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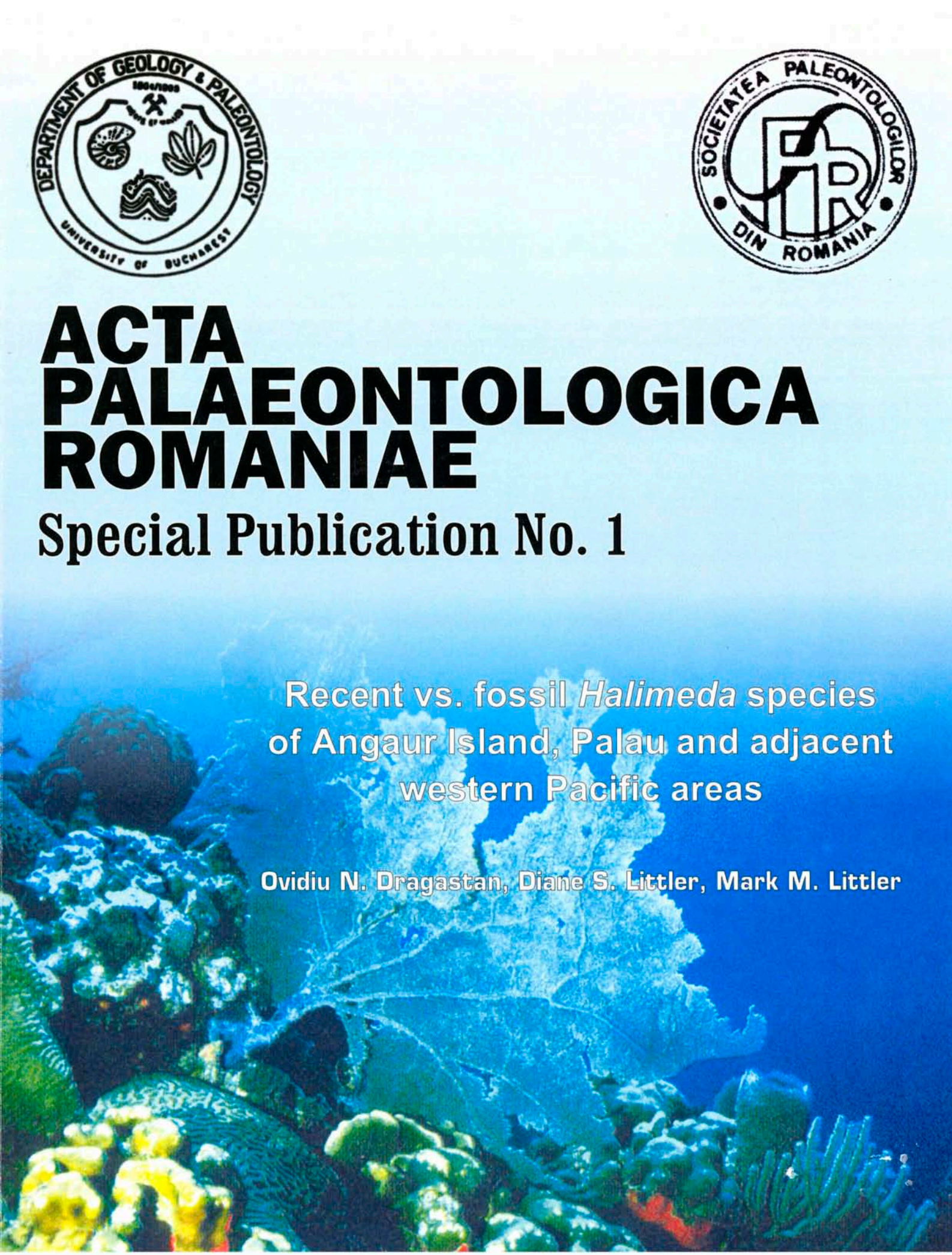

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Front cover: Reef community indicative of healthy condition of environment
(after Littler & Littler 2000)

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Recent vs. fossil *Halimeda* species of Angaur Island, Palau and adjacent western Pacific areas

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Abstract

Previously unstudied Late Miocene–Pleistocene samples and thin sections from Angaur Island limestones, Palau, Western Pacific (Harlan J. Johnson Collection, Department of Palaeobiology, Smithsonian Institution) revealed a diverse, *Halimeda* dominated, species association. We also examined other well-preserved *Halimeda* specimens in limestone drillings from Eniwetok Atoll, Bikini Atoll and the Kita-Daito-Jima area. These fossil materials are described in detail and compared with Recent *Halimeda* to clarify problematic fossil taxa erected solely on the basis of isolated segment fragments. The present study revealed a wide variability in both external morphology and internal anatomy (from base to apex) in all 33 of the Recent species of *Halimeda* examined. We believe that the wide-ranging *H. cylindracea*, showing only two segment morphotypes (predominantly cylindrical, although becoming sub-spherical toward the apex) and with the cortical system showing three to five utricle layers, has generated the large number of segments upon which many Late Triassic, Jurassic, Cretaceous and Cenozoic "taxa" were based. The following 21 Mesozoic and Cenozoic taxa are herein synonymized with *H. cylindracea*: *H. helladica* Dragastan (Late Triassic), *H. marondei* (Flügel) (Late Triassic), *H. fluegeli* Bucur (Early Cretaceous), *H. elliotti* Conrad & Rioult (Late Cretaceous, Turonian), *H.* cf. *elliotti* Conrad & Rioult (Late Cretaceous, in Schlagintweit 1992), *H. entogensis* Yu-Jing (Paleocene-Early Eocene), *H. camenitzae* Dragastan & Bucur (Late Aptian), *H. praemonilis* Morellet & Morellet (Paleocene-Early Miocene), *H. nana* Pia (Paleocene), *H. lingulata* Yu-Jing (Middle-Late Eocene), *Lekhamptonella llewellyae* Elliott (Middle Jurassic), *Arabicodium aegagrapioides* Elliott (Early Cretaceous), *A. aninensis* Bucur (Early Cretaceous), *A. tibeticum* Yu-Jing (Paleocene-Early Eocene), *Boueina hochstetteri* Toula (Late Triassic-Jurassic-Cretaceous; including var. *liasica* and var. *moncharmonti*), *B. pygmaea* Pia (Cretaceous-Paleogene), *B. globosa* Dragastan, Bucur & Demeter (Late Aptian), *B. chirakhanensis* Pal (Late

Cretaceous), *Banatea bucurii* Dragastan *nomen nudum*. A second phyletic line is illustrated by *H. incrassata*, characterized by cylindrical to reniform, subcuneate, smooth or ribbed thallus segments and a cortex system with three to five utricle layers. This line originated during the Cretaceous (Late Cretaceous) and continued into the Cenozoic, until the Present. The following seven fossil taxa are considered to be synonymous with *H. incrassata*: *H. chiplonkari* Badve & Kundal, *H. agharkari* Badve & Kundal, *H. corneola* Badve & Kundal, *H. densituba* Badve & Kundal, *H. pipaldehlaensis* Badve & Kundal, *H. robusta* Badve & Nayak, *H. triradiata* Badve & Nayak; all of which were reported from the Late Cretaceous but may more probably be Paleocene or Eocene in age. A third phyletic line includes taxa with extremely variable thallus segments, ranging from flat to somewhat contorted, cuneate-ovate to discoid, with truncate, auriculate, lobed to ribbed margins. Members of this line first appeared around the Cretaceous/Paleocene boundary and continued into the Present, as the species *H. opuntia*. At this time, only two fossil species, *H. eocaenica* Morellet & Morellet (Eocene) and *H. johnsonii* Pal (Maastricht-Paleocene), are included as synonymous with *H. opuntia*. Interestingly, the thallus segments of *H. discoidea* found in Pleistocene material consistently showed three anatomical layers of utricles, whereas only two utricle layers are characteristic of Recent specimens of this species.

The most important character for the identification of fossil species it isn't the shape of segment which represents a small part of the thalli, but the cortical system with various shape and orders of utricles remains the key to solve the misidentification of fossil materials and to find the correspondent in the real stock of Recent species. Generally speaking a few taxa of fossil *Halimeda* are true species, mostly are considered in this study "*Nomini dubiosum*".

Geological Setting and Stratigraphy

Descriptions of living and fossil algae from western Pacific Islands have been published by Taylor (1950) and Johnson (1954b, 1961a), respectively. Prior to 1950, Johnson visited a number of Pacific islands and collected or received samples of both living and fossil algae from the region. However, many of the limestone samples, including thin sections, have remained unstudied since that time. Among these materials were six interesting samples of limestones from Angaur Island (Palau Archipelago) received by Johnson from the geologists Cleaves L. Rogers and Paul O. Elmquist (United States Geological Survey), who participated in mapping expeditions under the auspices of the Pacific Islands Geologic Mapping Program. The geological data and stratigraphy from this report were published in 1956.

The approximately 350 islands comprising the Palau Archipelago (Fig.1) are located in the southwestern part of Micronesia upon a submarine ridge 170km long running from north to southwest. Tectonically, this group of islands is disposed toward the eastward margin of the Philippines plate, near the boundary with the Pacific plate. Angaur is the farthermost island toward the southwestern region of the Palau Archipelago and contains both barrier and fringing reef limestone deposits. The island is 4.5 km in length and less than 3.5 km wide, with a maximum

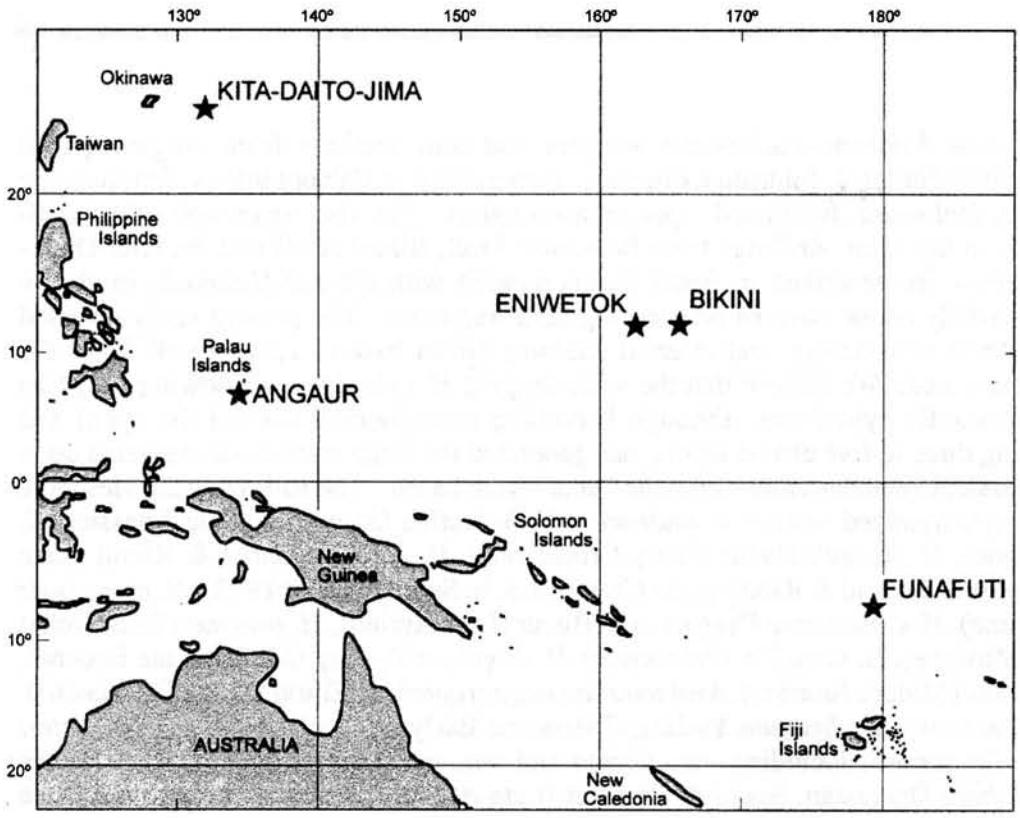

Figure 1.
Position of Angaur Island (Palau) and the sites of deep drill-hole collections at Eniwetok, Bikini and Kita-Daito-Jima of the Western Pacific.

altitude of 46 m above sea level. The limestone reef stratigraphy of the Palau Islands was established by the work of Hobbs (1926), Bridge & Goldich (1948), Tayama (1935, 1939, 1951) and by the U.S. Army Forces, Far East Team, which produced the 1956 report "Military geology of Palau Islands, Caroline Islands".

Tayama(1951) considered the limestones of Angaur Island to be different in age, but so similar in external appearance that it is almost impossible to distinguish them stratigraphically in the field. Fossils of mollusks, corals, echinoids, foraminifera, the red alga *Lithothamnion* and the green alga *Halimeda* abound. In spite of this stratigraphic problem, it is possible to establish an order of succession and Tayama (1951) introduced the concept of six formations, the oldest two being designated as the "Older Palau limestone formation" and the "Younger Palau limestone formation". We became interested in the reef limestones of Angaur Island because they are composed primarily of segments of the green alga *Halimeda,* rather than the remains of animals such as corals and sponges.

Foraminifera from deposits collected by Bridge and Ladd from the Palau Archipelago, including Angaur Island, have been described by Cole (1950), and descriptions of the mollusks have been provided by Hanzawa (1951) and Hatai (1951) as well. A list of fossil foraminifera from the Older and Younger Palau limestones was published by Hanzawa (1951), which contained 17 benthic species (in the genera *Acervulina, Amphistegina, Calcarina, Gypsina* and *Sorites*) as well as five pelagic species (in *Globigerina, Orbulina* and *Globorotalia*). The age of both Palau limestone formations according to the foraminiferan associations was considered to be Pliocene to Recent inclusive. However, the Older Palau limestone was referred to Pliocene–Pleistocene in age.

In the U. S. Army Forces report (1956), both of Tayama's "formations" were unified as a single formation of Palau limestone based on the presence of species of *Lepidocyclina*, *Miogypsina* and *Operculina*, which characterize Miocene or Middle Miocene to early Pleistocene age. The lower boundary of the formation corresponds to a gap bridging the Oligocene–Miocene and the upper one is an nonconformity between Palau and Peleliu formations, the latter being Pleistocene to Recent in age (Table 1).

Upon reconsidering Hanzawa's list of foraminifera from Angaur Island, the 22 species identified show different stratigraphic ranges and are revised as follows: 6 species = Recent, 2 species = Pliocene to Recent, 8 species = Miocene to Recent, 1 species = Oligocene to Recent and 5 species = Eocene to Recent. Only *Sphaeroidinellopsios dehiscens* Parker & Jones is a marker for Miocene to early Pliocene and was reported from the Younger Palau limestone. Taking into account other assemblages, including foraminifera, red algal species of *Lithophyllum* and *Lithoporella* and some *Halimeda* species (such as *H. opuntia)*, the Palau limestones cover the stratigraphic time span of Miocene, Pliocene and early Pleistocene.

The age of limestone samples USNH loc No. 35994 (= USNH No. 519484) and USNH loc No. 35998 (= USNH No. 519485) is Late Miocene, according to assemblages that include the foraminifera *Cycloclypeus carpenteri* Bradleyi, *Cribrorotalia obesa* Hornibrook, *Globigerina bulloides* d'Orbigny, *Orbulina universa* d'Orbigny, *Miogypsina* sp. and *Heterostegina* sp., along with red algae such as *Lithoporella melobesioides* Foslie and *Lithophyllum prelichenoides* Lemoine. Limestone sample USNH loc No. 36152 (= USNH No. 519488) contained an association with only benthic species such as *Discogypsina vesicularis* Silvestri, *Amphistegina* sp., *Hetereostegina depressa* d'Orbigny, *Borelis melo* (Fichtel & Mol), *Sorites orbiculus* (Forskal), *Pseudotriloculina lecalvezae* (Kaaschietev) and the red alga *Lithophyllum* cf. *racemus* (Lamarck) Foslie, mostly indicating a Pliocene age. Sample USNH loc No. 36146 (= USNH No. 519487), with some large cavities and benthic foraminifera such as *Schlumbergerella floresiana* (Schlumberger), *Calcarina* sp. and *Marginopora* sp., is also Pleistocene in age.

Authors	Tayama & Hanzawa (1951)	U. S. Army Forces, Far East (1956)
Age	Formations	
PLEISTOCENE	Older Angaur limestone	Peleliu limestone
PLIOCENE	Younger Palau limestone	Palau limestone
	Older Palau limestone	
MIOCENE		

Table 1. The age and litho-stratigraphic correlation between different limestone formations from Palau Islands.

Materials and Methods

Materials examined.- All materials cited are deposited in the collections of the National Museum of Natural History, Smithsonian Institution (USNH), unless otherwise noted. Limestone samples of Angaur Island originated from the Harlan J. Johnson Collection housed in the Smithsonian Institution Museum Support Center, Silver Hill, Maryland. The storage locations of the Angaur Island limestone samples are as follows: Drawer 85 –PJ–75–3 contains sample No. 36146 and, in position PJ–52–2, sample No. 36152. Drawer 83 contains sample No. 36027. Drawer 82 contains in position PJ–75–2, sample No. 35994 and, in position PJ–77–3, sample No. 35998. More than 30 thin sections were studied from the same collection taken from Pleistocene drill holes at Eniwetok Atoll (E1, 40 E 1), Bikini Atoll (B4 hole, 1340 hole and B2 hole) and Kita-Daito-Jima (2138 hole). The samples of limestone belonging to the Palau formation are compact, hard and light in color (whitish or light brown), very rich in CaCO3 (96.88%) with a low Mg content (1.01%, U. S. Army Forces, Far East 1956). The Late Miocene–Pliocene samples are denser and harder in comparison to the Pleistocene samples, which are less consolidated and more porous or contain cavities. All of the limestone samples were processed as thin sections from large slides (4.5 x 2.5 cm) in the Laboratory of the Department of Paleobiology, Smithsonian Institution or in the Institute of Geology, Ruhr University, Bochum, Germany.

Morphology and state of preservation of Halimeda *thalli.*—The Recent species of *Halimeda* show morphologically variable shapes of the segments, with a concomitant wide range of internal anatomical differences. The catenulate thallus of *Halimeda* is composed of a variable number of segments, with up to 10 in *H. discoidea* and as many as 700 in *H. incrassata* (Dragastan et al. 1997), usually as a function of thallus age. Along the regions of the thallus, the segments can have one, two or three external shapes: cylindrical, disc-like, or trilobed (*H. monile*). Multiple subshapes can also occur within the same thallus, ranging from cylindrical, disc-like to reniform (*H. simulans*), subcuneate, discoidal-sub-reniform (*H. macroloba*), trilobed (*H. opuntia* f. *triloba*) to contorted discoidal (*H. discoidea*, Littler & Littler 1997, 2000).

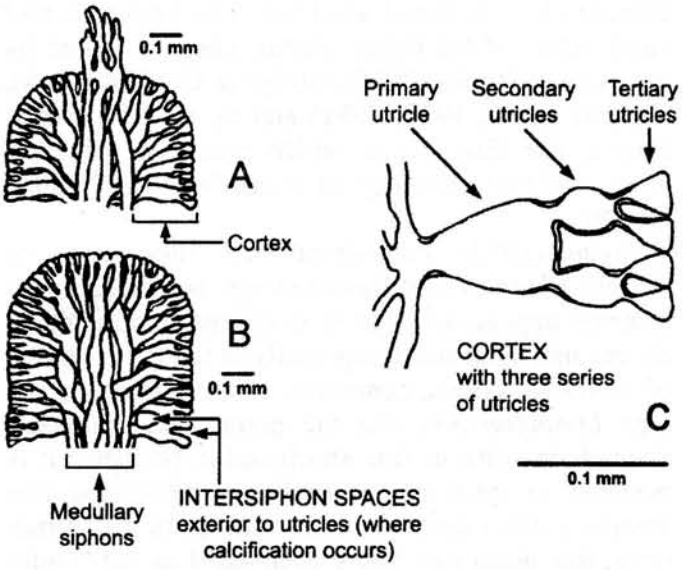

Figure 2.
A, B. Longitudinal sections of a segment of *Halimeda incrassata*; C. Enlarged utricle of the cortex (from Hillis Colinvaux 1980).

In *Halimeda incrassata*, the segments vary in shape from the base towards the apex of the thallus (i.e., proximal to distal), from cylindrical to subcuneate, either planular, ribbed or reniform towards the outer margin, becoming flattened, entire, undulated or deeply lobed. *Halimeda* is a major carbonate producer in the tropics and is well preserved in many rock formations, due to calcareous aragonite accumulations between the utricles within its calcareous segments. However, it is problematical to interpret the shapes of isolated fossil segments or fragments as new species or genera, as in the case of the fossil genus *Boueina* (described by Toula 1884). Moreover, it is likely that such fragment-based fossil taxa could have been the products of a single variable species.

The genus *Halimeda* is known without question from Triassic deposits (Dragastan et al., 2000). It is accurate to assign many of the preserved "different segments" to this genus, which encompasses (by its extremely plastic morphology) almost the entire spectrum of shapes from the Mesozoic (i.e., mostly cylindrical, globular with a compressed tendency) and Cenozoic (i.e., flattened shapes that are identical to Recent species).

Species	Section level	Outer diameter of thallus	Inner diameter (*medulla)	Thickness of cortex	Diameter of medullary siphons	Length of terminal siphons (*utricle)	Number of utricle layers
Halimeda	1 (base)	2.8-5.7	1.9	0.45	0.07	0.08	4-5
incrassata	2 (middle)	1.6-6.6	0.67	0.33	0.04	0.06	4
	3 (top)	0.86-3.60	0.46	0.20	0.04	0.04	2-3

Table 2. Variability of morphometric parameters along the thallus of *Halimeda incrassata,* segments sectioned at different levels: 1, 2, 3 (after Dragastan et al. 1997.)

Anatomically, the thallus of *Halimeda* is characterized by an axial region containing medullary siphons surrounded by a cortex with two or more zones of utricles (expanded tips = siphons in paleobiology, Fig. 2). As alluded to above, in a majority of cases paleoalgologists study only thallus fragments (segments or branches). By studying intact Recent *Halimeda* specimens (e.g., *H. incrassata*), we observed that the segments sectioned from different levels along the thallus [Table 2, base (1), middle (2) and top (3)] show variable numbers of utricle layers and other morphometric parameters from one level to another. For example, we found a large degree of variation regarding the siphon diameters within the inner portion of the medullary zone, as well as a variable number of utricle layers. However, less variation occurs within the base and middle regions of the thallus segments, with variability increasing and utricle layers decreasing toward the top (distally). Therefore, if the thallus segments were to become disconnected during fossilization (highly likely), individual segments would then present varying numbers and dimensions of utricle layers. Consequently, such segments from the base versus those from the middle or top might be mistakenly interpreted as separate species. In the case of fossil thalli, all of the morphometric parameters are extremely important, with the cortex system providing some of the most valuable characters to accurately discriminate the different *Halimeda* species in either the fossil state or in Recent specimens.

As a further example, the same large variability is readily observed in the Recent species *Halimeda cylindracea* (Fig. 3) in terms of outer segment morphology in transverse (horizontal) section, as well as in other morphometric parameters. It is clear from examining such variable characters as the inner or outer shape of the thallus segments along the complete plant thallus, that in many fragment-based fossil cases the identification to species remains difficult and in most instances uncertain. Also, as demonstrated by the examples of *Halimeda* species examined in Palau limestones, we need to remember Gould's (1981) concept that....species arise in geological time with the differences established from the start and do not change substantially for long periods....a valuable reminder for all scientists who work with fossil algae.

