Parapholas quadrizonata (Spengler, 1792), dominating dead-coral boring bivalve from the Maldives, Indian Ocean

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Abstract. Endolithic bivalves were studied to establish abundance ranking and bioerosive impact on Maldivian coral reefs. In samples of dead coral, *Parapholas quadrizonata* (Spengler, 1792) was by far the most numerous bivalve borer. The assemblages of variously sized and aged specimens, their spatial situation and the resulting behaviour are described and discussed. The morphology of shells and boreholes is illustrated. Intra-species competition for space may have restricted the individual growth but was not necessarily lethal. The borings show unique internal features that allow distinction from those of *Gastrochaena* species, whereas the borehole apertures are undistinguishable between the two genera.

Keywords. Bioerosion, boring bivalve, *Parapholas quadrizonata*, Martesiinae, Pholadidae, coral reef, Maldives

Introduction

The present paper is based on observations made in the Indian Ocean during the Coral Reef Expedition Maldives 2007, conducted from March 15 to 29, under the leadership of Karen and Wolfgang Loch (http://www.expeditionmaldives2007.org). During the cruise four atolls were examined in the central part of the republic (Fig. 1). The main goal of the expedition was to compare the state of live coral cover of the reefs of today and half a century ago and its recovery by resettlement after the severe coral bleaching event of 1998 (Scheer 1958, 1972, 1974; Pillai and Scheer 1976; Loch et al. 2002, 2004; Schuhmacher et al. 2005; Loch and Loch 2006; Wallace and Zahir 2007). The present study focused on collecting samples of endolithic bivalves and their substrate to establish a preliminary ranking of their abundance and to assess the presumed bioerosive impact on the reef frame-builders. Bioerosion is a major threat for the maintenance of stressed reefs, particularly if live coral cover drops below 50%. Therefore, a preliminary study of the present situation in the Maldivian reefs was undertaken (http://bufus.sbg.ac.at/info/Info%2037/Info37-home.htm).

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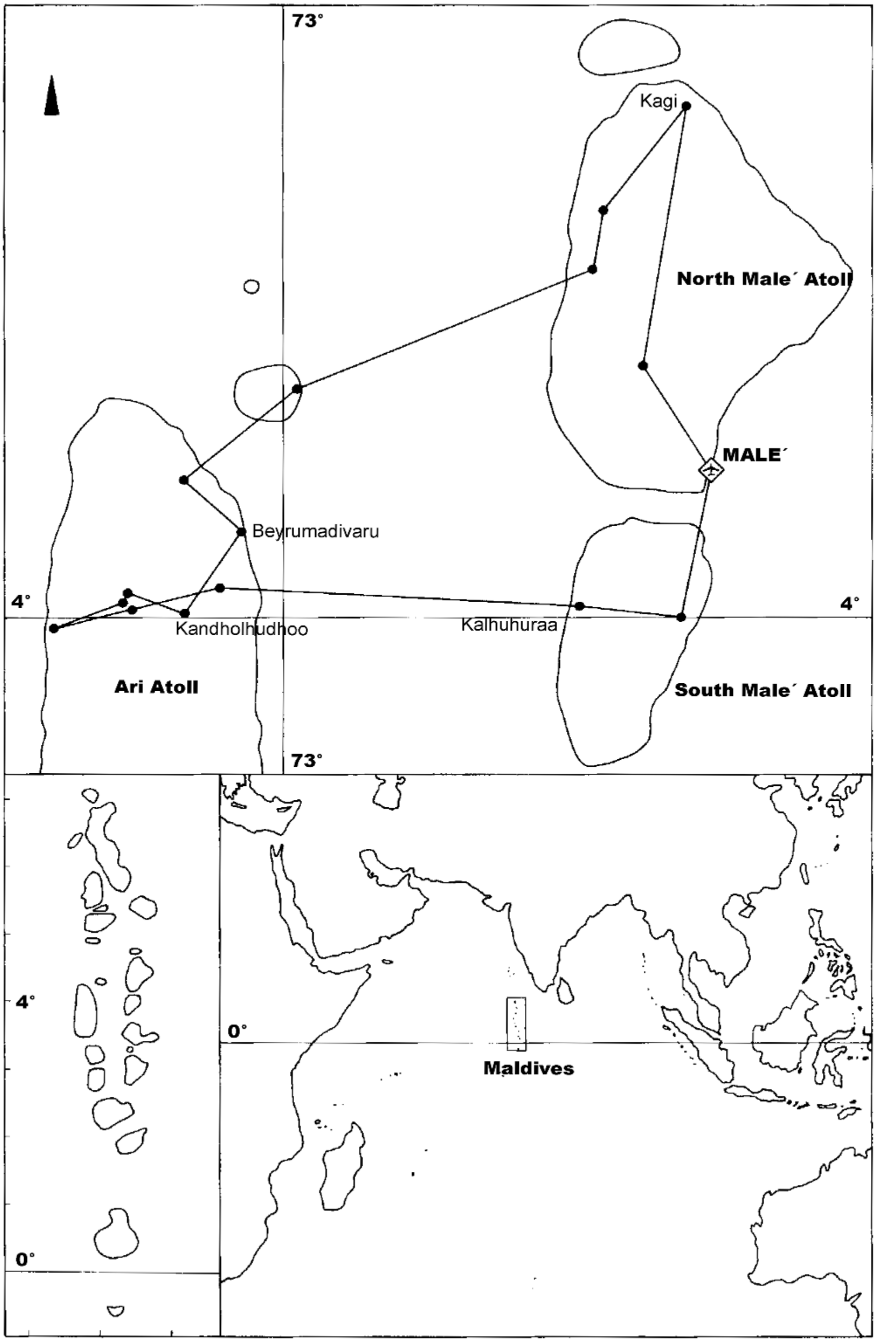


