**Cupuladria canariensis** (Busk)—Portrait of a Bryozoan

by R. Lagaaij

**Abstract.** The lunuliform bryozoan *Cupuladria canariensis* (Busk) is a benthonic marine organism, whose calcareous colonies can easily be recognised with a hand-lens or under the microscope.

This species is eurythermal (2–300 fathoms), eurytherm (12–31°C), and reasonably euryhaline (28–37...), and requires a stable carbonate or carbonate sand bottom. It is present widely distributed over the continental shelves of the Atlantic and East Pacific between the 14°C surface isotherms and had an equal distribution during the Late Tertiary and Quaternary.

The occurrence of *C. canariensis* in Miocene and Pliocene marine sediments of the southern part of the North Sea basin calls for sea-water surface temperatures of at least 14°C, higher than those obtaining at present in this area. Its occurrence in the Miocene, Pliocene, and Early Pleistocene marine sediments of Spain, Italy, and Rhodes suggests that the Mediterranean was somewhat less saline in the geological past than it is at present.

Although lunuliform Bryozoa range from the Upper Cretaceous to Recent, *C. canariensis* first appears in the Lower Miocene (Aquitanian). Its presence or absence among lunuliform bryozoan assemblages may serve as a criterion for establishing the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf sediments on both sides of the Atlantic. On this criterion a large part of the ‘Caribbean Oligocene’ is to be considered as Lower Miocene.

*Cupuladria canariensis* was named in 1859 by the English bryozoologist George Busk, who discovered it in material collected from the sea bed in the neighbourhood of Madeira and the Canary Islands. Later in the same year he reported its occurrence in the Pliocene Coralline Crag in East Anglia. In the last hundred years the number of records has increased enormously, and the data are widely dispersed in the biological and palaeontological literature. It seemed worthwhile to try to assemble these widely scattered data so as to give a comprehensive picture of the species in space and time.

Such a synthesis is of considerable geological interest. It will be shown that a study of *Cupuladria canariensis* can not only give an insight into certain ecological, climatological, and hydrological conditions in the geological past, but can also help resolve the problem of determining the Oligocene–Miocene boundary in sequences of ancient tropical and subtropical shelf deposits.

Its interest for the palaeo-ecologist is implied in a variant of Grimsdale’s golden rule for systematic palaeontologists: ‘...one detected synonym is worth from ten to one hundred new species’ (1951, p. 467). Perhaps this account will help to establish that one ecologically well-known species is worth more than a hundred tabulatæ ramosæ.

**Zoogeography and Ecology**

1. Distribution

*Cupuladria canariensis* (Bryozoa: Cheilostomata, Anascea) belongs to the so-called lunuliform Bryozoa (Pl. 25, fig. 1), all of which possess the same zoarial form as the genus *Lumulites* Lamarck, 1816. The fully grown colony, or zoarium, has the shape of a dome or flattened cone and consists of a single layer of cells, or zoecia, opening on the convex side of the dome. In addition to the normal cells, or autozoecia, in which

the polypides reside, there are other cells, the vibracula, each bearing a long, whip-like vibracular seta. In the genus *Cupuladria* there is, without exception, a vibraculum situated distally to each autozoocoeum; the tip of each seta is capable of describing a 180° arc in the median plane of its autozoocoeum (text-fig. 1).

Practically nothing is known with certainty concerning the function of these setae. It has been suggested, notably by Busk (1854, pp. 100, 104, 106; 1859, p. 79), that in certain lunulitiform species the setae might be 'subservient to locomotion'. Alternative views are that they function as defensive or cleansing organs (Busk 1859, p. 79). In my opinion, it is clear that they serve to stir up the water in the colony's immediate vicinity, not so much in order to fan food particles towards the polypides' mouths as to prevent clay particles settling on the colony.

If this view is correct, then the possession of these setae must be a valuable asset to the lunulitiform Bryozoa, since it would make them some of the least sensitive to clay sedimentation. It is certainly no coincidence that of all the possible zoarial growth-forms it is precisely two lunulitiform genera, *Cupuladria* and *Discoporella*, that venture most closely, on both sides, to the mouths of the Mississippi distributaries (text-fig. 2). On this map the distribution pattern of the Bryozoa can clearly be divided into three zones:

- **a.** An inner zone between the shore and the 5 fathom line, in which swell and breakers begin to disturb the sea bottom. Here, where the water is turbulent, no lunulitiform Bryozoa occur (for reasons given on p. 187) though other types do, such as those that attach themselves to plants or shells.

- **b.** An outer zone between the 50 and 100 fathom lines, having a steep slope and an irregular topography and situated on the outer edge of the continental shelf. Deposition of clay along the outer margin of many continental shelves is notoriously slight to nonexistent (Kuenen 1939; Shepard 1948, p. 160); and the Gulf of Mexico is no exception (Pilger 1959, p. 650; 1960, p. 288). The low rate of deposition and the local presence of hard substrata explain why Bryozoa with other growth-forms have been able to settle in this zone.
c. A middle zone, which coincides with the broad plateau lying between the 5 and 50 fathom lines. A large part of the clay brought down to the sea by the Mississippi is deposited on this plateau, and it is in this area that only lunuliform species of Bryozoa, being equipped with vibracular setae, are able to survive.

![Map of Louisiana](image)

**Legend**

- **Number of Bryozoa per 30 gramme sample**
  - 1-3
  - 4-10
  - 11-30
  - 31-100
  - >100
- **Bryozoa present, but in unknown quantity**
- **Barren sample**
- **Lunuliform Bryozoa as percentage of total assemblage**
- **Lunuliform Bryozoa present, but percentage unknown**

**Text-fig. 2.** Predominance of lunuliform Bryozoa in the bottom sediments of the Mississippi Delta area. Sources: (a) collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KUPE, Rijswijk; (b) Parker 1956.

There are five characteristics which in combination are responsible for the ability of this type of bryozoan to occupy an exceptionally wide range of environments:

(i) The ability to tolerate a certain amount of clay sedimentation owing to the possession of vibracular setae.

(ii) The ability to exist on almost any kind of bottom as long as the latter consists of small particles.
(iii) The ability to withstand a wide range of temperatures (eurythermal).
(iv) The ability to withstand moderate salinity variations (eurhaline).
(v) An insensitivity to hydrostatic pressure, light penetration, and other factors directly concerned with depth.

This combination of characteristics is the reason for the wide area of distribution of *Cupuladria canariensis*, which includes the tropical and subtropical Atlantic, the eastern Pacific, and the Mediterranean (text-fig. 3), and which has been generally the same throughout the Later Tertiary and Quaternary (text-fig. 4). Yet its distribution is not merely wide on a global scale. Within fairly restricted areas such as the Gulf of Mexico (text-figs. 5, 6) and the Nigerian shelf (text-fig. 7), or in the marine Pliocene of the Low Countries (text-fig. 8) and in the Miocene basin of eastern Venezuela (text-fig. 9), it is also widely distributed on a provincial scale.

2. Larval stage

One may wonder whether there is not perhaps a sixth characteristic contributing to this organism’s wide distribution: the duration of its larval stage. Like all Bryozoa, the lunuliforms are sessile, colonial organisms but they possess a free-swimming larval
stage. The larvae are able to swim by means of their cilia, and the duration of this free-swimming stage is conceivably one of the factors contributing to the geographical distribution of a bentonic species (Cloud 1959, p. 951).

Unfortunately, the larval stage of *C. canariensis* is still unknown. Within the order Cheilostomata, however, two completely different types of larvae occur. One of these, the so-called *Cyphonantes* larva, which is characterized by the possession of a functional alimentary canal, may spend a period of up to two months in this condition. The large majority of the Cheilostomata, however, have the second type of larva, in which this structure is rudimentary or entirely lacking. According to current views, such larvae are therefore drastically limited in the duration of the free-swimming stage (to no more than 12-24 hours, depending on the supply of yolk), so that they do not become truly pelagic. Nevertheless, there are species of Cheilostomata that have this second type of larva and which, in spite of this, have a very wide, or almost cosmopolitan distribution (e.g. *Microporella ciliata*).

This is a baffling paradox with which every student of Bryozoa is sooner or later confronted and for which various solutions have been proposed, e.g. continental drift, dispersal via ancient archipelagos or shelf bridges, or trans-oceanic rafting on floating objects by surface currents. Recently Cheetham (1960), in a stimulating paper, discussed
TEXT-FIG. 5. Quantitative distribution of Cephalodella carnicola in bottom sediments of the north-eastern Gulf of Mexico.
the merits of each of these three hypotheses in the light of Early Tertiary cheilostome distribution. He clearly favours the third alternative, but did not fully consider the possibility of long-distance dispersal in the larval stage. Yet it is precisely this fourth alternative that most strongly suggests itself in the case of those zoarial form-groups that are most unlikely to become attached to seaweed or other 'rafts'. If the distribution of such species, including *C. canariensis*, is amphitropical, and if the Wegenerian hypothesis that the surface and bottom configuration of the Miocene Atlantic Ocean were drastically different is rejected, the conclusion is inevitable that their free larval stage must under certain conditions be, and have been, able to last a long time.