The state or mode of preservation of different species of Recent calcareous algae also was examined for the stipe and capitulum regions of *Penicillus* and for the catenulae (segments) of *Halimeda*, mostly from Caribbean, Pacific and Indian Ocean specimens housed in the Algal Collection, U. S. National Herbarium.

Because the taphonomic processes leading to the fossilization of calcareous algae are poorly known, it is important to understand the following:

- that the fossil "segments" of a given thallus are often incompletely preserved as broken fragments or thallus parts, especially the cortex area;
- that the medullary siphons of fossil thalli attributed to the genera *Halimeda*, *Arabicodium* and

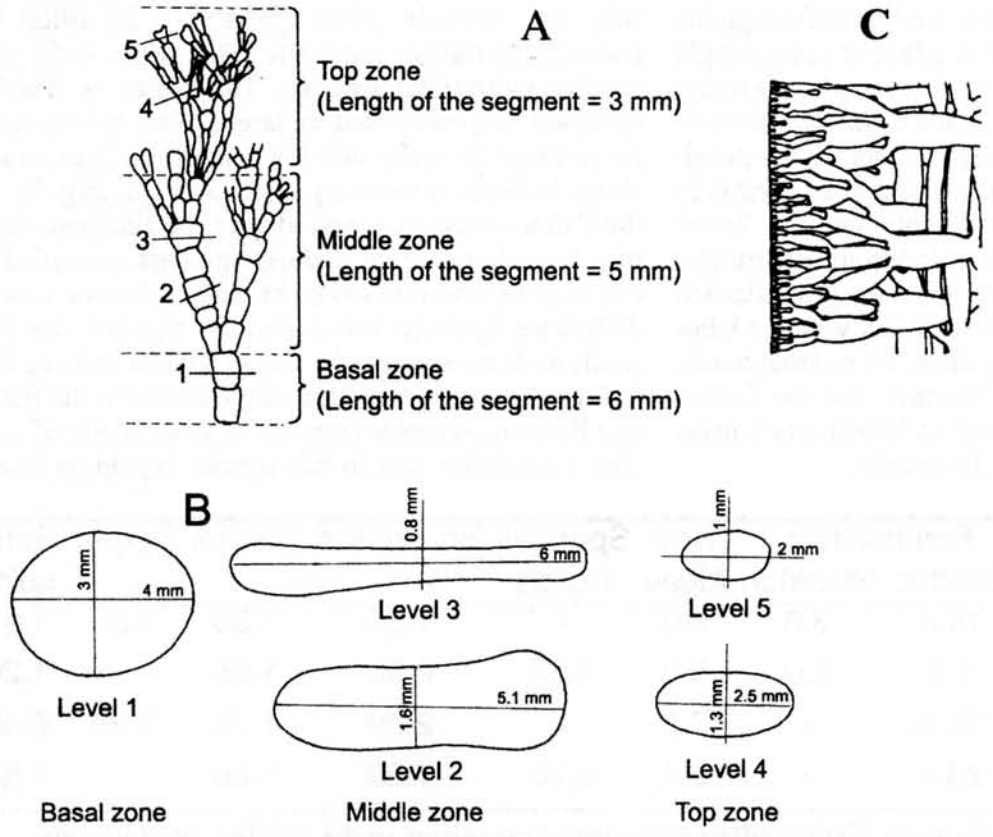

Figure 3.
A. *Halimeda cylindracea* and position of various sectioning levels of the segments along the thallus. B. Different profiles and dimensions of cross sections of segments represented in illustration A ; C. Cortex system and the morphology of utricles series (from Hillis-Colinvaux, 1980).

Banatocodium, for example, are not preserved at all in many cases.

It is possible to interpret these problems by starting with the observation that the degree (state) of calcification (light or heavy) is a response to a physiological stress or requirement and bears no relationship to a pathological process. The presence in the fossil state of many thallus segments from Triassic to Pleistocene fossils ascribed to the genera *Arabicodium, Leckhamptonella, Boueina*, or to some species of *Halimeda*, without adequate preservation of the medullary siphons (empty central area), necessitates a reconsideration of the calcification process at the siphon level, depending on $CaCO_3$ disposition in the medullary or cortical zones.

Upon examining the various siphon levels in Recent *Halimeda* collections, it is apparent that the medullary siphons are not as heavily calcified as the cortical utricles. This finding can be explained by the direction and steps of calcification, which grades from the pigmented (photosynthetic) exterior toward the interior of the thallus. In the Harlan Johnson Collection, there are specimens of fossil *Halimeda* (Pliocene to Pleistocene) in which the central medullary area in whole segments is completely empty or hollow (Pl. 10, Figs. 1, 2, 7), while, at the same time, there are many broken thalli in which only the cortex area crossed by utricles (= outer siphons) has been preserved (Pl. 8, Figs. 4, 5, 9). This kind of fossilization reflects the fact that medullary and cortical regions show different degrees of calcification. We hypothesize that such differences in calcification between the interior and the cortical areas represent a response to a physiological balance in two ways: first, cytoplasmic circulation is facilitated through the uncalcified medulla; second, the flux of seawater pH during photosynthesis in the utricles results in precipitation of aragonite crystals in the utricular spaces of the pigmented cortex, in direct relation to the possible function of the outer thallus layer (i.e., cortex) in deterring herbivory and also maintaining the 'erect' thallus position (i.e., stiffening) in the aquatic milieu. The result is that the outer cortex is heavily calcified in comparison with the inner medulla, with the latter providing flexibility during times of hydrodynamic shearing disturbances (e.g., storms), and the former being relatively well preserved as broken thalli making it possible to determine the species.

The limestones of Angaur Island are well known as *Halimeda* limestones, because they are built almost entirely by thallus segments. The percentage contribution of *Halimeda* to the construction of these limestones varies with the age of the deposits as follows: Late Miocene = 70 to 75% *Halimeda* segments, Pliocene = 63% and Pleistocene = 61% (Table 3).

During the Miocene, especially toward the Miocene/Pliocene boundary, the abundance of *Halimeda* segments reached a maximum, after which, during the Pliocene and also the Pleistocene, there was a diminution in the contribution of *Halimeda* species. The other organisms associated with *Halimeda* species in the Palau limestones show varying percentages of participation (see Table 3).

Systematic Account

Phylum Chlorophyta
Order Bryopsidales
Family Halimedaceae
Genus *Halimeda* Lamouroux, 1812

Halimeda discoidea Decaisne, 1842
Pl. 1, figs. 1–5, pl. 8, figs. 1–9, pl. 10, figs. 1–5

See also Littler & Littler 1997: 109. Littler & Littler 2000: 400.

Description.—The thallus segments are variable in shape, ranging from flat, oval, disc-like to wedge-shaped. In longitudinal or oblique longitudinal sections, the subcylindrical segments have a narrow medulla with four axial "lines" of long parallel siphons (Pl. 1, Figs. 1–3). In oblique tangential section, the medulla often appears to be filled by coarsely crystalline aragonite (Pl. 1, Figs. 4–5) with smaller cylindrical siphons. The cortex is heavily calcified and composed of large, oval, sub-triangular, conical, primary utricles supporting four small, short, bulbous, secondary utricles (Pl. 1, Fig. 3). In the Palau limestones, and also in the Pliocene samples, heavily calcified thallus segments are cylindrical, slightly compressed or broken and show a clear difference between the medullary siphons that are small in diameter and the thick cortical utricles (Pl. 8, Figs. 1, 4). The structure of the cortex in the Palau and Pliocene samples consists of three layers of utricles, a condition that in this species is seldom found

Samples	Halimeda	Foraminifera		Red	Sponges	Bryozoans	Gastro.	Serpul.	Echi-
	(%)	Benthic	Plankton	Algae	Corals				noids
No. 35994	70.0	14.0	3.0	7.0	-	1.50	1.50	1.50	1.00
No. 35998	75.0	8.0	5.0	5.0	1.25	2.50	1.25	-	1.20
No. 36152	63.4	22.5	-	7.2	-	2.50	1.70	0.85	0.40
No. 36146	61.0	24.4	-	2.4	5.70	1.50	1.60	-	1.50

Table 3. Quantitative contributions (%) by different groups of organisms to the building of *Halimeda* limestones on Angaur Island, Palau.

in Recent material. The primary utricles are conical, large and more inflated toward their distal ends. These primary utricles support secondary utricles that are short, subconical and bulbous. The secondary utricles support very short, small (often having a surface opening), tertiary utricles (Pl. 8, Figs. 2, 6).

Remarks.—The Late Miocene specimens have a reduced number of medullary siphons, 4 to 6 (up to 8 in the Pliocene). There are some minor dimension and shape differences in both the primary and secondary utricles between the species with two utricle layers (Late Miocene) and those with three utricle layers (Pliocene).

Measurements.—For specimens with a cortex of two layers of utricles: segment length 5.7–8.0 mm; segment thickness 0.50–0.75 mm; medulla diam. 0.3–0.4 mm; cortex thickness 0.36–0.45 mm; medulla siphon diam. 0.09–0.12 mm; primary utricle diam. proximal 0.09 mm, distal 0.15–0.18 mm; primary utricle length 0.25–0.27 mm; secondary utricle diam. 0.025–0.030 mm; secondary utricle length 0.045–0.060 mm.

Measurements.—For specimens with a cortex of three layers of utricles: segment length 2.5–3.0 mm; segment thickness 1.54–2.80 mm; medulla diam. 0.36–0.56 mm; cortex thickness 0.48–0.60 mm; medulla siphon diam. 0.12–0.14 mm; primary utricle diam. 0.18–0.25 mm; primary utricle length 0.18–0.25 mm; secondary utricle diam. 0.035–0.045 mm; secondary utricle length 0.06–0.08 mm; tertiary utricle diam. 0.030–0.035 mm; tertiary utricle length 0.025–0.040 mm.

Material examined.—Palau limestone, USNH loc No. 35994, Late Miocene; USNH loc No. 36152, Pliocene; USNH loc No. 36146, Pleistocene.

Halimeda gracilis Harvey 1887
Pl. 1, figs. 6–8, pl. 3, figs. 1–4, 6, 8

See also Hillis Colinvaux 1980: 144, fig. 44. Littler & Littler 2000: 402.

Description.—Thallus segments are strongly calcified, disc-like, oval to reniform with many, small, thin, medullary siphons. The cortex consists of long, tubular, primary utricles, increasing in diameter distally and often becoming claviform. These primary utricles support numerous secondary utricles which are short, tubular and slightly conical in the distal areas (Pl. 1, Fig. 6, Pl. 3, Figs. 1–4). The secondary utricles rarely, but occasionally, bear fine, small, tertiary utricles.

Measurements.—Segment length 3.3–3.5 mm; segment thickness 1.50–1.65 mm at base, to 0.4 mm distally; medulla diam. 0.28–0.60 mm; cortex thickness 0.45–0.50 mm; medulla siphon diam. 0.38–0.045(0.060) mm; primary utricle diam. proximal 0.025 mm, distal 0.035–0.060 mm; primary utricle length 0.25–0.30 mm; secondary utricle diam. 0.028–0.030 mm; secondary utricle length 0.080–0.12 mm.

Material examined.—Palau limestone, USNH loc No. 35994 and USNH loc No. 35998, Late Miocene.

Halimeda cylindracea Decaisne 1842
Pl. 2, figs. 1–3

See also *Halimeda* sp. Johnson 1954b, pl. 197, fig. 5, Bikini, Hole 2, 190 feet (62 m). *Halimeda* sp. Johnson 1961, pl. 280, fig. 1 (left side of photo, large specimen). Hillis Colinvaux 1980: 100, figs. 4–5, 104.

Description.—Segments in transverse section are cylindrical with undulating contours. The medulla appears large and hollow, often filled with coarsely crystalline aragonite, different bioclasts and quartz grains (Pl. 2, Fig. 1). The thick cortex consists of four utricle layers. The primary utricles are long, cylindrical-conical and increase in diameter distally. The primary utricles support secondary utricles which are small and tubular. These secondary utricles bear tertiary utricles which are short, tubular or a little inflated distally and these ultimately support the fourth layer which consists of extremely small utricles (Pl. 2, Figs. 2–3).

Remarks.—The specimen illustrated by Johnson (1954b, Pl. 197, Fig. 5) from the Pliocene of Bikini, Hole 2 (62 m) is an oblique transverse section of a cylindrical segment showing a large medulla and four cortical layers. The specimen shown in Johnson (1961a, Pl. 280, Fig. 1, left side of photo) represents a large cylindrical segment in axial-longitudinal section, well preserved in the Pleistocene limestone drilled at Kita-Daito-Jima Reef.

Measurements.—Segment thickness 3.15 mm; medulla diameter 1.8 mm; cortex thickness 0.78 mm; primary utricle diam. proximal 0.03 mm, distal 0.09 mm; primary utricle length 0.10–0.12 mm; secondary utricle diam. 0.02–0.06 mm; secondary utricle length 0.03–0.08 mm; tertiary utricle diam. 0.015–0.030 mm; tertiary utricle length 0.020–0.025 mm; quaternary utricle diam. 0.010–0.015 mm; quaternary utricle length 0.010–0.015 mm.

Material examined.—Palau limestone, USNH loc No. 35994, Late Miocene.

Taxonomic synonyms.—*Halimeda helladica* Dragastan et al. 2000: 144, pl. 3, figs. 1–2. *H. marondei* Flügel 1988: 126, figs. 1–12. *H. fluegeli* Bucur 1994: 15, pl. 3, figs. 1–5. *H. elliotti* Conrad & Rioult 1977: 85–89, text fig. 3, pls. 1–3. *H.* cf. *elliotti* Conrad & Rioult in Schlagintweit, 1992: 3, pl. 1, figs. 1–6. *H. entogensis* Yu-Jing 1976: 426, 451–452, pl. 12, figs. 3–4. *H. camenitzae* Dragastan & Bucur 1979: 113–114, pl. 5, figs. 1–4; pl. 6, figs. 1–2. *H. praemonilis* Morellet & Morellet 1940: 201–202, 204–205, fig. 1. *H. nana* Pia 1932: 7, 15–17, pl. 2, fig. 4. *H. lingulata* Yu-Jing 1976, 426, 452, pl. 12, figs. 1–2. *Lekhamptonella llewellyae* Elliott 1982: 432, pl. 45, figs. 1–6. *Arabicodium aegagrapiloides* Elliott 1957: 228, pl. 1, figs. 7–10. *A. aninensis* Bucur 1994: 14–15, pl. 2, figs. 3, 4, 6, 7. *A. tibeticum* Yu-Jing 1976: 453, pl. 12, figs. 6–8. *Boueina hochstetteri* Toula 1884 (including var. *liasica* Le Maitre

1937: 16–17, pl. 3, figs. 1–6 and *moncharmonti* De Castro 1963: 114–115, pl. 6–8). *B. pygmaea* Pia 1936L 12–13, pl. 5, figs. 1–9. *B. globosa* Dragastan, Bucur & Demeter 1977: 17, 28–29, pl. 1, pl. 15, figs. 6–8, pl. 19, fig. 1. *B. chirakhanensis* Pal 1971: 134–135, pl. 1, fig. 3. *Banatea bucurii* Dragastan *nomen nudum*, 2000.

Halimeda monile (J. Ellis & Solander) J. V. Lamouroux 1816
Pl. 2, figs. 4–5

See also *Corallina monile* Ellis & Solander 1786, pl. 20, fig. c. Littler & Littler 1997: 111, fig. 160. Littler & Littler 2000: 104.

Description.—Oblique longitudinal section shows a thallus consisting of cylindrical segments. The medulla is partially evident and hollow. The cortex is formed by three layers of utricles (Pl. 2, Fig. 4). In transverse section, the thallus segments are round with large cylindrical medullary siphons. The primary utricles of the cortex are sub-triangular to conical. The primary utricles support numerous medium, short, conical and dichotomously branched secondary utricles. The secondary utricles bear short, small, tertiary utricles that are broadly expanded distally.

Measurements.—Segment thickness 2.10 mm; medulla diam. 1.2 mm; medulla siphon diam. 0.09–0.10 mm; cortex thickness 0.3–0.6 mm; primary utricle diam. proximal 0.03 mm, distal 0.060–0.065 mm; primary utricle length 0.15 mm; secondary utricle diam. 0.030–0.035 mm; secondary utricle length 0.09 mm; tertiary utricle diam. 0.025–0.030 mm; tertiary utricle length 0.06 mm.

Material examined.—Palau limestone, USNH loc No. 35994, Late Miocene

Halimeda bikinensis Taylor 1950
Pl. 2, figs. 7–9, pl. 6, figs.1–10, pl. 7, figs. 1–5, pl. 11, figs. 2–3, 5

See also *Halimeda bikinensis* Taylor 1950: 87, pl. 48, fig. 1. Hillis Colinvaux 1980: 141, fig. 43. *Halimeda* sp. Johnson 1961a, pl. 33, fig. 2. Johnson 1961b, pl. 280, figs. 1–2.

Description.—Thallus segments are sub-cuneate, discoidal to sub-reniform with margins slightly undulated and infolded. The segments in various sectional planes show a moderately large medullary zone and a thin cortex of three utricle layers (Pl. 6, Figs. 9–10). The primary utricles are sub-triangular and support numerous medium, short, tubular-conical, dichotomously branched, secondary utricles. The secondary utricles bear various short, small, tertiary utricles (Pl. 2, Figs. 7–9, Pl. 6, Figs. 1, 6). In transverse section, the segments appear oval or ellipsoidal, compressed laterally (Pl. 6, Figs. 8–10) with a compact area between the medullary siphons and the thin cortex.

Remarks.—Specimens illustrated by Johnson (1961a, Pl. 33, Fig. 2) from Bikini Atoll, although not well oriented, show the inner structural characters of *H. bikinensis*. In the same year, Johnson (1961b, Pl. 280, figs, 1–2) published another paper which presents better longitudinal and transverse sections of segments of *H. bikinensis* from the Pleistocene of Kita-Daito-Jima.

Measurements.—Segment length 3.30–4.20 mm; segment thickness 1.20–1.40 mm; medulla diameter 0.50–0.56 mm; cortex thickness 0.30–0.45 mm; medulla siphon diam. 0.060–0.12 mm; primary utricle diam. 0.052–0.060 mm; primary utricle length 0.060–0.15 mm; secondary utricle diam. 0.030–0.045 (0.052) mm; secondary utricle length 0.10–0.12 mm; tertiary utricle diam. 0.015–0.030 mm; tertiary utricle length 0.040–0.045 mm.

Material examined.—Palau limestone, USNH loc No. 35994, Late Miocene; USNH loc No. 36152, Pliocene.

Halimeda incrassata (J. Ellis) J. V. Lamouroux 1816
pl. 3, fig. 7

See also *Corallina incrassata* J. Ellis 1768: 408, figs. 20–27. Littler & Littler 1997: 110, fig. 159. Littler & Littler 2000: 402.

Description.—In transverse section, segments are disc-like with acute, pointed and narrow margins. The medullary siphons are large in diameter. The cortex consists of three utricle layers. The primary utricles are sturdy, cylindrical-conical towards the distal end and large in diameter (Pl. 3, Fig. 7). The primary utricles support tubular, medium long, dichotomously branched, secondary utricles, which in turn bear tertiary utricles that are short, triangular in shape and very small.

Measurements.—Segment length 6.0 mm; segment thickness 1.1–2.5 mm; medullary siphon diam. 0.12–0.15 mm; primary utricle diam. proximal 0.028 mm, distal 0.06 mm; primary utricle length 0.12–0.14 mm; secondary utricle diam. 0.045–0.060 mm; secondary utricle length 0.09–0.10 mm; tertiary utricle diam. 0.010–0.015 mm; tertiary utricle length 0.025–0.032 mm.

Material examined.—Palau limestone, USNH loc No. 35998, Late Miocene.

Taxonomic synonyms.—Halimeda chiplonkari Badve & Kundal 1986: 155, figs. 11–13, *H. agharkari* Badve & Kundal 1986: 156, figs. 14–15, *H. corneola* Badve & Kundal 1983: 140–143, pl. 6, fig. 11, text fig. 4, *H. densituba* Badve & Kundal 1983: 142, pl. 6, figs. 6–7, text fig. 3, *H. pipaldehlaensis* Badve & Kundal 1983: 140, pl. 6, figs. 1–2, 4, 10, text fig. 2, *H. robusta* Badve & Nayak 1983: 140, pl. 6, figs, 9, 12, text fig. 1, *H. triradiata* Badve & Nayak 1983: 142, pl. 6, figs. 3, 5, 7, text fig. 5.

Halimeda tuna (J. Ellis & Solander) J. V. Lamouroux 1816
Pl. 4, figs. 1–3, pl. 11, figs. 7, 8, pl. 12, figs. 1–6

See also *Corallina tuna* Ellis & Solander 1786: 111, pl. 20, fig. e. *Halimeda tuna* Lamouroux 1816: 309. Hillis Colinvaux 1980: 122, fig. 35. Littler & Littler 1997: 113, fig. 164. Littler & Littler 2000: 408.

Description.—The transverse sections show flat disc-like segments with the lateral margins undulating and pointed at the extremities. The segments have large medullary siphons which are round or elongated in shape (Pl. 4, Figs 1–2). The cortex consists of two to three utricle layers. The primary utricles are relatively short, robust, conical and inflated distally. The primary utricles support numerous secondary utricles which are tubular, short and dichotomously branched. The secondary utricles bear various small, short, tubular or needle-like, tertiary utricles.

Measurements.—Segment length 2.4–3.6 mm; segment thickness 0.36–0.60 mm; medulla diam. 0.06–0.09 mm; cortex thickness 0.10–0.12 mm; primary utricle diam. proximal 0.025 mm, distal 0.060–0.065 mm; primary utricle length 0.040–0.075 (0.090) mm; secondary utricle diam. 0.030–0.0.35 mm; secondary utricle length 0.08–0.10 mm; tertiary utricle diam. 0.015–0.017 mm; tertiary utricle length 0.025–0.032 mm.

Material examined.—Palau limestone, USNH loc No. 35998, Late Miocene.

Halimeda tuna f. *platydisca* (Decaisne) E.S. Barton 1901
Pl. 4, figs. 4–5

See also *Halimeda platydisca* Decaisne 1842: 102. Littler & Littler 2000: 408.

Description.—The oblique longitudinal section shows a flat, disc-like segment having smooth or slightly rippled margins. The segment in transverse section is tubular, with large diameter medullary siphons disposed axially in two "rows" or parallel to one another. The cortex is composed of three utricle layers. The primary utricles are heavily calcified and conical to bulbous in shape (Pl. 4, Fig. 5). The primary utricles support tubular, slightly inflated distally, dichotomously branched, secondary utricles, while these in turn bear short and sub-conical or pot-like tertiary utricles (Pl. 4, Fig. 5).

Measurements.—Segment length 1.0–1.5 mm; segment thickness 0.35 mm; medulla diam. 0.14–0.15 mm; cortex thickness 0.09–0.10 mm; primary utricle diam. 0.035–0.050 mm; primary utricle length 0.050–0.075 mm; secondary utricle diam. 0.03–0.04 mm; secondary utricle length 0.06–0.07 mm; tertiary utricle diam. 0.03–0.05 mm; tertiary utricle length 0.045–0.050 mm.

Material examined.—Palau limestone, USNH loc No. 35998, Late Miocene.

Halimeda fragilis Taylor 1950
Pl. 5, figs. 1–9

See also *Halimeda fragilis* Taylor 1950, 80, pl. 48, fig. 2. Hillis Colinvaux 1980: 151, fig. 47.

