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Autor: Hottinger, Lukas / Caus, Esmeralda

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Marginoporiform structure in *Ilerdorbis decussatus* n.gen. n.sp., a Senonian, agglutinated, discoidal foraminifer

By LUKAS HOTTINGER[1]) and ESMERALDA CAUS[2])

ABSTRACT

Ilerdorbis decussatus n.gen. n.sp. from Early Campanian shallow water deposits on the southern margin of the Pyrenean basin produces an agglutinated, planispiral-evolute, discoidal shell with a crosswise-oblique stolon system and a corresponding pattern of the endoskeleton similar to *Marginopora*. Comparable endoskeletal patterns in agglutinated Foraminifera were known so far only in uniserial-conical orbitolinids s.l. Their occurrence in discoidal agglutinated forms points to the general analogous nature of endoskeletal patterns arising in independent taxonomic groups at different geologic times. As a taxonomic consequence, two new subfamilies of discoidal agglutinated Foraminifera are proposed.

RÉSUMÉ

Ilerdorbis decussatus n.gen. n.sp. découvert dans des sédiments campaniens d'eau peu profonde déposés en marge méridionale du bassin pyrénéen produit une coquille agglutinée, planispiralée-évolute, discoïdale avec un système de stolons obliques-entrecroisés et un endosquelette correspondant, similaire à celui des *Marginopora*. Parmi les foraminifères agglutinés, des endosquelettes de type similaire n'étaient connus jusqu'à présent que chez les coquilles unisériées-coniques des orbitolines s.l. La présence d'un endosquelette orbitoliniforme chez un foraminifère agglutiné discoïdal démontre la nature analogue des types d'endosquelettes apparaissant indépendamment dans des groupes taxonomiques les plus variés à des époques géologiques différentes. Comme conséquence systématique, deux nouvelles sous-familles de foraminifères agglutinés discoïdaux sont proposées.

Introduction

A structural analysis and description of the genus *Ilerdorbis* discovered in Late Cretaceous shallow water deposits on the southern margin of the Pyrenean basin was undertaken in order to demonstrate the general independence of endoskeletal patterns from shell shape or shell ultrastructure in larger Foraminifera. Particularly in agglutinated Foraminifera, radial stolon disposition seemed to be restricted to planispiral, peneropliform and discoidal chamber arrangement (HOTTINGER 1967) as for instance in orbitopsellids (Lias), anchispirocyclinids (Upper Jurassic-Lower Cretaceous) and in the *Broeckinella-Saudia* group (Paleocene, DROBNE & HOTTIN-

[1]) Geologisches Institut, Bernoullistrasse 32, CH-4056 Basel, Switzerland.
[2]) Dept. Paleontologia, Universidad Autónoma, Bellaterra (Barcelona), Spain.

GER 1971). Their uniserial, conical counterparts have usually stolon systems arranged in an overcrossed-oblique pattern as for instance in orbitolinids or dictyoconids (HOTTINGER & DROBNE 1980). Is there a functional link between shell shape and endoskeletal patterns in agglutinated Foraminifera? In porcellaneous Foraminifera, both radial and obliquely-overcrossed stolon systems (HOTTINGER 1978) occur in discoidal forms substituting each other in the same shallow water environment: In the Tethyan realm, Early Tertiary orbitolitids with a crossed stolon system are replaced by discoidal archaiasinids with a radial stolon system during Oligo-Miocene times and again by *Amphisorus* and *Marginopora* with an overcrossed stolon system from Late Miocene to recent. Therefore, in porcellaneous forms, shell shape and endoskeletal patterns are independent. The present study puts foreward an example of an agglutinated, planispiral-evolute foraminifer with a discoidal shell having an obliquely-overcrossed stolon system and a corresponding endoskeletal pattern similar to *Marginopora.* The systematic description of this new foraminifer serves to point out once more the striking structural homoeomorphies in larger Foraminifera arising independently in unrelated taxonomic groups at different geologic times. In agglutinated Foraminifera also, there is no link between shell shape and endoskeletal pattern.