Fig. 1 Location of the Maldives in the Indian Ocean and the route of the expedition in the central area of the archipelago, starting from Male northwards on March 15th, 2007

Methods

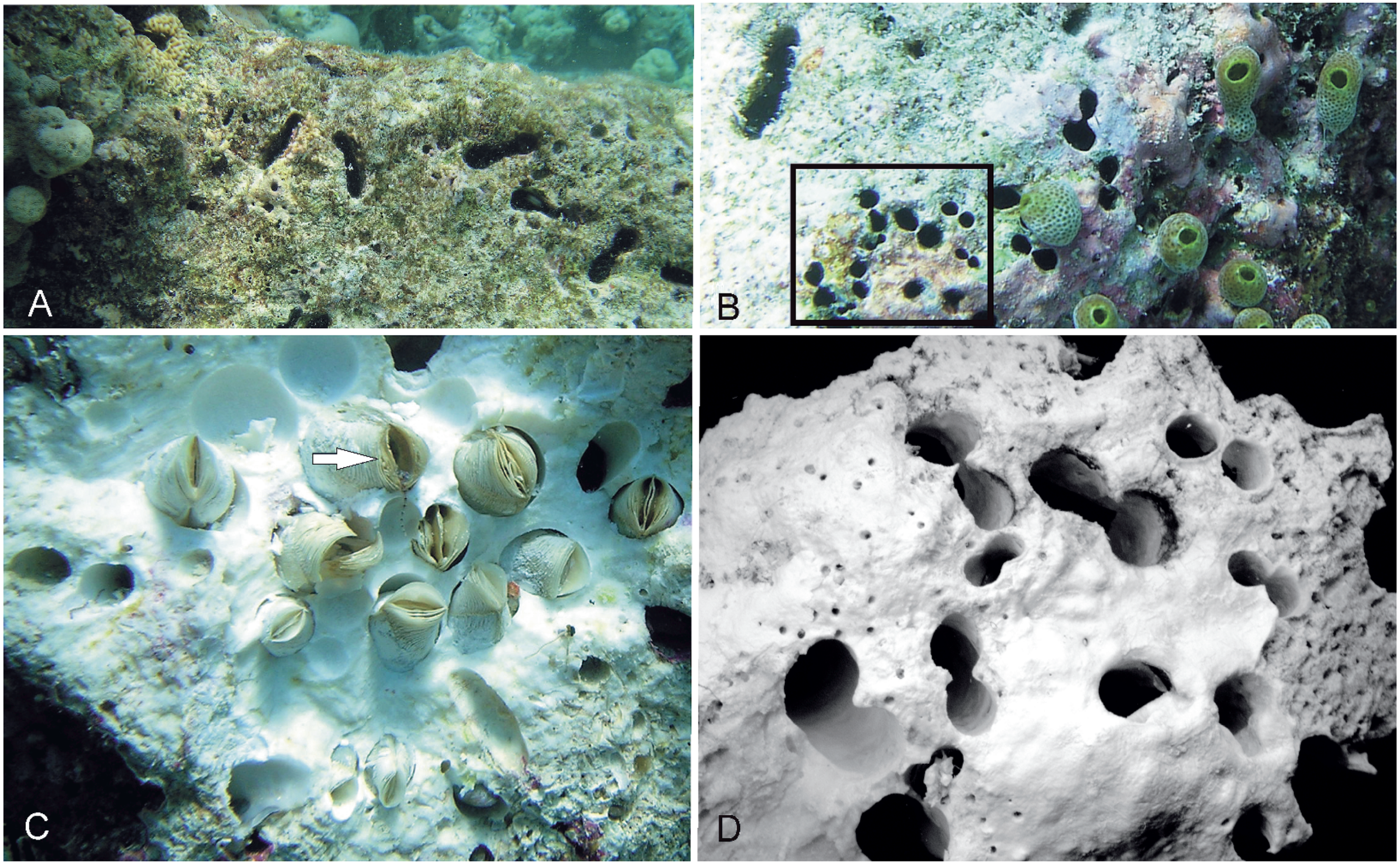
Dead coral surfaces with apertures of endolithic bivalves were selected from the reef top down to 12 m depth using SCUBA. From sites of special interest, images were taken with a digital camera (Camedia 350 Zoom) in an under-water-housing before and after opening the dead coral with hammer and chisel. The coral was split open in several steps in order to preserve as many of the bivalves as possible undamaged and to observe more details of the endolithic community structure. All dislodged specimens were put into small mini-grip plastic bags, which were secured in a wide-necked plastic bottle and attached to the dive jacket for safe transport to the vessel, where further treatment followed. Small specimens were preserved in pure ethanol for DNA analysis. Others were put in 70% ethanol or 5-10% formaldehyde in seawater. In the laboratory, bivalves and coral samples were investigated in more detail using a dissecting microscope, dental surgery tools, callipers and photographic equipment (Coolpix 4500). Corals were cleaned with household bleach and H_2O_2.