Description.—The thallus segments are flattened and subcuneate, with the upper margins tri-lobed (Pl. 5, Fig. 1) or with truncate or ear-like appendages (Pl. 5, Fig. 4). The medulla has long, undulating siphons disposed vertical-axially in 8–10 parallel "rows". The cortex is comprised of three to four utricle layers. The primary utricles are long, tubular and claviform at the distal end. The primary utricles support secondary utricles that are tubular, conical, dichotomously branched and occasionally opened distally (Pl. 5, Fig. 7). The secondary utricles bear short, tubular and dichotomously branched tertiary utricles, while these support a fourth layer of small, fine, tubular-cylindrical utricles (Pl. 5, Fig. 8).

Measurements.—Segment length 3.0–12 mm; segment thickness in the lobed area 0.9–3.0, between lobes 0.48–0.60 mm; medulla diam. 0.3–0.6 mm; cortex thickness 0.15–0.40 mm; medullary siphon diam. 0.06–0.09 mm; primary utricle diam. proximal 0.02, distal 0.05, primary utricle length 0.15–0.30 mm; secondary utricle diam. 0.030–0.042 mm; secondary utricle length 0.12–0.27 mm; tertiary utricle diam. 0.010–0.015 mm; tertiary utricle length 0.030–0.045 mm; quaternary utricle diam. 0.01 mm; quaternary utricle length 0.015–0.030 mm

Material examined.—Palau limestone, USNH loc No. 36152, Pliocene.

Halimeda simulans Howe 1907
Pl. 7, figs. 6–8, pl. 9, figs. 3–4

See also *Halimeda simulans* Howe 1907, 503. pl. 29. Hillis Colinvaux 1980: 103, fig. 26. Littler & Littler 1997: 112, fig. 163. Littler & Littler 2000: 408.

Description.—In oblique axial longitudinal section segments appear subcuneate to reniform with a medulla filled with medium diameter, tubular siphons. The strongly calcified thick cortex is formed by three layers of utricles (Pl. 7, Figs. 7–8). The primary utricles are conical in shape. The primary utricles support secondary utricles of a similar shape but are somewhat shorter, smaller, more bulbous and dichotomously branched. The secondary utricles bear tertiary utricles which are short, tiny, subcylindical and slightly inflated at the apices (Pl. 7, Fig. 8).

Measurements.—Segment thickness 1.35–1.50 mm; medulla diam. 0.6 mm at the basal part of segments; medullary siphon diam. 0.065–0.075 mm; cortex thickness 0.60–0.75 mm; primary utricle diam. proximal 0.025 mm, distal 0.06–0.07 mm; primary utricle length 0.15 mm; secondary utricle diam. 0.03–0.04 mm; secondary utricle length 0.075–0.090 mm; tertiary utricle diam.

0.020–0.025 mm; tertiary utricle length 0.030–0.035 mm.

Material examined.—Palau limestone, USNH loc No. 36152, Pliocene.

Halimeda cf. *bikinensis* Taylor 1950
Pl. 7, figs. 9–10

Description.—The lateral-longitudinal section shows a disc-like segment with an undulating, large margin. The segment consists of a moderately large medullary area filled with long tubular siphons, more or less disposed parallel (Pl. 7, Fig. 10). The cortex has only two utricle layers. The primary utricles are cylindrical-conical, occasionally claviform distally. The primary utricles support much smaller, short, conical, secondary utricles. This specimen differs from *H. bikinensis* because of the unique shape of primary and secondary utricles comprising the cortex.

Measurements.—Segment length 5.4 mm; segment thickness 0.9–1.2 mm; medulla diam. 0.3 mm; medulla siphon diam. 0.06 mm; cortex thickness 0.27 mm; primary utricle diam. proximal 0.025, distal 0.06–0.07 mm; primary utricle length 0.24–0.25 mm; secondary utricle diam. 0.010–0.012 mm; secondary utricle length 0.015–0.025 mm.

Material examined.—Palau limestone, USNH loc No. 36152, Pliocene.

Halimeda opuntia (Linnaeus)
J. V. Lamouroux, 1812
Pl. 9, figs. 1–2

See also *Corallina opuntia* Linnaeus 1758, 805. *Halimeda opuntia* (Linnaeus) Lamouroux 1812: 3, 181–188. Hillis Colinvaux 1980: 110, figs. 19, 51, 52. Bassoullet et al. 1983: 490, pl. 7, fig. 9.

Description.—The thallus segments are highly variable in shape, flat, oval-ellipsoidal with the upper margin entire, undulated or microlobed. In axial longitudinal section, the medulla consists of long, tubular, parallel, sometimes fused siphons, diverging at the margin or forming protuberances or microlobes (Pl. 9, Fig. 1). The cortex is thick and formed by multiple (most commonly four or five) utricle layers (Fig. 4). The primary utricles are long, tubular and slightly inflated distally. The primary utricles support tubular, medium long, dichotomously branched, secondary utricles, which in turn support short, tubular, cylindrical-conical (distally), dichotomously branched, tertiary utricles. The third layer of utricles often support tiny, extremely small, almost dot-like (punctiform) quaternary utricles (Pl. 9, Fig. 2).

Measurements (mm).—Segment length (height) 5.0–6.0 mm; segment thickness 3.0–3.2 mm; medulla diam. at middle part of segment 0.3 mm, in the lateral lobes 0.15–0.20 mm; medulla siphon diam. 0.050–0.065 mm; primary utricle diam. 0.030–0.045 mm; primary utricle length 0.14–0.15 mm; secondary utricle diam. 0.05–0.06 mm (distal); secondary utricle length 0.18–0.20 mm; tertiary utricle diam. 0.025–0.030 mm; tertiary utricle length 0.10–0.11 mm; quaternary utricle diam. 0.010–0.014 mm; quaternary utricle length 0.010–0.018 mm.

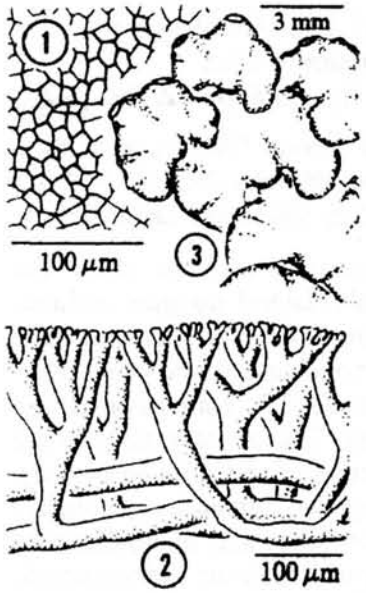

Figure 4.
Halimeda opuntia: Surface view (1); Surface utricles (2) in the longitudinal section; Habit of apical segments (3) (from Littler & Littler, 2000)

Remarks.—This species was reported from Miocene and Pliocene deposits from Buton Island, Malaysia by Keyser (1953) and recently from Eocene (Dragastan & Soliman, 2002). We consider *Halimeda opuntia* as a Miocene–Pliocene ancestor of Pleistocene–Recent *H. opuntia* f. *opuntia*. Also, the specimens illustrated by Bassoullet et al. (1983) as *H. opuntia* from the Recent (Tahiti) correspond to the subspecies *opuntia*. Although Morellet & Morellet (1922) incompletely described the new species *H. praeopuntia* from the Oligocene of France, showing only detached segments and only one longitudinal section (in Bassoullet et al. 1983, pl. 7, Figs. 10–11), we consider this taxon different from *H. opuntia* and a valid fossil species. In Bassoullet et al. (1983), the specimen at the upper left side of Fig. 10 belongs to *H. opuntia* f. *triloba*. The longitudinal section of Morellet & Morellet's (1922) *praeopuntia* species has clear, long, tubular medullary siphons, which is quite distinct in siphon disposition and distribution from the medullary siphons seen in fossil *H. opuntia* species. The Morellet & Morellet fossil species could be valid in spite of inconsistencies concerning missing internal details of the cortical structure, dimensions of thallus segments and other internal parameters.

Material examined.—Palau limestone, USNH loc No. 36152, Pliocene.

Taxonomic synonyms.—Halimeda eocaenica Morellet & Morellet 1940: 203–205, fig. 2. *H. johnsonii* Pal 1971: 133–134, 138, pl. 1, fig. 1.

Halimeda opuntia f. *triloba* (Descaisne)
J. Agardh 1887
Pl. 10, figs. 6–9, pl. 11, figs. 1, 4, pl. 12, fig. 8

See also *Halimeda triloba* Decaisne 1842: 102. Littler & Littler 1997: 113, fig. 162. Littler & Littler 2000: 406.

Description.—Segments of the thallus are considerably variable in shape, from flat with very little con-

tortions to highly contorted and often with three cylindrical to contorted lobes (Pl. 12, Fig. 8), which are often incompletely preserved. The segments have a large medulla in the central part and a narrow medulla in the lobed areas (Pl. 11, Fig. 1). The segment cortex is thick, well calcified and is formed by three to four utricle layers. The primary utricles are short and slightly conical at the distal end. The primary utricles support short, cylindrical, robust, dichotomously branched, secondary utricles that bear small, conical, tertiary utricles (often opened to the exterior).

Measurements.—Segment length (height) 1.5–1.8 mm; segment diam. (width) 1.35–4.00 mm; medulla diam. in central part of segment 0.8–0.9 mm, in lobes 0.3–0.4 mm; medullary siphon diam. 0.05–0.10 mm; cortex thickness 0.45–0.60 mm; primary utricle diam. 0.070–0.12 mm; primary utricle length 0.25–0.30 mm; secondary utricle diam. 0.042–0.058 mm; secondary utricle length 0.15 mm; tertiary utricle diam. 0.015–0.040 mm; tertiary utricle length 0.05–0.06 mm; height of lobe 1.0–1.5 mm; diam. of lobe 1.5–1.8 mm.

Material examined.—Palau limestone; Johnson Collection, Eniwetok, Hole E1, 10 m deep, USNH 36146, Pleistocene; sand beach near la Habana, Cuba, USNH No. 2023530, Recent.

Halimeda opuntia f. *opuntia* (Linnaeus) J. V. Lamouroux 1816
Pl. 12, fig. 7

See also *Corallina opuntia* Linnaeus 1758: 805. *Halimeda opuntia* J. V. Lamouroux 1816: 308. Littler & Littler 1997: 110, fig. 161. Littler & Littler 2000: 406.

Description.—Segments are heavily calcified, flat, contorted, often ribbed and oval to ear-shaped, occasionally with two small lateral protuberances (Pl. 12, Fig. 7).

Measurements.—Segment height 2.5–3.0 mm; segment width 3.5–5.0 mm; segment thickness 0.6–1.0 mm.

Material examined.—Sand beach near la Habana, Cuba, USNH No. 2023530, Recent.

Halimeda micronesica Yamada 1941
Pl. 11, figs. 6, 9

See also *Halimeda micronesica* Yamada 1941, 121, fig. 15. Hillis Colinvaux 1980: 149, fig. 46.

Description.—Thallus segments mostly discoidal to subcuneate. In oblique longitudinal section, the large medulla contains long, siphons. The cortex is formed by four layers of utricles. The primary utricles are tubular or cylindrical and support tubular, slightly inflated distally, dichotomously branched, secondary utricles. These secondary utricles bear short, cylindrical (slightly conical distally), dichotomously branched, tertiary utricles. The fourth cortical layer consists of tiny conical utricles that are open to the exterior. In oblique transverse section, the segments are oval and compressed; however, the large medulla appears hollow with bioclasts. The cortex clearly has four layers of utricles.

Measurements.—Segment length 2.0 mm; segment thickness 1.0–1.5 mm; medulla diam. 0.30–0.45 mm; cortex thickness 0.15–0.30 mm; medullary siphon diam. 0.090–0.17 mm; primary utricle diam. 0.036–0.050 distal mm; primary utricle length 0.15 mm; secondary utricle diam. 0.024–0.036 mm; secondary utricle length 0.10–0.15 mm; tertiary utricle diam. 0.025–0.030 mm; tertiary utricle length 0.080–0.087 mm; quaternary utricle diam. 0.020–0.022 mm; quaternary utricle length 0.060–0.075.

Material examined.—Johnson Collection, Kita –Daito-Jima, 2138 hole, 10 m deep, Pleistocene, Coll. Smithsonian Institution USNH.

Rhodophyta
Order Corallinales
Family Corallinaceae
Genus *Lithophyllum* Philipi 1837

Lithophyllum praelichenoides Lemoine 1917
Pl. 4, fig. 7

See also Johnson 1961: 54, pl. 1, fig. 3.

Description.—The crustose thallus covers the surface of an algal nodule (rhodolith) which has a bryozoan core. The hypothallus is coaxial and formed in regularly curved layers. The hypothallus cells are small, high and narrow in width. The perithallus is not uniform in thickness. The basal portions are thin because of attachment to the core, while the upper part or outer perithallus is more developed with a very distinct, but empty, conceptacle.

Remarks.—Lithophyllum praelichenoides was described by Lemoine (1917) as a crustose thallus from the Miocene and Pliocene in Europe and North Africa and reported by Johnson (1961b) and Johnson & Adey (1965) from the Miocene of Saipan Peninusula, Japan.

Material examined.—Palau limestone, USNH loc No. 35998, Late Miocene.

Lithophyllum cf. *racemus* (Lamarck) Foslie 1898
Pl. 9, fig. 5

Description.—This thallus appears to be branched and stands erect. The branch is composed of large coaxial hypothallus cells which are quadrangular in shape and disposed in regular curved layers. The perithallus is thin and consists of small cells arranged in horizontal rows. No conceptacles were preserved.

Remarks.—This species has been previously reported from Miocene and Pliocene deposits.

Material examined.—Palau limestone, USNH loc No. 36152, Pliocene.

List of Halimeda species from Palau limestones, Angaur island and other areas

Smithsonian Institution Collection:

Sample USNH loc No. 35994/USNH 519484 (Late Miocene) contains the following taxa:

1. *Halimeda discoidea* Decaisne
2. *Halimeda gracilis* Harvey ex J. Agardh
3. *Halimeda cylindracea* Decaisne
4. *Halimeda monile* (J. Ellis & Solander) J. V. Lamouroux
5. *Halimeda* cf. *bikinensis* Taylor

Sample USNH loc No. 35998/USNH 519485 (Late Miocene) contains the following taxa:

6. *Halimeda bikinensis* Taylor
7. *Halimeda gracilis* Harvey ex J. Agardh
8. *Halimeda incrassata* (Ellis & Solander) J. V. Lamouroux
9. *Halimeda tuna* (J. Ellis & Solander) J. V. Lamouroux
10. *Halimeda tuna* f. *platydisca* (Decaisne) E. S. Barton

Sample USNH loc No. 36152/USNH 519488 (Pliocene) contains the following taxa:

11. *Halimeda fragilis* Taylor
12. *Halimeda bikinensis* Taylor
13. *Halimeda simulans* Howe
14. *Halimeda* cf. *bikinensis* Taylor
15. *Halimeda discoidea* Decaisne
16. *Halimeda opuntia* (Linnaeus) J. V. Lamouroux

Sample USNH loc No. 36146/USNH 519487 (Pleistocene) contains the following taxa:

17. *Halimeda discoidea* Decaisne
18. *Halimeda opuntia* f. *triloba* (Decaisne) J. Agardh

H. J. Johnson Collection thin sections:

Eniwetok:

19. *Halimeda opuntia* f. *triloba* Decaisne J. Agardh, Pleistocene
20. *Halimeda micronesica* Yamada, Pleistocene
21. *Halimeda bikinensis* Taylor

Bikini:

22. *Halimeda tuna* (J. Ellis & Solander) J. V. Lamouroux, Pleistocene.

Kita – Daito – Jima:

23. *Halimeda micronesica* Yamada, Pleistocene

Dragastan Collection:

24. *Halimeda opuntia* f. *opuntia* (Linnaeus) J. V. Lamouroux, Recent, sand beach near la Habana, Cuba, USNH No. 2023530.
25. *Halimeda opuntia* f. *triloba* (Decaisne) E. S. Barton, Recent, sand beach near la Habana, Cuba, USNH No. 2023530.

Discussion

This study revealed the presence of a wide variability in both external morphology and internal anatomy (from base to apex) in all 33 of the Recent species of *Halimeda* that we examined from the extensive collections of Littler and Littler (US), Hillis (US, STRI) and the University of California, Berkeley Herbarium (UC). It is widely known that the number of thallus segments is variable, ranging from 6–10 (in *H. discoidea*) to as many as 700 (in *H. incrassata*). Moreover, in the above collections, there are taxa with thalli showing only two different segment morphologies (cylindrical to spherical or subspherical), as well as taxa with up to six different segment morphologies (ranging from cylindrical, cuneate, trapezoidal, reniform, ovoid to discoid). As elaborated below, two different morphological series can be recognized within the Recent *Halimeda* species; a third one is related to the second series, but shows less diversified, more flattened, segment morphologies.

The first of these morphological series, characterized by cylindrical, compressed or terete segments at the base of the thallus, includes the following 23 species: *Halimeda incrassata, H. favulosa, H. monile, H. cylindracea, H. stuposa, H. simulans, H. macroloba, H. opuntia, H. minima, H. reinschii, H. velasquezii, H. copiosa, H. cuneata, H. lacunalis, H. gigas, H. discoidea, H. taenicola, H. bikinensis, H. gracilis, H. lacrimosa* (spherical moniliform segments), *H. fragilis, H. melanesica* and *H. goreauii*. The second morphological series includes the following 6 species that show cuneate-ovoid, subcuneate, discoid to reniform or ovoid-elliptical segments from the base of the thallus: *H. distorta, H. tuna, H. scabra, H. macrophysa, H. micronesica* and *H. cryptica* (this last with a unique structure of the segments and siphons).

The above distinction was made for two reasons:

1. The long fossil history of the Suborder *Halimedineae*, beginning with the Ordovician, shows only small evolutionary modifications in segment morphology throughout the Mesozoic and Cenozoic and continuing up to the Present.
2. The large number of fossil *Halimeda*-related taxa described from an insufficient amount of material, usually only 1–4, or at most 8, sections made in different parts of poorly preserved segments, not to know entire thalli.

Because a number of these fossil "genera" and "species" were documented solely by an insufficient number of disoriented thin sections made in poorly preserved material, we are faced with an artificially high number of taxa. In light of our studies on Recent *Halimeda*, we believe that such fossil 'taxa' often represent only isolated parts of thalli belonging to one, or not more than 2–3, wide-ranging species that show a broad spectrum of segment variability within a single thallus. As mentioned above, in several instances, fossil descriptions are based on single iso-

lated specimens and/or lack morphometric data, which are especially important in the case of the cortical siphons, a critical character used in separating the different species of *Halimeda*.

Founded on the thallus segment morphology, the following three main lines can be discerned in the evolutionary history of the *Halimedineae*:

(1) The first, and oldest, of these lines originated in the Paleozoic and included forms with cylindrical, spherical or ovoid (sometimes laterally compressed) thallus segments that made their first appearance in the Ordovician Period and continued until the Permian; such as *Dimorphosiphon, Dimorphosiphonoides, Litania, Maslovina, Lowvillia, Orthriosiphon, Palaeoporella, Siamporidium, Succodium, Tauridium* and *Aphroditicodium* (Permian). It is possible that the genus *Saxonia* (invalidated, since two individuals were proposed as the holotype of the taxon) is synonymous with *Halimeda*. Poncet (1989) described *H. soltanensis* from the Permian based on an array of differently oriented segments, which indeed show features characteristic of the genus *Halimeda*. A part of these Paleozoic and some Mesozoic taxa constitute the Protohalimedaceae group or family (new family, introduced herein), a line that continued through *H. cylindracea* during the Mesozoic, crossed the Cretaceous/Paleocene boundary and survived until the Present.

Taking into account all described taxa included first in order *Siphonales* by Shuysky (1987) and reconsidered now as Suborder *Halimedineae*, four families (3 fossils and 1 fossils and Recent) are classified as follow:

1. The Family **Dimorphosiphonaceae** Shuysky, 1987 (Ordovician – Devonian, rarely Jurassic) with thalli composed by cylindrical segments crossed by multiaxial medullar siphon (4 up to 10 siphons) and primary cortical siphons, rarely secondary (genera included *Ampullipora, Litanaia, Litanaella, Prealitanaia, Botryella, Bacilloporella, Botrys, Abacella, Clibeca, Dimorphosiphon and Dimorphosiphonoides*);

2. The Family **Lanciculaceae** Shuysky, 1987 (Devonian) included thalli formed by cylindrical, spheroidal or conoidal segments crossed by uniaxial medullar siphon (like a central hollow) and only primary cortical, simple not branched siphons (genera *Lancicula, Hasticula, Lanciculella, Lepidolancicula, Planolancicula, Lanciculina, Cauculicula, Voycarella and Semilancicula*);

3. The **Protohalimedaceae** nov. family (Silurian-Permian, Late Triassic-Cretaceous) is comprised of thalli with cylindrical, subcylindrical, rarely spheroidal or flabelliform (somewhat flattened, Mesozoic). The segments are crossed by uni– or multi–axial medullary siphons and the cortex has both simple or dichotomously branched primary and secondary siphons in Paleozoic material and multi–series siphons (1–4, not more) in Mesozoic taxa. This family includes the Paleozoic genera: *Orthriosiphon, Orthriosiphonoides, Aphroditicodium, Lowvillia, Palaeoporella, Siamporidium, Succodium, Uva, Funiculus, Tauridium, Maslovina*; and from the Mesozoic: *Felixporidium, Fagetiella, Pinnatiporidium, Nipponophycus, Cortiporidium, Margueritiella, Cupasiella, Akrokorinthiella, Johnsonicodium, Tethysicodium, Carpathocodium.* The genus *Bacinellacodium* is excluded (all Mesozoic taxa were described by Dragastan, 1985, 1988, 1990, 2000, 2002 and Richter et al. 1992, except *Nipponophycus* described by Yabe & Toyama, 1928; *Consinocodium* Endo, 1961 and *Pycnoporidium* Endo, 1960).

4. The Family **Halimedaceae** Link, 1832 (Permian - Recent) thalli segments with, multishapes or morphae from cylindrical until disk – like flattened crossed by multiaxial medullar siphons and cortex with many utricles series from 2 up to 7 (genera *Halimeda, Juraella, Hydracara, Hikorocodium and Corallecodium*).

(1) **The first phyletic line** is *Halimeda cylindracea* which was noted from the Late Miocene and, based on the cylindrical or spherical segment morphology described in several Mesozoic taxa, it is probable that it made its appearance in the Mesozoic. The following 21 Mesozoic and Cenozoic taxa are herein synonymized with *H. cylindracea*: *H. helladica* Dragastan (Late Trisassic), *H. marondei* (Flügel) (Late Triassic), *H. fluegeli* Bucur (Early Cretaceous), *H. elliotti* Conrad & Rioult (Late Cretaceous, Turonian), *H.* cf. *elliotti* Conrad & Rioult (Late Cretaceous, in Schlagintweit 1992), *H. entogensis* Yu-Jing (Paleocene-Early Eocene), *H. camenitzae* Dragastan & Bucur (Late Aptian), *H. praemonilis* Morellet (Paleocene-Early Miocene), *H. nana* Pia (Paleocene), *H. lingulata* Yu-Jing (Middle-Late Eocene), *Lekhamptonella llewellyae* Elliott (Middle Jurassic), *Arabicodium aegagrapiloides* Elliott (Early Cretaceous), *A. aninensis* Bucur (Early Cretaceous), *A. tibeticum* Yu-Jing (Paleocene-Early Eocene), *Boueina hochstetteri* Toula (Late Triassic-Jurassic-Cretaceous; including var. *liasica* and *moncharmonti*), *B. pygmaea* Pia (Cretaceous-Paleogene), *B. globosa* Dragastan, Bucur & Demeter (Late Aptian), *B. chirakhanensis* Pal (Late Cretaceous) and *Banatea bucurii* Dragastan nomen nudum. These taxa, some described beginning in 1884, were based upon cylindrical or spherical-ovoid "thalli" segments found isolated in calcareous rocks. However, the fragment remains (=segments) they were described from do not represent complete thalli (the critical diagnostic feature for any species), so that the taxonomic validity of these taxa is doubtful at best. Moreover, because of problems with the orientation of the thallus sections, the incomplete descriptions lacking clear depiction of the cortical system, as well as the utricle anatomy and dimensions one of the most important characters to distinguish species (see Littler & Littler, 2000), an

artificial increase of so-called Mesozoic and Cenozoic "fossil taxa" has resulted.

