CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH

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PALAEONTOLOGICAL LABORATOR

CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH Volume V, Part 2, April, 1954

100. DISCUSSION OF SOME THECAMOEBINA DESCRIBED ERRONEOUSLY AS FORAMINIFERA H. M. Bolli and J. B. Saunders Pointe-à-Pierre, Trinidad, B. W. I.

ABSTRACT—The thecamoebian fauna of certain Trinidad rivers is discussed briefly and a number of faunal zones are distinguished. The position of the Thecamoebina within the Rhizopoda is mentioned and the synonymy that has arisen between some thecamoebian and foraminiferal genera is outlined. There follows a more detailed description of thecamoebian genera and species that have been described erroneously as Foraminifera. The paper is concluded with some examples from literature of the inclusion of recent, fresh water thecamoebian species in descriptions of fossil and recent foraminiferal assemblages.

INTRODUCTION

During the collection of samples in Trinidad rivers the writers came across a rich fauna of simple, arenaceous Protozoa. Subsequent investigation showed that these forms belong to the Thecamoebina. The Group has been studied extensively especially by G. Deflandre to whom the writers sent a number of types for identification. According to him the majority of the species that were sent have already been described.

While studying the group it became apparent to the writers that quite a number of fresh water Thecamoebina had been included erroneously in descriptions of fossil, marine, as well as recent, brackish water, foraminiferal assemblages. This discussion brings to light some of these errors.

Fossil Thecamoebina have been recorded from rocks as old as Middle Eocene though it is almost certain that the group is of far more ancient origin. The writers consider that the presence of fossil Thecamoebina in either recent or fossil foraminiferal assemblages is so unlikely that it may be ignored. In addition, it may be stated quite definitely that all material studied by them, including types sent from the U. S. National Museum, is recent.

INVESTIGATIONS IN TRINIDAD

As a preliminary to a more detailed publication that the authors hope to produce, a brief account is given here of the distribution of some species of Thecamoebina in the Caroni River with two of its tributaries and the Burro River. Investigations show that a number of faunal zones can be erected in these tropical rivers based on the distribution of these species. The accompanying map (Figure 1) shows these zones and a brief description of their characteristics may be found below.

Before defining the zones a short description of the sampling methods is given. Samples were collected at regular intervals from source to mouth of each river. Each sample consisted of approximately 2 pounds of mud, including submerged vegetation such as plant leaves, collected from the river bed. After washing through 105 micron and 62.5 micron sieves the thecamoebian tests were separated from the residue by flotation with carbon tetrachloride. Assemblages were prepared for each station and from these, distribution and frequency charts were constructed.

ZONE I

Water conditions.—Swiftly flowing rivers with pools and small waterfalls in mountainous rain forest. Water clear and well aerated.

Thecamoebian fauna.—Characterised by the abundance of the genus Centropyxis, especially Centropyxis (Cyclopyxis) stellata Wailes, Centropyxis (Centropyxis) ecornis Leidy and Centropyxis (Centropyxis) aculeata Stein and certain species of the genus Difflugia e.g. Difflugia capreolata Penard and Difflugia carona Wallich.

Distribution.—In the Arima River from head waters at approximately 2500 feet down to approximately 500 feet; that is, in the steep gradient section of the river.

In the Maracas River (and Acono River branch) which flows parallel to the Arima River and shows similar conditions.

In the Burro River from head waters at 1000 feet down to the region of tidal influence. This is a small river flowing straight from the mountains to the sea and not possessing central and lower portions as represented by Zones II and III in the Caroni River.

Isolated samples taken from pools in a very precipitous stream high up on the flanks of El Tucuche (at approximately 2500 feet) yielded a rich Zone I fauna.

ZONE II

Water conditions.—Rivers flowing, in the upper part of the zone in forest and lower down in cultivated land. Water clear to slightly turbid and though flowing appreciably, not as fast as in Zone I.

Thecamoebian fauna.—Characterised by the abundance of the genus Difflugia, especially common being Difflugia urceolata Carter. The genus Centropyxis is reduced in numbers in this zone, those remaining belonging mostly to the subgenus Centropyxis.

Distribution.—In the Arima River from approximately 500 feet down to 50 feet.

In the Maracas River from approximately 500 feet down to the junction with the Caroni River.





ZONE III

Water conditions.—Rivers flowing through cultivated land. Water turbid, slow flowing or semi-stagnant.

Thecamoebian fauna.—Rather impoverished. Best represented is the genus Difflugia, especially a form near to Difflugia cf. acuminata Ehrenberg.

Distribution.—In the Caroni River where there is a long stretch of alluvial plain; from 50 feet to the zone of tidal influence.

ZONE IV

Water conditions.—Rivers bordered by swamp vegetation (Mangroves etc.). Water brackish and turbid, slow flowing or semi-stagnant.

Thecamoebian fauna.—Exceedingly impoverished fauna. The specimens collected were not studied for protoplasm but it is the authors' opinion that they are more likely to have been carried down than to be living there.

An increasing number of brackish water Foraminifera appears as the salinity rises.

Distribution.—In the Caroni and Burro Rivers from the highest point of tidal influence to their mouths.

CLASSIFICATION AND TAXONOMY

The Group Thecamoebina of the Subphylum Rhizopoda has been studied in considerable detail since the middle of last century.

The essential difference between the Thecamoebina and the Foraminifera is in the structure of the pseudopodia and in the habitat.

As Deflandre is one of the leading authorities on this subject, the writers give here his view as to the position of the Thecamoebina within the Rhizopoda (Deflandre, 1952):

Subphylum: Rhizopoda

Class 1: Lobosa

Order 1: Amoebina

Order 2: Thecamoebina lobosa (Testacea

Class 2: Filosa

Order 1: Aconchulina Order 2: Thecamoebina filosa (Testacea

Class 3: Granulo-reticulosa

Order 1: Athalamia

Order 2: Thalamia

Order 3: Foraminifera

According to this classification the Thecamoebina fall within two classes; those with digitate pseudopodia in the Class Lobosa and those with filate pseudopodia in the Class Filosa. As many of the orders in the above classifications are not represented by fossils, Deflandre suggests a somewhat simplified classification of the Rhizopods with tests especially for use in paleontological work. This is as follows:

Group 1: Thecamoebina s.l.-practically all

fresh water forms

lobosa)

filosa)

Group 2: Foraminifera—practically all marine and brackish water forms

After studying the literature, the writers have come to the conclusion that a considerable synonymy has arisen between genera and species of Thecamoebina and Foraminifera. The following lists and discussion contain the writers' views on this synonymy:

Synonymy between Genera of Thecamoebina and Foraminifera

Thecamoebina	Foraminifera
Centropyxis(Cyclopyxis)	part Leptodermella
Centropyxis (Centropyxis)	part Millettella
Difflugia	part Lagunculina
	part Proteonina

Synonymy between Species of Thecamoebina and Foraminifera

Thecamoebina	Foraminifera
Centropyxis (Cyclopyxis) sp.	Leptodermella salsa
Centropyxis(Centropyxis)sp.	Leptodermella
	excentrica
Centropyxis(Cyclopyxis)sp.	Leptodermella arenata
probably not belonging to the Thecamoebina	Leptodermella turbanica Leptodermella maestrichtiensis
Centropyxis(Centropyxis)sp.	Leptodermella variabilis
Centropyxis(Centropyxis)sp.	Millettella eocenica
Centropyxis (Centropyxis) sp.	Millettella elongata
aff. Centropyxis (Centropyxis) aculeata	Millettella spinata
Centropyxis(Centropyxis)sp.	Millettella glabrella
probably not belonging to the Thecamoebina	Millettella pleurostomelloides Lagunculina urnula
Difflugia urceolata	Lagunculina vadescens
Centropyxis(Centropyxis)sp.	Urnulina compressa
Difflugia sp.	Urnulina rotundata
probably not belonging to the Thecamoebina	Urnulina difflugiaeformis Proteonina difflugiaefor- mis var. limnetica
aff. Pontigulasia compressa	Proteonina eocenica
aff. Difflugia oblonga	Proteonina prolixa
Difflugia sp.	Proteonina lagenaria
Pontigulasia compressa	Proteonina hancocki

CENTROPYXIS - LEPTODERMELLA and MILLETTELLA

A. Description of Genera

Genus Centropyxis Stein, 1857

Genotype: Arcella aculeata Ehrenberg, 1838

Genus description (after Deflandre, 1929).—Test discoidal or oboval flattened at top and bottom, hemispherical or subhemispherical, ventral side more or less deeply invaginated at the aperture, dorsal side rounded. Aperture rounded or irregular, polygonal, lobate or even crenulated; central or excentric but always ventral. The test may be ornamented with a variable number of horns or spines though these are totally absent in several species. The test is chitinous often with a punctate appearance, more or less covered with minral grains or with particles of different sorts (e.g. diatoms) which are seldom completely absent.

Deflandre subdivides the genus into two subgenera which he describes as follows:

1. Cyclopyxis.—Test circular in dorsal and apertural views with a central aperture (therefore axially symmetrical); regularly domed.

Type species: Centropyxis arcelloides Penard 1902.

2. Centropyxis.—Test dorso-ventrally symmetrical with excentric aperture; more inflated towards the posterior end.

Type species: Centropyxis aculeata (Ehrenberg) 1838.

Genus Leptodermella Rhumbler, 1935

Genotype: Pseudarcella arenata Cushman, 1930

Genus description.—Test planoconvex, Arcella-like, circular when viewed from above and more or less cone-shaped from the side; base flat, dorsal side convex; wall very thin, glassy, keratinous with adherent grains. Aperture in middle of ventral side.

Genus Millettella Rhumbler, 1904

Genotype: Reophax pleurostomelloides Millett, 1899

Genus description.—Test egg-shaped, free; wall thin with fine sand grains on it. Aperture large, half moon shaped and placed in a depression slightly set back from the anterior end.

B. Description of Species recorded as Leptodermella Leptodermella salsa Cushman and Brönnimann, 1948

(Fig. 2, Nos. 8a, 8b)

Described from inshore mud of the brackish water mangrove swamps on the west coast of Trinidad.

The writers' work shows that, whereas in the habitat mentioned by Cushman and Brönniman (1948a) this



FIGURE 2: Some representative Thecamoebina from Trinidad Rivers All Figures \times 75

II rigures × 75

No. 1 Difflugia urceolata Carter; side view.

- 2 Difflugia capreolata Pénard; side view.
- 3 Difflugia oblonga Ehrenberg; side view.
- 4 Pontigulasia compressa (Carter); a) front view; b) side view.
- Centropyxis (Centropyxis) ecornis Leidy; a) apertural view; b) side view.
- 6 Centropyxis (Centropyxis) constricta (Ehrenberg); a) apertural view; b) side view.
- Centropyxis (Cyclopyxis) stellata Wailes; a) apertural view; b) side view.
- 8 Centropyxis (Cyclopyxis) sp; a) apertural view; b) side view.

species is very scarce, it is living in large numbers in the Island's rivers. The greatest density occurs in Zone I (see Figure 1) but the species is found infrequently all the way down into Zone IV. It is obvious that this is a fresh water form but whether it is able to live under the unfavourable conditions of the Brackish Zone would be difficult to prove due to its scarcity there.

Specimens of Leptodermella salsa sent to G. Deflandre were determined by him as Centropyxis (Cyclopyxis) sp. It remains to be checked whether this species has been described already under the Thecamoebina.

Another species with the same distribution as Leptodermella salsa is Centropyxis (Cyclopyxis) stellata Wailes (see Figure 2, Nos. 7a, 7b).

Leptodermella excentrica Cushman and Brönnimann, 1948

A species with more or less the same distribution as Leptodermella salsa. Due to its excentric aperture it belongs to Centropyxis (Centropyxis).

Leptodermella arenata (Cushman), 1930

Examination of a paratype from the Eocene Twigg's Clay (Cushman, 1945) shows that it belongs to the genus *Centropyxis* (*Cyclopyxis*). According to the literature, the samples were collected from "a gully at the head of a branch of Lamars Creek" which would suggest that the Eocene samples were contaminated with recent river mud.

Leptodermella turbanica Rhumbler, 1935

Rhumbler describes this form from mud in 15 m. of water in Kiel Bay. The illustrations show that it differs somewhat from the other described *Leptodermella* species. Possibly this is a true marine form as the locality suggests.

Leptodermella maestrichtiensis Visser, 1951

The illustration given by Visser is inadequate and the writers are thus not in a position to discuss this species.

Leptodermella variabilis Parker, 1952

Described from facies 1 of the Connecticut and Housatonic Rivers (for a further discussion of Parker's facies 1 see page 51 of this paper). The description states that the species has an asymmetrical, pouch-like test with the aperture placed at the upper part of the ventral side. From this and from a study of the illustrations (Parker 1952, Plate 1, Figures 11 and 12) it would appear that this species belongs to the genus *Centropyxis* (*Centropyxis*).

C. Description of Species recorded as Millettella Millettella eocenica Cushman, 1945

Described from the Eocene Twigg's Clay of Georgia. Having examined a paratype it is apparent to the writers that this is a *Centropyxis* (*Centropyxis*) derived from river mud in the same way as *Leptodermella* arenata described from the same locality.

Millettella elongata Cushman, 1945

Again described from the Twigg's Clay. No material was available for study as there exists only a single specimen in Cushman's collection, but description and illustrations make it clear to the writers that it belongs to *Centropyxis* (*Centropyxis*).

Millettella spinata Cushman and Cahill, 1933

The figures given by Cushman and Cahill (1933) show that this form is very near to Centropyxis (Centropyxis) aculeata.

Millettella glabrella Cushman and McCulloch, 1939

This species was described from 4 fathoms in San Francisco Bay, Colombia. Examination of a paratype shows that this is a *Centropyxis* (*Centropyxis*) and it can only be presumed that fresh water forms have been introduced to this shallow water, marine locality by rivers.

Millettella pleurostomelloides (Millett), 1899

Described from marine stations in the Malay Archipelago. Having not seen any of the original material and not knowing the exact localities, the writers do not wish to comment on this species. However, the figures given suggest that it could belong to *Centropyxis* (*Centropyxis*).

DIFFLUGIA - LAGUNCULINA, URNULINA and PROTEONINA

A. Description of Genera

Genus **Difflugia** Leclerc, 1815

According to a written communication from G. Deflandre, he is engaged at the moment on a revision of this genus. From the literature it can be seen that there are already several subgenera in existence; in the following discussion all species are treated as belonging to $Difflugia \, s. \, l.$

In a broad sense the test of *Difflugia* may be defined as follows: fusiform with anterior end either truncated or drawn out to form a neck. Posterior end either rounded, with or without spines, or drawn out into a single central spine. Aperture rounded or polygonal, entire, lobate or crenulate; some species having a lip. Chitinous wall covered with mineral grains.

Genus Lagunculina Rhumbler, 1904

Genotype: Ovulina urnula Gruber, 1884

Genus description.—Flask shaped with a broad neck turning over at the aperture to form a lip. Test consisting of very fine sand grains, those at the aperture being smaller and less closely fused than those on the rest of the test.

Genus Urnulina Gruber, 1884

Genotype: Urnulina difflugiaeformis Gruber, 1884 Genus description.—Small, urn-shaped, composed of closely fused sand particles. Posterior end somewhat pointed, middle portion inflated and anterior end narrower. Aperture at anterior end, wide, circular and surrounded by a fine regular rim.

Genus Proteonina Williamson, 1858

Genotype: Proteonina fusiformis Williamson, 1858

Genus description.—Shell free, irregular, fusiform, or compressed and with a slight disposition in its young state to become convoluted; arenaceous. Septal orifice at the extremity of the shell, single, irregular in size and form.

B. Description of Species recorded as Lagunculina Lagunculina urnula (Gruber), 1884

Described from the harbour of Genoa where it was found living in a marine habitat. Gruber was aware of the existence of the fresh water genera *Difflugia* and *Pseudodifflugia* which he mentions as differing from the marine *Lagunculina* mainly in structure and behaviour of the protoplasm.

Lagunculina vadescens Cushman and Brönnimann, 1948

(Fig. 2, No. 1)

This form was described from inshore mud of the brackish water mangrove swamps of the west coast of Trinidad. Whereas the species is rare in the habitat given by Cushman and Brönnimann (1948a), the present writers found it living in large numbers in rivers where it is especially abundant in Zone II (see Figure 1) though occurring infrequently down to the Brackish Zone. It seems probable that those individuals found in the latter have been washed down the river and probably are not living there.

Specimens of Lagunculina vadescens sent to G. Deflandre by the writers were identified by him as Difflugia urceolata Carter.

C. Description of Species recorded as Urnulina Urnulina compressa Cushman, 1930

Described from the Miocene Choctawhatchee formation of Florida. According to the type description the sample was collected from a creek.

Since the aperture lacks a rim and is set back slightly from the anterior end, this species does not fit Gruber's description of the genus Urnulina. Furthermore, closely allied if not identical forms referred to the genus Centropyxis (Centropyxis) can be found in the rivers of Trinidad. The present writers suspect that there has been contamination of the type sample with recent, fresh water material.

Urnulina rotundata Cushman and Cahill, 1933

Described from the Miocene of the Eastern United States. Judging from illustrations and description (Cushman and Cahill, 1933, Plate 1, Figures 4a, 4b) this is a species of *Difflugia*.

Urnulina difflugiaeformis Gruber, 1884

Like Lagunculina urnula, Gruber described this species from the harbour of Genoa. Only one specimen was found with protoplasm preserved. Further studies would be required to prove whether or not this is a case of contamination from a fresh water source.

D. Description of Species recorded as Proteonina Proteonina difflugiaeformis var. limnetica Hada, 1937

Described from a small lake of very low salinity connected with the mouth of the Sendai River in Japan. This habitat and the figures given (Hada, 1937, Textfig. 5) suggest that this species might be a *Difflugia*.

Proteonina eocenica Cushman, 1945 (Fig. 2, Nos. 4a, 4b)

This species described from the Eocene Twigg's Clay of Georgia obviously has to be considered in conjunction with the other Thecamoebina from this locality. The writers have examined paratypes which belong to the genus *Pontigulasia* and it is probable that the species is close to *Pontigulasia compressa* (Carter) a form found especially abundantly in the writers' Zone I. *Pontigulasia* differs from *Difflugia* in that it has a laterally compressed test.