Material

Ilerdorbis n. gen. described in this paper originates from sample AC55 collected by A. Cornella and E. Caus from the base of the Campanian sedimentary sequence in the Serra de Montsec (Lerida prov., Catalonia, northern Spain) as seen in the Pedroneta Section (CAUS et al. 1981, fig. 8, loc. 1, unit 7). The *Ilerdorbis* beds are also the type level of *Calveziconus lecalvezae* CAUS & CORNELLA 1982. Its particular characteristics are the exclusive presence of the two mentioned genera, the absence of larger miliolids, particularly *Lacazina elongata* and its abundance in *Orbitokathina vonderschmitti.* This faunistic assemblage corresponds to a particular type of facies comparable to the marginal low-energy deposits of Paleocene and Eocene facies sequences rich in conical Foraminifera described by HOTTINGER & DROBNE (1980, p. 15, 16, text fig. 2).

The Early Campanian age of this horizon is given by orbitoids and siderolitids occurring below and above the Ilerdorbis-Calveziconus-beds (CAUS & CORNELLA 1982).

42 thin sections prepared from sample AC55, a light-brown, micritic limestone, offer about 120 random sections of *Ilerdorbis.* A minority of the sections are perfectly conserved; many specimens show slight to heavy recrystallisations in the last two or three chambers.

Structural analysis (fig. 1, 2)

The internal structures in the discoidal shell analyzed here are strikingly similar to structural patterns seen in large, discoidal orbitolinids. However, the mode of growth in this new foraminifer is fundamentally different from the growth of a discoidal orbitolinid: Whereas in *Orbitolina,* discoidal, uniserial chambers are transformed in late growth stages to chamber rings by suppression of growth in the central part of the chamber disc, the new genus described here generates annular chambers by elongating evolute, planispiral chambers as in so many peneropliform genera. This fundamental difference in the mode of growth is reflected by the position of the lateral, exoskeletal structure: In *Orbitolina*, the lateral chamber partitions formed below the cone mantel, remain on one side of the disc in the annular growth stage whereas in a discoidal foraminifer generated by peneropliform growth the exoskeletal structure appears symmetrically beneath both lateral surfaces of the shell disc (fig. 1 B).

Oblique sections of the discoidal shell at very low angles in respect to the equatorial plane (fig. 1 A, B) show best the main structural features of this agglutinated foraminifer: The marginal zone below both lateral surfaces of the disc is subdivided by primary elements perpendicular to the septum and very shallow secondary elements parallel to the septum (Pl. 1, Fig. 2). This marginal structure is not a polygonal, subepidermal network as in spirocyclinids but a comparatively coarse compartmentation of the lateral chamber spaces. The lateral chamber wall is not differentiated as an epiderm but keeps a considerable thickness and the same microgranular structure as the rest of the shell. There are no marginal apertures corresponding to the lateral chamber partitions. Consequently, these partitions have to be interpreted as exoskeleton with beams and shallow rafters. The latter are comparable to structures in *Fallotella alavensis* MANGIN (HOTTINGER & DROBNE 1980, Fig. 5, p. 25).

In the equatorial zone of the disc, the overcrossed stolon system is strikingly evident by the triangular pattern (Pl. 1, Fig. 3) formed by the crossing stolon ramps (LEHMANN 1961) in the endoskeleton as it can be easely observed in superficial sections parallel to the cone mantel line in *Orbitolina* or in sections perpendicular to the disc axis in *Orbitolites*. However, the structure seems less regular in this agglutinated discoidal form if compared in particular with *Orbitolites*. The seeming irregularity is due to the alternating position of the stolons in the two superposed, overcrossing layers as seen best in sections parallel to the axis of the disc and tangential to an annular septum (Pl. 2, Fig. 9–12; Fig. 1C).

As endoskeleton and exoskeleton merge in order to form continuous chamber partitions running from one lateral wall to the other, the alternation of the stolon position is reflected by the disposition of the merged skeletal elements alternating with the same rhythm in the two main chamber compartments (Fig. 1C, D). The endoskeleton is conditioned by the oblique-overcrossed stolon system and separates the shell cavities in the equatorial plane almost completely (Fig. 2B). Vertical connections (parallel to the shell axis) between two superposed main chamber partitions in same chamber ring are exceptional at least in adult growth stages.

During ontogeny, the endoskeleton appears early, already in the juvenile, planispirally coiled growth stages, separating the two stolon planes. For about a dozen cyclical growth stages, the number of stolon planes remains restricted to two. In large, presumably microspheric specimens (Pl. 2, Fig. 1), late growth stages admit supplementary stolon planes when the margin of the discoidal shell is considerably thickened.

