

# *Argyrotheca furtiva* n. sp. and *Joania arguta* (GRANT, 1983) two micromorphic megathyrid brachiopods (Terebratulida, Megathyridoidea) from the Indonesian Archipelago

by Eric SIMON

## Abstract

*Argyrotheca furtiva* n. sp. and *Joania arguta* (GRANT, 1983) two micromorphic brachiopod species (Terebratulida, Megathyridoidea) have been discovered in the Indonesian Archipelago. These species were collected from old shipwrecks which are remarkable environments for the development of cryptic marine animals, especially for brachiopods. *A. furtiva* n. sp. is known from off Donggala, Central Sulawesi (Pacific waters) whereas *J. arguta* has been found off Donggala, Central Sulawesi and off Tulamben, Bali (Indian Ocean waters). The transfer of *Argyrotheca arguta* (GRANT, 1983) to the genus *Joania* ALVAREZ *et al.*, 2008 is discussed.

**Key words:** Brachiopods, *Argyrotheca*, *Joania*, Indonesia, new species.

## Résumé

Deux espèces de brachiopodes micromorphiques (Terebratulida, Megathyridoidea) ont été découvertes dans l'Archipel Indonésien: *Argyrotheca furtiva* n. sp. et *Joania arguta* (GRANT, 1983). Ces deux espèces ont été récoltées dans d'anciennes épaves de bateaux qui se sont révélées être des environnements de qualité pour le développement d'espèces marines cryptiques en particulier des brachiopodes. *A. furtiva* n. sp. a été découverte à Donggala, Sulawesi Centrale (eaux de l'Océan Pacifique) tandis que *J. arguta* a été trouvée tant à Donggala qu'à Tulamben, Bali (eaux de l'Océan Indien). Le transfert d'*Argyrotheca arguta* GRANT, 1983 vers le genre *Joania* ALVAREZ *et al.*, 2008 est discuté.

**Mots-clefs:** Brachiopodes, *Argyrotheca*, *Joania*, Indonésie, espèce nouvelle.

## Ringkasan

*Argyrotheca furtiva* n. sp. dan *Joania arguta* (GRANT, 1983) dua spesies brachiopod micromorphic (Terebratulida, Megathyridoidea) telah ditemukan di kepulauan Indonesia. Spesies ini diambil dari bangkai kapal tua yang merupakan lingkungan yang luar biasa untuk pengembangan hewan laut samar, terutama untuk brachiopoda. *A. furtiva* n. sp. dikenal dari luar Kabupaten Donggala, Sulawesi Tengah (Pasifik perairan) sedangkan *J. arguta* telah ditemukan

dari Kabupaten Donggala, Sulawesi Tengah dan off Tulamben, Bali (perairan Samudera Hindia). Pengalihan *Argyrotheca arguta* (GRANT, 1983) kepada genus *Joania* ALVAREZ *et al.*; 2008 dibahas.

**Kata kunci:** Brachiopoda, *Argyrotheca*, *Joania*, Indonesia, spesies baru.

## Introduction

The megathyrid brachiopod genera *Argyrotheca* DALL, 1900 and *Joania* ALVAREZ *et al.*, 2008 have a worldwide distribution and they are now represented by 26 living species. Fossil *Argyrotheca* species have a similar large distribution and this genus is known from the Late Cretaceous (BOSQUET, 1859; STEINICH, 1965; LEE *et al.*, 2006) ranging back, at least, to the Upper Campanian (SIMON, 2000). *Joania* is a genus known from the Cenozoic since the Eocene. An exhaustive list of the papers dealing with fossil forms of *Argyrotheca* (including forms of *Joania*) collected throughout the world was published by HILLER *et al.* (2008). These authors illustrated also the world distribution of the fossil and Recent species with a map (fig. 1, p. 168). The highest diversity of species is observed in European and Caribbean waters (COOPER, 1977; LOGAN, 2007). However these genera have been discovered in the tropical-equatorial zones of the Atlantic, Pacific and Indian Oceans. Arctic and Antarctic zones seem to be devoid of this type of brachiopod. Surprisingly, living megathyrid brachiopods have not been reported from a wide zone of the Indo-Pacific region which covers Indonesia, the Philippines, the China Sea and Japan (ZEZINA 1985, fig. 19, p. 66; LOGAN 2007, fig. 1954, p. 3107). Absence of living *Argyrotheca* species in Indonesian waters is still more astonishing as this genus is represented there by three different fossil species collected from the Early Miocene of Central Java

(COOPER 1978, p. 9; pl. 1, fig. 5). However, a similar situation is observed for the New Zealand fauna. No living species have been reported up to the present but several species have been collected and described by HILLER *et al.* (2008) from the Eocene, the Oligocene and the Miocene.

An absence in the literature does not mean that these brachiopods are really absent in these large geographical areas. Megathyrid brachiopods are micromorphic species and they can be easily overlooked. For instance, in the Mediterranean Sea, which has been intensively studied for many years, the discoveries of the micromorphic rhynchonellid brachiopod *Tethyrhynchia mediterranea* LOGAN, 1994 (in LOGAN & ZIBROWIUS, 1994) and of the megathyrid brachiopod *Gwynia capsula* (JEFFREYS, 1859) are quite recent observations (LOGAN, MACKINNON & PHORSON, 1997; SIMON & WILLEMS, 1999). These micromorphic species are living in cryptic habitats such as dark rocky crevices, reef recesses or submarine caves and they cannot be easily trawled. Scuba diving is a suitable alternative for reaching such special habitats.

But small size and cryptic habitat cannot fully explain the difficulty of finding megathyrid brachiopods in the Indo-Pacific region. In Europe for instance, it is relatively easy to collect *Argyrotheca cuneata* (RISSO, 1826), *A. cistellula* (SEARLES-WOOD, 1841) or *Joania cordata* (RISSO, 1826) and they are generally present in abundance in the investigated samples. On the contrary, extremely small Indo-Pacific species are rare (COOPER, 1978, p. 9). For the Australian living species, HILLER *et al.* (2008) were obliged to base their study on only four specimens of *Argyrotheca australis* (BLOCHMANN, 1910) and on six specimens of *A. mayi* BLOCHMANN, 1913. In fact, these brachiopods are not living in dense populations. In the Indonesian samples investigated for this study, megathyrid brachiopod specimens appeared always isolated from each other and the discovery of a representative was never frequent. Collected pieces of substrate, with a size varying between 10 and 25 cm, never offered two specimens of a megathyrid brachiopod found on the same fragment. This indicates that these species are living in very sparse populations with isolated individuals and a great number of specimens for a study can never be expected.

This study points out, for the first time, the presence of megathyrid brachiopods in the Indonesian Archipelago, which straddles both Indian and Pacific Oceans. These results improve the knowledge of the geographical distribution of these genera. The material used in this study (Fig. 1) was collected in Indonesia off Tulamben on the north-eastern coast of Bali (Java Sea) which is considered part of the Indian Ocean and off the harbour

of Donggala in the Bay of Palu (Province of Central Sulawesi), on the western coast of Sulawesi (Strait of Makassar) which belongs to Pacific waters.

It is noteworthy that the studied samples were collected inside wrecks. It seems that, for the first time, brachiopods are found and collected in such conditions. In fact, stores in shipwrecks are extremely dark places, subject to water currents and acting as relatively closed submarine caves. These peculiar ecological conditions are very favourable for brachiopods. They are suspension feeders that do not appreciate well lit environments with a significant level of competition. In these wreck stores, brachiopods are mainly living together with serpulids, annelid worms, bryozoans and sponges. Brachiopod species discovered are quite numerous. The main group of species consists of thecideid brachiopods but craniid, rhynchonellid and terebratulid brachiopods are also observed. All this material, the habitat of these species and their association will be described later in further studies.

Two species of megathyrid brachiopods were discovered and they are representatives of two distinct megathyrid genera: *Argyrotheca* DALL, 1900 and *Joania* ALVAREZ *et al.* 2008. The differences between these genera have been pointed out by ALVAREZ *et al.* (2008). Representatives of the genus *Joania*, such as *J. cordata* which is the type species, have generally an inverted heart-shaped outline, a narrow hinge line, a prominent cardinal process, stubby crura in the adult stage of growth, an indented dorsal septum with tuberculate antero-ventral edge, and radial ridges terminating anteriorly in marginal tubercles. In the genus *Argyrotheca*, the shell outline can be quite variable. Species such as *A. cuneata*, possessing a semi-circular outline, generally show a wider hinge line, a small cardinal process and the internal valve floor is devoid of radial ridges terminating anteriorly in tubercles. The two species discussed in this paper are excellent examples of these generic distinctions.

## Material and methods

All brachiopod specimens used in this study were collected in August 2009 by a scuba diver who had the opportunity to pay visits to old shipwrecks in Tulamben (Bali, Indonesia) and in Donggala (Central Sulawesi, Indonesia).