Results

General observations and species found

In the field, the relatively large, 2-4 cm wide and dumbbell-shaped borehole openings of the mytilid bivalve *Leiosolenus obesus* (Philippi, 1847) were very conspicuous, especially when in small groups in dead massive coral (Fig. 2A). This species was the largest lithophagine bivalve in the collected material, with specimens reaching almost 10 cm in length (Kleemann 1984; Owada 2007). Next in length was *Lithophaga nigra* (Orbigny, 1842), known from the Maldives and other Indo-Pacific reefs under the junior synonym *Lithophaga teres* (Philippi, 1846); (see Kleemann 1984). Only a few specimens occurred in the samples of dead coral and the largest measured 65.2 / 16.0 / 13.0 mm in length / height and width (diameter), respectively. Further species found in this material consisted of quite common specimens of *Leiosolenus malaccanus* (Reeve, 1857), a single individual of the crenellinine *Gregariella coralliophaga* (Gmelin, 1791), two petricolids *Petricola lapicida* (Gmelin, 1791), and a few specimens of the gastrochaenid *Gastrochaena cuneiformis* (Spengler, 1783), *G. dentifera* (Dufo, 1840) and unidentified species (Carter et al. in press). Unexpectedly, the martesiinid *Parapholas quadrizonata* (Spengler, 1792) was most numerous and occurred in very dense assemblages. The external coral surfaces are riddled with the paired apertures which lead to the flask-shaped chambers occupied by the shells themselves. Each paired aperture may be figure-of-eight shaped and lined with a calcareous sheath (equivalent to *Teredolithus* Bartsch, 1930; see Kelly and Bromley 1984: 796; Fig. 2B), a configuration generally well-known from species of *Gastrochaena* Spengler, 1783 (Carter 1978; Nielsen 1986; Kleemann 1998).

Population density of boring bivalves in general seemed to be distinctly higher (1) on the reef flat near the reef edge and the shallow reef slope to about 3 m depth than in deeper samples, and (2) in massive dead coral versus those in ramose corals and coral rubble. No quantitative samples were taken.


