

A new Late Maastrichtian species of *Isocrania* (Brachiopoda, Craniidae) from The Netherlands and Belgium

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Abstract

Species of the craniid genus *Isocrania* JAEKEL, 1902 are known to have been able to adapt to various ecological parameters during their evolutionary history, which ranged in the Cretaceous from the Turonian to the Late Maastrichtian. For quite some time, specimens of *Isocrania* assignable to the “*costata* group”, which were adapted to life in current-swept environments and which occur abundantly in fossil hash levels directly above the Lichtenberg Horizon (= base of the Maastricht Formation, Late Maastrichtian) at Maastricht (The Netherlands), have posed a taxonomic problem. This material is revised here, and a new species of *Isocrania* is erected.

Keywords: Brachiopods, Upper Maastrichtian, The Netherlands, Belgium, new species.

Résumé

Les espèces de Craniidae du genre *Isocrania* JAEKEL, 1902 se sont adaptées à de nombreux paramètres écologiques tout au long d'une évolution s'étendant du Turonien au Maastrichtien. Des spécimens d'*Isocrania*, appartenant au « groupe *costata* », bien adaptés aux forts courants et abondants dans les niveaux fossilifères au-dessus de l'horizon de Lichtenberg (base de la Formation de Maastricht, Maastrichtien Supérieur) à Maastricht (Pays-Bas), représentaient depuis longtemps un problème taxonomique. Ce matériel a fait l'objet d'une révision et une nouvelle espèce d'*Isocrania* a été érigée.

Mots-clés: Brachiopodes, Maastrichtien Supérieur, Pays-Bas, Belgique, nouvelle espèce.

Introduction

Craniid brachiopods have often been considered

problematic fossils, which explains why they have been the subject of numerous taxonomic debates. RETZIUS erected the genus *Crania* and described *Crania Egnabergensis* (1781, p. 75, pl. 1, figs. 4-7) and later J. SOWERBY (1823, vol. 4, pl. 35, fig. 6) introduced *Crania costata* (the description of this species was by J. SOWERBY and not J. DE C. SOWERBY as explained by SURLYK in 1973). Ever since the first appearance of these species names, there has been confusion about their status. Such confusion is seen in DAVIDSON (1852) or NIELSEN (1909), as already noted by SURLYK (1973, p. 233). However, later authors interpreted *Crania costata* correctly, e.g. HOENINGHAUS (1828, pl. 1, fig. 11), GOLDFUSS (1840, pl. 162, fig. 11), VON HAGENOW (1842, pl. 9; fig. 1) and POSSELT (1894, pl. 1, figs 1-4). *Crania egnabergensis* was considered to be a distinct species by LUNDGREN (1885). Later, CARLSSON (1958) shared their views, but still there was confusion in their assignments, as pointed out by SURLYK (1973, p. 237).

Fortunately, in 1902, the genus *Isocrania* was erected by JAEKEL for these two species, and the general interest in these peculiar brachiopods grew again.

The confusion surrounding *Isocrania egnabergensis* and *I. costata* was resolved finally by SURLYK (1973), who published a detailed comparative autecological and taxonomic study. The specific morphological characters of these two species were pointed out and the relationships between shell structure and ecological adaptations were determined. Both *I. egnabergensis* and *I. costata* are now interpreted as free-living species at the adult stage, but the former was adapted to a high-energy, turbulent environment, whereas *I. costata* developed greater shell stability on a muddy, white chalk sea floor.

In 1984, ERNST erected several new species

of *Isocrania* from a white chalk section (Middle Coniacian to Lower Maastrichtian) at Lägerdorf-Kronsmoor (northern Germany). He pointed out two essentially different ecological adaptations for species collected from this sequence: species living fixed to a substrate and adapted to a turbulent environment and secondarily free-living species well adapted to a tranquil environment with soft bottom.

Isocrania borealis ERNST, 1984 lived attached during its entire life to a substrate by a relatively large attachment surface whereas *Isocrania costata* was a free-living species at the adult stage, thus confirming SURLYK's views (1973)

In fact, ERNST (1984) developed the concept of two distinct groups of species of *Isocrania* occurring in white chalk sections of Turonian to Early Maastrichtian age, namely the "borealis group" and the "costata group".

The "borealis" group includes species which lived fixed to a substrate at the adult stage. Species and subspecies such as *I. borealis*, *I. borealis tardestriata* ERNST, 1984, *I. borealis multistriata* ERNST, 1984, *I. restricta* ERNST, 1984 and *I. barbata* (VON HAGENOW, 1842) have a large, well-developed attachment

surface, and are well represented in the Turonian to Upper Campanian interval. Subsequently, they were unable to develop further as the bottom consisted essentially of muddy oozes.

The second group evolved during the Campanian and Maastrichtian, and comprises forms in which the attachment surface (which is still rather large in the primitive *Isocrania campaniensis* ERNST, 1984), disappeared progressively as a free-living adult stage was favoured, as is shown by development of a conical ventral valve first during the Early Maastrichtian (*Belemnella sumensis* Zone), with the occurrence of the first specimens of *Isocrania costata*. This conical ventral valve improved shell stability on the chalky sea bottom, allowing elevation of the commissure above the muddy surface. This adaptation prevented the lophophore from being clogged by mud particles in suspension (SURLYK, 1973, pp. 224-226).

Intermediate forms between *I. campaniensis* and *I. costata* were described by ERNST (1984). *Isocrania praecostata* ERNST, 1984 from the *Belemnella pseudobtusa* Zone (Lower Maastrichtian), which still possessed a small attachment surface at the adult stage, was a typical intermediate evolutionary