In Tulamben, the shipwreck is the US army cargo "Liberty" which was torpedoed in 1942. It lies on a sand bank just 30 m off the beach. The top of this wreck is 3 m. underwater and the bottom is at 29 m depth. Inside



Fig. 1. — Map of Indonesia and local maps of Sulawesi and Bali showing collecting areas which are the shipwreck “Mutiaara” (- 30 m) off Donggala (Central Sulawesi) and the shipwreck “Liberty” (- 25 m) off Tulamben (Bali).

one of the dark stores of the wreck, situated at a depth of 25 m, the upper part of the muddy sediment accumulated on the floor was carefully collected.

In Donggala, the visited shipwreck is the “Mutiaara” which was sunk 57 years ago just off the entrance of the harbour. It is lying on the bottom at a depth of 30 m. Three stores, which are under the influence of relatively strong currents, were accessible and two of them are completely dark. The upper part of the muddy sediment found on the floor was collected. Moreover, in this wreck it was possible to collect several fragments from the metallic walls. This provided us with brachiopods kept in living position.

The sediments collected in wreck stores have been washed and sieved. A sieve of 0.5 mm was used for

the smallest fraction. The sieved material was air dried and the brachiopods were picked out under a binocular microscope.

Half of the fragments picked up from the wreck walls were air dried. The remaining fragments were preserved in ethanol 70%.

Digital macrophotography was carried out using a Pentax K20D. Shells of specimens selected for scanning electron microscope were treated with household bleach (5% hypochlorite) to remove all remaining soft parts. Specimens collected in living position and preserved in ethanol were passed through successive ethanol/formaldehyde dimethyl-acetal treatments (respectively 100/0 – 75/25 – 50/50 – 25/75 – 0/100 in %) and critical point dried. All the samples subsequently were coated

with gold and observed using a low vacuum SEM - an ESEM FEI Quanta 200.

Suprafamilial classification follows WILLIAMS *et al.* (1996) and WILLIAMS *et al.* (2000, pp. 22-27) and the hierarchy within the superfamily Megathyridoidea DALL, 1870 follows LEE *et al.* (2006, pp. H2217-2222).

Specimens illustrated in this paper have been deposited under general number I.G. 31608 in the collections of the Department of Recent Invertebrates of the Belgian Royal Institute for Natural Sciences in Brussels (RBINS). Registered specimen numbers are given below in the text.

### Systematic descriptions

Phylum Brachiopoda DUMÉRIL, 1806

Subphylum Rhynchonelliformea WILLIAMS *et al.*, 1996

Class Rhynchonellata WILLIAMS *et al.*, 1996

Order Terebratulida WAAGEN, 1883

Suborder Terebratulidina MUIR-WOOD, 1955

Superfamily Megathyridoidea DALL, 1870

Family Megathyrididae DALL, 1870

**Genus** *Argyrotheca* DALL, 1900

Type species: *Terebratula cuneata* RISSO, 1826.

*Argyrotheca furtiva* n. sp.

Pl. 1, Fig. 1-4; Pl. 2, Fig. 1-3; Table 1.

DERIVATIO NOMINIS: lat. *furtivus*, *a*, *um* meaning "secret" or "hidden", an allusion to the difficulty in observing this small species fixed to its substrate.

HOLOTYPE: *Argyrotheca furtiva* n. sp. Plate 1, Figures 1-4, preserved in the collections of the Institut royal des Sciences naturelles de Belgique, RBINS - RI - BRA 7. The morphological characters of the holotype are indicated in Table 1.

LOCUS TYPICUS: Shipwreck "Mutiar", Bay of Palu, off Donggala Harbour. Donggala near Palu, Province of Central Sulawesi, Indonesia.

MATERIAL: Six specimens. Two shells were found in the sieved sediment collected on the floor of the store in the shipwreck. Four specimens were discovered in living position attached to their substrate (two were air dried and two were preserved in ethanol).

DIAGNOSIS: Small, thick, ventribiconvex shell,

subpentagonal in outline with obtuse wing-like lateral extremities, lenticular in lateral profile. Four radial incipient costae on either valve in opposite folding. Shell surface regularly tuberculate under SEM examination. Rectimarginate anterior commissure and sinuous lateral commissure. Large pedicle collar not buttressed by the low blade-like ventral septum, which extends for two-thirds of the valve length. Obtusely pointed crural processes. Weakly defined descending branches fused up to the mid-valve with valve floor and raised on the lateral slopes and the posterior part of the dorsal septum. Dorsal septum rather low, narrowly subtriangular in lateral profile with anterior slope straight, not serrate nor tuberculate. Strong adductor muscles scars developed in the posterior part of the dorsal valve with one large puncta present on either internal side of these scars.

### DESCRIPTION:

EXTERNAL CHARACTERS: The ventribiconvex shell is small (maximum width: 1.5 mm. See Table 1), wider than long with a transversely subpentagonal outline and obtuse wing-like lateral extremities. The straight hinge line is nearly as wide as the width of the shell. The maximum width of the shell is situated at the tips of the wing-like lateral extremities. The shell is relatively thick as the thickness represents up to 60 % of the length. Its lateral profile is lenticular. Two low costae are developed on either side of a wide shallow median sulcus. In anterior view, the opposite folding and the resulting bilobate shell structure are visible. Under binocular examination the shell surface seems to be smooth. However SEM examination shows numerous incipient sinuous growth lines. The shell surface of the protogulum is slightly wrinkled whereas the shell surface of the early growth stages is smooth. On the contrary, the shell surface of the later growth stages is regularly and incipiently tuberculate. The shell is coarsely punctate with  $\pm 340$  pores/mm<sup>2</sup>. The anterior commissure is rectimarginate whereas the lateral commissure is sinusoidal (Pl. 1, Fig. 2c). The straight beak is attrite, subtruncate with clear beak ridges building an apical angle of 124°. The shell surface of the lateral parts of the beak is devoid of tuberculation (Pl. 1, Fig. 2c). Interareas are flat, apsacline with a striated aspect (Pl. 1, Fig. 2a). The hypothryid, triangular foramen is large, limited by two very narrow, blade-like deltidial plates. In lateral profile these deltidial plates have a long triangular shape (Pl. 1, Fig. 2c).

INTERNAL CHARACTERS: Ventral valve with a pedicle collar half as long as delthyrium. Teeth long and hooked. A

Table 1. – *Argyrotheca furtiva* n. sp. Morphological characters measured (in mm) on the holotype (RBINS - RI - BRA 7) and the paratype (RBINS - RI - BRA 8) collected in August 2009 from the shipwreck “Mutuara” off Donggala, Central Sulawesi, Indonesia (depth: 30 m.). L = length, W = width, T = Thickness, LDV = length of the dorsal valve, WH = width of the hinge line, HA = height of the interarea, Øfor. = diameter of the foramen,  $\beta$  = apical angle (in degrees). L/W = ratio length (L) to width (W), T/W = ratio thickness (T) to width (W), LDV/W = ratio length of dorsal valve (LDV) to width (W), WH/W = ratio width of the hinge line (WH) to width (W), Øfor./W = diameter of the foramen (Øfor.) to width (W).

Specimens	L mm	W mm	T mm	LDV mm	HA mm	WH mm	Ø for. mm	$\beta$ degrees	L/W	T/W	LDV/W	WH/W	Ø for./W	Punctae Nbr/mm <sup>2</sup>
Holotype	0.9	1.5	0.6	0.7	0.2	1.3	0.4	0.4	0.61	0.39	0.48	0.86	0.24	340
Paratype	1.1	1.5	n.m.	1.0	0.4	1.3	0.4	0.4	0.75	n.m.	0.65	0.89	0.25	348

low blade-like median septum extends from below the pedicle collar up to two-thirds of the valve length (Pl. 2, Fig. 3c, 3d). The pedicle collar is independent and it is not buttressed by the ventral median septum (Pl. 1, Fig. 4b). A small pit for accommodating the crest of the dorsal septum is developed in front of the anterior end of this ventral septum (Pl. 1, Fig. 4c, 4d).

Dorsal valve with socket ridges poorly developed and occupying less than 25% of the width of the hinge line. The outer socket ridges are elongate and very low (Pl. 1, Fig. 3e). The inner socket ridges (Pl. 1, Fig. 3a; Pl. 2, Fig. 2b) are short with vertical straight anterior parts. The cardinal process is incipiently developed as a small depression between socket ridges. Crura are not developed. Obtuse, pointed crural processes are present. Descending branches are directly attached to the anterior side of the inner socket ridges and they are rapidly fused with valve floor till mid-valve. A free small hole remains between the posterior part of the descending branches and the valve floor (Pl. 1, Fig. 3d; Pl. 2, Fig. 2d). Descending branches are also visible on the lateral sides and behind the crest of the dorsal septum. In lateral profile the dorsal septum is subtriangular with a flat crest. Its anterior part is straight, not indented or tuberculate. It is rather low as seen in anterior view but it is relatively thick (Pl. 1, Fig. 3b; Pl. 2, Fig. 2e). Posteriorly the median septum is very low. In anterior view, the tip of the median septum is obtuse. Strong posterior adductor muscle scars are well visible in the posterior part of the valve on either side of the median area and one very large puncta is present on either internal side of these muscle scars (Pl. 1, Fig. 3b; Pl. 2, Fig. 2e).