Harmer (1910, p. 520) suggested 'that it does not follow that because we know that a larva may, under favourable conditions, fix itself a few minutes after it becomes free, we should be justified in assuming that that larva would not retain for a long period the power of undergoing a normal metamorphosis should it be drifted away from suitable fixing-grounds'. Silén's (1944, pp. 30, 31) hypothetical concept of external food absorption in larvae which are devoid of an alimentary canal is also interesting in this connexion.

3. **Substratum**

After a brief or protracted period of wandering, the larva settles on a hard substratum. It would seem to make a very careful choice in this matter, as if it knew in advance that the substratum on which it settled would have to be raised above the sea floor and eventually become lodged in the apex of the conical structure which is the adult *zoorium*. 
TEXT-FIG. 8. Distribution of *Cupuladria exarciensis* in the eastern part of the Pliocene North Sea basin (distribution of marine facies after van Voorthuysen 1956).
Above all, therefore, this substratum must not be too big, and it is for this reason that we usually find coarse quartz grains, glauconite pellets, small shell fragments, broken echinoid spines, even moderately large Foraminifera such as *Amphistegina gibbosa* and *Globorotalia menardii*, or fragments of other lunuliform Bryozoa functioning as nuclei for *Cupuladria*. The ideal biotope for the Lunuliform Bryozoa is therefore a small-particle (quartz and/or carbonate sand) bottom. They never occur on a bottom consisting

text-fig. 9. Distribution of *Cupuladria canariensis* in the Miocene basin of eastern Venezuela (shaded area).

entirely of clay, and are never found encrusting rocks, large pebbles, piles, larger shells, or other such large objects. It is not without reason that lunuliform colonies are commonly called 'free' (though this is incorrect) as opposed to 'encrusting' forms. So unusual, in fact, is the appearance of an 'encrusting' *C. canariensis* that Silén (1942, p. 14) refers to a juvenile colony on a small stone from Anguilla in the West Indies as only 'possibly belonging to this species'.

The question arises whether the larva's power of discrimination is real or apparent. On the one hand one might suppose that the larva settles indiscriminately on all kinds of substrata and that it develops into a colony only on those that are suitable. In that case the selection is the work of external circumstances and not of inherent 'intelligence' in the larva. On the other hand, selectivity on the part of pelagic larvae has definitely been observed in other groups of marine invertebrates. According to Thorson (1955, p. 390), Wilson (1952 and earlier papers) has shown 'that the larvae of several polychaetes,
when ready to metamorphose, will critically examine the bottom substratum to which they are exposed. If they find it attractive, they settle. If they find it less attractive or directly repellent, they will continue their pelagic life for days or even weeks. During such a prolonged larval life these larvae test the substratum at intervals as they are transported by the current directly over the bottom.\footnote{As far as Cypialdris is concerned, the following example is pertinent. Plate 25, figs. 2a, b, show two specimens of Cypialdris (not C. canariensis, but an allied species, having affinity with C. pyriformis Busk) from the subsurface Oligocene formation (Miocene) of eastern Venezuela. The larva of both specimens, and of several others from the same shale samples, originally singled out, and settled upon, specimens of Planoorbitinella trinitatis (Nuttall) and persistently neglected several other species of smaller Foraminiferida. This choice seems to have been prompted by the absence of quartz sand; for in a sandy facies with both quartz grains and Planoorbitinella available in good quantities, such as is found along the southern boundary of the eastern Venezuela basin, settling invariably occurred on the quartz grains only.}

4. Astogeny

Having attached itself to a suitable substratum, the larva then rapidly undergoes its metamorphosis into the first individual, the 'ancestrula', of the future colony. Further development takes place by a process of budding. It is interesting to follow the juvenile colony through the early stages of this development, especially since Harmer in 1931 (p. 162) was still able to say: 'there is no conclusive evidence with regard to the earliest stages in the discoidal or conical colonies, and a mere count of the number of surrounding zooecia is not enough to settle the matter', and no pertinent observations have been made since then.

By the time the number of zooecia has increased to twenty-six, the zoarium has passed through several separate stages of growth (text-fig. 10):

(a) The single ancestrula. Despite prolonged searching I have never observed a single ancestrula. Thus it would seem that the process of budding sets in very soon after the metamorphosis is complete.

(b) The three-cell zoarium. This, the earliest zoarial growth stage observed, invariably consists of three zooecia forming the pattern shown in text-fig. 10b. I have recorded several dozens of these three-cell colonies. They display distinct bilateral symmetry. From their mutual relationships it may be inferred that the ancestrula has given rise to two proximo-lateral first-generation zooecia.

(c) The four-cell zoarium. A fourth zooecium is added proximally in the plane of symmetry (text-fig. 10c). The circle is closed and the colony is ready to start its radial growth.

(d) The six-cell zoarium. By the addition of two zooecia in the angles between the ancestrula and the two first-generation zooecia, the colony assumes the shape of a six-pointed star (text-fig. 10d). The plane of symmetry through the ancestrula is still clearly apparent.

(e) The eight-cell zoarium. Two new proximo-lateral zooecia appear (text-fig. 10e).

(f) The ten-cell zoarium. Two more zooecia are added distally, one on either side of the ancestrula (text-fig. 10f; Pl. 25, fig. 3).

(g) The twelve-cell zoarium. Two new lateral zooecia appear (text-fig. 10g). At this stage the colony is still markedly stelliform; the bilateral symmetry can be seen without
difficulty. No zooecia are yet in proximal contact with the vibracula of preceding cells, but this situation changes in the next stage. This earliest, central, part of the colony is therefore relatively less densely covered by vibracular setae than later, peripheral, additions. It is therefore probably no coincidence that preferably (although not exclusively) these central zooecia sometimes regenerate into large vibracula of the type first described by Hastings (1930, p. 714; see also Silén 1942, text-fig. 8), whereas in other lunulitiform species they tend to develop a calcareous closure.

(b) The eighteen-cell zoarium. Six new zooecia have appeared at the periphery (text-fig. 10b), probably via two intermediate stages. The first slight departure from the original plan of symmetry is now apparent, since the proximal and the distal indentations
at the periphery in the median line are too large to be filled by a single zoecium and yet too small to accommodate a pair of zoecia. The filling of the gap therefore takes place asymmetrically.

1. The twenty-six-cell zoarium. A further departure from bilateral symmetry takes place (text-fig. 10). By now the colony has attained a diameter of 1.9 mm. and is well on its way to adulthood.

Two points emerge from these observations:

i. Waters's (1926, p. 426 and text-fig.) concept of a double ancestrula in Cupuladria, the two being turned in opposite directions, and each giving off three distal zoecia, is untenable. Although Waters specifically mentioned C. canariensis in connexion with his observations, it is clear from the occurrence of partially closed zoecia and from the provenance of his material (Princess Charlotte Bay, Queensland, Australia), that he was actually dealing with C. guineensis (Busk).

ii. Silén's (1942) theory of spiral growth is no longer valid in the case of the genus Cupuladria.

I should like to emphasize that the astogeny outlined above only applies to ideal cases, and that deviations from this scheme are common and may appear at an early stage (Pl. 25, fig. 4). Usually such deviations are closely bound up with irregular configurations of the small-particle substratum, or with an eccentric position of the ancestrula on the substratum. The eight-cell zoarium figured in Plate 25, fig. 4 deviates in that it has developed a zoecium (on the left) in a position that would normally not be occupied until the twelve-cell stage, while the usual place for the eighth zoecium (on the right-hand side) remains vacant. Occupation of the latter position, which projects beyond the edge of the particle, would have involved building a stronger dorsal wall than the extremely thin one required in the position now preferred, where it is supported by the substratum. Obviously less building energy is required for growth on the substratum than for expansion beyond its edges.

5. Mode of life of lamelliform colonies

The mode of life of the adult colony and, closely connected with that, its orientation with respect to the sea bottom, are controversial matters, and widely differing suggestions

**EXPLANATION OF PLATE 25**

Fig. 1. *Cupuladria canariensis* (Busk). Adult colony. a, View of the convex surface; b, View of the concave surface. Q.S. 173, Pleistocene of Pobrede 41, Rock, Netherlands, 15 00-20 00. m. x 10. (After Lagaan 1922.)

Fig. 2. *Cupuladria sp.*, Concave side of juvenile colonies, showing larval predilection for the foraminiferal *Planorbulinella trinitensis* (Nuttall): Lower Miocene (Officina formation) of Texas Petroleum Company well Mata 1, Estado Aracateigi, Venezuela; a, 2,100-8,170 ft.; b, 8,300-8,820 ft. x 20.

Fig. 3. *Cupuladria canariensis* (Busk). Juvenile colony (ten-cell stage) in normal symmetrical development. Recent, Mees Cremer 1959 Sta. 98, Nigeria, 14 fms. x 20.

Fig. 4. *Cupuladria canariensis* (Busk). Juvenile colony (eight-cell stage), showing early departure from bilateral symmetry. Recent, Mees Cremer 1958 Sta. 376, Nigeria, 11 fms. x 20.

Fig. 5. *Cupuladria canariensis* (Busk). Regenerated colony, showing sector of original large flattened conical colony with peripheral outgrowth in radial direction. Recent, Ras-el-Amouh, Mediterranean, 45 fms. x 10. (After Danerevel 1935.)
have been made, none of which, according to Harmer (1931), have been supported by pertinent observations. Four tenable hypotheses have been put forward (text-fig. 11).

