THE 'WATER-TRAP' SPINY OYSTER, *SPONDYLUS VARIUS* G.B. SOWERBY I, 1827 (MOLLUSCA: BIVALVIA: SPONDYLIDAE) FROM AUSTRALIA

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Spondylus varius G.B. Sowerby I, 1827, the largest member of the pectinoidean family Spondylidae, is recorded for the first time from Australian waters. Previously known from the Philippines, the Solomons and New Caledonia, it is now recorded from Orpheus and Lizard Islands in northern Queensland. A neotype is established for *S. varius* because: 1) no type material appears ever to have been deposited and no illustrations accompany Sowerby's original description; 2) validity of the species has been questioned; 3) juveniles of *S. varius* can potentially be confused with other species of *Spondylus* (especially *S. echinatus* and *S. castus*). Aside from its exceptionally large size (rv height up to 400mm), *S. varius* is also unique among the Spondylidae in often producing water/gas-filled chambers (defined by thin, shell septa) in one or both of the valves in mature specimens (> 100mm, sometimes occurring in subadult specimens) especially those living in coral overhangs or threatened by epibiont smothering. These chambers possibly play a role in maintaining the position of the animal in relation to the shell margin, thereby optimising water current flow (and therefore feeding and respiration). Given the extremely odorous quality of the enclosed liquid (an acidic, saline solution) the chambers could also act as a last resort deterrent to predation. A total of 55 species of Spondylidae are now recorded from Australia. ❐ *Spondylidae, Pectinoidea, spiny oysters, bivalves, Australian fauna, new record, neotype.*

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The waters around the Australian coastline are prolific in bivalve molluscs but especially so in tropical and subtropical areas which share several species with adjacent regions of the Indo-Pacific (Lamprell & Whitehead, 1992; Lamprell & Healy, 1998). Featuring prominently within the Australian molluscan fauna are the Spondylidae ('spiny oysters'), with 54 previously recorded species (Lamprell & Healy, 1998). Although several species are known from the southern states, including some endemics (Lamprell, 1992), the Spondylidae are more speciose off the subtropical to northern Australian coastline.

During November 1998, one of us (JK) collected a very large spondylid from shallow water off Orpheus Island, northern Queensland. After cleaning and close inspection, the species was determined as *Spondylus varius* G.B. Sowerby I, 1827 — a new record for the Australian bivalve fauna. A subsequent search of the collections of the Australian Museum (Sydney) revealed other specimens of this species. *Spondylus varius* is probably the largest spondylid to have ever existed, reaching a maximum of 400mm in shell height (umbones to ventral margin — measurement based on in situ measurements of Solomon Islands specimens, P. Clarkson, pers. comm.). Only the tropical Atlantic species *S. limbatus* G.B. Sowerby II, 1897, rivals the dimensions of *S. varius* (up to 267mm maximum height according to Eisenberg (1981)). Together with the giant clams (Tridacnidae) and pen shells (Pinnidae), *S. varius* and *S. limbatus* rank among the largest of the extant Bivalvia. In addition to its exceptionally large size, *S. varius* is also unique among the Spondylidae for its habit of often producing fluid and gas-filled chambers sometimes referred to as water-traps' (Lamprell, 1986) in one or both valves. This phenomenon was investigated by Sir Richard Owen (1837, 1838) who concluded that chamber production in *S. varius* was probably a response of the animal to overgrowth from encrusting life such as corals.

Juvenile *S. varius* differ from adults in colour and, usually, in the absence of water-filled chambers, leading to difficulty in identifying immature specimens and confusion with other species such as *S. echinatus* Schreibers, 1793 and

S. castus Reeve, 1856. Tomlin (1937: 350) considered Sowerby's (1827b) original description as vague and possibly based on material of more than one species.

The purposes of the present account are to: 1) record *Spondylus varius* in Australian waters; 2) establish a neotype; 3) clarify the publication date; 4) provide a revised diagnosis based on material from the entire known range and 5) discuss possible functions of the fluid and gas-filled chambers.

MATERIAL AND METHODS

The living specimen of *Spondylus varius* G.B. Sowerby I, 1827 was collected at depth of 10m, attached to a slight coral overhang, off the point between Pioneer Bay and Hazard Bay, Orpheus Island (18°36'S,146°29'E) during November, 1998. The specimen was photographed in the aquarium at the Orpheus Island Research Station to record the distinctive mantle pattern. After removal of the animal (for later gonad studies) the shell was partially cleaned of excessive coral encrustations by overnight immersion in 10% w/v sodium hypochorite solution. The shell is now deposited at the Queensland Museum (QMMO67048). For comparison with the Australian specimen, material from the Solomon Islands and the Philippines (all Lamprell Collection), and the Natural History Museum (London) (the specimen figured by G.B. Sowerby II (1847) and Reeve (1856)) are also figured. Height measurements are from umbones to ventral margin; width measurements are from anterior to posterior margins.

Abbreviations: AMSC = Australian Museum, Sydney; BMNH = Natural History Museum, London; I = Island; KL = Lamprell Collection; lv = left (or top) valve; pv = paired or conjoined valves; Qld = Queensland; rv = right (or lower) valve.

SYSTEMATICS

FAMILY SPONDYLIDAE Gray, 1826

Spondylus Linnaeus, 1758.

TYPE SPECIES. *Spondylus gaederopus* Linnaeus, 1758, by subsequent designation of Schmidt, 1818: 61.

