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Fungiacava eilatensis burrows in fossil *Fungia* (Pleistocene) from the Sinai Peninsula

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[Plates 36–39]

The striking morphological resemblance of the burrows, found in both Recent and Pleistocene fungiid corals, establish a possible link between the living *Fungiacava eilatensis* (Soot Ryen) (Bivalvia, Mytilidae) and their hereto unknown fossil ancestry.

Introduction

Fungiacava eilatensis (Soot-Ryen) (Bivalvia, Mytilidae) was first found in 1963 near the site of the now Eilat Marine Station, Israel. It is a delicately shelled commensal mussel, living ventral side uppermost, in its own burrow near the columella of the skeleton of some Fungiid reef corals: *Fungia scutaria* (cf. figure 1, plate 36), *Fungia fungites*, *Cycloseris sinensis* and *Diaseris distorta*. The description, biology, distribution and mode of boring, have been given in earlier papers by Goreau, Goreau, Neumann & Yonge (1968); Goreau, Goreau, Soot-Ryen & Yonge (1969); Goreau, Goreau, Yonge & Neumann (1970); Goreau, Goreau & Yonge (1972); Yonge (1974).

Location of samples

In the summer of 1969, the senior author, examining the coral reefs along the coast of the Sinai Peninsula, in the Red Sea, collected coral specimens of the genus *Fungia* from the living Recent coral reef, and fossil samples from the uplifted coral reef facies. He was searching for a possible link between the living *Fungiacava* mytilid and their hereto unknown fossil ancestry. At Marsa Bareika, in the skeleton of a *Fungia scutaria*, found *in situ* in the fossil reef, he recognized an undoubted *Fungiacava*-like burrow, but the valves were missing. This site was approximately 1.5 m above modern sea level, in a section where numerous fossil Fungias were in the process of being weathered out by erosion. However,

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the corals and algae in this facies appeared not to have undergone diagenesis. The specimen's mineralogy was determined by X-ray crystallography and shown to be aragonite.

A collection of fossil fungiid corals was taken from the 'raised outcrop' at Marsa Bareika, a small embayment at the eastern side of the tip of Ras Muhammad. The exact location, as taken from the official Israel Survey Department 1:250000 map of the Sinai Peninsula is 27° 47.3′ N by 34° 14.5′ E. The two headlands, surrounding the small inlet on the north side of Marsa Bareika, are part of a fossil coral reef. The formation, from sea level to *ca.* 12 m to the terrace above, is a relatively undisturbed fore reef type deposit, with many of its large corals in a position of growth. Unlike the fossil corals seen at Ras a Tantur and Ras Nasrani, the corals in these outcrops appear to be aragonitic.

In preservation and general relation to modern sea level this formation resembles those at Braco (Falmouth) and Rio Bueno, Jamaica (Cant 1970; Land 1973), Barbados (Bender, Taylor & Matthews 1973), and New Guinea (Bloom *et al.* 1974) which have all been dated at 125000–130000 years.

Moshe Goldberg at the Israel Geological Survey has used uranium-thorium dating to establish the ages of various corals in the raised reefs which have not undergone substantial diagenesis, and found that the 13 m terrace at Marsa Umm Mureikha (27° 57.1′ N, 35° 23.3′ E) was roughly 150000 years old (M. Goldberg, private communication). The raised reef at Marsa Umm Mureikha is 23.75 km from Marsa Bareika, but the fact that in both places the higher terraces have all been recrystallized to calcite (Gvirtzman, Buchbinder, Nir & Friedman 1973) and the relationship of the terrace to sea level give confidence that these terraces are contemporaneous despite the complicated tectonic history of the area (J. Erez, private communication).

More recent observations of the Sinai 1969 collection at Marsa Bareika, besides the fossil *Fungia scutaria* mentioned, uncovered other specimens of the genus *Fungia* showing, in various stages of preservation, excavation burrows like those

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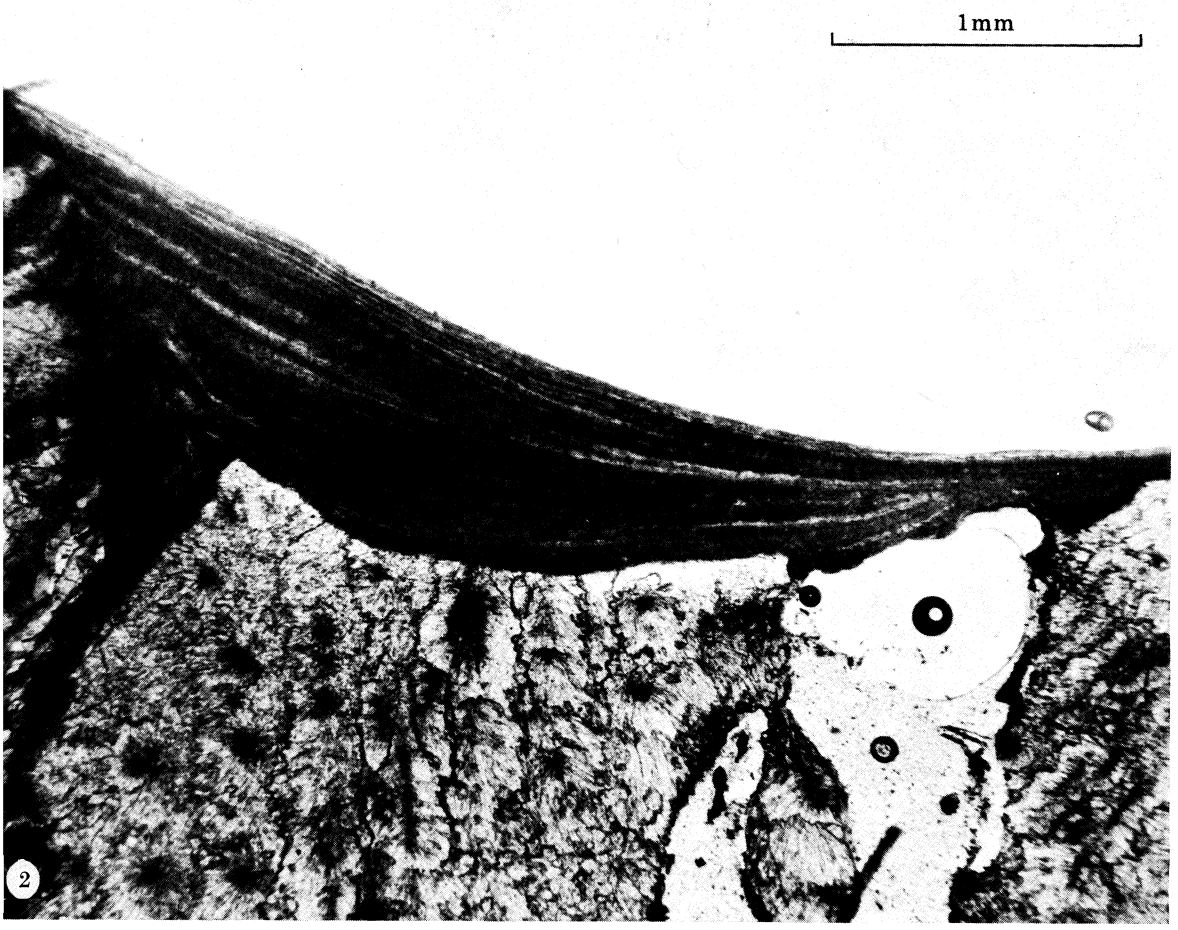
Description of plate 36

