Morphology, Taxonomy and Lifestyle of the Maastrichtian Rudist Bivalve *Thyrastylon*

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Abstract: The rudist bivalve *Thyrastylon* is redescribed based on extensive material collected from Jamaica. The new material shows that the left valve contains slits, and that this is the diagnostic feature of the genus. The genus is redefined as follows: a radiolitid rudist with no ligamental infold, stretched cellular microstructure and compact layers in the outer layer of the right valve; the radial bands are partially infolded into the shell layer of the right valve; the left valve has oscules developed above the radial bands and has concentric, slit-like pores that penetrate the shell and open out onto the inner part of the commissure close to the body chamber. Two species are recognized, the type species *Thyrastylon adhaerens* (Whitfield) from the mid to late Maastrichtian of Jamaica and Guatemala and *T. chubbi* Alencáster from the lower to mid Maastrichtian of Mexico (Chiapas) and Jamaica. The slits allow a reassessment of the feeding strategy of radiolitid rudists. Water entered around the entire length of the commissure, was carried across the apertural surface and expelled through the slits; the gills acting both to create the current and filter suspended detritus from seawater. The oscules acted to carry pseudofaeces out of the mantle cavity. The increase in thickness of the outer layer of the right valve in radiolitids is seen as an adaptation to increase the area of the commissure and increase filter feeding efficiency; it was not for the harboring of symbiotic algae.

Key Words: Rudist Bivalve, Cretaceous, *Thyrastylon*, feeding strategy, Radiolitid

Mastrihtiyen Rudist Cinsi *Thyrastylon*'nun Morfolojisi, Taksonomisi ve Yaşam Tarzı

Özet: Jamaika'dan derlenen çok sayıdaki materyale göre *Thyrastylon* rudist cinsi yeniden tanımlanmıştır. Yeni materyal sol kavkıda cinsin diyagnostik özelliğini oluşturan yarıklar içerir. Cins, izleyen verilere göre yeniden tanımlanmıştır: ligament çıkıntısı içermeyen bir radiolitid rudistidir, sağ kavkı dış tabakası kompakt ve yaygın hücreli mikroyapılıdır, radyal bandları sağ kavkı duvarına kısmen girmiştir, sol kavkı radyal bandlar üzerinde gelişmiş boşluklar ve kavkı duvarı içine giren ve kavkı birleşme yerinin iç kısmına açılan dairesel yarık şeklinde porlar içerir. Cinsin iki türü tanımlanmıştır: Jamaika ve Guatemala orta–geç Mastrihtiyeni'nden tip türü *Thyrastylon adhaerens* (Whitfield) ve Meksika (Chiapas) ve Jamaika erken–orta Mastrihtiyen'inden *T. chubbi* Alencáster. Yarıklar radiolitidlerin beslenme stratejilerinin yeniden değerlendirilmesine olanak sağlar. Kavkı birleşme yeri uzunluğunca su girişleri, açık yüzeyler ve yarıklar boyunca oluşmuştur; kalınlaşmış çene kısmı akıntıları düzenleme ve deniz suyundaki kırıntıları süzme görevini üstlenmiştir. Delikler manto boşluğundaki dışkıların atılmasını sağlar. Radiolitidlerde sağ kavkı dış tabakasının kalınlığının artışı, kavkı birleşme alanının büyümesi ve besin süzme etkinliğinin artması şeklinde görülmektedir; simbiyotik algler bu alanda barınmamıştır.

Anahtar Sözcükler: Rudist Bivalvia, Kretase, *Thyrastylon*, beslenme düzeni, Radiolitid

Introduction

The rudist bivalve *Radiolites adhaerens* Whitfield 1897 was originally described from the Maastrichtian (Late Cretaceous) limestones of Logie Green from the parish of Clarendon, Jamaica. Whitfield (1897, plate X–XII) figured two specimens of this species together with a drawing of a longitudinal cross-section. The species was subsequently revised by Trechmann (1924), Mac Gillavry (1934) and Chubb (1955, 1956, 1971). Trechmann (1924) erected two new species aligned to Whitfield's *R. adhaerens*, *Biradiolites coryi* and *B.*