Spondylus varius G.B. Sowerby I, 1827 (Figs 1-6)

Spondylus varius Sowerby, 1827; G.B. Sowerby I, 1827b:1-2; Tomlin, 1937: 350; 1943: 143.
Spondylus varius Sowerby, 1829; [sic] Fulton, 1915: 358, sp. 71; Lamprell, 1986: 68, pl. 25, fig. 2.
Spondylus varians Sowerby, [sic, no date specified]; G.B. Sowerby II, 1847: 426, pl. 86, figs 21, 22; Reeve, 1856: sp. 3, pl. 1, fig. 3; Hanley 1842-56: 293
Spondylus varians Sowerby, 1829 [sic]; Springsteen & Leobrera 1986: 325, pl. 92, fig. 16.
Spondylus delessertii Chenu, 1845: 5.

TYPE LOCALITY. Not stated by Sowerby (1827b); type locality of neotype (here designated; specimen BMNH 1952.10.30.3): 'Pacific Islands' (locality as stated on label).

TYPE MATERIAL. NEOTYPE (here designated; Figs 1A-E, 6B): 1 pv BMNH 1952.10.30.3, 'Pacific Islands' (locality as stated on label). Figured by Sowerby, 1847, pl. 86, fig. 21 and Reeve, 1856, pl. 1, sp. 3. Dimensions of neotype (excluding spines): lv height 154mm, width 137mm; rv height 169mm, width 140mm; pv height 169mm, width 140mm, depth 70mm; (measurements including spines) - lv height 163mm, width 143mm; rv height 174mm, width 155mm, pv height 179mm, width 155mm, depth 75mm.
OTHER MATERIAL. (all measurements excluding spines; Table 1) AUSTRALIA: AMSC104588 Watson Bay, Lizard I., Qld, 14°40' S, 145°27'E, 2.5m among corals and sand lv height 195mm, rv height 255mm, pv depth 100mm; AMSC150016 Orpheus I., Qld, 18°36'S, 146°29'E, 10m base of bommie, 1pv, lv height 155mm, rv height 200mm, pv depth 80mm, water chambers on lv; 1pv QMMO67048 approximately 10 m depth attached to a slight coral overhang off the point between Pioneer Bay and Hazard Bay, Orpheus I., Qld, 18°37'S, 146°30'E, rv height 170mm, lv height 138mm, pv depth 94mm, water chambers in both valves (see Figs 2A-D, 3A,B). NEW CALEDONIA: AMSC100790 Noumea, ex- aquarium, lv height 175mm, rv height 220mm, pv depth 90mm, water chamber on lv; one rv with water chamber (no data); Sud nouvelle Caledonie 2pv Grotte Merlet, 22°42.4'S, 166°41.2'E, 20-30 m, 21.1.1993, lv height 190mm (for figures see Lamprell & Healy, 2000). SOLOMON ISLANDS: AMSC303014, 1 pv, off Bonegi I shipwreck (lv height 115mm, rv height 135mm, pv depth 80mm, water chambers in both valves) (specimen figured by Lamprell, 1986); KL, 4 pv, off Bonegi I. shipwreck, 43m: spec 1 lv height 85mm, rv height 93.2 small water chamber in lv; spec 2 lv height 62mm, rv height 72.2mm, large water chamber in lv; spec. 3 lv height 56mm, rv height 65mm, water chamber in lv; spec. 4 lv height 36mm, rv height 42mm, water chambers absent (Fig. 3C,F); PHILIPPINES: KL, off Cebu I., spec 1 lv height 94mm, rv height 113mm, water chambers absent; spec 2 lv height 99mm, rv height 113mm, water chambers in both valves (Fig. 3D,E); NO DATA: KL, ex Rombouts collection, 1 pv, no locality data lv height 210mm, rv height 240mm, water chamber (empty) in both valves (senescent specimen; Fig. 5A-C).

DIAGNOSIS. Shell height of pv to 400mm; elongate-ovate; inequivalve, top valve (lv) usually depressed to slightly inflated; lower (rv) appreciably deeper than lv. Sculpture of lv with numerous, low, irregular, radial ribs ornamented with dense, slightly flattened, raised or depressed