Consequently, we consider that the wide-ranging *Halimeda cylindracea*, showing only two segment morphotypes (predominantly cylindrical, although becoming sub-spherical toward the apex) and with the cortical system showing three to five utricle layers, has generated the large number of segments upon which these Late Triassic, Jurassic, Cretaceous and Cenozoic "taxa" were based. However, we do not include within this series those species of the genus *Arabicodium* that show thalli crossed by medullary cavities and a cortex having simple or multiple siphons, which belong to the genus *Pseudopenicillus* Dragastan et al. (1997), included within the Family *Udoteaceae*.

(2) **The second phyletic line** is illustrated by *Halimeda incrassata*, characterized by cylindrical to reniform, subcuneate, smooth or ribbed thallus segments and a cortex system with three to five utricle layers. This line originated during the Cretaceous (Late Cretaceous) and continued into the Cenozoic, until the Present. The following seven fossil taxa are considered to be synonymous with *H. incrassata: H. chiplonkari* Badve & Kundal, *H. agharkari* Badve & Kundal, *H. corneola* Badve & Kundal, *H. densituba* Badve & Kundal, *H. pipaldehlaensis* Badve & Kundal, *H. robusta* Badve & Nayak, *H. triradiata* Badve & Nayak; all of which were reported from the Late Cretaceous but may more probably be Paleocene or Eocene in age. These species are characterized by cylindrical or subcuneate segments, with a faintly visible internal morphology, except for those illustrated in Plate VI, figs. 4, 11 by Badve & Nayak (1983). From the description of the cortical system, it appears that these fossil taxa had three to four utricle layers, corresponding in shape and number to those seen in the Recent species *H. incrassata*.

(3) **The third phyletic line** includes taxa with extremely variable thallus segments, ranging from flat or somewhat contorted, cuneate-ovate to discoid, with truncate, auriculate, lobed or ribbed margins. Members of this line first appeared around the Cretaceous/Paleocene boundary and continued into the Present, as the species *Halimeda opuntia*. This pantropical species shows a wide morphological variability of the segments at all levels along the thallus; such variability, in conjunction with post-mortem fragmentation during the preservation of a large number of differently shaped individual thallus segments, also is responsible for the introduction of an additional large number of "fossil taxa". The cortical system of this species is made up of up to five utricle layers. *Halimeda paucimedullaris* Schlagintweit & Ebli, from the Late Cretaceous (Turonian-Santonian), described on the basis of variously oriented sections as having a cylindrical thallus, is placed very close with *H. opuntia* or *H. tuna*, **but not synonymous**. However, the illustrations most probably represent 2–3 different types of flattened, fan-shaped, discoid segments. It is quite obvious that figure 4 from Pl. I of Schlagintweit & Ebli (1998) shows a transverse section within a flat, fan-shaped or discoid, compressed segment, whereas Pl. I, figs. 1–2 are oblique transverse sections in the lateral part of a discoid segment, Pl. I, figs. 3, 6 represent vertical sections through a fan-shaped segment, while Pl. I, Fig. 5 is a tangential section. The shape of these thallus fragments thus can be reconstructed as being flat, fan-shaped and nearly discoidal. The cortical system is

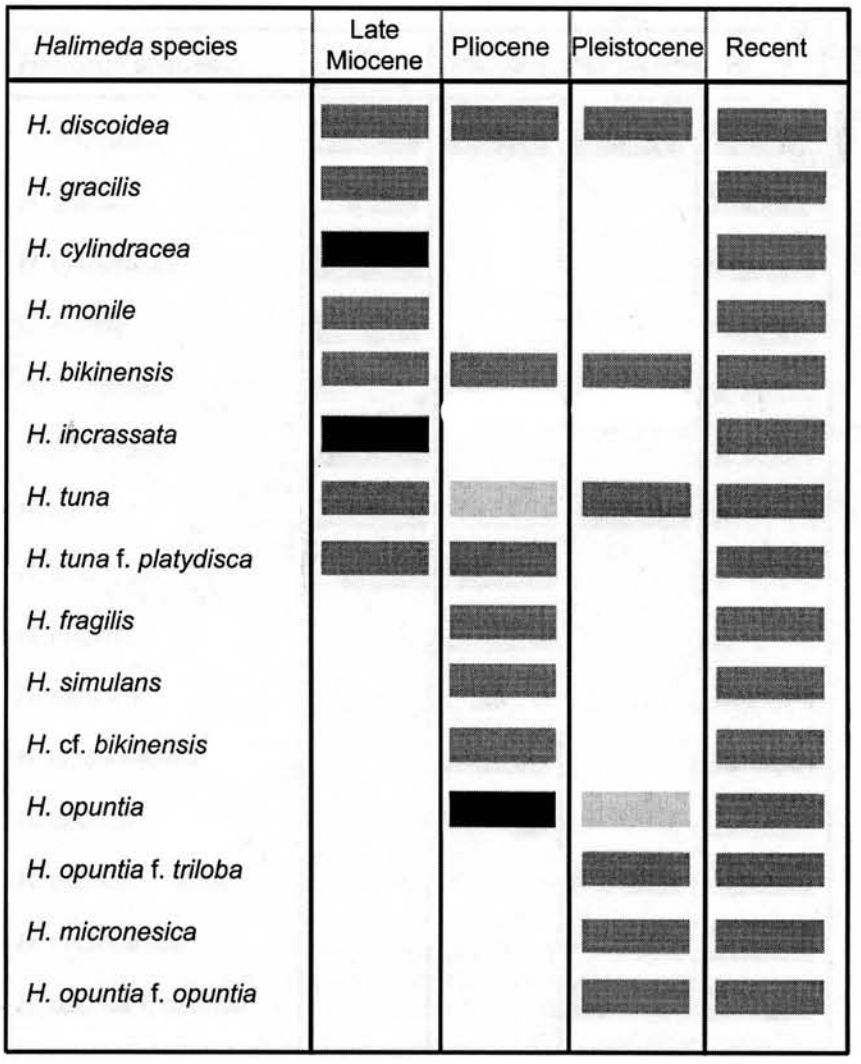

Figure 5.
Stratigraphic range of *Halimeda* species from Palau limestones (Angaur Island), Eniwetok, Bikini and Kita-Daito-Jima, Western Pacific. Black bar = main stock of the phyletic lineages of the "fossil species". Dark gray bar = common in the material examined. Light gray bar = rarely encountered in the material examined.

composed of five series of utricle layers similar to the condition of the Recent species *H. opuntia* and *H. tuna*.

The species *Halimeda eocaenica* Morellet & Morellet (Eocene), unknown in thin sections, also has variable shaped, but always flattened, fan-shaped segments with simple, undulating, vaguely lobed margins (in Bassoullet et al. 1983, from Morellet & Morellet 1940); these segments are strikingly similar to those of the Recent *H. opuntia*. Other taxa that might prove to be synonymous with *H. opuntia* include the poorly described *H. johnsonii* Pal (Maastrichtian-Paleocene), characterized by leaf-like segments. Fossil materials of the subspecies *H. opuntia f. opuntia* and *H. opuntia f. triloba* are reported in the present study from the Palau Pleistocene Formation of Angaur Island, Palau, Western Pacific (Fig. 5).

Given the current state of knowledge, the two evolutionary lines of fossil Halimedaceae, described by Dragastan et al. (2000) and established on the basis of structure of the cortical system, cannot be correlated with the three phyletic lines based on segment morphology and entire thalli proposed above. We emphasize again that fossil species of *Halimeda* have never been described from complete thalli, but have been solely based on segment forms, thereby rendering the validity of these "taxa" as highly questionable. The different orientation of the sectioning planes may yield vertical or horizontal "cylindrical" forms if executed in flattened, discoid or fan-shaped segments; however, the arrangement of the siphons will appear different in such sections, suggesting the actual form of the segment. In vertical sections, the medullary siphons appear tubular-cylindrical and oriented axial-longitudinally, while in horizontal sections, they appear circular or oval-ellipsoidal; aspects that are rarely observed in many fossil taxa. It is rather probable that this has led to the description and introduction of exclusively fossil taxa such as *Boueina, Leckhamptonella, Arabicodium* and *Banatea* among others.

Following this line of reasoning, ***Halimeda cylindracea*** made its first appearance in the Late Triassic, ***H. incrasata*** in the Early Cretaceous and ***H. opuntia*** in the Late Cretaceous at the Cretaceous-Paleocene boundary. Moreover, the microscopic anatomical features indicate many similarities among fossil and extant taxa of Halimedaceae and suggest that the Recent species are indeed living fossils (Kooistra et al. 1999). For the Recent *Halimeda* species, three phylogenetic lineages were separated by Hillis (2000): 1. Section Opuntia; 2. Section Rhipsalis and 3. Section Halimeda. There is a distinct possibility that the three phyletic lines separated herein, starting from the Mesozoic, could be coincident with these three Recent sections of Hillis (2000), and might originate from the Paleozoic group of Protohalimedaceae.

However, several fossil taxa, at the moment, cannot be synonymized with the genus *Halimeda* and they remain valid and independent. These are *Juraella bifurcata* Bernier, 1984 (Jurassic-Early Cretaceous), *Hydracara kubeae* Dragastan, 2000 (Late Triassic) and *Collareocodium* Brandner & Resch, 1980 (Middle Triassic). Other taxa, such as *H. praeopuntia* Morellet & Morellet, 1922 (Oligocene-Miocene) and *H. discreta* Dragastan, 2000 (Late Triassic), *Halimeda* (?) sp. (Oligocene) illustrated by J.P. & R. Beckmann (1966), *H. paucimedullaris* Schlagintweit & Ebli (1998), also remain valid species, with distinct structure and morphology that cannot be referred to any of the Recent species of the genus. *Permocalculus ? halimedaformis* Bucur, 1994 (Lower Aptian) is closely related to, if not synonymous with, the Recent *H. discoidea*.

The above-mentioned potential synonymies between various fossil genera and *Halimeda* were first suggested by Hoeg (1927), again by Elliott (1965) and emphasized further by Johnson (1969). The last two authors considered, and consequently recommended, that fossil genera such as *Boueina* and *Arabicodium* "which are similar to the genus *Halimeda*", be included in this taxon because of "priority". In the opinion of Elliott (1965), "the early (Late Triassic–Cretaceous), small-segmented *Halimeda* are considered to have developed from hybridizations between the species-groups of *Arabicodium* and *Boueina*". However, Recent processes of interspecific hybridization within the *Halimeda* group have not yet been demonstrated.

The presence of such a long historical record, beginning from the Ordovician (including here the family Dimorphosiphonaceae Shuysky 1987, Ordovician – Devonian, rarely Jurassic and the family Lanciculaceae, Shuysky 1987, Devonian), but surely from the Permo-Triassic, has the potential of providing considerable information about the evolutionary history of the genus. The presence of many 'segment-based' species of *Halimeda* in the geological record does not realistically reflect the degree of proliferation of the species, which seems to be much less when compared with the Present. These new data contradict the hypothesis that the Messinian crisis (occurring between 7.12 and 5.32 Ma; Gradstein and Ogg, 2000) was accompanied by massive extinctions of marine life and that the *Halimeda* flora either did not survive this environmental deterioration or, at most, existed as relict floras scattered throughout the Indian and Pacific Oceans; whereupon some surviving species of *Halimeda* even achieved a pan-tropical distribution. This conclusion is further supported by the discovery by Martin et al. (1997) of a Late Miocene bioherm built entirely by *Halimeda* thalli on the southern slope of the Sorbas Basin in southeastern Spain. These authors illustrated (p. 447, fig. 7a) three discoid-flat segments, whereby the different orientation of the sections (one vertical and two horizontal) shows a morphology that closely corresponds to that of the Recent species *H. tuna*.

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Plate 1. ▶

Figs. 1–5. *Halimeda discoidea.* **Figs.1–3.** Axial longitudinal sections of a disc-like segment, the medullary siphons (m) are few but large. Cortex with primary (1) and up to 4 bulbous, inflated, secondary utricles (2). **Figs. 4–5.** Transverse oblique section of segment. **Figs. 6–7.** *Halimeda gracilis* illustrating oblique and transverse sections of subcuneate to reniform segments, small-diameter, numerous, medullary siphons (m) and cortex with long, tubular, primary utricles (1), secondary utricles (2) short, tubular, conical distally and what appear to be tiny tertiary utricles (3). **Fig. 8.** *Cycloclypeus carpenteri* (c, foraminiferan Family Nummulitidae). **Fig. 9.** Late Miocene association including *Halimeda* cf. *cylindracea*, *Heterostegina* sp. (h), *Miogypsina* sp. (m) and *Globigerina bulloides* (g). Late Miocene, Sample USNH loc No. 35994, Palau Limestone.

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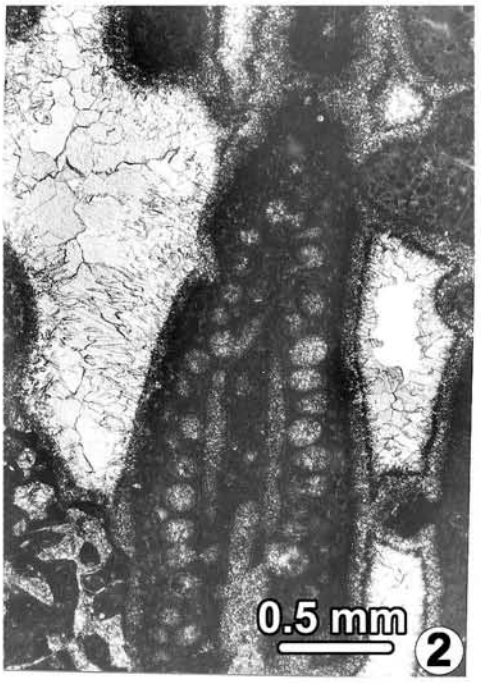
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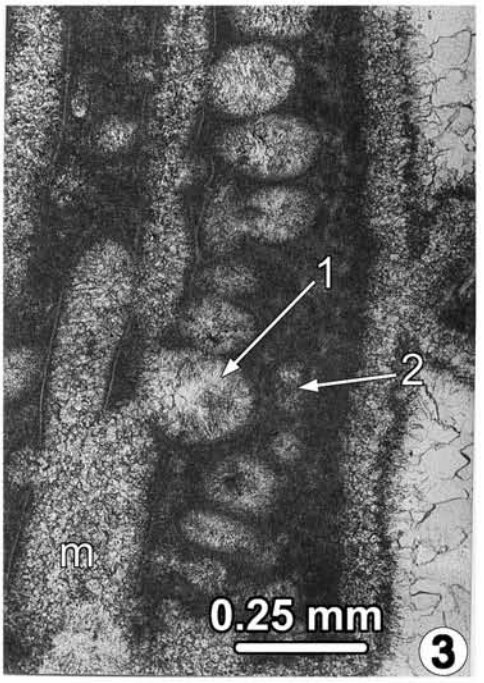
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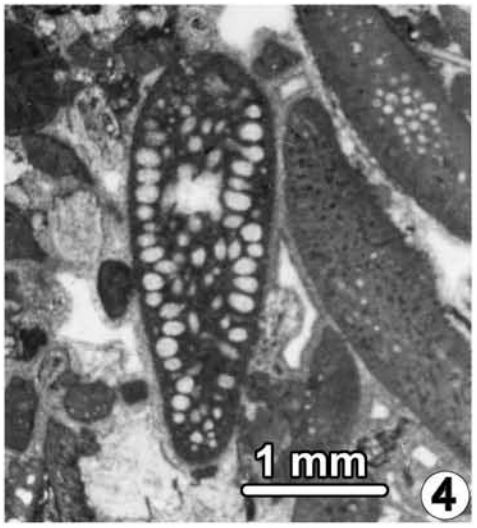
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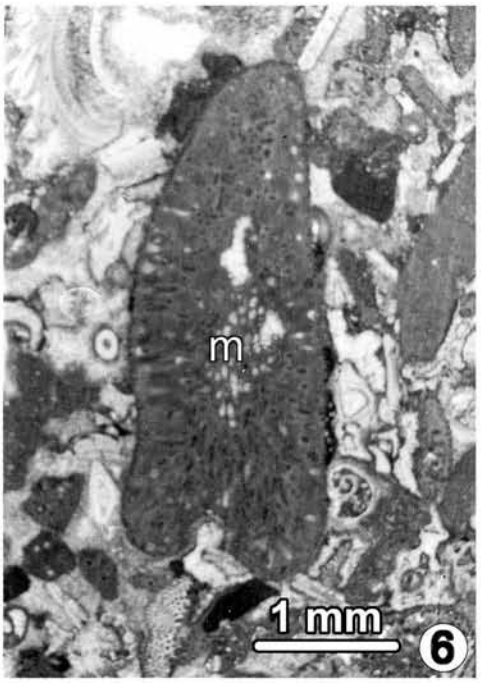
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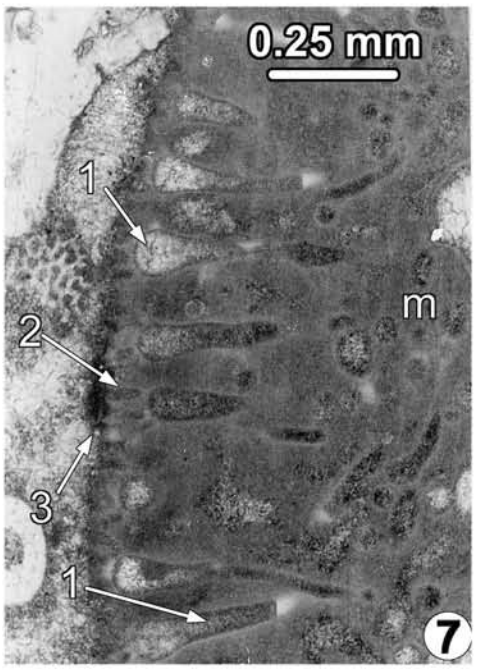
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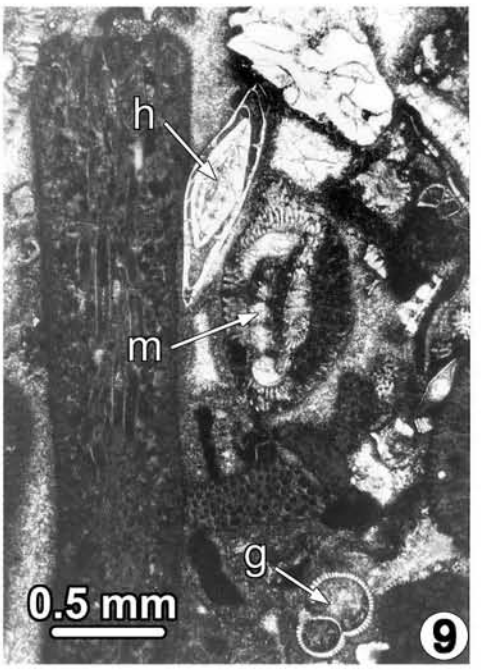
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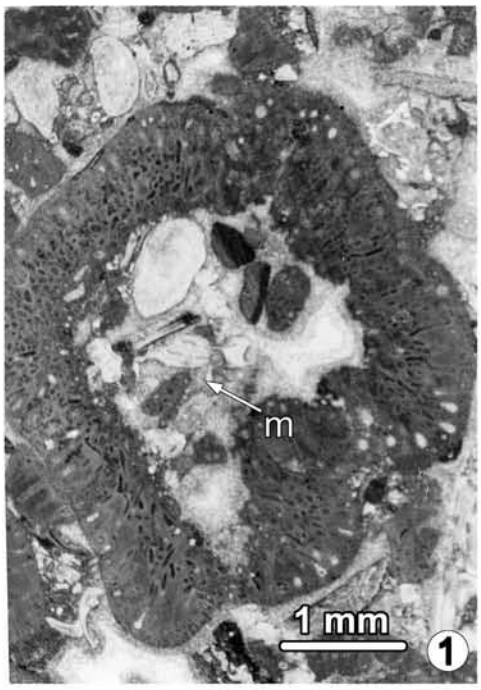
Plate 2. ▶