### Comparison with other Indo-Pacific *Argyrotheca* species

Comparison with *Argyrotheca australis* (BLOCHMANN, 1910)

This species is restricted to the southern gulfs of southern Australia (for instance off Cape Willoughby, Kangaroo Island, South Australia). It has been illustrated recently by HILLER *et al.* (2008, fig. 4, p. 170). Its presence off the Glorieuses Islands (Mozambique Channel), mentioned by ZEJINA (1987, p. 558; table 1, p. 552) is not supported by any detailed description nor by any illustration and needs further investigation.

*A. australis* has a L/W ratio value around 0.86 whereas it is near 0.60 for *A. furtiva* n. sp. This is due to the more transversely ovate outline of *A. furtiva* n. sp. The shell surface of *A. australis* is not regularly tuberculate and its growth lines are more step-like. *A. australis* has three costae on either side of the median sulcus. *A. furtiva* n. sp. has only two very incipient costae on either side. The interareas of *A. furtiva* n. sp. are strongly striated whereas those of *A. australis* appear smooth. The dorsal median septum of *A. australis* is thinner. The adductor muscle scars are much stronger in *A. furtiva* n. sp. and the large punctae present on either internal side of these muscle scars are not present in *A. australis*.

Comparison with *Argyrotheca mayi* BLOCHMANN, 1913

This species is known from the South coast of Australia and recently illustrated by HILLER *et al.* (2008, fig. 5, p. 172).

The cordiform elongate outline of *A. mayi* prevents all possible confusion with *A. furtiva* n. sp. Moreover *A. mayi* has a smooth shell with numerous growth lines and with a shallow median sulcus. The pedicle collar in *A. mayi* is buttressed by the posterior part of the median septum. In the dorsal valve crura are present.

Comparison with *Argyrotheca jacksoni* COOPER, 1973

This species has been collected in the Red Sea and is illustrated in COOPER (1973 pl. 3, fig.9-13).

This larger species is very different in outline and the shell surface is ornamented with numerous costae (11). The beak is more pointed triangular with a smaller apical angle. The anterior margin shows no clear opposite folding as in *A. furtiva* n. sp. The interareas are not transversely striated.

Comparison with *A. somaliensis* COOPER, 1973

A species collected off the north-eastern coast of the Somali Republic and is illustrated in COOPER (1973 pl. 5, fig. 1-19).

This *Argyrotheca* species is much larger and has a longer and more pointed beak with a narrow apical angle. Many costae are visible. The descending branches are strong and complete till they meet the dorsal septum. The pedicle collar is much shorter.

In *A. furtiva* n. sp., which is much smaller, the beak is lower and the apical angle is much wider. The shell has only four incipient costae. The descending branches are weakly defined and fused at mid-shell with the valve floor. The pedicle collar is wider and longer.

Comparison with *Argyrotheca angulata* ZEZINA, 1987

This species is only known by the holotype collected from off the Glorieuses Islands at -450/500 m. (Mozambique Channel). Only a drawing showing the specimen in posterior view has been given as illustration by ZEZINA (1987, fig. 2, p. 558). A comparison of the internal structures is rather difficult to do and it can only be based on the given description.

The specimen is larger (width: 3.3 mm). Its shell surface is smooth except for "two ridges visible on each half on both valves" (incipient costae?). The width represents 157% of the length. Interareas are transversely striated. The pedicle collar is "grown together with the septum in its posterior half" (ZEZINA, 1987, p. 558). The descending branches are attached directly to the front of the socket ridges.

Some characters are similar in *A. furtiva* n. sp. and must be pointed out. The width represents also 150 % of the length. Incipient costae are developed (= folds between the ridges described for *A. angulata*?). The interareas are also transversely striated. The descending branches are directly attached to the front of the socket ridges.

However some obvious differences are also clearly visible. The tuberculate shell surface visible in *A. furtiva* n. sp. has not been indicated by ZEZINA for *A. angulata*. The ratio thickness/width has a value of 0.65

in *A. angulata* (after the drawing of the holotype). In *A. furtiva* n. sp. this ratio turns only around 0.40. *A. furtiva* n. sp. is more ventribiconvex whereas *A. angulata* appears just biconvex. The pedicle collar is totally free from the ventral septum and not buttressed by the ventral median septum in *A. furtiva* n. sp. The foramen in *A. furtiva* n. sp. is more triangular and it reaches the umbo of the valve. In *A. angulata*, the foramen is more subrectangular and it does not reach the umbo.

**Genus *Joania* ALVAREZ, BRUNTON & LONG, 2008**

Type species: *Terebratula cordata* RISSO, 1826.

***Joania arguta* (GRANT, 1983)**

Pl. 3, Fig.1-6; Pl.4, Fig. 1-6; Text-Fig. 2; Table 2.

- 1954 *Argyrotheca* sp. – COOPER, p. 318; pl. 81, fig. 11-22.
- \* 1983 *Argyrotheca arguta* – GRANT, pp. 178-180; fig. 1.
- . 1987 *Argyrotheca arguta* – GRANT, table 2, p.79; p. 80.
- ? 2008 *Argyrotheca* sp. – BITNER, pp. 439-440; fig. 10,A & B.
- . 2008 *Argyrotheca arguta* – ALVAREZ *et al.*, p. 401.

NOMENCLATORIAL NOTE: *Argyrotheca arguta* GRANT, 1983 is transferred to the genus *Joania* ALVAREZ *et al.*, 2008 because this species has a variable outline from rounded subquadrate to subpentagonal, a complex cardinal process, a dorsal median septum with tuberculate antero-ventral edge, weakly defined descending branches of the brachidium present posteriorly and at the edges of the median septum and a valve floor with numerous radial ridges terminating anteriorly in marginal tubercles.

MATERIAL: Off Tulamben, Bali, Indonesia. In sediment collected from a dark store in shipwreck "Liberty" at 25 m deep and sieved (> 0.5 mm): 14 complete articulated shells, and 5 ventral valves and 1 dorsal valve.

Off Donggala, Central Sulawesi, Indonesia. Specimens collected from dark store in shipwreck "Mutiarra" at 30 m deep.

In sediment collected on the floor in the wreck store and sieved (< 0.5 mm): 39 complete articulated shells.

On wall fragments extracted from the store in the wreck (all air dried): 7 specimens in living position.

EMENDED DIAGNOSIS: An emended diagnosis is needed as important generic morphological characters pointed out by ALVAREZ *et al.* (2008, pp. 400-402) and new SEM observations described in this paper are missing in the original diagnosis published by GRANT (1983, p. 178).

Shell dorsibiconvex, small, known width less than three mm; white or translucent or light tan most

Table 2 – *Joania arguta* (GRANT, 1983). Morphological characters measured (in mm) on the specimens collected in August 2009 from the shipwreck “Liberty” off Tulamben, Bali, Indonesia (depth: 25 m) and from the shipwreck “Mutiara” off Donggala Harbour at Donggala, Central Sulawesi, Indonesia (depth: 30 m). These origins of the material are symbolized by “T” (Tulamben) and “D” (Donggala) in the table. L = length, W = width, T = Thickness, LDV = length of the dorsal valve, WH = width of the hinge line, HA = height of the interarea, Øfor. = diameter of the foramen,  $\beta$  = apical angle (in degrees). L/W = ratio length (L) to width (W), T/W = ratio thickness (T) to width (W), LDV/W = ratio length of dorsal valve (LDV) to width (W), WH/W = ratio width of the hinge line (WH) to width (W), Øfor./W = diameter of the foramen (Øfor.) to width (W).

Specimens	Origin	L mm	W mm	T mm	LDV mm	HA mm	WH mm	Ø for. mm	L/W	T/W	LDV/W	WH/W	Ø for./W
RBINS - RI - BRA 1	D	1.5	1.5	0.7	1.3	0.2	1.4	0.4	0.97	0.46	0.84	0.90	0.24
RBINS - RI - BRA 2	D	1.4	1.6	0.6	1.1	0.3	1.3	0.4	0.88	0.37	0.69	0.84	0.27
RBINS - RI - BRA 4	D	1.8	2.0	0.8	1.6	0.2	1.4	0.5	0.92	0.41	0.83	0.74	0.24
RBINS - RI - BRA 5	T	1.5	1.8	n.m.	1.3	0.3	1.4	0.4	0.84	n.m.	0.69	0.76	0.19
RBINS - RI - BRA 3	D	0.8	0.8	0.3	0.7	0.1	0.4	0.2	1.02	0.36	0.88	0.57	0.27
RBINS - RI - BRA 6	T	0.9	0.8	n.m.	0.7	0.2	0.5	0.2	1.05	n.m.	0.9	0.60	0.22
Off Tulamben N=14													
MIN	T	0.8	0.8	0.3	0.7	0.1	0.4	0.2	0.77	0.33	0.5	0.57	0.18
MAX	T	1.8	2.0	0.8	1.6	0.1	1.5	0.5	1.05	0.46	0.91	0.90	0.27
MEAN	T	1.32	1.5	0.58	1.13	0.24	1.17	0.33	0.9	0.38	0.74	0.77	0.22
Off Donggala N=39													
MIN	D	0.9	0.8	0.3	0.7	0.1	0.4	0.2	0.86	0.36	0.67	0.52	0.17
MAX	D	2.5	2.5	1.1	2.1	0.5	2.0	2.4	1.13	0.52	0.96	0.88	0.30
MEAN	D	1.76	1.85	0.79	1.44	0.32	1.4	0.46	0.96	0.42	0.79	0.75	0.22
All specimens N=53													
MIN		0.8	0.8	0.3	0.7	0.1	0.4	0.2	0.77	0.33	0.50	0.52	0.17
MAX		2.5	2.5	1.1	2.1	0.5	2.0	2.4	1.13	0.52	0.96	0.88	0.30
MEAN		1.75	1.83	0.78	1.42	0.3	1.38	0.4	0.94	0.41	0.77	0.76	0.22

