by Gatun Lake, but abundant specimens of this species can be obtained from many localities in this area which are above the level of the lake (Woodring, 1958, p. 24). The type locality of this species is assigned by Woodring (1957, p. 29, 117) to the middle member of the Caimito formation of Oligocene age. Recently, Cole (1953*b*, p. 18) redescribed and illustrated this species.

L. (*L.*) *canellei* has been reported elsewhere from Venezuela (Gravell, 1933, p. 24), Jamaica (Vaughan, 1928, p. 290; Cole, 1956, p. 213) and Trinidad (Vaughan and Cole, 1941, p. 70). Vaughan (1933, p. 15) reported a "dwarf variety of *L. canellei* at Arbol Grande station, near Tampico."

Vaughan (1928, p. 292) named specimens from Jamaica *L.* (*Lepidocyclina*) *matleyi*, a species which Cole (1956, table 3) considered to be a synonym of *L.* (*L.*) *canellei*. Vaughan and Cole (1932, p. 510) gave the name *L.* (*L.*) *pancanalis* to small specimens from U. S. G. S. loc. 6025, a locality formerly known as Bohio Ridge Switch, Panama Canal Zone. They reported that *L. pancanalis* occurred also in Antigua (Vaughan and Cole, 1932, p. 511) and in Trinidad (Vaughan and Cole, 1941, p. 71). Later, Cole (1953*b*, p. 18) decided that *L.* (*L.*) *pancanalis* was based on small specimens of *L.* (*L.*) *canellei* and was another synonym of *L.* (*L.*) *canellei*.

R. Douvillé (1907, p. 307) described *L.* (*L.*) *giraudi* from specimens obtained from the Oligocene of Pointe Macabou and vicinity, Martinique, French West Indies, where it was associated with *Spiroclypeus bullbrooki* Vaughan and Cole (1941, p. 54), the only species of *Spiroclypeus* known to date from the Americas.

Vaughan and Cole (1941, p. 71) found *L.* (*L.*) *giraudi* in Oligocene sediments in Trinidad where it was associated with *Spiroclypeus bullbrooki*. In Trinidad these two species are associated with *Heterostegina antillea* Cushman, *Lepidocyclina* (*Eulepidina*) *tempanii* Vaughan and Cole (=*L.* (*E.*) *tournoueri* Lemoine and R. Douvillé), *L.* (*E.*) *undosa* Cushman and *L.* (*E.*) *yurnagunensis* Cushman. Vaughan and Cole (1941, p. 120) noted that certain specimens from Trinidad which they referred to *L.* (*L.*) *giraudi* "might without great impropriety be referred to *L. parvula* Cushman."

Cushman (1919, p. 58) described a species from the Oligocene of Antigua to which he applied the name *Lepidocyclina parvula*. Vaughan (1933, p. 16) discussed this species in detail and described (1933, p. 17) from Arbol Grande near Tampico, State of Tamaulipas, Mexico, and several other Mexican localities, a variety which was named *L. parvula crassicosta* Vaughan and Cole.

In 1928 Cole (p. 21) named specimens found in a quarry on the golf course of the Huasteca Petroleum Company opposite Tampico *L.* (*L.*) *waylandvaughani*. Vaughan wrote Cole (1928, p. 22) concerning these specimens: "It appears to me to be more closely related to *L. parvula*

Cushman, but that species is usually thicker through the center, even to being inflated and the papillae are coarser. However, there is a tremendous amount of variation. Since I have not yet reached a positive decision regarding what to do with the form I hesitate to advise you. Because of the two differences above mentioned, I should hesitate to apply the name *parvula* to it, but the form runs very close to the flatter varieties of *parvula*."

At this same locality Cole (1928, p. 22) found microspheric specimens in association with *L.* (*L.*) *waylandvaughani* which he identified as *Lepidocyclina* aff. *L. morgani* Lemoine and R. Douvillé. Vaughan (1933, p. 16) assigned these specimens to *L.* (*L.*) *parvula,* but at the same time he (1933, p. 13) accepted *L.* (*L.*) *waylandvaughani* as a valid species.

Cole (1945, p. 30) accepted this revision by Vaughan in which the megalospheric specimens from this locality at Tampico were assigned to *L.* (*L.*) *waylandvaughani,* whereas the associated microspheric specimens (Cole, 1945, fig. 9, pl. 7) were referred to *L.* (*L.*) *parvula.*

Still another specific name was introduced when Vaughan (1927, p. 4) gave the name *L.* (*L.*) *miraflorensis* to certain specimens from the Panama Canal Zone which Cushman (1918, p. 93) had misidentified as *L.* (*Eulepidina*) *vaughani.* Cole (1953*a*, p. 333) studied topotype specimens of *L.* (*L.*) *miraflorensis* and published several new illustrations.

Woodring (1960, p. 29) has remarked that "The still younger La Boca marine member of Panama formation, also assigned to the early part of the early Miocene, contains the last species in the Canal Zone: two lepidocycline species *L. miraflorensis* and *L. parvula* (Cole, 1953*a*). *L. parvula* later was synonymized with *L. giraudi* (Cole, 1957*a*, p. 41). The Culebra and La Boca species of *Lepidocyclina* also occur in late Oligocene formations in the Canal Zone, with the exception of *L. miraflorensis*."

Nuttall (1932, p. 34) described a stellate species from the Alazan formation (Oligocene) of the Tampico Embayment area of Mexico as *L.* (*L.*) *asterodisca.* Gravell and Hanna (1937, p. 528) found stellate specimens in cores from the Anahuac formation (Oligocene) from a well in Texas which they named *L.* (*L.*) *texana.* Cole (1953*b*, p. 18) combined these two species, and later discussed and illustrated (1958*a,* p. 201) additional specimens from Cuba.

Thus, the specific names *L.* (*L.*) *asterodisca, L.* (*L.*) *canellei, L.* (*L.*) *giraudi, L.* (*L.*) *miraflorensis, L.* (*L.*) *parvula and L.* (*L.*) *waylandvaughani* became established. However, in a study of the variation which may occur in species of *Lepidocyclina* Cole (1957*a*, p. 41) demonstrated

that *L.* (*L.*) *parvula* was a synonym of *L. giraudi,* a conclusion which was accepted by Grimsdale (1959, p. 28). At the present time six species, as *L.* (*L.*) *mantelli* must be included, of *Lepidocyclina* (*Lepidocyclina*) are recognized as occurring in the Americas above the top of the Eocene.

The thesis developed in the next section of this discourse is that there are only two species of the subgenus, *L.* (*L.*) *canellei* and *L.* (*L.*) *mantelli,* in the Americas. *L.* (*L.*) *asterodisca, L.* (*L.*) *giraudi,* L. (*L.*) *miraflorensis* and *L.* (*L.*) *waylandvaughani* are synonyms of *L.* (*L.*) *canellei* as they were based upon selected "forms" within a variable species.

VARIATION

It has long been known that *L.* (*L.*) *asterodisca,* except for a stellate pattern, is similar in equatorial section to specimens referred to such species as *L.* (*L.*) *giraudi* and *L.* (*L.*) *waylandvaughani.* As a stellate pattern has been assumed to be a specific charater in the genus *Lepidocyclina,* it was possible to prepare a key for the recognition of the species in which this feature was used (Cole, 1957*a*, p. 33). In the use of this character the internal structures were ignored. In addition, the other Oligocene species assigned to the subgenus *Lepidocyclina* were placed in the key on the characteristics of the vertical sections as it was admitted that all of these species had similar, if not identical, equatorial sections.

Since that time certain problems have arisen which cast doubt on the validity of this key, and, thereby, on the species which the key was assumed to differentiate. As additional thin sections were prepared and studied, it became apparent that *L.* (*L.*) *asterodisca, L.* (*L.*) *canellei, L.* (*L.*) *giraudi, L.* (*L.*) *miraflorensis* and *L.* (*L.*) *waylandvaughani* were one species. The various specific names were based upon the superficial "form" of certain specimens rather than upon an analysis of the basic structures of the test.

Moreover, environmental factors influence the development of the test. Therefore, one kind of test normally predominates at a given locality. At locality 4 many of the specimens (figs. 1, 4, Pl. 30; fig. 2, Pl. 34) are similar to the types of *L.* (*L.*) *parvula* Cushman (1919, figs. 3-7, pl. 3) (=*L.* (*L.*) *giraudi*), whereas at locality 5 the specimens (fig. 9, Pl. 30; figs. 2, 6, 7, Pl. 38; figs. 1, 3, 9, Pl. 39) which are topotypes of *L.* (*L.*) *waylandvaughani* have an appearance which is distinctive and at first glance different from those at locality 4. Moreover, the small to medium size specimens at locality 5 are so similar to *L.* (*L.*) *canellei* that Vaughan (1933, p. 15) considered them to be a dwarf variety of that species.