A
B
C
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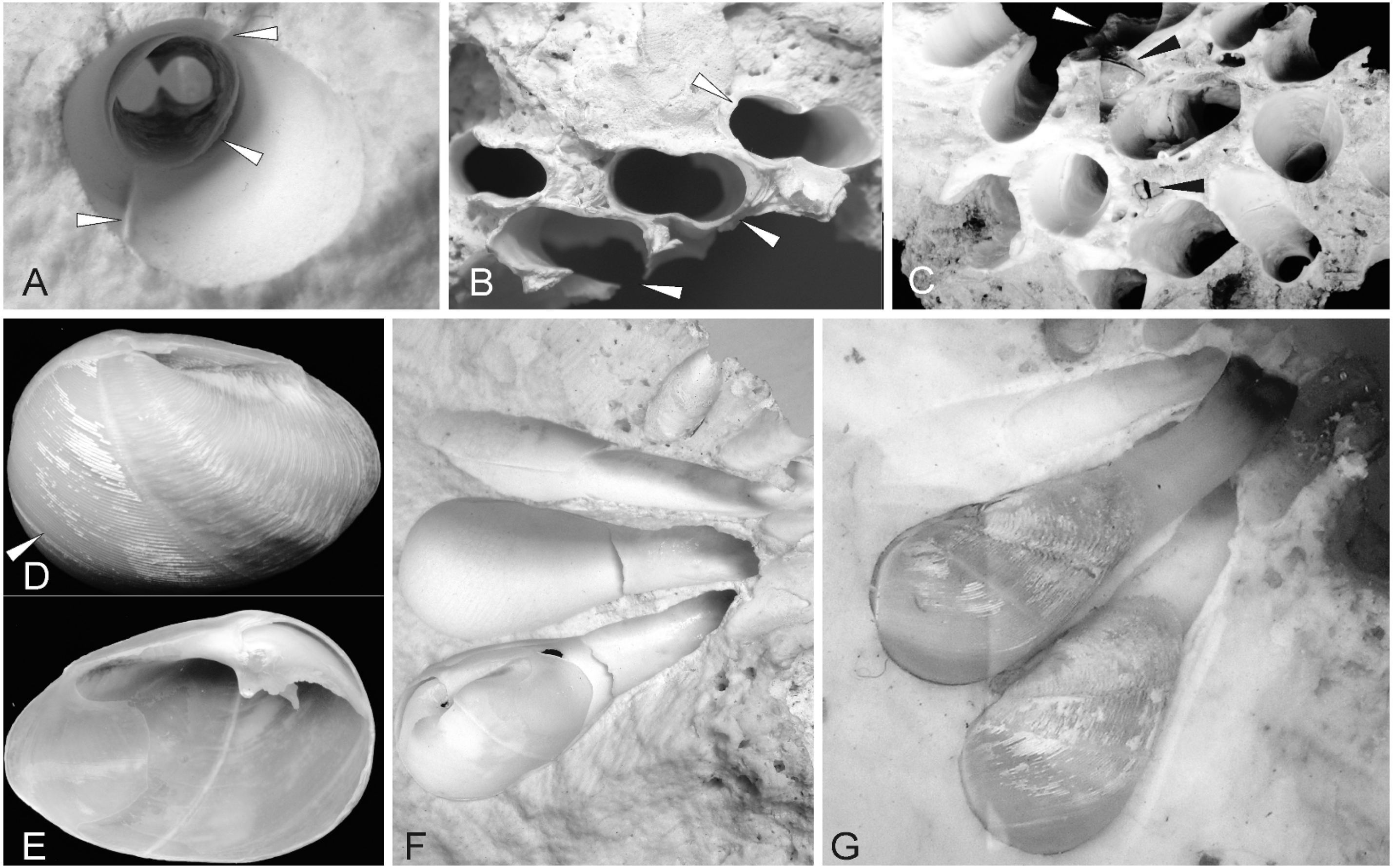
The shell morphology

The living shell of *Parapholas quadrizonata* and its borings are shown in Figures 2C and 3D-G. The general morphology is explained in Figure 4 and measurements are given in Table 1.

According to Turner (1998: 375), *Parapholas* Conrad, 1848, as a member of Martesiinae, has an apophysis, mesoplax, metaplax and hypoplax, and the presence of the callum is the most distinctive feature of the subfamily. Nielsen (1986) pointed out the commarginal sculpture of fine wavy ridges anteriorly, with the posterior part being covered by overlapping, fan-like protrusions of the straw-coloured periostracum. Additional features include the *'wide, drop-shaped pedal gape, which in the adult phase becomes closed by a callum from each valve meeting in the middle and united by a narrow zone of thin, brown periostracum.'*. He did not mention the middle lateral part of the shell, lying between two separate lines, which run different lengths from the umbo posteriorly to the ventral shell edge, yielding an oblique and arcuate, slender triangular field, named *'disk'* (Kelly 1988: 348; Fig. 3D). Anteriorly, the surface of this field is smoother than the anterior part of the shell, and posteriorly it becomes somewhat more coarsely sculptured at the beginning of the posterior part of the shell, resulting in an elevated stripe (Fig. 3D). Dorso-posteriorly of the middle part, the calcareous shell surface is still sculptured by commarginal but more pronounced and spaced ridges (Fig. 3D), and is covered by protruding periostracal lamellae (Figs. 2C, 3G). They are closely arranged like short scales in a series of increasing width and length towards the posterior. The periostracal lamellae cover the actual posterior shell surface and prolong its rim up to several millimetres forming a collar, e.g., a calcareous shell measuring 28.5 mm in length is extended by 4.5 mm giving a total of 33 mm by measuring the periostracum. The collar extends into the narrow space between the wall of the shell-chamber and the obliquely protruding constriction at the beginning of the siphonal tube (see below). In household bleach, the periostracum may be dissolved completely and therefore the lamellae are missing in Figures 3D-F and the line-drawing Figure 4.