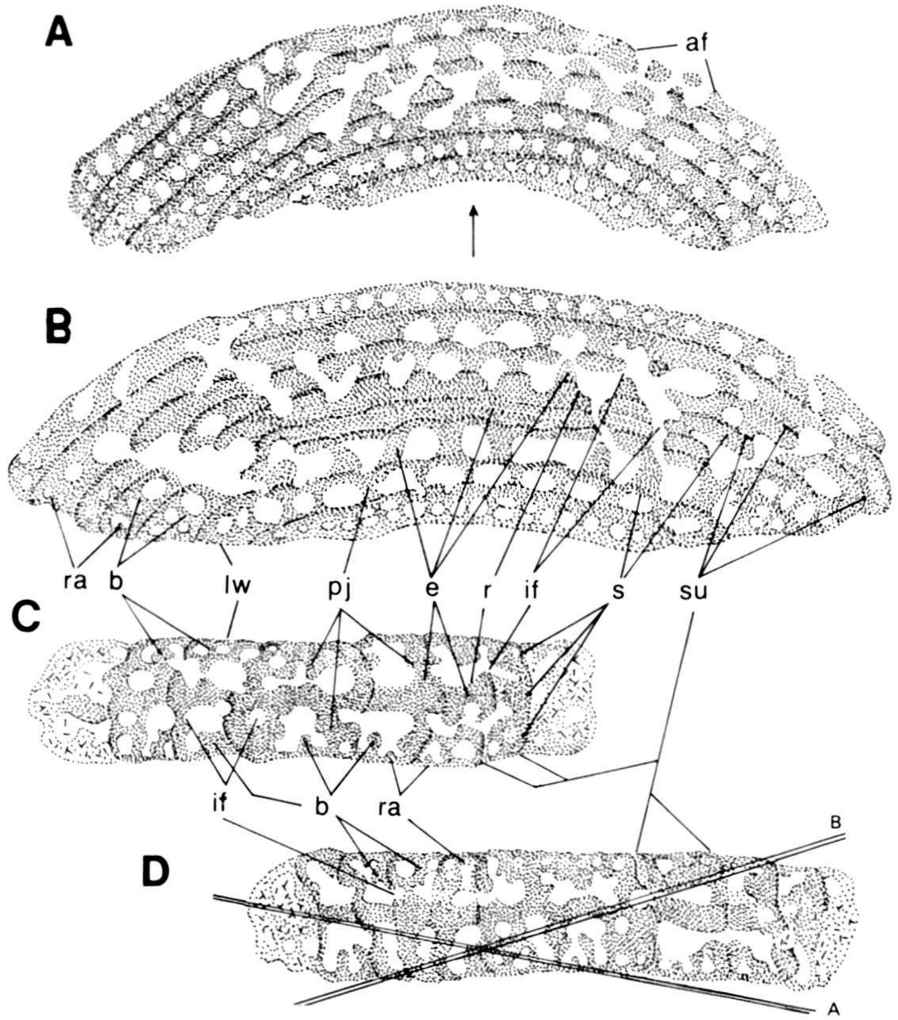

Fig. 1. *Ilerdorbis decussatus* n. gen. n. sp. Camera lucida drawings of selected random sections. Chamber sutures interpreted by darker shades in order to facilitate orientation. Compare with photographs on Plate 2. × 50.

A = shallow tangential section at low angle in respect to equatorial plane. B = oblique section at low angle in respect to equatorial plane. C = transverse section at low angle to axial plane. D = transverse section parallel to axial plane

Legend: af = annular apertural face in equatorial plane; b = beam (of exoskeleton); e = endoskeleton; if = intercameral foramen (stolon); lw = lateral wall; pj = point of junction between exo- and endoskeleton; ra = rafter (of exoskeleton); s = septum; su = suture. Arrow = direction of radial growth.

Systematic description

Ilerdorbis n. gen.

Type species: I. decussatus n. sp.

Diagnosis. – Finely agglutinated-microgranular shell generated by a peneropliform mode of growth: Early planispiral-evolute chambers are elongated during ontogenesis until becoming annular. The genus is defined by the structural characteristics of the discoidal shell (Fig. 1, 2): exoskeleton consisting of simple beams merging alternatively with the endoskeleton, and shallow rafters. No differentiation