At locality 1 specimens (fig. 2, Pl. 30) occur which are the same as the types of *L.* (*L.*) *waylandvaughani* and other specimens (figs. 5, 6, 13, Pl. 30) are identical with *L.* (*L.*) *parvula* (= *L.* (*L.*) *giraudi*). The microspheric specimens (fig. 3, Pl. 36) at locality 5 had been referred to *L.* (*L.*) *parvula* (=*L.* (*L.*) *giraudi*) although the associated megalospheric specimens had been named *L.* (*L.*) *waylandvaughani.*

Thus, in one population (loc. 4) the megalospheric and microspheric specimens had been assigned to the species *L.* (*L.*) *parvula* (=*L.* (*L.*) *giraudi*). At a second locality (loc. 5) the megalospheric specimens had been named *L.* (*L.*) *waylandvaughani,* whereas the microspheric specimens had been referred to *L.* (*L.*) *parvula* (=*L.* (*L.*) *giraudi*). At the third locality (loc. 1) both species seemingly are present.

Although there are inconsistencies in this terminology in referring megalospheric and microspheric specimens to different species, it might still be possible that there are several distinct species. Therefore, numerous thin sections were made and other localities were studied.

Specimens (figs. 1, 3-7, Pl. 34) from locality 3 were first identified as *L.* (*L.*) *miraflorensis* because of their size, shape, and the open, regularly aligned lateral chambers (fig. 7, Pl. 34). But, other specimens (fig. 3-5, 7, Pl. 34) from this sample which seemingly contained only one species of *Lepidocyclina* were similar to topotype specimens of *L.* (*L.*) *waylandvaughani.*

Additional thin sections (figs. 4-8, Pl. 39) of *L.* (*L.*) *canellei* from locality 9 were prepared to supplement those already published (Cole, 1953*b*, figs. 1, 3, 4, 11, 12, 16, pl. 16).

The vertical sections which are illustrated can be grouped into species by superficial form as follows:

1. *L.* (*L.*) *canellei* Lemoine and R. Douvillé

Plate 30, figures 8, 9; Plate 38, figures 2, 7; Plate 39, figures 3-6 8, 9.

2. *L.* (*L.*) *giraudi* R. Douvillé

Plate 30, figures 1, 4, 5, 6, 10, 12, 13; Plate 34, figures 2, 8; Plate 36, figure 3; Plate 37, figure 3; Plate 38, figure 1.

3. *L.* (*L.*) *miraflorensis* Vaughan

Plate 34, figure 7.

4. *L.* (*L.*) *waylandvaughani* Cole

Plate 30, figures 2, 3, 7, 11; Plate 34, figures 1, 3-6; Plate 38, figures 3, 6; Plate 39, figures 1, 2.

Admittedly, this is a subjectively determined listing as such features as the strength of the pillars became the critical feature upon which the specimen was assigned to a given species.

The specimen illustrated as figure 1, Plate 38 (*L. giraudi* kind) has the same internal structure as does figure 4 of this same plate except it is more inflated and the pillars on one side are stronger. Figure 3, Plate 38 is almost identical with figure 1, Plate 39 (a topotype of *L. waylandvaughani*) except the roofs and floors of the lateral chambers are slightly more curved in figure 1, Plate 39 than they are in figure 3, Plate 38. Other topotype specimens (Cole, 1952, figure 10, plate 18) of *L.* (*L.*) *waylandvaughani* have lateral chambers with straight roofs and floors. Thus, it seems logical to group these specimens under one specific name rather than two as the specimen illustrated as figure 4, Plate 38 is intermediate between the other two specimens.

If illustrations of *L.* (*L.*) *miraflorensis* (Cole, 1953, pl. 43) are compared with those given of *L.* (*L.*) *canellei* on Plate 39, it will be observed that the internal structure of those two species is the same. Likewise, specimens such as those illustrated by figures 3, 9, Plate 39, have the same internal structure as *L.* (*L.*) *canellei* does. But, specimens such as those illustrated by figures 8, 9, Plate 30 are intermediate between *L.* (*L.*) *canellei* and *L.* (*L.*) *waylandvaughani.*

Cole (1958*a*, p. 201) has given a number of illustrations of equatorial and vertical sections of *L.* (*L.*) *asterodisca.* If these are compared with the illustrations given in this article, it will be observed that the internal structure of this species which was named because of its stellate pattern is the same as specimens assigned to *L.* (*L.*) *canellei.* The first comparison should be between the specimen illustrated as figure 3, Plate 38, and the one shown as figure 10, plate 23 (Cole, 1958*a*).

In the study (Cole, 1958*a*) of *L.* (*L.*) *asterodisca* it was found that the associated microspheric specimens where not stellate, only the megalospheric specimens developed the stellate pattern.

Another pair of species should be mentioned in this connection. They are *L.* (*Eulepidina*) *tournoueri* Lemoine and R. Douvillé (figure 5, Plate 32) and *L.* (*Eulepidina*) *dartoni* Vaughan (Cole, 1953*b*, figures 1-8, plate 19). Except for the stellate pattern, it is impossible to separate these two species.

They should be combined under the name *L.* (*E.*) *tournoueri.* It should be recognized that in *Lepidocyclina* the stellate pattern is produced

only by certain individuals, probably under the influence of ecological conditions, and that this pattern is not genetically produced. Therefore, it does not have value as a specific character.

Specimens assigned previously to the species *L.* (*L.*) *asterodisca*, *L.* (*L.*) *canellei*, *L.* (*L.*) *giraudi*, *L.* (*L.*) *miraflorensis* and *L.* (*L.*) *waylandvaughani* have identical equatorial sections. The species, therefore, have been recognized by differences in the shape of the test and by the structure observed in the vertical sections.

Although *L.* (*L.*) *mantelli* (Morton) (Cole, 1957*a*, p. 38) has a similar equatorial section to that of *L.* (*L.*) *canellei*, the vertical section is markedly different. In *L.* (*L.*) *mantelli* the lateral chambers have noticeably thick roofs and floors, the chamber openings are slitlike, and they are never in alignment. Therefore, *L.* (*L.*) *mantelli* is retained as a valid species.

The supposed differences used in the recognition of these species are summarized in Table 2.

Such differences as do appear can be more readily interpreted as the result of individual variation in most cases produced by ecological rather than genetically produced structures. Moreover, it has been well established that all of these supposed species have the same stratigraphic ranges. The only useful purpose in retaining different specific names would be to define populations developed under different ecological conditions. However, any advantage so gained would be offset in concealing the fact that only one species was present at the different locilities. Moreover, the usual concept of a species would be violated.

THE SPECIES ILLUSTRATED

Many of the specimens illustrated have been mentioned already in the text. However, other specimens which may not have been mentioned are included in the illustrations for completeness and may be useful in making additional comparisons. With the exception of localities 4 and 9 all the species of larger Foraminifera found at the other localities are illustrated.

Camerina cojimarensis (D. K. Palmer) .... Plate 28
dia (Cole and Ponton) .... Plate 29

Table 2.—Major differences between the species

Species	Shape	Pillars	Lateral chambers	
			Roofs and floors	Alignment
L. (*L.*) *asterodisca*	Stellate	Few, small	Identical with *L. waylandvaughani*	
canellei	Compressed to inflated lenticular	Few, small	Thin	Regular
giraudi	Inflated lenticular	Many, large	Moderately thick	Some irregularity
miraflorensis	Compressed lenticular	Few, small	Identical with *L. canellei*	
waylandvaughani	Compressed lenticular	Few, small	Moderately thick	Some irregularity

Lepidocyclina (*Lepidocyclina*) *canellei* Lemoine and R. Douvillé . . . Plate 30; Plate 31; Plate 32, figures 1-4; Plate 33; Plate 34, figures 1-8; Plate 35, figures 1, 2, 4, 5; Plate 36; Plate 37; Plate 38

(*Eulepidina*) *tournoueri* Lemoine and R. Douvillé . . . Plate 32, figure 5; Plate 34, figure 9; Plate 35, figure 3.

PALEOECOLOGICAL IMPLICATIONS

At locality 1 there were abundant specimens of *Camerina dia* in association with a modest number of specimens of *Lepidocyclina* (*Lepidocyclina*) *canellei.* At locality 3 there were abundant, large size specimens of *L.* (*L.*) *canellei* and a modest number of specimens of *C. dia,* or just the reverse of the situation at locality 1.