Fig. 2 **A** Dumbbell-shaped borehole apertures of aggregated *Leiosolenus obesus* in massive dead coral, ~3 m depth, Kagi, North Male Atoll (N 04°40.5' E 73°30.8'). Frame size ~40 x 20 cm. **B** Mainly figure-of-eight-shaped apertures of predominating *Parapholas quadrizonata* and, in the upper left corner, one of *L. obesus*, in massive dead coral; the synascidian *Didemnum* Savigny, 1816 specimens at right indicate a steeply inclined surface. Water depth ~2 m, Beyrumadivaru, Ari Atoll (N 04°07.3' E 72°56.5'). Whole frame size ~15 x 7.5 cm, secondary frame ~45 x 30 mm (enlarged in D). **C** Assemblage of *Parapholas quadrizonata* in borings, with siphons completely retracted, in anterior view in freshly broken dead coral depicted in B. The serial periostracal lamellae form a collar at the shell posterior; the last-formed are not yet the longest. Note also the varying orientations of specimens. From the largest empty shell one arm of an ophiuroid (arrow) is protruding. Frame size ~15 x 11 cm. **D** Coral fragment from framed area in B. Note the different sizes of figure-of-eight apertures of *Parapholas quadrizonata*, rarely separated into two openings of the same calcareous tube (two at the right). This indicates the repeated, probably more than annually occurring infestation of the same spot by successive generations of veligers. Frame size ~45 x 30 mm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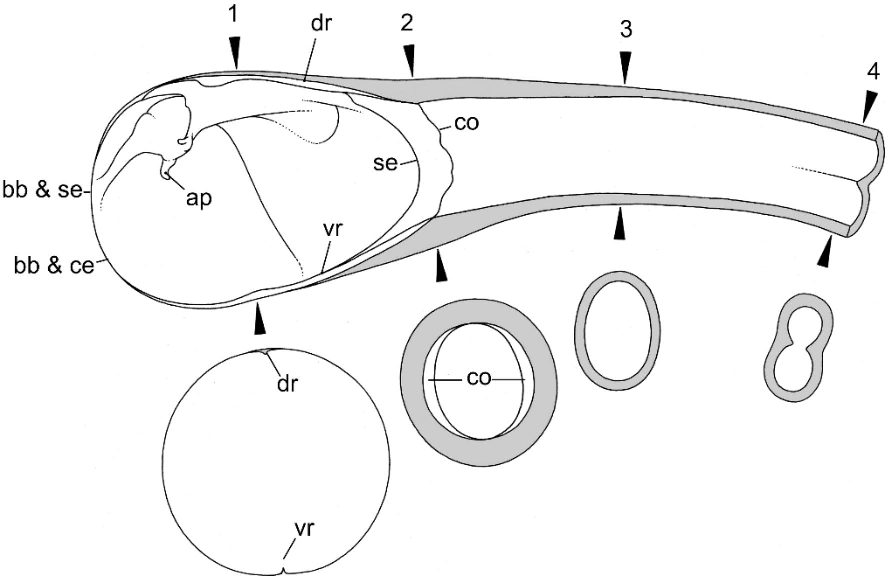

Fig. 4 Line drawing of the right valve of *P. quadrizonata* in its boring in lateral, internal view. Numerals 1-4 indicate the location of cross-sections, the pairs of black pointers show their respective position along the boring. ap = apophysis, bb = borehole base, ce = callum edge, co = constriction, dr = dorsal ridge, se = shell edge, vr = ventral ridge. Note the variation in thickness of the calcareous lining (shaded) between cross-sections 1-4. Note the three unique features of the boring, which are a dorsal and a ventral ridge and the velum-like constriction (Fig. 3A, C, F). The valve lacks periostracal lamellae on its posterior shell edge due to dissolution in commercial bleach (compare with Figures 2C and 3G)