As Harmer (1931, pp. 150-1) has shown, the conventional view that the colony rests on its flat ‘base’ (text-fig. 11a) was first disputed by Maplestone (1910, p. 3), who expressed the opinion that ‘the conical forms in their living state have the base uppermost’. Although at this time Maplestone was only referring to the conical colonies of the genus

![Image](image-url)

a RESTING ON BOTTOM WITH GROWING EDGE

b ATTACHED BY RHIZOLES SPRINGING FROM CIRCUM-
ANCESTRAL "RADICULAR" ZOOGIA

c FIXED UNDER THE FRONDS
OF ALGAE

d ROTATION AND ASCENSION
TO ESCAPE BURIAL

TEXT-FIG. 11. Various hypotheses regarding the mode of life of lobuliform colonies.

Conecharella, later authors have extended his contention to include other genera whose colonies are conical. Moreover, Maplestone was not certain whether the conical colonies of Conecharella hang point downwards from some foreign object, or whether they retain this position on the bottom by means of anchoring filaments.

Canu (1915, p. 21) adopted and elaborated on both hypotheses. His early reasoning is not generally known (cf. Harmer 1931, p. 151), but later re-statements of his views have profoundly influenced later workers. It is therefore necessary to quote Canu in full on this point: ‘Les espèces flottantes comme les Lunolites ont le zozarium conique, la pointe en bas. Tantôt il est maintenu sous les Algues [text-fig. 11c], tantôt il est attaché à de petits objets par des radicelles [text-fig. 11d]. Celles-ci proviennent de Zoécies radiculaires (= Zoécies avortées de l'Orbigny) disposées autour de l'ancestrale. . . . Les zoécies radiculaires sont d’abord des zoécies hydrostatiques. La larve, en effet, se fixe sur un grain de sable; l'ancestrale qui se développe émet immédiatement des zoécies radiculaires qui l'enveloppent et permettent à l’animal de commencer son ascension sous une Algue loin du sable dangereux à son développement. . . . Soit attachés par des radicelles, soit retenus sous les Algues, les Lunolites, par leur forme turbinée, sont de position très instable: ils chavirent au moindre filet d’eau. L’animal maintient sa position
normale à l'aide de longs filaments articulés appelés vibraculaires. Ce sont donc des appareils de stabilisation un peu analogues au balancier des danseurs de corde.

The same views, essentially unchanged, are repeated by Fauré and Canu (1916), Canu and Bassler (1920, pp. 238 ff.), and Canu and Lecointre (1927, p. 35). Waters (1921) was quick to oppose these views, which have in fact largely been confined to the French school. I refer in particular to his statement (1921, p. 401): '...though sometimes the growth is on a much larger stone, as in some specimens of Cupuladria canariensis from Petit Tahou, Liberia. It would seem impossible for a colony so heavily weighted on the bottom to maintain its equilibrium even in the water, in a position absolutely contrary to the ordinary laws of statics', invoked rotation as a means of conserving its position (text-fig. 11c), first for Conesclaterella (1929, p. 482) and later for Lunulites (1931, p. 9): 'Ils vivent donc l'apex en bas au voisinage du fond sableux. Ils s'émagent par rotation et ascension pour éviter l'enlisement'; and (1931, p. 19) 'Les Lunulites sont de petites coupes en perpétuelle rotation pour se dégager du sable et changer de place'.

Dartevelle also attributed a planktonic mode of life to Lunulites (1933, p. 69) and to Cupuladria (1943, p. 108): 'Leur mode de vie est semblable à celui, bien connu, des Lunulites, c'est-à-dire que la colonie flotte entre deux eaux, les zoéces tournées vers le dessous, la face concave vers le haut,...' The designation 'face supérieure' for the concave side and 'face inférieure' for the convex, siphuliferous side of lunuliform colonies still persists in recent French literature (Vigneron 1949; Buge 1957).

Dartevelle (1933, p. 57), moreover, provided a novel explanation of the role played by the small foreign particle at the downward directed apex of the cone: 'La présence de ce substratum constitué par un morceau de coquille, une nummulite, un grain de sable, contribue à maintenir l'équilibre de la colonie et à l'empêcher d'être chavirée par les vagues'; it served, in other words, as ballast, and as such would profoundly influence the shape of the colony. According to Dartevelle (loc. cit., p. 70) the lighter the substratum, the flatter the zoolithic cone, and, conversely, the heavier the particle, the higher and more dome-shaped the colony would have to become in order to keep the ballast as low as possible; '...ce qui guerriera donc la colonie, c'est la souci d'éviter le renversement et de maintenir le meilleur équilibre possible au sein du fluide.'

Harmer's presidential address to the Linnean Society of London in 1931 made it abundantly clear that Canu and Bassler's reasoning was based entirely on inference and not on direct observation. He added (1931, p. 151): 'I have failed to find any evidence that is really conclusive with regard to the question at issue. Except for Whitelegge's very brief account, I am acquainted with no observations made on living specimens, and in my judgment the matter should for the present be regarded as undecided.' Harmer's statement is still as valid today as it was thirty years ago. Here is clearly a case where laboratory experiment could be of value. It should not be too difficult to collect some living specimens of Cupuladria and keep them under observation in a sea-water aquarium.

Another example of reasoning by inference, the emphasis in which is laid on the
orientation of the ancestrula and of later zoocia with respect to the small-particle substratum, occurs in Silén (1947, pp. 5-6, 8, 15 and text-fig. 8). He concluded (correctly, in my opinion) that the colonies of Cupuladria rest freely on the sea bottom with the apex pointing upwards. Silén thereby reverted to the conventional view (see, however, Silén 1942, p. 13).

Two further arguments, both arising from the ecology of C. canariensis, support this conventional view, or rather conflict with the hypothesis of a planktonic mode of life postulated by Caru and his school. In the first place, if C. canariensis were indeed a planktonic organism, one would expect to find its skeletons distributed over different kinds of bottom and a very wide range of depths. However, its remains are found only on the small-particle bottoms to which it is confined in life by the special requirements of the larvae. Secondly, there is a direct relationship between the maximum depths at which C. canariensis has been observed in the various marine areas, and the temperature of the bottom water in those areas (see p. 189). Both these observations suggest that C. canariensis is a truly benthonic organism.

6. Minimum depth

Cupuladria canariensis occurs mainly on small-particle bottoms and is hence a full member of that rather select level-bottom community described by Petersen (cf. Thorson 1955). A type of small-particle bottom from which it is excluded, however, is one where the sand grains have a tendency to shift under the influence of water movements. The minimum depth at which the larvae of C. canariensis and other lunuliform species, such as Discoporella umbellata (Defrance), can settle and develop into adult colonies therefore depends on the intensity of the water turbulence over the bottom, i.e. on the depth of the wave base and on the strength of the bottom currents. Since both these factors are determined by the degree of exposure of the shelf and by oceanographical factors, the minimum depth mentioned above varies from place to place (text-fig. 12).

Cupuladria colonies are therefore unlikely to be washed up on the shore, and there are no records that this has ever occurred, although 'one dead and worn' colony of D. umbellata has been found on the shore at Balboa, Panama Canal Zone (Hastings 1930, p. 718). As Stach (1936, p. 63) has put it, 'their free mode of life prohibits their existence in the littoral zone where wave action is strongly felt'. The lunuliform Bryozoa thus seem to be confined to the stable small-particle bottoms below wave base. This conclusion is quite contrary to that of Dartevelle (1933, 1935), who inferred an agitated, current-infested biotope from the common occurrence of broken and regenerated lunuliform colonies in the Eocene of Belgium. Yet there is no reason why fragmentation should be due solely to mechanical breakage in a highly turbulent environment; the destructive activity of other marine organisms in deeper, quieter water might just as easily be responsible (Ginsburg 1957, p. 83). It is known that holothurians (sea cucumbers) include the lunuliform Bryozoa in their diet. Silén (1942, p. 13) records eight colonies of C. canariensis taken from the stomach of the sea-urchin Moena ventricosa, and I have observed the occurrence of fragments and of several entire colonies of C. canariensis among the coarser debris in the stomach of a holothurian in the north-western Gulf of Mexico (Cavalière 1956 Station 227, at a depth of 37.5 fathoms). Dartevelle (1935) gives Recent examples of regenerated zoaria of C. canariensis (Pl. 25, fig. 5) taken from the Mediterranean locality Râs-el-Amouch at a depth of 45 fathoms, which is well below that at
TEXT-FIG 12. Minimum depths at which *Cymatodrila cuspidata* has been found in various areas. Notice shallowest occurrences in sheltered, deepest occurrences in exposed biotopes.
which sand transport could occur, let alone transport and breakage of far larger objects such as bryozoan colonies.