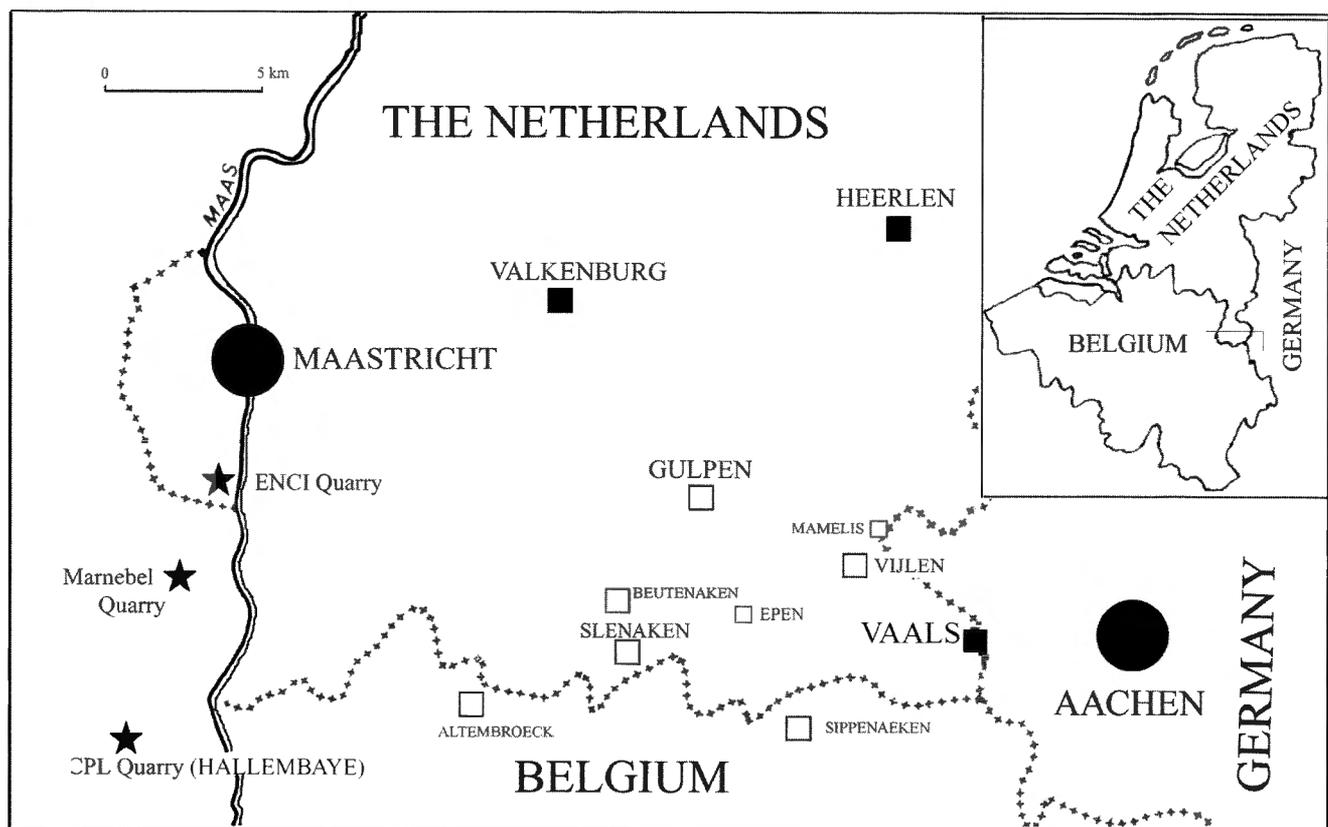


Fig. 1 — Map of southern Limburg (The Netherlands) and contiguous Belgian and German territories showing localities (stars) from which the material has been collected.

DANIAN		Geulhem Member	
		— Vroenhoven	
M A A S T R I C H T I A N	U P P E R	M A A S T R I C H T I A N F O R M A T I O N	Meerssen Member
			— Caster
			Nekum Member
			— Laumont
			Emael Member
			— Romontbos
			Schiepersberg Member
			— Schiepersberg
			Gronsveld Member
			— St. Pieter
	Valkenburg Member		
	Lichtenberg		
	L O W E R	G U L P E N F O R M A T I O N	Lanaye Member
			— Nivelle
Lixhe 1-3 Members			
— Wahlweiler			
Vijlen Member			
— Bovenste Bosch			
CAMPANIAN			
		Beutenaken Member	
		— Slenaken	
		Zeven Wegen Member	
		— Zeven Wegen	

Fig. 2 — Local lithostratigraphic subdivision of Campanian-Maastrichtian strata (after W.M. FELDER, 1975) with indication of horizons separating the different members.

step between *I. campaniensis* and *I. costata*. Later, another representative of the “*costata*” group, adapted to a non-white chalk environment was discovered: *I. phosphatica* SIMON, 1998 from the Phosphatic Chalk of Ciplý (*Belemnella obtusa* Zone, Lower Maastrichtian). This species has a very flat ventral valve, with a posteriorly positioned attachment

surface. Such shell form was better adapted to current action than to a muddy bottom sea floor.

The Late Maastrichtian specimens of *Isocrania* studied for the present paper have long posed a taxonomic problem. They cannot be assigned to any previously described species from the Upper Cretaceous. Late Maastrichtian material collected from limestones of the Debovo Formation near Shumen (Bulgaria), described by MOTCHUROVA-DEKOVA (1996, fig. 9(6); pp. 302-303) as *Isocrania* sp. ex gr. *costata*, does not match the specimens discussed here. This Bulgarian material has a simple conical flat dorsal(?) valve with relatively weak costae and smooth interspaces. In contrast, our Maastrichtian material shows specimens with distinct costae separated by interspaces with a strong radial, spiny ornamentation.

Specimens studied here were collected mainly from the fossil hash levels directly overlying the Horizon of Lichtenberg at the ENCI quarry (Fig. 1) near Maastricht (The Netherlands) also representatives of a non-white chalk environment. They are known not only from this level, but also (Fig. 2) occur sporadically in the underlying Lanaye Member (top of the Gulpen Formation) and range to the base of the Meerssen Member (top of the Maastricht Formation), invariably in coarse-grained sediments. For a discussion of lithostratigraphic units, facies interpretation and biozonation, see JAGT (1999, pp. 27-31).

This species of *Isocrania* was listed by BOSQUET (1860, n° 544) as *Crania Ignabergensis* RETZ. Much later, KRUYTZER (1969, pp.30-34) referred to it as *Crania (Isocrania) ignabergensis* RETZIUS, 1781 (note the misspelling “*ignabergensis*” instead of “*egnabergensis*”; see SURLYK, 1973). Both authors erred in considering this material to be conspecific with *I. egnabergensis*, which is a subrectangular (longer than wide) species with ornamentation consisting of 30-70 fine radials ribs and which, in fact, is restricted to the upper Lower Campanian in southern Sweden. The material from the Maastricht area studied here is much closer to *Isocrania costata* and cannot be confused with *I. egnabergensis*. Although this form is a member of the “*costata*” group, it is quite distinct from *Isocrania costata*, which is why a new species is here introduced to accommodate it.

Material and methods

A considerable portion of the material studied was collected

in 1993 by J. Reynders from a 30 kg bulk sample taken at the fossil hash level directly overlying the Horizon of Lichtenberg at the ENCI quarry near Maastricht (The Netherlands) (Fig. 1). After washing and sieving, this sample (>1mm) yielded two articulated specimens as well as 312 ventral valves, 36 dorsal valves and numerous fragments. This material is relatively well preserved but is certainly allochthonous, having been transported over a short distance. Dorsal valves are much rarer than ventral valves as they suffered much more from current transportation. The dorsal valve surface near the umbo is often worn, reflecting the abrasive current action. This also explains why no juveniles were found amongst the specimens from this level; the lack of juveniles implies that no precise population structure could be established.

Some well-preserved specimens in the D. Eysermans collection (Vosselaar, Belgium) were also available; several years of collecting from the level above the Horizon of Lichtenberg resulted in the find of a few rare juveniles. The same collection also contains juvenile specimens from the Marnebel Quarry (Fig. 1) at Eben-Emael (Liège Province, Belgium), collected from the Lanaye Member (between flint layers 12 and 14), a few metres below the Horizon of Lichtenberg. These juveniles allow a more complete morphological description of this new species to be made and are also useful for understanding its entire development.

Also represented in the Eysermans collection are a few adult specimens from levels other than the Horizon of Lichtenberg, as follows:

- 10 specimens from the Lanaye Member (between flint layers 11 and 13) at the ENCI quarry.
- 2 specimens from the Marnebel Quarry, Lanaye Member (between flint layers 22-23).
- 5 specimens from the Marnebel Quarry, Lanaye Member (between flint layers 14-20).
- 5 specimens from the Marnebel Quarry, Valkenburg Member.

The material studied was measured and scatter diagrams were plotted. The method of taking measurements followed parameters used by ERNST (1984, p. 14). The ventral and dorsal valves were measured for length, width, distance from posterior side to the umbo (Lp), and distance from the umbo to the anterior side (La). The number of primary costae and the total number of costae were counted.

In addition, the thickness of both ventral and dorsal valves was measured as the relative flatness of the ventral valve is considered an important adaptation to current action (SURLYK 1973, pp. 231-232). The size of the attachment surface on the ventral valve has also been considered.

Suprafamilial classification follows WILLIAMS *et al.* (1996) and WILLIAMS *et al.* (2000, pp. 22-27), and classification within the order Craniida WAAGEN, 1885 follows BASSETT (2000, pp. H169-183).

Taxonomic description

Phylum Brachiopoda DUMÉRIL, 1806
 Subphylum Craniiformea WILLIAMS *et al.*, 1996
 Order Craniida WAAGEN, 1885
 Suborder Craniidina WAAGEN, 1885
 Superfamily Craniioidea MENKE, 1828
 Family Craniidae MENKE, 1828
 Genus *Isocrania* JAEKEL, 1902

Type species : *Crania egnabergensis* RETZIUS, 1781.