Proteonina prolixa Cushman, 1945 (Fig. 2, No. 3)

Paratypes from the Twigg's Clay have been examined. In shape and general appearance they are very close to *Difflugia oblonga* Ehrenberg though the latter is larger.

Proteonina lagenaria (Berthelin), 1880

The original type was described by Berthelin from a Lower Cretaceous sample taken from a river bank in France. He recorded that the species was extremely rare. From a study of description and illustrations and taking into consideration the type locality, the writers consider that this is almost certainly a recent species of *Difflugia*.

References are made to the presence of *Proteonina* lagenaria in recent samples by Cushman and McCulloch (1939), Parker (1952) and Parker, Phleger and Peirson (1953). At first glance the comparison of recent types with a Lower Cretaceous species might seem strange. However, taking into account the fact that Berthelin's species is almost certainly a recent form, there is more justification for the comparison.

Proteonina hancocki Cushman and McCulloch, 1939 (Note: Proteonina hancocki is a new name for Proteo-

nina compressa Cushman and McCulloch, 1939)

The species was described originally by Cushman and McCulloch (1939) from Ketchikan, Alaska and subsequently by Parker (1952) from facies 1 in the Connecticut River. Very similar if not identical forms have been found by the present writers in great numbers in Zone I of Trinidad rivers. A number of specimens sent to G. Deflandre were identified by him as *Pontigulasia compressa* (Carter).

REFERENCES TO LITERATURE IN WHICH THECAMOEBINA HAVE BEEN DESCRIBED ERRONEOUSLY AS FORAMINIFERA

Several references have been made to Cushman's publication on the Eocene Twigg's Clay of Georgia (1945). The Thecamoebina described as Foraminifera (Plate I, Figures 1-6) are quite foreign to the otherwise entirely calcareous, fossil fauna. This suggests contamination.

Another paper mentioned before is by Cushman and Cahill (1933) in which a Miocene age was attributed to a number of forms which, in the writers' opinion, are recent Thecamoebina (Plate I, Figures 2-5).

As regards Cushman (1930), it is apparent that at least some of the species described as Miocene, marine Foraminifera are in reality recent, fresh water Thecamoebina (Plate I, Figures 3a, 3b).

Under the descriptions of Leptodermella salsa, Leptodermella excentrica, and Lagunculina vadescens will be found references to Cushman and Brönnimann (1948a, 1948b). Investigations by the writers show that the above forms are, in reality, fresh water Thecamoebina found in great numbers in Trinidad rivers.

A paper that includes a number of forms discussed here is that by Parker (1952). It is interesting to note that the species considered by the writers as belonging to the Thecamoebina (Proteonina hancocki, Proteonina lagenaria, Proteonina sp. B, Lagunculina vadescens, Urnulina compressa, Urnulina difflugiaeformis and Leptodermella variabilis) are all confined to Parker's facies 1. This facies is developed best in the Connecticut River mouth and to a lesser extent in the Housatonic River mouth where very low salinity values are recorded. The only exception to the above distribution is Proteonina lagenaria which occurs also in facies 2 though at much lower percentages. Apart from the above mentioned forms, facies 1 contains such brackish water types as Ammoastuta salsa and Miliammina fusca. As Parker points out, a close parallel may be drawn between these Long Island Sound area facies and the brackish facies faunas of Trinidad. It is the present writers' belief that sampling in the fresh water sections of the Connecticut and Housatonic Rivers would reveal the presence and real habitat of the Thecamoebina as has been found to be the case in Trinidad.

The paper by Parker, Phleger and Peirson (1953) contains references to a number of types under discussion (Lagunculina vadescens, Lagunculina sp., Leptodermella variabilis, Proteonina lagenaria, Urnulina compressa, Urnulina sp. A and Urnulina sp. B as shown on Plate I, Figures 1-3 and 5-10). These authors group the environments under 4 facies headings of which their River Facies, comprising samples from the Guadaloupe Delta, is characterised by the above forms. By analogy with Trinidad conditions the present writers would expect to find these species, which at best are not common here, increasing greatly in frequency as soon as the fresh water portion of the river is reached. Again it remains to be proved whether these forms found in waters of low salinity within the delta are living under these conditions or have been carried down the river from their normal fresh water habitat.

Cushman and McCulloch (1939) describe arenaceous Foraminifera from off the west coast of North and South America. In this paper the present writers find a number of species that would appear to belong to the Thecamoebina. They are as follows: Proteonina difflugiaeformis var. lagenaria, Proteonina compressa, Millettella spinata, Millettella glabrella and Leptodermella arenata. All these forms, with the exception of Leptodermella arenata, occur together in a sample taken in 8 fathoms off the wharf at Ketchikan in Alaska. From the illustrations it is quite definite that they are Thecamoebina in which case they must have been washed in by a river, though without more knowledge of the locality this cannot be proved.

A publication in which Thecamoebina have been recognised as such is that by Lowman (1949). He discusses the distribution of recent foraminiferal species in the Mississippi Delta region. The landward end of his area of sampling is covered by fresh water cypress swamps and grassy marsh. Here he records that Foraminifera are absent but that their place is taken by "their close relatives *Difflugia* and *Centropyxis*." In Lake Salvador, where he obtained salinity figures as low as 0.1 parts/thousand, the fresh water thecamoebian fauna had given way already to a brackish foraminiferal fauna consisting predominantly of the genus *Ammobaculites*.

CONCLUSIONS

The writers hope that this note will serve its purpose in so far as it draws attention to a number of taxonomic errors that have arisen. The errors arose due to the fact that where contamination of foraminiferal faunas with Thecamoebina had occurred, it was not recognised. The similarity between the tests of Thecamoebina and certain genera of the Saccamminidae led to the description of the former as Foraminifera.

The ease with which contamination can occur is well illustrated here in Trinidad where there are many cases on record of recent Thecamoebina in river outcrop samples and even in auger samples. In the latter case, the river water used as a lubricant while drilling the holes seems to have caused the contamination. Where barren beds are being drilled, Thecamoebina derived from the water may constitute the entire fauna. Before the true nature of these forms was realised, attempts were made to use them as stratigraphic markers.

As Thecamoebina are known not only from rivers and lakes but also from swamps, peat bogs and other moist places, the difficulty of preventing the contamination of field samples is considerable. The best solution seems to be an awareness of the existence of such forms and a knowledge of what their presence implies. When studying recent, foraminiferal material from the lower reaches of rivers and from estuaries it seems essential that some sampling is done in the fresh water sections of these same rivers. From this, an indication may be obtained of the fauna that is likely to be carried down into the brackish water sections and even out into adjoining bays.

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CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH Volume V, Part 2, April, 1954

101. CHITINOSIPHON, A NEW GENUS OF THE RHIZAMMINIDAE Hans E. Thalmann and Pedro J. Bermudez

In various bottom samples, taken by the expeditions in 1938 and 1939 of the "Atlantis" under the joint auspices of the Universidad de la Habana and Harvard University in the waters surrounding Cuba, the following genus of monothalamous Foraminifera, of the family Rhizamminidae, was observed at depths ranging from 285 to 1800 fathoms:

Chitinosiphon Thalmann and Bermudez, n. gen.

Genoholotype.—(monotypic): Chitinosiphon rufescens Thalmann and Bermudez, n. sp.

Diagnosis.—A new genus of the family Rhizamminidae, characterized by its free, slightly curved, tubular test with entirely chitinous wall and terminal aperture.

Occurrence.—Frequent, in moderate to deep water. Description.—See description of the genoholotype below.

Remarks.—This new genus is related to Bathysiphon M. Sars, 1872, but differs from it by its entirely chitinous wall of the test. In Bathysiphon the wall consists of a fine arenaceous paste, often with inclusion or agglutination of minute sponge spicules, or spicules from other marine organisms. Most authors, as f.i. Cushman (1950), Galloway (1933), Höglund (1947), Avnimelech (1952), and others, who have described representatives of Bathysiphon state, that this genus is provided with two apertures, a proximal and distal one at each end of the tubiform test. In our material from the "Atlantis"-Expedition, however, numerous juvenile specimens of Bathysiphon rufus Folin occur in which the test begins undoubtedly with a small slightly inflated proloculus. Such a proloculus is observed not only in Chitinosiphon but also in the majority of other tubular Foraminifera. The proloculus is followed by a tubular test with a single aperture at its distal end. The incorrect statement regarding the presence of two apertures in Bathysiphon can be ascribed to the circumstance that nearly all specimens pertaining to this genus are found as fragments, as is also the case in most fossil ones.

Chitinosiphon rufescens Thalmann and Bermudez, n. sp.

Description.—Test free, delicate, very elongate, cylindrical, thin, strongly tapering towards initial part, slightly curved, with small ovaliform, slightly inflated proloculus followed immediately by a long tubular test with occasional node-like thickening and feeble constrictions, possibly caused by seasonal growth; wall thin, entirely chitinous, solid, resistant, with highly polished surface (hammer finish), and of deep brownish-red color; aperture rounded, terminal, open, somewhat smaller than the maximum diameter of the test.

Measurements.—(in millimeters, made by K. Küpper): Holotype (Text fig. 1): Length: 3.14; aperture: 0.10; greatest width (distal part of test): 0.13; smallest width (just after proloculus): 0.07.

Paratypes (Text figs. 2, 3 and 4): Length: 2.90, 2.26, and 1.49 respectively; aperture: 0.07, 0.07, 0.07 respectively; greatest width (distal part of test): 0.13, 0.13, 0.13 respectively; smallest width (just after pro-loculus): 0.07, 0.08, 0.07 respectively.

Holotype.-Text fig. 1.

Paratypes.-Text figs. 2, 3, and 4.

Occurrence.—In rich pteropod mud at a depth of 1600-1800 fathoms off Baracoa, Eastern Cuba, Atlantic Ocean. Harvard-Havana "Atlantis"-Expedition Station 2970, approx. Lat. 20° 27' N, Long. 74° 26' W. Frequent.



Text Figs. 1-4: Chitinosiphon rufescens Thalmann and Bermudez, n. gen., n. sp., Recent, off Cuba. Fig. 1: Genoholotype; Figs. 2-4; Paratypes. All \times 25. (Drawn by Guillermo Colom).

The species occurs also at the following stations:

- Station 2952 Lat. 21° 52' N., Long. 85° 00' W. at 570 fathoms, Yucatan Basin of the Caribbean Sea, off western end of Cuba.
- Station 2953 Lat. 21° 47′ 30″ N., Long. 84° 32′ 30″ W., same basin, 617 fathoms.
- Station 2954 Lat. 21° 51' N., Long. 84° 34" W., same basin, 900 fathoms.
- Station 2967 Lat. 19° 47' N., Long. 75° 06' W. Off Bahia de Guantamano, East Cuba, 1530 fathoms.
- Station 2969 Lat. 19° 47' N., Long. 74° 59' W., same as preceding station, 1075-1145 fathoms.
- Station 3374 Lat. 20° 45' N., Long. 75° 19' W., off northeastern tip of Cuba, Atlantic Ocean, 300 fathoms.
- Station 3376 Lat. 20° 44′ 30″ N., Long. 75° 18′ W., same as preceding station, 285 fathoms.

Depository.—Holotype (text fig. 1) and Paratypes (Text figs. 2-4); Cushman Collection, U. S. National Museum, Washington, D. C.; Topotypes: Department of Micropaleontology, American Museum of Natural History, New York, Collections of Creole Petroleum Corporation, Caracas, and Bermudez Collection.

The holotype has been given Cushman Collection number 64581 and the other three specimens (Text figs. 2-4) numbers 64582, 64583, and 64584, respectively.

Remarks.—The species is easily recognizable in the foraminiferal assemblages due to the deep brownishred color and the delicate, although resistant, chitinous test. In all stations the specimens were well preserved.

In its general long and slender form *Chitinosiphon* rufescens resembles *Bathysiphon argenteus* Heron-Allen and Earland, 1913. The test of the latter species (Recent, off Ireland), however, is built up of minute

spicular, rod-like bodies of uniform size, possibly of crystalline origin and presumably secreted by the organism itself. Bathysiphon argillaceus Earland, 1934, from the Antarctic region has a test made of very fine mud or clay and the form of the tubular test does not taper towards the proloculus. Bathysiphon capillaris Folin, 1886, from the Gulf of Gascogne, France, makes its test with a paste of quartz dust, as is the case with B. rufus Folin, 1886, from the same Gulf, and which attains a much larger size (5 to 12 millimeters), and also includes minute spicules in the paste of quartz dust used as building-material for the test. Bathysiphon flexilis Höglund, 1947, although having the same slender tubiform test and the same size as Chitinosiphon rufescens, constructs the wall of its test with several layers of extremely minute and thin mica (?)plates embedded in a muddy mortar-mass or paste.

Chitinosiphon rufescens is, so far, the only entirely chitinous representative of the family Rhizamminidae.

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CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH Volume V, Part 2, April, 1954

102. UPPER CRETACEOUS ORBITOIDAL FORAMINIFERA FROM CUBA

PART I. Sulcorbitoides n. gen.

P. Bronnimann

Habana, Cuba¹

Upper Cretaceous strata of Cuba yield a rich and extraordinary orbitoidal² fauna of which the genera Vaughanina, Pseudorbitoides, Orbitoides, Omphalocyclus, Torreina, Asterorbis, and Lepidorbitoides s.l. have been reported. Notwithstanding the classic study of D. K. Palmer (1934), and the later researches of M. G. Rutten (1935), Thiadens (1937), Vaughan and Cole (1943), and others, the generic features and the stratigraphic distribution of some of these genera are not well known. They deserve a critical revision based on a detail morphologic investigation of the individual species.

Furthermore, the rotaliform genus Sulcoperculina must be considered in such a revision, for it is shown to be the ancestor of Vaughanina and related groups. Sulcoperculina is represented by a number of widely distributed species. Possibly its significance for the stratigraphy of the Caribbean Upper Cretaceous may be similar to that of Nummulites for the stratigraphy of the European Tertiary.

In addition to the genera mentioned, other undescribed orbitoidal genera occur in the Upper Cretaceous of Cuba. This paper, the first in a series of studies on these Foramin fera, contains the description of Sulcorbitoides n. gen., which is related to Sulcoperculina Thalmann 1938, and to Vaughanina Palmer 1934. The family relationship of Sulcorbitoides is not yet known. The new genus is therefore provisionally assigned to the Pseudorbitoidinae M. G. Rutten 1935, a subfamily of the Orbitoididae Schubert 1920. Its systematic position will be clarified in the course of the revision of Vaughanina and of Pseudorbitoides H. Douvillé 1922.

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The described material has been collected by G. Flores, P. Truitt and H. Wassall, geologists of Gulf Oil Corporation in the course of fieldwork in Camagüey and Las Villas Provinces. The original samples are in the collections of Cuban Gulf Oil Company, Habana. The holotype and figured material will be deposited in the U. S. National Museum, Washington, D.C., U.S.A.

Family ORBITOIDIDAE Schubert, 1920 Subfamily PSEUDORBITOIDINAE M. G. Rutten, 1935

Genus Sulcorbitoides Bronnimann, n. gen.

Genotype: Sulcorbitoides pardoi Bronnimann n. sp. Definition.-The orbitoidal adult test is divided into a single equatorial layer and two lateral layers. The lateral layers completely cover the equatorial layer. The sulcoperculinoid juvenarium consists of a bilocular embryo and a single periembryonic spiral of variable length. Radial stolons pierce the outer walls of the periembryonic chambers in the plane of the equatorial layer. The neanic stage is characterized by two alternating systems of vertical radial plates, which project from both sides into the equatorial layer. The two systems are separated by a narrow median gap. Toward the periphery, the radial plates may develop irregularities. Radial plates from the top and bottom of the equatorial layer may fuse, or may become longer until they cut across the equatorial layer. The lateral chambers rest directly on the radial plates. The equatorial layer is not limited toward the lateral layers by roof and floor. There are no annular walls. The neanic stage is short in comparison with the juvenarium. The quotient of diameter of the juvenarium and diameter of the test ranges from about 0.2 to about 0.9 (see p. 59 of this paper). The equatorial layer is not divided by "additional floors" into horizontal divisions. Lateral chambers are arranged in regular tiers of two to nine layers. They are connected by basal stolons and by fine pores. Pillars are present.

Diagnosis.—Sulcorbitoides differs from Sulcoperculina Thalmann 1938, by the orbitoidal features in the adult, and from Vaughanina Palmer 1934, by the absence of annular walls, and of floor and roof of the equatorial layer. The revision of the morphologic features of Vaughanina (in press) has shown that the two genera are related. The following comparison between Sulcorbitoides and Vaughanina is based on the results of this revision:

¹ Gulf Oil Corporation.

² Orbitoidal is herein used in its widest sense as including all foraminiferal tests which can be divided in an equatorial layer and two layers of lateral chambers or the homologues of these parts.

	Juvenarium	Neanic stage
Sulcorbitoides	Sulcoperculinoid.	Two alternating systems
	Long compared	of vertical radial plates.
	with neanic	Annular walls absent.
	stage.	Lateral chambers rest
		directly on the radial
•		plates of the equatorial
		layer. Lateral cham-
		bers cover the equato-
		rial layer completely.
Vaughanina	Sulcoperculinoid.	Two alternating systems
	Short compared	of vertical radial plates.
	with neanic	Annular walls present.
	stage.	Lateral chambers and
		radial plates are sep-
		arated by roof and floor
		of the equatorial layer.
		Lateral chambers do not
		completely cover the
		equatorial layer.
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Sulcorbitoides and Vaughanina are regarded as two different lineages both derived from Sulcoperculina Thalmann.

Occurrence.-Cuba, Texas.

Age.—Upper Cretaceous.

Sulcorbitoides pardoi Bronnimann, n. sp. Plates 9-11; Text figures 1-5

Vaughanina sp. or Pseudorbitoides sp., DE VLETTER, 1946, Thesis, Utrecht, p. 12, pl. 3, figs. 1-3.

