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Bryozoan borings in shells of Costa Rican Miocene oysters

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Abstract

Borings of bryozoan colonies are rare fossils and hitherto unknown from Central America. Four different types of zoaria, belonging to *Spathipora* sp., *Terebripora* sp. A, *Terebripora* cf. *falunica* and *Iramena* sp., were recognized. They are developed on shells of Miocene oysters (*Saccostrea* sp. and *Ostrea* sp.) from shell - beds of the Venado-Formation (Northern Limón – San Carlos Basin, Costa Rica). The period of colonization and growth by bryozoans and/or a few other benthic invertebrates was probably a short - term event, followed by suffocation from accumlating sediment.

Key words: Bryozoa, Ctenostomata, fossils, borings, bioerosion, ichnology, Miocene, Costa Rica

INTRODUCTION

Along the Atlantic side of Costa Rica, a considerable series of Tertiary sediments accumulated within the San Carlos Basin. While the Oligocene was characterized by deposition of mainly turbiditic sediments in a rapidly subsiding trough, more neritic and shallow marine conditions dominated Miocene times (Amann, 1993, Bottazzi et al., 1994). Starting at the end of that epoch and going on through the Pliocene, the sea retreated continuously to the east and terrestrial sediments were deposited within the San Carlos Basin.

During the Miocene and until the early Pliocene the northern part of the San Carlos Basin was filled by shallow marine to lagoonal sediments. They constitute the so called Venado Formation (Malavassi and Madrigal, 1970; Obando, 1986). As Calvo and Bolz (1987) recognized, the formation is composed by two depositional systems: one of lagoonal sediments and a second of bars of calcareous sands. The calcareous series are nearly 130 m thick with an extension of some 5 km^2. Typical rocks contain mixtures of bivalve and balanid shells, embedded in a matrix of bioclastic sand with terrigenous material (lithoclasts, quartz grains, clay).

The fauna, collected from a shell bed near the type locality (Fig. 1), is a typical taphocenosis, composed by allochthonous and parauthochthonous material. Isolated, but well preserved shells of *Saccostrea* sp. make up nearly 70% of the material. Another 15% are shells of *Aequipecten plurinominis*, frequently pre-served with articulated valves. The third major com-ponent consists of skeletal elements of *Balanus* sp., from which complete walls as well as isolated plates are found. Accessory findings include isolated valves of *Anadara* (?*Grandiarca*) sp., *Patinopecten candelariae* and of *Ostrea* sp.. Taphonomic studies show, that the material was accumulated by short events of high water energy, caused by storms. The major part of it was de-rived from the nearer surroundings of the place of deposition.

After deposition the shells constituted a secondary hard ground for epilithic organisms, like encrusting agglutinated foraminifera, colonies of cheilostomate bryozoans, and small individuals of *Tetrabalanus* sp.. Endoliths are documented by borings. Besides borings of sponges (*Entobia* sp.) and of polychaetes (*Polydora*-like forms), borings made by bryozoans can be found. The latter are first identified from Costa Rica and Central America in this study. Bryozoan borings are