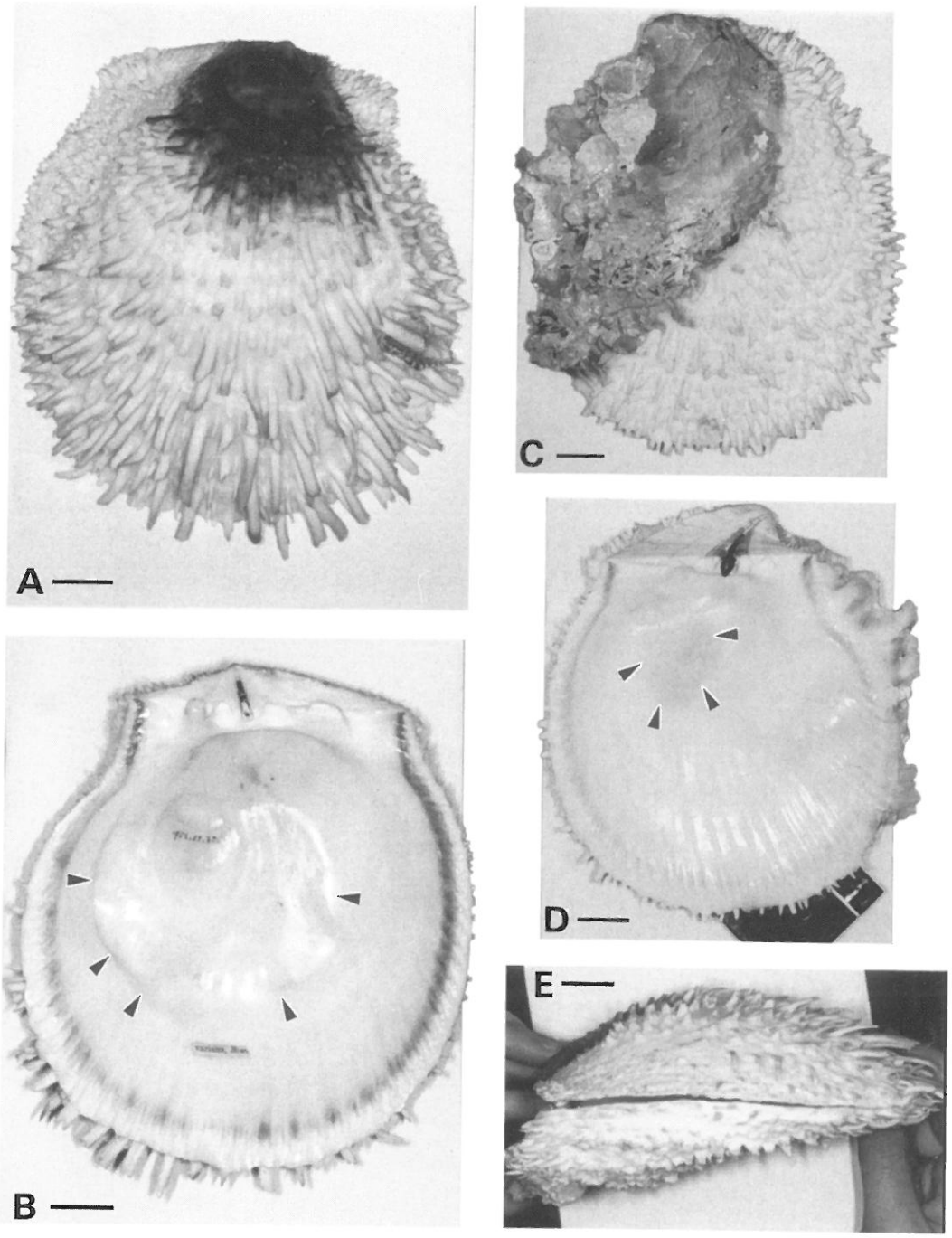

FIG. 1. *Spondylus varius* Sowerby, 1827. Neotype (here designated) 1 pv BMNH 1952.10.30.3, 'Pacific Islands' (locality as stated on labels). Figured by G.B. Sowerby II, (1847) in the Thesaurus Conchyliorum: pl. 86, fig. 21 (see Fig. 6B herein) and Reeve, (1856) in the Conchologia Iconica: pl. 1, sp. 3. A, External view of lv. B, Internal view of lv showing visible (but empty) water chamber (arrow heads). C, External view of rv. D, Internal view of rv showing visible (but empty) water chamber (arrow heads). E, Profile view of pv. Scale bars = 20mm.