7. **Maximum depth (minimum temperature)**

The maximum depth of occurrence of *Cupuladria canariensis* is determined by the temperature of the bottom water. The maximum depths at which *C. canariensis* has been found in three marine provinces is as follows:

<table>
<thead>
<tr>
<th>Province</th>
<th>Depth (Fathoms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NW Gulf of Mexico</td>
<td>138</td>
</tr>
<tr>
<td>NE Gulf of Mexico</td>
<td>117</td>
</tr>
<tr>
<td>Straits of Florida</td>
<td>122</td>
</tr>
<tr>
<td>Jamaica</td>
<td>150</td>
</tr>
<tr>
<td>E of Jacksonville, Florida</td>
<td>440</td>
</tr>
<tr>
<td>N of St. Thomas, Virgin Islands</td>
<td>300-470</td>
</tr>
<tr>
<td>Sénégal</td>
<td>118</td>
</tr>
<tr>
<td>Nigeria</td>
<td>120</td>
</tr>
</tbody>
</table>

Since the recent geographical distribution of *C. canariensis* is roughly limited both in the Atlantic and in the eastern Pacific by the 14°C surface isotherms (text-fig. 3) and it must be remembered that the bottom water at shelf depths will be a few degrees colder it may reasonably be assumed that this approaches the minimum temperature at which *C. canariensis* can survive. The maximum depths of occurrence and the corresponding bottom-water temperatures of approximately 12°C observed in various marine areas seem to confirm this assumption (text-fig. 13).

The deep occurrences along the western and southern confines of the Sargasso Sea are of particular interest. In all three cases the data refer to living specimens. The hydrography of this region (text-fig. 14) is almost unique in featuring a lenticular body of water of uniform temperature (18°C) and salinity (approx. 36.5‰) down to a depth of 300-400 metres (Worthington 1959). Below this depth a gradual decrease of temperature takes place down to the main thermocline. Clearly it is only the peculiar temperature conditions prevailing in this area that permit the occurrence of *C. canariensis* at such unusually great depths.

8. **Maximum temperature**

It is at the shallow end of its depth range that one has to seek the maximum temperature which the species will tolerate. This will be in shallow coastal waters, where the effects of atmospheric heat exchange are most strongly felt.

It will be readily understood, however, that the determination of this parameter will be far less precise than that of the minimum temperature, since the absolute maximum may vary from year to year. Thus, *C. canariensis* may conceivably form part of the bottom fauna of a shallow bay during the normal summer of a particular year, but the following year an abnormally hot summer may bring its occupation of that bay to a sudden termination. The best approximation will therefore be found by taking the average maximum temperature in the warmest month, recorded over a number of years.

Areas where such shallow occurrences of *C. canariensis* coincide with the necessary amount of regularly recorded temperature data are Tampa Bay, Florida, and Breton
Sound, Louisiana, where C. canariensis occurs at minimum depths of 4 and 2 fathoms respectively (text-fig. 12).

According to the records published by the U.S. Coast and Geodetic Survey (1955), the average maximum temperature in the warmest month (July) for the years 1947-54 at St. Petersburg (Tampa Bay) was 31°C. Since this figure is based on surface measurements, the corresponding value for the shallow bottom water is bound to be somewhat less extreme.

[Image: Diagram showing relation between deepest occurrences of Cupuladria canariensis and bottom-water temperature.]

Text-fig. 13. Relation between deepest occurrences of Cupuladria canariensis and bottom-water temperature.

In Breton Sound, where C. canariensis is known to occur in 2-3 fathoms depth in the lee of Breton Island (Parker 1956), surface-water temperatures during the summer reach an average absolute maximum of about 31-32°C (Scrutton 1956, p. 2937). According to Scrutton (loc. cit.), "vertical stratification is stronger in the summer than at other times, so that bottom temperatures in Breton Sound proper probably seldom reach 32°C."

9. Maximum salinity

The clue to the maximum salinity that C. canariensis will tolerate lies in the Mediterranean. From its occurrences elsewhere, on the Florida shelf and in the West Indies, one may infer that it still thrives in salinities of approximately 36-5%o. In the Mediterranean, on the other hand, salinities at the surface are everywhere higher than 37%o (and increase with depth), except where the surface current carries water of Atlantic origin and an original salinity of about 36-25%o through the Strait of Gibraltar along the
north coast of Africa as far east as Tunisia (Sverdrup, Johnson and Fleming 1960, pp. 643, 646).

The extent of this Atlantic water in the Mediterranean coincides exactly with the Recent Mediterranean distribution of *C. canariensis* (text-fig. 15f). The easternmost Mediterranean record of the species is from Cape Rosa, Algeria, 40 km. east of Bône. *C. canariensis*, like all other lunuliform species, is conspicuously absent among the bryozoan fauna of the eastern Mediterranean, for example in Tunisia (Canu and Bassler 1930), Egypt (O’Donoghue and De Watteville 1939), and Syria (Gautier 1957). Since this entire area lies south of the 14° C. surface isocline (text-fig. 15d) and since
bottom temperatures in the Mediterranean, even at great depths, nowhere drop below about 13°C (Nielsen 1912; Furnestin 1960). It is clear that here the limiting factor is not the water temperature but the $\geq 37\%_o$ salinity.

This conclusion has the interesting implication that the Miocene, Pliocene, and early Pleistocene Mediterranean (text-fig. 15a-c) was somewhat less saline than it is at present. The difference was most marked in the Sicilian, when $C. canariensis$ (and by inference salinities $< 37\%_o$) extended into the Levantine basin (Rhodes), where present-day salinities constantly remain about $39\%_o$ (Wüst 1960, figs. 2, 5; pl. 7).

10. Minimum salinity

Data on the minimum salinity which $C. canariensis$ will tolerate must be inferred from its occurrence in the shallow coastal waters, where precipitation and run-off are most effective in lowering the salinity.

Reduced salinities have been observed in the following shallow areas where $C. canariensis$ is known to occur:

a. Breton Sound, leeward of Breton Island, Louisiana; depth 2-3 fathoms (Parker 1956); bottom salinity $28-35\%_o$, measured in the autumn of 1951 during flood tide; the ebb tide produces still lower salinities (Scruton 1956, p. 2927).

b. South of Calcasieu Pass, Louisiana; depth 5-8 fathoms (text-fig. 12). Salinities measured at neighbouring stations (Bandy 1954, fig. 8, Sta. 106, Sta. 108) are of the order of $28-29\%_o$. To all appearances these figures are based on surface measurements, but in this shallow turbulent part of the Gulf of Mexico vertical stratification is bound to be slight and the corresponding bottom salinities will therefore probably not be very different.

$C. canariensis$ is absent in the Gulf of Mexico off Grand Isle, Louisiana, presumably because here salinities at 10 feet below the surface may drop periodically to as low as $21\%_o$ in June and July, and $14\%_o$ in February (Geyer 1950, p. 103). The lowest monthly average in this area is $22.6\%_o$ (March 1949).

11. Recognition

Another, more subjective, factor which affects the boundaries of the known distribution of $C. canariensis$ is the ease with which the species can be recognized. Large undamaged colonies may easily attain a diameter of 1.5 cm., and their aesthetically satisfying shape makes them conspicuous among the other members of the macro-fauna. Unfortunately, $C. canariensis$ is rather fragile and during rough handling in nature or in

Explanations of Plate 26

Fig. 1. Detail of the broken surface, showing the characteristic fine, parallel, vertical striation. Lower Miocene (Carapita formation) of Mene Grande Oil Company well SB-133, Estero Monagas, Venezuela, 3,825-3,840 ft., $\times 40$.

Fig. 2. Middle Miocene (Reineke/Dingdener Stufe) of Twistringen, SSW of Bremen, Germany, $\times 20$.

Fig. 3. Lower Miocene of Shell-BP Petroleum Development Company well Itik-1, Nigeria, 3,320-3,780 ft., $\times 20$.

Fig. 4. Lower Miocene (Chickasawhay formation) of Limestone Creek, Wayne County, Mississippi, U.S.A., $\times 20$.

Fig. 5. Upper Miocene (Cubagua formation) of Socony Mobil Oil Company well Cubagua-1, Cubagua, Venezuela, 218 ft., $\times 20$. 
TEXT-FIG. 15. Fossil and recent distribution of Cupuladria canariensis in Europe and North Africa (Middle Miocene and Pliocene base maps after Wilks 1951).
the laboratory is apt to break almost always along the radial lines on the concave surface. The smallest recognizable fragments take the form of tiny rectangular prisms (Pl. 26, fig. 1), whose dorsal ends correspond to the rectangular compartments visible on the concave surface (text-fig. 16). These compartments are perforated, and so consequently, are the dorsal ends of the individual prisms. The vertical faces are flat and show line, parallel, vertical striation (Pl. 26, fig. 1). Thus even very small fragments can be recognized (Pl. 26, figs. 2-5), and for this reason C. canariensis may be regarded as a component of both the macro- and the microfauna.

APPLICATIONS

1. Shifts in sea water temperature since the Miocene

Palaebotany holds the key to the interpretation of Tertiary climates in north-west Europe. It is known that the north-west European climate gradually cooled from tropical (Eocene) through subtropical (Miocene and early Pliocene) to warm temperate (late Pliocene) conditions, after which even more marked and rapid cooling to subarctic conditions introduced the Pleistocene.

At present both summer and winter air temperatures in north-west Europe are strongly influenced by the temperature of the water in the eastern Atlantic and the North Sea. It is not unreasonable to assume, therefore, that the subtropical and oceanic climates prevailing in north-west Europe during the Miocene and Pliocene periods bore a direct relationship to considerably higher sea-water temperatures in these latitudes.