lacking costae; outline variable from subquadrate to heart-shaped, subpentagonal with emarginated anterior margin. Hinge line straight, narrower than the shell. Ventral valve with a microtuberculate external shell surface. Ventral valve with apical angle around 124°-131°; large pedicle collar; robust teeth given off dorsally; low blade-like ventral median septum; valve floor with radial ridges terminating in tubercles near the anterior margin. Dorsal valve with median sulcus producing a slightly sulcate anterior commissure; strong, deep sockets with elevated inner socket ridges; complex strong cardinal process; strong triangular serrate dorsal septum; valve floor with radial ridges terminating in marginal tubercles; loop circling laterally with short pointed crural processes, descending branches weakly defined fused rapidly with valve floor and attached to lateral sides of dorsal septum. Shell coarsely punctate with 250/280 punctae/mm<sup>2</sup>.

DESCRIPTION: This description fits in with the morphological observations made by COOPER (1954,

p. 318) and confirms the descriptions given by GRANT (1983, p. 178). However some new morphological characters are added and some variations of the morphological characters are taken into account.

EXTERNAL CHARACTERS: The adult shell is dorsibiconvex, rather small (Table 2), slightly wider than long with variable outlines, either a subquadrate outline (Pl. 3, Fig. 1a & 4a) or a transversely subpentagonal outline (Pl. 3, Fig. 2a & 5a). These two different outlines are already visible on the material collected from Bikini Atoll (COOPER 1954, pl. 81, fig. 14). The maximum width of the shell is therefore placed in the posterior part of the shell if the outline is subpentagonal or placed at mid-shell if the outline is subquadrate. In lateral profile the shell is sublenticular, relatively thick (Table 2) and the maximal thickness is placed in the posterior part of the shell. The greatest depth of the dorsal valve is at mid-valve whereas the greatest depth of the ventral valve is in its posterior part. The hinge line is straight and narrower than the width of the shell. The cardinal

extremities are gently rounded, not wing-like. The shell is anteriorly emarginate. A low median sulcus, beginning one third the valve length, is developed on the dorsal valve. The lateral sides of the sulcus can form broad folds determining steep postero-lateral slopes. In the Indonesian specimens studied, no costae have been observed. The shell is smooth, white, and translucent when observed under binocular conditions. However, under SEM conditions, the shell surface appears microtuberculate and the shell surface of the ventral

valve is much more tuberculate than the shell surface of the dorsal valve (Pl. 3, Fig. 1f, 1g, 2f, 2g). The position of the microtubercles alternates with the position of the punctae (Pl. 3, Fig. 2g). The anterior commissure is slightly unisulcate. The lateral commissure is curved, concave dorsally. The straight beak is often attrite with an apsacline cardinal area which has a striated surface when it is not abraded. The apical angle varies between 124° and 131°. Beak ridges are poorly defined. The hypothryid, triangular, large foramen is limited by

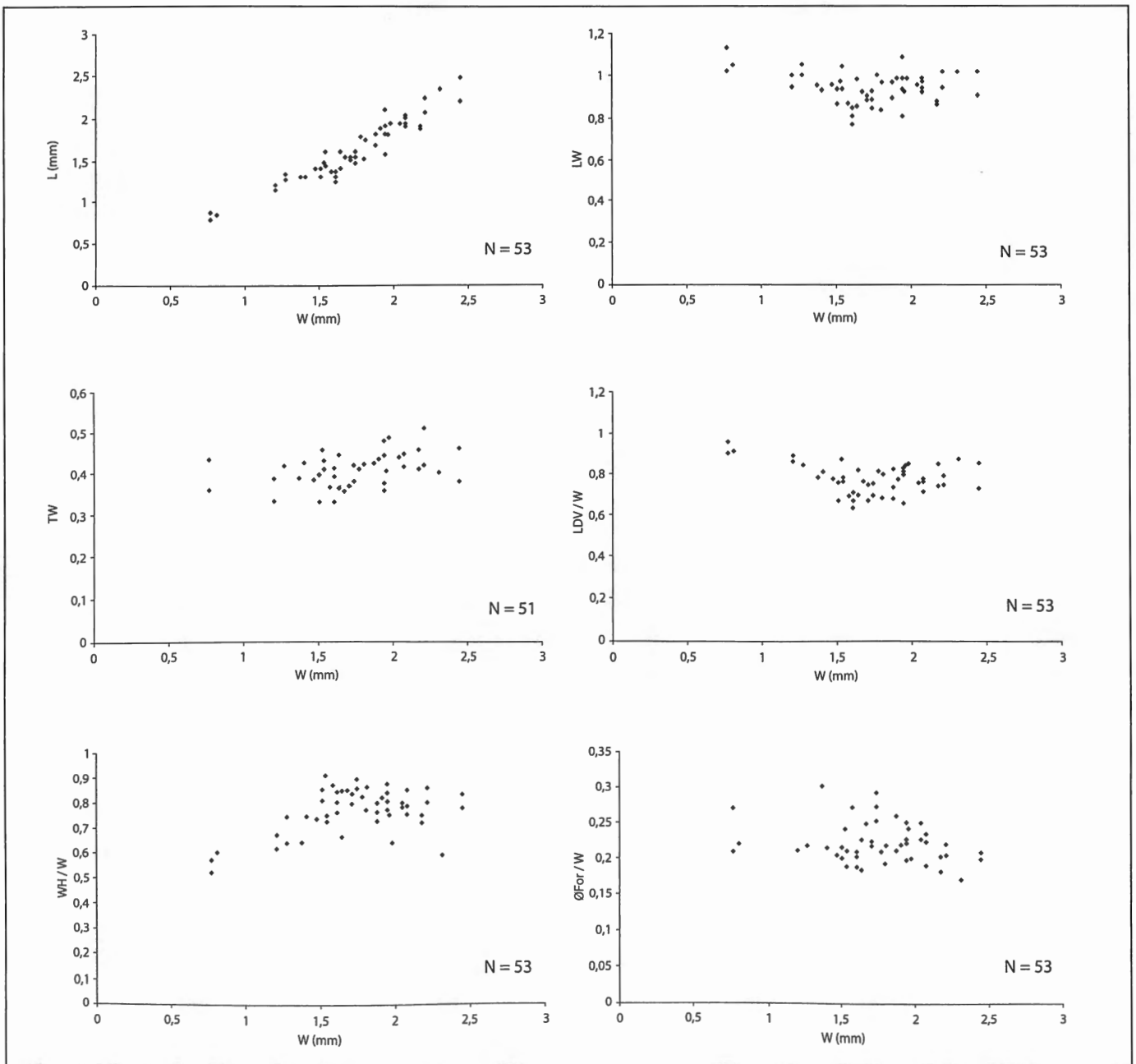


Fig. 2 – Scatter diagrams for *Joania arguta* (GRANT, 1983) collected in Indonesia from the shipwreck “Liberty” off Tulamben, Bali (25 m deep) and from the shipwreck “Mutiarra” off Donggala, Central Sulawesi (30 m deep). L: length (mm); W: width (mm); LDV: length of dorsal valve (mm); T: thickness (mm); WH: length of hinge line (mm); Ø For.: diameter of the foramen (mm). Relationships between L and W; between ratios L/W and width; LDV/W and width; T/W and width; WH/W and width; Diam. For/W and width.



narrow triangular, blade-like deltidial plates. The shell is coarsely endopunctate and the number of punctae varies from 250 to 280/mm<sup>2</sup>.

On the specimens observed in living position, the pedicle was extremely short and the shell was firmly fixed against the substrate.

Juvenile shells are longer than wide with an ovate outline. The apical angle is clearly lower (115° - 120°). The shell is anteriorly emarginated and a very short low dorsal median sulcus is already visible. This sulcus gives a slightly unisulcate anterior commissure for very young specimens (Pl. 3, Fig. 3d). The hinge line is rather narrow in juveniles. This indicates that the hinge line strongly increases during growth (Text-Fig. 2). On intact juvenile shells the protogulum is visible and its surface is wrinkled (Pl. 3, Fig. 6b). The early stages of growth produce a smooth shell surface devoid of coarse punctae (Pl. 3, Fig. 6a, 6b).