Figs. 1–3. *Halimeda cylindracea.* Transverse sections of the more or less infolded cylindrical segments showing a large medullary cavity (m) filled with bioclasts and quartz grains, and a thick cortex consisting of fourth level utricles (= siphon layers), primary long tubular utricles (1), secondary tubular utricles (2), slightly inflated distally, tertiary short utricles (3), conical, more distally separated quaternary utricles(4), that are tiny, short, tubular or filiform and dichotomously branched. **Figs. 4–5.** *Halimeda monile.* **Fig. 4.** Oblique longitudinal section of thallus crossed by large medullary siphons (m) and cortex with primary long, tubular, claviform utricles (1), tubular dichotomously branched secondary utricles (2) and short, conical, very small diameter tertiary utricles (3). **Fig. 5.** Transverse section of thallus segment showing large medullary siphons (m) and cortex with three utricle layers. **Fig. 6.** *Cribrorotalia obesa*, a benthic foramaminiferan of Miocene age. **Figs. 7–9.** *Halimeda bikinensis* illustrating a longitudinal oblique section of a subcylindrical segment crossed by vertical medullary siphons (m) and cortex with 2 or 3 utricle layers. **Fig. 7.** Enlarged cortical area (in the middle-left of the thallus, see Fig. 8 arrows) showing the long tubular (somewhat distally claviform) primary utricles (1) and short coniform secondary utricles (2), and very small tertiary utricles (3). **Fig. 9.** Enlarged area on the middle-right portion of thallus (Fig. 8 arrows) with axially disposed medullary siphons (m) and the cortex with primary (1), secondary (2) and tiny fine tertiary utricles(3). Late Miocene, **Figs. 1–6** from Sample USNH loc No. 35994 and **Figs. 7–9** from Sample USNH loc No. 35998, Palau Limestone.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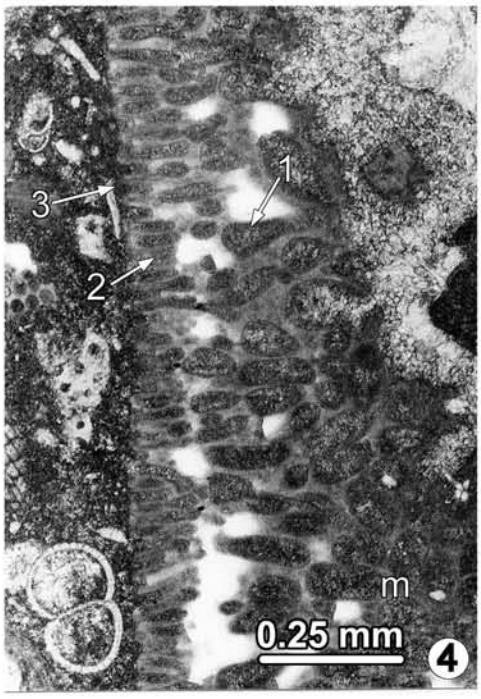
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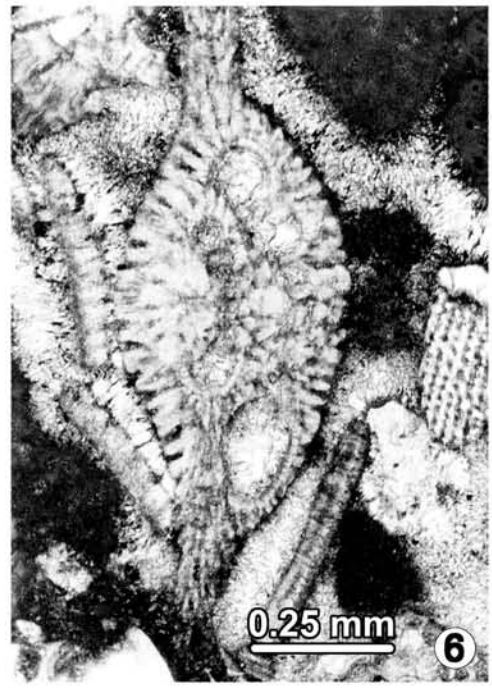
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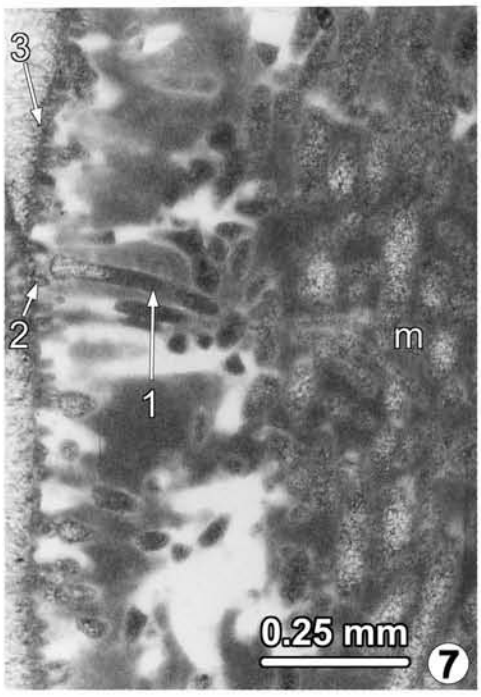
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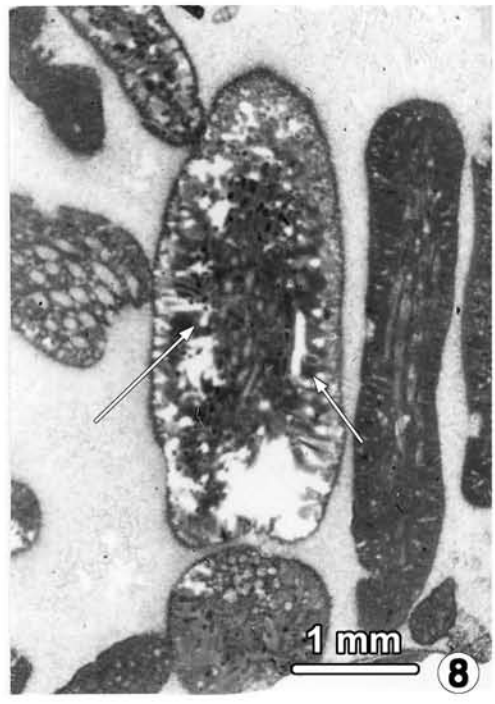
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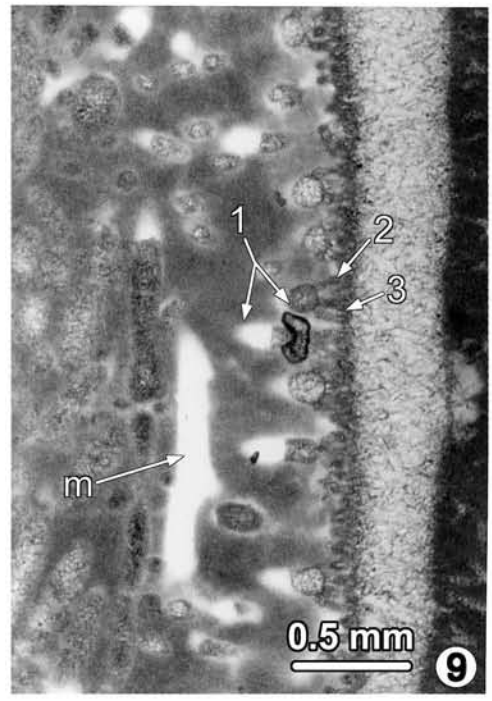
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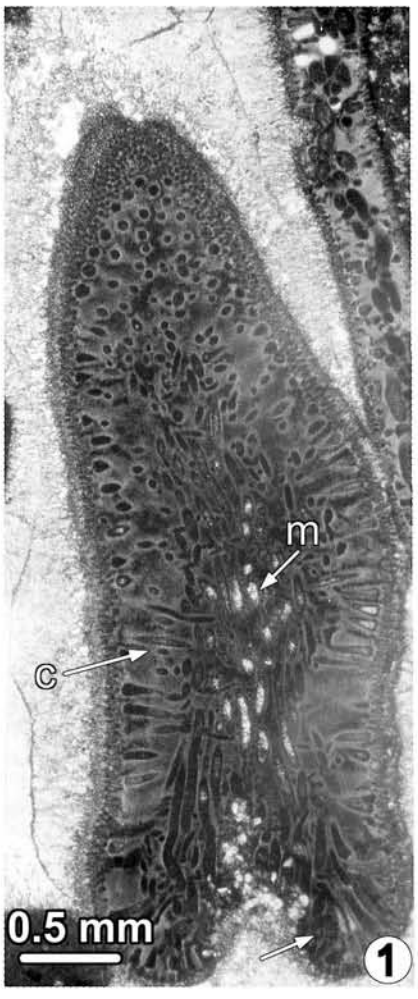
Plate 3. ▶

Figs. 1–4, 6, 8. *Halimeda gracilis.* **Figs. 1–2.** Vertical oblique sections of disk-like oval segments. The segments are crossed by vertical medullary siphons (m) and the cortex consists of 2 utricle layers (c). **Figs. 3–4.** Enlarged cortex system from Figs. 1 and 2 showing 2 utricle layers (l, 2). **Figs. 6, 8.** Transverse sections of enlarged areas, the medullary siphons are round in shape (m) and the cortex is crossed by long primary tubular utricles (1), secondary conical dichotomously branched utricles (2) and short tertiary utricles that are also conical in shape (3). **Fig. 5.** Pelmicrosparite with the planktonic foraminifera *Globigerina bulloides* (g) and *Orbulina universa*, gastropods and echinoid bioclasts. **Fig. 7.** *Halimeda incrassata* illustrating transverse section in a subcuneate disk-like segment showing large medullary siphons (m) and cortex with 3 utricle layers having a strong, cylindrical-conical primary layer (1), medium, short, dichotomously branched, secondary layer (2) and small, short, fine, tertiary utricle layer (3). Late Miocene, Sample USNH loc No. 35998, Palau Limestone.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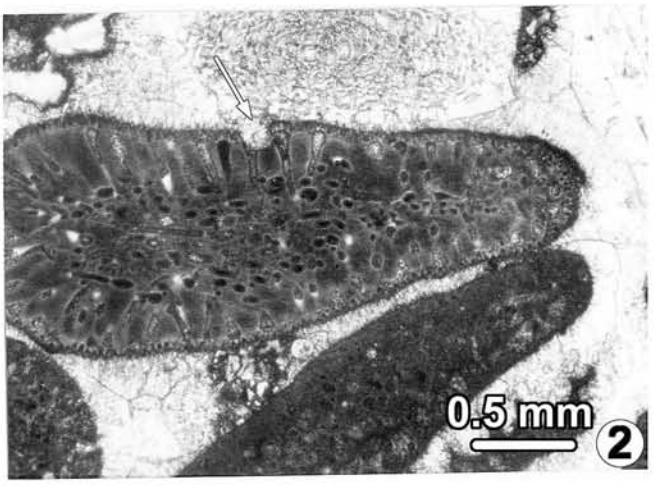
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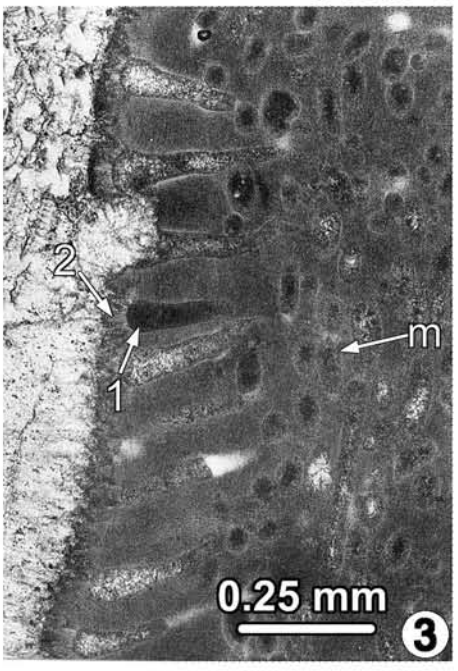
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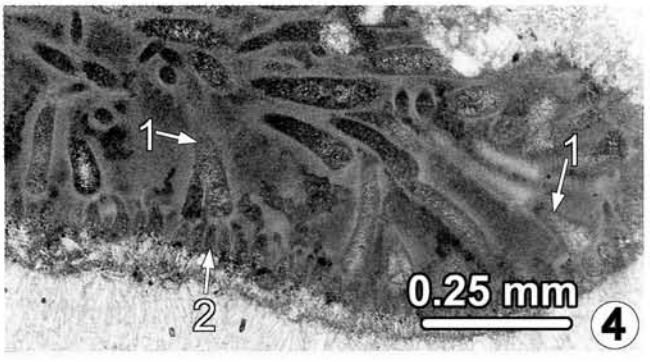
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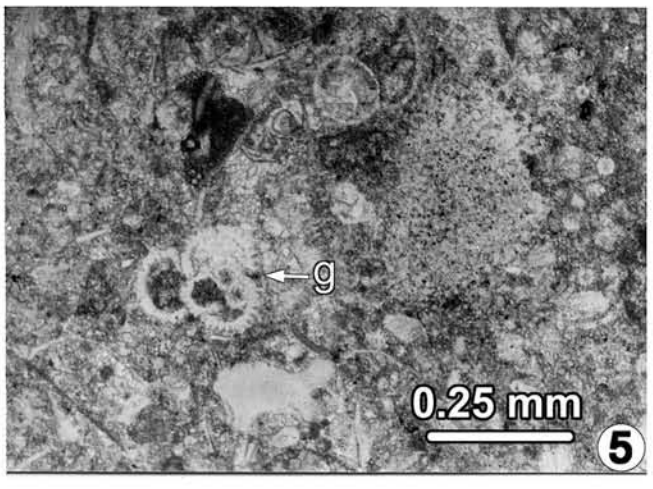
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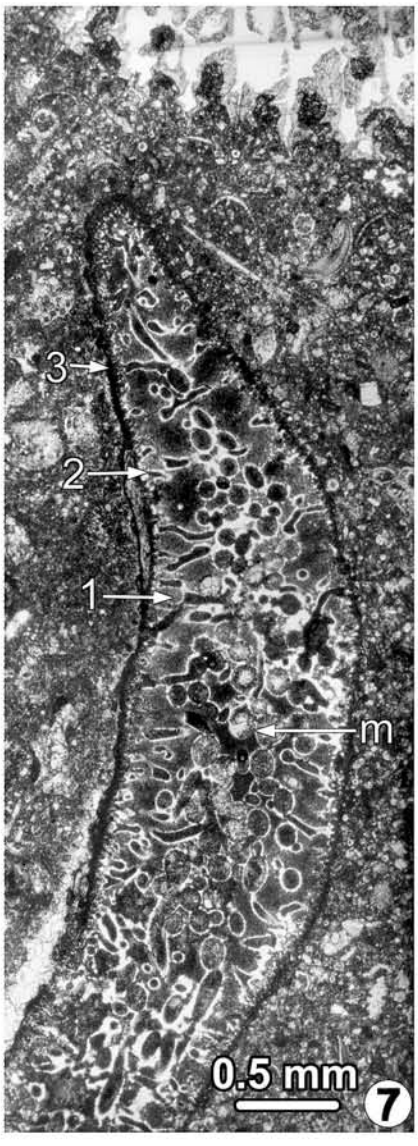
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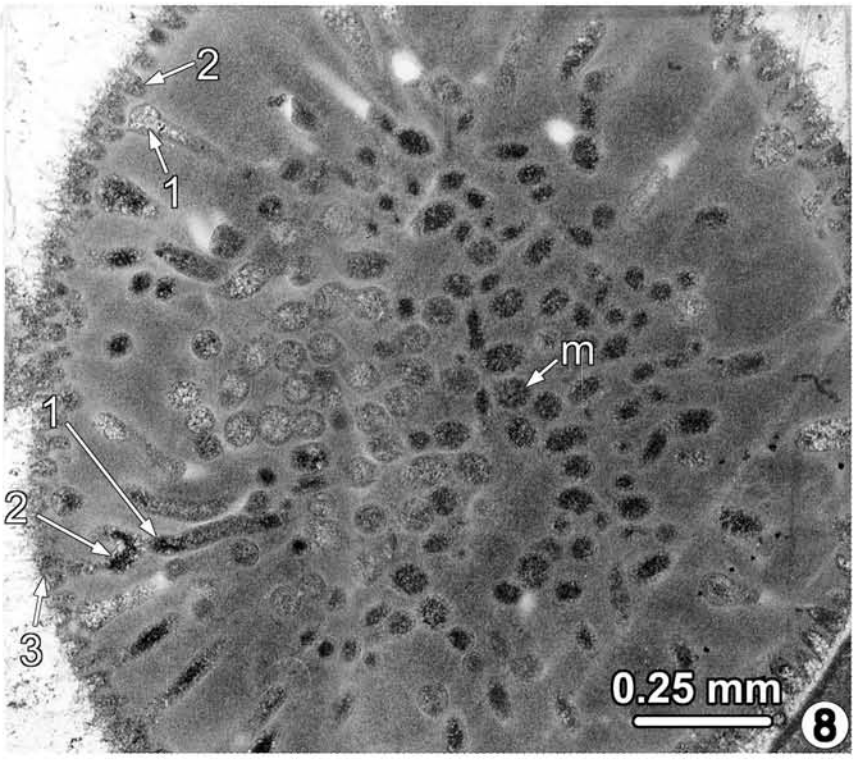
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Plate 4. ▶

Figs. 1–3. *Halimeda tuna*. **Fig. 1.** Vertical oblique section. Fig. 2. Transverse sections of a disk-like segment crossed by large medullary siphons (m) and the cortex with 2 or 3 utricle layers. Primary utricles are robust, conical, more inflated distally, secondary utricles are short, dichotomously branched and tertiary utricles appear short and very small in diameter. **Fig. 3.** Transverse section of a disk-like segment showing only 4 "rows" of axial-medullary siphons (m) and the cortex with 3 utricle layers (1, 2, 3). **Figs. 4–5.** *Halimeda tuna* f. *platydisca*. Oblique longitudinal sections of a disk-like segment with only 2 "rows" of large medullary siphons (m). In **Fig. 5,** the lower-right side of the thallus-segment is enlarged (Fig. 4 arrow) showing large medullary siphons (m) and strongly calcified primary (1), secondary (2) and tertiary (3) utricles. **Fig. 6.** Rhodolith (red algal nodule) formed as a large bryozoan core surrounded by the crustose coralline alga *Lithoporella melobesioides*. **Fig. 7.** Rhodolith formed around a bryozoan core covered initially by a layer of thin *Lithoporella melobesioides* and finally by a thick layer of *Lithophyllum prelichenoides*. **Fig. 8.** Pelimcrosparite containing many planktonic foraminiferans (e.g., *Globigerina*, *Orbulina*) and a segment of *Halimeda incrassata*. Late Miocene, Sample USNH loc No. 35998, Palau Limestone.

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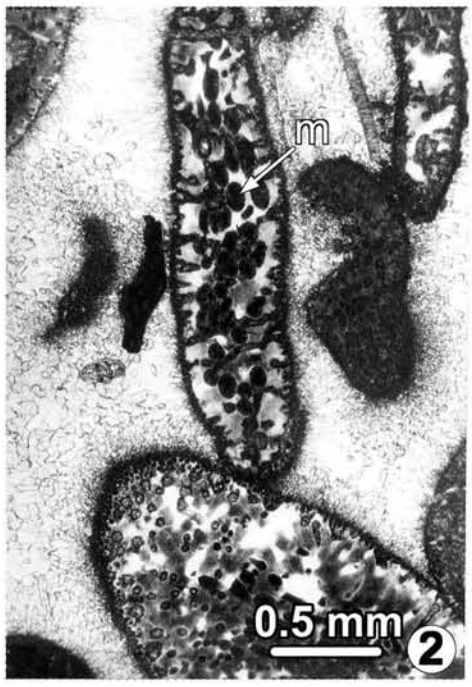
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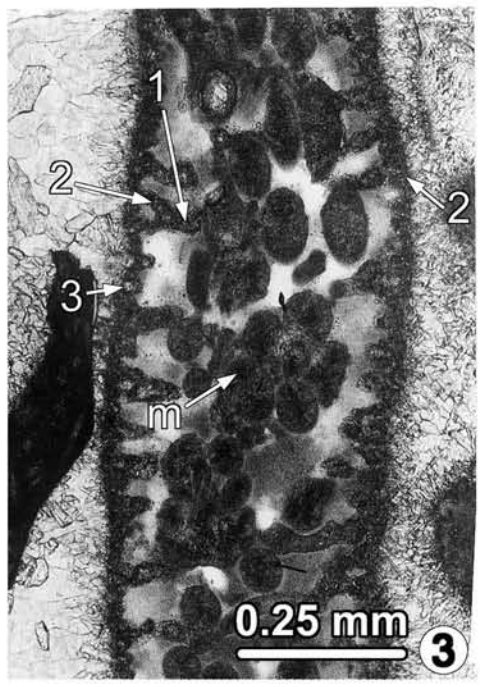
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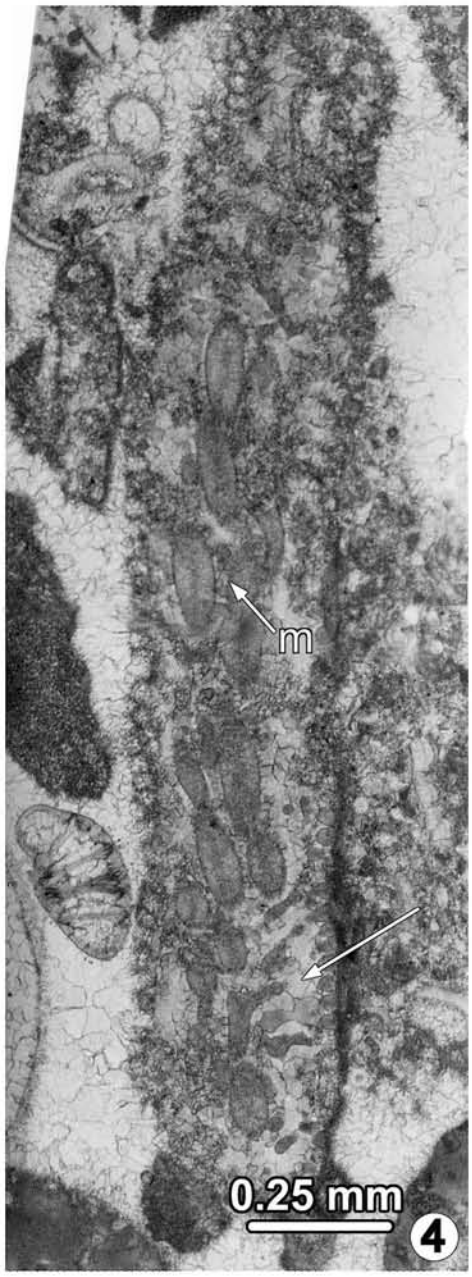
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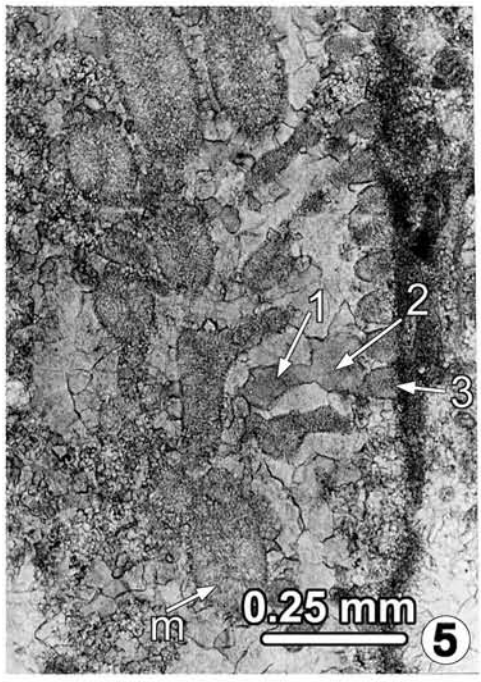
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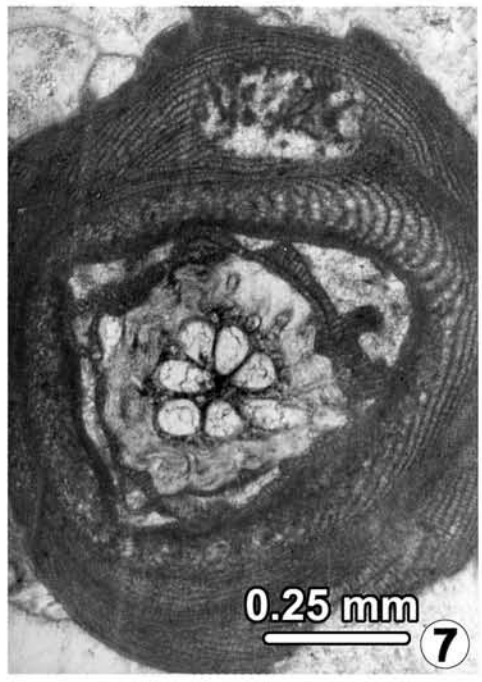
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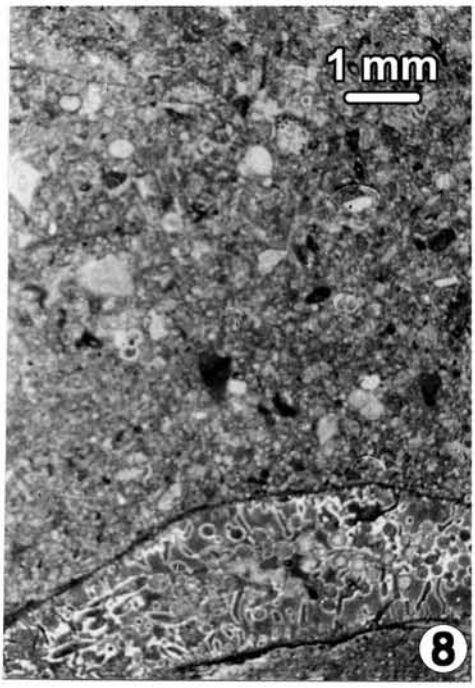
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Plate 5. ▶

Figs. 1–9. *Halimeda fragilis.* **Figs. 1, 4.** Transverse sections of subcuneate blade segments with auriculate upper margins; the segments are crossed by medullary siphons in which the auriculae form a compact structure (m), sometimes filled by coarsely crystalline aragonite (see Fig. 4) and the cortex consisting of three or four utricle layers. **Figs. 2, 3, 5, 8.** Axial longitudinal sections of segments with truncate margins showing the distribution of the medullary siphons (m) and the cortex system. In **Figs. 3, 6, 7** some parts of the thallus segments have been enlarged to show the primary long, cylindrical, slightly inflated, distal utricles (1), secondary, cylindrical, dichotomously branched utricles (2), tertiary, short, subcylindrical utricles (3) and quaternary, tiny, fine utricles (clearly shown in Fig. 6). **Fig. 9.** Transverse section of an auriculate margin, or lobe area, showing the disposition of the medullary siphons (m) and the cortex system with four utricle layers. Pliocene, Sample USNH loc No. 36152, Palau Limestone.