semiannulosus. Biradiolites coryi Trechmann, from near Catadupa in the parish of St. James, Jamaica, was characterized by a large attachment area; a single specimen was figured (Trechmann, plate XXV, figure 5). Two specimens of *Biradiolites semiannulosus* Trechmann from Logie Green were figured (Trechmann, plate XXV, figures 6–7); they have very small attachment areas. Mac Gillavry (1934) figured a specimen of *Biradiolites adhaerens* (Whitfield) from Guatemala, together with a specimen from Jamaica, and suggested that this species should probably be placed in a new genus. In 1955, Chubb introduced the generic name *Thyrastylon* for the three Jamaican species: *R. adhaerens*, *B. coryi* and *B. semiannulosus*, with the former species as the type. An additional species, *Biradiolites persicus* Douvillé 1904, from Iran (Persia) was also included in the genus based on the similarity of its radial bands. Subsequently, a further species, *Thyrastylon chubbi* Alencáster 1971, was described from the Maastrichtian Ocozocuautla Formation from the state of Chiapas, Mexico. In the literature, the diagnostic features of *Thyrastylon* are considered to be the infolding of the radial bands of the right valve and the development of oscules above the radial bands in the left valve (Chubb 1956, 1971; Dechaseaux & Coogan 1969). In this paper the genus *Thyrastylon* is investigated and revised using large stratigraphic collections from Jamaica that include exceptionally well-preserved material. New features not recognized before are described, and their value in diagnosing and understanding the lifestyle of *Thyrastyon* are presented.

Morphology of *Thyrastylon*

The right valve (RV) of Thyrastylon is conical to cylindrical, it has a thin inner shell layer and a thick outer shell layer composed of radial plates. The attachment area of the RV is variable; it may be small or large, and in some cases may occupy the entire dorsal side of the shell. Shell growth (Skelton & Gili 1991) may be vertical (elevator or radial clinger morphotypes) or parallel to the attachment surface (frictional clinger morphotype) and is, at least in part, dependent on orientation of the attachment surface. Trechmann (1924) used the size of the attachment area and the relative height of the left valve (LV) to distinguish his species *coryi* and *semiannulosus* from *adhaerens*. Yet attachment area is generally regarded as having little value at the species level in rudist bivalves (cf. Marincovich 1975) and *coryi* and *semiannulosus* are placed in synonymy with *adhaerens* herein.

The radial bands (RB1 and RB2: Mitchell & Ramsook 2009) of the RV are represented by grooves, RB1 being a spatula-shaped upfold, and RB2, a flat-topped crenulated upfold. The radial bands form strong protuberances on the apertural surface. The lateral flanks of the radial bands may be partially or completed covered by outfolds/downfolds of the funnel plates, this varies within populations and with growth morphology and appears to have little taxonomic significance. The relative width of the radial bands and interband in relation to the size of the body cavity does appear to have taxonomic significance, and can be used to distinguish the earlier *T. chubbi* from the later *T. adhaerens*. The apertural surface may be smooth or plicated; with the proportion of specimens with plications, as well as, the intensity of plications, increasing up-section; this allows the stratigraphic position of populations of *T. adhaerens* to be determined. Additional plications may develop within furrows in the middle or outer part of the apertural surface. The outer surface of the RV is generally irregular; although, where plications are present, a crude vertical striation is sometimes developed (cf. Mac Gillavry 1934).

The microstructure of the RV has been investigated on specimens that have been naturally split parallel to the funnel plates and is complex; it consists of sectors of parallel straight or curved muri, with the muri of individual sectors orientated radially, concentrically or at an oblique angle to the radius. In some specimens the sectors may be arranged to form chevrons, particularly in strongly plicated forms, but in others the arrangements appear more random. The muri may coalesce, particularly between plications, and may be broken up to form granules. On the inner part of the funnel plates of some specimens, only an irregular rough granulation is developed. This pattern can be referred to as stretched cellular in the terminology of Pons & Vicens (2008). Some specimens have radial vascular impressions that may bifurcate once.

The left valve (LV) may be convex, flat or have a central dome and a broad brim. The central region of the LV is clearly distinguished from the brim even in flat and concave forms. Within any population, there is a range of forms and the height of the central dome has low taxonomic significance (in *T. chubbi* it is concave to a low dome; in *T. adhaerens* it is a low to medium dome, and only rarely a high dome). It is possible that the dome is higher in populations from more muddy (clastic) substrates, but this has not been investigated statistically. The dome of the LV is ornamented with flat-topped ridges alternating with flat-floored grooves. Typically 15 to 20 grooves are present. A broad ridge corresponds with RB2, whereas a normal ridge corresponds to RB1. The brim extends across the apertural surface formed by the funnel plates and may be flat or plicate (matching the funnel plates of the RV). The brim rises up toward, and is folded around the protuberances formed by the radial bands on the apertural surface; when the radial bands are deeply infolded the brim may completely surround the protuberances and oscules are developed. The outer ends of the flat-floored grooves of the central boss penetrate the LV as a series of concentric, slit-like pores. The pores are orientated outwards and downwards and open onto the inner part of the funnel plates close to, or at, the body cavity. When plications are developed, the pores correspond with furrows on the aperture surface, suggesting that the plications may have had a functional significance. The myocardinal apparatus consists of two teeth that fit into grooves on the inner layer of the RV, and two myophores.