### Internal characters

**VENTRAL VALVE:** A wide subtriangular, flat to slightly concave dorsally, pedicle collar is developed. It is not buttressed by the ventral median septum (Pl. 4, Fig. 1j, 6h). Strong teeth are given off dorsally. Radial ridges terminating in clearly defined tubercles near the valve commissure are visible on the valve floor. These radial ridges are sometimes weak (Pl. 4, Fig. 1f) sometimes much stronger (Pl. 4, Fig. 4e, 6e). A low, blade-like ventral median septum is developed. In lateral view (Pl. 4, Fig. 1i, 2f, 4f) it has a wide triangular shape. Its height decreases at mid-valve but it still extends as a very low median septum near the anterior commissure. In this zone, small pits accommodate the crests of the dorsal septum. The number of pits is variable but in some shells four pits are visible.

In juvenile specimens the ventral median septum is much lower and its height decreases rapidly in the posterior third of the valve (Pl. 4, Fig. 3d). However a very low median ridge extends near the front margin (pl. 4, Fig. 3e).

**DORSAL VALVE:** The socket ridges are relatively strong, deep and they extend over 35-38% of the width of the hinge line. The sockets are relatively wide to accommodate robust teeth (Pl. 4, Fig. 1e). Outer socket ridges are very low whereas inner socket ridges are high.

In juvenile specimens the socket ridges appears proportionally larger as the hinge line is relatively reduced.

A very strong cardinal process is developed between the inner socket ridges. The cardinal process does not have

a short shaft but it occupies a low depression. Crura are extremely short but robust (Pl. 4, Fig. 4b). The crural processes are short and pointed. The weakly defined descending branches are rapidly fused with the valve floor and they are raised in the posterior third of the valve. A very small hole remains visible between the descending branches and the valve floor in their posterior part (Pl. 4, Fig. 4b). The descending branches are also apparent in the anterior part of the valve where they are attached on the lateral sides and the tip of the dorsal septum (Pl. 4, Fig. 6f). The dorsal septum is strong, pointed triangular and serrate in lateral view. The highest height of the septum is nearly at mid-valve. The anterior edge is variably tuberculate. For large specimens, the number of serrations commonly reaches four to five. Radial ridges terminating in marginal tubercles are clearly visible on the valve floor. The number of tubercles increases with the size of the specimens but not always. The specimen illustrated (Pl. 4, Fig. 1a) is an example of an adult shell with very few tubercles developed near the margin.

In juvenile specimens the dorsal septum is much lower and its triangular elevation begins at the anterior margin of the valve (Pl. 4, Fig. 3b, 3c, 5a, 5c). Very few marginal tubercles are present (Pl; 4, Fig. 3a, 5a).

### Comparison with *Joania cordata* (Risso, 1826)

The outline of the shell of *J. cordata* is quite variable (ALVAREZ *et al.* 2008, fig. 11, p. 401) from elongate subpentagonal to transversely rounded or even heart-shaped. A great variability in the outline is also observed in *J. arguta* as it varies from broadly subquadrate to transversely subpentagonal. However the apical angle is always much lower in *J. cordata* than the apical angle observed in *J. arguta*. The shell of *J. cordata* is ornamented with two or four weak costae whereas the shell of *J. arguta* is without any costae (in our Indonesian material) or rarely with very incipient costae (as reported by GRANT, 1983). The hinge line in *J. cordata* is relatively narrow whereas the hinge line of *J. arguta* is relatively wide. This gives a more transversely subpentagonal or subquadrate outline for *J. arguta*. The cardinal process of *J. cordata* is said to be trifold but it is shortly shafted. In *J. arguta* the cardinal process is without a shaft and it is placed in a low depression. It is not really trifold but it exhibits multiple strong crenulated myophores. The dorsal septum is serrate in both species but the number of serrations is slightly higher in *J. cordata*. Radial ridges terminating in marginal tubercles are developed in both species.

## Discussion

Wrecks are "artificial" environments made of old corroded "metallic walls". However it seems that they allow a large development of brachiopod representatives. They represent wide dark spaces (much larger than small crevices present in the marine environment) submitted to good hydrodynamic conditions and facilitating the circulation and the fixation of larvae. The good hydrodynamic conditions are confirmed by the development of a fauna consisting essentially of suspension feeders. There, brachiopods are protected from competition with organisms depending directly or indirectly on the presence of light. Brachiopods are also protected from several predators that feed by grazing the surfaces. For research, wrecks represent an interesting alternative because scientific sampling does not alter any natural environment. Shipwrecks represent large spaces promoting the development of cryptic species and they can be excellent situations for discovering more easily many species which are living in hidden or inaccessible deep small crevices.

Megathyrid brachiopods have a worldwide distribution. However this paper is the first mention of the presence for the genera *Argyrotheca* and *Joania* in the Indonesian Archipelago. This increases our knowledge about their detailed distribution. *Argyrotheca* representatives in the Pacific or Indian Oceans are rarely found as they are quite small and cryptic species. Moreover, representatives of these genera seem present in their biotopes in quite loose populations. The new species described here, *A. furtiva* n. sp. has been recognized, for the moment, only off Donggala, Central Sulawesi and it is quite rare in its *locus typicus*. However this species should not be now considered as endemic. Other intensive researches are necessary for establishing more completely its distribution. It has not been found off Bali but the sampling there was too scarce (one sample) in order to conclude definitively that *A. furtiva* is not present there.

The discovery in Indonesia of specimens of *Joania arguta* was surprising as this species was considered as endemic to the Marshall Islands. This small cryptic species is now known from two Indonesian places separated from each other by 950 km; Donggala in the Strait of Makassar (Pacific waters) and Tulamben, Bali (Indian Ocean waters). The Indonesian Donggala station is separated from Bikini Atoll in the Marshall Islands, where *J. arguta* was initially discovered, by 5,800 km. The endemic character of *J. arguta* cannot be maintained. The discovery published in 2008 by BITNER (pp. 439-440; fig. 10 A, B) of a shell supposed to be *J.*

*arguta* ( which seems not different from the specimens studied in this paper) and collected from Fiji, Bligh Water by the French cruise MUSORSTOM 10 extends the distribution of this species to the South-West Pacific. *J. arguta* becomes now an Indo-Pacific brachiopod species with an extremely wide distribution. All these new results give also a more complete bathymetric range for this species as it is found from a depth of 30 m. in Enewetak (Marshall Islands) to 100 m. off Bikini (Marshall Islands). In the Indonesian archipelago it is found at depths between 25 and 30 m. In Fiji Island it has been dredged at 251-257 m. (BITNER, 2008).

The reasons for transferring *Argyrotheca arguta* to the genus *Joania* have been explained here in a nomenclatural note. It must be pointed out that a variable outline, an emarginated anterior margin, a dorsibiconvex shell, radial ridges terminating in marginal tubercles, a very strong cardinal process, a serrate dorsal septum and weakly defined descending branches of the loop are observed in both species *Joania cordata* and *J. arguta*. But the ventribiconvex shell, the two or four rounded weakly defined costae, the narrow hinge and the cardinal process with a shaft are specific characters of *J. cordata* and they are not observed in *J. arguta*. These characters are not generic. However, the fact that the hinge line is always shorter than the width of the shell is a character observed in both species and it seems of generic value.

In this work, it was sometimes difficult to make detailed comparisons with some species because they are poorly illustrated. It is thus necessary to insist on the need for precise illustrations to help in recognizing correctly the different species of brachiopods. The distinctions between species could sometimes be difficult as they are based on minor morphological characters. Brachiopods have also asymmetrical shells and all the projections i.e. dorsal, ventral, lateral, anterior and posterior are absolutely useful for considering the different aspects of the shell. Of course external and internal views of the specimens should be given as often as possible.

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Eric SIMON

Département de Paléontologie (Invertébrés)  
Institut royal des Sciences naturelles de Belgique  
Rue Vautier, 29  
B-1000 Bruxelles  
Belgique.  
ericssimon98brach@yahoo.fr

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## Plate captions

### PLATE 1

*Argyrotheca furtiva* n. sp. collected in the shipwreck "Mutiarra" off Donggala Harbour, Donggala, Central Sulawesi, Indonesia at - 30 m. Holotype, RBINS - RI- BRA 7, housed in the RBINS, Brussels, Belgium. Size of the specimens given by scale bars.

- Fig. 1. – Holotype in living position attached on a shell fragment of *Neopycnodonte* sp. **1a**: Oblique dorsal view showing the incipient costae and the median sulcus. **1b**: Slightly oblique anterior view illustrating the incipient opposite folding with bilobate shell structure and the rectimarginate commissure. Material air dried.
- Fig. 2. – SEM observations of the complete shell. The specimen has been bleached for removing all organic parts. Noteworthy is the slightly tuberculate structure of the shell surface. This aspect is very difficult to observe using a conventional binocular microscope. **2a**: Dorsal view. The shell is semi-circular with short wing-like lateral extremities. Four incipient radial costae are visible and a wide median sulcus is developed. The surface of the dorsal protogulum is wrinkled whereas the early growth stages of the shell are smooth. The latter growth stages produce a slightly spino-tuberculate shell surface. **2b**: ventral view. **2c**: lateral view. The shell is strongly ventribiconvex with an apsacline cardinal area. The beak with a hypothryid foramen is attrite. The lateral parts of the beak are not tuberculate. The lateral commissure is sinuous. **2d**: anterior view. The incipient costae, the opposite folding and bilobate shell structure and the rectimarginate commissure are clearly visible. **2e**: posterior view. The hypothryid foramen is limited by long, narrow deltidial plates. The beak is attrite. The interareas are striated.
- Fig. 3. – SEM observations of the disarticulated dorsal valve. The specimen has been bleached for removing all organic parts. **3a**: ventral view. Obtuse crural processes, descending branches attached to the internal side of inner socket ridges and fused to the valve floor and small median septum well visible. **3b**: oblique anterior view. The small median septum with its obtuse tip is clearly visible. Posteriorly two typical strong adductor muscle scars are developed. Descending branches are attached on the anterior end of the median septum. **3c**: detailed oblique anterior view showing the subtriangular strong adductor muscle scars placed in the umbo of the valve. **3d**: oblique lateral view. The sockets, crural processes, descending branches and the subtriangular obtusely pointed median septum are clearly visible. **3e**: oblique posterior view showing the outer and inner socket ridges as the posterior aspect of the loop and of the dorsal septum.