Isocrania sendeni n. sp.

Pl. 1, Figs 1-4; Pl. 2, Figs 1-4; Pl. 3, Figs 1, 2 ;
 Tables 1, 2 ; Text-Figure 3

pp 1860 — *Crania Ignabergensis* Retz. — BOSQUET, n° 544.
 1969 — *Crania ignabergensis* Retzius 1781 — KRUYTZER,
 pp. 31-35, fig. 12a-d (*non* fig. 12e).

Diagnosis

Medium-sized *Isocrania* with subcircular outline. Both valves have an ornamentation of (16)18 - 38(42) costae, the postero-lateral ribs being slightly curved posteriorly. Interspace surface densely covered with radially directed spines. New costae formed by intercalation. Ventral valve thick, heavy, very flat, depressed centrally, with trace of very small attachment surface in posterior position. Attachment surface equals highest point of ventral valve. Dorsal valve "capuliform" with umbo curved backwards and placed posteriorly. Ventral valve with anterior adductor muscle scars placed centrally. Dorsal valve with elliptical posterior adductor muscle scars, strong hatchet-style anterior adductor muscle scars and well-developed elevator muscle scars. Long ridge present on the valve floor of dorsal valve bearing well-developed protractor muscle scars.

Derivatio nominis

The species is dedicated to the late Mr. F.M.H. Senden, who was a well-known fossil collector in the Maastricht area. His collection, now housed at the Natuurhistorisch Museum Maastricht, has contributed substantially to a better understanding of brachiopod faunas from the Maastrichtian type area.

Locus typicus

ENCI quarry (Heidelberg Cement Group), Maastricht, southern Limburg, The Netherlands.

Stratum typicum

Fossil hash level directly on top of Horizon of

Specimens illustrated	Iconography	Valve type	L mm	W mm	T mm	La mm	Lp mm	Lp/La	1ary costae	2ary costae	total costae
Holotype MI, 11033	Pl. 1, Fig. 1	VV	8.8	9.5	2.0	6.1	2.7	10.44	11	22	33
Paratype MI, 11034	Pl. 1, Fig. 2	VV	6.1	6.3	1.2	4.3	1.9	0.44	13	15	28
Paratype MI, 11035	Pl. 1, Fig. 3	DV	7.1	8.2	2.3	5.4	1.7	0.32	10	17	27
Paratype MI, 11036	Pl. 1, Fig. 4	DV	8.3	9.6	3.0	6.9	1.4	0.20	11	32	43
Paratype MI, 11037	Pl. 2, Fig. 1	VV	11.4	11.9	2.1	9.2	2.2	0.24	11	14	25
Paratype MI, 11038	Pl. 2, Fig. 2	VV	8.1	9.1	1.7	6.9	1.2	0.17	11	20	31
Paratype MI, 11039	Pl. 2, Fig. 3	DV	7.2	7.7	2.0	5.8	1.4	0.24	12	23	35
Paratype MI, 11040	Pl. 2, Fig. 4	VV	3.9	4.1	0.6	2.3	1.8	0.79	11	7	18
Paratype MI, 11040	Pl. 2, Fig. 4	DV	3.9	4.1	1.0	2.4	1.5	0.63	13	6	19
Paratype MI, 11041	Pl. 3, Fig. 1	VV	2.6	2.8	0.4	1.5	1.0	0.69	10	4	14
Paratype MI, 11042	Pl. 3, Fig. 2	DV	2.7	2.8	0.8	1.5	1.2	0.82	9	2	11

Table 1 — Measurements (in mm) of specimens of *Isocrania sendeni* n. sp. described and illustrated in the present paper; all housed in the Institut royal des Sciences naturelles in Brussels (IRScNB). VV: ventral valve. DV: dorsal valve. L: length. W: width. T: thickness (height of valve at the umbo). La: distance from the umbo to the anterior side of the valve. Lp: distance from the umbo to the posterior side of the valve. 1ary costae: number of primary costae. 2ary costae: number of secondary costae.

Lichtenberg, Valkenburg Member (base of Maastricht Formation), Late Maastrichtian, Upper Cretaceous.

Type

The holotype (Pl. 1, Fig. 1a-e; Table 1) is a fully adult ventral valve preserved in the Royal Belgian Institute for Natural Sciences in Brussels (IRScNB MI 11033), collected in 1993 from the hash level overlying the Horizon of Lichtenberg at the ENCI quarry by J. Reynders from a bulk sample of 30 kg net weight. Morphological characters measured on the holotype are listed in Table 1.

Description

Outline

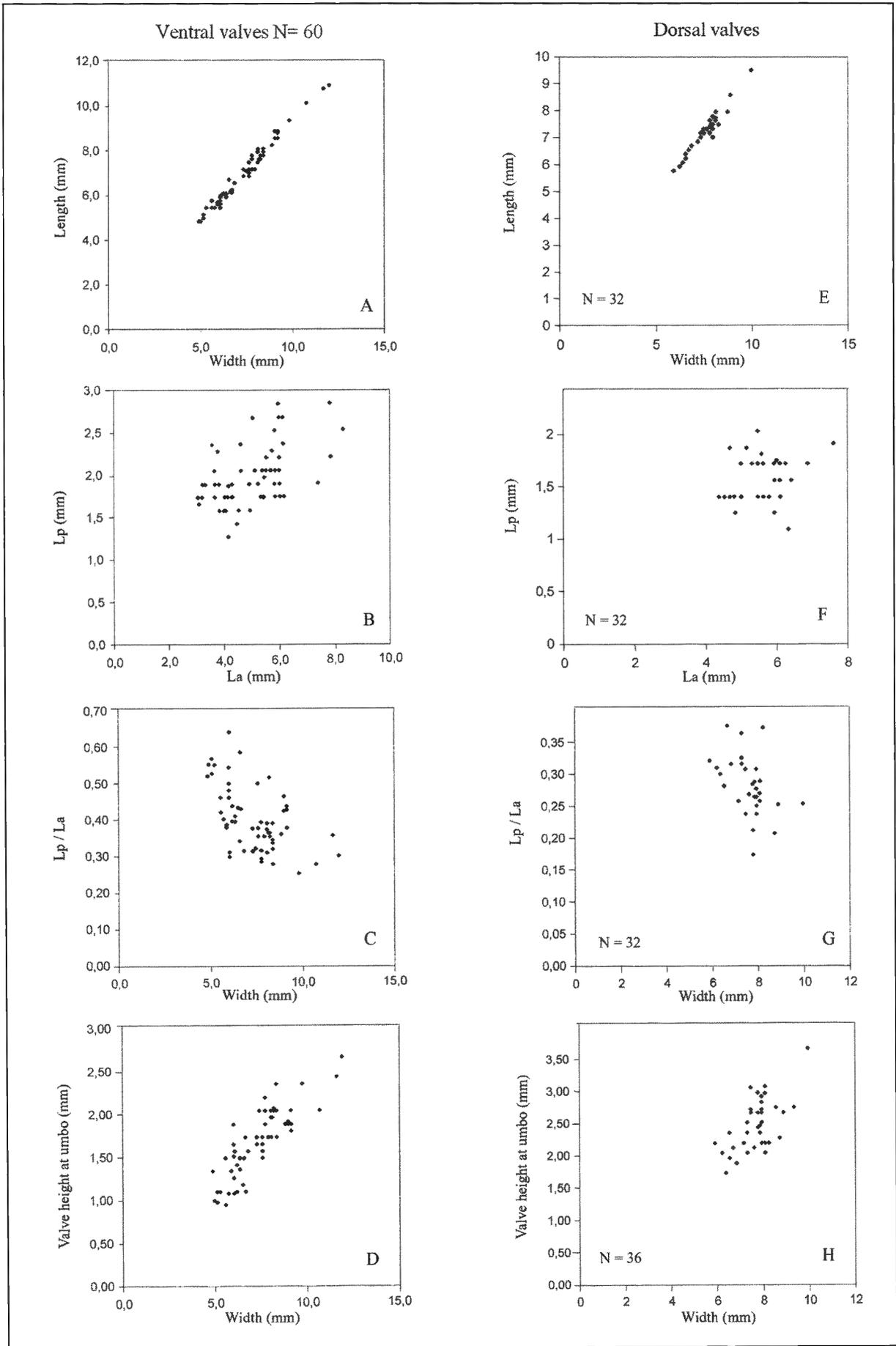
Subcircular, with posterior margin slightly truncated, which explains why the anterior margin is wider than the posterior. The valves are always slightly wider than long with their maximum width at mid-length. Anterior and lateral margins are rounded.