The diagnosis of the genus *Thyrastylon* Chubb, 1956, needs to be amended to indicate that slit-like, concentrically arranged pores are present in the LV, a unique morphological feature of *Thyrastylon*, of prime diagnostic value. Two species of *Thyrastylon* are accepted here: *T. chubbi* Alencáster from the lower Maastrichtian of Jamaica and Chiapas, which has wide radial bands and a relatively narrow interband; and *T. adhaerens* (Whitfield) [= *T. coryi* (Trechmann), *T. semiannulosus* (Trechmann)] from the mid to upper Maastrichtian of Jamaica and Guatemala, which has narrow radial bands and a relatively wide interband. Populations of *T. adhaerens* show a progressive increase in overall size and in the strength of plications on the commissure throughout the mid to upper Maastrichtian.

Systematic Palaeontology

The material described in this paper is preserved in the Geology Museum, in the Department of Geography and Geology at the University of the West Indies (UWIGM numbers) and the Natural History Museum, London (BMNH numbers).

Genus *Thyrastylon* Chubb 1956

Type Species. Radiolites adhaerens Whitfield 1897, upper Maastrichtian, Logie Green, parish of Clarendon, Jamaica.

Diagnosis. A radiolitid rudist with no ligamental infold, stretched cellular microstructure and compact layers in the outer layer of the RV; the radial bands are partially infolded into the shell layer of the RV. The LV has oscules developed above the radial bands and has concentric, slit-like pores that penetrate the shell and open out onto the inner part of the commissure close to the body chamber.

Species Included. Thyrastylon adhaerens (Whitfield) from the Middle to Late Maastrichtian of Jamaica and Guatemala, and *T. chubbi* Alencaster from the Early to Mid Maatrischtian of Mexico (Chiapas) and Jamaica.

Discussion. Chubb (1956) included *Biradiolites persicus* Douvillé from Iran (Persia) within this genus. The lack of knowledge of the LV prevents the species being included in *Thyrastylon* at the present time.

Thyrastylon adhaerens (Whitfield 1897)

Figure 1a–d.

v. 1897   *Radiolites adhærens* n. sp.: Whitfield, p. 188–189, plate X, figures 2–3 (same specimen), plate XI, figures 1–2 (same specimen), figure 3 (section of specimen), plate XII, figure 1 (same specimen as plate X, figure 1).

v. 1924   *Biradiolites adhaerens* Whitfield; Trechmann, p. 400–401.

v. 1924 *Biradiolites coryi* sp.nov.; Trechmann, p. 401, plate XXV, figure 5.

v. 1924 *Biradiolites semiannulosus* sp. nov.; Trechmann, p. 401–402, plate XXV, figure 6–7.

v. 1934 *Biradiolites adhaerens* (Whitfield) Trechmann; Mac Gillavry, p. 4–6, figures 1–2 (Guatemala specimen), figure 3 (Jamaican specimen).

v. 1955 'Radiolites' *adhaerens* Whitfield; Chubb, p. 3.

v. 1956 *Thyrastylon adhaerens* (Whitfield); Chubb, p. 36, plate 6, figures 1–3, plate 7, figures 5–9.

v. 1956 *Thyrastylon coryi* (Trechmann); Chubb, p. 37, plate 7, figures 1–3.

v. 1956 *Thyrastylon semiannulosus* (Trechmann); Chubb, p. 38.

v. 1971 *Thyrastylon adhaerens* (Whitfield); Chubb, p. 190–191, plate 38, figures 1–6.

v. 1971 *Thyrastylon coryi* (Trechmann); Chubb, p. 191, plate 38, figures 7–9, plate 39, figures 1–3.

v. 1971 *Thyrastylon semiannulosus* (Trechmann); Chubb, p. 191–192, plate 39, figure 4.

v. 1996 *Thyrastylon adhaerens* (Whitfield 1897); Scott, p. 304, plate 2, figures 10–12, figure 6C.

v. 2003 *Thyrastylon adhaerens* (Whitfield); Mitchell, p. 154–155, plate 7a–d, plate 8a–d.