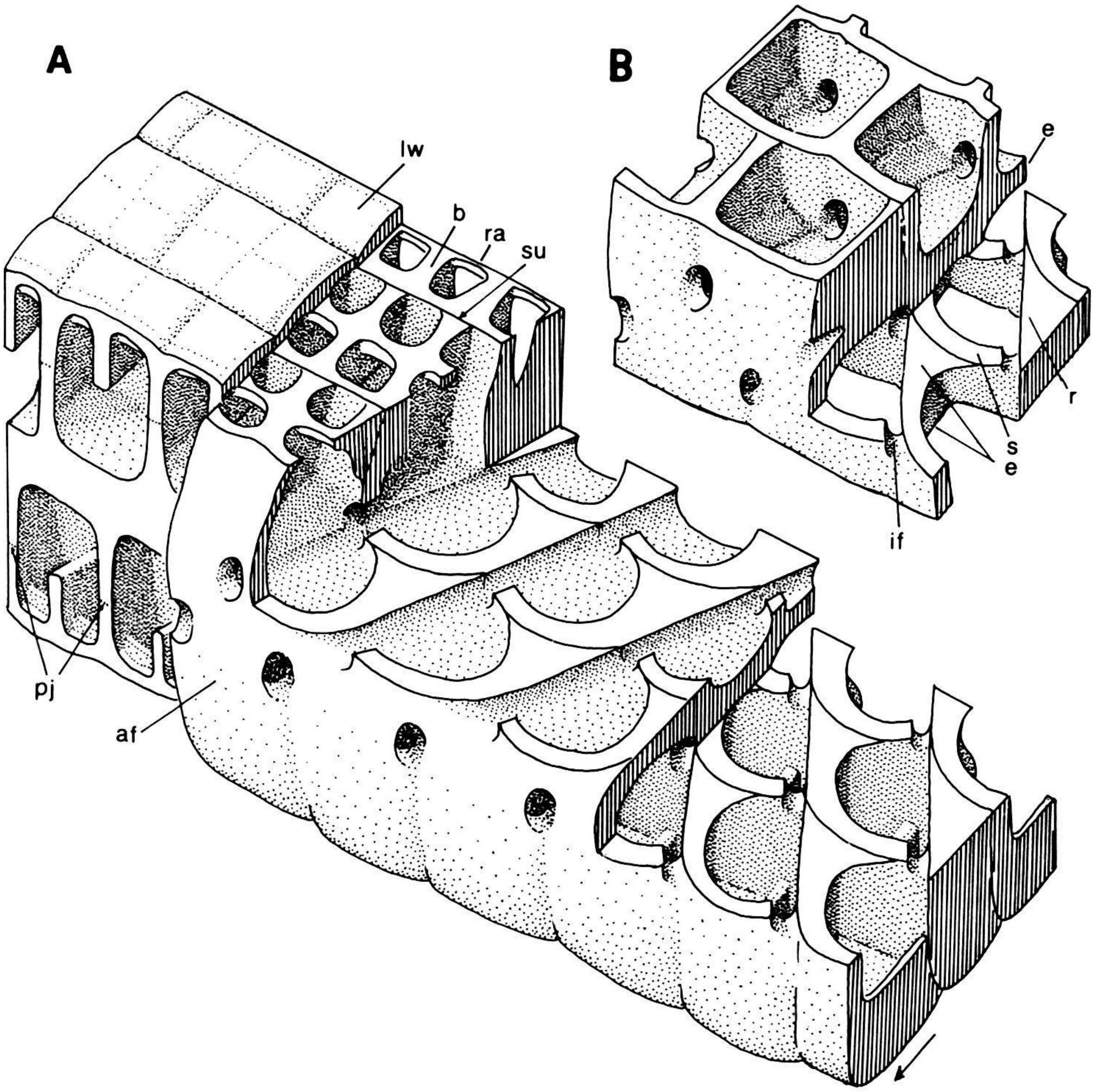

Fig. 2. Stereogramme of structural elements in *Ilerdorbis decussatus* n. gen. n. sp.
A = Annular segment of two and a half chambers cut in transverse, tangential, oblique and radial directions. In equatorial direction, two parallel sections run in the two stolon planes. Exoskeletal and endoskeletal elements are shown. B = endoskeletal elements only. Legend as in Figure 1.

of the lateral chamber wall in an epiderm nor of a polygonal subreticular network as in spirocyclinids or in orbitolinids.

Endoskeleton present, conditioned by the cross-wise oblique stolon system, merging laterally with the beams of the exoskeleton and dividing almost completely the chamber lumen in two equal parts in the equatorial plane of the shell. On the apertural face, the oblique apertures are disposed in two rows above and below the equator of the shell. Their radial position is alternating. The stolons in a stolon layer (parallel to the equatorial plane of the shell) are alternating their radial position from one annular chamber to the next. The angle between shell radius and stolon axes is thus defined by the ratio between half the chamberlet's annular and its total radial extension.