Such an hypothesis is strongly supported by a comparison of the present-day occurrences of C. canariensis with those during Miocene and Pliocene times (text-fig. 17). As has been already mentioned (p. 189), the northern boundary of its present area of distribution in the northern hemisphere coincides with the 14°C surface isotherm (text-fig. 3). Consequently, Miocene and Pliocene winter surface-water temperatures in the North Sea basin must have been at least 14°C, February surface-water temperatures in this area now average between 5°C and 6°C (J. H. Sverdrup, Johnson, and Fleming 1960, chart II). In the Miocene and even in the Pliocene the water in the southern part of the North Sea must therefore have been at least 8°C or 9°C warmer than it is at present. This conclusion accords well with the figures derived by the Polish palaebotanist Szafir for the amount by which Pliocene air temperatures in Europe north of the Alps exceeded those now prevailing: January +11°C, July +9°C, yearly average +9°C (J. H. Sverdrup, Johnson, and Fleming 1960, p. 266).

This conclusion is particularly interesting, however, because both in the Middle Miocene (text-fig. 13) and in the Pliocene (text-fig. 15b) the land area at present occupied by the British Isles was connected to the continent of Europe. C. canariensis (and the entire warm-water fauna associated with it) must therefore have migrated to the North Sea area of those times by a path lying to the north of Scotland. In view of the present-
day confinement of the species by the 14° C. surface isotherm must have lain to the north of Scotland in both the Miocene and Pliocene periods and probably resembled in shape the present-day 5° C. isotherm, which under the influence of the Gulf Stream curves around Scotland and penetrates into the North Sea (text-fig. 17). The strandings of a loggerhead turtle, Caretta caretta (Linn.), on the Norwegian coast in December 1891 (Willgoos 1953) and the capture of a flying fish, Cypselurus heterurus, in Oslo Fiord in 1848 and in 1937 (Brunner 1938) are indications that even today the Gulf Stream occasionally carries tropical and subtropical marine organisms along this ancient migration route.

During the Pleistocene C. canariensis did not have a chance to migrate once more into the North Sea region (text-fig. 15c). This sea-water temperature did not rise sufficiently to allow this, even in the interglacial periods, when the climate was somewhat warmer than it is now. From the composition of the molluscan fauna of the Dutch Eemian (the last, late-Pleistocene, interglacial), van Straaten (1956, pp. 224, 225) concluded that the temperature of the sea-water at that time could only have been about 4° C. higher than that of the present North Sea, and might have been no more than 2° or 3° C. higher. It is interesting to note that Spätm (1958, p. 31) concluded that the southern element of this Eemian fauna must also have reached the Dutch coastal area by the route north of Scotland.

2. The Oligocene-Miocene boundary in the Gulf Coast and Caribbean areas

During the past decade, several attempts have been made to correlate the Tertiary formations on either side of the Atlantic. The problem of defining the Oligocene-Miocene boundary in the Caribbean area has been closely connected with these attempts and has still not definitely been solved.

A detailed discussion of this problem lies outside the scope of this paper. Those who are interested are referred to the paper by Eames (1953), through whose activity the problem became critical, to the ensuing discussion between Stainforth (1954) and Eames (1954), to the later restatement of the problem by Stainforth (1960a; 1960b, with extensive bibliography) and to the renewed discussion between Eames et al. (1960a; 1960b) and Stainforth (1960c). The arguments put forward by Eames et al. have now been stated in full detail in their book on Mid-Tertiary stratigraphical correlation (1962).

Briefly, the Oligocene-Miocene boundary in the Caribbean area has undergone a progressive lowering during the past decade. All concerned agree that this move was justified; there is no agreement, however, about the level in the Caribbean sequence of planktonic foraminiferal zones where this boundary should finally be drawn. Stainforth (1960b, p. 226) is undecided whether the whole Globigerina ciperoensis zone and part of the Globigerina dissimilis zone or only part of the Globigerina ciperoensis zone represents the whole Oligocene. Eames (1955, p. 86), on the other hand, implied complete absence of marine Oligocene sediments in Trinidad by his statement that “probably all the Cipero formation is of Lower Miocene age”. Eames et al. (1960a; 1960b, 1962) have since corroborated this view and have even extended it so that not only the Cipero but also the underlying San Fernando formation is included. If their opinion is correct, a major hiatus occurs in the Trinidad sequence between the Eocene (Navet and equivalents) and the Miocene (San Fernando, Cipero and equivalents) marine deposits.
It is important to discover whether, and to what extent, the lunuliform Bryozoa, and in particular Cupuladria canariensis, throw light on the matter.

Lunuliform Bryozoa, which range from the Upper Cretaceous to Recent, have long been of interest to palaeontologists. Lunulites, the eponymous genus, was introduced by Lamarck in 1816 and since then a considerable number of fossil species have been recorded from Tertiary and Quaternary strata both in Europe and in North America. The accompanying range charts (text-fig. 18) show the time-stratigraphic distribution of these species in the two hemispheres.

Comparison of these two charts reveals several interesting facts:

a. There are no Eocene and Oligocene species of Lunulites common to both hemispheres. It is possible that a thorough systematic revision of the group might alter this situation. But whether it would or not, it is significant that there is a similar lack of common species among the contemporaneous larger Foraminiferida of both hemispheres.

b. The disappearance of the genus Lunulites clearly did not take place contemporaneously in both hemispheres. In North America it probably no longer occurs in situ in the post-Vicksburg formations, whereas in Europe it persists into the Miocene. It should be borne in mind, however, that several living species of Lunulites have been recorded from Australian seas.

c. Several names common to both charts, of which one is C. canariensis, first appear in the Miocene of Europe and in the post-Vicksburg formations of the southern U.S.A. This new appearance of modern lunuliform genera and species, which, as has been seen in the case of C. canariensis, possess exceptional environmental tolerance leading to wide and rapid dispersal, may well serve as a criterion for establishing the Oligocene-Miocene boundary in sequences of ancient tropical and subtropical shelf sediments on both sides of the Atlantic.

By this criterion the Vicksburg group correlates with some part of the European Oligocene (absolute hegemony of Lunulites), whereas such post-Vicksburg formations as the Chickasawhay of Mississippi and Alabama and the subsurface Upper Frio of Texas cannot be considered older than Aquitanian (since both contain C. canariensis). Although most North American stratigraphers, e.g. Cooke et al. (1943), MacNeil (1944), and oil companies do not share this view, it is clear that it was held as long ago as 1934 by others, such as Howe (1934) and McGuirt (1941).

Some of the evidence underlying text-fig. 18 is brought out in greater detail on the correlation chart of the Gulf Coast Oligocene and Miocene formations (text-fig. 19), which shows the known occurrences of the genus Lunulites and C. canariensis according to the published records and my own observations. Conspicuous on this chart is the wide distribution of these lunuliform Bryozoa throughout the marine Tertiary sediments, even though information on several southern states is still incomplete.

It is interesting to study the Caribbean area in the light of what is known about Europe and the Gulf Coast, where modern lunuliform species and genera first appear in the Aquitanian and post-Vicksburg formations respectively.

It has already been shown (text-fig. 9) that lunuliform Bryozoa, in this case C. canariensis, are widely distributed throughout the ‘Oligocene-Miocene’ basin of eastern Venezuela. The vertical distribution of C. canariensis in various parts of the basin is
TEXT-FIG. 18. Time-stratigraphic distribution of Tertiary and Quaternary Nummuliform species.
shown in text-fig. 20. As far as the problem of the Oligocene-Miocene boundary is concerned, the oldest occurrences are the most relevant.

In northern Guairejo the earliest occurrence is to be found in the upper part of the 'Oligocene' Robleicto formation of well GX1-5. In the Rio Arcos of northern Montana C. canariensis occurs at the base of the Aroe Shale, directly above its contact with the Los Jabillos formation (text-fig. 21). The Aroe Shale is generally considered to be the lateral equivalent of the lower part of the NairiTul formation of the Barcelona area.

<table>
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<th>Age</th>
<th>Occurrence</th>
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</thead>
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<td>Robleicto</td>
<td>Upper part</td>
</tr>
<tr>
<td>Louisiana</td>
<td>Oligocene</td>
<td>Robleicto</td>
<td>Upper part</td>
</tr>
<tr>
<td>W. Mississippi</td>
<td>Oligocene</td>
<td>Robleicto</td>
<td>Upper part</td>
</tr>
<tr>
<td>C. Mississippi</td>
<td>Oligocene</td>
<td>Robleicto</td>
<td>Upper part</td>
</tr>
<tr>
<td>SW. Alabama</td>
<td>Oligocene</td>
<td>Robleicto</td>
<td>Upper part</td>
</tr>
<tr>
<td>NW. Florida</td>
<td>Oligocene</td>
<td>Robleicto</td>
<td>Upper part</td>
</tr>
</tbody>
</table>

Text-fig. 19. Occurrences of Lunulites spp. and of Cupuladria canariensis throughout the Oligocene and Miocene formations of the Gulf Coast.

which itself was considered to be of Lower Oligocene, and possibly even Upper Eocene, age (Renz et al. 1958, p. 576). This age assessment can no longer be maintained. Since they contain C. canariensis, both the upper part of the Robleicto and the Aroe Shale (and for that matter the NairiTul) cannot be of more than Aquitanian (or post-Vielsburg) age. The correctness of this interpretation is reinforced by the fact that C. canariensis is accompanied in both cases by Discoporella umbellifera, another 'modern' lunuliform species.