Holotype.—S. pardoi Bronnimann, fig. 5, pl. 10; Upper Cretaceous (Turonian-Maestrichtian), Cuba. CUGOC Ser. No. 12337 B, Section of Arroyo Hondo, near town of Camagüey, Camagüey Province, Cuba. The species is named for G. Pardo, chief geologist of Cuban Gulf Oil Company.

Exterior.—Free specimens have not been found. Thin sections indicate that the test is lenticular and more or less strongly umbonate. The surface is papillate. The outline is finely pectinate (fig. 5, pl. 10). The diameter of the tests ranges from 0.5 to 1.7 mm., and the thickness from 0.4 to 1.1 mm.

Interior.—The morphologic description of the interior is based on many oblique and a few oriented sections. Exactly centered sections have not been encountered.

In order to facilitate the description and the understanding of the morphology of this unusual foraminifer a model of a part of the equatorial layer covered on one side by a few lateral chambers is presented in text fig. 5. Equatorial section .---

1) Juvenarium. Horizontal sections of the megalospheric sulcoperculinoid juvenarium are illustrated by figs. 1, 3 of pl. 9 and by fig. 5 of pl. 10. Microspheric specimens have not been encountered. Although one of the specimens (fig. 1, pl. 9) is tangentially cut, it displays a bilocular embryo, consisting of a subspherical protoconch and an arcuate deuteroconch, followed by a single nepionic spiral of more than 30 chambers arranged in almost three volutions. Other figured horizontal sections do not exhibit the embryonic chambers. The specimens illustrated by fig. 3 of pl. 9, and by fig. 5 of pl. 10, have about 20 to 30 spiral chambers arranged in two to three volutions. The spiral chambers increase gradually in size; however, the last chamber or chambers may be smaller than the preceding ones. The septa of the periembryonic chambers consist of two thin lamellae which enclose fissural or vacuolar lumina, which communicate with the equatorial layer (figs. 1, 2, pl. 9). As in Sulcoperculina, an intramural system of true canals seems to exist.

2) Neanic stage. The neanic stage is characterized by two alternating systems of vertical radial plates. They project from both sides into the equatorial layer and are separated by a narrow median gap. The plates and the median gap are best seen in excentric vertical and in oblique vertical sections (text figs. 3, 4). In oblique equatorial sections, the median gap can be detected by groups of abruptly ending and abruptly beginning radial plates (fig. 5, pl. 10). This characteristic pattern produced by the radial plates in equatorial section is a feature differentiating Sulcorbitoides from the Cuban Upper Cretaceous orbitoidal Foraminifera, which were described and figured by M. G. Rutten (1935) as Pseudorbitoides israelskyi¹ Vaughan and Cole 1932 and Pseudorbitoides trechmanni H. Douvillé 1922. Only the very early ontogenetic stage of these orbitoids has the two systems of vertical radial plates separated by the median gap; in the later ontogenetic stage it is superseded by a single system of radial plates. The irregularities in the structure of the radial plates toward the periphery in Sulcorbitoides (see p. 58 of this paper) can be interpreted as the initial stage of the development of the single system of radial plates, typical of the forms described by M. G. 1 The species name "israelskii" was formed by Vaughan

and Cole (1932) for Merle C. Israelsky. It should be spelled "israelskyi."

FIGS.

EXPLANATION OF PLATE 9

PAGE

FIGS. 1-4 Sulcorbitoides pardoi n. sp. All from CUGOC Ser. No. 12337 B, Section of Arroyo Hondo, near town of Camagüey, Camagüey Province. All approx. 80 \times .

- 1, 3. Oblique equatorial sections displaying the large sulcoperculinoid initial stage, radial plates of the equatorial layer and lateral chambers. The irregular pattern of the radial plates is in the lower right side of fig. 3. No annular walls exist.
- right side of fig. 3. No annular walls exist. 55 2, 4. Vertical sections with low elongate lateral chambers. The Sulcoperculina-stages are large, with distinct sulci and the equatorial layers short. The equatorial layer of fig. 2 shows the lower and upper radial plates and the median gap. The equatorial layer is short and slightly wedge-shaped. 56,57



Bronnimann: Upper Cretaceous Sulcorbitoides from Cuba

Plate 10



Bronnimann: Upper Cretaceous Sulcorbitoides from Cuba

Rutten, which evidently are directly related to Sulcorbitoides. The relationship between Sulcorbitoides and the species referred to by Rutten will be discussed after the morphologic revision of topotypes of P. trechmanni and P. israelskyi. De Vletter (1946, pl. 3, figs. 1-3) figured three oblique sections of an orbitoid from Upper Cretaceous tuff series of Oriente Province, Cuba, which he considered to belong either to Pseudorbitoides H. Douvillé or to Vaughanina Palmer. The photographs show lateral chambers and radial plates. The irregular arrangement of the coarse radial plates, especially on the right side of his fig. 3, suggests the existence of a median gap. The oblique thin section of a Sulcorbitoides pardoi n. sp. (pl. 11, fig. 10) from Las Villas Province, displays a similar arrangement of the radial plates as de Vletter's thin section (pl. 3, fig. 3). De Vletter's specimens are definitely representatives of Sulcorbitoides, and being comparable in the other features to Sulcorbitoides pardoi, they are herein tentatively assigned to this species.

Two systems of vertical radial plates, separated by a median gap, are also found in the sulcus of Sulcoperculina dickersoni (Palmer) 1934 and of Sulcoperculina cubensis (Palmer) 1934. However, the plates are much shorter than in Sulcorbitoides. They are shown by Palmer's figures of the sideviews of a cotype of S. dickersoni and of the holotype of S. cubensis (1934, figs. 6, 7, pl. 14) and by the horizontal section of S. dickersoni illustrated by fig. 12 of pl. 11 of this paper. Radial plates in the sulcus of the later whorls are also figured by the horizontal sections of Sulcoperculina obesa de Cizancourt 1949 (de Cizancourt, 1949, fig. 9, pl. 24) and of S. dickersoni and varieties (Cole, 1947, figs. 1-9, pl. 2). Cole (1942, p. 640) mentions in the description S. dickersoni "two rows of closely packed plates" which are the two systems of radial plates described in this paper.

The sulcus of *Sulcoperculina* and of the neanic stage of the equatorial layer of *Sulcorbitoides* are morphologically equivalent.

Annular walls do not exist in *Sulcorbitoides*, and thus no chambers are formed as in the equatorial layer of *Vaughanina*.

Vertical section.-

Vertical sections (pl. 9, figs. 2, 4; pl. 10, figs. 1, 3, 6, 9) display the prominent sulcoperculinoid juvenarium, the comparatively short equatorial layer and the lateral chambers. In the material studied, the number of layers of lateral chambers varies from two or three to about ten. A series of specimens, arranged according to the number of lateral layers, is illustrated by the vertical sections figs. 2-7 of pl. 11. Figures 2 and 3 show two or three layers, and figure 7 about ten layers of lateral chambers.

There are two types of lateral chambers, which are rather low and arranged in regular tiers. One type, represented by figs. 2 and 4 of pl. 9 and by fig. 9 of pl. 10, is characterized by relatively thin-walled and open lateral chambers. The other type, illustrated by fig. 1 of pl. 10 and by fig. 2 of pl. 11, has thicker chamber walls and smaller chamber cavities.

These differences in the lateral chambers are striking and possibly may be used for further taxonomic division. For the present, however, the two types are grouped together in the same species.

The initial Sulcoperculina-stage is asymmetric, trochospiral. The "ventral" side carries a strong axial plug. In centered vertical sections the sulcus is a peripheral V-shaped indentation (figs. 2, 4, pl. 9; fig. 1, pl. 10). Two or three parallel lines represent the sulcus in excentric vertical sections (figs. 1, 8 and 9, pl. 11). A portion of the tangentially cut sulcus represented by two parallel lines in the center, and four sep-

FIGS.

EXPLANATION OF PLATE 10

FIGS. 1-9 Sulcorbitoides pardoi n. sp.

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Figs. 1, 3, 5, 6, 8, 9 from CUGOC Ser. No. 12337 B, Section of Arroyo Hondo, near town of Camagüey, Camagüey Province.

- Fig. 2 White's Asphalt Quarry, 4.5 miles southwest of Blewett, Uvalde County, Texas. (Donated by A. Carter).
- Figs. 4, 7 from CUGOC Ser. No. 15396, Santa Clara area, Las Villas Province.

1. Vertical section of worn specimen with thick walled and low lateral chambers. The Sulcopercu-

- lina-stage is large, with distinct sulci. 76 ×.
- 2. Rock thin section of Anacacho limestone, with oblique equatorial and vertical sections. $27 \times \dots 57,60$
- 3. Vertical section with reduced Sulcoperculina-stage. The same figure contains also an oblique verti-
- cal section of Sulcoperculina cf. vermunti (Thia dens). $28 \times .$ 57 59 4, 7. Excentric vertical sections showing the two alternating systems of radial vertical plates. $66 \times .$ 60

 - Oblique vertical section with few radial plates on the right hand side. The sulcus is deeply incised.
 28 ×.

 - Excentric vertical section, displaying a portion of the sulcus of the previous whorl (the two parallel lines in the center), and the basal apertures of the final whorl of the Sulcoperculina-stage. The apertures are asymmetric in regard to the position of the sulcus. 77 ×.



TEXT FIGURES 1-5

tal apertures are shown by the excentric vertical section reproduced by fig. 9 of pl. 10. The apertures of the Sulcoperculina-stage are on the "ventral" side, asymmetric in respect to the sulcus. This agrees with the observations made by Cole (1947, p. 12) who described the aperture of Sulcoperculina dickersoni (Palmer) as being asymmetric. In a specimen with a large Sulcoperculina-stage and few layers of lateral chambers, axial plugs are developed on both sides of the test (fig. 3, pl. 11). Toward the periphery, the axial plugs appear to split and to form the pillars of an orbitoidal test. Occasionally, the axial plugs exhibit long, thin canals. The Sulcoperculina-stage of Sulcorbitoides pardoi is similar to the small tests of a thickwalled, strongly trochospiral Sulcoperculina, associated with Sulcorbitoides pardoi (figs. 3, 8, pl. 10; fig. 11, pl. 11). This Sulcoperculina species appears to be related to Sulcoperculina vermunti (Thiadens) and Sulcoperculina sp. described by de Cizancourt (1949, figs. 1, 12, 14, pl. 24) from the Upper Cretaceous of San Sebastian, State of Guarico, Venezuela.

By comparing the vertical and slightly oblique vertical sections, one obtains the impression that a distinct relationship exists between

- a) the diameter of the juvenarium,
- b) the diameter of the neanic stage (equatorial layer), and
- c) the number of layers of lateral chambers.

Individuals with a large initial portion have a small number of lateral layers and a short neanic stage. On the other hand, individuals with a small juvenarium have many lateral layers and a long neanic portion of the equatorial layer. An index characteristic of this relationship is the quotient of diameter of juvenarium and diameter of test.

		TABLE	1	
Number of	Diameter	Thickness	Diameter of	Diameter of
layers of	of test	of test	juvenarium	juvenarium
lateral	in mm	in mm	in mm	Diameter of
chambers				test
2-3	1.457	0.896	1.155	0.79
	0.770	0.410	0.640	0.83
3	0.704	0.570	0.512	0.73
4	1.092	0.767	0.640	0.59
5	1.150	0.832	0.670	0.58
	0.895	0.576	0.512	0.57
6	1.280	0.778	0.640	0.60
	1.089	0.960	0.641	0.54
	1.402	0.770	0.640	0.45
	1.150	0.640	0.512	0.44
7	1.150	0.920	0.500	0.43 ·
8	1.150	0.962	0.512	0.44
9	1.660	1.030	0.384	0.23
10	1.150	0.896	0.256	0.22

mintr -

The quotient of the diameter of juvenarium and the diameter of test ranges in the tabulated specimens from 0.22 for a test with ten layers of lateral chambers and a small juvenarium to 0.83 for a test with two to three layers of lateral chambers and a large juvenarium. High quotients indicate primitive individuals with a large Sulcoperculina-stage and a low number of lateral layers. Low quotients indicate advanced individuals in which the Sulcoperculina-stage is reduced in relation to the orbitoidal neanic development. The degree of reduction of the nepionic stage therefore can be expressed numerically, and by applying Tan's principle of nepionic acceleration (1935), the phylogenetic position of a certain Sulcorbitoides population can be established by the determination of the quotients of the dimensions of juvenarium and test. The measurements can be taken in more or less centered vertical and oblique ver-

TEXT FIGURE 1 Sulcorbitoides pardoi n. sp.

CUGOC Ser. No. 12333, Section of Arroyo Hondo, near town of Camagüey, Camagüey Prov., Cuba; $100 \times$. Excentric vertical section across the sulcus showing the initial stage of the two alternating systems of radial plates.

TEXT FIGURE 2 Sulcorbitoides pardoi n. sp.

CUGOC Ser. No. 12333, Section of Arroyo Hondo, near town of Camagüey, Camagüey Prov., Cuba; $100 \times$. Slightly excentric vertical section across the *Sulcoperculina*-stage showing sulci and vertical radial plates.

TEXT FIGURE 3 Sulcorbitoides pardoi n. sp.

a) CUGOC Ser. No. 12333; b-f) CUGOC Ser. No. 12327; All from Section of Arroyo Hondo, near town of Camagüey, Camagüey Province, Cuba; all 100 \times . Oblique and excentric vertical sections across the equatorial layer displaying the two alternating systems of vertical radial plates. The lateral chambers are resting directly on the radial plates.

TEXT FIGURE 4 Sulcorbitoides pardoi n. sp.

CUGOC Ser. No. 12327, Section of Arroyo Hondo, near town of Camagüey. Camagüey Province, Cuba; $100 \times$. Slightly oblique section across the nearic stage exposing the two systems of radial plates separated by the median gap, and stolons (stippled) leading from the peri-embryonic chamber into the equatorial layer.

TEXT FIGURE 5 Sulcorbitoides pardoi n. sp.

Model of a portion of the equatorial layer near the juvenarium, covered by a few lateral chambers. The front of the model is directed toward the periphery of the test. The right side of the model cuts across the sulcus of the *Sulcoperculina*-stage.

tical sections where the sulci appear as peripheral Vlike indentations. Such sections are often common in a single rock thin section. This method does not require the time-consuming preparation of oriented thin sections of individual specimens and, therefore, can be used in routine work.

Excentric vertical sections (pl. 10, figs. 4, 7; text figs. 1, 3) exhibit the two alternating systems of vertical radial plates. The radial plates of *Sulcorbitoides* are short and thick and the pattern is much coarser than in *Vaughanina* Palmer.

Near the periembryonic chambers, the radial plates are almost indiscernible (pl. 11, fig. 9; text fig. 1). They grow somewhat irregularly toward the periphery. Plates from the top and bottom of the equatorial layer seem to fuse, or to grow longer and to cut across the equatorial layer. The median gap disappears in places, and the two systems of radial plates can no longer be clearly distinguished. The lateral chambers rest directly on the radial plates (text fig. 3). Floor and roof of the equatorial layer are not developed; however, the thick walls of the low elongate lateral chambers resting on the radial plates may give the impression of a separating wall between equatorial layer and lateral layers (text figs. 1, 3).

The equatorial layer is single throughout. There are no annular walls, and oriented vertical sections which run more or less parallel to the radial plates lack the chambered division of the equatorial layer of the Orbitoididae. The equatorial layer appears to be void of any distinct structures, and only by careful examination of very thin vertical sections, can the two systems of radial plates or the median gap be recognized. In specimens with long neanic stages the equatorial layer is slightly wedge-shaped. Pillars are regularly distributed. In individuals with large *Sulcoperculina*-stage, the pillars seem to develop from the axial plugs.

Dimensions of the taxonomically important structural elements have been measured in vertical sections of two groups of individuals from the localities CUGOC Ser. No. 15396, Santa Clara area, Las Villas Province, and CUGOC Ser. No. 12327, Camagüey Province. They are listed in table 2. Dimensions of lumina are inner dimensions.

TABLE 2

Dimensions of structural elements in microns (µ) SER. No. 15396.

Thickness of wall of embryonic chambers ± 20 Thickness of wall of last whorl of *Sulcoperculina*stage 120-150

Thickness of walls of lateral chambers 10-25 Length of lateral chambers near periphery 60-100 Height of lateral chambers near periphery 10-30

Ser. No. 12327.

Length of radial plates 120-150 Thickness of radial plates \pm 10 Distances between radial plates 10-15 Diameter of initial chamber ± 45 Thickness of wall of juvenarium 25-40 Thickness of wall of lateral chambers ± 12 Length of lateral chambers ± 60 Height of lateral chambers ± 15 Height of equatorial layer near periphery ± 100

Age and Occurrence.—Sulcorbitoides pardoi n. sp. has been found in limestones of Upper Cretaceous age in Cuba and Texas.

Cuba

1) Las Villas Province.

Santa Clara area, CUGOC Ser. Nos. 15396, 15413 and 22015.

Upper Cretaceous yellow-cream fragmental limestone boulders containing igneous-derived fragments are redeposited in an Eocene conglomerate. The boulders contain abundant and, in part, worn Sulcorbitoides pardoi n. sp., Sulcoperculina cf. S. vermunti (Thiadens), rare Globotruncana lapparenti tricarinata (Quereau), Globigerina cretacea d'Orbigny, Gümbelina cf. G. globulosa (Ehrenberg), Oligostegina spp., Archaeolithothamnion sp. algae, rudists, echinoid fragments and other organic remains.

2) Camagüey Province.

Section of Arroyo Hondo, near the town of Camagüey, CUGOC Ser. Nos. 12327, 12327b and 12333.

Upper Cretaceous brown fragmental limestones containing igneous-derived fragments are interbedded with tuffs. These strata are *in situ*. The limestones contain Sulcorbitoides pardoi n. sp., Sulcoperculina cf. S. vermunti (Thiadens), Globotruncana lapparenti tricarinata (Quereau), small rotalids, Oligostegina spp., Archaeolithothamnion sp., algae, rudists, and gastropod and echinoid fragments.

3) Oriente Province.