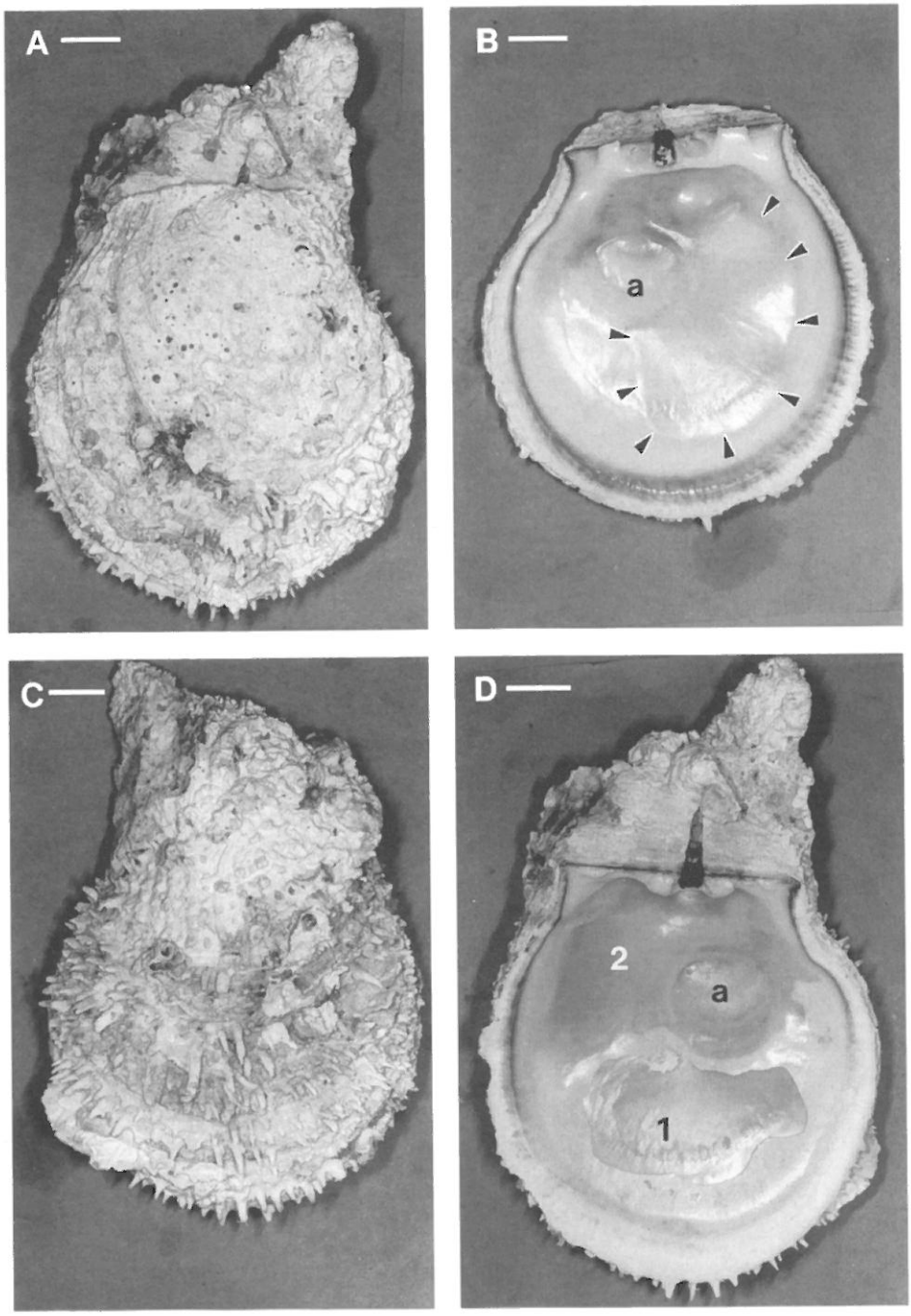

FIG. 2. *Spondylus varius* Sowerby, 1827. A-D, Specimen from 10m, between Pioneer Bay and Hazard Bay, Orpheus I., Queensland, 18°37'S, 146°30'E (QMMO67048). A, External view of pv from aspect of lv. B, Internal view of rv showing the visible water chamber (arrow heads). C, External view of pv from aspect of rv. D, Internal view of rv showing two visible water chambers. Note broken uppermost water chamber overlying most of lower (intact) water chamber (the latter indicated by arrow heads). Scale bars = 20mm.

ribs in juvenile specimens (< 100mm rv height), becoming longer towards ventral margin. In mature specimens (100-400mm rv height) spines sometimes long but usually short, blunt and appressed (extremely stunted in specimens over 200mm rv height); interstices in uneroded specimens have fine, dense appressed spines. Rv with similar radial ribs to those of lv; ornamentation of foliations extending out from umbonal (fixation) area; remainder of rv similarly spined to lv. Hinge line broad, straight, showing typical spondylid dentition of two, large, isodont teeth on rv, fitting into sockets on lv; ligament and ligament pit between teeth/sockets. Auricles broad. Externally, shell usually white, almost always with a clearly defined orange-red-purple area umbonally which occasionally extends into the spines or over entire shell length (especially in small juveniles < 50mm rv height). Internally, glossy white with yellow-orange margin. Radiating ribs visible internally, stronger marginally forming a strong, wide crenulated margin. Mature and senescent specimens (height of rv 100-400mm, excluding spines) often exhibiting fluid and gas-filled, vertically-stacked chambers within one or both valves. Chamber septa composed of smooth, translucent shell, associated with or completely surrounding the adductor scar (rarely passing partially under scar). Chambers sometimes also occurring in juveniles (of rv height 60-80mm, excluding spines) but absent in smaller specimens (rv height < 60mm). Fluid from chambers usually lost through evaporation over an extended period of dry storage (or rapidly if septum is cracked). Table 1 lists the incidence of externally detectable water chambers in material examined herein. For material <100mm in shell height the absence of chambers represents a verifiable absence of these structures, whereas in thicker, more mature specimens, the absence of visible, surface chambers (that is, ones which are fluid/gas-filled in fresh material) in one or both valves does not necessarily preclude the presence of one or more lower (empty) chambers.

OBSERVATIONS ON LIVE-COLLECTED SPECIMENS. The live-collected specimen from Orpheus I. (Figs 1A-D, 2A-D, 3A,B, 4A,B) has lv 170mm in height, and 130mm in width (from anterior to posterior margin in the lv). Although considerably encrusted with calcareous material, treatment with commercial hydrochloric acid soon revealed the external colour to be white with some traces of red-purple umbonally. The rv contains two visible water chambers, one overlying the other (Figs 2B,D, 4A,B) whereas the lv exhibits only a single visible chamber. The presence of fluid within the chambers is clearly indicated by the large gas bubbles which move around when the shell is tilted. During the initial stage of shell cleaning after removal of the animal, the uppermost of the two water chambers lining the inside of the rv was accidentally broken, thereby allowing release of the clear, faintly yellowish fluid contents. This fluid was slightly more viscous than water and extremely foul-smelling (? partly due to the gas within the traps) — both characteristics suggesting decomposing proteinaceous material. The septum of the broken chamber consists of translucent-white, glossy, shell material and has a thickness of approximately 0.3mm (lamella thickness). Internally both valves are white with the exception of the crenulated, brown-purple margins and the regions associated with the water chambers which appear brownish owing to the discoloured fluid contained therein.

Live *Spondylus varius* has an extensive and gaping mantle which exhibits large, irregularly-shaped mottlings (Fig. 3B; white on a black background in Orpheus I. specimen, this study; orange on green background in Solomon Islands specimens, P. Clarkson, pers comm; white on yellow background (Slack-Smith, 1998, pl. 12.5). Variation in mantle colour is possibly associated with age, sex of the animal or represents some degree of geographical variation. Edges of the mantle are red-orange in colour and ornamented with numerous blue ocelli. The ocelli are associated with rapid closure of the valves during disturbances including the approach of a diver. Large specimens of *S. varius* may weigh several kilograms, and live to be at least ten years of age (P. Clarkson, pers. comm.).

HABITAT AND DISTRIBUTION. *Spondylus varius* is usually found cemented umbonally to gently sloping reefs, vertical drop-offs, shipwrecks and concrete pylons, in depths from 3m to more than 60m water in prominent positions exposed to nutrient laden currents. Specimens with particularly well-developed spines occur in sheltered positions within shipwrecks, where they are attached to a variety of surfaces and obscured by silt or sponges rather than calcareous encrusting organisms. They commonly provide habitat for other molluscs, including other cemented bivalves (other Spondylidae, Chamidae, Ostreoidea) and gastropods such as cowries and muricids. *S.*