It is interesting to compare these occurrences with the Caribbean planktonic foraminiferal zonation locally established by the Creole Petroleum Corporation.

According to Creole, the Aroe Shale represents the upper two-thirds of the Globorotalia opima opima zone and the whole of the Globigerina ciperoensis ciperoensis zone. The oldest known occurrences of C. canariensis at the base of the Aroe Shale thus fall in the lower half of the G. opima opima zone.

The underlying Los Jabillos formation has hitherto generally been considered as Upper Eocene (ibid Fio-Codexito 1956, p. 331; Renz et al. 1958, p. 576). This age assessment, too, needs revision in the light of newly acquired evidence. According to Creole, the Los Jabillos formation must be post-Eocene, since its stratigraphical position falls slightly above the base of the G. opima opima zone.
TEXT-FIG. 20. Occurrences of Cupuladria canariensis throughout the Tertiary formations in the eastern Venezuela basin (map and correlation chart after Renz et al. 1958, modified).
Again according to Creole, the Los Jabillos formation is underlain by shales with *Globigerina ampliapertura* (not present in the Rio Aoro outcrop section shown in text-fig. 21). It is this *G. ampliapertura* zone that on planktonic foraminiferal evidence correlates with the Vicksburg (Boll 1957, p. 107). Thus one might expect to find a different suite of lunulitiform Bryozoan at this level. Unfortunately, there are no earlier records of this group of Bryozoan from Eastern Venezuela than those mentioned above. All one can say is that the Vicksburg, as it is defined in the southern U.S.A., is characterized, from the point of view of the lunulitiform bryozoan sequences, by the absolute hegemony of the genus *Lunulites* (text-fig. 18b) and therefore correlates with some part of the European Oligocene (text-fig. 18a). This would imply that the *G. ampliapertura* zone is also Oligocene.

In summary it appears that Eames *et al.* were substantially correct in lowering the Oligocene-Miocene boundary in the Caribbean area farther than any of their critics were prepared to go. From the presence of modern lunulitiform Bryozoan, it must be concluded that at least the upper two-thirds of the *Globorotalia opima opima* zone is Miocene (Aquitanian or younger). On the other hand, Eames *et al.* (1960a, p. 448; 1962, pp. 48, 49, fig. 5) would definitely seem to be going too far in wishing to submit the Vicksburg to the same rejuvenation course. The Vicksburg lunulitiform bryozoan assemblages have a distinct Oligocene character, and if the planktonic foraminiferal correlation is correct, this would imply that the *Globigerina ampliapertura* zone of the Caribbean sequence of planktonic foraminiferal zones is also Oligocene. The Oligocene-Miocene boundary in the Caribbean, subject of so much discussion in the past decade, would thus be pinpointed in eastern Venezuela somewhere between the top of the *Globigerina ampliapertura* zone and the top of the lower one-third of the *Globorotalia opima opima* zone.

The earliest occurrences of *C. canariensis* in Nigeria of which I am aware have so far been found in the wells Ituk-1 (range 3,320-3,780 feet) (PI. 26, fig. 3) and Ituk-2 (range 2,770-2,950 feet) in the Calabar flanks area, and in Ihuo-I (range 2,062-2,085 feet).

Acknowledgements. The author wishes to thank the staffs of the museums, the numerous oil companies, and the many friends and colleagues who have provided the material which forms the basis of this study, or who have offered suggestions and help in many other ways and whose contribution is not specifically mentioned in the text.

He is particularly indebted to the staff of the Creole Petroleum Corporation, who, in their comments on the manuscript, made available important information on the planktonic foraminiferal zonation in eastern Venezuela and suggested several corrections to text-figs. 20 and 21.
The Dutch manuscript was translated by Mr. R. W. Barke; Mr. W. R. Mulder executed the text figures with great care; Messrs. J. Foumier and J. H. H. van Gijch took some of the photographs.

REFERENCES


— 1955. The Miocene–Oligocene boundary in the Caribbean region. Ibid., 92, 86.


WATER, A. W. 1921. Observations upon the relationships of the (Bryozoa) Selenniidae, Concórrhenniidae, &c., fossil and Recent. J. Linn. Soc. (Zool.), 34, 399–427, pl. 29, 30.


APPENDIX

I. Synonymy


1921 *Cupulifera caryensis* Busk: WATER, A. W. Observations upon the relationships of the (Bryozoa) Skenethidae, Coescheschellidae, etc., fossil and Recent. *J. Linn. Soc.* (Zool.), 34, p. 410 (partie), pl. 29, figs. 1–5; pl. 30, figs. 11, 12, 21, 22, 23.


1930 *Cupulifera caryensis* (Busk): HASTING, A. R. Chelostomatous Polypora from the vicinity of the Panama Canal collected by Dr. C. Crossland in the Cruise of the S.S. “St. George.” *Proc. zool. Soc. Lond.* 47, p. 714, pl. 8, figs. 38, 40.


2. Documentation of maps and figures

All cited papers are listed either in the References or the Synonomy.

BAMS: British Museum (Natural History).
KNS: Koninklijke Shell Exploratie en Produktie Laboratorium, Vomeronk 6, Rijswijk, Z.H., Netherlands.

1. Cap Rons, Algeria
2. Tanger Bay, Morocco
3. Ouz, Algeria
4. Tangier Bay

All the selected localities shown are:

1. Cap Rons, Algeria
2. Tanger Bay, Morocco
3. Ouz, Algeria
4. Tangier Bay
<table>
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<th>Reference or repository</th>
<th>Location</th>
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<tr>
<td>5. Vannneau Sta. XXIX, Morocco</td>
<td>Canu and Bassler 1925b</td>
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<td>6. Cape Sagres, Portugal</td>
<td>Silen 1942</td>
</tr>
<tr>
<td>7. Off Punta Delgada, Azores</td>
<td>Bassler 1899a; Normann 1899</td>
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<td>8. Madeira</td>
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<td>9. 'entrée de la Bocayna', Canary Islands</td>
<td>Calvet 1907</td>
</tr>
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<td>10. Gran Canaria, Canary Islands</td>
<td>Silen 1942</td>
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<td>13. Cape Verde, Senegal</td>
<td>Bassler 1889a</td>
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<td>14. Conakry, Guinea</td>
<td>Bassler 1889a</td>
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<td>15. Petit Faho, Liberia</td>
<td>Waters 1889, 1921</td>
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<td>16. Accra, Ghana</td>
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<td>17. SE of Lagos, Nigeria, 13 fms</td>
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<td>22. Albatross Sta. 2415, E of Jacksonville, Fla.</td>
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**REF. 4.** The selected localities shown are:

- **Mioceine**
  1. Twistringen, SSW of Bremer, Germany
  2. Berningen, Netherlands
  3. Wernheim, near Antwerp, Belgium
  4. Vienna Basin, Austria
  5. Benczyn, near Wadowice, Poland
  6. Turin, Italy
  7. Ferriere l'Arcon, Indre-et-Loire, France
  8. Dept. Girond, France
  9. Barcelona province, Spain

- **Reinbek-Dinglen Steine, Middle Miocene (Pl. 26, fig. 2)**
  10. Diebolingen 15°154-195 m., Middle Miocene
  11. Lower Diestian (Deurnian), Upper Mioceine
  12. Torrington, Middle Miocene
  13. Aulitzan and Burdigalian, Lower Miocene
  14. Helvetian, Middle Miocene

- **ex Dr. C. W. Drooger**
  15. Lagoaia 1953
  16. Lagoaia 1952
  17. Manzoni 1877a; Canu and Bassler 1925a
  18. Maleev (1951)
  19. Scotii 1936
  20. Siggemue 1979
  21. Canu and Leconte 1925b; Bogen 1957
  22. Cana 1917; Daubiere 1920; Vignaux 1949
  23. Fauna 1914; Fauna and Canu 1916
10. Niger Delta, Nigeria
11. Calabar area, Nigeria
12. Misselle River, 10 km. N of Tiko, E of Mount Cameroon, Nigeria
13. French Cameroon
14. Monroe County, Florida
15. Jackson’s Bluff, Ochlockonee River, Leon County, Florida
17. Limestone Creek, Wayne County, Mississippi
18. East Baton Rouge Parish, Louisiana

19. Laguna Atocosa, Cameron County, Texas
20. Goliad County, Texas
21. Gulf of Mexico, off Nueces County, Texas
22. Bowden, Jamaica
23. Cercado de Mao, Santo Domingo
24. Port Limón, Costa Rica
25. Río Coro, at Caracas, Dist., Miranda, Estado Falcón, Venezuela
26. Cuyo Blasico, near Maiquetia Airport, Dist., Federal, Venezuela
27. Estado Guairac, Venezuela
28. Estado Anzoategui, Venezuela
29. Estado Monagas, Venezuela
30. Estado Monagas, Venezuela
31. Cubagua Island, Venezuela
32. Concord quarry, Point à Pierre, Trinidad

Exploration well Oloibiri-1, 9,560–9,570', Miocene
Exploration well Ikuk-1, 3,320–3,720', Miocene (Pl. 26, fig. 3)
Lower Miocene