Type Specimens. Whitfield (1897) figured two specimens using photographs and a drawing of a third specimen that had been sectioned longitudinally. These specimens represent the syntypes of the species and are preserved in the American Museum of Natural History in New York. No valid selection of a lectotype has been made, and either of the specimens figured photographically by Whitfield would suffice. No lectotype is selected herein, pending a study of the syn-types.

Type Locality. Logie Green, Clarendon, Jamaica (Whitfield 1897).

Description. A medium- to large-sized species of *Thyrastylon* occurring as weakly- to strongly-attached elevators or clingers. Elevators occur singly or in bouquets numbering up to 20 or more individuals. The RV is cylindrical to conical, up to 10 cm long and 7 cm in diameter. The margin is broadly rounded and irregular, with relatively narrow radial bands, and a wide interband. Aperture with or without radial plications and/or vascular impressions. Transverse cross sections of the RV show a thin inner layer (less than 0.5 mm) and a thick (up to 15 mm) cellular outer layer. Compact shell layers are developed around the infolded radial bands. Longitudinal sections show the upward projecting funnel plates, with occasional layers of compact microstructure, which is also concentrated adjacent to the infolded radial bands.

The LV is cap like, with a central raised dome and a wide, thin brim that extends across the apertural face. The dome is ornamented with flat-topped ridges alternating with 15–20 flat-floored grooves. The grooves penetrate the LV as a series of concentric, slit-like pores, that open onto the inner part of the funnel plates close to, or at, the body cavity. RB2 is represented by a broad ridge, whereas RB1 is represented by a normal ridge. The LV has two oscules developed above the radial bands.

Geographical and Stratigraphical Distribution. The species occurs abundantly in the *Titanosarcolites* Limestones of Jamaica. Specific records come from the Guinea Corn Formation (Middle to Late Maastrichtian) of the Central Inlier (Mitchell 2003), and the Maldon and Vaughansfield Limestones of the Maldon Inlier (Gunter & Mitchell 2005). Mac Gillavry (1934) and Scott (1996) illustrate specimens from the Maastrichtian of Guatemala. Specimens have been reported from Cuba (Rojas & Iturralde-Vinent 1996), but with the lack of figures, these specimens cannot be assigned to *T. adhaerens* at the present time.

Thyrastylon chubbi (Allencáster 1971)

Figure 1e–f.

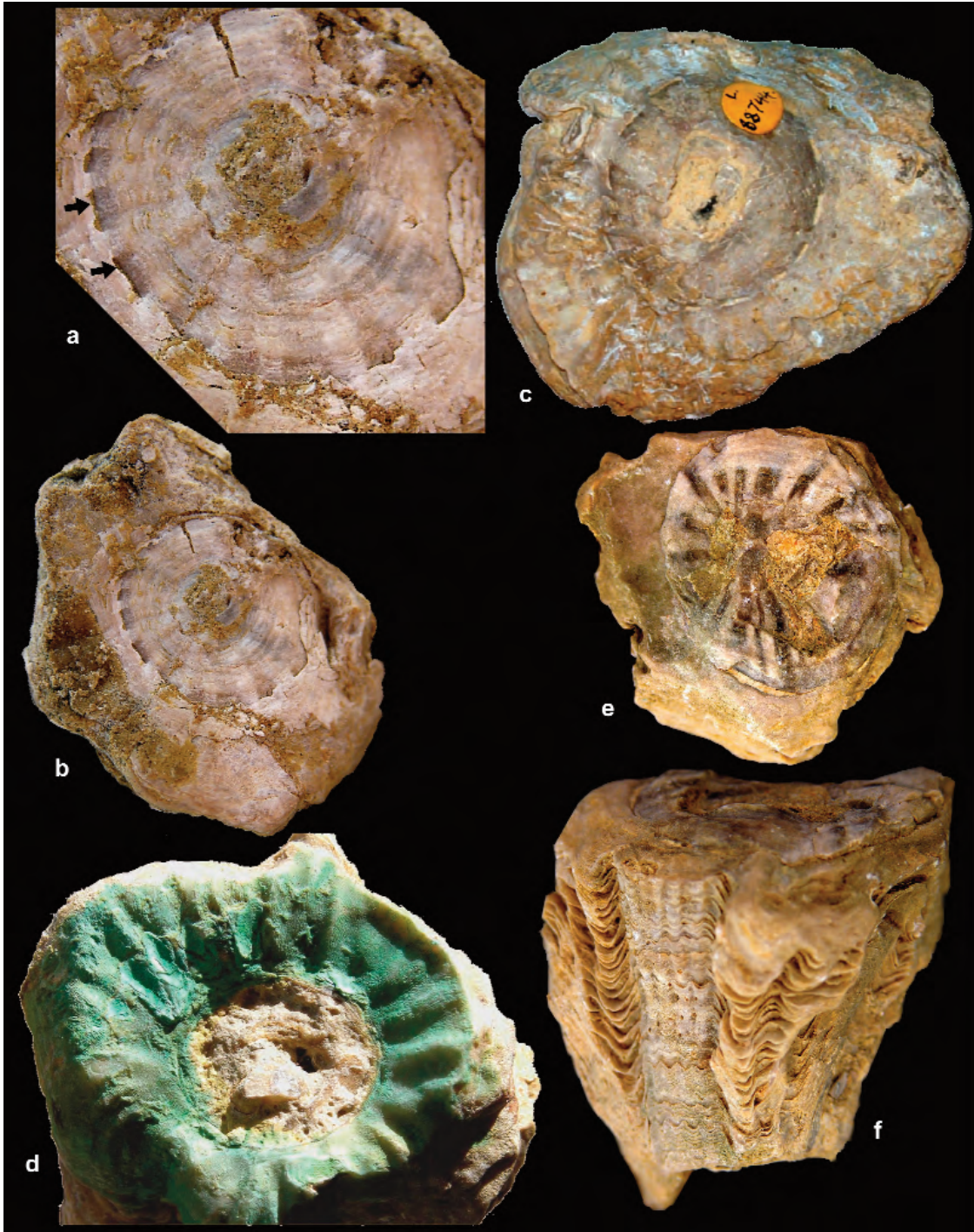?1961 *Biradiolites* sp.; Chubb, p. 3–4.