The form reported and figured as *Pseudorbitoides* sp. or *Vaughanina* sp. by De Vletter (1946, p. 12) from blue limestones of the tuff series (Localities F 160 and F 166) cropping out in the western part of middle Oriente is identical with *Sulcorbitoides pardoi* n. sp.

Texas.

Upper Cretaceous yellow, porous, orbitoidal limestone from the Anacacho limestone exposed in White's Asphalt Quarry, 4.5 miles southwest of Blewett, Uvalde County, Texas, yields abundant *Sulcorbitoides pardoi* n. sp., rare *Sulcoperculina* sp., algae and other organic remains. A thin section of this limestone (fig. 2, pl. 10), illustrates vertically cut specimens with sulcoperculinoid juvenaria and lateral chambers and an oblique-horizontally cut specimen with about 26 spiral chambers.

Sulcorbitoides is a closely related but less advanced form than either Vaughanina or Pseudorbitoides. Phylogenetically, this indicates that it is older. There are also stratigraphic indications which support this conclusion.

Vaughanina has not been recorded from strata older than Maestrichtian. In Cuba its life range appears to be restricted to the *Globotruncana mayaroensis* zone (middle to late Maestrichtian).

Pseudorbitoides israelskyi was originally described by Vaughan and Cole (1932, p. 614, pl. 2, figs. 1-6) from a subsurface stratigraphic unit in Louisiana, now called the Monroe gas cap-rock of Navarro age (Maestrichtian). Vaughan and Cole also reported this species from the Anacacho limestone of early Taylor age (Campanian or possibly slightly older) in Texas, and thus assumed that the type specimens from Louisiana were of the same age. Today this correlation cannot be maintained, for the form from the Anacacho limestone is in fact Sulcorbitoides pardoi, not Pseudorbitoides israelskyi.

In Cuba, the life range of Sulcorbitoides pardoi is difficult to establish because of redeposition and structural complications. The only diagnostic microfossil encountered in thin section, Globotruncana lapparenti tricarinata (Quereau), is known from Turonian-Maestrichtian strata. De Vletter (1946, pp. 12, 13) referred the blue limestones of the tuff series in middle Oriente Province to the Maestrichtian, basing this age determination on a form which he regarded to be either Vaughanina or Pseudorbitoides, two Maestrichtian genera. However, his form is Sulcorbitoides pardoi, an ancestral form of the two Maestrichtian genera. Therefore it could indicate a pre-Maestrichtian age for the blue limestones, which, according to de Vletter, are remarkably similar to those of Turonian-Coniacian age collected by Thiadens (1937) in southern Santa Clara (Las Villas) Province and by Hermes (1945) in eastern Camagüey and western Oriente provinces.

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CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH VOLUME V, PART 2, APRIL, 1954

SYNONYMS OF GUBLERINAS 103. P. BRONNIMANN AND N. K. BROWN, JR.

Gulf Oil Corporation, Habana, Cuba

Recently de Klasz (1953), and Brönnimann and Brown (1953) independently described new representatives of the Upper Cretaceous foraminiferal genus Gublerina Kikoïne. According to de Klasz (letter, dated January 10, 1954), his paper was first mailed September 23, 1953. The paper by Brönnimann and Brown (1953) was first mailed October 29, 1953.

Comparison of the holotype of Gublerina hedbergi Brönnimann and Brown with metatypes of G. acuta robusta de Klasz reveals that these two names represent the same form. Thus G. hedbergi is a junior synonym; the valid trivial name is robusta.

Gublerina aff. G. cuvillieri Kikoïne described by de Klasz (1953, p. 248, footnote 1, pl. 8, fig. 2a, b) is the same as G. glaessneri Brönnimann and Brown.

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EXPLANATION OF PLATE 11

PAGE

	FIGS. 1-10 Sulcorbitoides pardoi n. sp.
	FIG. 11 Sulcoperculina cf. vermunti (Thiadens)
	FIG. 12 Sulcoperculina cf. dickersoni (Palmer)
	Figs. 1-11 from CUGOC Ser. No. 15396, Santa Clara area, Las Villas Province, Cuba.
	Fig. 12 Gravell Station 7480, 500 m south-east of km 16.4 of Bahia Honda Road, Pinar del Rio
	Province.
1, 8, 9.	Excentric vertical sections displaying the sulcus of one of the whorls of the juvenarium. The two systems of radial plates can be seen in the excentric section of fig. 9. Fig. 1, 93 \times ; figs. 8,
	9, 21 ×
2-7.	Series of vertical sections with increasing number of layers of lateral chambers and decreasing size of the juvenarium. $21 \times$
10	Oblique equatorial section exhibiting the radial plates 21×57

que equatorial section exhibiting the radial plates. 21 imes. 57 11. 12. Sulcoperculina cf. S. dickersoni (Palmer). 61 ×. 57

FIGS.

Contrib. Cushman Found. Foram. Research, Vol. 5

PLATE 11



Bronnimann: Upper Cretaceous Sulcorbitoides from Cuba

Contrib. Cushman Found. Foram. Research, Vol. 5

Plate 12



Küpper: Genus Orbitoides in America

CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH VOLUME V, PART 2, APRIL, 1954

104. NOTES ON CRETACEOUS LARGER FORAMINIFERA

Genus Orbitoides in America

KLAUS KÜPPER

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INTRODUCTION

I.

This is the first of a series of studies on American Upper Cretaceous Orbitoids, the purpose of which is to determine their evolutionary development and relationship with European species. The writer, together with A. Papp of the University of Vienna has studied Orbitoids in a stratigraphically known sequence from various localities in Austria and has found that they can be used for detailed stratigraphic subdivision of the Upper Cretaceous. Comparison of Austrian and other European populations of Orbitoides with collections from Cuba and Florida show that the trend of evolution among this genus is identical and that the morphological differences are too small for establishment of separate subspecies.

In any population variation usually exists. This variation may be in the form of number of auxiliary chambers, number of stolons, number of embryonic cells and less significant other features. The method of study is essentially that of Tan Sin Hok applied in his studies of Tertiary larger Foraminifera, in which detailed investigation of the central part of the test and variation within populations and their evolution in time are involved. It would not be appropriate to designate every variation in a population a species, and the writer is of opinion that populations with the same predominant type of variation can be regarded as conspecific. Some authors object to the emphasis placed on the embryonic apparatus by Tan Sin Hok and others, but this manner of investigation offers definitions of species which correspond to natural units, if carefully applied.

Morphogenetic study has as its ultimate aim the establishment of a nomenclature with a phylogenetic background. It is, in effect, not only a "systematic search for index fossils" as indicated by Tan Sin Hok but also a logical explanation why species are index fossils.

Acknowledgments.—I am indebted to the following gentlemen and institutions for submitting materials for

study: P. J. Bermudez, B. F. Ellis, the Paleontological Research Institution (Palmer Collection), and the Humble Oil Co. Thanks are due to H. E. Thalmann for his encouragement and help in the progress of this study.

Genus Orbitoides Orbigny, 1847

Diagnosis.—Test lenticular, more or less symmetrical, surface smooth or in some species with pillarheads or vermicular radiating costae. Embryonic apparatus enveloped in a thick perforated wall. Earliest species quadrilocular, later species trilocular and bilocular in the megalospheric generation. Median chambers of variable form communicating with each other through a complicated system of stolons. Lateral chambers observable and characteristic for all species of this genus. Pillars more or less developed.

EXPLANATION OF THE ANATOMICAL TERMS

Embryonic cells.—The central part, usually termed the embryonic apparatus, is enveloped in a thick perforated shell. It differs from the embryonic apparati of all other orbitoidal foraminifers in its general configuration and, therefore, the term cell is used. The embryonic apparatus of *Orbitoides media* is subdivided into four separate cells (Text fig. 1a). In horizontal sections cells I and II are centrally located but which



PAGE

FIGS.

EXPLANATION OF PLATE 12

1, 2.	Orbitoides tissoti tissoti Schlumberger, vertical and horizontal section, topotype material of "Orbi-	
	toides palmeri Gravell," Campo Florida, Habana, Cuba.	65
3,4.	Orbitoides media media (Archiac), vertical and horizontal section, Lawson, Florida.	66
5,6.	Orbitoides apiculata browni (Ellis), vertical and horizontal section, Habana formation, coll. Ber-	
	mudez.	66
7,8.	Orbitoides apiculata apiculata Schlumberger, vertical and horizontal section, Palmer station 812	66
	All Figures 16 \times .	



of these is the protoconch can only be determined in vertical sections (Text fig. 1b). Cell I is round to oval and embraced by cell II which is kidneyshaped. Cells III and IV on the left and right sides respectively are semicircular in outline. Cells I and II correspond with the proto- and deuteroconch in *Lepidorbitoides* but they are vertically not horizontally compressed. Cells III and IV have the position of auxiliary chambers in *Lepidorbitoides* in that they are partially embracing I and II. However, the term periembryonic chambers is applied to those chambers surrounding the embryonic apparatus enclosed in the thick perforated wall. Periembryonic chambers.—In some sections stolons are observed in the thick perforated wall surrounding the embryonic cells. In such sections auxiliary chambers among the periembryonic chambers are always distinct. The stolons are the primary connections between the embryonic cells and the med an layer. The number of auxiliary chambers is variable, but increasing in time. From each auxiliary chamber a row of chambers is observed growing into the direction of the next auxiliary chamber, meeting with the row of chambers from the opposite side at a point halfway between. Such a row is called a spiral. In Orbitoides there are two spirals emanating from each auxiliary chamber.

Stolons in median chambers.-Median chambers are connected with each other through diagonal stolons. No distal stolons have been observed so far although special attention has been paid to this question. The system of stolons can be revealed in its entire complexity in vertical sections only, because here it is possible to observe the number of stolons superimposed in a wall. Douvillé recorded 7 stolons superimposed in Orbitoides apiculata Schlumberger. Similar conditions have been described by Vaughan 1934.

Lateral chambers .-- Lateral chambers are very variable in form and size. They communicate with each other and with median chambers through stolons and very thin perforations in the walls. Lateral chambers have been recorded in all species of Orbitoides and are here regarded as typical for the genus.

SPECIES PREVIOUSLY DESCRIBED

To the best of my knowledge no species of Orbitoides has been recorded from the continental Americas. All the recorded species so far have been found in Central American Islands:

1. "An orbitoidal foraminifer approaching O. apiculata Schlumberger determined by Dr. A. Morley Davies" in C. A. Matley 1929 from Jamaica.

2. Orbitoides palmeri Gravell 1930 from Cuba.

3. Gallowayina browni Ellis 1932 from Cuba. The systematic and stratigraphic position of this genus was corrected by Vaughan (1934) and Palmer (1934).

4. Orbitoides apiculata Schlumberger recorded from Cuba by Vermunt (1937). Although it is apparent from his description that he did not have O. browni (Ellis) his determination may be questioned. His statement: "embryonic chambers quadrilocular" evidently excludes the elementary species O. apiculata which is characterized by a bilocular embryonic apparatus.

5. Several authors recorded Orbitoides sp. from various localities but unfortunately exact identification is impossible from the figures and descriptions available.

DESCRIPTION OF SPECIES

Orbitoides tissoti tissoti Schlumberger

Plate 12, figures 1, 2; Text figure 2, 12-15

1902 Orbitoides tissoti Schlumberger, p. 259, Pl. 8. fig. 21-25, p. 260, fig. 3.

1920 Orbitoides tissoti Douvillé, p. 214, Fig. 1, 10.

1930 Orbitoides palmeri GRAVELL, p. 269, pl. 22, fig. 1-10.

Description.-Test flat, umbo not very distinct. Test generally smooth, a few pillars concentrated on the umbo. Small, 2.5 - 3.0 mm. in diameter, thickness 0.75 - 1.2 mm. The embryonic apparatus is typical quadrilocular, the first two cells are separated by a wall generally perpendicular to the median layer. There are always four auxiliary chambers and eight spirals in the periembryonic chambers. The median chambers are of irregular outline even in correctly oriented sections. Usually chambers communicate with each other through one or two stolons. Only in one case a median chamber has been observed with three stolons. Very distinct lateral chambers of considerable size are present in vertical sections.

A re-examination of topotype material of Orbitoides palmeri Gravell established its identity with Orbitoides tissoti Schlumberger. All the specimens figured here are from the type locality of Orbitoides palmeri Gravell.

Occurrence.-Orbitoides tissoti tissoti Schlumberger has been first described from the lower Campanian of Algeria. It also occurs in the Campanian of Austria.

EXPLANATION OF TEXT FIGURE 2

The species are arranged in stratigraphic order. Note the increase of auxiliary chambers (x) and the change of the arrangement in the embryonic cells from the stratigraphic oldest (bottom) to the youngest (top) occurrences.

- Orbitoides apiculata apiculata Schlumberger, Palmer Station 812. Specimen with 14 auxiliary 1. chambers, bilocular type of embryonic apparatus. Maestrichtian s. str. Magnified 60 X.
- Same. Specimen with 10 auxiliary chambers, bilocular type of embryonic apparatus. Magnified 2. $60 \times .$
- Specimen with 14 auxiliary chambers, bilocular type of embryonic apparatus. El Silen-3. Same. cio, Cuba. Magnified 30 ×. Orbitoides apiculata browni (Ellis). Habana formation, coll. Bermudez. Specimen with 6
- 4. auxiliary chambers, quadrilocular type of embryonic apparatus. Lower Maestrichtian. Magnified 40 \times .
- Same. Specimen with more than 6 auxiliary chambers. Magnified 40 \times . 5.
- Specimen with 9 auxiliary chambers. Magnified $60 \times$. Same. 6.
- Specimen with 12 auxiliary chambers, trilocular type of embryonic apparatus. Magni-7. Same. fied 30 \times .
- 8. Orbitoides media media (Archiac). Lawson Limestone, Florida. Specimen with 4 auxiliary chambers, quadrilocular type of embryonic apparatus. Upper Campanian. Magnified 40 X.
- 9 Same. Magnified $36 \times$.
- 10. Same. Magnified 30 \times .
- 11.
- Same. Specimen with 6 auxiliary chambers. Magnified $36 \times .$ Orbitoides tissoti tissoti Schlumberger. Topotype of "Orbitoides palmeri Gravell." Specimen with quadrilocular type of embryonic apparatus, 4 auxiliary chambers. Middle (?) Campanian. Mag-12. nified 33 \times .
- 13-15 Same as 12. Magnified $33 \times$.

Auxiliary chambers are marked with a cross. (x)

The locality in Cuba, containing this species probably has to be correlated with the same zone. The type level of *Orbitoides palmeri* (= *Orbitoides tissoti tissoti*) is within the Habana Formation, generally considered to be Maestrichtian of age. The occurrence of *Orbitoides tissoti* indicates, however, a possible Campanian age for part of the Habana formation.

Locality.—Well at a depth of 950 feet, a short distance NW of the village Campo Florido, Havana Province, Cuba.

Orbitoides media media (Archiac)

Plate 12, figures 3, 4; Text figure 2, 8-11

1799 "Numismale" FAUJAS DE SAINT-FOND, pl. 34, figs. 1-4.

- 1837 Orbitolites media Archiac, p. 178.
- 1849 Orbitoides media ORBIGNY, (I.) p. 193, fig. 163.

1852 Orbitoides media ORBIGNY, (II.) p. 852, fig. 557.

1901 Orbitoides media Schlumberger, p. 464, Pl. 7, Figs. 1-7.

1920 Orbitella media DOUVILLÉ, p. 215, figs. 11, 13.

1954 Orbitoides media media PAPP and KÜPPER, K. p. 73-74; Pl. 1, figs. 5-7; Pl. 2, Fig. 4; Pl. 3, fig. 2.

Description.—Test disc-shaped with pronounced umbonal thickening. Diameter 3.5-5.0 mm., thickness 1.0-1.75 mm. The surface is ornamented with distinct isolated pillarheads and vermicular radiating costae. The embryonic apparatus is quadrilocular, the cells I and II are divided by a wall inclined to the median layer, clearly observable in vertical sections, and indicated in horizontal sections by its indistinct outline and the lack of a typical black central line. The embryonic apparatus is larger than in Orbitoides tissoti tissoti. The number (4) of auxiliary chambers is identical, at least in the predominant number of specimens in our populations. Only a few specimens with six auxiliary chambers have been observed, indicating a higher degree of specialization.

The median chambers are ogival in outline. They communicate with each other through a stolon system more specialized than in *Orbitoides tissoti tissoti*. Usually three stolons are observed in median chambers of an intermediate position and 4-5 in peripherically located median chambers. This corresponds with the drawing fig. 11 by Douvillé (1920) of topotype material from Royan, France.

In vertical sections large median chambers and more than two centrally located and well-developed pillars are present.

Occurrence.—Orbitoides media media does not occur at the type locality of Maastricht (see Visser 1950) but at various localities in S. France and the Alps is restricted to an intermediate horizon between lower Campanian with Orbitoides tissoti tissoti and Orbitoides apiculata, which is restricted to the Maestrichtian (type locality) and correlated deposits. Since the detailed position of the Maestrichtian-Campanian boundary is not yet settled it is difficult to allocate Orbitoides media either to the uppermost Campanian or to the lowermost Maestrichtian.

Locality.-Lawson Limestone, Gilchrist County, Florida, Sun Oil Co., Well No. 1. Navarro formation.

Orbitoides apiculata browni (Ellis)

Plate 12, figures 5, 6; Text figure 2, 4-7

1932 Gallowayina browni Ellis, p. 4, Figs. 1-7. 1934 Orbitoides browni Vaughan, p. 70-72.

Description .- Test planoconcave, smooth surface with a starlike ornamentation on the top of the concave side, on the basal side an ornamentation of vermicular radiating costae present in some specimens. Diameter 5.5-7.0 mm., thickness 3.0-4.0 mm. The embryonic apparatus is still quadrilocular, but the wall dividing cell I and II is already very close to the wall enclosing the embryonic apparatus. Auxiliary chambers vary in number, specimens with 6, 8, 9, 12 have been found but evidently most specimens in our population have 8 or 9 auxiliary chambers. The median chambers are arranged in a smoothly curved plane. The chambers communicate with each other through a highly specialized system of stolons. The distal chambers have up to 7 superimposed stolons, as has been figured by Douvillé (1920) in Orbitoides apiculata Schlumberger from Latoue, Haute-Garonne, France. Although this subspecies differs in some respects from the elementary species it is allocated to it because the variation of its embryonic apparatus already trends towards the bilocular type characteristic of Orbitoides apiculata. However, the predominance of specimens with a quadrilocular embryonic apparatus does not allow identification with this species. Therefore, subspecific status is proposed to indicate the close relation with Orbitoides apiculata and to account for the differences.