Figure 1. Broken edge of a recent *Fungia scutaria* showing two large burrows of *Fungiacava eilatensis*. One of the bivalves is still in place with its contracted siphon in the position it occupies in life, toward the columella of the coral. The wall of the cavity is lined with a smooth chalky white veneer of aragonite secreted by the bivalve, the texture of which contrasts with the more translucent coral skeleton. There is no distortion of the coral despite the large size of the bivalves which inhabit it. Note bumps in the exposed surface of the mytilid. (Magn. × 1.875.)

Figure 2. *Fungia scutaria*, thin section through the corallum showing calcereous infilling lining the roof of a burrow of *Fungiacava eilatensis*. Seen under crossed Nicols to show appearance in polarized light. The maximum thickness of the laminated deposit is 0.8 mm and it is clearly differentiated from the spherulitic structure of the *Fungia*'s corallum. The banded structure corresponds to growth lines due to change in position of the *Fungiacava* mussel within its burrow.



FIGURES 1 AND 2. For description see opposite.

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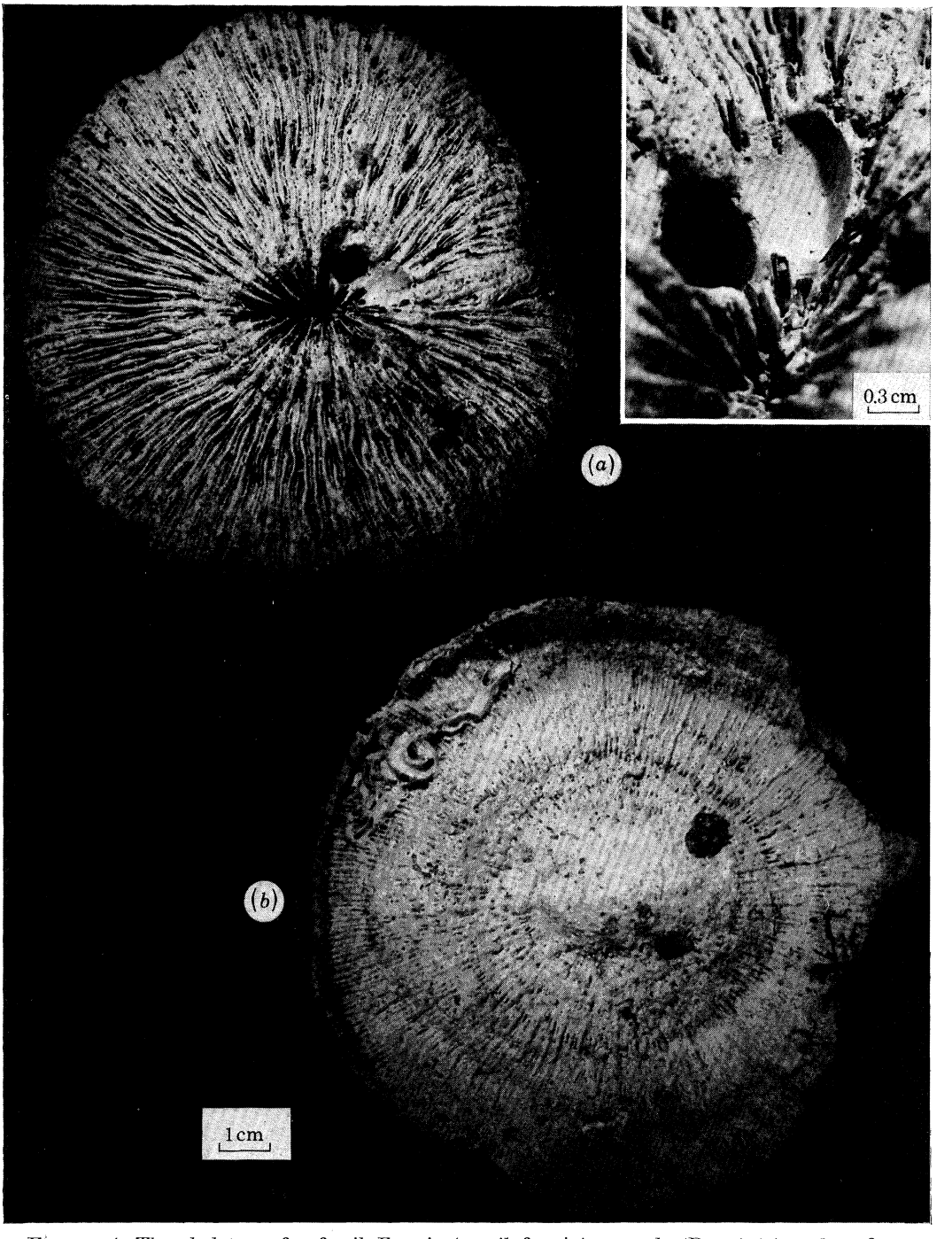


FIGURE 4. The skeleton of a fossil *Fungia* (verrilofungia) *repanda* (Dana) (*a*) oral surface at upper left, with enlarged enclosure at right, to show burrows made by Pleistocene ancestor of *Fungiacava*. From the black hole near the columella, we obtained Latex casts seen in figures 5*h* and *i*, plate 38. The smooth white lining near the black hole shows, at the point of the arrow, the typical canal trace of the mytilid siphonal position. The visible burrows are partially damaged by abrasion of the coral. (*b*) aboral surface of same specimen with a smooth, eroded hint of the anthocaulus basal scar and the perforations characteristic of the species.