At locality 4 *Heterostegina antillea* in modest numbers occurred with rare specimens of *C. dia* and numerous specimens representing two species of *Lepidocyclina, L.* (*L.*) *canellei* and *L.* (*E.*) *undosa.* At localities, such as locality 5, *L.* (*L.*) *canellei* in abundance was associated with numerous specimens of *Streblus mexicanus mecatepecensis* (Nuttall) and *Elphidium.*

At locality 9 *L.* (*L.*) *canellei* in abundance occurred with *Miogypsina antillea* (Cushman) and other species of *Lepidocyclina.* However, camerinids were not found at this locality.

These associations suggest that ecological controls were operative to some extent. Cole (1957*b,* p. 751) had written ". . .*Heterostegina* require(s) warm, shallow protected situations. *Operculina* (=*Camerina*) favors partly protected conditions, but is more tolerant of greater depth and lower temperatures." Elsewhere he (Cole, 1959, p. 354) stated "The average depth at which *Heterostegina* occurred in the vicinity of Bikini and the Philippine Islands was 25 to 32 fathoms."

Bandy (1960, p. 11) wrote, "Most rotaloids with pillars are inner shelf inhabitants, as represented by the cosmopolitan *Streblus*. . . *Streblus* is euryhaline and eurythermal whereas the others mentioned are stenohaline and stenothermal."

The abundance of *Streblus* and *Elphidium* at locality 5 as well as the character of the sediments, massive cross-bedded sandstones between which occur thin, fossiliferous beds of sandy clay, suggest that these sediments accumulated in shallow water in a somewhat protected situation such as a large bay. This is the environment suggested for such localities as 1, 3

and 5 of which locality 5 represents the shallowest environment with the most variable conditions and locality 3 represents the deepest environment of these three localities.

In contrast to these localities the sediments at locality 9 in which *Miogypsina* occurred with *Lepidocyclina*, but without camerinids seemingly were deposited in waters which were too deep or too cold for the camerinids.

The faunal association at locality 4 is suggestive of conditions which represent intermediate conditions, probably those which occur near the lower limit of the ecological controls favorable to the camerinids.

Specimens of *L.* (*L.*) *canellei* with weak pillars and thin floors and roofs of the lateral chambers would be those of the deeper environments, whereas specimens with larger pillars and thicker floors and roofs of the lateral chambers would represent kinds which inhabited shallower and probably warmer water. Stellate specimens of *L.* (*L.*) *canellei* are associated commonly with abundant specimens of *Heterostegina,* and seemingly are developed in the situations which are optimum for the development of *Heterostegina.*

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PLATES

This study was made subsequent to the ones by Cole and Applin and Cole which had been accepted for publication (Contrib. Cushman Found. Foram. Res., v. 12, pt. 4, 1961). Therefore, some of the specific names of *Lepidocyclina* used in those articles have been changed.—Editor's note.

Explanation of Plate 28

Figure Page

1-7. **Camerina cojimarensis** (D. K. Palmer) 378, 379

1. Central part, X 40, of a median section of a megalospheric specimen.

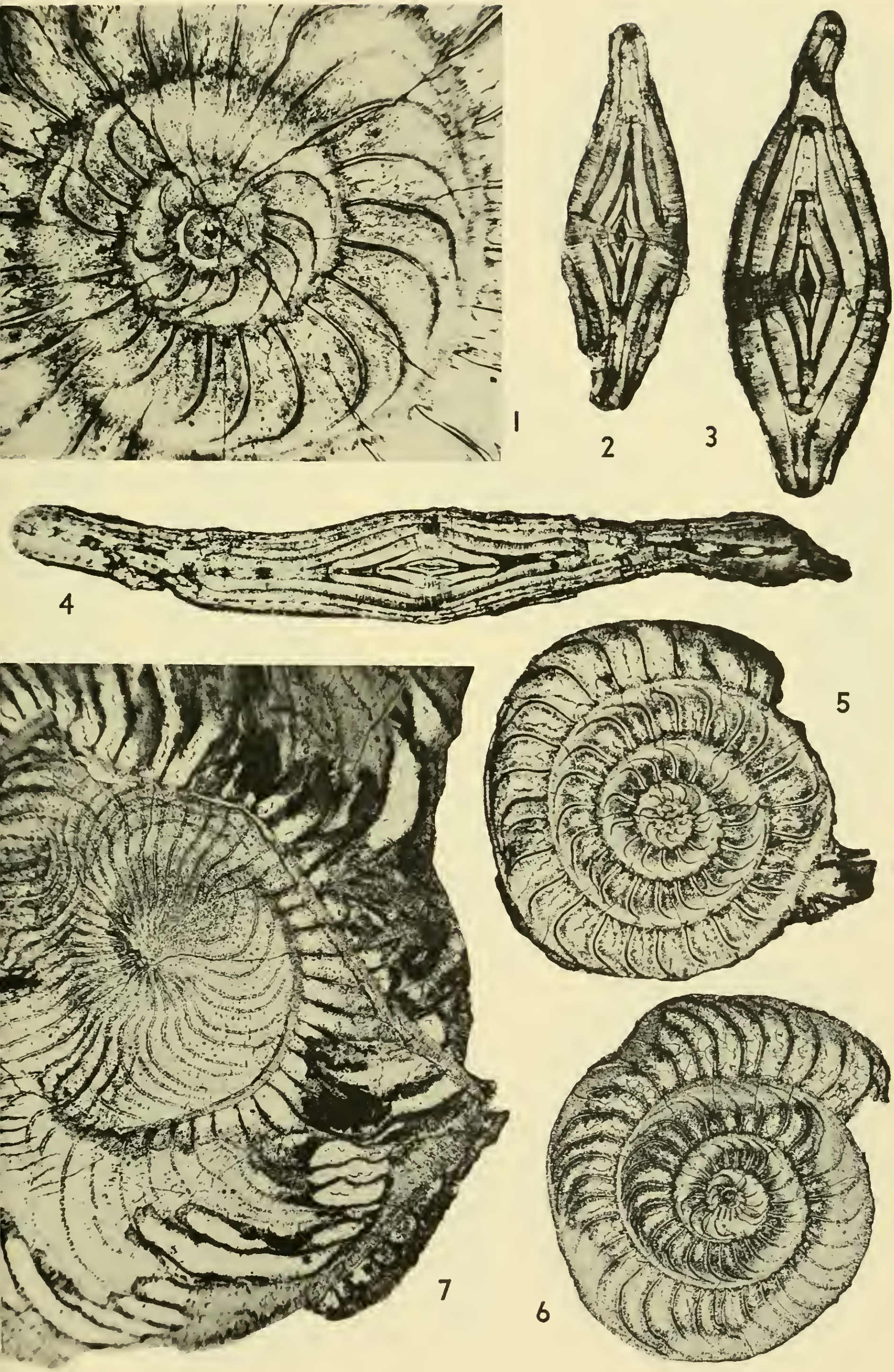
2. Transverse sections; 2, X 20; 3, X 12.5; of megalospheric specimens.

4. Transverse section, X 12.5, of a microspheric specimen.

5,6. Median sections; 5, X 20; 6, X 12.5, of megalospheric specimens.

7. Part of a median section, X 12.5, which is not ground to the median plane in the central area of a microspheric specimen.