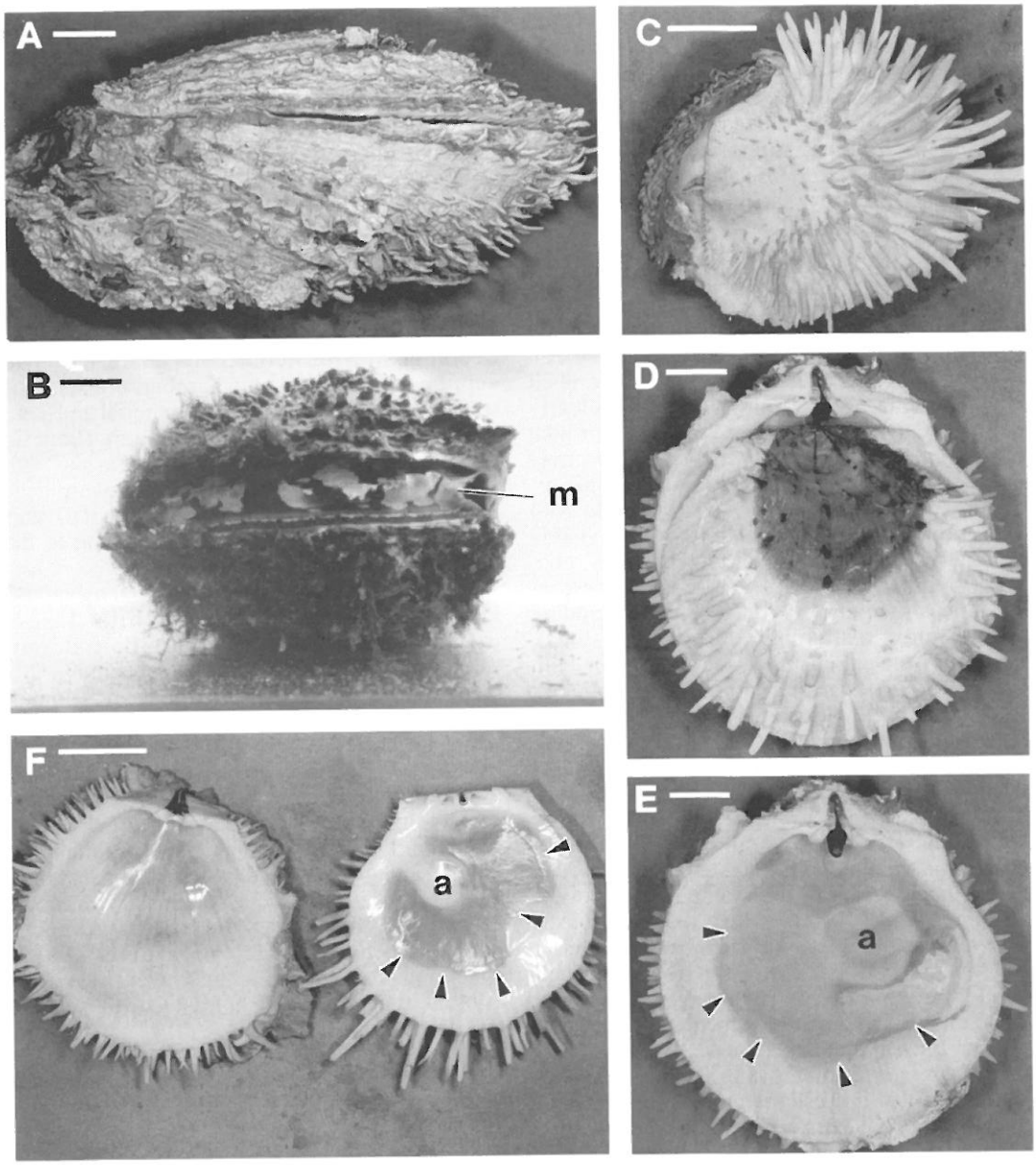

FIG. 3. *Spondylus varius* Sowerby,1827. A, Profile of pv from 10m, between Pioneer and Hazard Bays, Orpheus I., Queensland (QMMO 67048). B, Same specimen photographed alive in aquarium at Orpheus I. Research Station. Clearly visible is the black and white mottled mantle. C, Pv of juvenile from 43m off, Bonegi Island wrecks, Solomon Islands showing long spines (KL). D, External of lv of juvenile specimen from off Cebu I., Philippines — note darker shell colour (purple in this case) of younger portion of shell (KL). E, Rv of same specimen as Fig. 3D showing water chamber (arrow heads). F, Internal views of left valve (at right) and right valve (at left) of juvenile specimen from 43m, off Bonegi I. wrecks, Solomon Islands, showing water chamber in lv (KL). Scale bars = 20mm.

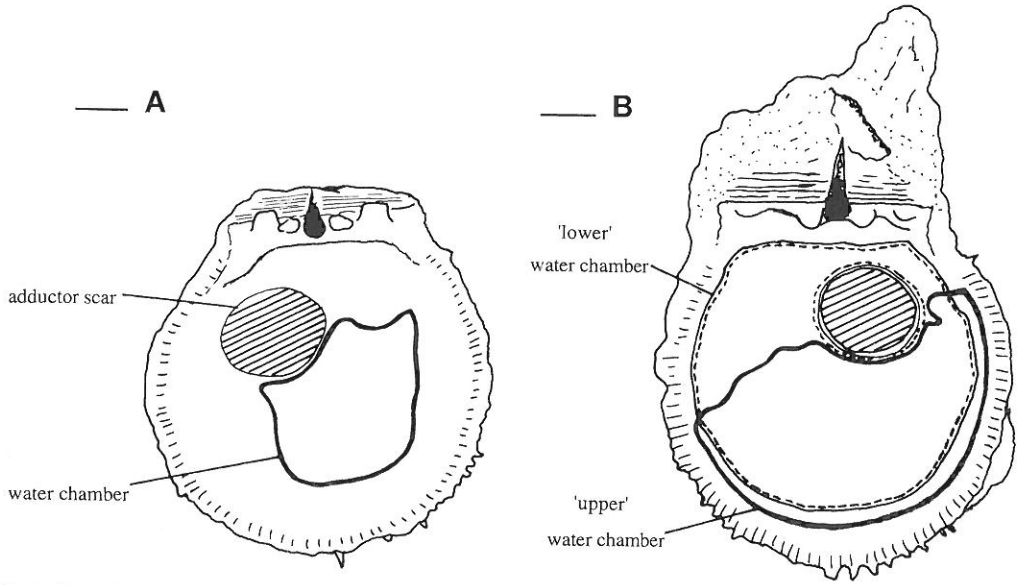

FIG. 4. *Spondylus varius* Sowerby,1827. Sketches showing extent of the water chambers (dotted lines) in QM MO67048. A, Lv; B, Rv – note two visible water chambers, the upper one broken. Scale bars = 20mm.