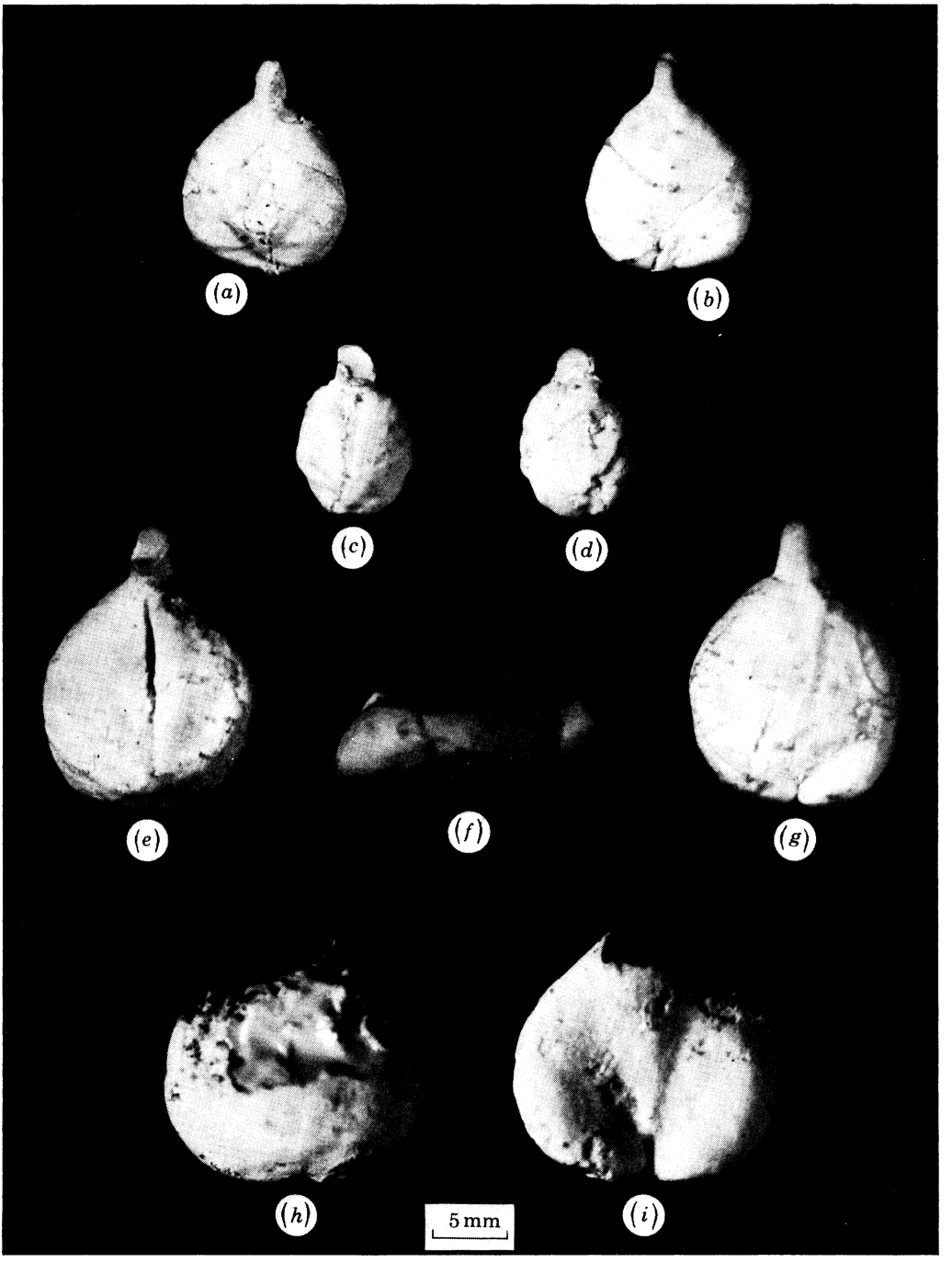


FIGURE 5. Latex casts of burrows made by *Fungiacava eilatensis* (Soot-Ryen). (*a*)–(*g*) Casts from a single specimen of the coral host, *Fungia scutaria*, collected alive at Eilat, Israel. The sets (*a*, *b*), (*c*, *d*) and (*e*, *f*, *g*) represent different view of three burrow casts, (*a*), (*c*), and (*e*) are the anatomically ventral side. (*b*), (*d*) and (*g*) are the anatomically dorsal side. (*f*) is a side view showing the position of the mytilid, which lies ventral side uppermost. Note bumps on the surface of (*c*) and (*d*). (*h*) and (*i*) are casts from the respectively ventral and dorsal sides of a fossil burrow in the large central black hole at the oral surface of figure 4*a*, plate 37. Note the similarity of the shapes of the burrows (*h*, *i*) to the ones made nowadays by the *Fungiacava* bivalves (*a*–*g*).

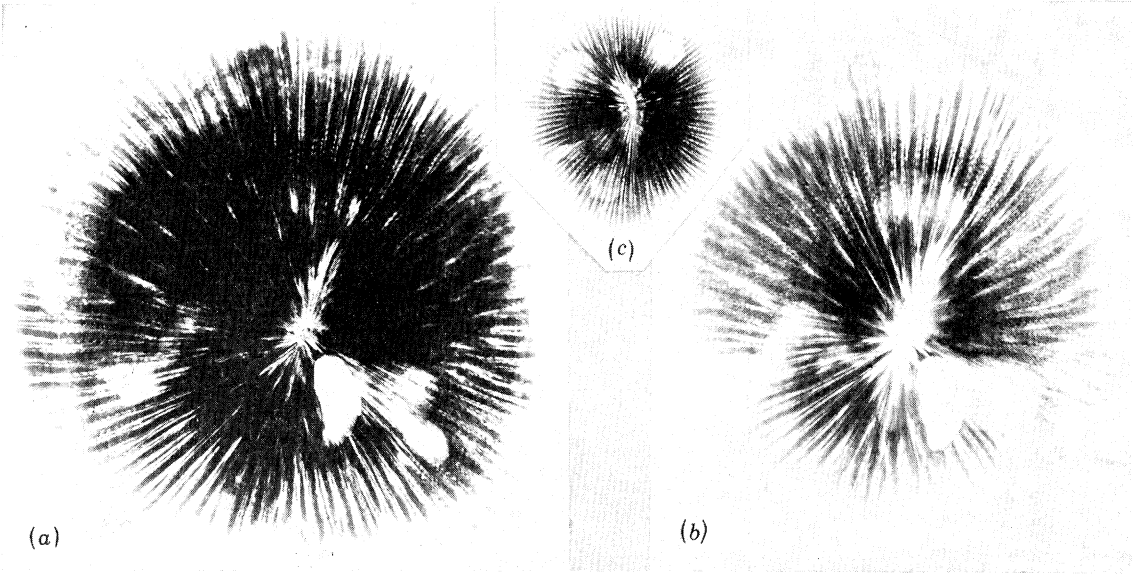


FIGURE 6. A fossil *Fungia repanda* with burrows. (*a*) Very high X-ray exposure to show burrows at 5 o'clock position. (*b*) Same as (*a*) at higher X-ray exposure to show more detail of the burrows in the interior at 12 and 6 o'clock. (*c*) Recent *Fungia scutaria* with burrows. Because of the lower density a much lower X-ray exposure was used. (All natural size.)