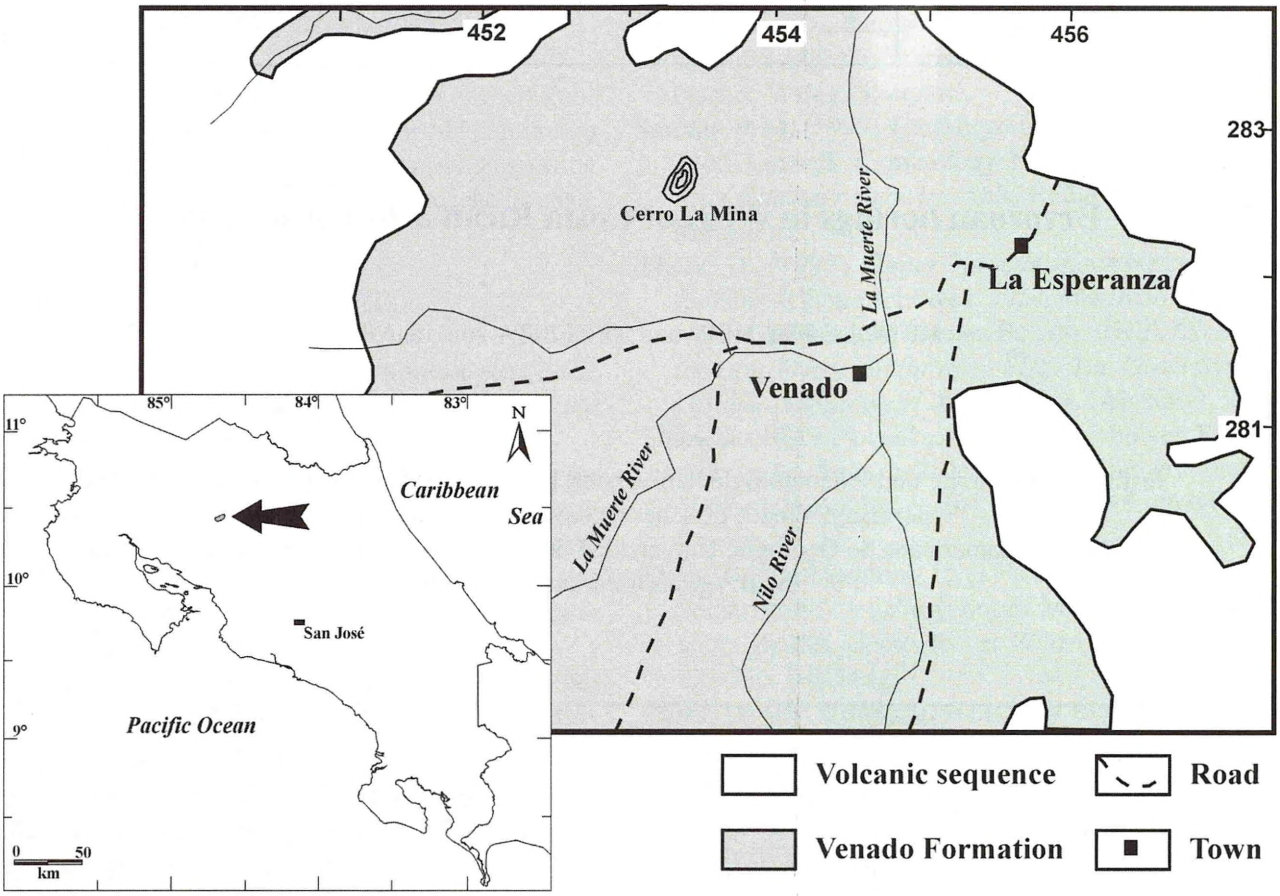

Fig. 1: - Exposure of the Venado Formation (Upper Miocene to Lower Pliocene) in the Atlantic part of Costa Rica and ubication of the type locality, from where the bryozoan ichnofossils are described.

rare fossils (Soule & Soule, 1969; Warme, 1975; Häntzschel, 1975), often disregarded by collectors.

The figured specimens and additional material are deposited in the paleontological collection of the Escuela Centroamericana de Geología, University of Costa Rica, San José (Code CO- 325, 328, 329-1/2).

THE BORINGS

Borings made by Miocene bryozoans are undoubtedly ichnofossils. To avoid nomenclatural confusion, borings are named as ichnotaxa, independent from the names of the extant organisms themselves (Boekschoten, 1966, 1970; Bromley, 1970; Bertling, 1995). Four morphologically different ichnospecies can be recognized in the studied material from Venado, Costa Rica. Two of them belong to the genus *Terebripora* and one each to *Spathipora* and *Iramena*. The last one was established by Boekschoten, 1970 as a genuine ichnogenus. *Terebripora* (d´Orbigny, 1847) and *Spathipora* (Fischer, 1866) were originally based on borings (Bassler, 1953), but later on were also applied to name biogenera.