Occurrence.—This subspecies has not been recorded from Europe. The morphologic development suggests a position in the phylogenetic system preceding Orbitoides apiculata. This would indicate an occurrence probably below the zone with Orbitoides apiculata (Maestrichtian s.s.) However, until Orbitoides apiculata browni has been found in an established sequence this stratigraphic position will remain open to question.

Locality.—This species was originally described from one kilometer below Baños, Cuba. The population figured here was found at Madruga, Cuba, (Abra con Cuidados), in the Habana Formation. Topotype material was available for comparison.

Orbitoides apiculata apiculata Schlumberger

Plate 12, figures 7, 8; Text figure 2, 1-3

- 1901 Orbitoides apiculata SCHLUMBERGER, p. 465-466, pl. 8, figs. 1, 4, 6, pl. 9, figs. 1, 4.
- 1920 Orbitella apiculata DOUVILLÉ, p. 216, 217, fig. 4-9, 12, 15-18.
- 1950 Orbitoides apiculata VISSER, p. 295-296, pl. 9, fig. 4, pl. 11, figs. 1-3.

1950 ? Orbitoides brinkae VISSER, p. 296-297, pl. 9, fig. 5, pl. 11, figs. 2, 5.

Description .- This species is identical with the previously described Orbitoides apiculata browni in every respect except for the embryonic apparatus and the number of the auxiliary chambers. Therefore, only these features are described in detail. Orbitoides apiculata apiculata has the typical bilocular embryonic apparatus in horizontal sections. Cell I is reduced, and Cell II is now in a central position. However, in vertical sections a very small wall is sometimes observable, indicating the reduced subdivision in Cell I and II. Cell III and IV are united and embrace Cell II. Intermediate stages are present as in Text fig. 2, 1, where cell III and IV are separated because the central Cell II still touches the opposite wall. There is a further increase in the number of auxiliary chambers compared with Orbitoides apiculata browni. In the specimens figured 10, 14 and 14 auxiliary chambers are observed.

Occurrence.—In Europe Orbitoides apiculata apiculata is restricted to the Maestrichtian (s.s.).

Locality.—1 km. S. of Central San Antonio in railroad cut, Habana Prov., Cuba, Palmer Sta. 812. W. of "El Silencia," Cuba, R. H. Palmer Sta. 65.

SUMMARY

- 1. Four representatives of the genus Orbitoides are described and compared with each other.
 - Orbitoides tissoti tissoti Schlumberger Orbitoides media media (Archiac)
 - Orbitoides apiculata browni (Ellis)

Orbitoides apiculata apiculata Schlumberger

- 2. An evolution of various features is observed, namely:
 - a. Increase of the number of auxiliary chambers from 4 to 14.
 - b. Increase of the number of stolons from 2 to 7.
 - c. Decrease of the number of embryonic cells from 4 to 2.

3. The genus *Orbitoides* is not restricted to the Maestrichtian as indicated in recent literature but also occurs in the Campanian.

4. The Habana formation of Cuba can possibly be zoned on the basis of species of *Orbitoides*.

5. A final interpretation of the stratigraphical position and distribution of the species and subspecies of the genus *Orbitoids* must await further intensive studies in the field and laboratory.

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105. THE STRATIGRAPHICAL VALUE OF *BOLIVINOIDES* IN THE UPPER CRETACEOUS OF NORTHWEST AUSTRALIA H. S. Edgell

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ABSTRACT—The occurrence and succession of five species and subspecies of **Bolivinoides** are noted from the Cretaceous of Northwest Australia. One new subspecies of **Bolivinoides decorata** is described and the correlative value of the **Bolivinoides** group is emphasized.

Introduction.—The Bolivinoides group is represented in the Upper Cretaceous of the Carnarvon Basin, Northwest Australia by at least five species and subspecies of restricted vertical range. They are Bolivinoides draco draco (Marsson) 1878, Bolivinoides decorata gigantea Hiltermann and Koch 1950, Bolivinoides decorata australis Edgell 1954, n. subsp. Bolivinoides decorata cf. delicatula Cushman 1927, and Bolivinoides strigillata (Chapman) 1892.

Four of these forms are known previously from Northwest Germany and North America where they occur in the same succession and provide some of the best index fossils for subdivision of the Upper Cretaceous. The single new subspecies is closely related to *Bolivinoides decorata decorata* (Jones 1886) from the Upper Senonian (=Campanian) of Europe.

The occurrence in Australia of these known and related subspecies of *Bolivinoides* enables a close correlation with the standard stages of the European Upper Cretaceous. In local correlation the characteristic and stratigraphically restricted members of this bioseries are equally valuable. Apart from their biochronologic value these Australian *Bolivinoides* are also of interest from a phylogenetic and paleogeographic point of view.

Occurrence.-Strata of Upper Cretaceous age outcrop over a wide area within the sedimentary province known as the Carnarvon or North-West Basin. They are exposed where the overlying Tertiary rocks have been removed by erosion and are also known in borings for water and oil. In connection with oil exploration in Northwest Australia the writer has examined several continuous outcrop and subsurface sections of the Cretaceous while employed by the Australian Bureau of Mineral Resources from 1950-1953. Several hundred isolated samples were also examined and many could be easily correlated on the basis of Bolivinoides alone. The most complete surface sections of Upper Cretaceous sediments are from the Giralia Anticline, a large meridionally trending domal structure 60 miles in length and about 15 miles in maximum width. This elongated dome is situated just south of the Exmouth Gulf and some 60 to 100 miles south of the North West Cape (see map fig. 1). Well-exposed Cretaceous deposits occur in the eroded core of the anticline and in watercourses cutting the west flank of the structure.

Most of the Bolivinoides described here are from this area except for Bolivinoides strigillata and Bolivinoides decorata cf. delicatula which are known from a lower level in the Brickhouse Bore near Carnarvon. Bolivinoides decorata australis n. subsp. occurs at a higher level in this bore and can be correlated with its re-



stricted occurrence in outcrop section in the Giralia-Cardabia area.

Stratigraphy.—Cretaceous strata are developed to a thickness of at least 1000 ft. in the Giralia Anticline. The basal beds unconformably overlying the Permian consist of sandstones and siltstones followed by a characteristic formation of white- to ochre-colored siltstone of probable Cenomanian age. This in turn is overlain by a poorly-exposed, grey, bentonitic siltstone formation from 500 to 700 ft. in thickness. The earliest *Boli*-



vinoides in this section occur abundantly in the Inoceramus marl overlying this grey siltstone formation. The ultimate forms of the Cretaceous Bolivinoides series are found in a thin ammonite-marl layer which conformably underlies a basal Tertiary greensand horizon.

About 150 miles south of the Giralia Anticline, near Carnarvon, Upper Cretaceous sediments are known in the Brickhouse bores. The generalized sequence as known from percussion boring consists of a thin basal sandstone bed overlain by more than a thousand feet of grey shale and silt-stone with occasional intercalations of marl. The uppermost Upper Cretaceous does not appear to be represented in this bore and Tertiary and Post-Tertiary sediments occur from the surface to a depth of 280 ft.

Material.—The samples from the Giralia Anticline, on which this study is based, were collected from measured sections by an Australian Bureau of Mineral Resources Survey Party between 1950 and 1952. The samples were taken at strata intervals of \pm 30 ft. and have been supplemented by samples taken at closer intervals by the writer in 1950 and 1952. Due to the prominent outcrops and gently folded strata in the Giralia area the stratigraphic positions of all samples are accurately defined.

The material from the Brickhouse Bore, obtained in boring for water, is not so reliable. Although samples were taken at intervals of less than 20 ft. the boring was by the percussion method so that only the uppermost ranges of species could be determined definitely.

Systematic Description.—With the exception of the newly described subspecies only a brief description and comparison is given of the forms of *Bolivinoides* known from Northwest Australia. Because of the detailed description and revision by Hiltermann and Koch (1950) of the same species and subspecies it does not seem necessary to discuss the systematics of the Australian forms in detail.

The salient features of the species and subspecies encountered are expressed in table I.

SPECIES OR SUBSPECIES	OUTLINE OF TEST	CROSS SECTION	SIZE (LENGTH)	L/BR INDEX	ORNAMENTATION
Bolivinoides draco draco	Kite-shaped to rhomboidal	compressed rhombus (acute margin)	0.59 mm. to 0.25 mm.	Mode 1.42 Limits 1.15 to 1.75	Two strong parallel median ribs with con- tinuous connected side ribs. Apertural end smooth and thickened.
Bolivinoides decorata gigantea	rhomboidal	elliptical, with pointed ends	0.81 mm. to 0.31 mm.	Mode 1.45 Limits 1.10 to 1.80	Continuous side ribs. Median sulcus absent. Ribs slightly with- drawn from initial end which is smooth and thickened.
Bolivinoides decorata australis n. subsp.	pear-shaped	elliptical	0.85 mm. to 0.30 mm.	Mode 1.52 Limits 1.2 to 1.9	Discontinuous side ribs breaking up into num- erous nodes towards initial end. Initial end generally thick- ened and smooth.
Bolivinoides decorata cf. delicatula	narrowly conical	elliptical to oval	0.50 mm. to 0.40 mm.	Limits 2.1 to 2.3	Lobes or small ribs confined to last cham- ber. Irregular nodes on earlier part of test.
Bolivinoides strigillata	narrowly conical with blunt end	roundedly oval to subquadrate	0.34 mm. to 0.38 mm.	Limits 1.9 to 2.1	Very irregular broad ribs and depressions. Test strongly thick- ened.

TABLE I. Main Characteristics of the Bolivinoides forms from N. W. Australia

The following is a short description and comparison of the *Bolivinoides* forms known from Northwest Australia.

Bolivinoides strigillata Chapman, 1892

Plate 13, figure 8; plate 14, figure 8 Synonymy.

Bolivina strigillata CHAPMAN, 1892 (p. 515, Pl. XV, fig. 10)

pars Bolivina strigillata Снарман, 1892 in Williams-Mitchell (р. 106)

Bolivina sim. draco WICHER, 1952, pp. 67-68 Pls. 23-26.

Material.—Four specimens from depths of 995 ft., 1015 ft., and 1055 ft. in the Brickhouse Bore are deposited in the Commonwealth Palaeontological Collection of the Bureau of Mineral Resources, Canberra, Australia.

Diagnosis.—(after Hiltermann and Koch 1950) "Test only slightly compressed, somewhat carrot-shaped. Cross section roundly oval; sides broad and rounded; sculpture consists of elongated nodes, which run at right angles to the chambers and which may be connected as ribs."

Description.—Test elongate, sides tapering gradually. Maximum width situated close to the apertural end. Maximum length of shell approximately twice maximum breadth. L/Br ratio varies from 2.14 to 1.82. Test small in size and characteristically round to oval in cross section. Apertural face broad. Aperture consisting of a short slit situated in slight embayment of last formed suture. Test ornamented with loosely connected nodes or broad irregular ribs running perpendicular to the sutures. Coarse ornamentation or secondary thickening of the shell is strongly developed in *B. strigillata* leaving only small unthickened depressions in the later part of the test. These depressions are often loosely connected to form a zic-zac, longitudinal, median furrow.

Remarks.—The representatives of *B. strigillata* from N.W. Australia differ from typical forms from the Quadraten Senon of N.W. Germany. They are generally smaller, more rounded and with more secondary thickening of the shell.

Occurrence.—This species is known from between the depth of 995 ft. and 1055 ft. in the Brickhouse Bore, Northwest Australia. This distribution can be correlated with its occurrence in the upper Santonian and lower Campanian of Germany, England, and the upper Austin of Texas.

Age.—Santonian.

Bolivinoides decorata (Jones) cf. delicatula Cushman, 1927 Plate 13, figure 7; plate 14, figure 7

Synonymy.

Bolivina decorata CUSHMAN (non Jones) Bull. Amer. Assoc. Petr. Geol., Vol. 10, 1926, p. 582, Pl. 15, fig. 11.

Material.—Two specimens from depths of 935 ft. and 995 ft. in the Brickhouse Bore are deposited in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra, Australia.

Diagnosis.—Test narrowly conical in outline but compressed to have an elliptical cross section. Ornamentation typically consisting of a network of rib-like lobes confined to each chamber. Initial chambers devoid of ornamentation.

Description.—The specimens examined from N.W. Australia are elongated almost parallel sided with a rounded initial chamber. They are larger than specimens of *B. strigillata* having a length of ca. 0.5 mm. and a Length-Breadth ratio (L/Br) of 2 or more. The cross section of this form is strongly compressed and elliptical and the aperture consists of a narrow median slit connected with the base of the terminal face of the last formed chamber. Ornamentation is poorly developed and consists of lobes at right angles to the sutures in the two last chambers. The earlier chambers possess occasional short lobes or nodes while the initial chambers are unornamented.

Remarks.—The Australian specimens closely resemble the type figured by Cushman from the Upper Cretaceous of Mexico and refigured by him in 1946. (U.S. G.S. Prof. Pap. 206. Pl. 48, fig. 10.) However, they are not nearly so highly ornamented as forms from N.W. Germany referred to this subspecies by Hiltermann and Koch (1950). Since the type description notes that the ornamentation is "much less definitely marked" the Australian forms are provisionally identified with it and as pointed out by Hiltermann (personal communication) they could be considered as a primitive form of *B. decorata delicatula*. There is also a resemblance to *Bolivinoides decorata laevigata* Marie but the Australian forms are more slender and their ornamentation though reduced is not restricted to the axial part of the test as in the former.

Occurrence.—The specimens described occur at depths of 935 ft. and 995 ft. in the Brickhouse Bore. They are rare in the material examined.

Age.—Basal Campanian.

Bolivinoides decorata (Jones) australis Edgell, n. subsp.

Plate 13, figures 5, 6; plate 14, figures 5, 6

Holotype.—Pl. 13, fig. 6. Deposited in Stanford Univ. Paleo. Type Coll. No. 8112.

- Paratype.—Pl. 13, fig. 5 and more than 50 other specimens. Deposited in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Australia.
- Type Locality.—C. Y. Creek, West flank of Giralia Anticline Northwest Australia (Bureau of Mineral Resources Sample Locality GC/304).

Material.—More than 100 specimens of this species were examined statistically and 50 of these are deposited as paratype material.

Diagnosis.—This is a form of Bolivinoides decorata which differs from Bolivinoides decorata decorata in that the early part of the test is ornamented by numerous prominent nodes whereas in the latter it is conspicuously smooth and thickened.

Description.—Outline of the test pyriform to almost kite-shaped. In cross section compressed to an elongated oval shape. Margin of the shell broadly rounded. Apertural end much thickened and smooth. Aperture as a slit-like or key-hole like opening which may be isolated on the apertural face or may be connected with the last formed suture.

A small initial portion of the test may be smooth. Most of the test covered with conspicuous nodes or tubercules which tend to coalesce into broken costae and finally into short ribs in the later part of the test. The subspecies is represented by large specimens up to 0.85 mm. in length thus exceeding in size the largest specimens of *B. decorata gigantea*.

The Length-Breadth ratio (L/Br) varies from 1.2 to 1.9. When plotted against the number of individuals in a population of this subspecies a bimodal curve results. The same curve has been obtained by consideration of several different populations. The two maxima of 1.4 and 1.6 show that these two Length-Breadth ratios are more common (see fig. 3). Thin sections of



_____ 53 specimens of <u>Bolivinoides</u> <u>decorata</u> <u>australis</u> (Sample GC/304) _____ 50 specimens of <u>Bolivinoides</u> <u>decorata</u> <u>australis</u> (Sample GC/303)



individuals belonging to each of these groups show a marked difference in size of the proloculus. Thus individuals with a Length-Breadth ratio of 1.4 would appear to be mostly megalospheric with a proloculus diameter of ca. 0.015 mm. while those with a ratio of 1.6 seem to be microspheric with a diameter of ca. 0.0075 mm. (see fig. 4). The recognition of alternate generations in Bolivinoides is supported by the presence of the same phenomenon in the related genus *Bolivina*.

Remarks.—Bolivinoides decorata australis n. subsp. is closely related to B. decorata decorata from N.W. Germany, and seems to occupy a similar stratigraphic position. However, comparison with typical specimens of B. decorata decorata kindly sent by H. Hiltermann



Text Fig. 4 Camera lucida drawings of thin sections of Bolivinoides decorata australis showing alternate generations.

show consistent differences which justify the establishment of a new subspecies.

Occurrence.—This subspecies occurs abundantly in the upper part of the *Inoceramus* marl which outcrops extensively in the Giralia Anticline. It is also known from the Brickhouse Bore between the depths of 320 and 355 ft.

Age.-Upper Campanian.

Bolivinoides decorata (Jones) gigantea Hiltermann and Koch, 1950

Plate 13, figure 4; plate 14, figure 4.

Synonymy.

Bolivina ex. aff. draco WICHER, 1942, p. 67, Pl. 26, 22.

Material.—More than fifty specimens were examined from the Giralia Anticline mostly from samples a few feet below the base of the Tertiary greensand. Forty of these specimens are deposited in the Commonwealth Palaeontological Collection of the Bureau of Mineral Resources, Canberra, Australia.

Diagnosis.—Test large, rhomboidal compressed with elliptical cross section. Initial chambers smooth. Ornamentation of numerous long thick unbroken ribs running at right angles to the sutures.

Description.—The outline of the shell is kite-shaped or rhomboidal in *B. decorata gigantea* with the maximum width nearer to the distal end than in *B. draco draco*. The test is large, up to 0.81 mm. in length and the Length-Breadth ratio is commonly between 1.4 and 1.5. The shape of a cross section through the last two chambers is biconvex with rounded ends. Thus the margin of the shell is rounded and not acute as in members of the *B. draco* group. The apertural end of the shell is smooth and thickened with the aperture as a large isolated slit on the terminal face of the last formed chamber.