Middle Miocene
Calyphiophora formation, Miocene
Chocarawhachic, Miocene

Shell River (type locality), Miocene

Chickasawhay, Miocene (Pl. 26, fig. 4)
Superior Oil Prod. Co.’s Dogleg well, No. 1 well, 7,671–7,687', Heterostegia zone; 8,091–8,101', Marginatum zone, Catahoula formation, Miocene

Shell Continental Corp. (Pl. 26, fig. 3)

Houash, Thompson & Crown Central C. G. Wood, I. 1, 3,193', updip limit of Anahume shaly wedge, Miocene

Gulf Oil Corp. and others, Block 899, 3–A, 10,300', Upper Frilo, Miocene

Bowden Beds, upper Middle Miocene

Middle Miocene

Lower Miocene
Cuyahoga formation, upper Middle Miocene

Playa Grande formation, Upper Miocene

Crespo Petroleum Corp., CXB-5, Reday formation, Miocene

Mercado Oil Co., OG-1, 2,185–2,250', Frattles formation; 3,700–4,215', Oficina formation, Miocene

Crespo Petroleum Corp., ORC-2, 3,000–4,200', Carapita formation, Miocene

Compania Shell de Venezuela, Caracas

Crespo Oil Co., Cero Negro-3, Frattles formation, Oficina formation, Miocene

Sociedad Minera, Cubagua-1, 2,185', Cubagua formation, Upper Miocene (Pl. 26, fig. 5)

Concord marl, Miocene

R. LAGANAIJ: THE BRYZOAN CUPULADRIA CANARIENSIS
PlIOCENE

I. Sutton, Suffolk, England
II. Antwerp, Belgium
III. Heurnesoord, Netherlands
IV. Rolen, Netherlands
V. Contigne, Maine-et-Loire, France
VI. Pignon-Blanc (Landreau), near Nantes, France
VII. Pontevedra, Portugal
VII. El Ampurdan, near Barcelona, Spain
VIII. Valle Andona, Asis, Piedmont, Italy
IX. Province of Modena, Italy
X. Artavilla, near Palermo, Sicily, Italy
XI. Nador, near Algiers, Algeria
XII. Terrebonne Parish, Louisiana
XIII. Minotimmi Creek, Bocas Island, Almirante Bay, Panama
XIV. Camarones, 10 km. E of Esmeralda, Ecuador

Gederean, Pliocene
Scaldian (prob. Luchthol horizon), Pliocene
Boring 1928, 102-40-109.03 m., Scaldian; Pliocene
Boring 114-22, 184.50-215.00 m., Pliocene
Redonian, Pliocene
Redonian, Pliocene
Pliocene
Pliocene
Aslian, Pliocene
Pliocene
Aslian, Pliocene
Pliocene
Pliocene
Pliocene
Pliocene
Pliocene

Pliocene

Bunker 18596
Cana 1920
Lagunaj 1952

Bunker (ex Dr. J. H. van Voorsluysen)
Roger and Bugge 1946; Bugge 1957
Cana 1920b; Roger and Bugge 1946; Bugge 1957
Calderon de Carvalho 1961
De Angeli 1895
Manzoni 1889; Cana 1913b
Najivas 1890
Cipolla 1921
Cana 1913a
McGuire 1941
Cana and Bassler 1928a

Cipolla (ex Mr. J. Brouwer)

Pleistocene

A. Livermore, Italy
B. Monte Mario and Farnesina, near Rome, Italy
C. Carrurture, Calabria, Italy
D. Palermo, Sicily, Italy
E. Rhodes
F. Gulf of Mexico, Mississippi River Delta area, Louisiana
G. Gulf of Mexico, High Island area
H. Gulf of Mexico, off Matagorda County, Texas
J. Cabo Blanco, near Maiquetia Airport, Dist. Federal, Venezuela
K. Estado Monagas, Venezuela
L. Puerto Militar, Bahia Blanca, Argentina

Sicilian, Pleistocene
Calabrian
Sicilian?
Sicilian?
Sicilian
South Pass, Block 6 Area, State Lease 29001, 500-1,000", Upper Marine, Pleistocene
Federal Block A 104, Shell Continental "Neptune-1", 750-900; 835-1,000", Pleistocene
Ohio Oil Company, State of Texas 401-1, 1, 537-598; 662-754; 1,035-1,997; Pleistocene
Marine formation, Pleistocene?
Compania Shell de Venezuela, Guanima-1, 640-670, Pari formation, Pleistocene
Pampana, Pleistocene

Neviani 1891
Manzoni 1889; Neviani 1895
Neviani 1905
Cipolla 1921
Manzoni 1877b; Pergens 1887; Salen 1942

CIPOLLA (ex Mr. J. J. Gouty)
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**Text-1, Source:** samples kept at KEMP, Rijswijk, Netherlands; the co-ordinates and depths are listed below:

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**Text-2, Source:** collections from the Exploration and Production Research Laboratory, Shell Development Company, Houston, Texas, now at KEMP, Rijswijk, Netherlands; (b) Parker 1956.
TEXT-FIG. 9. Southern boundary of eastern Venezuela Basin after Mencher et al. 1953, fig. 7; northern boundary coincides with 'mountain front'.

The following Miocene occurrences are shown:

- Cabo Blanco, near Maiquetia Airport, Dist. Federal
  - Cabugua Island, Socony Mobil Oil Company, Cabugua-1, 218°
- Estado Guárico, Socony Mobil Oil Company, GXB-2
  - Socony Mobil Oil Company, GXB-3
- Estado Guárico, Venezuelan Atlantic Refining Company, Tacurpiño-2
- Estado Guárico, Sinclair Oil & Refining Company, Pedro Azul-1
- Estado Guárico, Venezuelan Atlantic Refining Company, Guama-1
- Estado Guárico, Compañía Shell de Venezuela, Shothole 6081
  - Shothole 1146
- Estado Guárico, Sinclair Oil & Refining Company, Canaronco-1, 2,350-2,790'
- Estado Aragua, Compañía Shell de Venezuela, VC-1
  - Cagaita-1, 750-775'
  - Cagaita-2, 2,200-2,225'
  - Cagaita-3, 6,750-6,800'
- Estado Aragua, Mene Grande Oil Company, Casco-1, 750-1,225'
  - Casco-2, 3,025-3,425'
- Estado Aragua, Phillips Oil Company, B-1, 625-1,175'
  - Mene Grande Oil Company, OG-1, 2,125-2,150', 3,250-3,275'
- Estado Aragua, Texas Petroleum Company, Mata-1
  - Texas Petroleum Company, El Salto-1
- Estado Monagas, Compañía Shell de Venezuela, Cerro Negro 1
  - Compañía Shell de Venezuela, Cerro Negro 2
- Estado Monagas, Compañía Shell de Venezuela, Cerro Negro-3
  - Compañía Shell de Venezuela, Cerro Negro-4
  - Compañía Shell de Venezuela, Cerro Negro-5
  - Compañía Shell de Venezuela, Cerro Negro-6
- Estado Aragua, Compañía Shell de Venezuela, outcrop sample SL-2992
  - outcrop sample SL-3000
  - outcrop sample SL-301
- Estado Monagas, Compañía Shell de Venezuela, outcrop sample SL-781, Río Aro
- Estado Monagas, Compañía Shell de Venezuela, SIR-153, 925-1,250'
- Estado Monagas, Creole Petroleum Corp., JGE-28
  - Monag-1
  - JGE-28, 1,274, 5,325-6,790'
  - JGE-2, 2,000-3,800'
  - JGE-3, 2,900-4,200'
  - JGE-9
- Estado Monagas, Compañía Shell de Venezuela, OHS-3
  - Compañía Shell de Venezuela, OHS-3
- Estado Monagas, Creole Petroleum Corp., QGE-26, 2,900-4,300'

Playa Grande formation
  - Cabugua formation
  - Robleos formation
  - Chavezarama formation
  - Chavezarama formation
  - Chavezarama formation
  - Chavezarama formation
  - Upper Santa Inés
  - Naranja equivalent
  - Verde equivalent, Oficina formation
  - Moreno member
  - Verde member, Oficina formation
  - Moreno member, Oficina formation
  - Blanco member, Oficina formation
  - Blanco member, Oficina formation
  - Azul member, Oficina formation
  - Freites formation
  - Oficina formation
  - Oficina formation
  - Freites formation, Oficina formation
  - Freites formation, Oficina formation
  - Freites formation, Oficina formation
  - Freites formation, Oficina formation
  - Oficina formation
  - Oficina formation
  - Freites formation, Oficina formation
  - Freites formation, Oficina formation
  - Capaya formation
  - Capaya formation
  - Capaya formation
  - Capaya formation
  - Arco shale
  - Capaya and Capaya formations
  - Buena Vista shale - Arco shale
  - Carenia formation
  - Capaya formation
  - Capaya formation
  - Capaya formation
  - Carenia formation
  - Capaya formation
R. LAGAAN: THE BRYOZOA OF **CUPULADRIA CANARIENSIS**

Estado Montagas, Creole Petroleum Corp., GFE-29, . Carapita formation
Trinidad, Point-a-Pierre, Shell Trinidad Ltd., outcrop sample No. 207, Concord Quarry
Trinidad, Caroni County, Caura Ward, Springvale, near Caura, about 1 mile
S of Milton, outcrop sample (Mansfield 1925; Darrevelle 1943). C. conocephala