so very typically shaped nowadays by *Fungiacava eilatensis*. These corals were analysed by X-ray diffraction and the data shows that a large specimen represented in figure 4, plate 37, is aragonite with a trace of calcite, but visual comparison with Recent *Fungia scutaria* specimens, and the difficulty of obtaining good shadow X-rays indicate secondary recrystallization and micritization appear to have increased its X-ray density, compared to recent specimens.

Description of specimens

The large coral represented in figure 4, plate 37, is a fossil *Fungia* (Verrillofungia) *repanda* (Dana); although poorly preserved for identification, it shows the perforations on the under side which are characteristic of the species (J. W. Wells, personal communication). We made Latex casts of the burrows which are shown in figures (*h*) and (*i*) in figure 5, plate 38. To compare with the form and structure of the fossil burrows (*h*) and (*i*), we also made Latex casts of a Recent *Fungia scutaria* showing the typical burrows carved by the living mussel nowadays. The results are recorded also in figures 5*a–g*.

Figure 6, plate 39 represents a fossil *Fungia repanda* with burrows. Figure 6*a* is the result of very high exposure needed to show the three *Fungiacava* burrows at 5 o'clock position, in the very dense coral skeleton. Figure 6*b* is the same as figure 6*a* which was exposed to the X-ray for a longer time. The resolution of the edges is greatly reduced here since the specimen is less thick at the edges. However, much more detail is available to see extra burrows in the interior. The three burrows at 5 o'clock position are less well defined, except for the big one which seems to be sideways, not horizontal, and goes right through the skeleton which suggests that it may have been eroded mechanically after the death of the coral, or may even represent other mollusc boring organisms (cf. Goreau *et al.* figure (*a*), Plate I, 1973). The burrow at 8 o'clock is marked by a hole at the site of the columella. A small fainter burrow is seen at 6 o'clock and two more are clearly outlined at 12 and at 1 o'clock. The positions of the burrows in the fossil skeleton are the ones usually occupied by the living *Fungiacava eilatensis*, at the extreme ends of the long axis of the columella, which in life are favourable places for feeding because at the edges of the oral aperture of stomodeum the motions of the feeding mucus currents are stronger. Figure 6*c* is a recent *Fungia scutaria* containing burrows, included for comparison. The contrast in (*a*) and (*b*) is poor as compared with the recent specimen (*c*) because the greater thickness of the denser fossil skeleton results in a reduced X-ray density contrast. These photographs are all life size contact exposures. Out of nearly 110 whole and broken fossil *Fungias* X-rayed, Fungiacava burrows were found in two specimens and an additional five suspected possible *Fungiacava* burrows were seen in three specimens but the resolution in the X-ray negatives was insufficient to be sure, possibly due to varying recrystallization and micritic infilling and cementation.

In the Recent association, *Fungiacava eilatensis* is a boring bivalve commensal

in reef corals of the genera *Fungia*, *Cycloseris* and *Diaseris*. Fungiacava lives entirely inside the coral, in a burrow excavated in the skeleton of the coral host. The burrow carved by the mytilid is quite independent of the scleractinian corallum and bridge gaps (cf. figure 2, plate 36; also in Goreau *et al.* 1972). *Fungiacava* burrows by chemical means; the distinct layered structure is made by *Fungiacava*, the result of a dual process of dissolution of the coral substratum and secretion of a layered aragonitic lining. The delicate and fragile shells of the clam are unsuitable for mechanical boring; these are covered by the 'pallial envelope' which represents an outgrowth of the highly glandular middle fold of the mantle lobe. The pallial envelope, seen under ordinary light microscopy, is ciliated at the surface facing directly the burrow. The coral polyp has nothing to do with the carbonate deposition and it is significant that there is no reaction from the coral toward the boring mussel, either by way of compensating skeletogenesis, nor attempts to wall off the bivalve, nor changes in the symmetry of the coral. The growing *Fungiacava* continuously remodels its cavity by eroding the surrounding corallum and infilling voids with a deposit so that the internal surface of the burrow facing the mytilid is always covered by a smooth lining, which is in effect a mould of the animal. With growth, the bivalves often change their position within the host by removing corallum in the direction of migration and filling in the old part of the burrow with a plug of $CaCO_3$ (cf. figure 4*c*, plate 37, and plate II, Goreau *et al.* 1972).

Analysing closely the morphology of the matrices of the burrows made by Recent *Fungiacava*, we again confirm the fact that these conform closely to the shape of the shell valves. Thus, the latex casts of the burrows of the Recent *Fungiacava eilatensis* (cf. figures 5*a–g*, plate 38) are greatly compressed dorso-ventrally and are roughly heart-shaped when seen from the dorsal or the ventral views. However, some features of the Recent *Fungiacava* burrows seem to reflect more than a simple conforming to the surface of the bivalves.

The burrows represented by the latex casts of figures 5*c*, *d* are decidedly bumpy in outline, as in contrast with the other burrow casts (*a*, *b*, *e*, *f*, *g*) of the same plate (cf. also compared with the bumps seen in figure 1, plate 36). Such irregularity may represent a recent period of burrow enlargement, prior to completion of the lining. In addition, the burrows represented by the casts in figures *e*, *f* and *g* show prominent longitudinal ridges in the area of the pedal gape. This is also seen in life, the continuously moving pallial envelope which covers the whole mytilid shell presents, facing the burrow, a ciliated outer surface with a dendritic system of shallow grooves converging toward the pedal gape. These are in fact ciliated grooves which probably have the function of extracting foreign particles and maintaining circulation in the space between the bivalve and the wall of its burrow.