Ornamentation of the test characteristically consists of a large smooth initial portion from which arise thick continuous ribs running perpendicular to, and obscuring the sutures.

Remarks.—Comparison of the Australian specimens with typical material from N.W. Germany reveals little or no consistent differences. Perhaps the latter are slightly narrower and more pointed initially than the Australian forms. The distribution of the Length-Breadth index in 47 specimens from the Giralia Anticline shows an optimum of 1.45. According to Hiltermann and Koch (1950), their specimens show an average L/Br ratio of 1.5 to 1.6, but the difference is probably insignificant.

Occurrence.—In N.W. Australia this subspecies is common in a thin ammonite-marl bed of Maestrichtian age which outcrops in the Giralia Anticline at the top of the Upper Cretaceous sequence. B. decorata gigantea also occurs in the upper 10 ft. of the underlying *Inoceramus*-marl but always above the range of *B. decorata australis* n. subsp.

Age.—Maestrichtian.

Bolivinoides draco draco (Marsson), 1878

Plate 13, figures 1, 2, 3; plate 14, figures 1, 2, 3 Synonymy.

- Bolivina draco (MARSSON), 1878 (p. 157, Pl. 3, figs. 25a-d)
- Bolivinoides rhomboidea Cushman, 1926 (p. 19, Pl. 2, fig. 3)

Material.—Of the several hundred specimens examined, 120 are deposited in the Commonwealth Palaeontological Collection of the Bureau of Mineral Resources, Canberra, Australia. They come from a sample taken one foot below the base of Tertiary greensand in a sample pit at the north end of the Giralia Anticline.

Diagnosis.—Kite-shaped in outline, compressed rhomboidal in cross section, with acute or keeled margin extending to the base of the initial chamber. Apertural end smooth and conspicuously thickened. Strong median sulcus separating two strong parallel ribs. Side ribs generally continuous and confluent with median ribs.

Description.—The smaller forms of B. draco draco have a characteristic rhomboidal outline which becomes more elongated in larger specimens. The maximum width is always situated close to the proximal end. The Length-Breadth ration in 52 specimens is most commonly between 1.3 and 1.5. The average size of the test is about 0.4 mm. but some specimens range up to 0.64 mm. The shape of the cross section is narrowly rhomboid so that the median part of the shell has the greatest thickness while the margin is acute or keeled. This keeled margin extends even around the initial part of the test and is characteristic for the B. draco group. The proximal part of the last two chambers is thickened and smooth and the aperture is a marked notch in the middle of the upper part of the last formed suture.

The pattern of conspicuous ornamentation in B. draco draco characteristically consists of two parallel median ribs separated by a central sulcus. These two parallel ribs begin in the initial part of the test and extend to the last formed chamber. In some larger forms, however, they are replaced by overlapping side ribs in the later part of the test (see Pl. 13, figs. 1, 3). The two parallel, median ribs are bordered by, and generally confluent with prominent, continuous side ribs which traverse the sutures at right angles.

Occurrence.—Bolivinoides draca draco occurs associated with *B. decorata gigantea* in outcrops in the Giralia Anticline, Northwest Australia. However, it is always more numerous and in most samples at least twice as common as *B. decorata gigantea*.

Age.-Maestrichtian.

PHYLOGENY

The vertical distribution of *Bolivinoides* forms in Northwest Australia shows a succession of morphologically distinct subspecies. This sequence of types suggests a line of evolution in the genus, which is borne out by consideration of characters such as shape, size and ornamentation. These characters exhibit general trends as one passes upwards stratigraphically. It is of interest that the same succession has been noted by Wicher (1949) and Hiltermann and Koch (1950) in areas as widely separated as the Tampico Embayment of Mexico and North-West Germany. Thus the progressive changes in morphology are due to rapid evolution of new types and not to the influence of any ecological changes.

The shape of the test shows modification in three ways: 1) broadening of the test accompanied by a shift in the position of maximum width, 2) compression of the test and 3) a tendency towards an acute margin. The progressive increase in breadth of the test is shown by a general decrease in the Length-Breadth ratio from 2.1 in the earliest species, *B. strigillata*, through 2.2 in *B. decorata* cf. *delicatula* to ca 1.6 in *B. decorata australis* and ca. 1.5 in *B. decorata gigantea*. *B. draco draco*, which is contemporaneous with the last species, appears to be in an evolutionary line or side branch of its own and has a broad test with an average L/Br ratio of 1.4.

In cross section there is also a trend from a round section in the most primitive form (i.e. B. strigillata) through an oval section in B. decorata delicatula to an elliptical section in B. decorata australis and eventually to a slightly more elliptical section in B. decorata gigantea. This compression leads to the development of an increasingly marked margin. The most acute margin is developed in B. draco draco where it extends as a keel even to the base of the initial chamber. This strongly developed marginal keel and its rhombic cross section are features which remove B. draco draco from the *B. decorata* lineage to a separate phylogenetic branch. From the earliest form, B. strigillata, to the youngest form, B. decorata gigantea, there is a general increase in absolute length of the test from 0.36 mm. to 0.81 mm. However, B. draco draco is an exception to this general progression in size.

The known evolution in the size of the proloculus in the genus *Bolivinoides* has not been studied in the Australian forms but probably parallels the increase in overall size of successively younger forms.

The most striking and characteristic change is that of ornamentation. In the first appearing species, B. *strigillata*, there is only a general thickening of the test with a smooth initial part and irregular depressions along the later part of the test, leaving broad thickened areas between. The succeeding form, B. decorata cf. delicatula, shows the evolution of inconspicuous nodes in the early part of the test and in the last chambers they are developed into short ribs which are confined to these chambers. Higher in the stratigraphic sequence B. decorata australis has developed an early portion covered with prominent nodes which in the later part of the test coalesce to form discontinuous, and eventually continuous ribs crossing the sutures at right angles. *B. decorata australis* is succeeded by *B. decorata gigantea*, in which the nodes have entirely united to form continuous ribs obscuring the sutures. In *B. draco draco* continuous obliquely directed ribs are also developed with the addition of two parallel median ribs (see fig. 5).



Text Fig. 5 Phylogeny of Cretaceous Bolivinoides in N.W. Australia.

Correlation.—The Upper Cretaceous species and subspecies of the genus *Bolivinoides* are narrowly restricted stratigraphically and yet seem to have an almost world-wide distribution. Their vertical distribution is well-known in Northern Germany in terms of standard European subdivisions of the Cretaceous. The recognition of the same restricted subspecies in Europe, America and Australia would seem to provide a good basis for broad inter-regional correlation.

Thus Bolivinoides strigillata is known from the upper Santonian and lowermost Campanian in Germany and England as well as in the upper Austin of Texas. On this basis, together with the indications of the associated Globotruncana and Neoflabellina, beds containing B. strigillata in the Brickhouse Bore are correlated in a general way with the Santonian of Europe.

The form here identified as *B. decorata* cf. *delicatula* is similar to forms known from the lower part of the Upper Campanian and the upper part of the lower Campanian in N.W. Germany according to Hiltermann (personal communication). Similar forms are also figured by Cushman (1946) from the Taylor marl of Texas and the Cretaceous of Mexico. This distribution suggests a general Campanian age for the Australian occurrence.

The abundantly occurring new subspecies described here as *Bolivinoides decorata australis* is closely related to *Bolivinoides decorata decorata* and occupies the same position in the *Bolivinoides* bioseries. Thus beds containing *Bolivinoides decorata australis* can be assigned a general Campanian age and this is also indicated by other associated microfossils. Within the Upper Cretaceous deposits of the Carnarvon Basin *Bolivinoides decorata australis* also provides a valuable marker for local correlation. On the basis of its restricted occurrence the beds between 320 ft. and 355 ft. in the Brickhouse Bore have been correlated with those 150 miles to the north in the Giralia Anticline. *Bolivinoides decorata gigantea* and *Bolivinoides draco*

EXPLANATION OF PLATE 13

FIG	GS.	PAGE
	Photomicrographs of various Australian Bolivinoides types.	
1.	Bolivinoides draco (Marsson) 1878 (× 83).	73
	North end of Giralia Anticline, Giralia, Western Australia (Sample GE/11)	
2.	Bolivinoides draco (Marsson) 1878 (× 124).	73
	North end of Giralia Anticline, Giralia, Western Australia (Sample GE/11)	
3.	Bolivinoides draco (Marsson) 1878 (\times 80).	73
	C. Y. Creek, Cardabia, West flank of Giralia Anticline, Western Australia (Sample GC/301)	
4.	Bolivinoides decorata gigantea Hiltermann and Koch 1950 (\times 94).	72
	C. Y. Creek, Cardabia, West flank of Giralia Anticline, Western Australia (Sample GC/301)	
5.	Bolivinoides decorata australis Edgell 1954 n. subsp. (× 86).	71
	C. Y. Creek, Cardabia, West flank of Giralia Anticline, Western Australia (Sample GC/303)	
6.	Bolivinoides decorata australis Edgell 1954 n. subsp. $(\times 80)$	71
	C. Y. Creek, Cardabia, West flank of Giralia Anticline, Western Australia (Sample GC/304)	
7.	Bolivinoides decorata cf. delicatula Cushman 1927 (\times 106).	71
	Brickhouse Bore, East of Carnarvon, Western Australia Depth 935 ft.	
8.	Bolivinoides strigillata Chapman 1892 (\times 131).	70
	Brickhouse Bore, East of Carnarvon, Western Australia Depth 1015 ft.	

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PLATE 13



Edgell: Upper Cretaceous Bolivinoides in N. W. Australia

Contrib. Cushman Found. Foram. Research, Vol. 5

Plate 14



Edgell: Upper Cretaceous Bolivinoides in N. W. Australia

draco are good index fossils for the Maestrichtian in N.W. Germany. The latter is also known from the Mendez of Mexico. Both forms occur in the uppermost part of the Cretaceous in the Giralia Anticline in beds conformably underlying a greensand horizon with an abundant Paleocene microfauna. The Bolivinoides forms enable a correlation to be made between the uppermost Cretaceous (Maestrichtian) of Europe and the ammonite-marl (and topmost 15 ft. of the Inoceramus-marl) in the Giralia Anticline in N.W. Australia. The validity of this correlation made on the same restricted subspecies as known in Europe is supported by the Maestrichtian ammonites described by Spath (1926) from the ammonite marl outcropping in the Giralia Anticline.

CONCLUSIONS

This paper illustrates the restricted value of species and subspecies of *Bolivinoides* for local and interregional correlation within the Upper Cretaceous. It provides an instant of the cosmopolitan distribution of certain benthonic Cretaceous Foraminifera even to a subspecific level. These members of the *Bolivinoides* group also show the application of morphogenetic studies of the smaller Foraminifera.

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EXPLANATION OF PLATE 14

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CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH Volume V, Part 2, April, 1954

106. A NOTE ON FORAMINIFERAN SIEVE-PLATES¹ Zach M. Arnold

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The electron microscope has recently been directed toward the study of one of the most perplexing structures yet uncovered in the shell of the foraminifera the sieve plates. Brigitte Jahn, of the Deutsche Forschungshochschule in Berlin-Dahlem, has recently (1953) described and figured a series of sieve-like plates which were found preserved within the organic lining of the pore canals following the decalcification of certain unidentified Nonionid or Camerinid tests. The minute, discoidal plates (one micron in diameter) appear fairly regularly spaced, occur at node-like regions of the canals, and have a large number of circular and triangular (possibly even polygonal) micro-pores arranged in concentric rows. Each pore canal contains a number of sieve plates, some of which appear to have been dislodged from their nodal sites during preparation for electron photomicrography.

Arnold has recently (1954) described comparable organic structures, termed "pore plugs," lying as single, micro-porous plates at the base of the external pores of *Discorinopsis aguayoi* (Bermudez). The micro-pores which perforate these pore plugs are randomly distributed over the surface of the plug but are approximately equal in number to the round micro-pores observed by Jahn in the sieve-plates. The micro-pores of *Discorinopsis* are approximately 0.2 to 0.3 microns in diameter, while those of Jahn's material are 0.1 micron or less.

The demonstration of organic plates in the pore canals has confirmed and expanded the observations of Hofker (1927), Jepps (1942), Myers (1943) and Le Calvez (1947). The disclosure, by Jahn and Arnold, of the micro-porous nature of the sieve-plates or pore-plugs should provoke an inquiry into the role and significance of these minute structures in the animal's biological economy.

It may be that the sieve-like structures serve selectively to control the flow of cytoplasmic elements into and from the pseudopodia. It is known that, although there are several different types of formed bodies within the intratest cytoplasm of the Foraminifera, only certain of these elements actually enter the pseudopodia. Doyle (1935) has shown that only the "mitochondria" enter the pseudopodia of *Iridia diaphana* Heron-Allen and Earland, and Arnold (1953) has found that of a half-dozen or more different types of cytoplasmic inclusions only the very minute (0.1 to 0.3 micron) spherical or ovoidal elements enter the pseudopodia of Allogromia laticollaris Arnold. The exact chemical nature and physiological function of these migratory elements are still unknown, but the fact remains that some filtering action occurs to restrict the pseudopodial extravasation of the other cytoplasmic elements. In the two cases in which a filtering action has been noticed, no filtering structure has been observed, disconcertingly enough, but structures which seem admirably competent to perform a filtering action have been described in two genera of calcareous, perforate Foraminifera. So, there is a challenge for the paleontologist to determine the occurrence of such sieve-plates throughout the Order and for the biologist to investigate the role of these structures in the animal's physiology.

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¹ A contribution from the Museum of Paleontology, University of California at Berkeley.

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107. VARIATION AND ISOMORPHISM IN ALLOGROMIA LATICOLLARIS: A CLUE TO FORAMINIFERAL EVOLUTION¹ Zach M. Arnold

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INTRODUCTION

The foraminiferan Allogromia laticollaris is a typical member of the type genus of the family from which most paleontologists believe the other foraminifera arose. The species was first described from the littoral waters of the Bay of Saint Andrew, Panama City, Florida (Arnold, 1948), and laboratory cultures of it have been the subject of study by the writer for several years. A study of mass cultures as well as known-lineage or isolation cultures of this species has revealed a surprising amount of variation, variation which may shed some light on the origins of other morphologic types within the Order. The present study is intended to bring into focus not only this variation but also certain similarities between variants of this primitive form and more "advanced" foraminiferan types. Mere similarity of growth plan or other single morphological feature is not the sole basis for designating ancestral relationships within the Foraminifera-no such designations are intended or implied by the comparative discussions which follow-but it seems desirable at this point to record the observed similarities in basic test form and chamber arrangement ("plans of growth"), so that they may be evaluated through future investigations.

The study of morphological diversity at the infraspecific level will greatly facilitate the erection of a taxonomic scheme which shows fundamental relationships among the various groups of foraminifera. The paleontologist can investigate variation with the increased perspective afforded by the time dimension of the stratigraphic record, but, beyond his application of the demonstrated principles of inheritance, he cannot exercise a particular control over the lineages he examines and can only suggest the degree of phylogenetic or metagenetic relationship between any two specimens that he encounters in the fossil state. There is a rough continuity in the stratigraphic record, but this continuity is seldom if ever interpretable at the level of the individual foraminiferan and its immediate relatives. The biologist. on the other hand, though he never can be certain of the actual evolutionary significance of his experimentally-controlled functional data, can isolate a single animal and observe the relationship between successive generations with relatively fine chronologic control. This is the method which the biologist can apply

to the study of living representatives of paleontologically critical species as an additional approach to the interpretation of variation and evolutionary relationships in the fossil record.

The species Allogromia laticollaris is a particularly significant form upon which variation studies can be conducted, although it has never been reported in the fossil record, and it is doubtful that it can ever positively be identified in the fossil state. An investigation of variation within this species, however, could be expected to reveal information concerning its "evolution potential" and could, conceivably, give an insight into the basic evolutionary changes from which some of the early foraminiferal divergencies arose.

MATERIALS AND METHODS

Specimens of Allogromia laticollaris were first collected by the author in 1946 and have been maintained in laboratory cultures since that date. All observations contained within the present report were made on specimens from these cultures. The cultures have been maintained on mixed, unicellular algae in an enriched seawater culture medium known as "Erdschreiber" (Føyn, 1934). Cultures have been maintained routinely at room temperature, although thriving populations have been produced within the 14 to 32°C. range.

The variants described here were observed in either mass or isolation cultures and a detailed description of the techniques involved in maintaining and examining such cultures has been presented elsewhere (Arnold, in press).

Variants which have been illustrated to show internal details, such as peduncular sheath (entosolenian tube) and nuclei, were sectioned at 10 microns through the use of routine cytological procedures, while all other specimens were photographed *in vivo* without special preparation.

VARIATION

The most characteristic feature of this species is its flexibility, keynoted at the purely morphological level by test plasticity, but extending far beyond the structural organisation of the animal to the basic physiological and cytological processes upon which its biological existence depends. The present investigation of these variations has been pursued at the descriptive level, because of the incompleteness of the physiological and genetical background upon which an interpretive study would of necessity depend.

¹ A contribution from the Museum of Paleontology, University of California at Berkeley.

Test flexibility.—The "typical" test of this species is ovoidal or spherical, but it shows varying degrees of flexibility which may have some correlation with the animal's growth and developmental physiology. The test of young animals appears to be more flexible than that of older individuals, but this appearance could be deceptive and should, therefore, be tested by more critical methods (micromanipulation, for example) than have been available during the course of this study. Young schizonts recently freed from the confines of their parental incubation chamber typically show a circumferential unrest which is characterized by erratic distension and contraction at localized points along the periphery of the test.

This tendency is sometimes weakly expressed in adult individuals. Most laboratory cultures contain a few adults which show extreme test flexibility, but the number of such individuals rarely exceeds 3 per cent of the total population. An indication of the range of variation that has been observed in controlled lineages can be obtained from the following data: In a total of 4.250 individuals taken from 7 known-lineage cultures, only 58 individuals, approximately 1.4 percent of the total, showed variation from the typical ovoidal or spherical shape. Within this series the progeny of one of the lineages contained 51 abnormal individuals out of a total of 1,950, a variation incidence of 2.6 per cent. The progeny of a second lineage within the larger group included only 7 abnormal forms in a total of 2,300 offspring, a variation incidence of only 0.3 per cent.