1-7. Loc. 2—see text for locality descriptions.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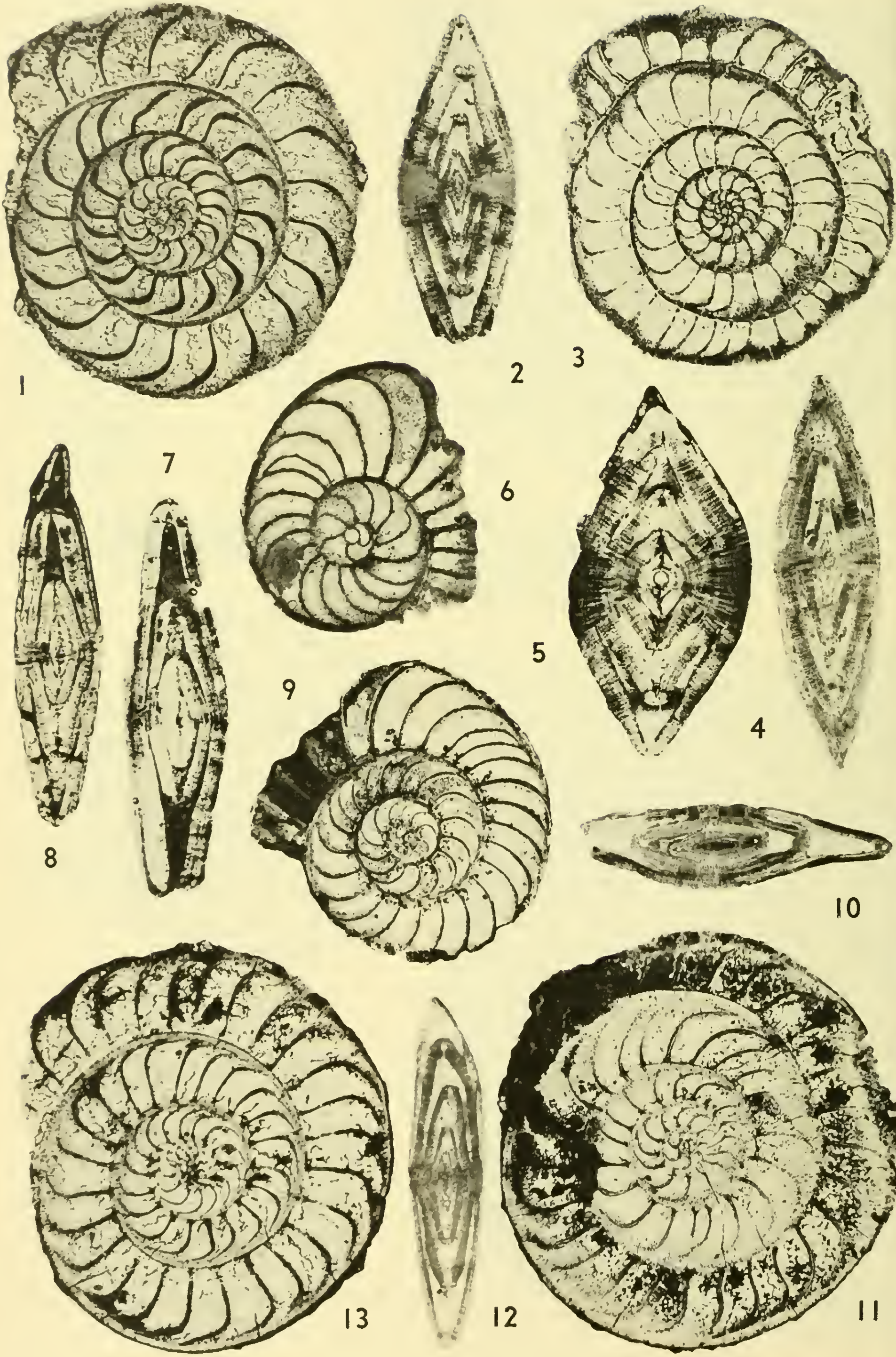
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Explanation of Plate 29

Figure	Page

1-13. Camerina dia (Cole and Ponton) 383

All figures, X 20.

1, 3, 6, 9, 11, 13. Median sections.

2, 4, 5, 7, 8, 10, 12. Transverse sections.

1-5, 12. Loc. 1—see text for locality descriptions.

6, 9, 10. Loc. 8.

7, 8, 11, 13. Loc. 3.

Explanation of Plate 30

Figure | Page

1-13. **Lepidocyclina (Lepidocyclina) canellei**
Lemoine and R. Douvillé.. 386, 387, 388, 391

Figures 1-7, 10, 11, X 20; 8, 9, 12, 13, X 40.

1-13. Vertical sections of megalospheric specimens to illustrate variation.

1, 4, 10. Loc. 4—see text for locality descriptions.

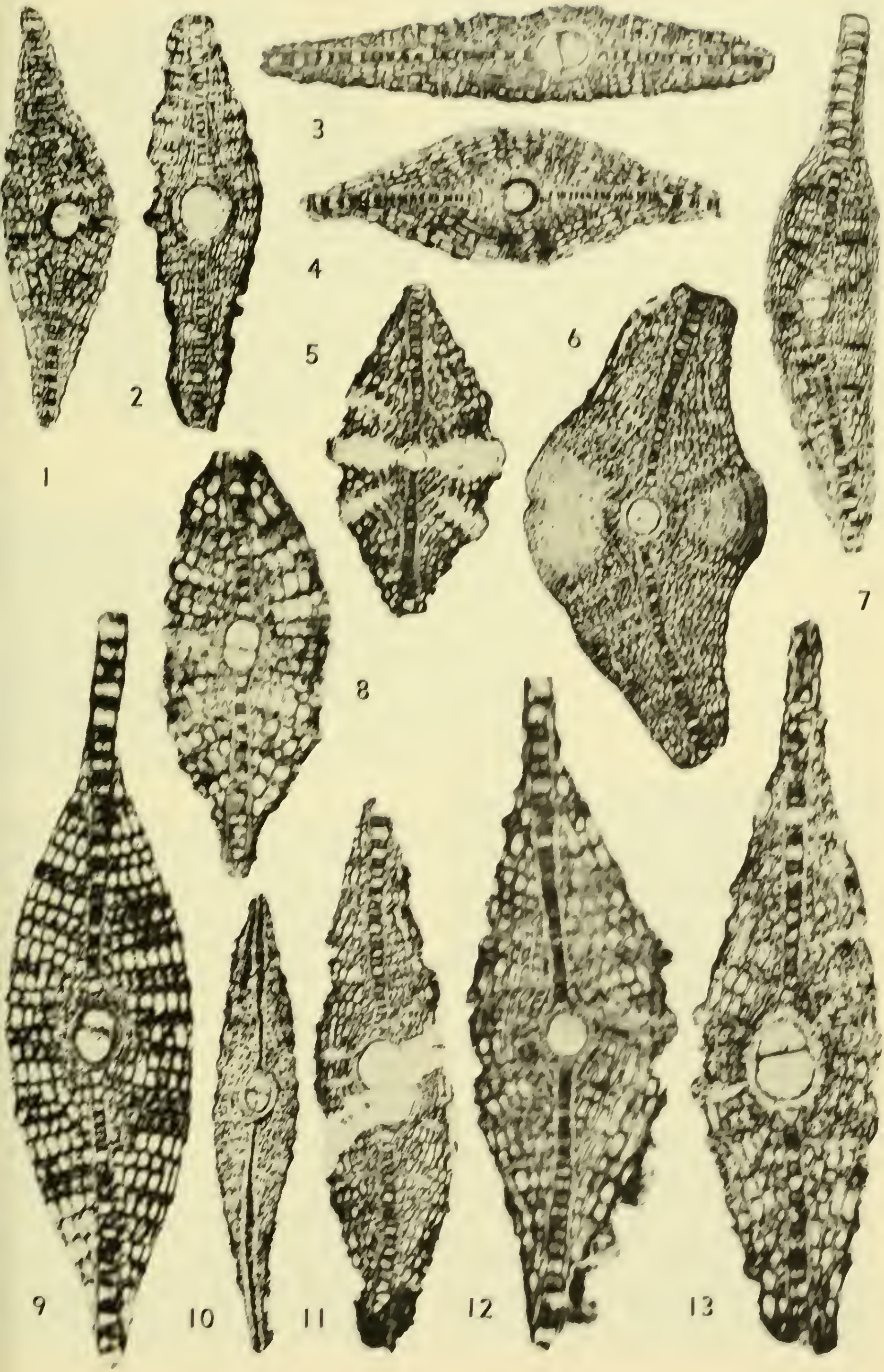
2, 5, 6, 13. Loc. 1.

3, 8, 11. Loc. 6.