The burrow, visible as a large hole in the fossil coral, *Fungia repanda*, figure 4*a*, plate 37, resembles strikingly the Recent *Fungiacava* burrow casts from the Recent *Fungia scutaria* and its heart shape, dorso-ventral compression, and

traces of the valve umbones in the doral view (figures 5*h* and *i*, plate 38). Judging from the partial cast, the complete fossil burrow was probably more compressed anterio-posteriorly than the casts of the Recent *Fungiacava*'s burrows (figures 5*a–g*). This variation is to be expected in the light of the great morphological variability resulting from growth changes, already observed in the burrows made by the Recent *Fungiacava eilatensis*, as the living young bivalves change from ovoid-elongate shapes to dorso-ventrally flattened and heart shaped adults. With the alteration of shape, caused by the growth of the mytilid, the burrow concomitantly is changed in form (Goreau *et al.* 1968, 1973).

The smooth lining, seen in the enlargement inset at the upper right, figure 4*a*, plate 37, belongs to a second burrow in the same specimen of *Fungia repanda*, which has been largely destroyed by abrasion. However, the lining shows traces of secretion giving an indication, at the point of the black arrow, of the position and relative size of the siphon protruding into the coelenteron of the coral host through a narrow canal near the columella.

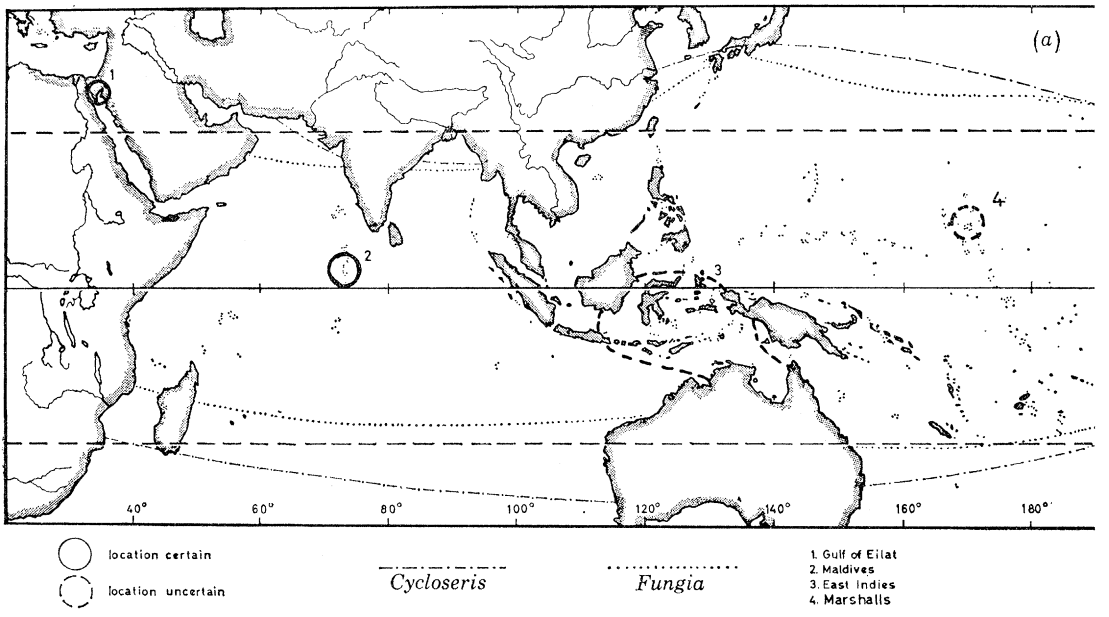
The similarity of the burrows found in the fossil forms, *Fungia scutaria* and *Fungia repanda*, to the burrows nowadays made by the mytilid *Fungiacava eilatensis* in the skeleton of their hosts, the fungiid corals, mostly *Fungia scutaria*, is extremely striking in the morphology of the matrix, the presence of a prominent burrow lining, and the position of the siphonal canals toward the columella of the coral host.

Discussion

The living populations of the Recent *Fungiacava* are concentrated in a few isolated and spatially restricted localities, dispersed throughout a vast area, ranging from the Gulf of Eilat, in the uppermost Red Sea, the central part of the Maldive archipelago, to a broad regional designation in the East Indian Ocean, and possibly to the Marshall Islands in the Central Pacific (cf. figure 3*a*). At the same time, the data set out a sporadic and disjunct pattern of distribution of the *Fungiacava* mytilid in relation to that of its coral hosts, the fungiids.

It is also worth noting that the genus *Fungiacava* still live successfully in the same region today, in the Gulf of Eilat (cf. figure 3*b*), as it did in the Pleistocene times, near 130000 years ago, as recorded in the Marsa Bareika fossil outcrop, near the northeast tip of Ras Muhammad, and one can merely speculate whether the paradoxical disjunct modern distribution of this commensal bivalve is a relic type, the animal having had a very much wider distribution in former times.

The lower incidence of *Fungiacava* in the fossil specimens compared to recent ones in areas where the association takes place could indicate either that the fossil locality was in some way marginal for the stability of the association, or that the symbiosis was historically recent when the raised reef was formed. The fossil record should show it.



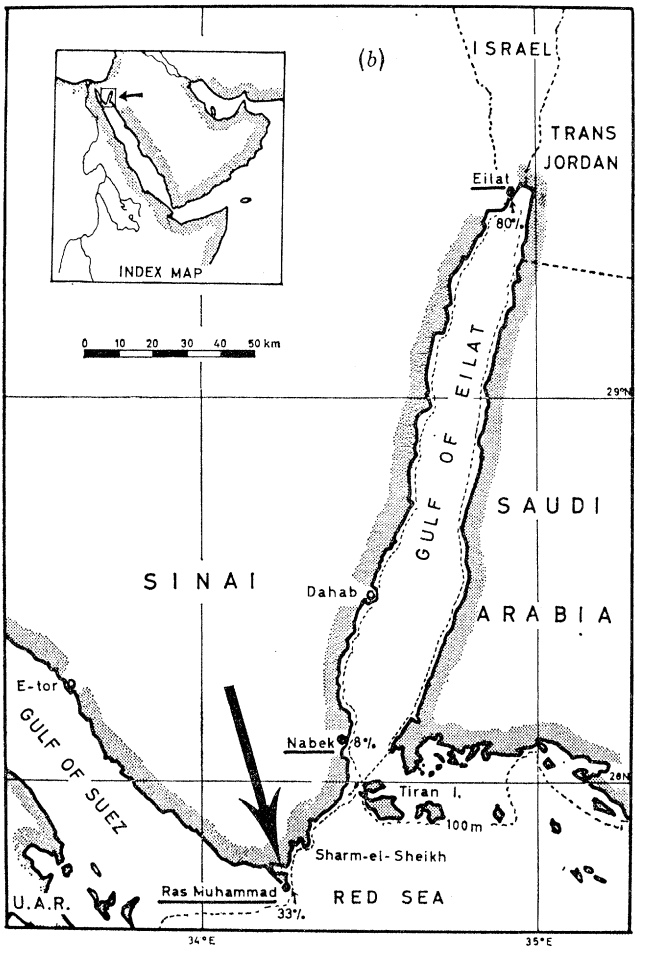


FIGURE 3. For description see opposite.