varius is recorded from the Philippines (Lamprell, 1986; Springsteen & Leobrera, 1986), Solomon Islands(Lamprell, 1986), northern Queensland and New Caledonia (Lamprell & Healy, 2001). The species has yet to be taken in the eastern Pacific, and we know of no Hawaiian records.

DISCUSSION. *General remarks and comparisons.* This is the first published record of this large and unusual bivalve from Australian waters, bringing the number of spondylid species known to occur in the region to 55. Sowerby (1827b) offered no precise locality data for *S. varius* other than to say that the material offered in the auction catalogue were 'shells collected by Mr. Samuel Stutchbury on the coast of some islands of the Australian and Polynesian groups'. Tomlin (1943) located a complete copy of the Sowerby auction catalogue which records in one annotation that catalogue specimens of *S. varius* were from 'Bow Island' ('one of the Paumoto group according to Tomlin (1943) = Hao Atoll, Archipel des Tuamoto, 9°22'S, 171°14, French Polynesia). Although we have not examined material from French Polynesia, there is no compelling reason to believe that *S. varius* does not occur there (possibly all of Stutchbury's material was collected at 'Bow Island'). Reeve (1856) gave the collection locality of the Cuming Collection specimen (designated herein as the neotype of *S. varius*) as 'Pacific Islands'.

Possibly because of its preference for semi-secluded habitats such as sunken ships or coral overhang, *S. varius* may have been observed previously by divers in Australian waters but not identified as such. Specimens of *S. varius* were also found in the collections of the Australian Museum, but somehow these have remained overlooked and undocumented until now. The exceptionally large size reached by *S. varius* (maximum height 400mm — measurement based on in situ measurements of Solomon Islands specimens — P. Clarkson, pers. comm.) could have precluded collection of specimens prior to this study as divers are generally hesitant to collect or even disturb large, attached molluscs such as these. The measurement of 450mm quoted by Lamprell & Healy (1998) for the Spondylidae (not stated by them but indirectly alluding to *S. varius*) was based on andecotal sources only. While diving on the reefs between Pioneer and Hazard Bays at Orpheus Island, one of us (JK) noted very large spondylids (estimated pv height of 250+ mm) in the vicinity of the *S. varius* specimen collected for this study. Almost certainly these were additional specimens of *S. varius* because no other spondylid occurring in the Western Pacific reaches this size.

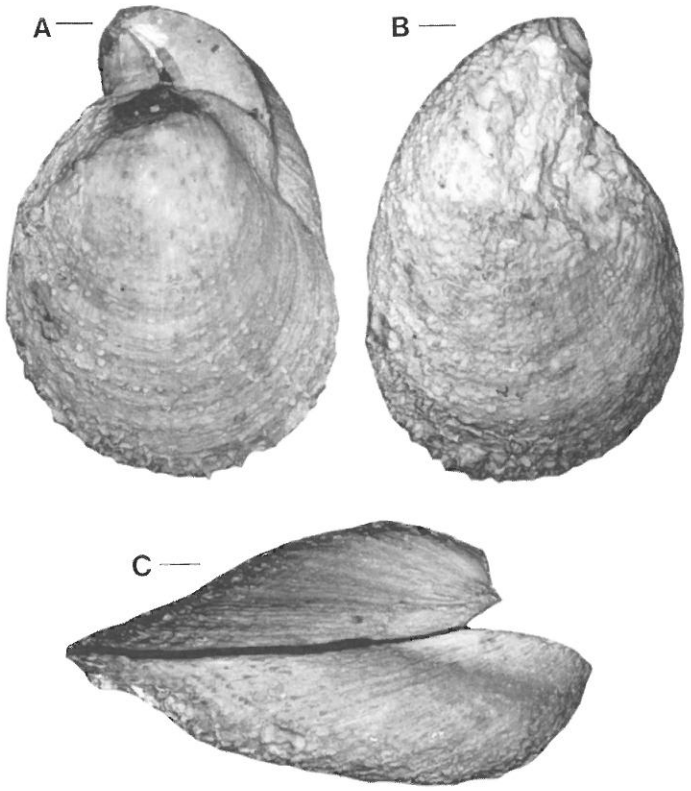

FIG. 5. *Spondylus varius* Sowerby,1827. A-C, Aged specimen showing stunted nature of spines (KL; no locality data), height from umbones to ventral margin 257mm; A, External view of pv from lv aspect; B, External view of pv from rv aspect; C, Lateral view of pv. Scale bars = 20mm.

In its juvenile state (and before any water chambers have developed), *S. varius* can potentially be confused with *S. echinatus* Schreibers, 1793 and *S. castus* Reeve, 1856. However, *S. varius* can usually be distinguished from these species by its umbonal colouration (white, or often orange-red-purple in *S. varius*; white with black speckling in *S. echinatus* and *S. castus*). *Spondylus wrightianus* Crosse, 1872 and *S. tenuitas* Garrard, 1966 also exhibit orange-red umbonal colouration like *S. varius*, but the former is smaller, solid and equivalved and the latter is a relatively small (65mm length), equivalved temperate Australian species with delicate spines.