The bryozoan borings are developed on valves of oysters (*Saccostrea* sp. and *Ostrea* sp.). They were studied with a stereoscopic microscope (Wild 208700). Both sides of the valves present different mode and intensity of the boring patterns. The borings are more or less abraded, simulating considerable variability of form and width of the zooids and, especially, of their apertures. The tracks of the stolons, - only slightly sunken into the substrate - are often completely lost. However, combina-tion of cuts to different depth levels in the substrate, permits a reconstruction of zooecial details, like vane

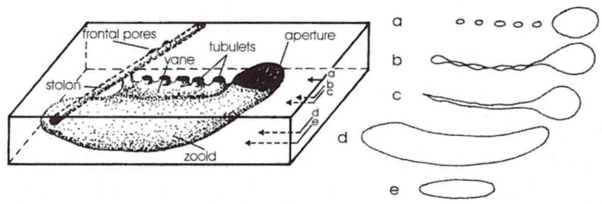

Fig. 2: - A zooid of *Spathipora* sp. is fixed at the stolon by a peduncle. A bladelike vane and tubulets are developed on its front. a - e: cuts at different depth below the surface show caracteristic contours which allow a three - dimensional reconstruction of the zooid in an abraded substrate.

Fig. 3: - Part of a zoarium of *Spathipora* sp. preserved on a shell of *Saccostrea* sp. (CO-330). The specimen shows the type of branching of the stolons and the alternating arrangement of the zooids. The angle between the stolon and the zooids opens in growth direction of the colony.

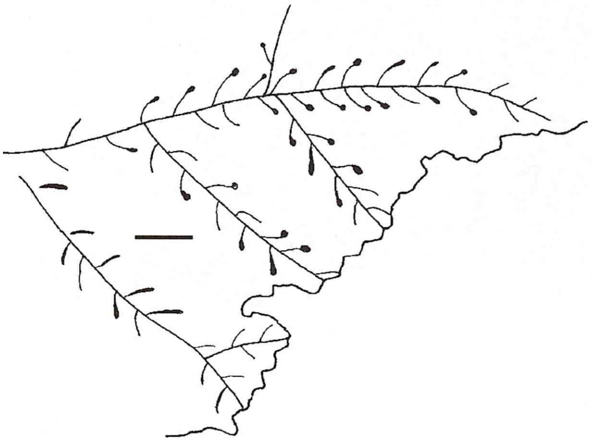

Fig. 4: - Sketch of the specimen photographed in Fig. 3, showing additional stolonial branches, visible under the microscope. Scale bar: 0.5 mm.

and tubulets (Fig. 2), which usually can only be studied on artificial resin casts (Pohowsky, 1974; Radtke, 1991).

Phylum Bryozoa Ehrenberg, 1831
Order Ctenostomata Busk, 1852
Family Spathiporidae Pohowsky, 1978

***Spathipora* sp.**
Fig. 2-5

Pohowsky (1978) emphasizes the arrangement of the inclined to horizontal zooids at a specific angle to the stolon, the staggered budding of stolons and zooids, and the comma-shaped pattern at the surface of the sub-strate, due to the form of aperture and vane, as cha-racteristic features of the genus.

Description: A typical zoarium of *Spathipora* sp. is developed on the interior of the right valve of *Saccostrea* sp. (CO-330). A principal stolon (more than 1 cm long) can be recognized from which several lateral stolons branch at varying intervals. The stolons have a diameter of 0.024 mm. Small, elongated and sac-like zooids (length up to 0.36 mm, width up to 0.09 mm) with a round aperture (diam. 0.07 mm) are alternately arranged along the stolons (Fig. 3-5). They are fixed on the sto-lons in a horizontal to slightly inclined position by means of a short peduncle, inserted in the proximal half of the zooid. The zooids show an angle of 45 to 50° between their length axis and the stolon. On specimen CO-329-2, a fragment of a free valve of *Ostrea* sp., the ancestrula is preserved. Three stolons start from it, a character held by Pohowsky (1978) as diagnostic for the genus.
The abraded outlines of the zooecia permit to deduce the existence of a vane and of tubulets on their frontal side. The comma - like contour of the zoecia of *Spathipora* can be seen, when aperture and vane are cut by an abrasion plane (Fig. 5). The commas are curved against the direction of the stolonal growth (Fig. 4, 5).