The University of Tel Aviv and the Geological Survey of Israel were hosts of Professor T. F. Goreau's visit to study the fossil and modern coral reefs of the Sinai Peninsula, a last and cherished stay which now makes possible this communication. We are personally indebted to N. Gudderman, D. Popper and A. Shoob, who assisted with the collection, and to L. Fishelson, Ch. Levinshon, Y. Loya and Y. Nir.

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Description of figure 3

Figure 3. (*a*) Distribution of recent *Fungiacava* in relation to its coral associates *Fungia* and *Cycloseris*. The geographic limits of the corals are indicated by the light dotted and dashed lines (adapted from Wells 1966, p. 233). The bivalve has so far been reported only in the four restricted areas shown on the map: the heavy open circles mark the Eilat and Maldives sites from which numerous specimens and precise locality records are available; the heavy dashed circle marks the approximate area from which single corals with *Fungiacava* were collected but no precise positions are known. Specimens were collected by the senior author and collections examined at the British Museum of Natural History (London), the Smithsonian Institution (Washington), and the S. Gardiner collection at Cambridge University. (*b*) Occurrence of *Fungiacava eilatensis* in the Gulf of Eilat and off the coast of the Sinai Peninsula. At Eilat, the type locality, more than 80 % of the shallow water *Fungia* carry one or more *Fungiacava*. The bivalve seems less common at Nabek (8 %) and at Ras Muhammad (33 %) but the extent and continuity of the *Fungiacava* populations in the arm of the Red Sea are not fully established. The fossil record of *Fungiacava*'s like burrows in Pleistocene *Fungia* specimens come from Marsa Bareika, near the northeast tip of Ras Muhammad, as indicated by large arrow.

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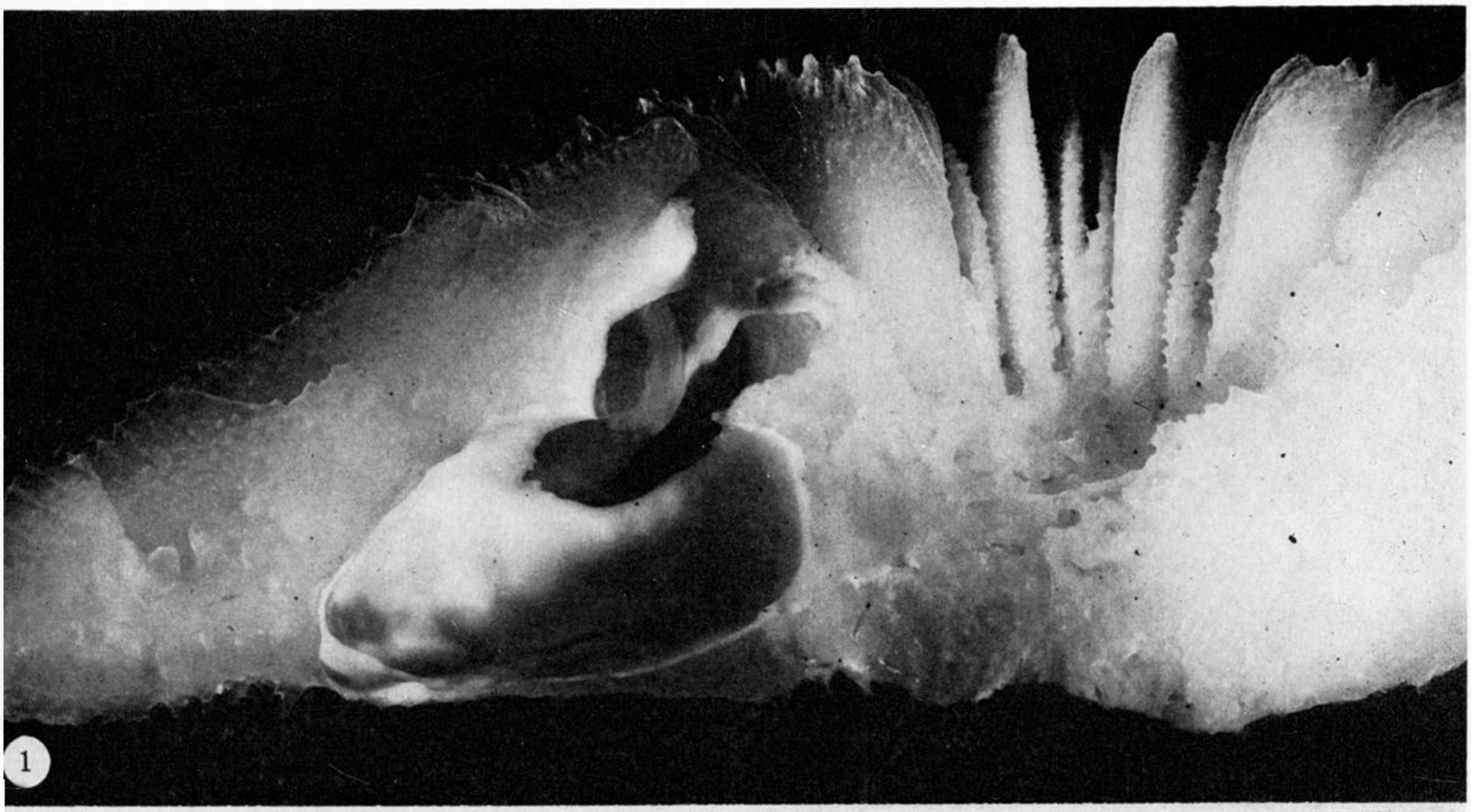
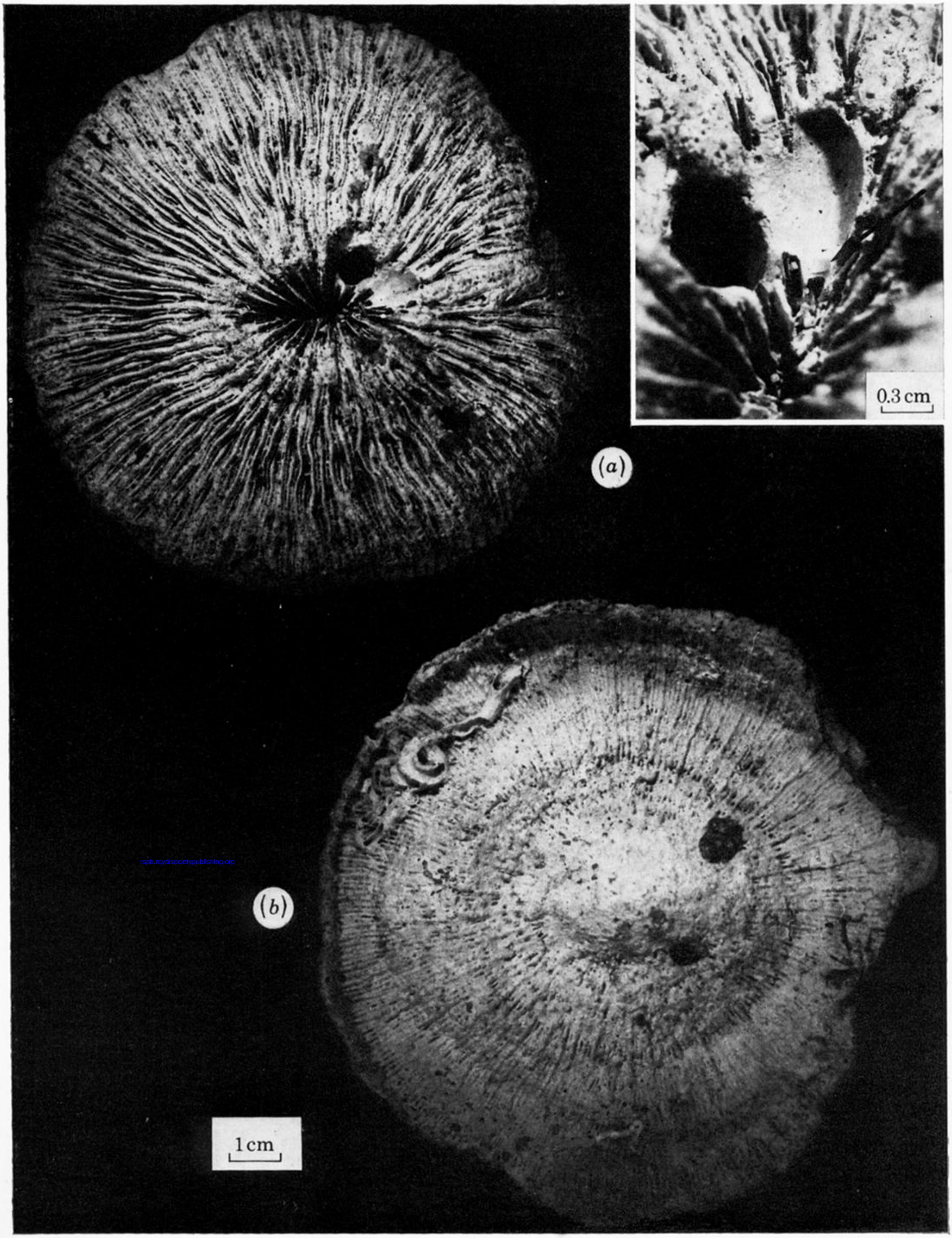