Ventral valve

The ventral valve is slightly thicker and heavier than the dorsal valve. In lateral view, this valve is very flat, with a depressed central area, and the protegular node, with the attachment surface, occupies the highest position. The protegular node, located posteriorly, is relatively small and flat. The size of the attachment surface is variable but smaller than the protegular node surface. In some specimens, the attachment surface is so diminutive that in many adult specimens

it is difficult to see without magnification. Such is the case in the holotype (Pl. 1, Fig. 1a, d). In contrast, several specimens show a wider, flat and subcircular attachment surface, as in one of the paratypes (Pl. 1, Fig. 2a, d). However, such a large attachment surface is relatively uncommon. The Lp/La ratio is rather low and has a mean value of 0.40 (Table 2; Text-Fig. 3B) indicating that the protegular node is posteriorly placed in this species. The Lp/La ratio has a higher value in small valves and decreases in larger specimens, indicating that the protegular node is positioned more posteriorly in gerontic specimens than in juveniles (Text-Fig. 3C). Juveniles collected from the Lanaye Member and from the fossil hash overlying the Horizon of Lichtenberg (Pl. 3, Fig. 1a, d) have a more central small protegular node, which allowed the animal to settle onto a small substrate such as bryozoans. This is demonstrated clearly by the higher value of the ratio Lp/La observed for juveniles (Table 1; specimens MI 11040, MI 11041 and MI 11042). The very small and occasionally barely visible attachment surface in adult specimens indicates that this species rapidly acquired a free-living life style. Rarely, fragments of the substrate used for fixation remain visible on the attachment surface of an adult specimen, as illustrated in Pl. 2, Fig. 1a.

The relation between Lp and La values measured for ventral valves (Text-Fig. 3B) is quite variable ($r = 0.51$). This relatively low correlation coefficient indicates that the relation between Lp and La was not subject to severe selection pressure. As seen in



	L mm	W mm	T mm	La mm	Lp mm	Lp/La	Costae 1 costae	Costae	total Costae
Ventral valves									
N	60.0	60.0	60.0	60.0	60.0	60.0	55	55	56
Minimum	4.8	4.9	0.94	3.1	1.3	0.25	9	7	16
Maximum	10.9	12.0	2.65	8.4	2.8	0.64	15	25	38
Mean	7.1	7.4	1.68	4.4	2.0	0.40	11.9	14.7	27
σ	1.42	1.56	0.40	1.21	0.34	0.088	1.22	4.13	4.45
Standard error	0.183	0.201	0.05	0.156	0.044	0.011	0.164	0.556	0.599
Dorsal valves									
N	32	36	36	32	32	32	20	20	30
Minimum	5.77	5.9	1.72	4.4	1.09	0.17	10	9	19
Maximum	9.5	9.98	3.65	7.59	2.03	0.37	16	26	38
Mean	7.25	7.71	2.46	5.62	1.59	0.28	12.2	16.9	29.3
σ	0.74	0.84	0.41	0.70	0.22	0.045	n.e.	n.e.	4.95
Standard error	0.12	0.14	0.07	0.11	0.04	0.081	n.e.	n.e.	0.90

Table 2 — Measurements (in mm) of specimens of *Isocrania sendeni* n. sp. collected (30 kg. bulk sample, washed and sieved) from a fossil hash level directly overlying the Lichtenberg Horizon (Upper Maastrichtian) at the ENCI quarry at Maastricht (The Netherlands). N: total number of individuals measured. For some characters, the number of specimens measured is lower because some valves are partly broken. Counting of the number of primary costae was sometimes impossible because the umbo of some valves is very erased. σ : standard deviation. This parameter is not evaluated for too small samples (n.e.)

SURLYK (1973, fig. 9, p. 236), this relation is much more accurate when measured for specimens of *Isocrania costata* or *Isocrania egnabergensis*. An accurate relation between Lp and La was also pointed out by SIMON (1998, text-fig. 9, p. 194) for *Isocrania phosphatica* from the phosphatic chalk at Ciply (*Belemnella obtusa* Zone, Lower Maastrichtian). In *I. sendeni* n. sp., the posterior position of the protegular node is a much more variable morphological character.

The number of primary costae varies between 9 and 15. New costae are produced by intercalation and the total number of costae has a mean value of 27

with a minimum of 16 and a maximum of 38. But, the total number of costae is quite variable in this species and this character seems relatively independent of specimen size. A rather low number of costae is present in the specimen illustrated in Pl. 2, Fig. 1a, but all kinds of intermediates (Pl. 2, Fig. 2) occur between paucicostate (Pl. 2, Fig. 1) and multicostate individuals (Pl. 1, Figs 1-4). The posterior costae are slightly curved backwards. Costae protrude beyond the valve margin but this character is more clearly developed in juvenile specimens. The shell surface of the interspaces is densely covered by coarse, radially directed spines. The fact that the costae are distinct

Fig. 3 — Opposite page

Scatter diagrams of *Isocrania sendeni* n. sp. collected from the fossil hash level directly overlying the Lichtenberg Horizon (base Valkenburg Member, Maastricht Formation; Upper Maastrichtian) at the ENCI quarry near Maastricht (The Netherlands). **Ventral valves** - 3A: Relationship between length and width ($y = 0.90x + 0.38$. $r = 0.98$). 3B: Relationship between the distance from the umbo to the anterior side (La) and the distance from the umbo to the posterior side (Lp) ($y = 0.15x + 1.22$. $r = 0.51$). 3C: Relationship between the ratio Lp/La and the width (Logarithmic curve fit: $y = 0.63 - 0.07 \ln x$. $r = 0.51$ and $r^2 = 0.26$). 3D: Relationship between the height of the valve at umbo and the width ($y = 0.17x + 0.42$. $r = 0.75$). **Dorsal valves** - 3E: Relationship between length and width ($y = 0.89x + 0.43$. $r = 0.94$). 3F: Relationship between the distance from the umbo to the anterior side (La) and the distance from the umbo to the posterior side (Lp) (no observable correlation). 3G: Relationship between the ratio Lp/La and the width (no visible correlation). 3H: Relationship between the height of the valve at umbo and the width. $y = 0.30x + 0.14$ $r = 0.63$).

and rather narrow, compared to the relatively wide interspaces, is a constant morphological character in this species. The width of the interspaces is reduced progressively when new costae develop by intercalation. However, the limit between interspaces and costae remains distinct. Costae never appear as wide folds of the shell surface as is the case in other species (see e.g. ROSENKRANTZ, 1964, pl. 5, fig. 1a-b; KRUYTZER, 1969, fig. 12e, p. 32).