7. Loc. 7.

9. Loc. 5.

12. Loc. 8.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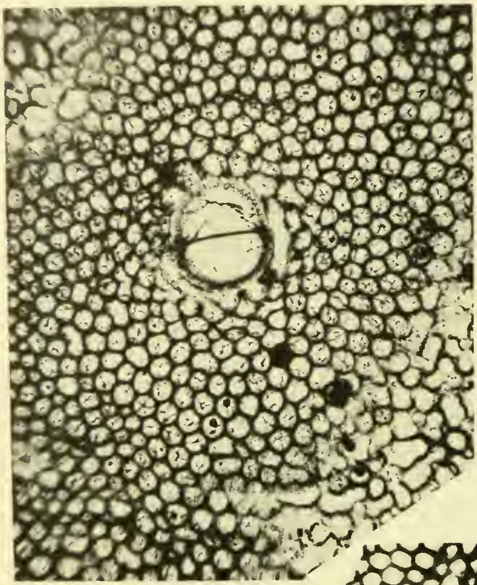

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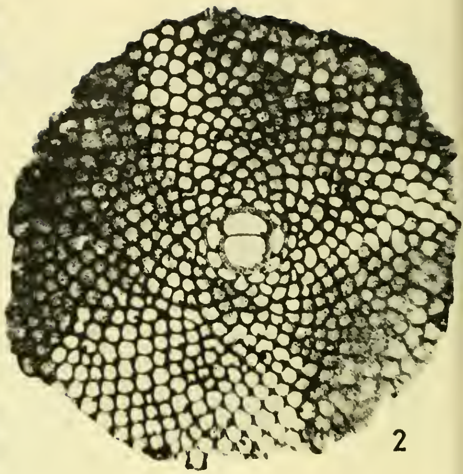

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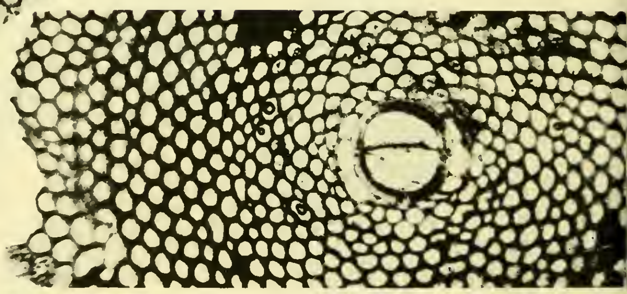

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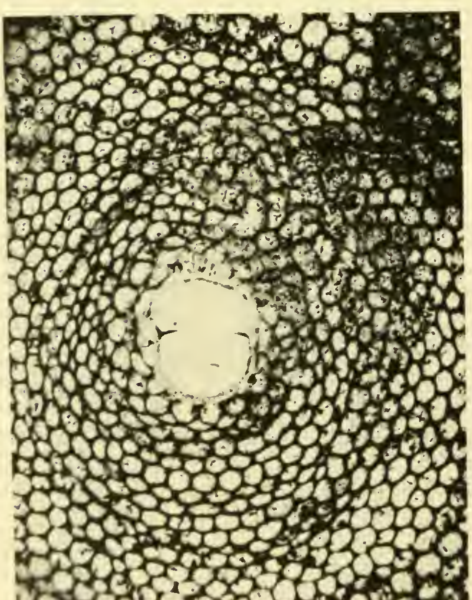

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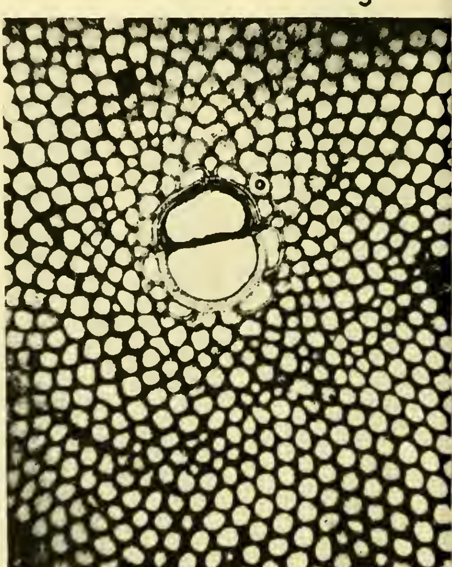


Explanation of Plate 31

Figure Page

1-5. **Lepidocyclina (Lepidocyclina) canellei** Lemoine and R. Douvillé 391

1. Part of an equatorial section, X 40, of a megalospheric specimen the peripheral equatorial chambers of which are illustrated as figure 1, Plate 36.
2. Equatorial section, X 40; the vertical section of a similar specimen is illustrated as figure 8, Plate 30.
3. Part of an equatorial section, X 40, of a specimen illustrated previously as figure 11, plate 7 (Cole, 1945).
4. Part of an equatorial section, X 40, the peripheral equatorial chambers of which are illustrated as figure 5, Plate 35.
5. Part of an equatorial section, X 40; the vertical section of a similar specimen is illustrated as figure 7, Plate 30.

1. Loc. 4—see text for locality descriptions.
2. Loc. 6.
3. Loc. 4.
4. Loc. 3.
5. Loc. 7.

Explanation of Plate 32

Figure | Page

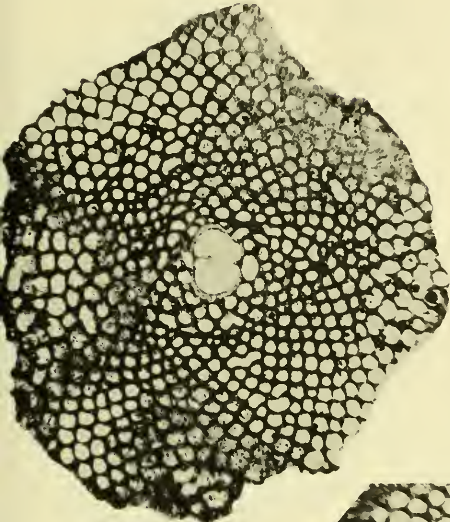
1-4. **Lepidocyclina (Lepidocyclina) canellei** Lemoine and R. Douvillé 391

1. Equatorial section, X 40; the vertical section of a similar specimen is illustrated as figure 8, Plate 30.
2. Equatorial section, X 40; the vertical section of a similar specimen is illustrated as figure 13, Plate 30.
3. Equatorial section, X 40; the vertical section of similar specimens are illustrated as figures 1, 4, Plate 30.
4. Equatorial section, X 40; the vertical section of a similar specimen is illustrated as figure 9, Plate 30.

5. **Lepidocyclina (Eulepidina) tournoueri** Lemoine and R. Douvillé 288 391

Equatorial section, X 40.

1, 5. Loc. 6—see text for locality descriptions.
2. Loc. 1.
3. Loc. 4.
4. Loc. 5.



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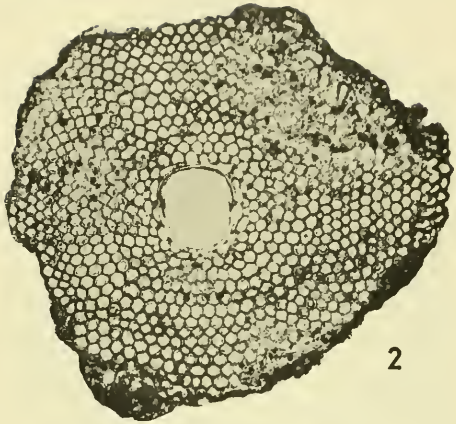

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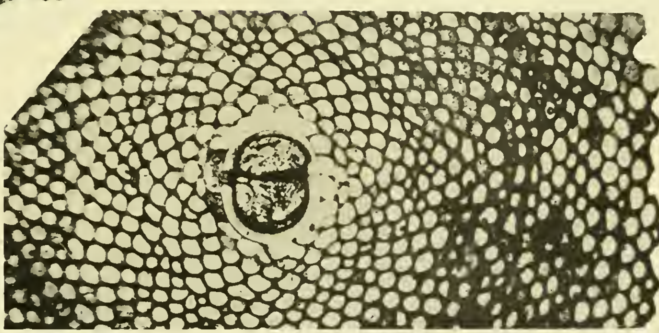

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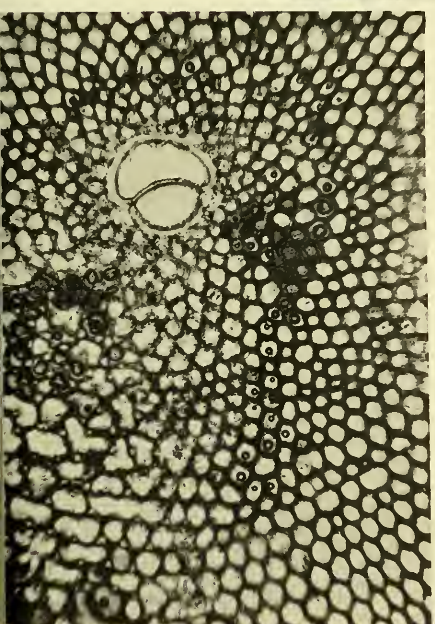