Figure 1. (a–d) *Thyrastylon adhaerens* (Whitfield) from the Guinea Corn Formation, Jamaica: **(a, b)** (UWIGM. 2009.01.0046), apertural view showing slits (a x 4, selected slits arrowed; b x 2), Upper C Beds (mid upper Maastrichtian), Cabbage Hill; **(c)** (BMNH L887414), specimen in Trechmann collection from Logie Green showing slits (x 2); **(d)** (UWIGM. 2009.01.0047) specimen from G Beds (upper upper Maastrichtian) at Tweedside showing strong plications (x 1.5). **(e, f)** (UWIGM. 2009.01.0048), *Thyrastylon chubbi* Alencáster, Jerusalem Mountain (upper lower or lower upper Maastrichtian), Jamaica (x 2).

*. 1971 *Thyrastylon chubbi* n. sp.; Alencáster, p. 45–48, plate 8, figures 1–5, plate 21, figures 3–4.

?1971 *Thyrastylon* sp.; Chubb, p. 192.

. 2006 *Thyrastylon adhaerens* (Trechmann 1897); Oviedo Garcia, p. 48–50, figure 35(1–10).

.2008 *Thyrastylon adhaerens* (Trechmann 1897); Pons and Vicens, figure 12.

Holotype. The holotype from the state of Chiapas was figured by Allencáster (1971, plate 8, figures 2–3).

Type Locality. Ocozocuautla Formation (?lower Maastrichtian), state of Chiapas, Mexico (Alencáster 1971)

Description (Jamaican Material). A small- to medium-sized species of *Thyrastylon* occurring as weakly-attached elevators, singly or in bouquets numbering two or three. The RV is cylindrical to conical, up to 5 cm long and 3 cm in diameter. The margin is broadly rounded and irregular, with relatively wide radial bands, and a narrow interband. The aperture is simple without radial plications or vascular impressions.

The LV is cap like, with a flat or gently raised central area, and a wide, thin brim that extends across the apertural face. The central area is ornamented with flat-topped ridges alternating with about 16 flat-floored grooves. The slit-like pores have not been seen; RB2 is represented by a broad ridge, whereas RB1 is represented by a normal ridge. Oscules are developed in the LV only in larger specimens with deeply incised radial bands.

Geographical and Stratigraphical Distribution. The species occurs in the Ocozocuautla Formation (?lower Maastrichtian), of the state of Chiapas, Mexico (Alencáster 1971) and in the Jerusalem Mountain Limestone (upper lower or lower upper Maastrichtian: Steuber *et al.* 2002) of the Jerusalem Mountain Inlier, parish of Westmoreland, Jamaica (reported herein).