- Fig. 4 – SEM observations of the disarticulated ventral valve. The specimen has been bleached for removing all organic parts. **4a**: dorsal view. A wide pedicle collar is developed and a low blade-like median septum is present. Teeth are relatively long and slender. **4b**: oblique anterior view. The pedicle collar is not buttressed by the median septum. **4c**: oblique lateral view showing the low blade-like median septum. **4d**: oblique posterior view. The pedicle collar, the median septum and the small pit accommodating the crest of the dorsal septum are visible.

#### PLATE 2

*Argyrotheca furtiva* n. sp. collected in the shipwreck “Mutuara” off the Donggala Harbour, Donggala, Central Sulawesi, Indonesia at – 30 m deep. Paratype, RBINS - RI- BRA 8, housed in the RBINS, Brussels, Belgium. This specimen has been preserved in ethanol and its valves were slightly disjoined due to shock during transportation. For this reason, valves have been treated separately and are presented disarticulated. Size of the specimens given by scale bars.

- Fig. 1 – Dorsal valve showing the lophophore critical point dried. The left inner socket ridge has been broken during transportation of the material. **1a**: ventral view. **1b**: oblique anterior view.
- Fig. 2 – Dorsal valve treated with household bleach (5% hypochlorite) for removing all organic matter. **2a**: external dorsal view showing the numerous wavy growth lines, the smooth aspect of the shell surface in early growth stages and the microtuberculate aspect of the shell surface in later growth stages. **2b**: internal aspect in ventral view showing the loop with obtuse crural processes, the descending branches attached to valve floor and to the anterior part of the median septum. The small, short median septum is visible. **2c**: detailed view of the posterior part of the valve. **2d**: oblique lateral view showing the socket, the obtuse crural processes, the descending branches and the subtriangular median septum with its obtuse tip. **2e**: oblique anterior view showing the small obtuse median septum and the deep adductor muscle scars in the posterior part of the valve. **2f**: oblique posterior view showing the outer and inner socket ridges, the incipient cardinal process and the obtuse crural processes.
- Fig. 3 – Ventral valve treated with household bleach (5% hypochlorite) for removing all organic matter. **3a**: external ventral view showing the tuberculate shell surface and the incipient radial costae. **3b**: internal dorsal view showing the low ventral median septum and the pedicle collar. The left tooth has been damaged during transportation. **3c**: Detailed view of the pedicle collar. The attrition of the tip of the beak is perceptible. **3d**: Detailed view of the blade-like median septum. **3e**: oblique lateral view showing the structure of the tooth and the blade like low median septum. **3f**: oblique anterior view. The pedicle collar is not buttressed by the median septum. **3g**: oblique posterior view showing the pedicle collar and the attrition of the tip of the beak. **3h**: a detailed view of the posterior part of the valve.

#### PLATE 3

*Joania arguta* (GRANT, 1983). Complete articulated specimens collected from the shipwreck “Mutuara” off the Donggala Harbour, Donggala, Central Sulawesi, Indonesia (depth: 30 m). All this material housed in the RBINS, Brussels, Belgium. **a**: dorsal view; **b**: ventral view; **c**: lateral view; **d**: anterior view; **e**: posterior view; **f**: portion of the shell surface of the ventral valve; **g**: detailed view of the shell surface of the ventral valve. Size of the specimens given by scale bars.

The four specimens illustrated here show a dorsibiconvex shell, are emarginate anteriorly, have a slightly unisulcate anterior commissure due to the development of a stronger dorsal sulcus, a dorsally concave curved lateral commissure, an apsacline interarea and a shell surface of the ventral valve which is more tuberculate than the shell surface of the dorsal valve.

- Fig. 1 – Specimen RBINS - RI- BRA 1, an adult individual found in living position on a small fragment of the wall extracted from the store in the wreck. The specimen is not bleached. On the left side this shell is slightly distorted due to a pressure against the substrate during growth. This shell distortion affects the whole shell outline which appears less regular. The detailed views of the tuberculate ventral shell surface (Fig. **1f**, **1g**) show that the position of the microtubercles is alternate with the position of the punctae.
- Fig. 2 – Specimen RBINS - RI- BRA 2, a fully adult individual found in the sieved sediment collected on the floor of the store in the wreck. The specimen has been bleached. Its outline is identical to the outline of the specimens described by GRANT and collected from the Marshall Islands. There are no real costae developed but a low, wide

median sulcus is clearly visible. The detailed illustrations of the tuberculation of the ventral shell surface (Fig. 2f, 2g) show again that the tubercles are in regular alternate position with the punctae.

- Fig. 3 – Specimen RBINS - RI- BRA 3, a juvenile with a much more ovate outline collected from the sieved sediment. This specimen is emarginate anteriorly. The hinge line is much narrower than in adult specimens. On the shell surface of the ventral valve the minute tubercles appear coarser than those observed for adult shells.
- Fig. 4 – Specimen RBINS - RI- BRA 4, a large shell collected from the sieved sediment. Its outline is more subquadrate. Such shells are frequent and represent a morphological variation.

*Joania arguta* (GRANT, 1983). Complete articulated specimens collected from the sediment accumulated in the store of shipwreck “Liberty” off Tulamben, Bali, Indonesia (depth: 25 m). All this material housed in the RBINS, Brussels, Belgium. Size of the specimens given by scale bars.

The two specimens illustrated show a dorsibiconvex shell, emarginate anteriorly and a shell surface of the ventral valve which is more tuberculate than the shell surface of the dorsal valve.

- Fig. 5 – Fully adult specimen (RBINS - RI- BRA 5). 5a: dorsal view. 5b: ventral view with tuberculate shell surface.
- Fig. 6 – Juvenile specimen (RBINS - RI- BRA 6) with a more ovate outline and shorter hinge line. 6a: general dorsal view. 6b: detailed view of the posterior part of the shell. The protegulum surface is slightly wrinkled. The early growth stages are smooth and do not exhibit punctae. The later stages of growth are coarsely punctate.

#### PLATE 4

*Joania arguta* (GRANT, 1983). Complete disarticulated specimens collected in the shipwreck “Mutiara” off Donggala, Central Sulawesi, Indonesia (depth: 30 m). All this material housed in the RBINS, Brussels, Belgium. Size of specimens given by scale bars.

- Fig. 1 – Specimen RBINS - RI- BRA 1, an adult individual found in living position on a small fragment of the wall extracted from the store in the wreck. For these internal views the specimen has been bleached. a: dorsal valve in ventral view showing dorsal median septum and several well defined marginal tubercles. b: detailed view of the complex strong cardinal process. c: dorsal valve in oblique anterior view showing the tuberculate anterior edge of median septum and radial ridges terminating anteriorly in tubercles. d: dorsal valve in oblique lateral view showing the serrate median septum. e: dorsal valve in oblique posterior view showing sockets, socket ridges and the posterior edge of the median septum. f: ventral valve in dorsal view. g: ventral valve in oblique posterior view showing pedicle collar, blade-like median septum and radial ridges on the valve floor. h: detailed view of the pedicle collar and the teeth in dorsal view. i: ventral valve in oblique lateral view showing the subtriangular shape of the blade-like median septum. j: ventral valve in oblique anterior view showing that the pedicle collar is not buttressed by the median septum.
- Fig. 2 – Specimen RBINS - RI- BRA 2, a fully adult individual found in the sieved sediment collected on the floor of the store in the wreck. The specimen has been bleached. Its outline is identical to the outline of the specimens described by GRANT and collected from the Marshall Islands. a: dorsal valve in ventral view showing dorsal median septum and a small number of well defined marginal tubercles. b: dorsal valve in oblique lateral view showing the serrate median septum. c: dorsal valve in oblique anterior view showing the tuberculate anterior edge of median septum and radial ridges terminating anteriorly in tubercles. d: dorsal valve in oblique posterior view showing sockets, socket ridges and the posterior edge of the median septum. e: ventral valve in dorsal view with blade-like median septum. f: ventral valve in oblique lateral view showing the subtriangular shape of the blade-like median septum.
- Fig. 3 – Specimen RBINS - RI- BRA 3, a juvenile with a much more ovate outline and shorter hinge line collected from the sieved sediment. a: dorsal valve in ventral view showing a incipient median septum emerging anteriorly from the valve floor and very few marginal tubercles. b: dorsal valve in oblique lateral view. c: dorsal valve in oblique anterior view. d: ventral valve in dorsal view showing a very short median septum in the posterior part of the valve.