A review of the Spondylidae from New Caledonia (Lamprell & Healy, 2001) uncovered several new species and a significant number of species previously unrecorded from that region including *S. varius*. It is therefore not surprising that *S. varius* should also occur on the Great Barrier Reef, and indeed it is likely that other Indo-West Pacific spondylids known from the Solomon Islands and New Caledonia will eventually be recorded from Queensland.

Taxonomic history of Spondylus varius. Confusion concerning the date of publication of the description of *Spondylus varius* stems from the fact that Sowerby I chose to publish this text in an appendix to the auction catalogue of Samuel Stutchbury's collection (principally of Polynesian shells and artefacts). Tomlin (1937) located incomplete copies of the catalogue, each with the date 'July 1827' added to a MS version of the missing title page and noted the discrepancy between this date and the tentative date '? 1829' written on the Natural History Museum's (then only) copy of the catalogue. Later a complete copy of the catalogue was sighted by Tomlin (1943) allowing him to clarify the date of the auction as July 26th, 1827. Tomlin concluded that this complete copy of the catalogue was probably Stutchbury's, for it is annotated and bound into the back of a copy of J.G. Children's *Lamarck's Genera of Shells* bearing Stutchbury's signature). Although it is impossible to state the exact date of publication of the auction catalogue, it seems almost certain that this occurred in the first few months of 1827, and not in 1826. For some reason, however, the year 1829 has regularly been associated with the name *Spondylus varius* Sowerby and, at present, the labels of the Natural History Museum specimen figured by G.B. Sowerby II (1847) and Reeve (1856) still bear the date 1829. Fulton (1915) appears to be the first author to cite 1829 as the authority year for *S. varius* Sowerby. Conceivably however, the first usage of this erroneous date may have been earlier than 1915, perhaps arising in dealers' listings and subsequently repeated by Fulton.

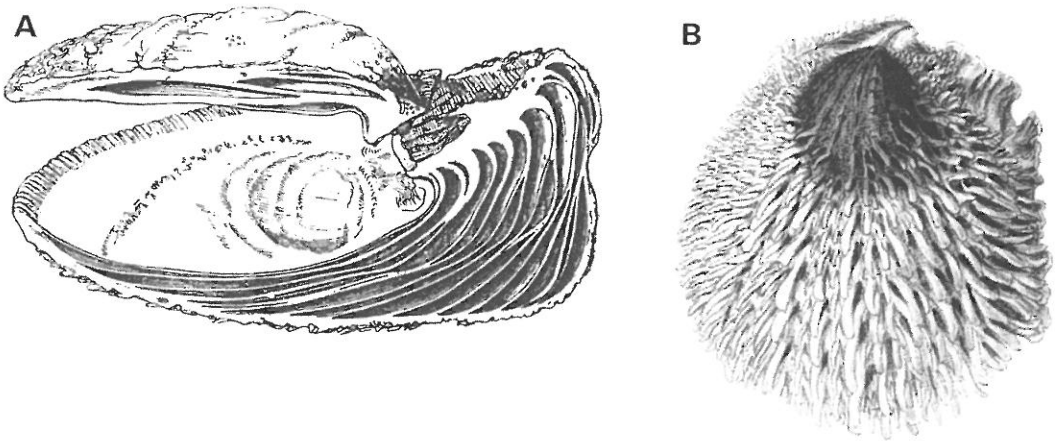

FIG. 6. *Spondylus varius* Sowerby, 1827. A, Illustration from Owen (1838, fig. 21) of a longitudinal section through pv of *S. varius* showing the multiple, vertically stacked, slightly offset septa of water chambers (note bifurcation of each septum into two lamellate layers). B, Illustration from Sowerby (1847, fig. 21, pl. 86) of *S. varius* here chosen as neotype (BMNH 1952.10.30.3): external view of pv from aspect of rv.

To our knowledge, alteration of the name *S. varius* to *S. varians* was first made by Sowerby (1847) and unaccompanied by any explanation. This name change appears deliberate and not a *lapsus calami* as it occurs not only in Sowerby's (1847) main text but also in his List of Figures and Alphabetical Index.

Tomlin (1937: 350) considered the original description of *S. varius* (Sowerby, 1827) to be 'rather vague, and one rather suspects that it may have been taken from a series comprising more than one species'. Undoubtedly this view was influenced not only by Sowerby's choice of name (*varius*) but also his admission that 'Under all other circumstances their form is exceedingly varied' (Sowerby, 1827b: 2). Sowerby (1827a, b) did not illustrate *S. varius* nor did he mention deposition of any type material. It is clear from Sowerby's original description that he was familiar with his new species outside of the series of specimens included in the auction ('Many of the specimens of this shell are extremely beautiful, and there is in the Sale an interesting series of specimens of different sizes and variously circumstanced', Sowerby, 1827b: 2). The neotype, figured by Sowerby (1847, pl. 86, fig. 21) and Reeve (1856, pl. 1, fig. 3.) (BMNH 1952.10.30.3.), has obvious historical significance, but to our knowledge, there is no surviving documentation to prove that it originated from the material offered in the auction catalogue or from other material used by Sowerby in his 1827 description (or from material collected after 1827). Associated with this specimen in the Natural History Museum is a note stating that it has no type status. Reeve (1856) referred to this shell as being from Cuming's collection ('Cuming Mus.') but as to the ultimate source of this specimen nothing is known, other than it was collected in the 'Pacific Islands'.