FIGURES 1 AND 2. For description see opposite.



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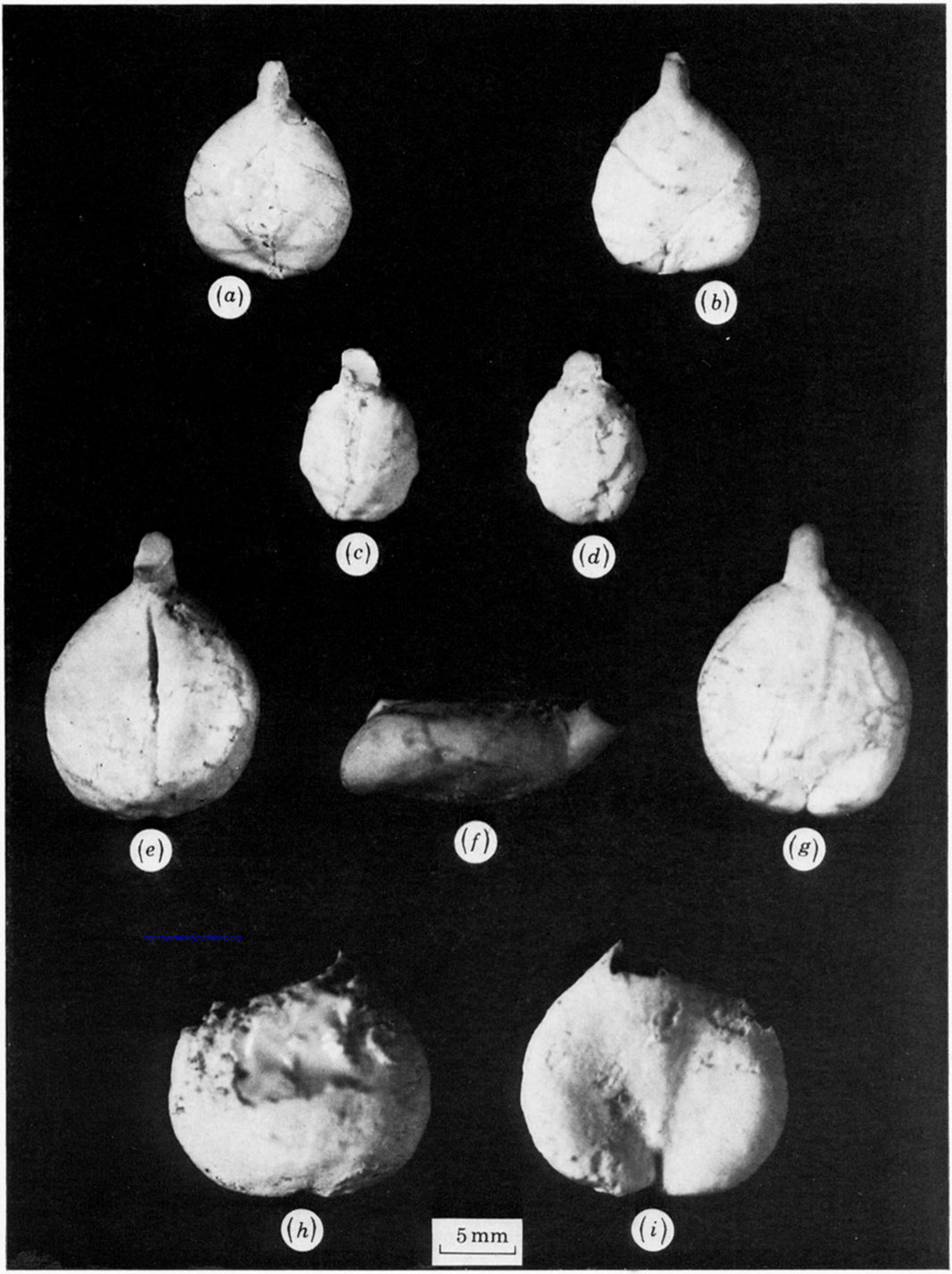