Proloculus consisting of a simple sphere followed by a hemispherical deuteroconch. Structural details of early growth stages not known in detail, particularly for the microspheric generation. Beams present in the third chamber of the megalospheric embryo. First appearence of endoskeletal elements presumably only few growth stages later.

Differential diagnosis. - So far *Ilerdorbis* is the only agglutinated foraminifer with a peneropliform-discoidal shell having an endoskeleton conditioned by a crosswise-oblique stolon system. The comparably agglutinated genus *Montsechiana* AUBERT, COUSTEAU & GENDROT has a radial stolon system with stolons in alternating radial position and an other type of exoskeleton (CAUS & CORNELLA 1981) whereas *Cyclopsinella* MUNIER-CHALMAS has a radial stolon system with stolons of superposed layers disposed in the same radial position and with undivided lateral chamber compartments (no exoskeleton; HOTTINGER 1978). All peneropliform spirocyclinids have radial stolon systems and a polygonal, subepidermal network as an exoskeleton. Agglutinated foraminifera with an exoskeleton similar to the one of *Ilerdorbis* and with a crosswise-oblique stolon system are uniserial-conical and have therefore a discoidal apertural face: The Campanian *Calveziconus* CAUS & CORNELLA (1982) has stolons disposed in radial rows on its apertural face as in *Orbitolina* whereas *Fallotella* MANGIN has a discontinuous, pillared endoskeleton (HOTTINGER & DROBNE 1980).

Structural patterns similar to *Ilerdorbis* are developed in porcellaneous larger peneroplids, particularely in *Marginopora,* a genus having marginal apertures and corresponding marginal shell compartments, and in late growth stages of particular species of *Amphisorus.* In *Orbitolites,* the apertures of superposed stolon planes are disposed in the same radial position forming vertical rows on its apertural face.

Systematic affinities and considerations

According to the hierarchy of characters adopted to construct the taxonomic system of Foraminifera *Ilerdorbis* may be attached to very different suprageneric units. Following the hierarchy of characters presented and discussed in detail by HOTTINGER (1978, p. 255) the crosswise-oblique position of the stolon axes in *Ilerdorbis* would be a suprageneric character of subfamily rank analogous to porcellaneous Soritinae if compared to Archaiasinae. The only agglutinated peneropliform-discoidal genus known to possess a crosswise-oblique stolon system is the genus *Dohaia* HENSON described in 1948 from Mid-Cretaceous deposits of the Middle East. *Dohaia* lacks an endoskeleton and has an annular passage and simple, radial partitions subdiving the lateral chamber lumen; it is considered here to fulfil an analogous structural relationship to *Ilerdorbis* as the relations between *Amphisorus* and *Marginopora* (HOTTINGER 1978) in porcellaneous Soritinae.

In present day systematics (LOEBLICH & TAPPAN 1964, 1974) *Dohaia* is grouped in the Dicyclininae, a subfamily with the type genus *Dicyclina.* This latter genus presents a cuneolinid, biserial growth type combined with a polygonal, subepidermal network as exoskeleton, a structure totally unrelated with most of the other genera figuring in this subfamily. Therefore, and before a comprehensive systematic revision can be carried out, we propose to remove *Dohaia* from its present subfamily in order to transfer this genus to a new subfamily Ilerdorbinae n.subfam. with *Ilerdorbis* as the type genus and with the following diagnosis: Finely agglutinated-microgranular shells with a peneropliform-discoidal mode of growth, simple exoskeleton and crosswise-oblique stolon system. This subfamily, restricted to Middle and Late Cretaceous forms, comprises so far only the genera *Dohaia* and *Ilerdorbis*.