Highly variable populations have been maintained at room temperatures, but some of the most variable ones have appeared in cultures maintained at 14°C. The available experimental data do not warrant the conclusion that a temperature correlation exists for this variation, but the phenomenon must be investigated further in an effort to determine the effect of temperature on test flexibility and on the expression of morphological variation.

Some of the individuals from two cultures that had been maintained for two months at a temperature of 14°C. are illustrated in Plate 15 (C, C1, C2, C3, C4, C_6 , C_7 , C_9 , D_2 , B_1 , B_1 , and A_1). Most of these have supernumerary mouths and are grotesquely deformed. Several underwent irregular binary or multiple fission within the few hours that they were being observed for photographing, and most of the others appeared to be on the verge of division. Normally-dividing forms appeared to be singularly absent from the two groups. "Normal" division in this species involves the production of numerous testate young within the parent test and their subsequent liberation as independent juvenile forms. The parent test remains intact after such normal multiple fission. In abnormal fission the number of offspring may be relatively low (as few as two) and the parental test may participate in the formation of the tests of the offspring.

Several aberrant forms of the types illustrated in the accompanying plate have been transferred to isolation cultures and have been observed to give rise to normal spherical or ovoidal young which possess a single test aperture and undergo normal reproduction, but the number of experiments of this type which have been performed does not warrant the generalization that this is the invariable fate of such animals and their progeny. Nothing can be said of the cytological relationships of most of these variants except that their nuclei are superficially indistinguishable from those of normal individuals.

It is interesting to note that the distortional forces generally seem to originate from or be applied at the oral regions and that these are the regions of active movement, while the inter-oral portions are passively stretched or wrinkled. Exceptions to this have been noted in the formation of bud-like protuberances such as those illustrated in A, A₁ and A₃ of Plate 15. Both forms of distortion, however, would seem to be a positive indication that distortional forces are autonomous and possibly the result of protoplasmic strains and stresses set up by both the intra-test protoplasm and the pseudopodia. The distortion observed in illustrated forms B, B₁, C, C₁, C₂, C₃, C₆, C₇, C₄, C₉ of Plate 15 is clearly correlated with pseudopodial activity, if not actually due to its action upon a flexible test. That distortion can occur without such activity is clear from an examination of A₃, D, and similar forms which possess a single aperture and are, therefore, subjected to unilateral pseudopodial stresses. It seems likely that strong protoplasmic flow against the inside of the oral region of the test actually produces distortion at times without the aid of pseudopodial action.

The question then arises: Why is the test of the animal not subjected to continual distortion by the force of intra-test protoplasmic currents? It may be that the degree of test flexibility is constant, that the degree of its expression in the form of test distortion is strictly related to, or a factor of, protoplasmic-current force, and that it varies simply with the number of apertures through which the protoplasm can flow. (These act as points against or through which a force can be applied.) There certainly seems to be strong correlation between the number of apertures and the degree of distortion, as an examination of the poly-oral forms illustrated in Plate 15 will show. On the other hand, however, there is the possibility that the degree of test flexibility varies and is genetically linked with factors responsible for the development of supernumerary mouths. The character of test flexibility has not been subjected to close scrutiny with adequate experimental methods, but this feature may be a clue to a number of interesting and taxonomically significant, morphological variations within the species.

Lobation.-Lobed individuals are not uncommon in the species, and the phenomenon may merely be the expression of distortional forces of the type described above, or it may develop in single-mouthed forms in which different distortional mechanisms must be invoked. Lobation is generally of a temporary nature and is frequently terminated by plasmotomy or budding. Lobed individuals frequently give rise to other individuals by these two processes, but occasionally lobed portions are simply resorbed and the animal's existence terminated with perfectly normal multiple fission long after the lobe has been resorbed.

Flattening.—To the list of variants must be added forms which show varying degrees of flattening. In general all cases of flattening appear to be environmentally induced and of a non-heritable nature (Arnold, 1953). The development of dense algal mats over healthy populations results in the flattening of many individuals which are trapped underneath the mat. These flattened animals do not immediately regain their sphericity when the pressure of overlying algae is relieved, but may remain flat for several days thereafter. Eventually, however, they become spherical again and reproduce normally. The young animals produced thereby are spherical and remain so unless they, too, are subjected to the same environmental pressures that deformed their parents.

During the course of preliminary experiments with semi-solid culture media individual specimens became characteristically flattened and remained so as long as they were grown on an agar substrate, but the offspring of such abnormally flattened parents were normal, spherical individuals which became flattened only when allowed to remain on the agar plates during their developmental period.

Apertures.—The test aperture of this species could well be the subject of intensive investigation, in view of the general importance of test apertures in foraminiferal taxonomy, but the structure and its variation have only been cursorily treated in the present study. Before a serious attempt could be made to relate this species to other forms, a detailed examination of apertural features, including morphogenesis and variation, must be made.

The aperture, in its typical development, is a single, permanent structure with a fixed position in the test wall. This position has not been observed to change during the life of the individual. Supernumerary mouths are not uncommon and the relative position of these accessory apertures also appears to remain constant during the life of the individual, although inter-oral distortion frequently gives a deceptive impression of positional changes.

The maximum number of apertures thus far observed in culture populations is six. The number of mouths remains constant until an animal reproduces, and supernumerary mouths apparently appear as the test of the young animal is formed. The post-natal formation of a mouth in a test-bearing individual has never been observed and the available information indicates that an animal emerges from the parent test with its full apertural complement, but the possibility of the de*novo* formation of such structures in completely formed animals must be considered. The nature of the causes of the variation in number of apertures is not understood at present and their study lies beyond the scope of the present work.

The test aperture of this species lies at the distal end of an entosolenian tube or peduncular sheath, and the opening itself is generally round but with a slightly wrinkled margin. A prominent collar of pseudochitinous wall material surrounds the aperture, which lies within the craterlike oral depression. In some specimens the wrinkles along the margin of the aperture are so prominent as to impart a strongly radiate appearance to the structure when seen from above. The orifice itself then becomes stellate and suggestive of the lagenid orifice. Since the entire oral apparatus, consisting of entosolenian tube (with its external and internal openings) and collar, is flexible, the external opening can be everted and come to bear an uncanny resemblace to certain Lagenids. As one looks at such a protruded mouth it is easy to imagine that some revengeful evolutionary hand reached through the Urschleim, froze those lips in their puckered condition, and plastered them with calcium carbonate to form a Lagenid.

The entosolenian tube shows variation in length, wall thickness and diameter of the opening which penetrates it. Occasional specimens show a tube which extends to the center of the animal's protoplasmic body, but these are grotesquely elongate in comparison to the normal tube length. The structure may be deflected from its normal path which is perpendicular to the wall of the animal; such deflection heightens its resemblance to Lieberkühnia. The tube permits the passage of protoplasm and contained food materials which frequently are larger than the tube opening itself. As a large food particle passes down the tube one is reminded of a Walt Disney ostrich swallowing golfballs. Some well-coordinated force can open the tube and close it again, but the mechanisms involved in this response have not yet been analyzed.

Other morphological features.—The average wall thickness of a healthy adult ranges from 1.5 to 3 microns, and thickening appears correlated, in some cases at least, with moribundity and senility . A test thickness of 15 microns has been recorded for some obviously moribund specimens and thicknesses ranging from 8-10 microns are not uncommon in old cultures.

The external surface of the test is occasionally found to be scalloped or wrinkled, although the typical test has a smooth surface. A budded portion of one parental test shows strong wrinkling that suggests incomplete inflation of the bud by the contained protoplasm,

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PLATE 15



Arnold: Variation and Isomorphism in Allogromia

but the variation has been encountered in so few cases that its significance remains uninterpreted.

Non-morphological variation.—This species is characterized by variation in many of its non-morphological features, including nutritional and reproductive habits as well as most of the other physico-chemical processes which govern and regulate its existence, but these variations are not included within the scope of the present paper.

ISOMORPHISM

Certain similarities in growth plan, body form and "chamber" arrangement have been observed to exist between variants of Allogromia laticollaris and other foraminifera. Representative variants have been assembled in Plate I in an attempt to show at a glance the range that has been encountered during this study. The typical test form is seen in the lowest photograph, while variants derived by each of a number of processes are grouped in lettered series leading from the basal figure. Solid lines leading from one morphological type to another indicate observed relationships, and broken lines merely suggest inferred relationships that have not been actually observed. The true significance of the following comparisons can only be determined after the accumulation of much additional data from the experimental study of living foraminifera and additional research upon fossil representatives of the group.

In few cases has the study of a living animal borne out more strikingly the paleontologist's predictions than the present one on *Allogromia laticollaris*. The paleontologist has long recognized the family Allogromiidae or a similarity composed complex as the basic, highly varied stock from which all foraminiferan familes must have evolved. The present study has shown how very fitting this designation has been. The choice of the type genus of this family was made without the realization of its variation potential, but it was a particularly fortunate choice.

This species, with its vast potential for variation, could well become the material upon which studies of the basic causes of variation in the foraminifera could be undertaken, for within its variants morphological similarities to at least six basic plans of test organisation have been observed. It would indeed be difficult to find another easily grown foraminiferan with such a variation potential.

Observed similarities have frequently been as striking between this species and certain "advanced" foraminiferal types as they have between this form and its more obvious relatives. This may be coincidence, but students of foraminiferal evolution and systematics should be cognisant of the fact as they attempt to reevaluate existing hypotheses of evolutionary origins and trends.

It is true that the similarities to higher forms may be as great as to the lower or more primitive forms on the basis of test organisation, chamber arrangement

and body form, but other striking and possibly much more fundamental differences may exist; these, too, of course, must be considered by the systematist. The sum total of such characters as test composition, chamber arrangement ("plans of growth"), chamber form, test aperture, body form, septal and sutural characters, ornamentation, wall structure and innumerable cytological, ontogenetic and metagenetic minutiae far outweighs mere morphological similarity in the evaluation of evolutionary and taxonomic relationships. This realisation tempers any desire to draw unwarranted conclusions on the basis of the superficial similarities described below. Yet they do suggest that in this primitive and highly plastic form there is, and has for a long time been, a vast evolution potential which could have been tapped for the subsequent production of several highly diverse foraminiferal stocks.

A typical specimen, such as the one shown in section at the bottom of Plate 15, has in general the same simple, spherical body form as that to be seen in such Saccamminids as Lagunculina, Saccammina, and Pilulina. The first two have a protruding aperture and the last one a slit-like opening, but both apertural types appear in variants of this Allogromiid. An exceptionally striking resemblance exists between this species of Allogromia and the Saccamminid Iridia lucida. The former secretes no chitinous disc-like base as does the latter, but in other respects the two are very similar indeed. Both have perfectly clear organic tests ("pseudo-chitinous"), both are generally spherical to ovoidal, both have a well-developed entosolenian tube, and both have strikingly similar nuclear morphology and organisation (see Le Calvez, 1936 and 1938). Other species of Iridia, such as I. diaphana and I. serialis are notably similar to variants of Allogromia laticolaris. Iridia serialis, for example, has the same linear separation of bud-like lobes as those shown in A3 of Plate 15, while I. diaphana resembles such forms as those of C7, C_8 and C_9 of the same plate.

Simple budding of the parental stock has been observed to produce an individual of type A. Budding is not an uncommon means of reproduction in this species, although asexual reproduction is usually accomplished by multiple fission, with the division of the parent cytoplasm into a number of separate units which form new tests around themselves and emerge from the parent test as complete, miniature reproductions of the parent. Budding, in every documented case, has been aboral in this species, but the possibility of adoral budding of the type described for the testacean Euglypha (Schewiakoff, 1888) must be considered.

Figure A_2 shows an intermediate stage in the budding process. In this animal the nucleus of the uninucleate parent has divided mitotically and a daughter nucleus can be seen migrating toward the budded half of the original animal. Budding may be terminated by the separation of a single individual, or the bud may remain temporarily attached to the parent and itself produce a bud. In some cases the process may be repeated several times, resulting in the formation of a temporarily multiloculine, rectilinear form of the type illustrated in A_3 . Each "chamber" of such an animal contains a single nucleus, although the illustrated section contains one "chamber" which appears to be enucleate. The adjacent frame of the sectioned series shows the missing nucleus. The illustrated specimen has a single aperture which is located at the lower portion of the photograph, and the mouth-bearing portion is superficially biserial. Animal A_3 will, upon reproduction, revert to the typical spherical form from which it arose.

Budding may in some instances be lateral instead of terminal and then produce a twisted or coiled uniserial body of the type shown in A_4 and A_5 . These animals have the body form and chamber arrangement of *Placopsilina* or *Bullopora* and have been observed ultimately to separate into a number of ovoidal to spherical animals which correspond in number and size to the individual lobes or "chambers" in the grotesque, parental concatenation. Type A_5 may arise by secondary contortion of animal A_3 , and, although this phenomenon has not been observed in living specimens, it seems most probable that type A_4 can arise in the same manner and merely represents an early stage in the subsequent separation of the lobes to form new, simple individuals.

The forms thus far discussed are produced by budding in a chain-like sequence. There is abundant evidence, however, that another type of budding does occur. Animal A₁, for example, has been produced as a result of multiple budding along the aboral surface of a single chamber. Successive buds have arisen not from each other, but alongside one another in the same hemisphere of the parent mass. No discernible spiral has been detected in the mass of closely packed buds, but the body form of this creature is strikingly similar to that of Tretomphalus pacificus Cushman when seen in side view. The large, bulbous parental lobe festooned with its halo of sub-globular chamber-like buds is impressive enough, but the isomorphism is climaxed by the presence of an entosolenian tube in the exact relative position that it occupies in Tretomphalus. There is, however, no evidence for a functional similarity between the two isomorphs.

Body form B, a straight tube with apertures at both ends, can arise directly from a spherical parent as a result of multiple fission, but it can also be produced as a result of the differential breakup of a stellate form of the type shown in C_7 or C_9 . An animal with form B usually pinches into two oval or spherical bodies as shown in B_1 , thereby eventually reverting to the spherical form of the earlier parental organism.

Animal C is intended to represent a variety of multiapertured forms which are derived on occasion from a single-mouthed, spherical or ovoidal parent; the illustrated specimen has four apertures. From such multiapertured forms may be derived a variety of body forms which may persist for most or all of the adult life of an individual but which eventually revert to the simple form of the parent by the separation of the various lobes into young individuals.

Animal C_1 represents one modification of the basic poly-oral test in which extenuation occurs to separate off a dual-mouthed tube and a single-mouthed sphere. This same animal may have grown and undergone some contortion to produce types C_2 and C_4 , forms which strongly suggest the early rotation observed in certain miliolids. The adjacent segments of a swollen animal of type C_1 have merely folded back on each other differentially to give the two contrasting appearances of C_2 and C_4 .

The Pennsylvanian miliolid Orthovertella is an isomorph of animal C_3 , an Allogromia with early chambers of the "milioline" type leading into an uncoiled, protrusive (and, in this case, protrusible as well) terminal chamber.

Continued growth and elongation of C_1 could eventually be followed by more intensive contortion to produce, via C_4 , an animal of type C_5 , an analogue of the coiled form illustrated in D. Animal C_5 was rapidly assuming the appearance of an irregular coil at the time it was killed, sectioned and stained, but the coil was produced by the bending and adhesion of one lobe to another, a very different process from the one involved in the production of D, as we shall subsequently see.

The earlier precursor of the entire C lineage could possess three mouths, as in C and C₆, or it could possess several, as in C₇. This latter animal is a near-perfect, unarmoured prototype of such typical Astrorhizids as *Astrorhiza* itself. In the highly elastic condition which seems to characterize this stellate form of *Allo*gromia laticollaris the animal passes through a pleomorphic spectrum ranging from a form isomorphous with *Astrorhiza* (C₇) and C₈ and C₉ to the tubular form of B. The protrusion of the apertural region of animal C₆ could and has been observed to produce a miniature, triradiate form that is an isomorph of *Rhabdammina abyssorum*.

Form D—one of the most remarkable isomorphs yet observed in this species—arose from a typical, spherical parent by a unique process of segmentation which involves a gastrulation-like process, the formation of folds in the test wall, and the ultimate pinching off of the lobes thus produced.

The first noticeable change in the normal, spherical adult is the development of a small depression along some part of its periphery (Stage 1, Fig. 1.) This depression deepens as the test wall appears to collapse, resulting in a form similar to that produced by pushing in one side of a hollow rubber ball (Stage 2, Fig.

1). The process is reminiscent of gastrulation as it occurs in the development of metazoan embryos, but the resemblance, of course, is superficial. The walls of the pocket then collapse or are forced together by protoplasmic turgor (Stage 3). Soon small depressions appear around the exposed outer surface of the animal's test (Stage 4). These depressions gradually deepen as the test wall grows inward toward the collapsed pocket. Slight depressions soon appear along the marginal walls of the collapsed pocket and begin to migrate toward the external furrows (Stage 5). Both groups of depressions or furrows are lined with test material and eventually unite to form a "septum" between adjacent protoplasmic lobes or "chambers." In some instances protoplasmic bridges between adjacent lobes persist for a time and the structures thus formed are suggestive of the retral processes of Elphidium crispum. The openings through which the protoplasm penetrates the septum are certainly analagous to, if not homologous with, true foramina.

Each segment of the protoplasmic body of the animals is found to contain a single nucleus, as illustrated in D of Plate 15. Eventually the individual lobes are completely separated by the confluent septal elements and begin to pull apart. Each lobe is soon found to contain its own aperture, but the time or mode of origin of these features has not yet been determined. Lobed specimens have been observed to contain at least two mouths before septal fusion occurs, but data concerning the development of additional apertures is still lacking. As Stage 6 shows, the prominently lobed mass next begins to unroll, giving an appearance of the type seen in D_1 of Plate 15. As the actual separation of the lobes into individuals begins, the relict coil becomes very loose (A4 of Plate 15) and the associated mass of young begins to pull apart, with the ultimate formation of as many normal, spherical, uninucleate young as there were lobes in the monstrous progenitor.