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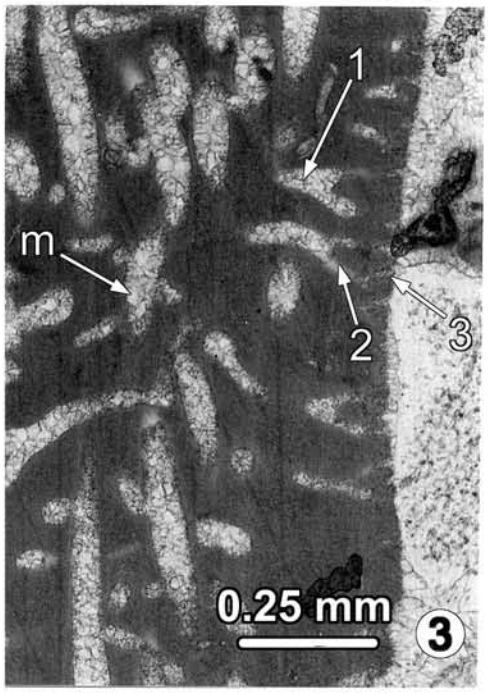
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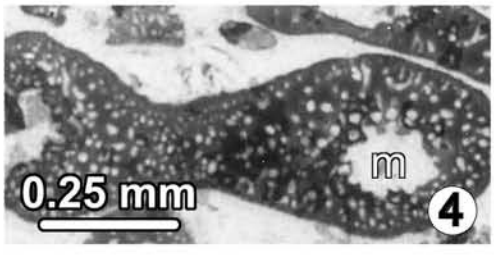
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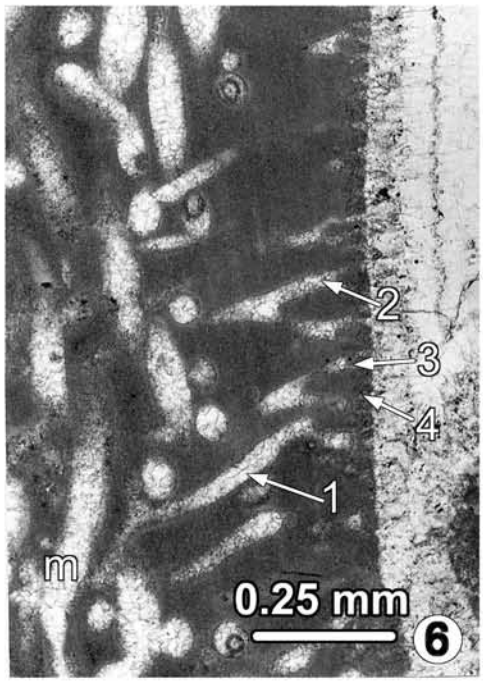
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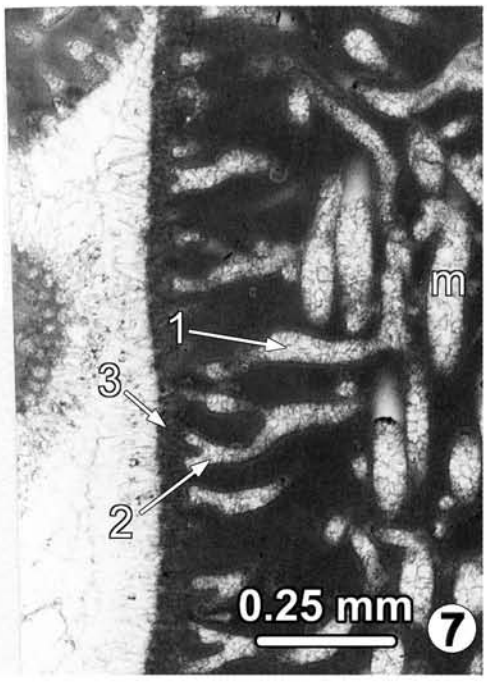
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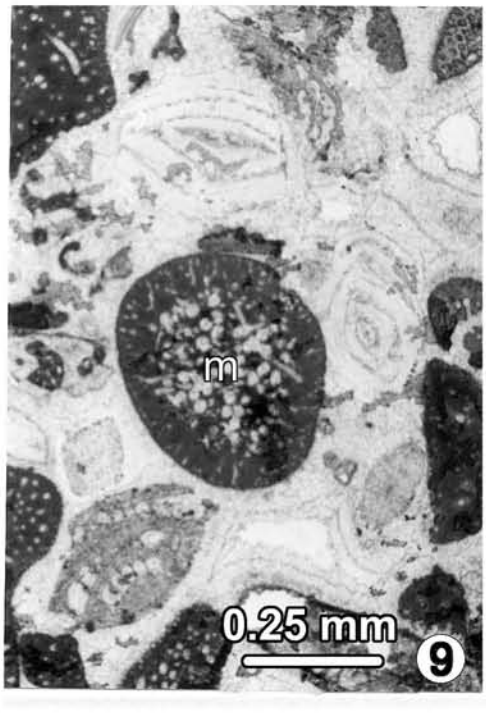
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Plate 6. ▶

Figs. 1–10. *Halimeda bikinensis*. **Figs. 1, 2, 7.** Transverse sections in the central region of discoidal-subcuneate segments having slightly undulating and infolded outer margins (see Fig. 7). **Fig. 2** shows an enlarged area from Fig. 1 of medullary siphons with large diameters (m) and cortex with 4 utricle layers; i.e., primary-1, secondary-2, tertiary–3 and quaternary–4 utricles. **Figs. 3–6**. Superficial transverse sections of a discoidal–subcuneate segment showing large medullary area with round siphons showing a small cavity filled with coarsely crystalline aragonite (m) and thinner cortex with only three utricle layers. **Figs. 8–10.** Transverse section of the lateral basal region of segment with more developed medullary area (m) and a thin cortex (see Fig. 10 enlarged) with primary (1), dichotomously branched secondary (2) and tiny tertiary (3) utricles. Pliocene, Sample USNH loc No. 36152, Palau Limestone.

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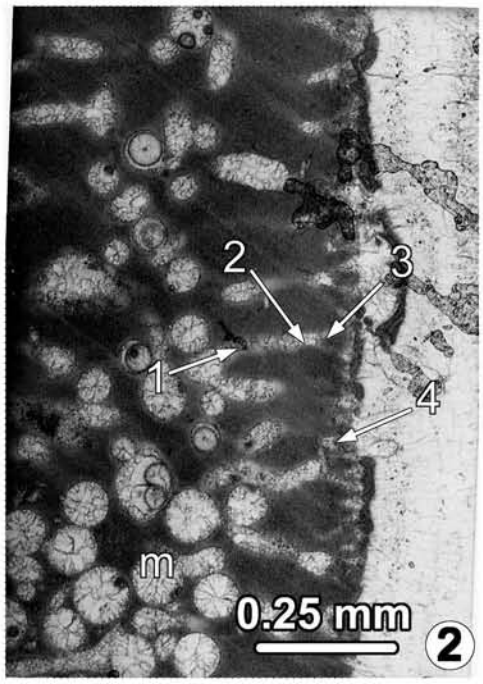
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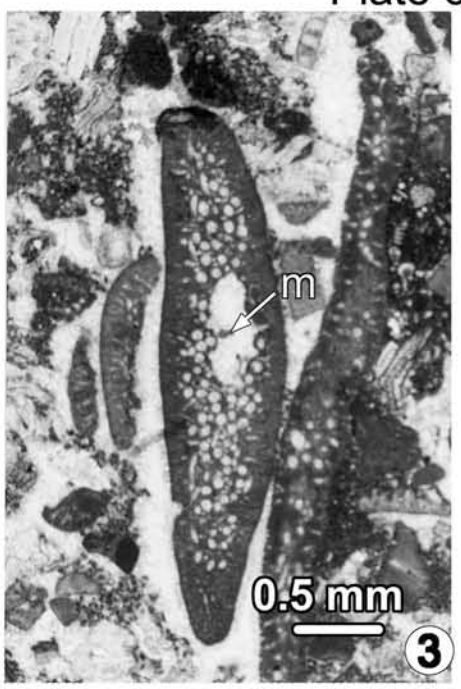
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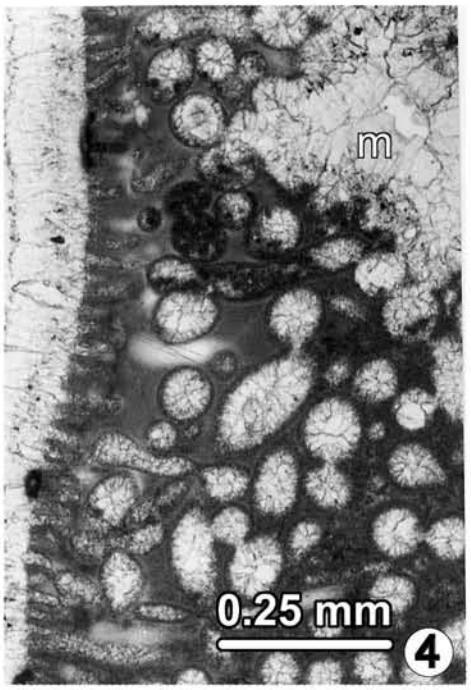
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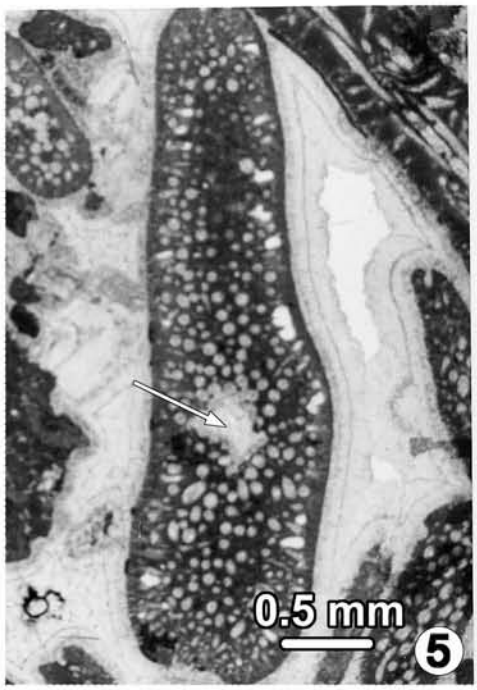
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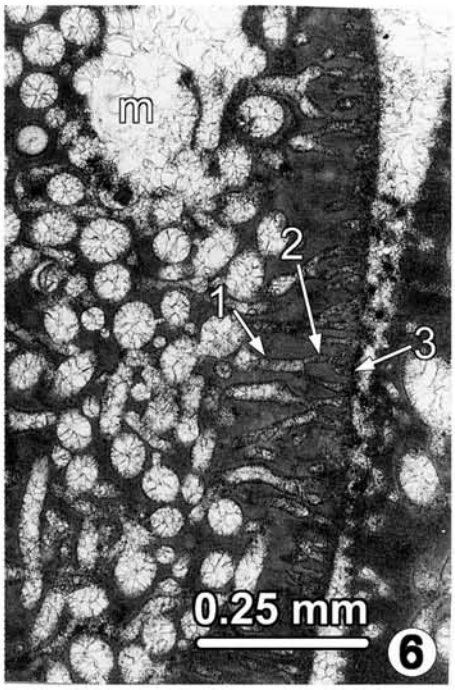
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3
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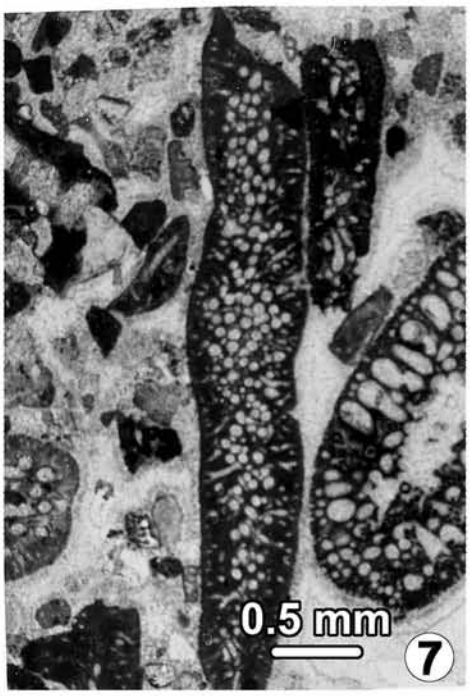
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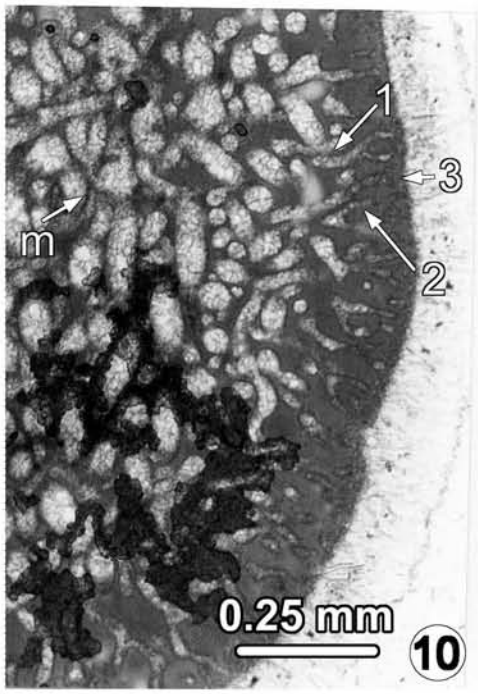
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3
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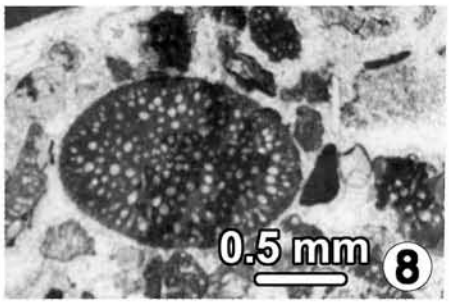
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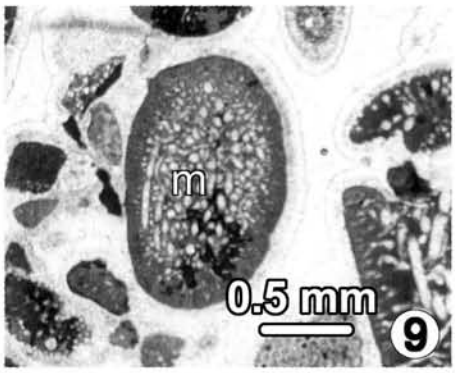
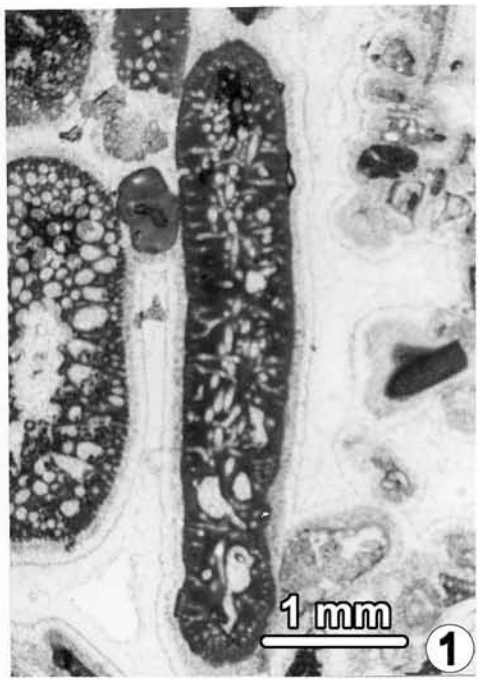

m
0.5 mm
9

Plate 7.

Figs. 1–5. *Halimeda bikinensis.* Transverse sections at different segment levels. In **Figs. 2 and 5**, the thallus segments are enlarged to show the disposition of medullary siphons (m) and the cortex with three utricle layers; i.e., primary (1), secondary (2) and tertiary (3) utricles. **Figs. 6–8.** *Halimeda simulans.* **Fig. 6.** Oblique axial longitudinal section in subcuneate or reniform segment with large medullary area (m) and moderately thick cortex. **Fig. 7.** Lower right side of enlarged segment (Fig. 6 arrows) showing the robust, conical, primary utricles (1) giving rise to short, bulbous, conical, secondary utricles (2) and short, tiny, subcylindrical tertiary (3) utricles. **Fig. 8.** Lower left side of enlarged segment showing portions of medullary (m) and cortex areas with primary (1), secondary (2) and tertiary (3) utricles. **Figs. 9, 10.** *Halimeda* cf. *bikinensis.* **Fig. 9.** Lateral oblique longitudinal section of a disk-like segment with undulating outer margin crossed by a moderately developed medullary area (m) and thin cortex. **10.** Left side of the segment further enlarged (see arrow at Fig. 9) showing the connection between medullary siphons (m) and cortex with primary long, subcylindrical, claviform (distally) utricles (1) and secondary utricles (2). Pliocene, Sample USNH loc No. 36152, Palau Limestone.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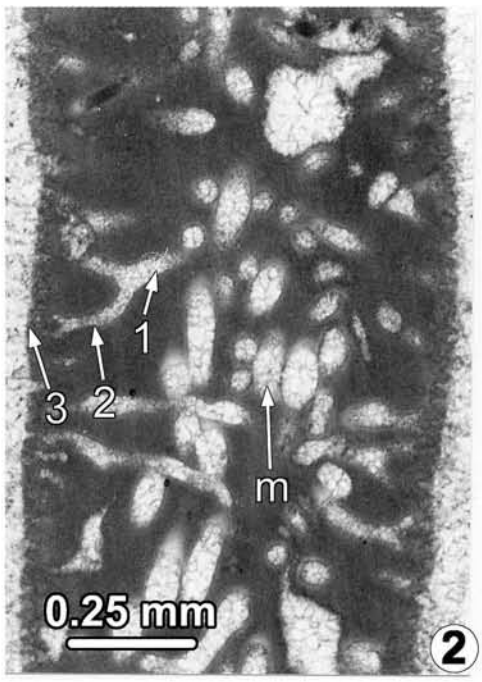
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2
m
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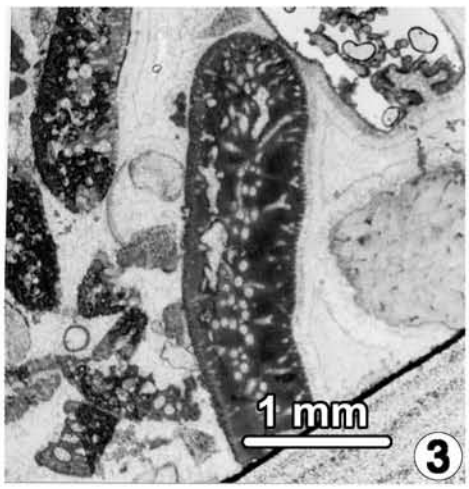
2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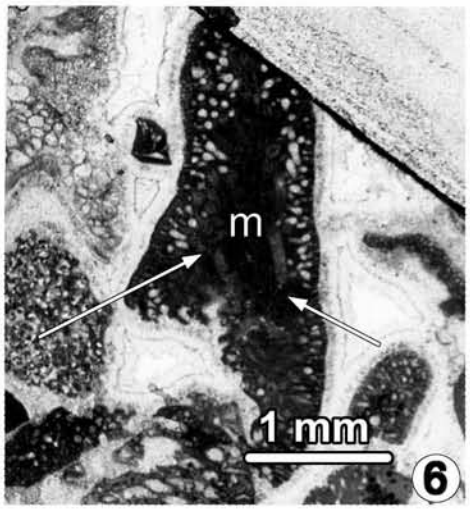
m
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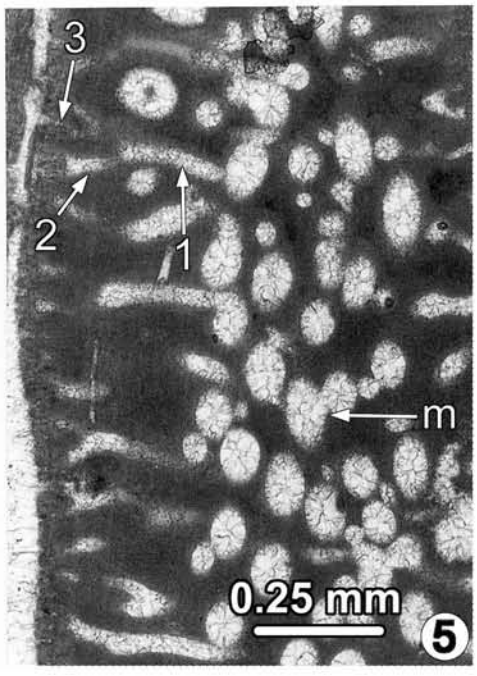
6