Remarks: The described species of *Spathipora* may be a new one, because it differs from all hitherto known forms. A certain similarity exists with the colonies of *Spathipora magnivorticellospis*, described by Pohowsky (1978) from the Pliocene of Italy, with respect to the pattern of branching and arrangement of stolons and zooids. In contrast, the zooidal aperture of the Costa Rican species is round and smaller than the triangular and large one of *Sp. magnivorticellopsis*.

Fig. 5: - Amplification of borings from *Spathipora* sp. on a shell of *Saccostrea* sp.. The shape of the zoecia varies as a function of the intensity of abrasion of the substrate.Width of the foto: 2 mm.

Fig. 6: - Borings of *Terebripora* sp. A on the outer side of a shell of *Ostrea* sp. (CO-329-2). The surface of the shell is slightly abraded: the tracks of the stolons are lost and the zooids appear as stab - like slits. Width of the photo: 9 mm.

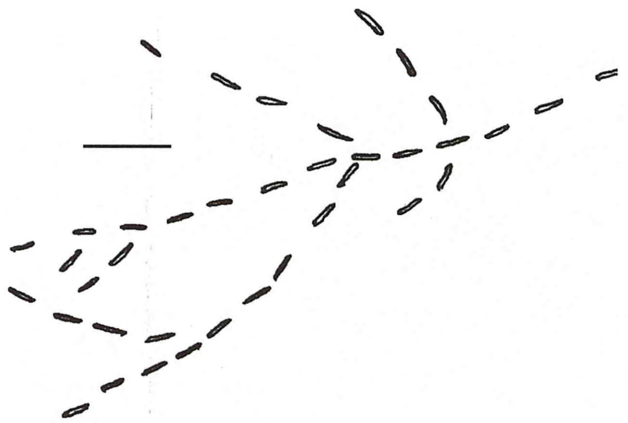

Fig. 7: - Sketch of a part of a zoarium of *Terebripora* sp. A , developed on a shell of *Ostrea* sp., showing the type of branching of a particular colony. Scale bar: 1 mm.

The observed colonies of *Spathipora* do not cross each other. They apparently invade the shells as first colonizers, starting near the border and then extending towards the center of the oyster shell. They reach population density of nearly 40 zooids / 9 mm^2. On the other hand, the borings of *Terebripora* cf. *falunica* and of sponges (*Entobia* sp.) cut the tracks of *Spathipora*, indicating a subsequent colonization.

Family Terebriporidae d´Orbigny, 1847

Following the emendated diagnosis by Pohowsky (1978), the Terebriporidae are non - pedunculated bryozoans with zooids arranged horizontally along the stolon and fixed on it by a narrow vane.

***Terebripora* sp. A**

Fig. 6-7

Description: The borings of *Terebripora* sp. A are the most frequent in our material and developed on all the studied oyster shells. They best can be observed on the external side of a free valve of *Ostrea* sp. (CO-329-2), which is densely colonized (more than 250 zooids per 9 mm^2). The zooids lie immediately below the stolon at which they are attached by a small vane. When shells are slightly abraded, the zooids appear as small (width 0.1 mm), stab-like slits of 0.3 mm length, which follow each other at a regular distance of 0.1- 0.2mm. Pohowsky (1978) mentions that the Terebriporidae have enantiomorphic zooids with the apertures located on the right or left side of stolon. No preserved apertures can be seen on the material, but it is a relic of enantiomorphism that the small slitlike zooids are alternatively slightly inclined towards the stolon (Fig. 7).