In dorsal view, a set of well-developed muscle scars is preserved. The posterior adductor muscle scars are strongly developed, wide, subcircular and close set. They are separated by a prominent development of the posterior part of the limbus, which forms two strong and distinct lobes, ornamented with some very large pustules. The largest pustules of these lobes are those medially placed, in anterior position. These two large pustules are separated by a narrow sulcus. The oblique lateral muscle scars are elongated and very small yet distinct. The strong anterior adductor muscle scars are set on both sides of a short, pointed rostellum. The anterior limit of the rostellum is in the centre of the valve. These crescent-shaped adductor scars comprise two drop-shaped parts, a wide one and a narrower one of which the longitudinal axes define an angle between 50° and 55°. The oblique internal muscle scars are elongated. A flat ridge is present, dividing the anterior part of the valve floor into two distinct depressions, but is better visible in gerontic specimens (Pl. 2, Figs 1b, 2b). However, this ridge is barely visible in other specimens (Pl. 1, Figs 1b, 2b). Traces of the mantle canal system are developed to a variable degree in well-preserved specimens (Pl. 2, Fig. 1b). The limbus is wide and pustulose.

Dorsal valve

Despite the fact that dorsal valves are more rare (36 valves), all morphological characters could be established. The outline is similar to the ventral valve but the dorsal valve is subconical with the umbo in a very posterior position. The Lp/La ratio has a rather low mean value of 0.28, except in juvenile specimens (Table 1; specimens MI 11041 and MI 11042). This low value could indicate that the dorsal umbo is set more posteriorly than the ventral umbo. However, more dorsal valves are needed to resolve this matter definitively. Moreover, the dorsal umbo tends to be curved backwards, and thus renders a typical "capuliform" lateral profile to this valve; this profile is highly typical of the species. Juveniles, however, exhibit a regular conical lateral profile. The curvature of the umbo is already visible in young specimens

that are 4.0 mm wide (Pl. 2, Fig. 4c). The costae on the dorsal valve are developed in the same way as on the ventral valve. In the material studied, the number of primary costae varies between 10 and 16, whereas the total amount of costae varies between 19 and 42. When the dorsal shell valve is not worn, the interspace surface is covered densely by coarse, radially directed spines.

The posterior adductor muscle scars are close set near the posterior margin of the valve; they are relatively large but a little smaller and more elliptical than the adductor muscle scars of the ventral valve. These posterior adductor scars are separated by a fairly coarse development of the limbus, which forms a kind of apophysis. The apophysis is divided into two parts which have two small cavities on their tip. The cavities are opposed to the two large pustules developed face to face in the ventral valve. This notable development, as well seen in well-preserved specimens, was very useful in determining correct valve adjustment by the living animal which was devoid of a hinge. Oblique internal muscle scars are oval-elongated and sometimes clearly visible. A relatively long, median ridge is variably developed. Anterior adductor muscle scars are strongly developed on both sides of the ridge and present a "hatchet" structure. The elevator muscle scars, placed on the lateral sides of the anterior adductor muscle scars, are clearly developed in this species and they appear as crescentic, narrow-elongated structures. The protractor muscle scars are set on the anterior part of the median ridge (Pl. 1, Fig. 4a); these oval-shaped scars are relatively thick. The position of the protractor scars, however, is quite variable. In some specimens they are placed very near the anterior adductor scars, whereas in others they are situated much more anteriorly.

Comparison with other species of *Isocrania*

Isocrania sendeni n. sp. is assignable to the "costata group" as defined by ERNST (1984). The evolution of this group is characterized by a progressive regression of the attachment surface. The root species, *I. campaniensis*, possessed a relatively large attachment surface whereas *I. costata*, with its minute attachment surface, was a free-living species and represented the terminal evolutionary stage in this group. *Isocrania sendeni* was a free-living species with a very small attachment surface.

Comparison with *Isocrania costata*

Isocrania sendeni n. sp. has a very limited attachment surface which is as small as those observed in

specimens of *I. costata*. As pointed out by SURLYK (1973, pp 221-226) for *I. costata*, *I. sendeni* n. sp. at the juvenile stage also lived attached to small substrates such as bryozoans or molluscan fragments, but young adults rapidly became free living. However, *I. sendeni* cannot be confused with *I. costata*; the latter possesses a typically conical ventral valve with a much higher L_p/L_a ratio, which indicates that the umbo of the valve is more central. The conical ventral valve with central protegular node of *I. costata* was a feature that offered shell stability in a chalky environment and also prevented the lophophore from becoming clogged by muddy sediments (SURLYK, 1973, p. 226).

In *I. sendeni* the ventral valve is a heavy, flat, disc-shaped structure, adapted to a sea bottom with coarse sand and shell fragments, in a high-energy (turbulent, current-swept) environment. The ventral valve was centrally depressed; it attached to the sediment by its spiny periphery and by its protegular node placed more posteriorly, near the posterior margin. The lateral profile of the dorsal valve in *I. costata* is conical with a pointed, straight umbo. Clear examples of this are illustrated by ERNST (1984, pl. 6, fig. 3b; pl. 7, figs. 1b, 3b, 4b and 6b). Even if the umbo of the dorsal valve is not very sharp, it is never curved backwards (ERNST, 1984, pl. 7, fig. 2b).

The lateral profile of the dorsal valve in *I. sendeni* is conical with its umbo curved backwards (Pl. 1, Figs. 3c, 4c; Pl. 2, Fig. 3c). This character is already visible in young individuals as small as 4 mm (Pl. 2, Fig. 4c). However, early juvenile dorsal valves possessed a conical lateral profile with a straight umbo.

Comparison with *Isocrania paucicostata* (BOSQUET, 1859)

This species is rather intriguing, as the original specimen described and illustrated by BOSQUET (1859, pl. 1, figs 5a-b, 6a-b) is apparently lost. It has been referred to in the literature on numerous occasions, e.g. by JAEKEL (1902, p. 1063, fig. 5), CARLSSON (1958, pp. 26-27), ROSENKRANTZ (1964, p. 522, pl. 5, fig. 1), KRUYTZER (1969, p. 32, fig. 12e) and MOTCHUROVA-DEKOVA (1996, p. 305, fig. 9-1a, b). These records are all probably confused. Recently, the author had the opportunity to study a single, uniquely bivalved specimen of *I. paucicostata* from the Lanaye Member near Maastricht in the D. Eysermans collection. This specimen has all the characters of the type specimen as illustrated by Bosquet. It is a rather large species (width +/- 15 mm, length 13.0 mm, total thickness of bivalved specimen 6.5 mm) with a low

number of costae (10 primary costae and 19 in total) well separated by wide interspaces. The shell surface of the interspaces is devoid of any spiny structure but numerous fine growth lines are clearly visible, as markedly represented on the type specimen by Bosquet. The umbo is set in a very posterior position and the attachment surface is well developed, rather deep, although not very wide. The ventral valve is low conical, not flat, suggesting a fixed way of life. The dorsal valve is "capuliform" with its umbo curved backwards. The posterior adductor muscle scars are medium-sized (they appear rather small compared with the large size of this shell) and subcircular to elliptical. In the ventral valve these scars are separated by a limbus which forms two triangular, prominent small projections. This character is also clearly visible in the type specimen. In the dorsal valve the curved scars of the anterior adductor muscles are clearly visible and the protractor scars are set on a short ridge near the adductor scars. *Isocrania paucicostata* could not be confused with *I. sendeni* n. sp. which has a flat, depressed ventral valve and interspaces ornamented with radially oriented spines. The muscle scar system in *I. sendeni* is also quite different.

The specimen illustrated by KRUYTZER (1969, fig. 12e, p. 32) under the name "*Crania ignabergensis* Retzius var. *paucicostata* Bosquet" is quite large (width = 14 mm) but it has clear interspaces with radially oriented spines. The development of the costae is totally different (see below). This specimen is not conspecific with *I. paucicostata* as interpreted here and, moreover, does not match the diagnosis of *I. sendeni* n. sp. Collected from a quarry near L oen (Li ege, Belgium) and claimed (KRUYTZER, 1969, p. 32) to be Upper Maastrichtian, this specimen of *Isocrania* has very thick costae, mainly structured as wide, high, folds of the shell surface. This material is strikingly similar to a specimen collected at Bochohnica (central Poland) and illustrated by ROSENKRANTZ (1964, pl. 5, fig. 1a-b) as "*Crania (Isocrania) paucicostata* Bosquet". Although found in strata referred to the Paleocene this specimen is considered to be a remani e fossil of Maastrichtian age (ROSENKRANTZ, 1964, p. 322). The interspaces of the Bochohnica specimen are also covered with radial spines. This character excludes *I. paucicostata* as a correct assignment for this material. Further study including a direct comparison of these specimens is needed to draw a more definitive conclusion, but at first impression they seem to represent two specimens of another species of *Isocrania*.