3
2
1
m
0.25 mm
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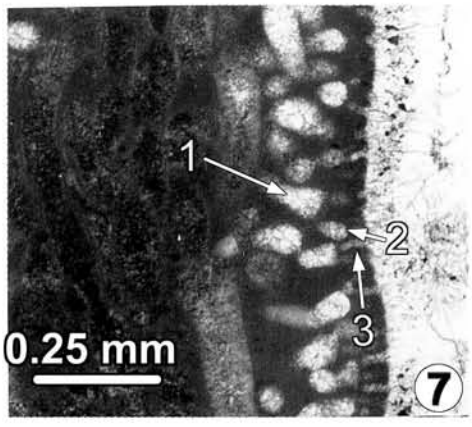
1 mm
4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2
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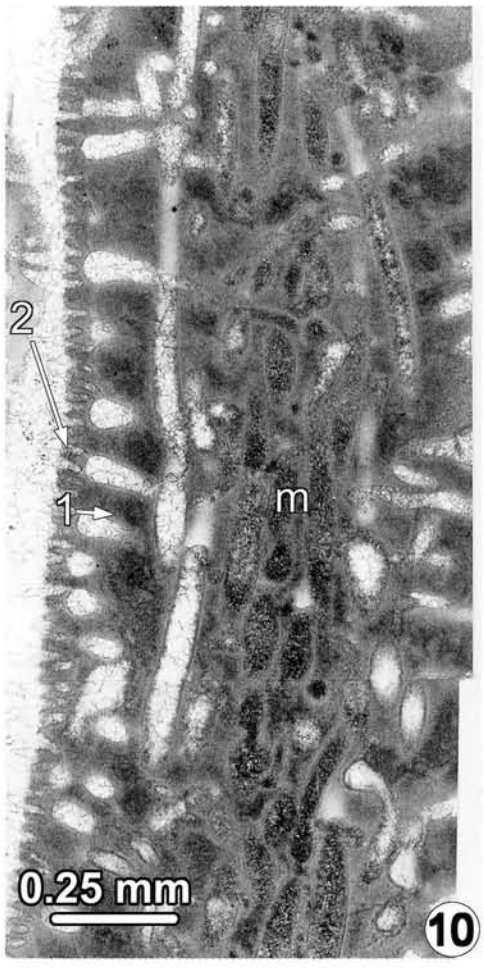
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m
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10

m
1 mm
9

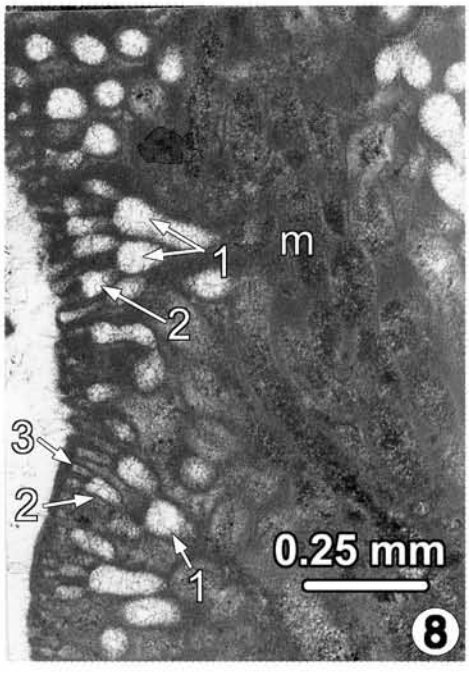
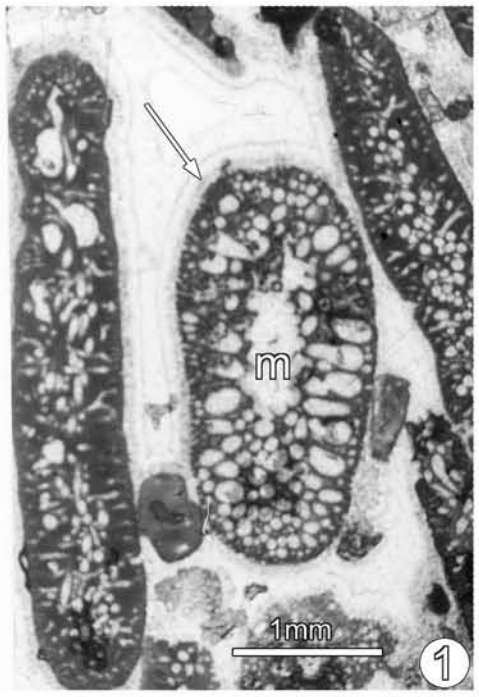

1
m
2
3
2
1
0.25 mm
8

Plate 8. ▶

Figs. 1–9. *Halimeda discoidea.* **Figs. 1–3, 6.** Oblique longitudinal and longitudinal sections in broken thalli and a cylindrical segment crossed by a medullary cavity (m) infilled with coarsely crystalline aragonite with a strongly calcified cortex consisting of primary large subconical utricles (1) contiguous with bulbous, short, conical secondary utricles (2) and short, tertiary, distally opened utricles (3). **Fig. 4.** Transverse section of a compressed subcuneate segment having a large medullary area (m) and thick cortex with rounded primary utricles (1) that are larger in diameter than secondary medullary utricles, which are also round in shape (2), and very small tertiary utricles (3). **Fig. 2.** Upper left side enlarged (see arrow Fig. 1) showing the structure of the cortex system. **Figs. 3, 6.** Longitudinal section of a broken thallus segment, with Fig. 6 showing part of the cortex much enlarged to reveal the three utricle layers. **Figs. 5, 7–9.** *Halimeda discoidea.* **Figs. 5, 7.** Oblique longitudinal and transverse sections at different levels of a disk-like, segment showing a very narrow medullary area (m) and a strong cortex with two utricle layers. **Fig. 8.** Transverse section of a subcylindical segment showing the medulla (m) and strong cortex crossed with primary (1) and secondary utricles (2). **Fig. 9.** Longitudinal section of a broken thallus segment showing only two utricle layers in the cortex; the primary utricles are large s(1) and secondary utricles small and subconical (2). Pliocene, Sample USNH loc No. 36152, Palau Limestone.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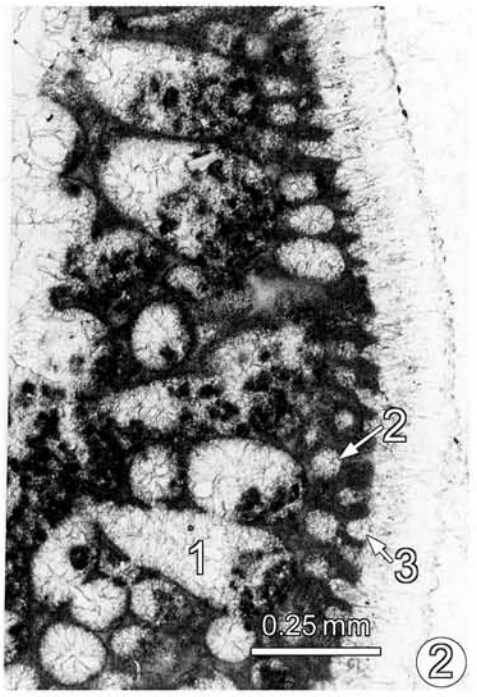
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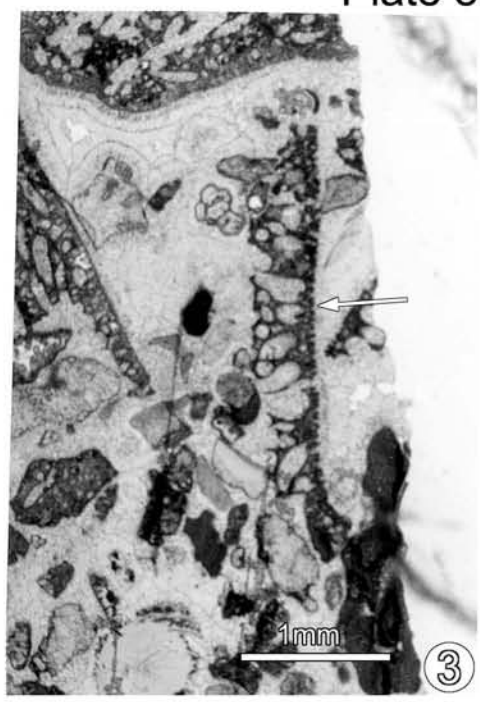
1mm
3

m
2
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c
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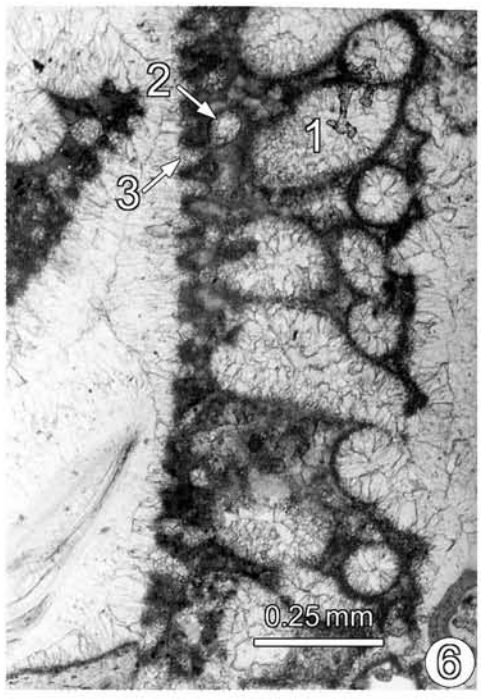
4

m
1mm
5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3
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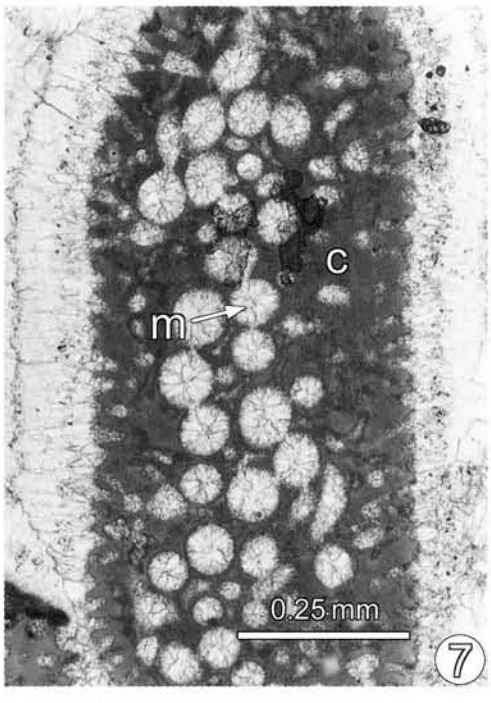
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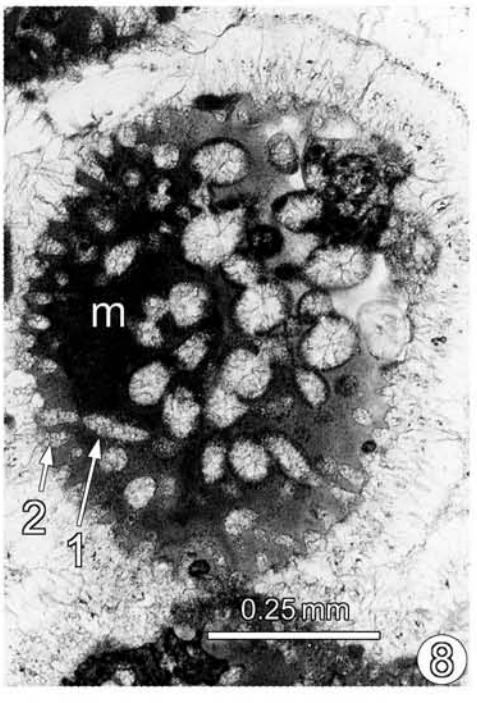
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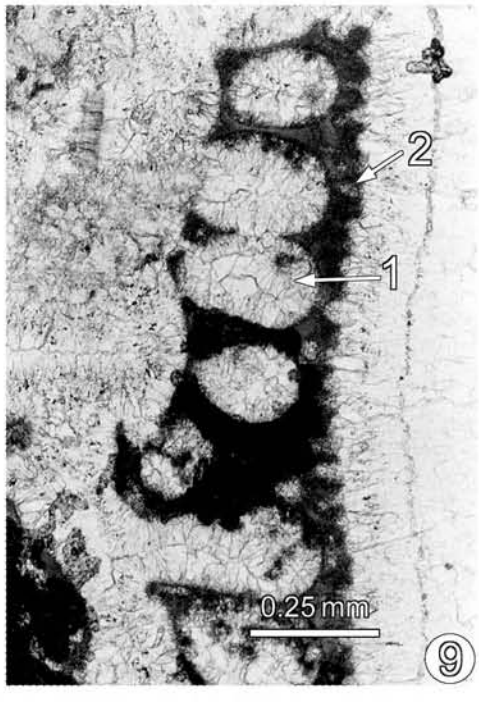
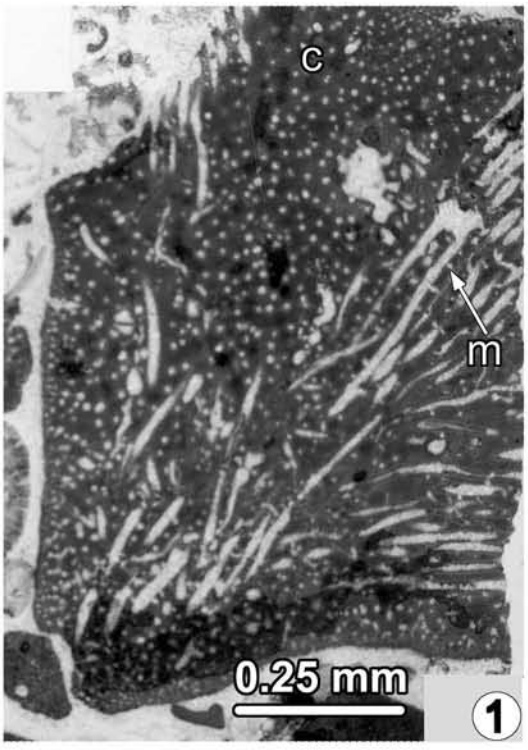

2
1
0.25 mm
9

Plate 9.

Figs. 1, 2. *Halimeda opuntia.* **Fig. 1.** Oblique longitudinal section of a contorted, ear-shaped segment with long, lax, medullary siphons (m) and thick cortex (c). **Fig. 2.** Oblique transverse section of an ear-shaped segment illustrating the long cylindrical primary utricles (1), secondary, cylindrical, dichotomously branched utricles (2), short, tertiary (3) and tiny quaternary utricles (4). **Figs. 3, 4.** *Halimeda simulans.* Oblique transverse section in the terminal part of a segment; the medullary area is mostly infilled with coarsely crystalline aragonite (m) and the cortex consists of primary (1), secondary (2) and tertiary (3) utricles. **Fig. 5.** *Lithophyllum* cf. *racemus.* Axial longitudinal section of a branched thallus showing a large coaxial hypothallus (h) and a thin perithallus (p). **Fig. 6.** Biosparite with different bioclasts, *Discogypsina vesicularis* (d), *Heterostegina depressa* (h) and *Pseudotriloculina lecalvezae* (p). **Figs. 7–8.** Different sections in *Amphistegina lessonii.* **Fig. 9.** *Borelis melo* (b) and fragment of *Sorites orbiculus* (s). Pliocene, Sample USNH loc No. 36152, Palau Limestone.

Plate 9


c
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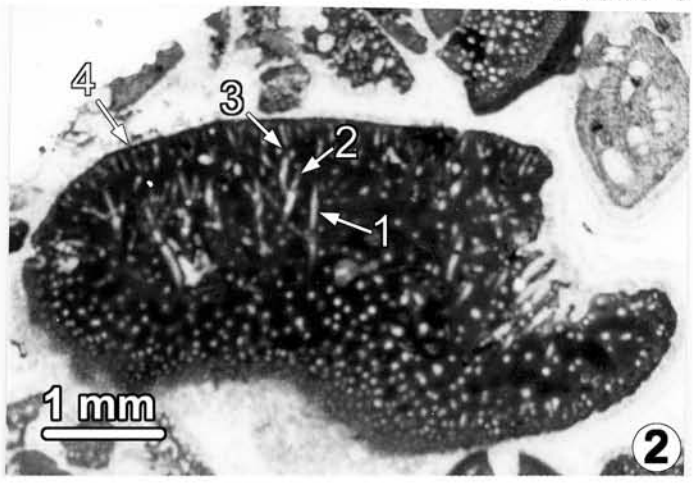
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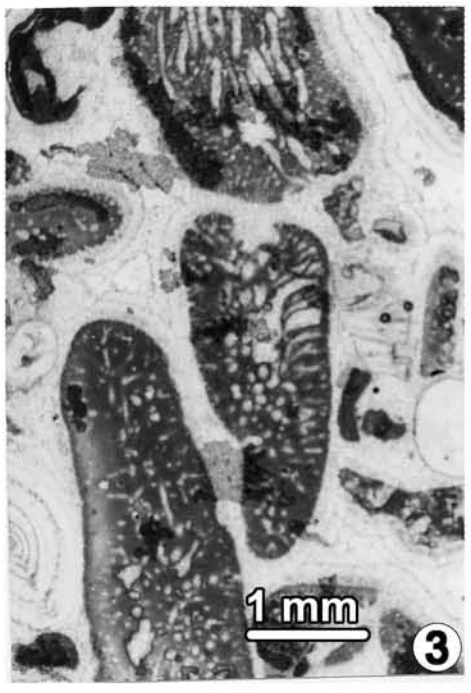
2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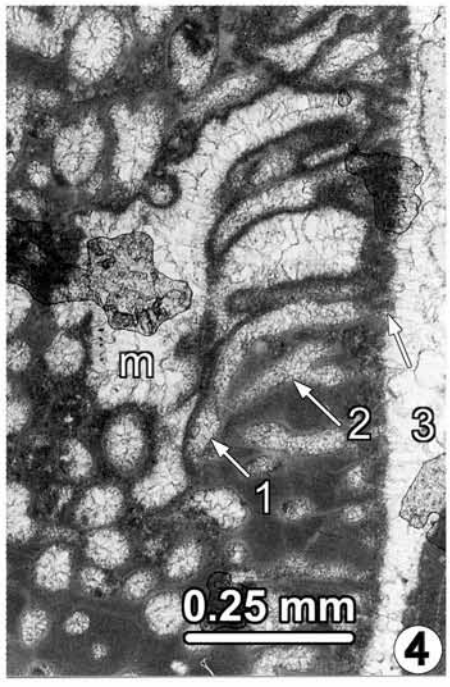
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1
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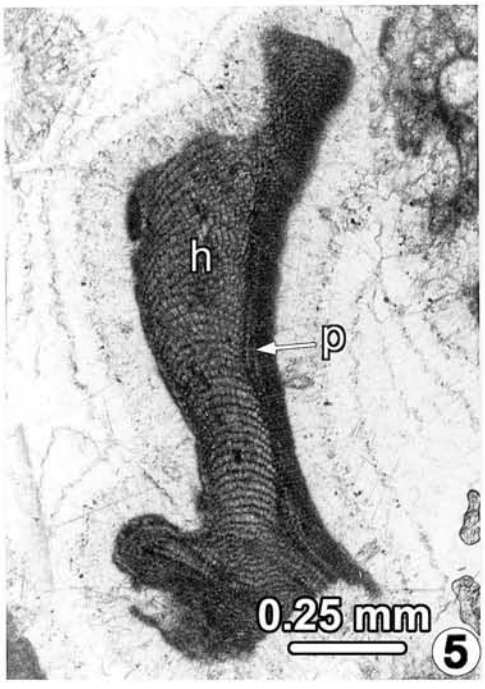
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p
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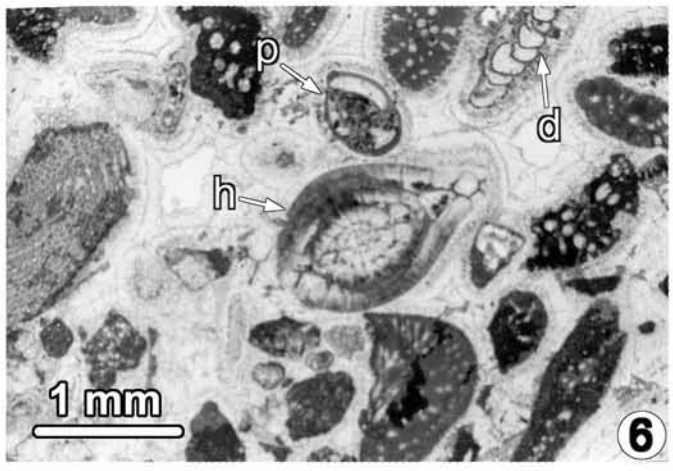
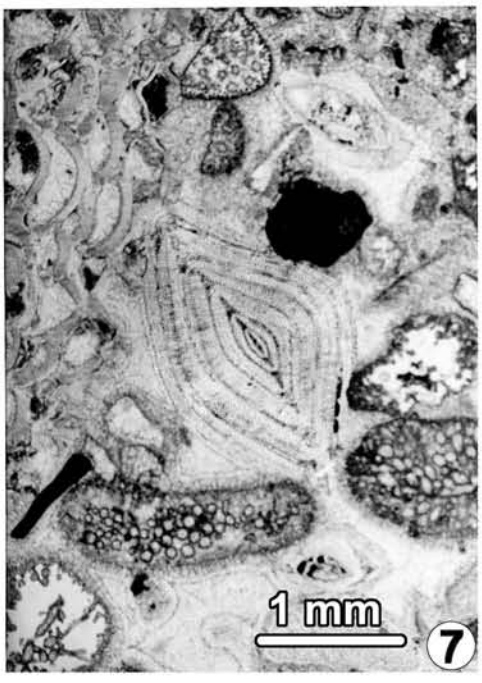
5


p
d
h
1 mm
6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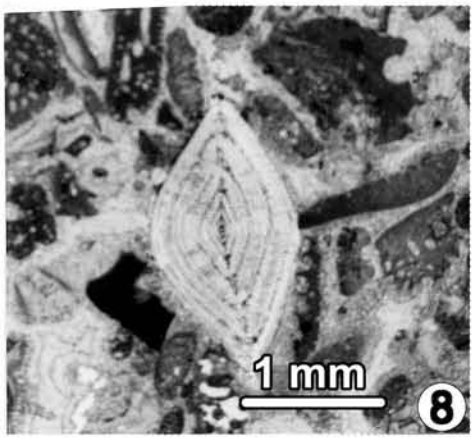
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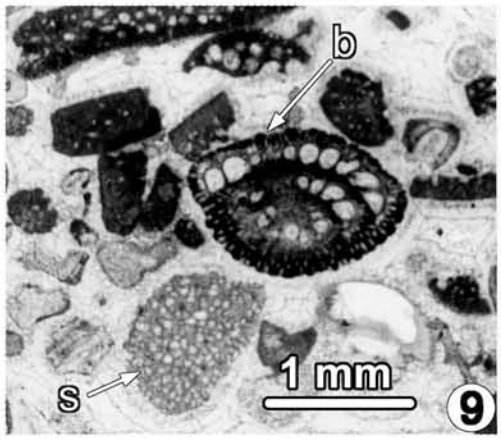
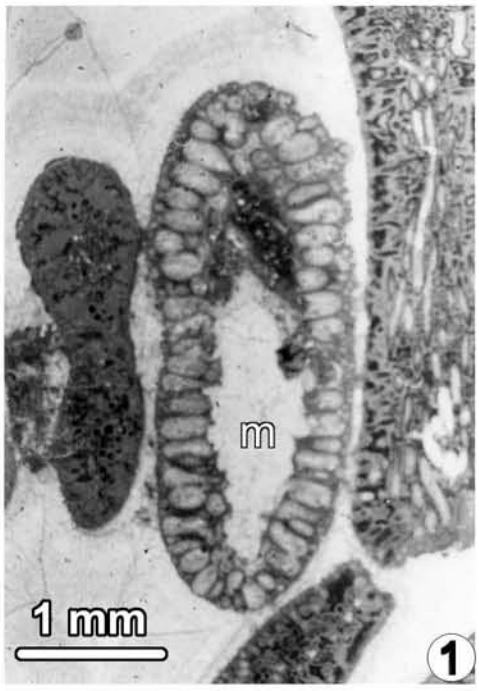
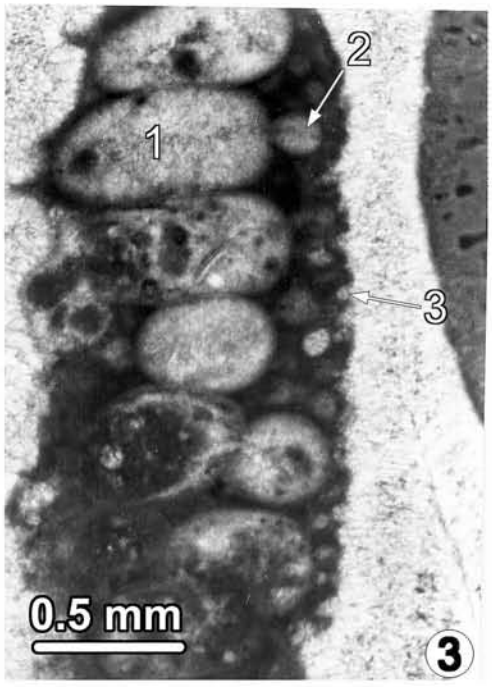

b
s
1 mm
9

Plate 10.