In analogy to soritid peneropliforms, we propose to regroup in a second subfamily discoidal agglutinated forms with a radial stolon system and simple exoskeletal elements such as *Orbitopsella* (HOTTINGER 1967): Orbitopsellinae n.subfam. with *Orbitopsella* MUNIER-CHALMAS as type genus. Diagnosis: Agglutinated shells with a peneropliform-discoidal mode of growth, simple exoskeleton and radial disposition of stolon axes. Apertures in alternating arrangement. This subfamily includes the jurassic representative of this structure: *Labyrinthina* WEYNSCHENK (= *Lituosepta* CATI) and *Orbitopsella*. Provisionally *Montsechiana* AUBERT, COUSTEAU & GENDROT could be placed into this subfamily whereas *Mangashtia* HENSON and *Zekritia* HENSON have a similar structure as exhibited by *Cyclopsinella* GALLOWAY and are transferred here to the subfamily Cyclolininae LOEBLICH & TAPPAN. The genus *Saudia* HENSON is structurally related to *Broeckinella* HENSON (DROBNE & HOTTINGER 1971). Both genera have to be united with *Spirocyclina*, *Choffatella* and *Pseudochoffatella*. On *Qataria* and *Orbitolinella* we have no opinion for the time being. The subfamily Dicyclininae LOEBLICH & TAPPAN has to be reserved in our opinion to biserial forms with a subepidermal reticulum: *Dicyclina* and *Cuneolina*. Both genera are restricted to the Cretaceous.

Ilerdorbis decussatus n. sp.

Pl. 1, Fig. 1–3; Pl. 2; Fig. 1, 2

Holotype. – Oblique section (Pl. 1, Fig. 3) deposited in the Natural History Museum Basel, NMB No. C 35468.

Type locality. – Pedroneta section in the Serra de Montsec, Lerida province, Catalonia, northern Spain.

Type level. – Base of unit 7 in Pedroneta Section (CAUS & CORNELLA 1981), Campanian, Upper Cretaceous.

Derivation of name. – *Ilerdorbis:* latin for Lerida-disc; *decussatus:* latin for crosswise divided (from latin root decem = X).

Diagnosis. – Discoidal shell with the structural characteristics of the genus *Ilerdorbis* n. gen. (see structural analysis and generic diagnosis with Fig. 1, 2). Largest observed diameter of shell 3.2 mm, average about 2 mm. Ratio diameter: thickness about 1:7 in a shell margin of 2 mm in diameter. About 15 annular chambers par 1 mm radial growth in adult stages. Lumen of megalospheric protochonch 0.1 mm, equatorial diameter of deuteroconch 0.05 mm. At least 6 spiral chambers following the deuteroconch (see Pl. 1, Fig. 1).

Remarks. – So far *I. decussatus* is the only species of the new genus *Ilerdorbis* known. Therefore, the structural characteristics defining the genus are also diagnostic for its type species until other species of the same genus are discovered. As the description is based exclusively on random sections in hard rock, the measurements of the specific proportions of the shell are approximate. The juvenile stages in particular are inadequately known. The specimen figured on Plate 1, Figure 1, is the only available centered section of a megalospheric specimen. The almost perfect axial section figured on Plate 2, Figure 1, is interpreted here as belonging to a microspheric specimen considering its unusually large size and its tightly coiled center where a comparatively large megalosphere would not fit in near the plane of the section.

I. decussatus is distinguished easily from the coexisting agglutinated discoidal Foraminifera of similar size, *Montsechiana montsechiensis* (Pl. 1, Fig. 4) by its crosswise-oblique stolon system, from *Cyclopsinella steinmanni* by the presence of an exoskeleton subdividing the lateral chamber lumen and from *Dicyclina schlumbergeri* by its annular-uniserial chamber arrangement. Transverse sections of early spiral stages in *Ilerdorbis* (Pl. 2, Fig. 7, 8) might be confused with similarly transverse sections of *Spirocyclina choffati*. The latter, however, has a subepidermal reticulum as exoskeleton subdividing the lateral chamber lumen in a much more complex way than in *I. decussatus*. Fragments of *I. decussatus* shells in oblique section are identified best by the U-shaped delimitation of the chamberlet lumen (arrow Pl. 2, Fig. 5) divided laterally by one exoskeletal element (compare stereographic model, Fig. 2).

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Plate 1

Fig. 1–3 *Ilerdorbis decussatus* n. gen. n. sp. Campanian, Serra de Pedroneta, Montsec, Lerida, Spain. × 50.

1 = oblique, centered section of megalospheric specimen showing irregular growth; a half disc perpendicular to the main disc is formed as a supplementary structure. Such supplementary structures are observed often in recent soritids living in tidal pools where salinity and temperature rise temporarily to extreme values. Note bilocular embryo followed by early planispiral whorl.

2 = oblique, almost centered section showing early spiral chambers and particularely well preserved exoskeleton. Note crosswise oblique stolon system.

3 = oblique, almost equatorial section showing triangular pattern of endoskeleton due to the crosswise-oblique stolon system. Holotype.

Fig. 4 *Montsechiana montsechiensis* CAUS & CORNELLA.