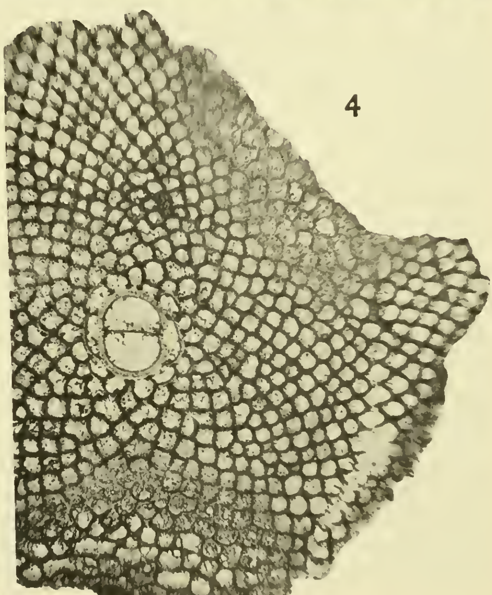

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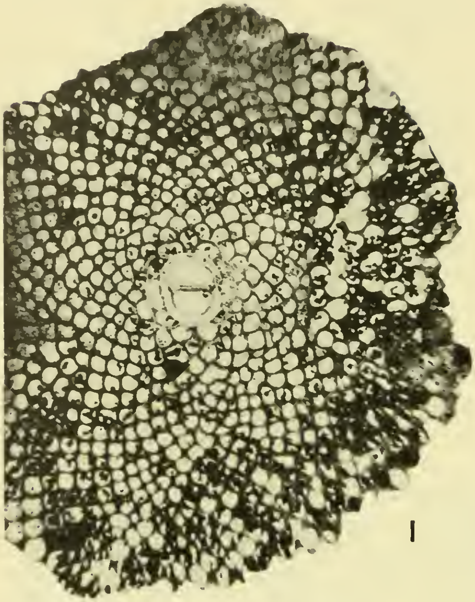

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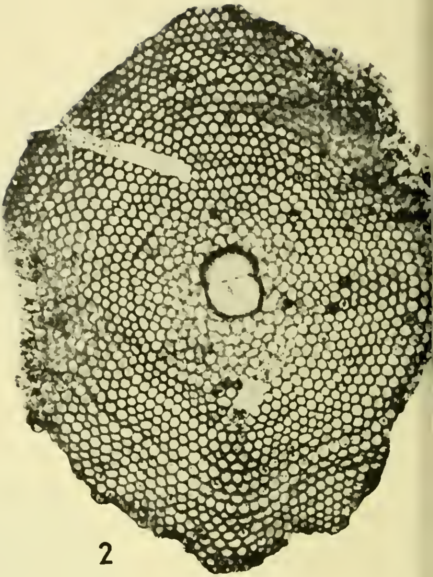

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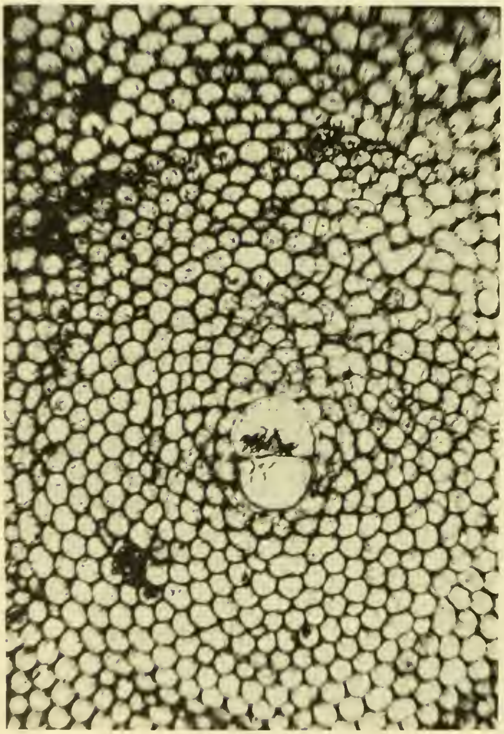

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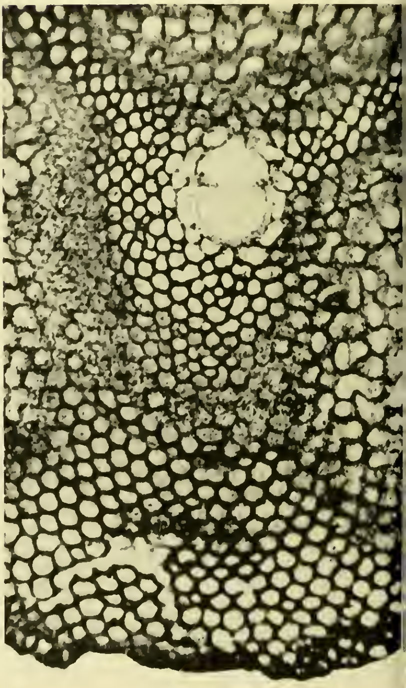


Explanation of Plate 33

Figure	Page

1-4. **Lepidocyclina (Lepidocyclina) canellei** Lemoine and R. Douvillé 391

1. Equatorial section, X 40.
2. Equatorial section, X 20; the vertical section of a similar specimen is illustrated as figure 2, Plate 30.
3. Part of an equatorial section, X 40, of the same specimen illustrated as figure 4, Plate 35.
4. Equatorial section, X 40; the vertical section of a similar specimen is illustrated as figure 6, Plate 30.

1. Loc. 6—see text for locality descriptions.

2, 4. Loc. 1.

3. Loc. 3.

Explanation of Plate 34

Figure — Page

1-8. **Lepidocyclina (Lepidocyclina) canellei** Lemoine and R. Douvillé 386, 387, 391

1. Part of a vertical section, X 40, of the same specimen illustrated as figure 3 of this plate.

2-5, 8. Vertical sections, X 20.

6, 7. Parts of vertical sections, X 40.

9. **Lepidocyclina (Eulepidina) tournoueri** Lemoine and R. Douvillé 391

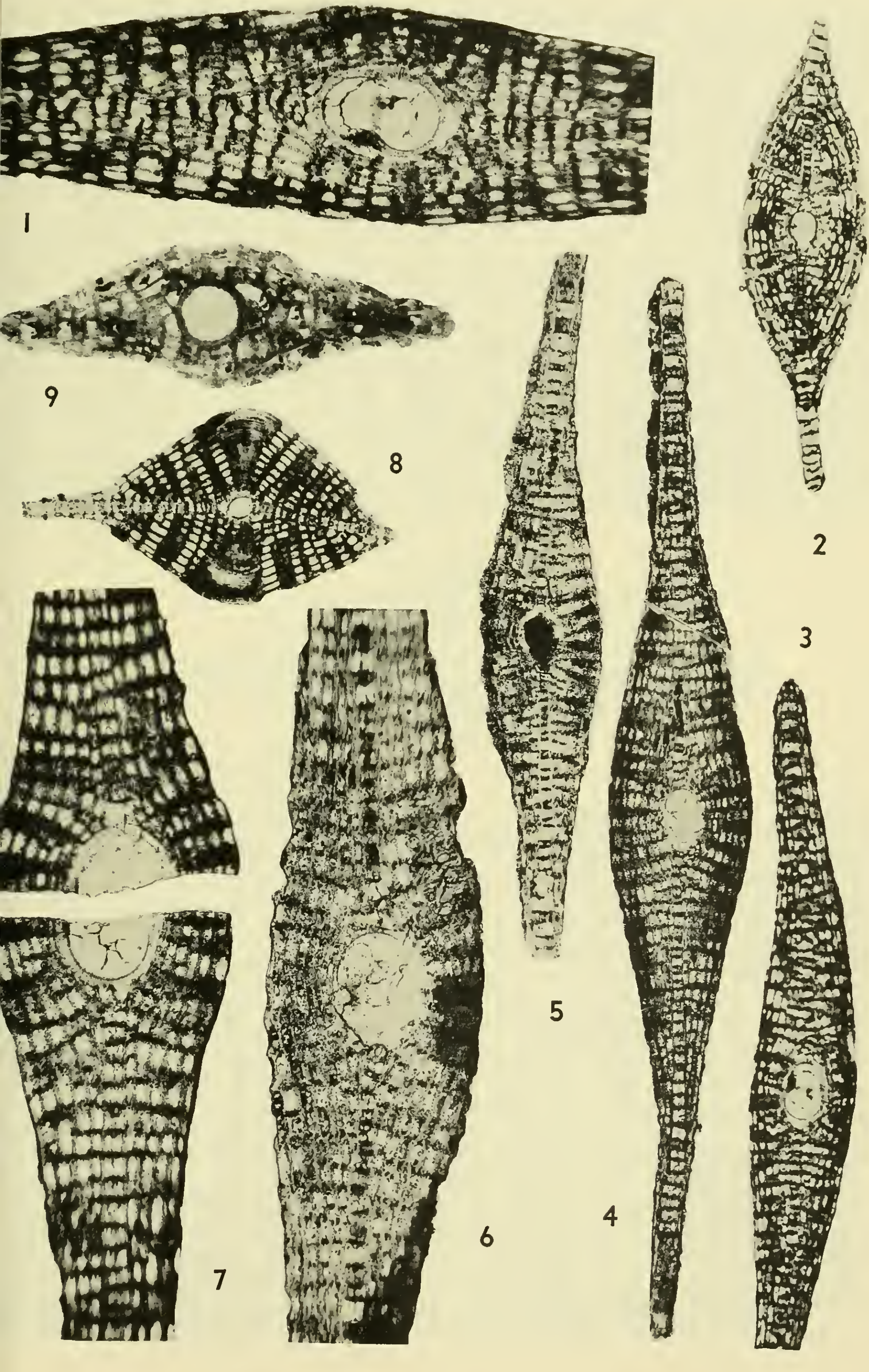
Vertical section, X 40, of a small specimen.