Fig. 3 **A** Transversely opened *P. quadrizonata* boring revealing the posterior part of the shell-chamber with the unique features, the dorsal and ventral ridge, both leading to the velum-like constriction (pointers). Note that the tube opening in the background is turned right about 45° from the sagittal plane of the chamber. Frame size ~3 x 2.5 cm. **B** External view of apertures of calcareous-lined siphonal tubes of several *P. quadrizonata* individuals penetrating dead coral. The exterior surface is slightly eroded. Three apertures are from borings illustrated in **G** (pointers). Length of central aperture 12.5 mm, frame size ~35 x 25 mm. **C** Lower surface of coral chip figured in figure 2D, with maximal thickness of 20 mm. Note two bivalves (black pointers), in situ in borings between densely packed adjacent borings; parts of the callum halves are exposed. These had no free space ahead, but survived long enough to construct a callum. The encrustations in one tube indicate the constructor died (white pointer). Frame size ~45 x 25 mm. **D** Left valve of *Parapholas quadrizonata*, 34.5 mm length, in lateral external view; showing the callum (pointer) – the typical feature of Martesiinae – but lacking the periostracum with lamellae through bleaching. See E for interior and G for life position. **E** Same specimen as in D in lateral internal view. For similar view of right valve F, lower left corner. **F** Similar view to G with most of the shell material and soft parts removed and specimen bleached; one right valve of *P. quadrizonata* remains in the lower boring showing the interior aspect. For left valve see D-E; see text and compare with line-drawing (Fig. 4). Frame size ~75 x 90 mm. **G** Freshly split longitudinally opened borings containing live *P. quadrizonata*. Note the tight fit of the shells in the chambers and the inhalent and exhalent siphon showing lengthwise fusion except at the distal ends. Frame size ~75 x 70 mm

Table 1 Shell dimensions of 42 *Parapholas quadrizonata*, collected from ~25 x 25 cm of the dead coral shown in Figures 2B-D and 3F-G. Measurements are given in millimetres for length (L; with lamellae, to the closest half mm), height (H) and width (W). Missing measurements, caused by fractured specimens, are indicated by '?'. Specimens marked with '*' indicate measurements of three specimens with an atypical calcareous girdle at their maximum diameter

Specimens with callum (n = 13, mean length 30.0 mm)			Specimens without callum (n = 29, mean length 22.4 mm)		
L	H	W	L	H	W
44.0	24.0	~24.0	34.5	16.5	18.4
41.5	23.2	23.2	33.0	15.8	17.8
40.0	22.6	22.1	33.0	14.9	16.2
37.0	~20.5	?	32.0	16.3	?
37.0	20.3	?	32.0	15.0	?
34.0	20.0	~20.0	31.0	15.6	15,8*
29.0	14.0	?	30.1	13.0	?
26.0	15.2	14.4	30.0	14.3	16.7
26.0	14.4	14.1	29.0	15.4	17.1
22.6	11.1	11.5	28.0	~13.5	?
19.0	10.7	10.3	~27.0	14.1	15.3
19.0	10.5	10.8*	22.5	11.5	12.2
15.0	8.2	7.7	22.0	10.6	10.9
			21.0	?	11.3
			20.3	?	?
			20.0	8.7	9.1
			19.5	10.5	10.6*
			18.5	9.0	10.3
			18.5	8.8	10.2
			18.5	8.8	9.1
			17.0	9.0	?
			~17.0	?	?
			16.0	8.5	9.6
			15.0	7.6	8.2
			15.0	7.0	7.3
			13.0	6.8	7.4
			12.0	6.1	7.1
			12.0	5.8	6.9
			11.0	5.3	5.9

In respect to the soft body, the large, drop-shaped base of the foot is worth noting, mirrored by the gape between the shells (as long as no callum halves are developed, separated by periostracum of individually differing width). Also, the longitudinally fused siphons, separated only at the distal end, form a paired opening with figure-of-eight shaped aperture formed by the calcareous tube they secrete (Figs. 2B, D, 3A-B).

The borehole morphology

These are very typical clavate bivalve borings, comparing well with those described by Kelly and Bromley (1984). From the outer coral surface into the substratum, the clavate borings are composed of a siphonal tube and a shell chamber, separated from the tube by a velum-like constriction, slightly protruding into the cavity on both longer sides of the slightly oval-shaped cross-section (Figs. 3A, C, F, 4). This structure is part of the solid lining of the borehole wall, and is not perpendicular but inclined towards the shell-chamber (Fig. 3A, C, F).

The right valve in Figure 3F fits so tightly into the chamber, despite the missing periostracum, that it is prevented from falling out by two ridges in the longitudinal, dorso-ventral plane. The dorsal ridge appears to be part of the calcareous lining of the boring by the bivalve, while the ventral one seems to be a remnant of the dissolved substrate, in this case the dead coral *Porites* Link, 1807. As shown in the drawing (Fig. 4), the shell-chamber, being distinctly wider than the siphonal tube and more or less circular in cross-section, has a hemispherical anterior and a somewhat conical posterior half. This closely mirrors the shape of the slightly smaller constructor due to the developed callum (Figs. 3D, G, 4). The siphonal tube reaches from the velum-like constriction (Fig. 3A), which separates it from the shell-chamber, to the outer substrate surface. There it is usually figure-of-eight-shaped, rarely separated into two rounded openings, of which the exhalent one is circular (Figs. 2B, D, 3A-B). Except near the outer surface, tube cross-sections are oval, widest near the chamber and narrowing gently towards the entrance to the boring, before flaring at the exterior surface (Fig. 4). Length / width of the apertures in Figure 2D is 4.5 / 2 mm, 5.2 / 2.4 mm, 6.7 / 3.2 mm, 7.5 / 3.5 mm, 8.0 / 4.5 mm, 9.0 / 4.6 mm, and 10.1 / 5.0 mm. Figure 2D shows a paired siphonal opening partly overgrown and constricted by post-mortal growth of coralline algae and therefore strictly should not be included, however estimated measurements are: 12.5 / 5.5 mm.