Form D_2 has the loosely-coiled, inner chambers characteristic of the later stages in the process described above, but the development of a long, terminal lobe or "chamber" gives it a form which is suggestive of the globigerinid *Hastigerinella*.

The changing patterns of development and isomorphism described in the preceding paragraphs have shown some of the morphological diversity that occurs within this primitive, gromoid species. There are numerous relationships which, for the sake of clarity, have been omitted from the illustrations. Any appendix to the earlier discussion of these relationships should, at this point, add no further detail but merely emphasize the fact that extreme morphological flexibility characterizes this species.

TAXONOMIC COMPLICATIONS

The "twilight" zone between the true Foraminifera and the true Testacea is occupied by a group of testate sarcodinians which have affinities with both groups—a typical boundary problem in taxonomy. It is impossible to so define the two groups as to accommodate the intermediate forms adequately unless some arbitrary and possibly artificial means of making the distinction is employed. Further investigation may eventually show that the basis currently used for the demarcation is invalid, but taxonomic expediency requires that a line be drawn at some point.

Rhumbler (1904) drew the line between a group of gromoid forms which had hyaline pseudopodia and a group which had granular pseudopodia. The first group was removed to a new Order, the Filosa, and the second was assigned to the favored position of the first family of the Foraminifera. Rhumbler's choice of pseudopodial granularity as a basis for the division seems to have been sound, since no better distinguishing characteristic has yet been found. It does seem that the presence or absence of pseudopodial granules may be a fundamental, organisational characteristic of far greater genetical significance and taxonomic value than any known morphological feature or group of features. Doyle (1935) has shown that mitochondria are the only protoplasmic granules which pass from the intra-test protoplasm of Iridia diaphana to the pseudopodia. If all pseudopodial granules are eventually shown to be mitochondrial, the presence or absence of pseudopodial granules can be expected to be of sufficient significance in the physiological organisation of the animal to justify considerable taxonomic recognition.

The type species of the genus *Gromia*, as originally constituted by Dujardin (1835), was *Gromia oviformis*. This huge sarcodinian (it frequently attains a diameter of 3 mm.) has hyaline pseudopodia and was removed to the Filosa by Rhumbler. Living specimens and



TEXT FIGURE 1. Observed ontogenetic changes in one variant of Allogromia laticollaris.

stained sections of specimens from the Scottish coast of the Atlantic Ocean and from numerous stations along the California coast of the Pacific Ocean (Arnold, 1951) offer convincing proof of the propriety of separating these beasts from the more delicate Allogromiid form. The basic difference between the pseudopodia is striking, but other important differences are known to exist between the two groups. Jepps (1926, 1934) and Lwoff (1925) have shown that flagellated zoospores are formed in G. oviformis, whereas Swarczewsky (1909) in his studies on Allogromia ovoidea and Arnold (1953unpublished Ph.D. dissertation) in cytological studies on A. laticollaris have encountered amoeboid gametes. Arnold (1952) has shown that the oral apparatus of G. oviformis is a fairly complicated structure, and unpublished observations on the structure of the oral apparatus in Allogromia laticollaris suggest that basic organisational differences between the two structures exist. The life history and cytology of the larger species are not known, but the above differences alone leave little doubt that basic differences exist between Gromia oviformis and the smaller Allogromiid ancestors of the true Foraminifera.

Rhumbler (1904) proposed the name Allogromia for the genus to which the gromoid forms with granular pseudopodia should be transferred when he shifted G. *oviformis* to the Filosa. The name is particularly appropriate, because the Allogromiidae do bear a striking superficial resemblance to the larger Gromia and obviously had been taxonomically treated as other Gromia until the time of Rhumbler's critical revision.

The Order Foraminifera contained 10 families at the time Rhumbler established the genus Allogromia. He assigned the genus to the Family Rhabdamminidae which then contained 8 subfamilies. Rhumbler used the name "Craterininae" in one place and Allogromiinae in another to designate the Subfamily containing Allogromia, but it seems probable that the former was erroneously retained in his text, since he mentioned in a footnote the pre-occupation of the generic term Craterina for a ciliate and was obviously aware of the impropriety of this name for the foraminiferan subfamily. Members of the Allogromiinae differ from the Myxothecinae in having a definite mouth structure and from the remaining subfamilies in the lack of adherent foreign particles on their test. The present study has produced no evidence which would contra-indicate this taxonomic treatment.

Rhumbler included six genera within the Subfamily Allogromiinae: Allogromia, Lieberkühnia, Shepheardella, Rhynchosaccus, Rhynchogromia and Diplogromia. The present study has shown that the characters which are of primary generic significance for each of the first four genera are developed to some degree by variants of A. laticollaris. The details of these similarities are as follows:

1. A constant, ovoidal or spherical shape is sup-

posedly characteristic of *Allogromia* and *Lieberkühnia* and separates these two genera from the remaining four. Variants of *A. laticollaris* assume shapes, in an incidence of 0.5 to 3% of the culture population, which are supposedly characteristic of the last four genera.

2. The laterally-displaced aperture is supposed to distinguish *Lieberkühnia* from *Allogromia*, but the entosolenian tube of *A. laticollaris* may be displaced from its perpendicular position so much as to make a differentiation on this basis alone quite difficult.

3. The genus *Shepheardella* is characterized by an elongate body with a mouth at each end, but the highly plastic individual illustrated as B in Plate 15 is an excellent replica of *Shepheardella's* form.

4. Rhynchosaccus, an elongate, irregularly contorted genus which has been described as parasitic on larger foraminifera or as an inhabitant of empty foraminiferal tests (Carpenter, 1877; Rhumbler, 1904), is paralleled morphologically by certain elongate variants of *A. laticollaris*, and, while no opportunity has arisen to determine whether or not these variants would assume similar "parasitic" habits, the morphological characteristics alone seem inadequate for distinguishing the two genera.

The last two genera, *Rhynchogromia* and *Diplogromia*, appear to be established on more reliable characters and would not be confused with any of the observed variants of *A. laticollaris*.

The morphological similarity between this species of Allogromia and various representatives of other Allogromiid genera is marked, but it would be unwise to propose taxonomic revisions within the subfamily until the representatives of the isomorphs could be examined in laboratory cultures. Type specimens of these genera are not available and before an adequate comparison could be made each species would have to be found in the type locality, established in laboratory cultures, and studied from a standpoint of variation. It has not been feasible to undertake this problem during the course of the present study.

Rhumbler (1904) included six species within his newly constituted genus Allogromia, as follows: mollis, lagenoides, ovoidea, dubia, terricola and fluvialis. It is not possible to arrive at positive conclusions concerning the taxonomic relationship of these forms and laticollaris without first studying the cytology and life history of each one in laboratory populations. There is no satisfactory morphological basis for distinguishing the species from observed variants of A. laticollaris, but at the specific level non-morphological characters are of greatest taxonomic importance within this genus. The features which have been used to separate A. laticollaris from A. ovoidea, the only other member of the genus which has been subjected (Swarczewsky, 1909) to detailed cytological investigation, have been previously discussed (Arnold, 1948). Further details of these comparisons will be published in the future.

The taxonomy of the genus and subfamily must eventually come to rest on cytological and metagenetic features in combination with more superficial morphological characters. Since comparative data on this totality of traits are lacking the present discussion has culminated not in a taxonomic revision of the genus but in a further evaluation of certain characters which have previously been used in indicating taxonomic relationships.

EVOLUTIONARY IMPLICATIONS

The essential features of two popular hypotheses concerning the evolution of test form and chamber arrangement are schematized in the upper two-thirds of Text Figure 2. Cushman (1948) does not clearly indicate such a relation between the stellate, tubular and spherical forms, but this is implied in his discussion on page 15. His Text Figure 8 is not in agreement with the textual presentation, but indicates that the Astrorhizidae and Rhizamminidae lie rather nebulously off to one side of the main trunk of development from the Allogromiidae to the Saccamminidae. The text explanation, moreover, somewhat disconcertingly omits the spherical Allogromiids from the lineage. Because of several apparent inconsistencies in his presentation the early relationships have been queried in the diagram. The remaining relationships are presented rather unequivocally by Cushman. Galloway's (1933) concept as diagrammed should be self-explanatory.

Early students of foraminiferal taxonomy (d'Orbigny, 1839, 1852, for example) based their classificatory schemes solely on test form and chamber arrangement. Schultze (1854) included number of chambers as well, and Reuss (1861) added test composition to the list of taxonomically critical criteria. Brady (1884) first attempted to use a multiplicity of traits, and Schubert (1907, 1920) suggested that both horizontal (geographical) and vertical (stratigraphical) distributional data be used, not in the form of traits, but as added clues to the evolutionary probabilities indicated by the fossil record. Most micropaleontologists, now aware of the many parallelisms and convergences in the fossil record of the Foraminifera, attempt to base their taxonomies on these precepts.

Phylogenetic studies have shown that a given test form or chamber arrangement may be encountered in members of widely divergent lineages. The present study of living foraminifera from laboratory cultures seems to furnish ontogenetic support for several paleontologically demonstrable parallelisms.

The remarkable morphologic plasticity of *Allogromia laticollaris* seems to lend support to the view that this or a similar form lies very close to the ancestral stock from which further foraminiferal diversification arose. Among variants of this highly flexible species may be found the chamber arrangements and basic test forms of six of the most prominent morphologic patterns in the Order, namely spherical, stellate, tubular, coiled, uncoiling and rectilinear. The fixation of each of these basic organisational patterns in an hereditary lineage, especially in association with the appearance of hardpart secretion as a trait, could have given rise to an equal number of morphologically distinct groups.

These observations have in no way aided in distinguishing the *basic* form from the *derived* forms, although the spherical or ovoidal form is the most common in culture populations.

SUMMARY

- 1. Allogromia laticollaris has been found in laboratory cultures to reveal a measure of morphologic plasticity which is very conveniently conformable with the paleontological concept of primordial foraminiferal flexibility and which seems to justify the retention of this and similar forms in the complex from which "higher" foraminiferal types have evolved.
- 2. The most common body form in this species is the sphere or oval, but stellate, tubular, rectilinear, coiled and uncoiling variants—isomorphs of a number of "higher" foraminiferal forms—are occasionally observed in laboratory cultures.
- 3. The variants are usually only transient stage between spherical progenitors and descendants.
- 4. A tube with apertures at each end may be produced either by pinching off from a stellate form or as a result of the multiple fission of a single-mouthed, spherical parent (i.e. *de novo*).
- 5. A coiled form may be produced either by the segmentation of a spherical body or by the coiling of an elongate body.
- 6. A stellate form has been observed to arise only from a spherical form, but other possible origins must be considered.
- Uncoiling may be true uncoiling, or it can be merely relict rectilinearity, a transient stage which ultimately leads to coiling.
- 8. A rectilinear form arises by the sequential budding of a spherical parent, or possibly by complete uncoiling.
- 9. The present observations give no indication of the most primitive form in the sequence.
- 10. The complex ontogenetic relationships which sometimes develop among variants of this species suggest that, in general, foraminiferal phylogenies may be complicated, and that, specifically, a given body form and/or chamber arrangement may arise in more than one way or from more than one ancestral type.
- 11. This study suggests that, although many resemblances exist between this species and certain inadequately characterized Allogromiids, taxonomic revisions should not be attempted until the range of variation exhibited by the latter has been defined through a study of laboratory populations of the questionable species.



TEXT FIGURE 2

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CONTRIBUTIONS FROM THE CUSHMAN FOUNDATION FOR FORAMINIFERAL RESEARCH Volume V, Part 2, April, 1954

RECENT LITERATURE ON THE FORAMINIFERA

Below are given some of the more recent works on the Foraminifera that have come to hand.

- ANDERSEN, HAROLD V., and MURRAY, GROVER E. Shallow Pleistocene fossils in St. Tammany Parish, Louisiana.—Journ. Pal., vol. 27, No. 6, Nov. 1953, pp. 845, 846, text fig. 1 (map).—Foraminifera are listed.
- BECKMANN, HEINZ. Palachemonella torleyi n. gen. et n. sp., eine neue Foraminifere aus den Schleddenhofer Schichten (Mitteldevon).—Geol. Jahrb., vol. 67, Febr. 1953, pp. 259-271, pls. A, B, text figs. 1-6.
- BRONNIMANN, P., and BERMUDEZ, P. J. Truncorotaloides, a new foraminiferal genus from the Eocene of Trinidad, B.W.I.—Journ. Pal., vol. 27, No. 6, Nov. 1953, pp. 817-820, pl. 87.—Truncorotaloides (genotype T. rohri n. sp.) differs from Truncorotalia in having supplementary dorsal apertures. Three new varieties are also described.
- CARSOLA, ALFRED J., and DIETZ, ROBERT S. Submarine geology of two flat-topped northeast Pacific seamounts.—Amer. Journ. Sci., vol. 250, July 1952, pp. 481-497, pls. 1-3, text figs. 1-6, table 2.—Foraminifera give evidence bearing on date of truncation.
- CASTANARES, AUGUSTIN AYALA. Note on Globotruncana spinea Kikoine (Upper Cretaceous of Mexico).—The Micropaleontologist, vol. 7, No. 4, Oct. 1953, p. 26.—Includes list of associated species.
- CHANG, LI-SHO. Tertiary Cyclammina from Taiwan and their stratigraphic significance.—Bull. Geol. Survey Taiwan, No. 4, March 1953, pp. 27-37, pls. 1-4, text fig. 1 (map), table 2.—Five species, none new.
- COLE, W. STORRS, and HERRICK, STEPHEN M. Two species of larger Foraminifera from Paleocene beds in Georgia.—Bull. Amer. Pal., vol. 35, No. 148, Dec. 24, 1953, pp. 1-16 (47-62), pls. 1, 2 (4, 5).—A Pseudophragmina and a new Operculinoides. Smaller Foraminifera are listed.
- COLLINS, A. C. Pleistocene Foraminifera from Port Fairy, western Victoria.—Mem. Nat. Mus. Melbourne, No. 18, May 1953, pp. 93-105, pl. 1.—One hundred twenty-six species are listed; four are described as new.
- CRESPIN, I. The Cape Range structure, western Australia, Part II, Micropaleontology.—Bureau Min. Res., Geol. Geophys. Bull. No. 21, 1953, pp. 43-75, pls. 7-10, tables 3-5.—Larger Foraminifera are illustrated. Many lists of Foraminifera are included, as well as a table showing distribution in five formations from lower Miocene to Pleistocene.
- DILL, ROBERT F., DIETZ, ROBERT S., and STEW-ART, HARRIS. Deep-sea channels and delta of the Monterey submarine canyon.—Geol. Soc. America, Bull., vol. 65, No. 2, Febr. 1954, pp. 191-193, pl. 1.
 —Presence and absence of Foraminifera in cores are used to interpret origin of submarine sediments and rapidity of deposition.
- DUNBAR, CARL O. A giant Permian Fusuline from Sonora, in Permian fauna at El Antimonio, western Sonora, Mexico, by G. Arthur Cooper et al.—Smithsonian Misc. Coll., vol. 119, No. 2, June 25, 1953, pp. 14-19, pls. 2, 3.—Parafusulina antimonioensis n. sp.

- ERICSON, DAVID B. Sediments of the Atlantic Ocean. —Lamont Geol. Observatory, Tech. Rept. on Submarine Geol. No. 1, Nov. 1953, pp. 1-34 (mimeographed), text figs. 1-6 (map, diagrams).—Climatic curves are based on proportion of warm- to cold-water planktonic species of Foraminifera. Correlation between undisturbed cores is possible by means of direction of coiling of Globorotalia truncatulinoides. Bottom distribution patterns of a few planktonic species shed light on the current systems in the Pleistocene.
- FEYLING-HANSSEN, ROLF W. Late-Pleistocene Foraminifera from the Oslofjord area, southeast Norway.—Norsk Geol. Tidsskrift, 33, 1-2, 1954, pp. 109-152, pls. 1, 2, text figs. 1-5.—A quantitative study in which the clays can be recognized on the basis of dominance of some species and presence of certain accessory species. Sixty-five species and subspecies are recorded and some of them illustrated.
- GILL, WILLIAM DANIEL. Facies and fauna in the Bhadrar beds of the Punjab Salt Range, Pakistan.— Journ. Pal., vol. 27, No. 6, Nov. 1953, pp. 824-844, pls. 88-91, text figs. 1-4.—Nummulites comprise most of the foraminiferal fauna. Eleven species, one new and two indeterminate, and one new variety, are described.
- HAGN, HERBERT. Die Foraminiferen der Pinswanger Schichten (Unteres Obercampan). Ein Beitrag zur Mikropaläontologie der Helvetischen Oberkreide Südbayerns.—Palaeontographica, Band 104, Abt. A, 1953, pp. 1-119, pls. 1-8, text figs. 1-27.—Included are 191 species and subspecies, of which 7 are new.
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- Chamber arrangement in Foraminifera.—The Micropaleontologist, vol. 8, No. 1, Jan. 1954, pp. 30-32.
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 Geol. Bavarica, No. 17, 1953, pp. 223-244, pls. 4-7.—
 Fourteen species and subspecies, 9 new and 2 indeterminate.

On the foraminiferal genus Gublerina Kikoïne.—Geol. Bavarica, No. 17, 1953, pp. 245-251, pl. 8.—A new species and new subspecies from Upper Bavaria.

- OBRADOVIC, SULTANA. Die Mikrofauna der Oberen Kreide in der Umgebung von Beograd.—Srpska Akad. Nanka, Belgrade, Zbornik radova, knj. 34, Geol. Instit., knj. 6, 1953, pp. 67-87 (pp. 85-87 German summary), pls. 1-5, 1 text fig. and map.—Thirty species, none new, are recorded and illustrated.
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 - The age of the clay-balls and origin of fauna in the Tortonian sands at Zabcice (Moravia, Extra-Alpine Neogene Basin).—Mem. Soc. Roy. Lett. Sci. Bohême, Cl. Sci., Ann. 1951, 1953, VIII, 7 pp.—A large foraminiferal fauna is listed from the clay-balls.
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