Comparison with *Isocrania praecostata*

The outline and ornamentation of both ventral and dorsal valves as well as muscle scars development in *I. sendeni* n. sp. are much more reminiscent of *Isocrania praecostata*. Both species have a similar total amount of costae with interspaces covered with coarse, radially directed spines. The strong development of the adductor muscle scars is obvious in both species. However, *Isocrania sendeni* n. sp. is distinguished from *I. praecostata* by several distinct characters. The attachment surface in adult shells of *I. sendeni* n. sp. is much smaller and set more posteriorly (mean value for $L_p/L_a = 0.40$); in *I. praecostata* this ratio is around 0.50. In lateral profile, the ventral valve of *I. sendeni* is extremely flat, depressed in its central part. This allowed the organism to completely cover the substrate, thus avoiding the possibility that currents could excavate substrate particles from under the shell. The ventral valve of *I. praecostata* is subconical, much more elevated and its central part is not depressed.

The anterior adductor muscle scars are set near the centre of the ventral valve in *I. sendeni*. The anterior part of the rostellum is set precisely in the centre of the valve. In *I. praecostata* the rostellum and the anterior adductor scars are set more posteriorly.

The dorsal valve of *I. sendeni* has its umbo set more posteriorly and is curved backwards. In *I. praecostata*, the umbo is simply pointed upwards and set more centrally.

A long ridge is developed in the median part of the dorsal valve in *I. sendeni* n. sp. This structure is absent in *I. praecostata*.

The hatchet-shaped anterior adductor muscle scars in *I. praecostata* comprise two drop-shaped parts in which the longitudinal axes form an angle of 90° (ERNST, 1984, p. 64, pl. 6, fig. 2). In *I. sendeni*, this angle varies between 50° and 55° . Although this is a variable character, the brachial protractor muscle scars are placed generally in a more anterior position in *I. sendeni*.

Comparison with *Isocrania phosphatica*

The interspace shell surface in *Isocrania phosphatica* is smooth. The attachment surface of the ventral valve is relatively wide and in a stable posterior position: the ratio L_p/L_a has a mean value of 0.28 and the relation between L_p and L_a shows a high correlation coefficient ($r = 0.723$ in SIMON 1998, text-fig.9). The ventral valve of *I. phosphatica* has a dome-shaped outline in lateral profile and the protegular node is below the top of the valve.

Isocrania sendeni n. sp. has a strongly developed spiny interspace ornamentation. The attachment surface is very tiny and its position is relatively variable, although generally set posteriorly (mean value $L_p/L_a = 0.40$). The lateral profile of the ventral valve of *I. sendeni* is not dome-shaped but is a flat disc, depressed centrally. The protegular node of *I. sendeni* is placed at the tip of the ventral valve. The dorsal valve of *I. sendeni* n. sp. is typically "capuliform" with its umbo curved backwards.

Comparison with *Isocrania egnabergensis*

As both *I. egnabergensis* and *I. sendeni* n. sp. were adapted to current-swept environments, their general outline is similar with a flat ventral valve associated to a "capuliform" lateral profile of their dorsal valve. However, they cannot be confused.

Isocrania egnabergensis has a subrectangular outline and is always slightly longer than wide. Its ventral valve is flat, but not depressed centrally. The shell ornamentation consists of very fine and more numerous radial ribs (30-70). The ventral umbo is near the posterior margin and this is a very stable morphological character for *I. egnabergensis* (SURLYK 1973, fig. 9, p. 236). The lateral profile of the dorsal valve is low conical and in specimens studied for the present paper the umbo is pointed slightly backwards. The lateral profile tends to be slightly "capuliform".

Isocrania sendeni has a subcircular outline and is always slightly wider than long. Its ventral valve is flat and is centrally depressed. The ornamentation consists of a lower number (16-42) of fine to coarse, radial costae. The position of the ventral umbo, although always set posteriorly, is more variable. In *I. sendeni*, the dorsal valve has an umbo which is curved more backwards.

Discussion and conclusions

Isocrania sendeni n. sp. is a Late Maastrichtian craniid which has long presented taxonomic problems, having been confused with *I. egnabergensis* by BOSQUET (1860) and KRUYTZER (1969). The morphological measurements made on a large series of specimens now show a relatively wide range of variation when some characters are taken into account. This is the case for the relation between L_p (length from posterior side to the umbo) and L_a (length from the umbo to the anterior side). The relation between L_p and L_a is important and quite distinct for species that lived in chalky facies (L_p/L_a relatively high) and

those which lived in more agitated waters (Lp/La relatively low). The variability for this parameter previously led to the notion that *I. sendeni* was an "under-group" of *I. costata* on its way to speciation. Such a view would mean that this *Isocrania* might be considered a subspecies of *I. costata*. However, other very stable morphological characters (flat depressed ventral valve and "capuliform" dorsal valve), typical of good adaptation to current flow, indicate that this *Isocrania* is better interpreted as a distinct species.

Isocrania sendeni shares with *I. egnabergensis* several characters because both were adapted to a similar, relatively high-energy environment. Both species exhibit a low, flat and heavy ventral valve with an umbo set posteriorly. Both species have a dorsal valve with a relatively worn shell surface, indicating current action. Both species have a subconical dorsal valve in lateral profile with a curved umbo placed backwards. *Isocrania egnabergensis* (upper Lower Campanian) and *I. sendeni* (Upper Maastrichtian) are two different species, which evolved within the "costata group", at two different intervals and at two different localities. The same ecological conditions produced the same effects. However, the species remain quite distinct and can easily be distinguished.

The suggestion formulated by SURLYK (1973, p. 241) "that this (= *I. sendeni* as here understood) is an Upper Maastrichtian off-shoot of the *I. costata* line rather than a direct descendent of *I. egnabergensis*" is thus corroborated entirely by the present study.

Predators

Numerous specimens of *I. sendeni* show drill holes of boring gastropods. The holes observed are often situated in the umbonal region, but some are also set in a more laterally position. Specimens may have been predated upon by several boring gastropods active in different places of the shell surface. Occasionally, drill holes are unfinished, as seen in the juvenile dorsal valve in Pl. 3, Fig. 2.

Following the opinion of SURLYK (1972, pp. 49-50) the shape of these holes, which is cylindrical, suggests attacks by muricid gastropods.

Occurrence

Upper Maastrichtian of southern Limburg (The Netherlands) and Liège Province (NE Belgium), currently known from Lanaye Member (Gulpen Formation) to Meerssen Member (Maastricht Formation). Numerous specimens from a level just above the Horizon of Lichtenberg, which separates the Gulpen and the Maastricht formations.

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Explanation of the plates

PLATE 1

Isocrania sendeni n. sp.

All material housed at the IRScNB (Brussels) and collected from the ENCI quarry near Maastricht, southern Limburg, The Netherlands. Upper Maastrichtian, fossil hash level resting directly upon the Lichtenberg Horizon, base of the Maastricht Formation, *Belemnitella junior* Zone.