The assemblages

The assemblages were composed of groups of specimens belonging to different size-classes, ranging from 11 to 44 mm in length. These values were also reflected in the sizes of the boreholes and their openings. The latter reach up to 14 mm in maximum length and 7.5 mm in maximum width of the usually undivided siphonal apertures (Figs. 2B, D, 3A-B). The distance between adjacent openings was often very narrow to minimal (Fig. 3B). Consequently, the space between the respective borings was even narrower (Fig. 3C), as their diameter increases with depth. Thus borings sometimes lie in direct contact with neighbours, but the calcareous linings do not generally intersect (Figs. 2C, 3B-C, F-G). In other borers, such as *Lithophaga* Röding, 1798 and *Leiosolenus* Carpenter, 1856, borings without and with calcareous linings do intersect (Kühnelt 1930; Kleemann 1974, 1980; Owada 2007). The largest assemblages of *P. quadrizonata* were found in massive coral, although smaller individuals were present in various dead corals including rubble.

Discussion

Regarding its biology, *Parapholas quadrizonata* is a poorly known bivalve, with few records in the literature, although its wide geographical distribution is Indo-Pacific (Oliver 1992: 203, noting it from Aden, Red Sea). Nielsen (1986) described the species from Phuket, Thailand, in association with the coral *Porites*. Turner (1998: 375) mentioned *Parapholas* as a member of Martesiinae occurring in Australia. I have observed only 21 specimens of *P. quadrizonata* (ranging from 7 to 30 mm in length) at Lizard Island, Great Barrier Reef (Australia) in three weeks, but none in the northern Red Sea during several months of study. According to the present findings, peak population densities probably occur at the Maldives.

The largest *P. quadrizonata* in the present study, measuring 44 mm in length, is only 6 mm short of the reported maximum size of 50 mm (Oliver 1992); the smallest specimen is 11 mm. On the other hand, Nielsen (1986) noted a maximum diameter of 34 mm (probably because shell length, without periostracal lamellae, is difficult to measure) in comparison with 24 mm in the Maldives samples; presumably, his 34 mm wide specimens from Phuket, Thailand, reached about 60 mm in total length including the periostracum.

The four zones of the shell, which give rise to the specific name *quadrizonata*, include the smooth callum (or the wide gape, if not developed), the fine, commarginally sculptured anterior part, the middle part between the two lateral oblique lines, and the dorso-posterior section, covered by the flexible lamellae (Fig. 3D, E, G).

As in gastrochaenids and various other boring bivalves, the calcareous lining, which changes markedly in thickness along the siphonal tubes (Figs. 3F-G, 4), is supposedly secreted from the bivalve's siphons and mantle tissue. The velum-like constriction (Fig. 3A, C, F) differs distinctly from structures found in some *Eufistulana* Eames, 1951, *Gastrochaena* and *Spengleria* Tryon, 1861 species (Gohar and Soliman 1963; Soliman 1973; Carter 1978; Morton 1983; Nielsen 1986).

The different size-classes of shells in the aggregations of *P. quadrizonata* may be primarily the result of successive generations, probably annual, of veligers infesting the same site. A second possibility must be considered due to intra-species space competition. When specimens become crowded by neighbours of probably the same age (Fig. 3C), they stop growing and build a callum as so-called stenomorphs (Bartsch 1923). Stenomorphs are adults of dwarf size but not necessarily immature. They appear to survive for years, feeding and reproducing, but unable to grow. Overlaps between adjacent borings in live *P. quadrizonata* were not observed. At Phuket, Nielsen (1986) noted a 15 mm shell as the smallest with a callum, the same size as one individual in the present material. A further reason to develop a callum before being fully grown could be if an individual has lengthy pauses between phases of growth or reproduction. There were, however, no indications for this based on shell structure. This may be worth investigating in more detail. There may also be clues hidden in the layered structure of the lining. Specimens less than ~10 mm in length may have been overlooked in the few samples available, or may be missing owing to collecting date (perhaps before or too soon after a new settling season).