The stolons are rarely preserved; their course and the direction of growth of the colony can be deduced by the arrangement of the zooids. A main stolon can be recognized from which lateral stolons branch. Dichotomical branching is preferred, especially on the lateral stolons. (Fig. 7). Lateral stolons arise on both sides of the stolon, but often one side is preferred. On specimen CO 329-2, the direction of growth and branching seems to be influenced by the ornament of the shell. On its outer side, stolons grow preferably parallel to the concentric growth folds. On the flat surface of the inner side, the borings of *Terebripora* sp. A are randomly distributed within their area of occurrence.

Remarks: *T.*sp. A differs from all described species of *Terebripora* by the regular arrangement of the zooids along a system of dichotomically branching stolons. The slitlike borings of *T.*sp. A resemble borings of cirripeds (Voigt, 1967), like *Zapfella* (Häntzschel, 1975:W135), *Rogerella* or *Simonizapfes* (Häntzschel, 1975:W130), especially when stolons are not preserved. They differ from those borings by their arrangement in rows and in their dimensions, which are significantly smaller.

***Terebripora* cf. *falunica* Fischer, 1866**

Fig. 8-9

Description: A small zoarium of a second species of *Terebripora* is exposed only on a small area on the outer side of the free valve of a *Saccostrea* sp.. Stolons form a dense network of borings (diam. 0.024 mm) with small meshes, all densely occupied by frontal pores and/or tubulets (Fig. 8). Zooids are irregularly distributed

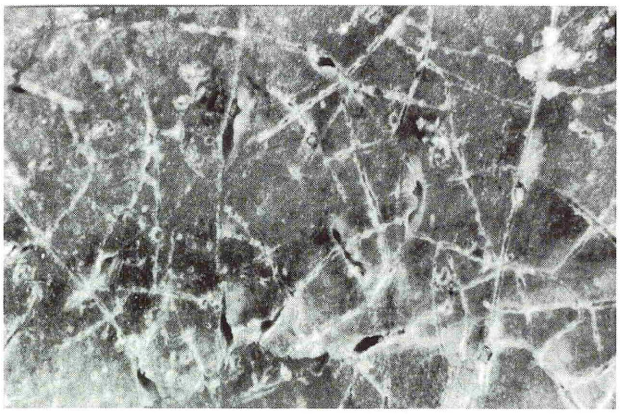

Fig. 8: - Part of the zoarium of *Terebripora* cf. *falunica* Fischer, 1866. On the surface of the stolons frontal pores are developed. They cause the nodular appearance of the stolonal tracks on the slightly abraded surface of the substrate. The zooids lay below the stolon and are slightly inclined. Their form is visible on translucent parts of the substrate (pale elongated shadows within the foto). Width of the foto: 2.5 mm.

Fig. 9: - Sketch of the stolonal tracks and zooids of *Terebripora* cf. *falunica*. The shapes of the zoecial apertures vary with abrasion depth of the substrate. Thin lines: stolonal tracks. Irregular lines: frontal pores on stolons. Dotted lines: Contour of zooids. Scale bar: 0.25 mm.

within the network. They always lie slightly inclined below the stolon to which they are attached by a small vane, extending from the aperture to half length of the zooid (Fig. 9). The zooidal aperture touches the stolon at its right or left. The aperture is round; when the vane is abraded, it has a slitlike proximal prolongation. The zooid is 0.3 mm long and 0.096 mm wide.

Remarks: The Costa Rican species resembles *T. falunica*, described by Pohowsky (1978) from Miocene localities from France and from Bay of Santos, Brazil. Nevertheless, the specifically diagnostic "presence of tubulets arising from frontal surface of autozooids" (Pohowsky, 1978:115) cannot be observed due to preservation.

? Family Immergentiidae Silén, 1946

The family comprises non-peduncular, boring bryozoans, with vertically penetrating zooids, which are joined together with processes, emanating from their distal end.

Iramena ichnosp.

Fig. 10

Description: Especially on the inner side of specimen CO-329-2 (*Ostrea* sp.) a further system of bryozoan borings is developed. It consists of a dense network of stolons, combined with circular openings (diam. 0.096-0.12 mm), which are in contact with the stolon on one side. The openings are the apertures of vertically penetrating zooids of unknown length. They are arranged on both sides of the stolons and show an irregular distribution. Some may be immediate neighbours, others are more distant. They cover the substrate with an average of 60-70 zooids per 9 mm^2.