Discussion. Althought the slits in this species have not been seen, the construction of the LV appears identical to that of *T. adhaerens*. *Thyrastylon chubbi* is distinguished from *T. adhaerens* by its smaller size, wider radial bands, and narrower interband.

Significance of slits in the Left Valve

Douvillé (1886) interpreted the radial bands, which are prominent features on the flanks of radiolitid rudists, as representing the inhalant (E or RB2) and exhalent (S or RB1) siphons. He used this to argue that the radiolitids, like other suspension feeding bivalves, used the gills to generate currents carrying water in through the inhalant siphon, across the gills where suspended detritus was filtered, and out through the exhalent siphon. Various other studies have accepted his interpretation (e.g., Chubb 1956, 1971; Yonge 1967; Philip 1972).

In contrast, however, Skelton (1979) questioned the existence of siphons based on his detailed studies of *Radiolites angeoides* (De Lapeirouse). He argued that since there was a very small distance (1 mm or so) between the matching scars for the attachments of the adductor muscles on the LV and RV, radiolitids could have only had a very small gape. This would have meant that insufficient water could have been passed over the short commissural lengths represented by the radial bands for feeding. Additionally, his reconstructions of the soft parts of early rudists (Skelton 1978) placed the gills close to the ventral margin of the commissure, much as in oysters. Thus, Skelton (1979) suggested that the radial bands rather that representing the inlets and outlets of feeding siphons served as the excretion sites for unwanted material (the pseudofaeces of Yonge 1967) from the mantle cavity. Consequently, Skelton (1976, 1978) argued that food entrapment was probably by the mantle margin rather than by the gills. In support of this, Skelton (1979) listed: the progressive restriction of the body cavity relative to shell size, implying atrophy of the gills; a concomitant expansion of the valve and consequently mantle margin, and reduction in active shell gaping.

Other authors (e.g., Philip 1972; Kauffman & Sohl 1974; Vogel 1975) have argued that the shell construction of certain radiolitid rudists was adapted for symbiontic algae, much as in the Recent bivalve

Tridacna. Rudist genera, such as *Durania*, have developed a thickened horizontal expansion of the outer shell layer of the RV that was covered by the thin, presumably translucent, brim of the LV; possible adaptations for symbiontic organisms.

The morphology of *Thyrastylon* allows a discussion of the feeding strategies of radiolitid rudists. The last representatives of *Thyrastylon* had a relatively thick outer shell layer of the RV and all specimens have this covered by the very thin brim of the LV. These match the morphology of *Durania* and functionally could be adaptations for the presence of symbionts. The elevation of the tips of the radial bands in the RV and the presence of oscules in the LV has been interpreted as a functional adaptation for carrying water with ejected pseudofecaes away from the shell's aperture (Steuber 1999). The presence of slits in the LV of *Thyrastylon* is particularly significant in terms of reconstructing feeding strategies. Functionally, the slits have to be interpreted as the entry or exit areas for seawater, either for feeding purposes or to release spat following reproduction. The presence of slits throughout ontogeny (the grooves on the central area of the LV) indicates that they were not for the release of spat; consequently, the slits must have been used for feeding. Judging from the relatively close proximity of the slits and the oscules, it seems unlikely that the slits would have been entry sites for seawater as this would likely carry waste material back into the mantle cavity. Thus, the most likely interpretation is that seawater entered at the shell margin, was drawn across the apertural surface and exited through the slits. This implies that a current was created within the mantle cavity, presumably by the gills, channeled by the plications (at least in later forms) on the apertural surface, and that the gills, rather than the mantle margin, were used to trap suspended detritus. So whereas the gape of the shell may have been too small to allow sufficient water to enter at the radial bands for feeding purposes as pointed out by Skelton (1979), if sea water entered around the entire commissural margin a small gape would suffice for feeding activities. The increase in shell diameter, with only limited increase in the size of the body cavity can be viewed not as an adaptation for gill atrophy or as an adaptation for symbiotic algae, but as a means to increase the length of the commissure and increase the efficiency of a gill-driven feeding system. *Thyrastylon* was a specialized late offshoot from the radiolitids, and it seems unlikely that it would have secondarily reverted to a gill-driven feeding system. Thus, all radiolitids presumably had gill-driven feeding systems, and the real success of the group was not the modification of the mantle margin for feeding, but the use of the entire commissure to allow seawater into the shell.

Acknowledgements

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