- Fig. 1 — Holotype, IRScNB MI 11033, a fully adult ventral valve. 1a: external ventral view (x 6.0). 1b: internal dorsal view (x 5.8). 1c: lateral view (x 5.8). 1d: external ventral view; detail of the umbo with very small attachment surface (x 10). 1e: external ventral view; detail of the spiny intercostal ornamentation (x 11).
- Fig. 2 — Paratype, IRScNB MI 11034, a fully adult ventral valve with a wider protegular node. 2a: external ventral view (x 8.0). 2b: internal dorsal view (x 8.0). 2c: lateral view (x 8.0). 2d: detail of the protegular node (x 22).
- Fig. 3 — Paratype, IRScNB MI 11035, a medium-sized adult dorsal valve with a well-preserved shell surface. 3a: external dorsal view. 3b: internal ventral view showing well-preserved muscle scars. 3c: lateral view showing the posterior umbo curved backwards (x 6.0).
- Fig. 4 — Paratype, IRScNB MI 11036, an average-sized adult dorsal valve with a worn shell surface. 4a: external dorsal view. 4b: internal ventral view showing well-preserved muscle scars. 4c: lateral view showing the posterior umbo curved backwards (x 5.2).

PLATE 2

Isocrania sendeni n. sp.

All material housed at the IRScNB (Brussels).

- Fig. 1 — Paratype, IRScNB MI 11037. A gerontic ventral valve ornamented with a low number of strong costae. Some particles are still fixed on its attachment surface. 1a: external ventral view. 1b: internal dorsal view. A flat ridge, dividing the anterior part of the valve floor into two distinct depressions, is present. Traces of the mantle canal system are clearly developed. 1c: lateral view (x 4.4). Specimen collected from the ENCI quarry near Maastricht, southern Limburg, The Netherlands. Upper Maastrichtian, fossil hash level directly overlying Lichtenberg Horizon, base of the Maastricht Formation, *Belemnitella junior* Zone.
- Fig. 2 — Paratype, IRScNB MI 11038. A fully adult ventral valve, very well-preserved and quite typical of the species. 2a: external ventral view. 2b: internal dorsal view. 2c: lateral view (x 5.9). 2d: detail of the protegular node (x 22). Specimen collected from the Marnebel quarry at Eben-Emael (Liège Province, Belgium). Upper Maastrichtian, Valkenburg Member, Maastricht Formation, *Belemnitella junior* Zone (ex D. Eysermans Colln.).
- Fig. 3 — Paratype, IRScNB MI 11039. A fully adult dorsal with a very well-preserved ornamentation. 3a: external dorsal view. 3b: internal ventral view. 3c: lateral view showing the umbo posteriorly placed and curved backwards (x 6.7). Specimen collected from the Marnebel quarry at Eben-Emael (Liège Province, Belgium). Upper Maastrichtian, Valkenburg Member, Maastricht Formation, *Belemnitella junior* Zone (ex D. Eysermans Colln.).

- Fig. 4 — Paratype, IRScNB MI 11040. Complete bivalved specimen collected as separate valves and reconstructed. Specimen collected from the Marnebel quarry at Eben-Emael (Liège Province, Belgium). Upper Maastrichtian, Lanaye Member, Maastricht Formation (ex D. Eysermans Colln.). 4a: Dorsal valve in external dorsal view. 4b: Ventral valve in external ventral view. 4c: Specimen in lateral view (x 13.5). 4d: Ventral valve, detail of the attachment surface (x 42.5).

PLATE 3

Isocrania sendeni n. sp.

All material housed at the IRScNB (Brussels) and collected from the ENCI quarry in Maastricht, southern Limburg, The Netherlands. Upper Maastrichtian, fossil hash level directly overlying the Lichtenberg Horizon, base of the Maastricht Formation, *Belemnitella junior* Zone. Material collected by D. Eysermans.

- Fig. 1 — Paratype, IRScNB MI 11041. Juvenile ventral valve. 1a: external ventral view. 1b: internal dorsal view. 1c: lateral view (x 26.5). 1d: external ventral view; detail of the protegular node (x 42). It is clearly observed that the attachment surface is much smaller than protegular node itself.
- Fig. 2 — Paratype, IRScNB MI 11042. Juvenile dorsal valve. 2a: external dorsal view. 2b: internal ventral view. 2c: lateral view; at this juvenile stage of growth, the lateral profile is simply conical. (x 26.5). 2d: external dorsal view; detail of the spiny ornamentation developing between the costae (x 46.5). This specimen was probably killed by a boring gastropod; the shape of this hole suggests a muricid gastropod.