**TEXT-FIG. 12.** The four stations shown are:
- Parker 1956, Sta. 321, lat. 29° 30' 30" N, long. 89° 15' W
- Tarpon Bay, Florida, lat. 27° 46' N, long. 82° 39' 36" W
- Cavalier 1956 Sta. 286, lat. 29° 40' 35" N, long. 93° 19' 40" W
- Mee Cramer 1959 Sta. 83, lat. 4° 10' 39" N, long. 6° 10' 25" E

**TEXT-FIG. 13.** The eight stations shown are:
- NW Gulf of Mexico: bathythermogram—Mabel Taylor 1932 Sta. 1106
  *C. canariensis*—Cavalier 1956 Sta. 314, 27° 48' 12" N, 93° 43' 48" W
- NE Gulf of Mexico: bathythermogram—Mabel Taylor 1932 Sta. 903
  *C. canariensis*—Atlantic 1951 Sta. 152, 28° 00' 09" N, 85° 07' 00" W
- Sargasso Sea: bathythermogram—Atlantic 1953 Sta. 1483, 21° 46' N, 62° 45' W
- Gulf of Guinea: bathythermogram—Meteor 1926 Sta. 235, 3° 33' 30" N, 5° 6' 42" E

**TEXT-FIG. 14.** The three occurrences shown are:
- Albarroba Sta. 2415, lat. 30° 44' N, long. 79° 26' W, 440 fms.
- Port Antonio, Jamaica, 150 fms.
- Caroline 1933 Sta. 94, lat. 18° 39' N, long. 63° 03' 30" W, 100-470 fms.

**TEXT-FIG. 15.** The Middle Miocene occurrences shown are those listed under text-fig. 4 as Nos. 1, 2, 4, 5, 6, 7, 8, and 9; the Pleistocene occurrences shown are those listed under text-fig. 4 as Nos. 1, II, III, IV, VI, VII, VIII, IX, X, and XI; the Early Pliocene occurrences shown are those listed under text-fig. 4 as Nos. A, B, C, D, and E; the Recent occurrences shown are those listed under text-fig. 3 as Nos. 1, 2, 3, 4, 5, and 6.

**TEXT-FIG. 17.** The Pleistocene occurrences shown are those listed under text-fig. 4 as Nos. I, II, III, IV, V, VI, VII, VIII, IX, X, and XI; the Recent occurrences shown are those listed under text-fig. 3 as Nos. 1, 2, 3, 4, 5, and 6.

**TEXT-FIG. 18a.** Compiled from Canu and Basler 1923, 1929, 1931; Darrevelle 1933, 1952; Münzen and others. Not shown on this chart, on the assumption of being junior synonyms, are:
- *Lumulites stahlinoides* von Münster (fide Canu and Basler 1929, p. 11)
- *Lumulites angulata* Canu and Basler (fide Darrevelle 1933, p. 57; 1952, p. 133)

**TEXT-FIG. 18b.** Compiled from Canu and Basler 1920, 1923, 1928a; McGuirt 1941; Uhlich and Basler 1954 and others; and incorporating own observations, e.g., the occurrence of *Lumulites angulata* (Canu and Basler) in the Byram marl of Byram, Pearl River, Mississippi, and the occurrences of *Lumulites canariensis*, *C. subata* (Orbigny) and *Decaporella mullikini* (Defrance) in the Pleistocene of the Gulf Coast at the localities listed under text-fig. 4 as Nos. F, G, and H.

**TEXT-FIG. 19.** Correlation chart largely based on one made by Mr. R. W. Barker, with the south Texas column (I) here added and the NW Florida column (II) adapted to include the latest views of Purk (1955). The following occurrences of *Lumulites spp.* are shown:

<table>
<thead>
<tr>
<th>Column 1 (Louisiana)</th>
<th>Column 2 (Mississippi)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rosserdell, Cachicota Parish</td>
<td>Vicksburg (McGuirt 1941)</td>
</tr>
<tr>
<td>Pont Springs, near Vicksburg</td>
<td>Miss Spiers, near Byram (ex Mr. J. J. Gouvy)</td>
</tr>
<tr>
<td>Byram</td>
<td>Byram marl (Canu and Basler 1920)</td>
</tr>
</tbody>
</table>
### Coluna 4 (E Mississippi)
- Red Bluff, Wayne County
- Horseshoe Mill Creek, near Highway 45, Wayne County
- Locality CN, W bank of Chickasawhay River, Wayne County

<table>
<thead>
<tr>
<th>Red Bluff clay (Cana and Buser 1920)</th>
</tr>
</thead>
<tbody>
<tr>
<td>basal Marnine limestone, ksp. (ex Mr. R. W. Barker)</td>
</tr>
<tr>
<td>Paynes Hammock sand (if fragment), ksp. (ex Mr. R. W. Barker)</td>
</tr>
</tbody>
</table>

### Coluna 5 (SW Alabama)
- One mile N of Monroeville
- St. Stephens Bluff, Tombigbee River

<table>
<thead>
<tr>
<th>'Chimney Rock' member of Marianna limestone (Cana and Buser 1920)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gleneden, ksp. (ex Mr. E. H. Rainwater)</td>
</tr>
</tbody>
</table>

### Coluna 6 (NW Florida)
- Road cut, U.S. Highway 90, at Chipola River

| Marianna limestone, ksp. |

The following occurrences of *Cupuladria canariensis* are shown:

#### Column 1 (E Texas)
- Gulf of Mexico, off Nueces County, Gulf Oil Corp. and others, Block 889, 3-A, 10,900' / Wood top 1, 2,165-3,493' / Upper Frio, ksp. (ex Mr. E. M. Wilkins) / Updp limit of Anahuac shale wedge, ksp. |

#### Column 2 (Louisiana)
- East Baton Rouge Parish, Superior Oil Producing Company’s Duplanier Community No. 1 well, 7,671-7,687' / Heterostegina zone, Catahoula formation (McGuirt 1941) |
- East Baton Rouge Parish, Superior Oil Producing Company’s Duplanier Community No. 1 well, 8,091-8,101' / Mettantia zone, Catahoula formation (McGuirt 1941) |

#### Column 4 (E Mississippi)
- Limestone Creek, Wayne County
- Chickasawhay, ksp. (ex Mr. R. W. Barker) |

#### Column 5 (SW Alabama)
- Choctaw Bluff, Alabama River, Clarke County
- Chickasawhay, ksp. (Mr. W. McAlhany Coll.) / ex Mr. R. W. Barker |

#### Column 6 (NW Florida)
- Shell Bluff, Shoal River, N of Mossyhead, Walton County
- W. D. McDaniel’s farm, near Red Bay, Walton County / Choctawhatchee stage, *Arca* facies, marl with *Arca rhuddanian* ksp. |

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### Text-fig. 20. The following occurrences of *Cupuladria canariensis* are shown:

#### Column 1 (Northern Guarico)
- Creole Petroleum Corp., GXB-5
- Sinclair Oil & Refining Company, Piedra Azul-1
- Venezuelan Atlantic Refining Company, Tucupido-2

#### Column 2 (Greater Antare area)
- Companhia Shell de Venezuela, Capacai-1, 750-775'
- Mene Grande Oil Company, Casca-1, 750-1,225'
- Socony Mobil Oil Company, Guarai-1, 1,675-1,700', 2,200-2,225'
- Phillips Oil Company, B-1, 625-1,175'
- Texas Petroleum Company, Mata-1
- Mene Grande Oil Company, OG-1, 2,125-2,150', 3,250-3,275'
- Companhia Shell de Venezuela, Cerro Negro-1
- Companhia Shell de Venezuela, Cerro Negro-3

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**Legend:**
- Reboleó formation
- Chaguaramas formation
- Naranja equivalent
- Verde equivalent, *Oicina* formation
- *Bacillo* member
- *Mewaco* member, *Oicina* formation
- *Azuel* member, *Oicina* formation
- *Baino* member, *Oicina* formation
- *Oicina* formation
- *Oicina* formation
- *Oicina* formation
<table>
<thead>
<tr>
<th>Column 5 (NW Anzoategui: 'mountain front')</th>
<th></th>
<th></th>
<th>Lower Santa Ines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Compañía Shell de Venezuela, VC 1</td>
<td></td>
<td></td>
<td>Capaya formation</td>
</tr>
<tr>
<td>Column 6 (N Anzoategui)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Compañía Shell de Venezuela, outcrop samples St. 2992, St. 3000</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Compañía Shell de Venezuela, outcrop samples St. 2992, St. 3000</td>
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<tr>
<td>Column 7 (Northern Monagas)</td>
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<tr>
<td>Creole Petroleum Corp., RC1-28</td>
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<tr>
<td>Mene Grande Oil Company, SB 133, 925–625'</td>
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<td></td>
</tr>
<tr>
<td>Creole Petroleum Corp., J-274, 5,325–6,700</td>
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<td></td>
</tr>
</tbody>
</table>

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Netherlands
LAGAAUI. *Cupuladria canariensis* (Busk)
LAGAAJ, Cupuladria camariensis (Busk)