1, 3-7. Loc. 3—see text for locality descriptions.

2. Loc. 4.

8. Loc. 1.

9. Loc. 6.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Explanation of Plate 36

Figure Page

1-5. **Lepidocyclina (Lepidocyclina) canellei** Lemoine and R. Douvillé.. 387, 391

1. Peripheral equatorial chambers, X 40, of the specimen illustrated as figure 1, Plate 31.

2. Part of an equatorial section, X 40, of a specimen similar to the one illustrated as figure 12, Plate 30.

3. Vertical section, X 20, of a microspheric specimen.

4. Part of an equatorial section, X 20, of a microspheric specimen.

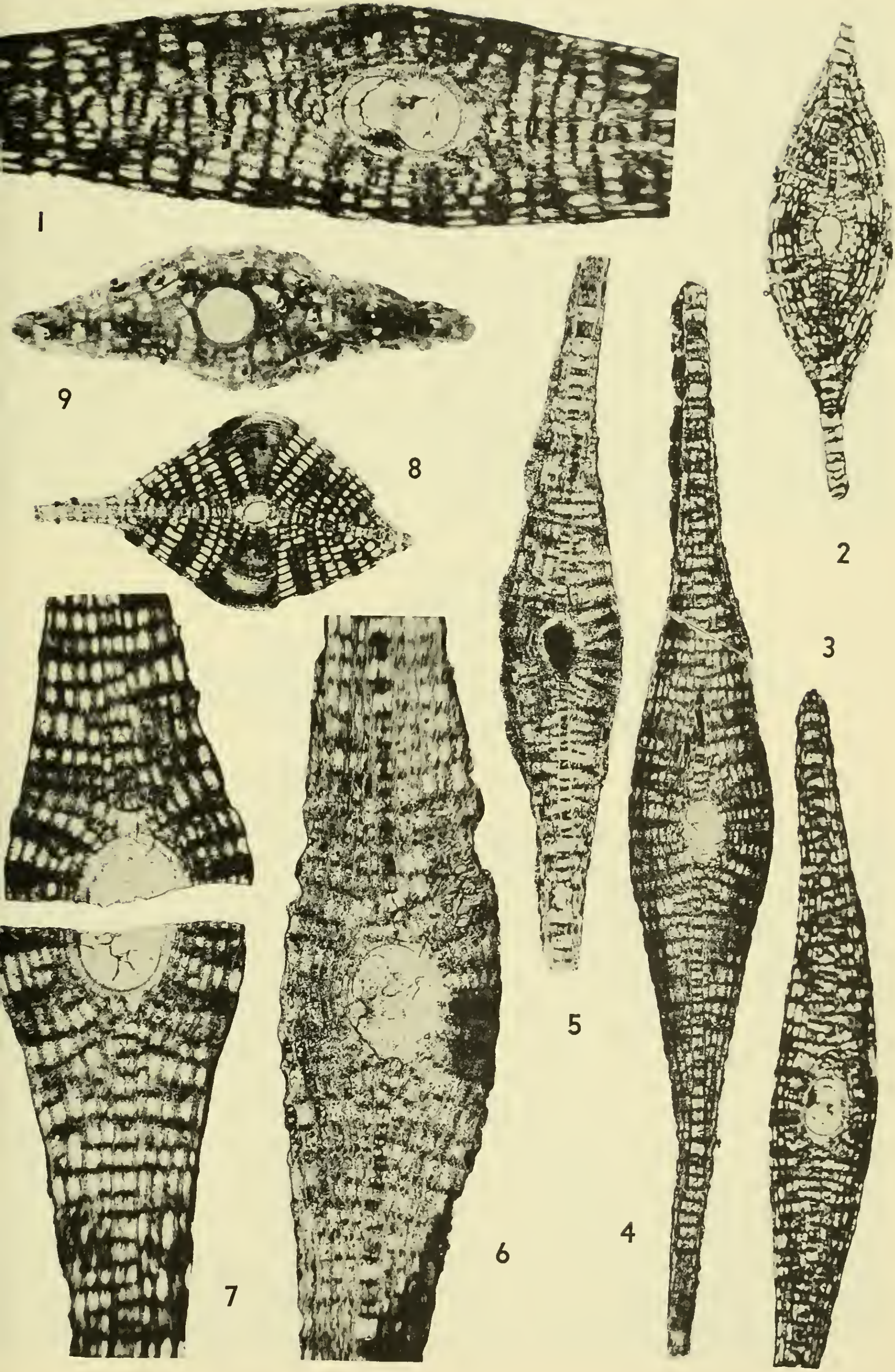
5. Part of an equatorial section, X 40, of a specimen similar to the one illustrated as figure 5, Plate 30.

1, 3. Loc. 5—see text for locality descriptions.

2. Loc. 8.

4. Loc. 7.

5. Loc. 1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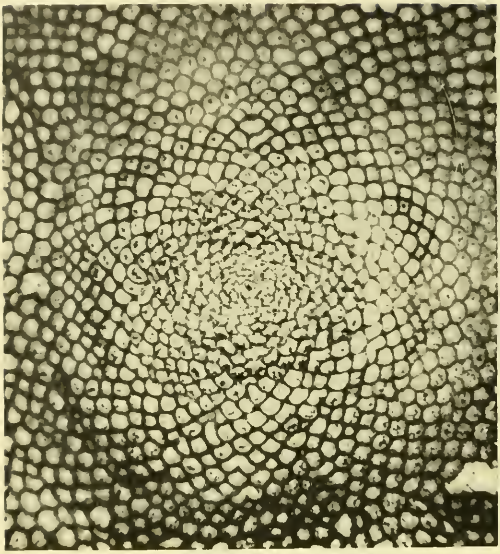

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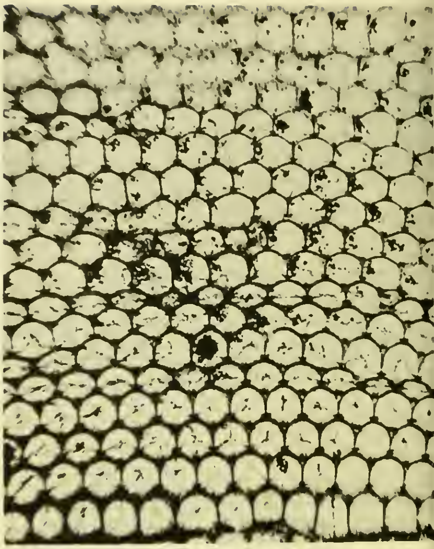

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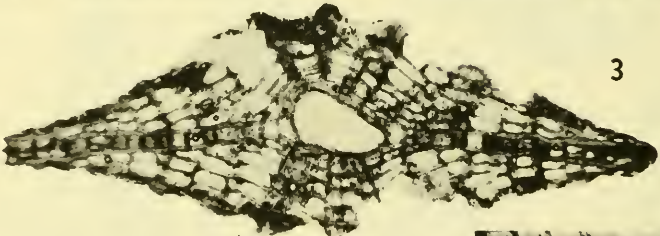

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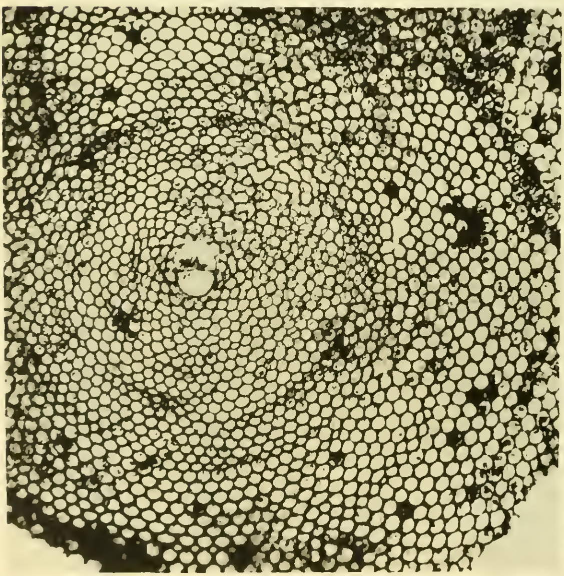

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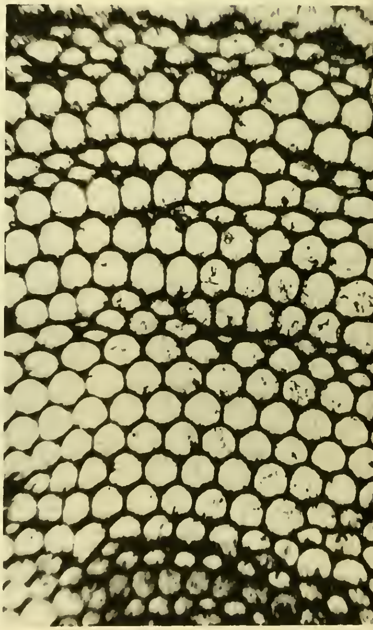


Explanation of Plate 37

Figure | Page

1-5. **Lepidocyclina (Lepidocyclina) canellei** Lemoine and R. Douvillé 391

1, 2. Parts of the same vertical section, X 20, of a microspheric specimen.