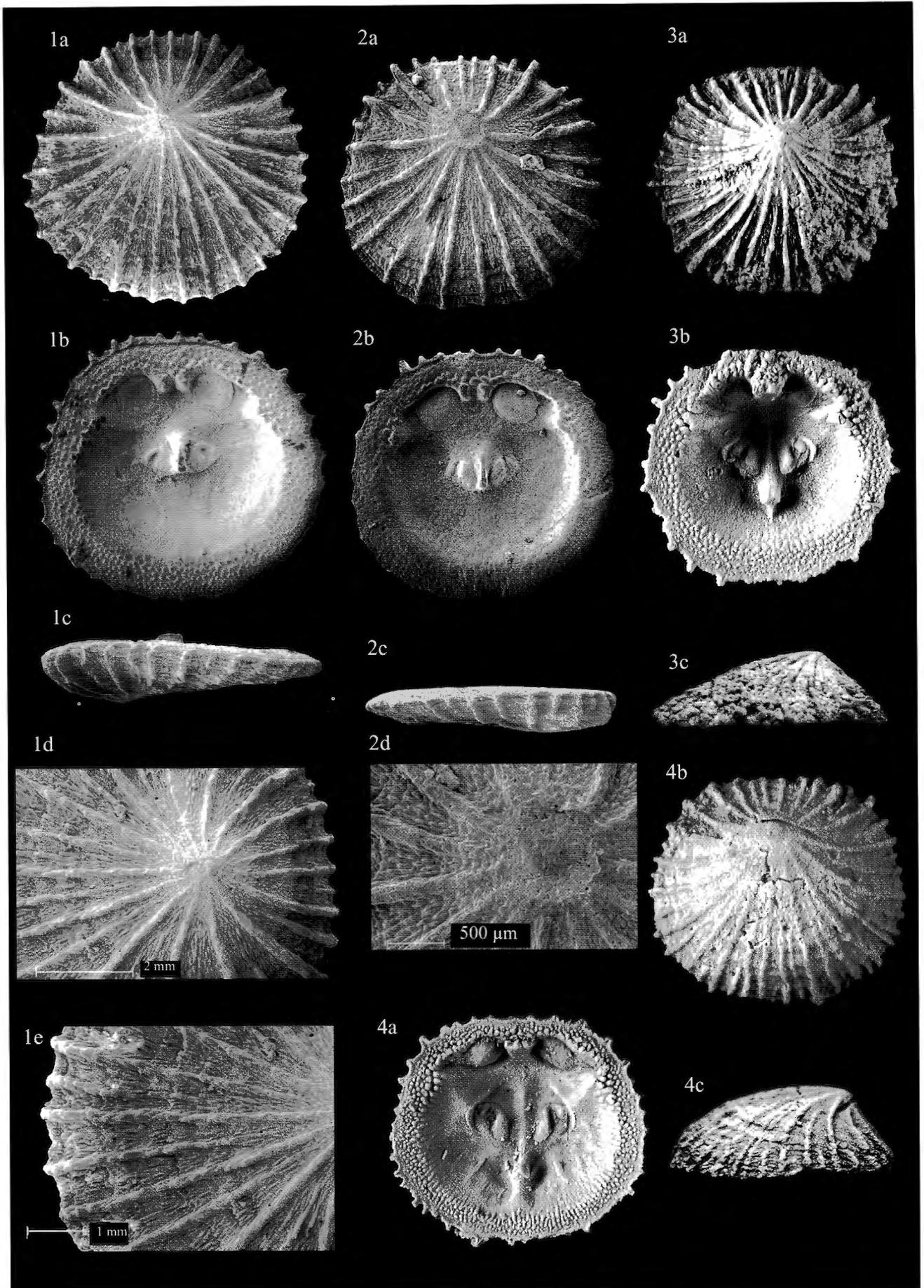


PLATE 1

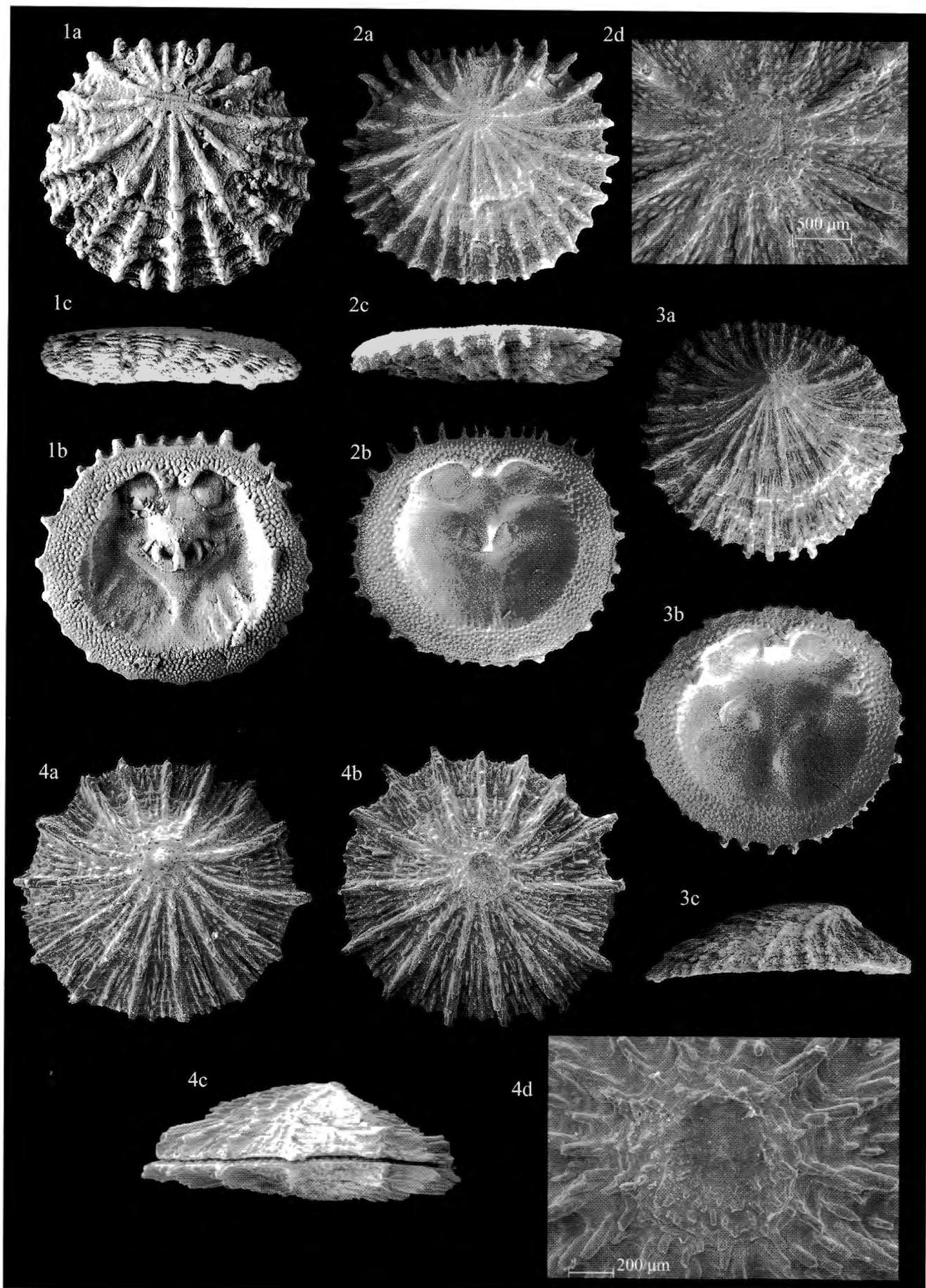


PLATE 2

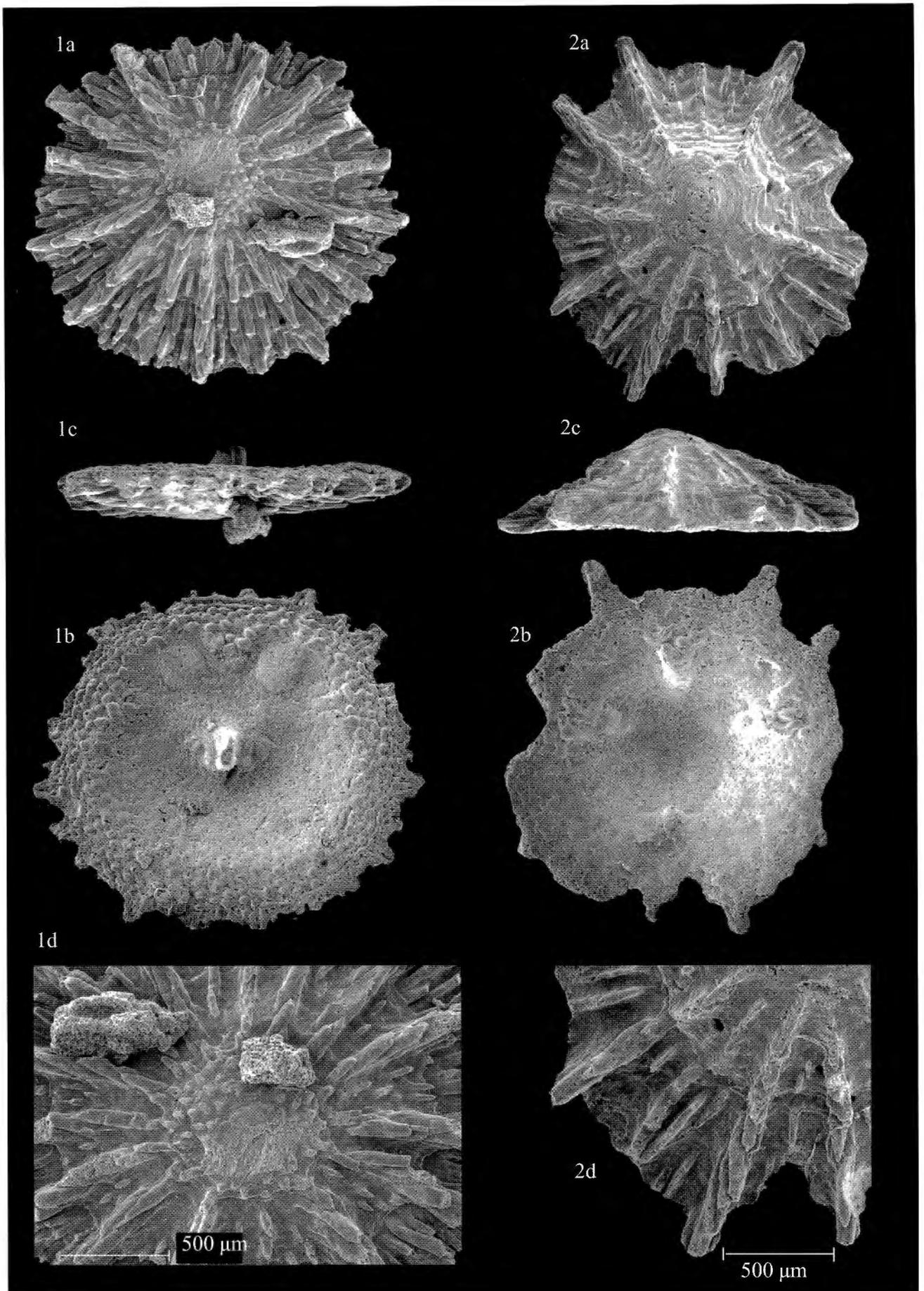


PLATE 3