- Fig. 4 – Specimen RBINS - RI- BRA 4, a large adult shell collected from the sieved sediment. Its outline is more subquadrate. **a:** dorsal valve in ventral view showing tuberculate dorsal median septum and a large number of well defined marginal tubercles. **b:** dorsal valve in oblique lateral view showing the serrate median septum. **c:** dorsal valve in oblique anterior view showing the tuberculate anterior edge of median septum and radial ridges terminating anteriorly in tubercles. **d:** dorsal valve in oblique posterior view showing sockets, socket ridges, the posterior edge of the median septum and the radial ridges terminating in strong marginal tubercles. **e:** ventral valve in dorsal view with wide triangular pedicle collar, blade-like median septum and teeth given off dorsally. **f:** ventral valve in oblique lateral view showing the subtriangular shape of the blade-like median septum. **g:** ventral valve in oblique posterior view showing pedicle collar, teeth given off dorsally, blade-like median septum and radial ridges on the valve floor.

*Joania arguta* (GRANT, 1983). Complete disarticulated specimens collected from the sediment accumulated in the store of shipwreck “Liberty” off Tulamben, Bali, Indonesia (depth: 25 m). All this material housed in the RBINS, Brussels, Belgium. Size of the specimens given by scale bars.

- Fig. 5 – Juvenile specimen (RBINS - RI- BRA 6) with a more ovate outline and shorter hinge line. **a:** dorsal valve in ventral view showing a incipient median septum emerging anteriorly from the valve floor and very few marginal tubercles. **b:** dorsal valve in oblique lateral view. **c:** dorsal valve in oblique anterior view.

- Fig. 6 – Fully adult specimen (RBINS - RI- BRA 5). **a:** dorsal valve in ventral view showing tuberculatè dorsal median septum and a large number of well defined marginal tubercles. **b:** detailed view of the strong complex cardinal process. (The right crural process has been broken and is visible on the internal side of the inner socket ridge). **c:** dorsal valve in oblique lateral view showing the serrate median septum. **d:** dorsal valve in oblique anterior view showing the tuberculate anterior edge of median septum and radial ridges terminating anteriorly in tubercles. **e:** dorsal valve in oblique posterior view showing sockets, socket ridges and the posterior edge of the median septum. **f:** detailed oblique postero-lateral view of the tuberculate dorsal septum septum. The descending branch is visible on the lateral and upper posterior parts of the septum. **g:** ventral valve in dorsal view with a blade-like median septum. **h:** ventral valve in oblique anterior view showing that the pedicle collar is not buttressed by the median septum.