3. Vertical section, X 20, of a microspheric specimen with large pillars.

4, 5. Parts of the same equatorial section, 4, X 40; 5, X 230, of a microspheric specimen to illustrate the initial equatorial chambers.

1, 2, 4, 5. Loc. 3—see text for locality descriptions.
3. Loc. 7.

Explanation of Plate 38

Figure Page

1-7. **Lepidocyclina (Lepidocyclina) canellei** Lemoine and R. Douvillé 386, 387, 388

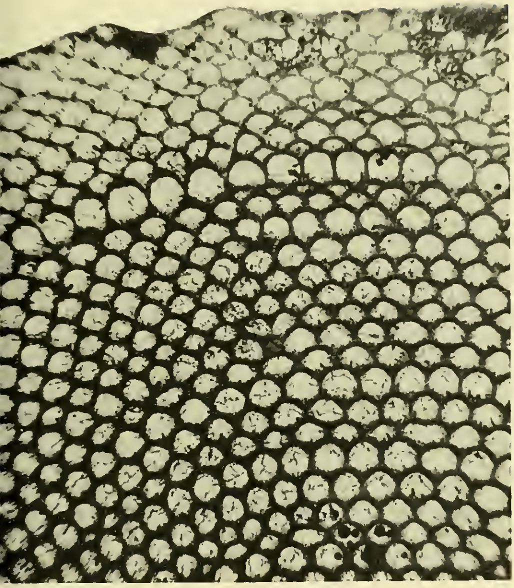
1. Part of a vertical section, X 40, of the specimen illustrated as figure 4, Plate 30.
2. Vertical section, X 40.
3. Part of a vertical section, X 40, of the specimen illustrated as figure 3, Plate 30.
4. Part of a vertical section, X 40, of the specimen illustrated as figure 2, Plate 30.
5. Part of an equatorial section, X 40.
6. Vertical section, X 20.
7. Part of a vertical section, X 40, of the specimen illustrated as figure 3, Plate 39.

1. Loc. 4—see text for locality descriptions.

2, 5-7. Loc. 5.

3. Loc. 6.

4. Loc. 1.



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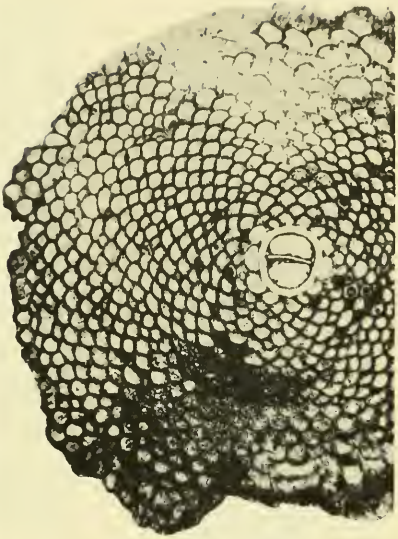

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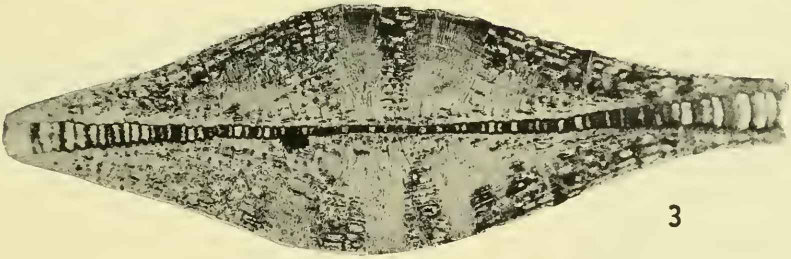

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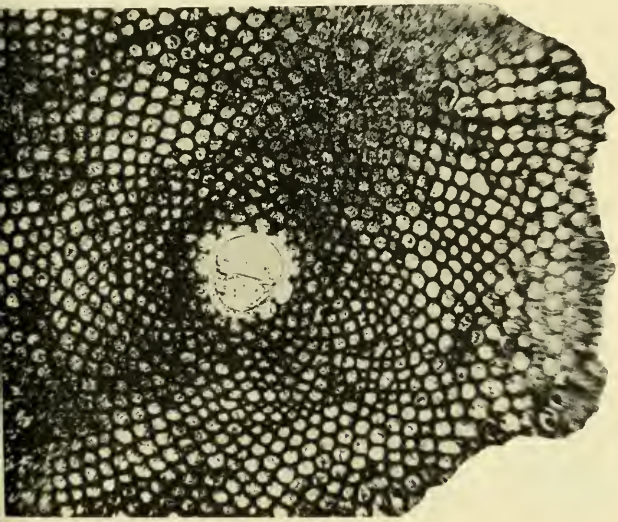

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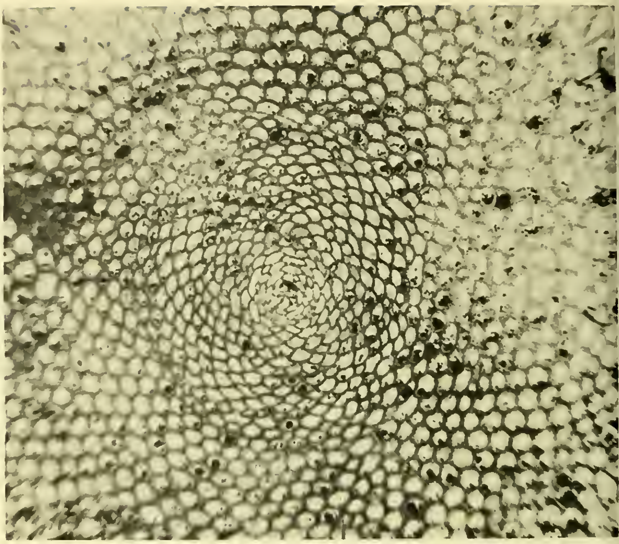

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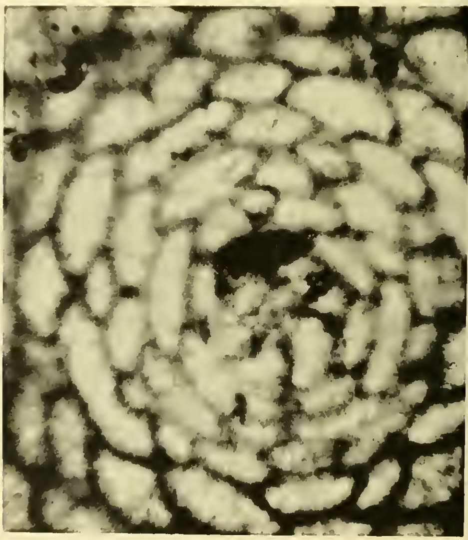

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Explanation of Plate 39

Figure Page

1-9. **Lepidocyclina (Lepidocyclina) canellei**
Lemoine and R. Douvillé 386, 387, 388

1. Part of a vertical section, X 40, of the specimen illustrated as figure 6, Plate 38.
2. Vertical section, X 40, of a small specimen.
3. Vertical section, X 20.

4, 5. Vertical sections, X 20.

6. Part of a vertical section, X 40, of the specimen illustrated as figure 4 of this plate.
7. Part of an equatorial section, X 40.
8. Part of a vertical section, X 40, of the specimen illustrated as figure 5 of this plate.
9. Vertical section, X 40.

1, 3, 9. Loc. 5—see text for locality descriptions.

2, 4-8. Loc. 9.