Specimen of similar size sectioned in approximately the same direction as Figure 3 for comparison. Note the different pattern of the endoskeleton caused by radial-alternating stolon axes. × 50.

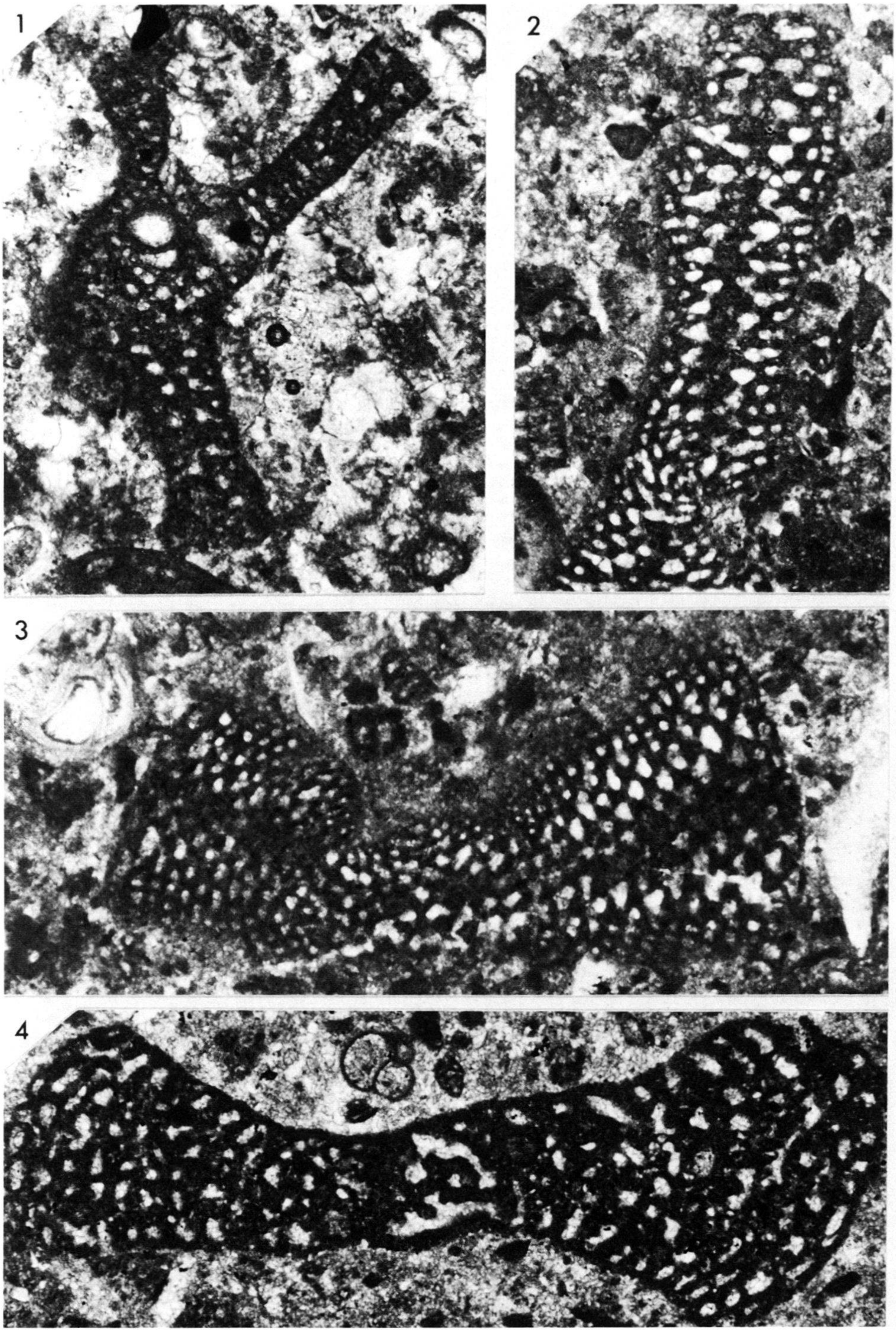
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Plate 2

Ilerdorbis decussatus n. gen. n. sp. Campanian, Serra de Pedroneta, Montsec, Lerida, Spain. × 50.

1 = axial section, almost centered, of presumably microspheric specimen.