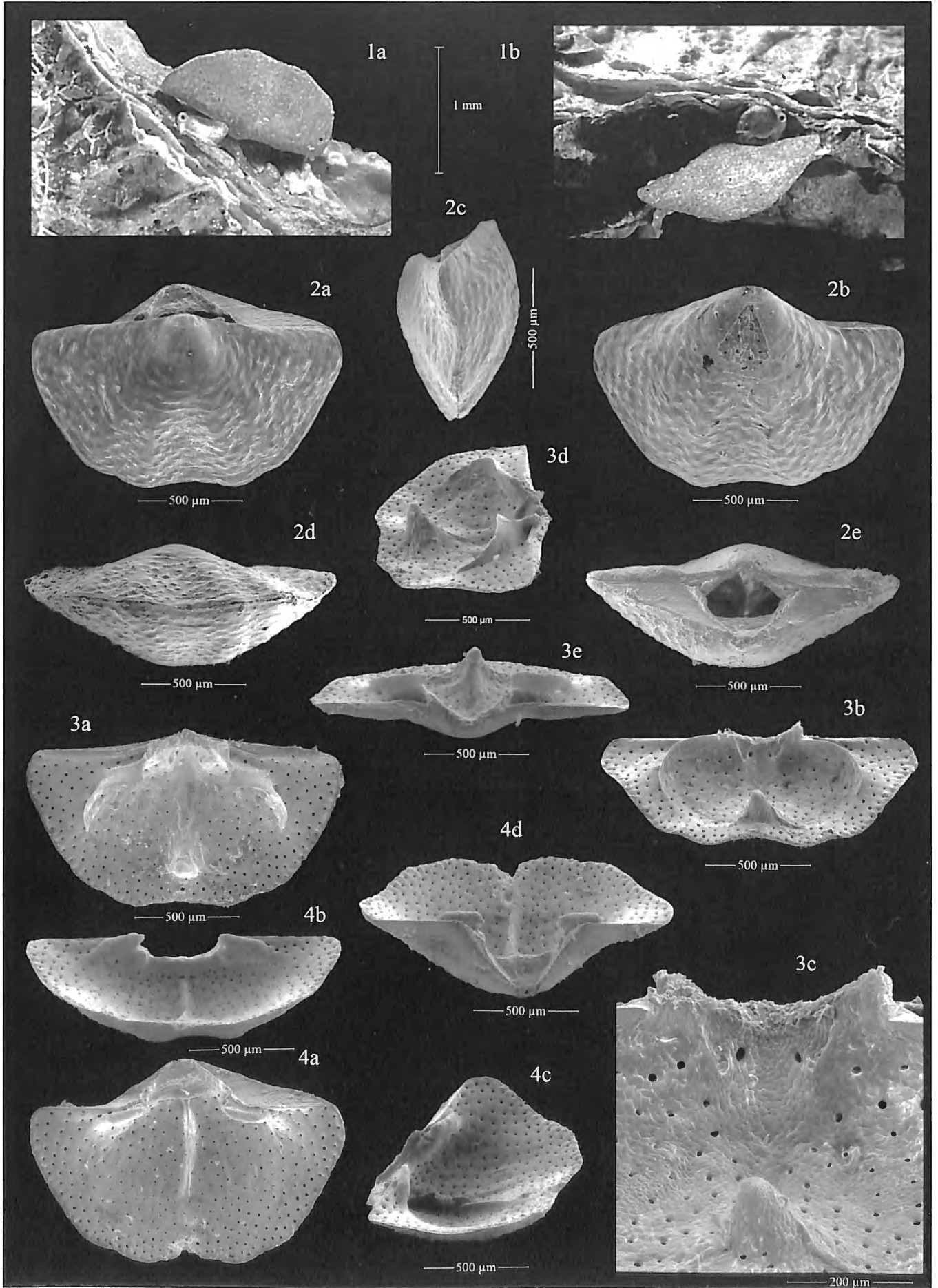


PLATE 1



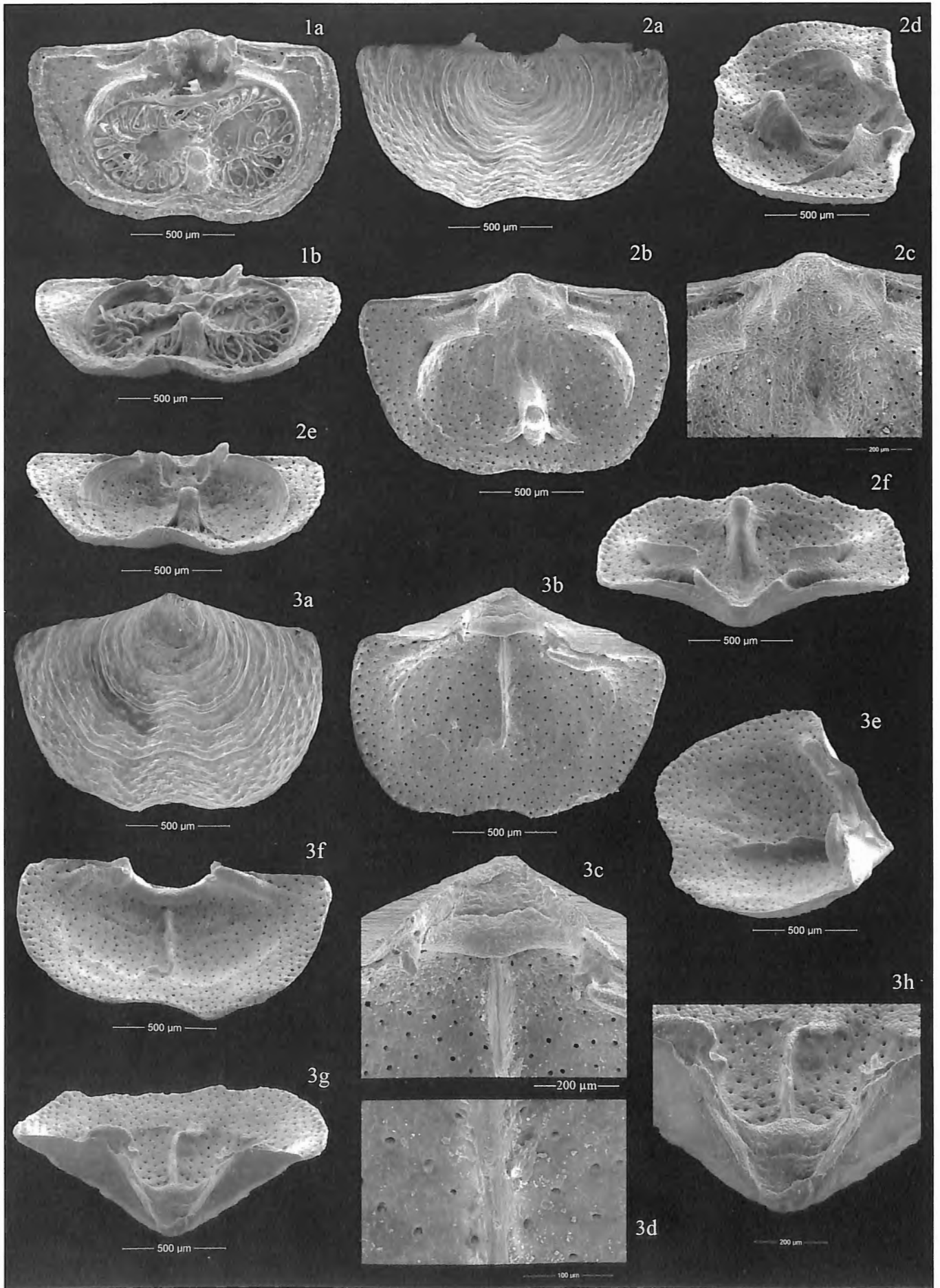


PLATE 2

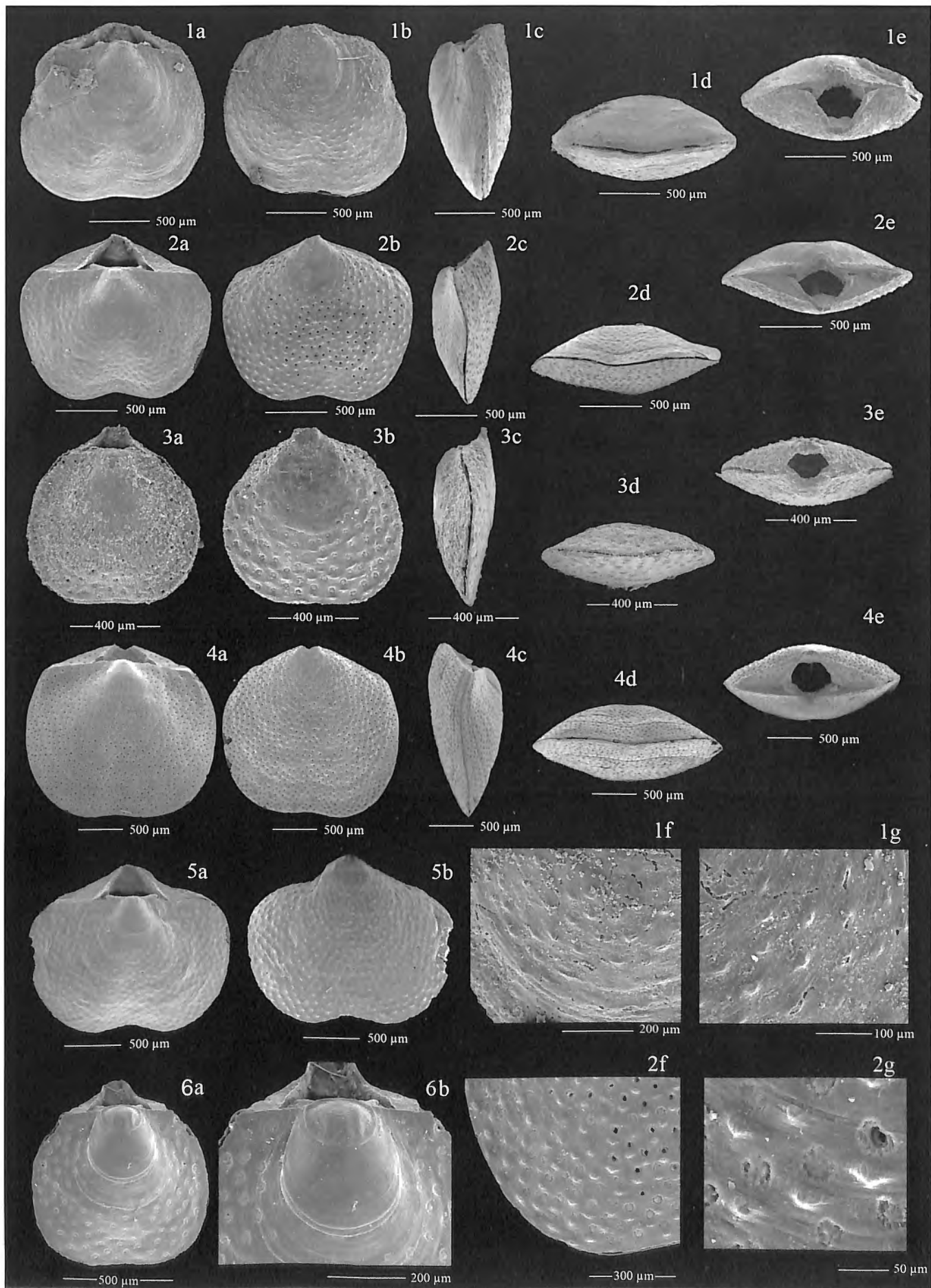


PLATE 3

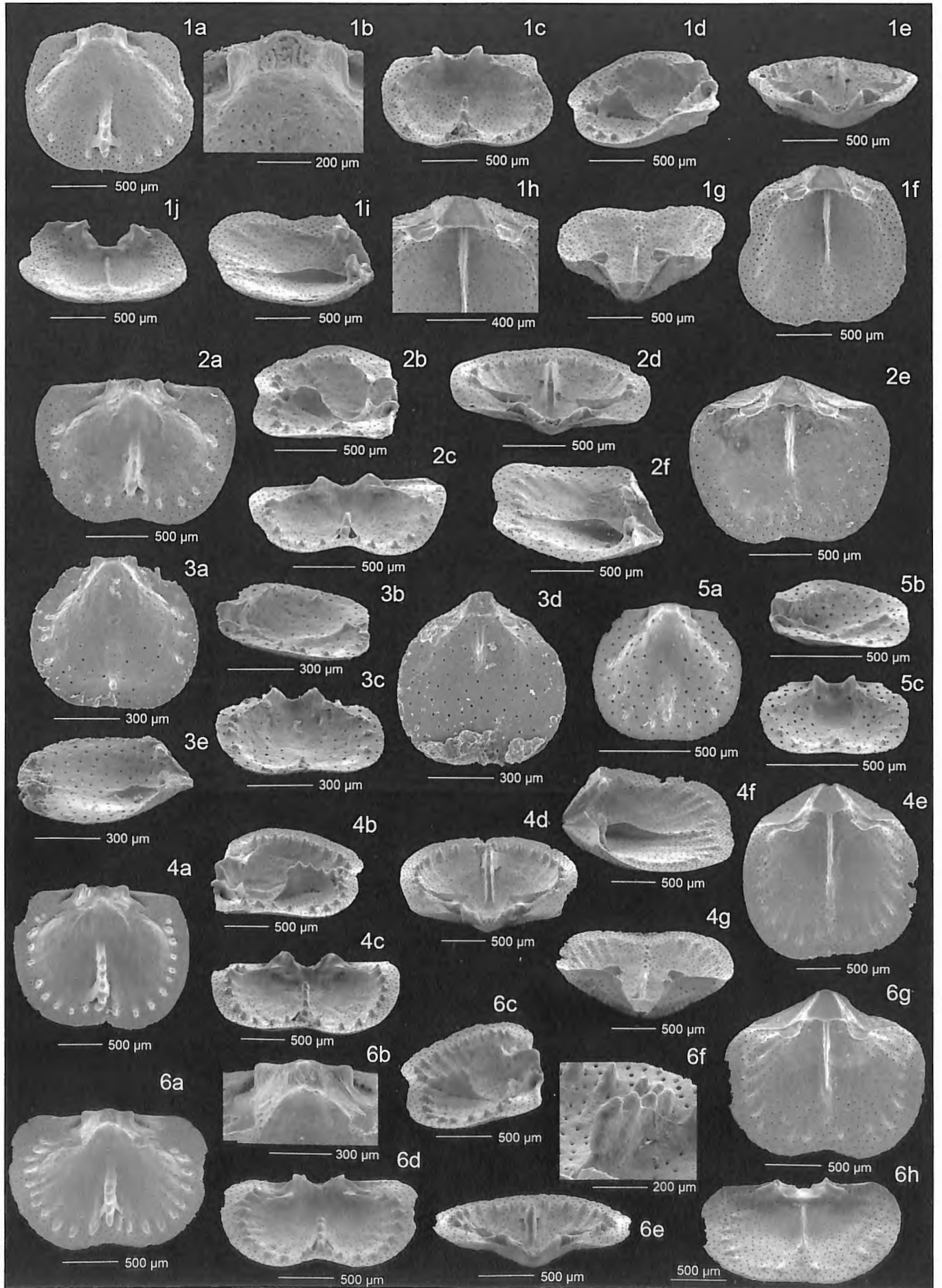


PLATE 4