Our reasons for nominating BMNH 1952. 10.30.3. as neotype are: 1) this shell was accepted both by G.B. Sowerby II (1847) and Reeve (1856) (and presumably also Sowerby I who died in 1854), as characterising the species, and is accurately illustrated in colour by both authors; 2) the specimen is in an excellent state of preservation, even though the liquid contents of the water chambers have been lost through gradual evaporation; 3) the locality data associated with this specimen ('Pacific Islands') reasonably accurately reflects the known distribution of *S. varius*, although the species has yet to be collected from the eastern Pacific or the Indian Ocean. Nomination of a neotype is here deemed necessary to eliminate any doubts concerning the validity of *S. varius* (e.g. Tomlin's (1937) comment that the species may have been based on specimens of more than one species).

Structure and possible function(s) of the water chambers. The function of the water chambers in *S. varius* remains unclear. Over 150 years ago, Sir Richard Owen investigated the structure of the fluid/gas chambers in this species in two brief, but highly informative, papers (1837, 1838). He demonstrated a sequence of 14 vertically-stacked, slightly off-set chambers (each defined

TABLE 1. Comparison of *Spondylus varius* specimens examined.

Collection Reference	Locality	Water Chambers (visible externally)	RV Height (excluding spines)	LV Height (excluding spines)
QMMO67048	Orpheus I., Qld	In both valves	170mm	138mm
AMSC150016	Orpheus I., Qld	In lv only	200mm	155mm
AMSC104588	Lizard I., Qld	In lv only	255mm	195mm
AMSC100790	New Caledonia	In lv only	220mm	175mm
AMSC303014	Solomon Is	In both valves	135mm	115mm
KL	Solomon Is	In lv only	65mm	56mm
KL	Solomon Is	In lv only	72mm	62mm
KL	Solomon Is	Chambers absent	42mm	36mm
KL	Solomon Is	In lv only	93mm	85mm
KL	Philippines	Chambers absent	113mm	94mm
KL	Philippines	In both valves	113mm	99mm
KL	No data	In both valves	240mm	210mm
BMNH 1952.10.30.3 (neotype)	Pacific Islands	In both valves	169mm	154mm

by shell septa) in the rv (lower valve) of a large specimen which he had sectioned longitudinally from umbones to ventral margin (Fig. 6A). The upper valve of his specimen contained fewer, more lenticular chambers, which Owen (1837) originally ascribed to a reduced shell-secreting capability of the lv (upper valve) mantle but later (1838) interpreted as a result of reduced demand for such a capability in this region of the mantle (that is, both the upper and lower valve mantle margins probably have equal shell-secreting abilities). Septa of the chambers in the rv were shown by Owen to bifurcate away from the attachment area of the valve, so that strictly each septum is composed of two thin lamellae for most of its length.

After discussing the phenomenon of septal production in other attached bivalves (ostreids and gryphaeids), in attached gastropods (vermetids and certain muricids) and in chambered cepahalopods, Owen (1837, 1838) hypothesised that the presence of septa in *S. varius* was probably a continuing response of the animal to impending overgrowth by corals. Hence the attached animal could effectively counteract overgrowth, and therefore maintain an unimpeded water flow for respiration and filter feeding, by raising the mantle edge on a series of successive shell platforms (= the septa defining the chambers). In support of this idea, Owen (1838) cited a personal communication from Stutchbury claiming that chambers only occurred in specimens associated with coral overhangs or other situations where over-growth by corals seemed imminent. In this species, water chambers may occur on the upper valve, the lower valve or commonly on both (Owen, 1837, 1838; Lamprell, 1986; Springsteen & Leobrera, 1986; present study), and even though it has been suggested that the fluid/gas chambers are only a feature of older specimens (Sowerby, 1827, 1848; Lamprell, 1986) we have sometimes observed them in relatively young shells (rv 72mm height) from the Solomons and the Philippines (Fig. 5C-F). We cannot definitively assess Owen's 'overgrowth' theory, but admit that his explanation is well argued and probably correct. However the chambers in some sub-adult *S. varius* — animals not as yet threatened by epibiont smothering — and the absence of such chambers in other spondylid species (including all other large species, Lamprell & Clarkson, unpubl. data), suggest that there may be additional functions for these structures. The foul-smelling odour of the fluid contained within the water chambers may offer another clue as to the function of these structures. Owen (1837,1838) had the fluid analysed by a colleague, Dr Bostock, who reported that 'it was turbid, had an acid-saline taste, and a rank disagreeable odour'. After allowing the fluid to settle for 24 hours he determined that the clear supernatant was essentially a saline (sodium chloride) solution, with some hydrochloric acid and a little sulphuric acid also present. Dr Bostock made a point of emphasising that the fluid differed in its composition from sea water, raising the question as to its origin. If Owen's (1837, 1838) proposed sequence of events for septal secretion is accepted, then sea water seems

the most likely source of the water chamber fluid. Possibly the mantle has an ability to chemically modify the contents of the fluid immediately before it is sealed off from the environment. More likely perhaps, chemical changes occur within the water once it is enclosed resulting in the precipitation of certain dissolved salts leaving a predominantly sodium chloride solution within the water chamber. In addition to the above results Dr Bostock isolated 'a little brown matter' which he tentatively concluded 'gave the fluid its peculiar flavour and odour'. We can certainly confirm the repugnant odour of the fluid (? and gas) in *S. varius* and given this property, and the brittle nature of the septa, it is possible that fluid/gas-filled chambers may act as a last-resort defence against predators once maturity has been reached. The use of repugnatorial chemicals for defence against predators is widely recorded in the animal kingdom, although in most cases species adopting such a strategy advertise their inedibility (or even poisonous nature) through the use of bright colours and patterns (for example many nudibranchs, xanthid crabs).

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authorship almost certainly G.B. Sowerby I, the auctioneer; catalogue printed sometime prior to the auction date, July 26, 1827, but presumably within the early months of 1827). Pp 1-10, plus two pages with hand-written notes (one identifying the copy as belonging to Stutchbury and one giving locality data for three species, including *Spondylus varius*]

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