Figs. 1–3. *Halimeda discoidea.* **Figs. 1, 2.** Longitudinal oblique sections of a cylindrical segment crossed by medullary cavity infilled with coarsely crystalline aragonite (m) and strongly calcified cortex. **Fig. 3.** Detail in the cortex of thallus segment from Fig. 2 showing large primary utricles (1) giving rise to short, bulbous, secondary utricles (2) and very small tertiary utricles (3). **Figs. 4–5.** *Halimeda discoidea.* Oblique longitudinal section of a disk-like segment crossed by a narrow medullary area (m) and a strongly calcified cortex (c). **Fig. 5.** Detail of medullary area (m) and cortex having only two utricle layers (primary and secondary). **Figs. 6–9.** *Halimeda opuntia* f. *triloba.* Different longitudinal sections of flat contorted segments with three lobes, sometimes broken, crossed by large medullary areas (m) and multiple cortical utricle layers (c). Pleistocene, Sample USNH loc No. 36146, Palau Limestone.


m
1 mm
1

m
1 mm
2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3
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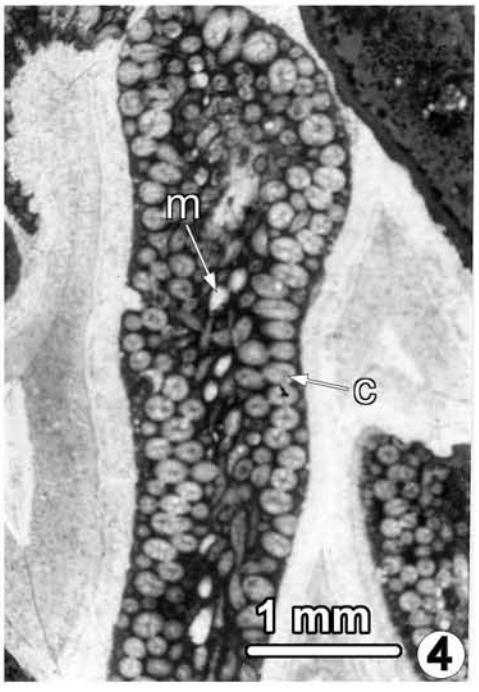
3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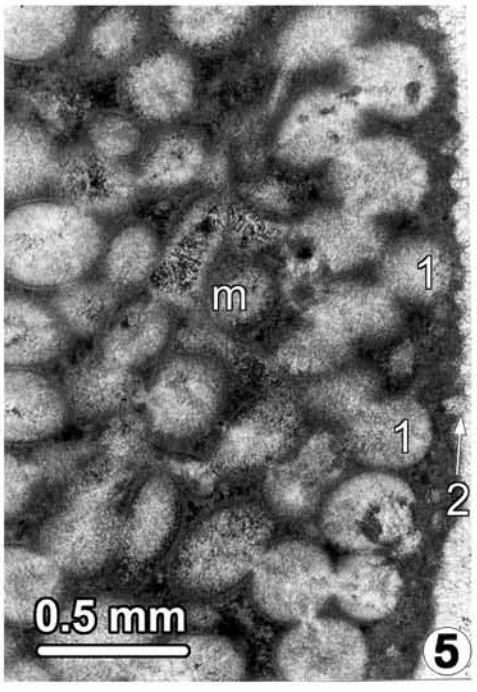
m
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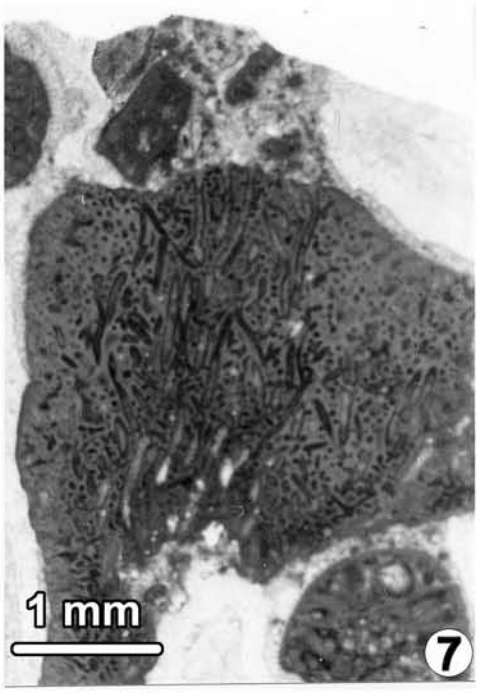
1
2
0.5 mm
5

m
1 mm
6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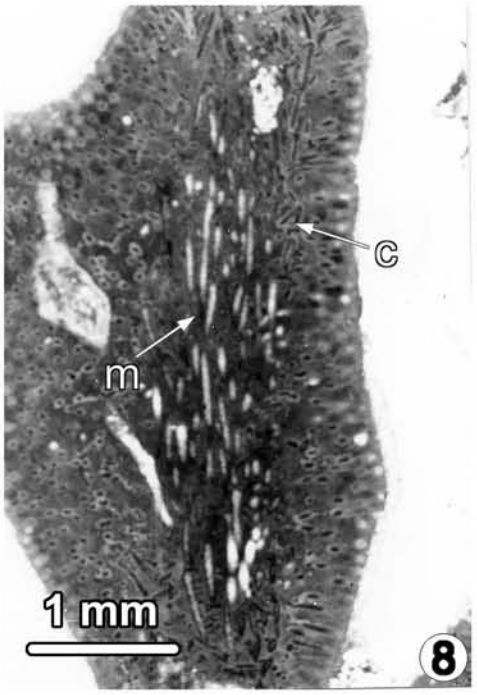

c
m
1 mm
8

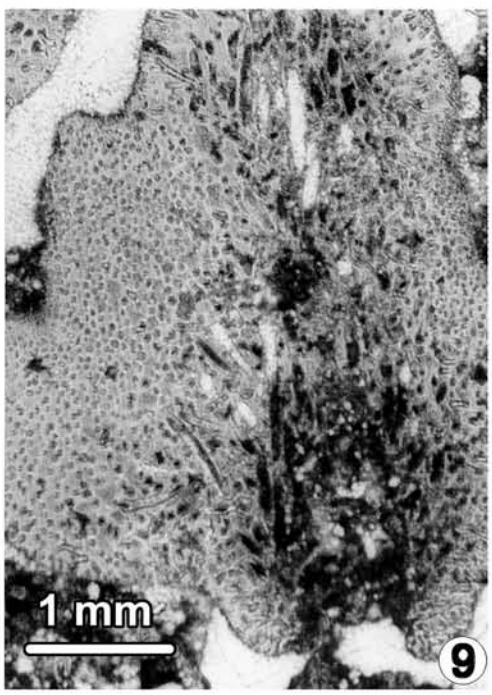
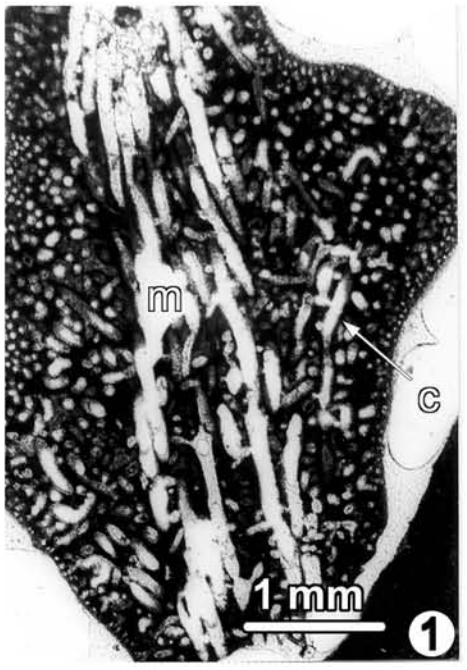
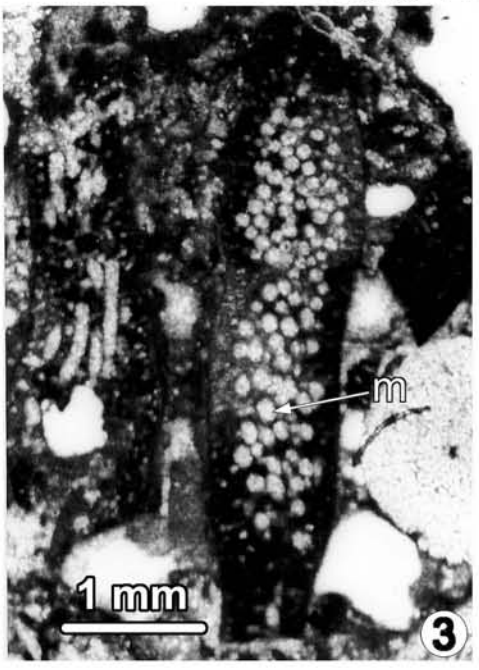

1 mm
9

Plate 11. ▶

Figs. 1, 4. *Halimeda opuntia* f. *triloba.* **Fig. 1.** Axial-longitudinal section of a flat tri-lobed segment crossed by medullary siphons (m) and thick cortex (c) having four utricle layers. Pleistocene, Eniwetok, Hole E 1, 10 m deep. **Fig. 4.** Tangential transverse section of a broken thallus segment with inconspicous medullary siphons (m) and thick cortex (c). Pleistocene, Bikini, Hole B 4, 21 m deep. **Figs. 2, 3, 5.** *Halimeda bikinensis.* **Figs. 2, 3.** Oblique longitudinal and transverse sections in different segments with large medullary areas (m) and relatively thin cortex. **Fig. 5.** Transverse section showing the large medullary area (m) and cortex (c). Pleistocene, Eniwetok, 40 Hole E 1, 27, 20–30, 6 m deep. **Figs. 7, 8.** *Halimeda tuna.* Axial and oblique longitudinal sections in disk-like segments crossed by medullary siphons (m) and by cortical utricles (c). Pleistocene, Bikini, Hole 1340, 26 m deep. **Figs. 6, 9.** *Halimeda micronesica.* **Fig. 6.** Oblique longitudinal section with large medullary area (m) and cortex with four utricle layers (1, 2, 3, 4, see upper left thallus). **Fig. 9.** Oblique transverse section in thallus segment crossed by a large, medullary cavity (m) and multiple utricle layers (1, 2, 3, 4 see lower right side of section). Pleistocene, Kita-Daito-Jima, Hole 2138, l0 m deep.


m
c
1 mm
1

m
1 mm
2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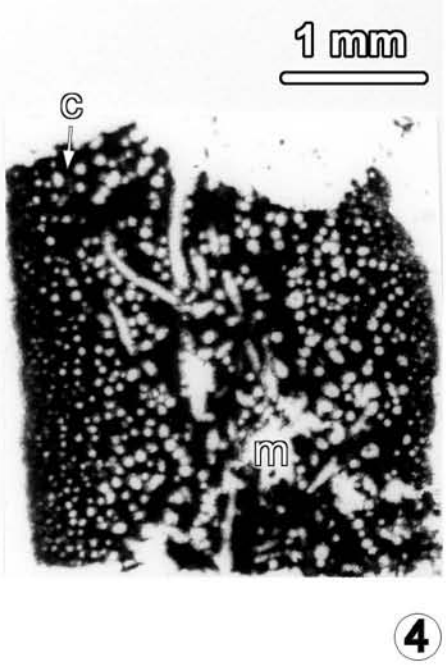
1 mm
3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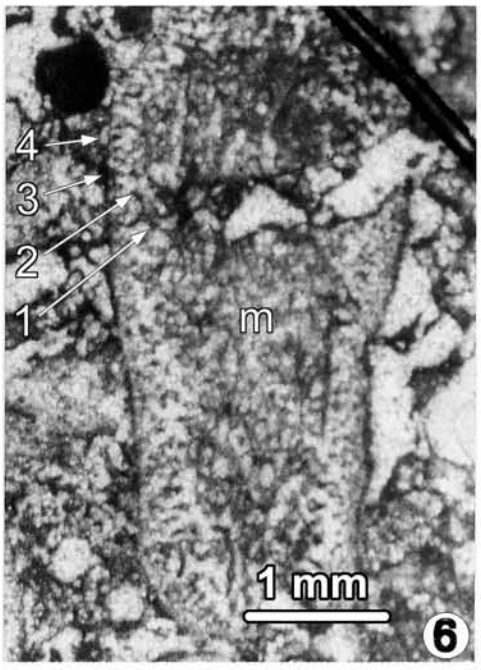
c
m
4

c
m
1 mm
5


4
3
2
1
m
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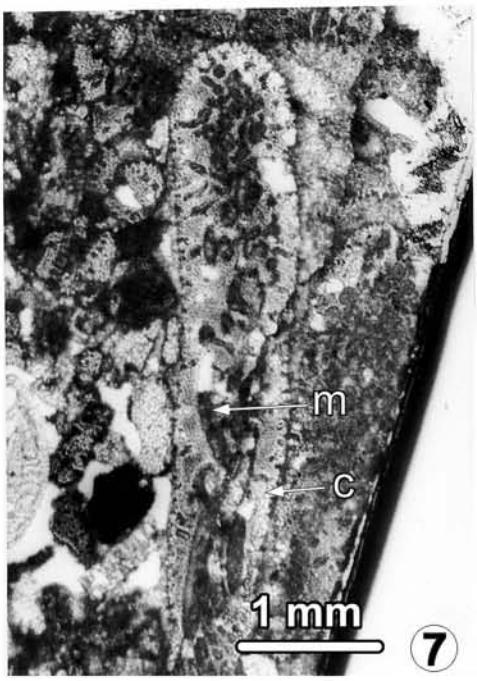
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c
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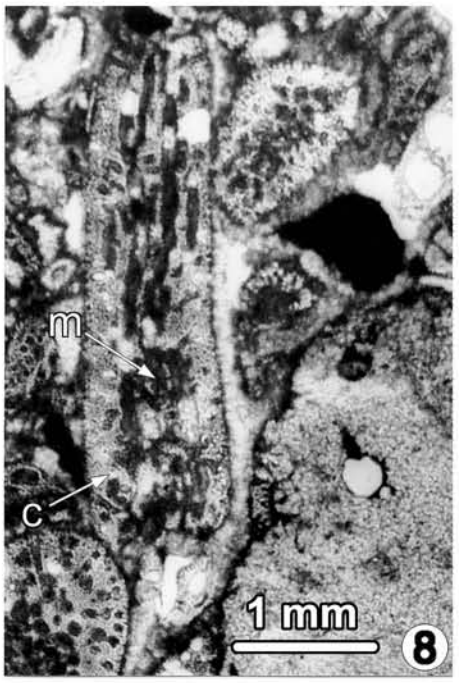

m
c
1 mm
8

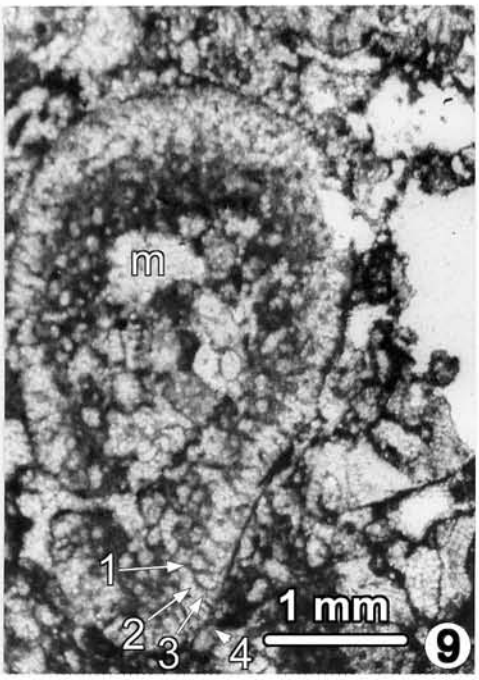
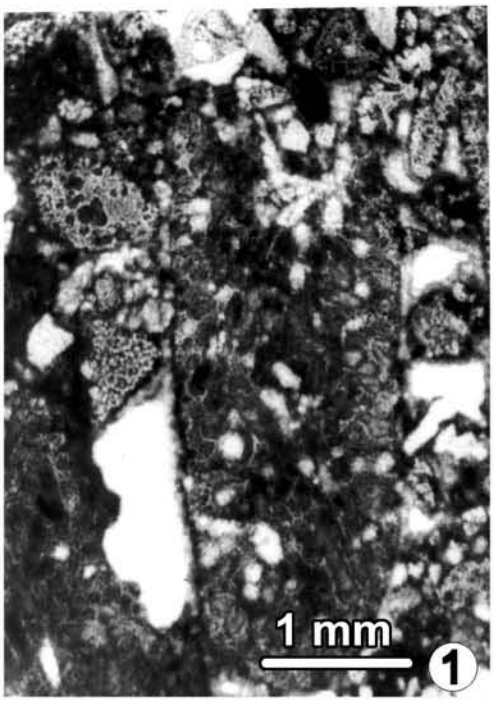

m
1
2
3
4
1 mm
9

Plate 12. ▶

Figs. 1–6. *Halimeda tuna.* Differently oriented sections of flat discoid segments cut at various levels of the thallus presenting large or moderate medullary cavities (m), sometimes with small areas infilled with coarsely crystalline aragonite (ca) and with a cortex of 2 or 3 utricle layers. Pleistocene, Bikini Hole B 2, 26 m deep. **Fig. 7.** *Halimeda opuntia* f. *opuntia.* Segment strongly calcified, flat to contorted and ribbed. Recent, sand beach near La Habana, Cuba. **Fig. 8.** *Halimeda opuntia* f. *triloba.* Segment flat and trilobed. Recent, sand beach near La Habana, Cuba, USNH No. 2023530.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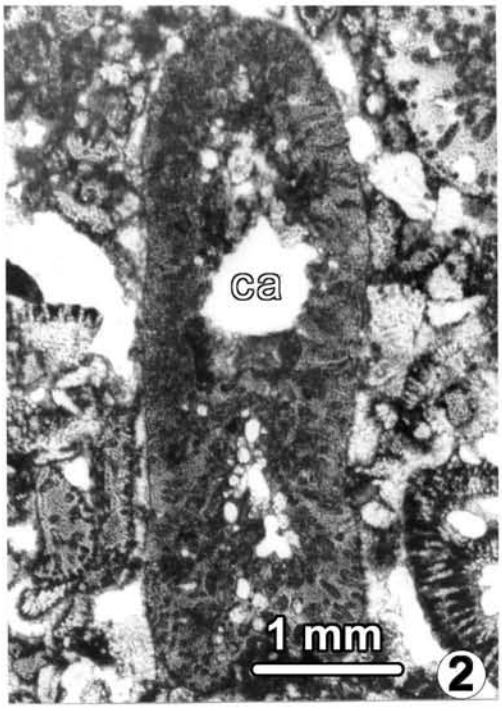
1


ca
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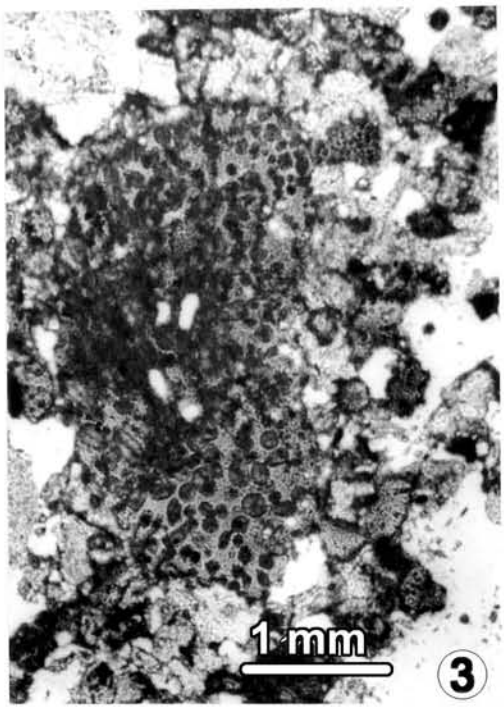
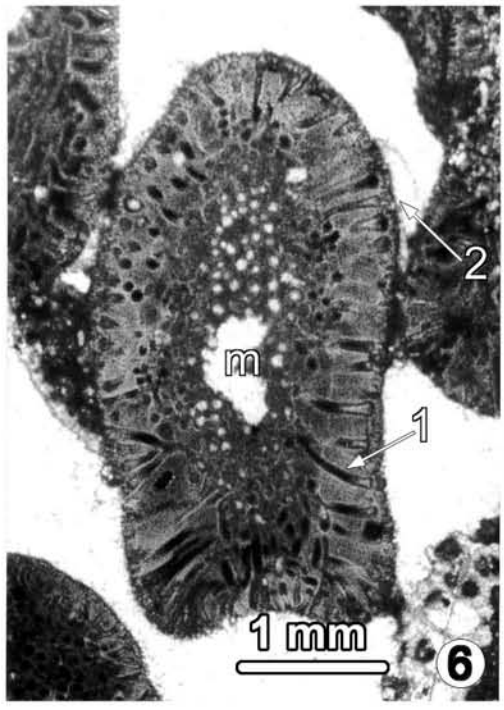
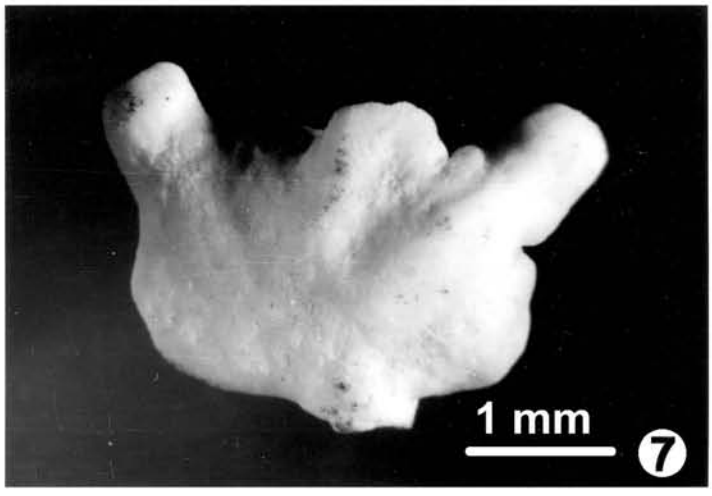
2


1 mm
3

1
2
1 mm
4

1 mm
5


2
m
1
1 mm
6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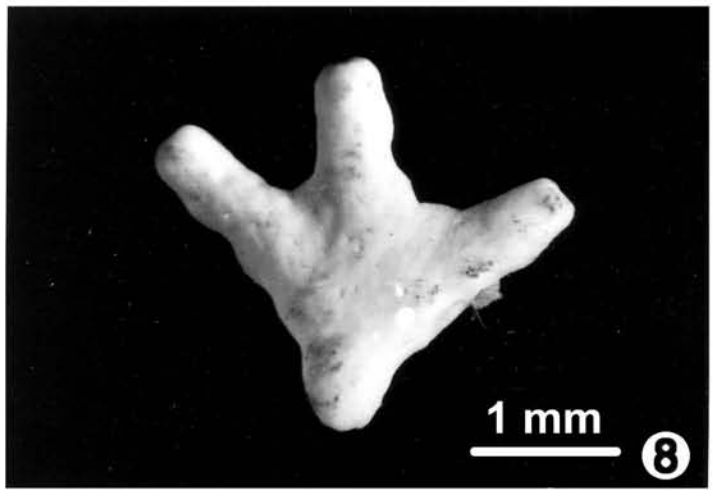
1 mm
8