Remarks: The described borings are typical for *Iramena*, an ichnogenus described by Boekschoten (1970). He defended a strict separation of ichnological and biological nomenclature and did not group the ichnogenus within a higher category. On the other hand, the morphology of *Iramena* ichnosp. resembles in details

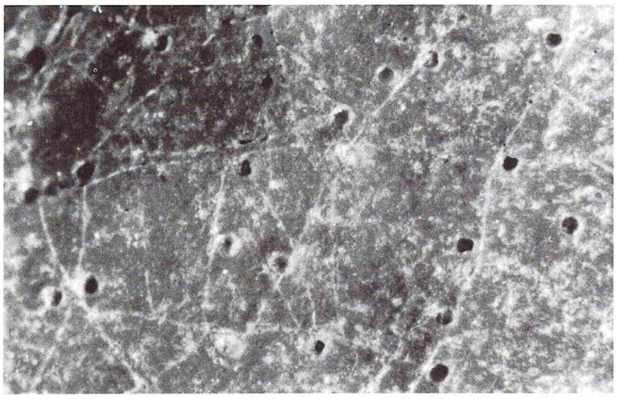

Fig. 10. Borings of *Iramena ichnosp.* on the inner side of an oyster shell (CO-329-2). A dense network of stolonal borings is combined with circular openings of vertically penetrating zooids, arranged along the stolons. Width of the photo: 4 mm.

recent and fossil borings made by species of the genus *Immergentia* Silén 1946 (see Pohowsky, 1978, Pls. 22-24) and it therefore seems reasonable to assign *Iramena* to the family Immergentiidae.

The area of the oyster shell, which is mainly occupied by the *Iramena* borings, also includes those of *Terebripora* sp. A and *Spathipora* sp. Within the center part of the valve, only *Iramena* borings occur, whereas those of *Terebripora* sp. A dominate within a broad strip along the margin of the shell. *Iramena* penetrates into that zone and cuts the preceding *Terebripora* borings. *Spathipora* sp. is a subordinate species.

PALAEOECOLOGICAL OBSERVATIONS

Borings and remains of epilithic organisms are found on isolated valves of *Saccostrea* sp. and *Ostrea* sp. as well, independent of their state of preservation, which may be more or less complete or fragmented. If the valves are arched, bryozoans (borings and skeletal crusts) and encrusting foraminifera are preferably found on their concave inner side. Borings of sponges and of polychaetes affect all carbonaceous skeletal elements in the same manner. Based on those arguments, we deduce the invasion of the skeletal material by epi- and endoliths after deposition as a shell bed. A high number of accumulated arched shells (lying in stable position = arched upwards) and of crowns of balanids resulted in cavity-rich sediment with a considerable circulation of water within it. That special protected habitat was inhabited by the enlisted benthic invertebrates.

The colonization of the shells occurred stepwise. It began with initial settling of boring bryozoans on oyster shells, where they preferred the lower side of arched shells. The studied material indicates that *Spathipora* sp. was usually the first colonizer, followed by other boring species of bryozoans. Borings of polychaetes (*Polydora* - like forms) and of sponges (*Entobia* ichnosp.) cut all other borings and crusts of epiliths and document the last step of colonization. The epilithic remains (encrusting foraminifera, dimyid bivalves and small balanids) do not allow to recognize a comparable succession.

In general, the number of benthic species is restricted and they all are poorly developed. The colonies of boring bryozoans are relatively small and their borings overlap only in a subordinate manner. The polychaete borings remain small and isolated; the borings of sponges affect only small restricted areas and are not extended over the entire skeletal element. Finally, the epilithic species are present as isolated individuals or small bryozoan zoaria and never form continuous crusts. Apparently, the conditions which allowed colonization and growth were of relatively short duration. It is probable that accumulation of sediment and its penetration into the interstitial cavities of the shell bed stopped the water circulation and suffocated the organisms within them.

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