FIGURE 5. Latex casts of burrows made by *Fungiacava eilatensis* (Soot-Ryen). (*a*)–(*g*) Casts from a single specimen of the coral host, *Fungia scutaria*, collected alive at Eilat, Israel. The sets (*a*, *b*), (*c*, *d*) and (*e*, *f*, *g*) represent different view of three burrow casts, (*a*), (*c*), and (*e*) are the anatomically ventral side. (*b*), (*d*) and (*g*) are the anatomically dorsal side. (*f*) is a side view showing the position of the mytilid, which lies ventral side uppermost. Note bumps on the surface of (*c*) and (*d*). (*h*) and (*i*) are casts from the respectively ventral and dorsal sides of a fossil burrow in the large central black hole at the oral surface of figure 4*a*, plate 37. Note the similarity of the shapes of the burrows (*h*, *i*) to the ones made nowadays by the *Fungiacava* bivalves (*a*–*g*).

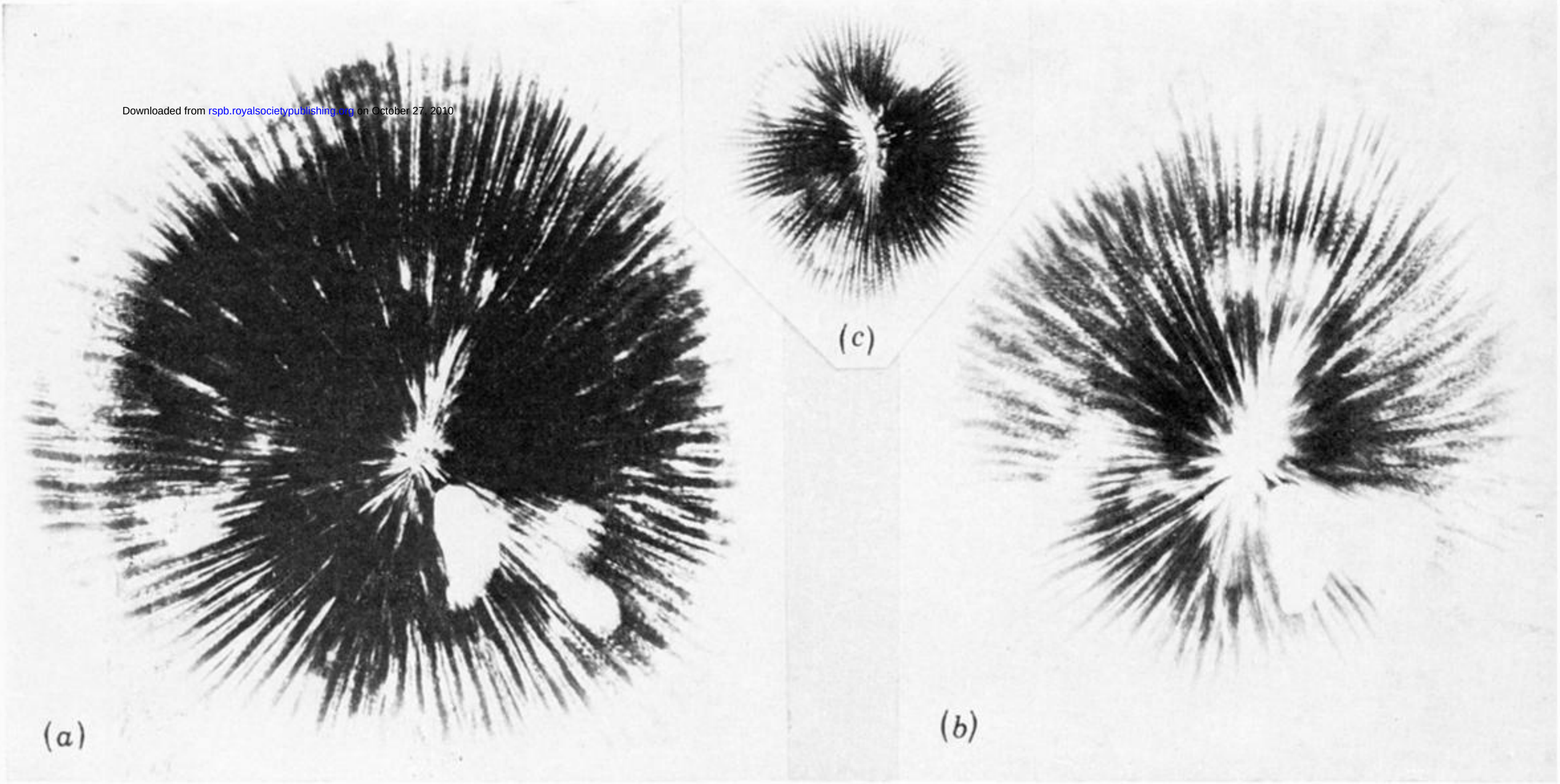

FIGURE 6. A fossil *Fungia repanda* with burrows. (*a*) Very high X-ray exposure to show burrows at 5 o'clock position. (*b*) Same as (*a*) at higher X-ray exposure to show more detail of the burrows in the interior at 12 and 6 o'clock. (*c*) Recent *Fungia scutaria* with burrows. Because of the lower density a much lower X-ray exposure was used. (All natural size.)