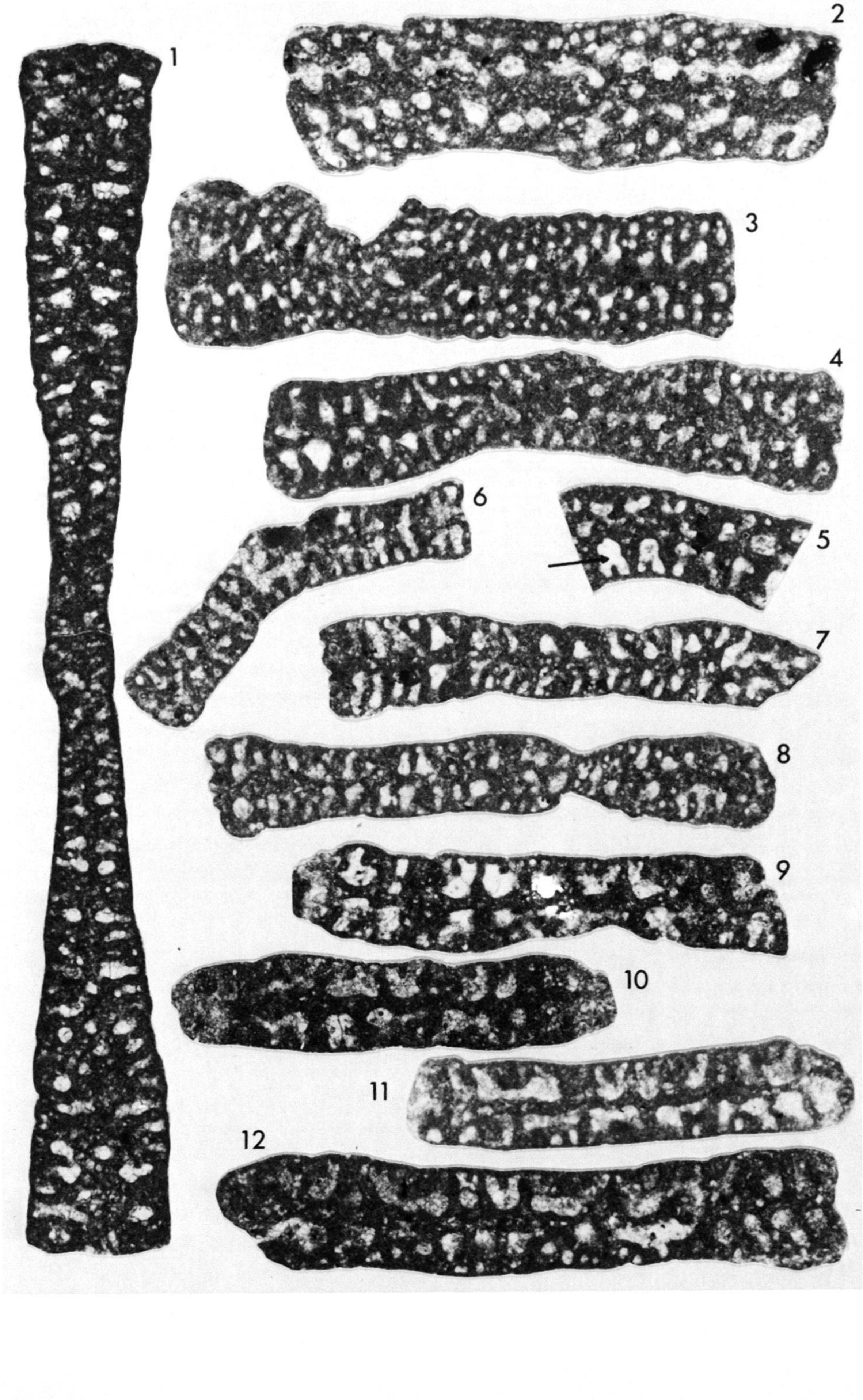
2–3 = oblique sections at low angles in respect to equatorial plane.

4–5 = oblique sections at low angles in respect to axial plane. Note in fragment Figure 5 the diagnostic U-shaped pattern of main chamberlet cavity (arrow).

6 = transverse section.

7–8 = transverse sections, almost centered, showing early spiral growth stages in approximately radial direction.

9–12 = transverse sections, more or less perfectly vertical, showing uninterrupted endoskeleton in the equatorial plane of the shell, the crosswise-oblique stolon system, the alternation of the points of fusion between exoskeleton and endoskelton in the upper and lower part of the shell disc (compare pj in the figures in the text) and the exoskeletal elements in cross section.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