The siphonal tube usually extends up to or a little above the substrate surface, but is not usually chimney-like and not separated into two openings, as stated by Nielsen (1986) in his findings at Phuket. No prominent elevations and only a few isolated ('closed' figure-of-eight) apertures were noted (Fig. 2B, D).

The borehole morphology of *P. quadrizonata* fits best to a mixture of *Gastrochaenolites dijugus* Kelly and Bromley, 1984 and *G. turbinatus* Kelly and Bromley, 1984 (Kelly and Bromley 1984: fig. 3). It shows some unique and thus characteristic features for a determination and differentiation from the otherwise very similar borings of certain *Gastrochaena* species, e.g., *G. dentifera* (Dufo, 1840). Alas, the fossilisation potential of these fine structures is poor and therefore the probability to establish a new ichnospecies is minimal. The size of intact tube apertures are suitable as a rough age indicator (because stenomorphs and *Gastrochaena* specimens are mostly rare), once a relation between size and age is established. So far only estimates can be proposed. Considering an estimated growth rate of 10 mm a^{-1} (no smaller specimens were found, but may have been overlooked), an estimated age of at least 4 years for the largest specimens (and apertures) should be on the conservative side because growth in length usually decreases with age.

The three unique borehole features of a dorsal and ventral ridge in the shell chamber, and the constriction at the beginning of the siphonal tube, are probably better recognisable in the cross-sections (1 and 2, respectively) than in the schematic longitudinal section of the boring with the right valve in the chamber preserved (Fig. 4, compare with Fig. 3A, C, F). These features are not always well developed, and three of the collected specimens have a calcareous girdle at their largest diameter. I have only a hypothesis for the former situation and no explanation for the latter circumstance. Presumably, growth is not a continuous process and the likely seasonal increase of a boring necessarily shifts the position of velum-like constriction. When the shell-chamber increases, the above features may become (partly) dissolved. The constriction of the boring probably functions as a holdfast in conjunction with the lamellae of the shell during hydraulic and / or boring activities, perhaps even as a lock in case of a major disturbance. At times of stress the bivalves can retract the extendable siphons completely (Figs. 2C, 3G). The cross-sections 3 and 4 (Fig. 4) through the siphonal tube are similar to or indistinguishable from those of certain *Gastrochaena* species (Gohar and Soliman 1963; Nielsen 1986; Kleemann 1998).

Considering (1) the common, dense aggregations of boring bivalves in dead coral rock at shallow depth in several Maldivian reefs, which probably promoted spawning success and yielded abundant larval recruits trying to find appropriate settling places, (2) the decrease of substrate volume up to ~50%, from its surface to ~2 cm depth (Figs. 2C, 3B-C), and the borehole dimensions of *P. quadrizonata* reaching 80 mm in length and 25 mm in diameter near the deep end and an estimated volume of up to ~20 ml, and (3) an estimated life-span of 3-8, probably 10 years, the impact of these bivalves on reefs with less than 50% live coral cover may be severe and accelerate their decline. Particularly accelerated by boring sponges, parrotfish and other bio-erosive organisms, competing for available space as well as food, destroy more substrate than frame-builders are able to construct at the same time. Therefore, the situation is already tense at some reefs with poor coral recovery since 1998, e.g., at Kalhuhuraa, South Male Atoll, while some others are in astonishingly good shape, e.g., at Kandholhudoo, Ari Atoll (Fig. 1; Wallace and Zahir 2007).

The biology – including life-span, local population density and depth distribution, growth, boring and succession rates – of this dominant boring bivalve needs to be investigated in detail for a better understanding of its impact on the reef system. This should provide answers to key questions such as: is spawning and reproduction a brief or a prolonged seasonal annual event or more or less permanent? Are there recognisable shifts in population density and local distribution within a few years?

Conclusions

- *Parapholas quadrizonata* is the most abundant dead-coral boring bivalve in the Maldives.
- The largest specimen measured 44 mm in length and 24 mm in width, the smallest 15 mm (with callum).
- Successive recruitment on massive dead coral lead to dense assemblages of variously sized and oriented individuals.
- No intra-specific competition was observed.
- Boreholes were up to 80 mm in length and 25 mm in diameter and borehole volume may reach 20 ml.
- Aperture size in borings may originally indicate size / age of occupant, but may be modified by bioerosion of outer surface by other organisms or by accretion.
- Borehole morphology and the presence of dorsal and ventral ridges and the velum can be used to distinguish the vacant boreholes of *P. quadrizonata* from those of *Gastrochaena* species.
- Boreholes resemble a mixture of *Gastrochaenolites dijugus* and *G. turbinatus*.

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