Geologia Croatica	57/1	15–53	3 Figs.	3 Tabs.	12 Pls.	ZAGREB 2004

On Some Peri-Mediterranean Lower Cretaceous Dasyclad Species (Calcareous Algae; Dasycladales) Previously Assigned to Different Genera

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Key words: Calcareous algae (Dasycladales), Taxonomy, Biostratigraphy, Lower Cretaceous, Dinarides, Croatia.

Abstract

The taxonomic position of some dasyclad species which were previously assigned to the same taxon or, alternatively, were assigned to different genera by different authors, is discussed and revised, respectively. The material described and figured as *Cylindroporella lyrata* MASSE & LUPERTO-SINNI is shown to be heterogeneous (also partly described as *Salpingoporella robusta* SOKAČ) and some figured sections are shown to possess new characteristic features. These forms are therefore singled out and described as *Biokoviella* n.gen. with two species: *B. robusta* (SOKAČ) n.comb. and *B. gusici* n.sp. *Macroporella aptiensis* SOKAČ is shown to represent the infertile (sterile) forms of *Neomeris cretacea* STEINMANN and, consequently, has to be regarded as the younger objective synonym of the latter. New material, with clearly visible morphological characteristics, has enabled the "resurrection" of the controversial genus *Korkyrella* SOKAČ & VELIĆ, 1981, and its species, *K. texana* (JOHNSON), which was originally invalidly described.

1. INTRODUCTION

Micropalaeontological analysis of numerous samples collected during field work from various Lower Cretaceous levels of the karstic Dinarides, led to the discovery of new, rich algal associations, particularly from Upper Barremian–Lower Aptian deposits. In a sample of algal limestone from Mt. Biokovo it was possible to determine, at species level, about 15 different taxa, some of which were identified for the first time in that area. However, there were several additional forms which were, at the same time or due to more detailed later analysis, or new descriptions, assigned to the same or different species and different genera. This triggered the re-evaluation of the material stored in our collection and deriving from the same levels at different localities. Thus the comparison of numerous existing and newly made thin sections made possible more detailed observations which resulted in some revisions regarding the morphology and/or the taxonomic position of particular species. Here, some species ascribed to the genera *Cylindroporella, Macroporella, Acroporella*, *Salpingoporella*, and *Korkyrella* are included. In total, 250 thin sections were made of the same algal-bearing sample, which almost excluded the possibility of random determinations and enabled assessment of the true variation range of various, sometimes visually different forms.

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2. TAXONOMIC DESCRIPTIONS

Genus *Cylindroporella* JOHNSON, 1954

Cylindroporella lyrata MASSE & LUPERTO-SINNI, 1989
Pls. I–II

Selected synonymy

1989 (part) *Cylindroporella lyrata* n.sp. – MASSE & LUPERTO-SINNI, p 30–39, pl. 1, figs. 1–3, part. figs. 5, 6, non fig. 4; pl. 2, figs. 2, 4, 5, 7, 9, non figs. 1, 3, 6, 8.

1991 non *Cylindroporella lyrata* MASSE & LUPERTO-SINNI – SCHLAGINTWEIT, p. 49–50, pl. 19, figs. 6–13, 15–16.

non 1993a *Cylindroporella lyrata* MASSE & LUPERTO-SINNI – LUPERTO-SINNI & MASSE, p. 411, pl. 31, fig. 5.

1993b *Cylindroporella lyrata* MASSE & LUPERTO-SINNI – LUPERTO-SINNI & MASSE, p. 300–304, pl. 5, fig. 6, non figs. 5, 7.

non 1994 *Cylindroporella ?lyrata* MASSE & LUPERTO-SINNI – BODROGI, BONA & LOBITZER, p. 241–242, pl. 16, figs. 1–5, 8–10.

non 1999 *Cylindroporella* cf. *lyrata* MASSE & LUPERTO-SINNI – BUCUR, p. 58, pl. 2, figs. 14, 19.

Remarks

In the original description, MASSE & LUPERTO-SINNI (1989) mentioned the following diagnostic characteristics: calcified, cylindrical thallus with alternating whorls consisting of alternating sterile and fertile branches. The main species-specific character is the shape of the sterile branches which look like a guitar: swollen in their proximal part, constricted in the middle, and again slightly swollen distally, sometimes acquiring a pyriform shape (MASSE & LUPERTO-SINNI, 1989, figs. 2/1, 2/2; pl. 1, fig. 2; pl. 2, figs. 2, 4–5). On their outer ends, the sterile primary branches bear short secondaries, which, as mentioned by MASSE & LUPERTO-SINNI (1989), appear as crosses in tangential section. Each whorl consists of regularly alternating sterile and fertile branches, their total number varying from 8–10. A further distinction is that fertile branches have a slender elongated stalk in their proximal part and a pronounced, bladder-shaped swelling along the outer half of their length.

With the above mentioned characteristics, the species has been properly described and its validity is not in doubt. The description is complemented by a graphic reconstruction (MASSE & LUPERTO-SINNI, 1989, fig. 2) and rather numerous sections on two plates. However, among the figured sections two different forms can be visually distinguished: one, with the typical characteristics of the species as described, is figured in the authors' pl. 1, figs. 1–3, as well as in the lower part (below the line along which the two photomicrographs are pasted together) of fig. 5, and the left and lower section in fig. 6; and in pl. 2, figs. 2, 4, 5, 7, and 9. Another form is figured in pl. 1, fig. 4, upper part of fig. 5 and right part of fig. 6, as well as in pl. 2, figs. 1, 3, 6, and 8. As distinct from the first one, the second form does not show alternating sterile and fertile branches; i.e., it does not show the diagnostic characteristics of the species (including the holotype), and consequently, it should be removed from that species. Therefore, the allegedly characteristic feature of cross-shaped sections of sterile primaries and their secondaries in *C. lyrata*, emphasized by MASSE & LUPERTO-SINNI (1989), becomes questionable, the more so because almost the same feature has been quoted as one of the key characteristics in the completed description of the genus *Acroporella* (PRATURLON & RADOIČIĆ, 1974, fig. 2d). Such, cross-shaped sections are almost impossible to imagine as derived from the tangential plane of a section as figured in MASSE & LUPERTO-SINNI (1989): compare fig. 4 in pl. 1 with figs. 1–3, and the lower part of fig. 5. Obviously, we are dealing here with two different forms; the second one, atypical for *Cylindroporella lyrata* and with only one type of branch (= fertile primaries, which bear a tuft of secondaries, with a different distance between the whorls and different density of branches within a whorl) can hardly be conceived as a consequence of a different calcification pattern during growth. To my mind, the original and the later descriptions and illustrations of *C. lyrata* (LUPERTO-SINNI & MASSE, 1993b, pl. 5, figs. 5–7) included two different forms that occur in the same algal assemblage, which is also the case in the Biokovo sample, discussed below. An apparent objection to the above interpretation can possibly be based on the already mentioned section figured in pl. 1, fig. 5 in MASSE & LUPERTO-SINNI (1989), in which, immediately below the joining line of the two photomicrographs, a normal (i.e., continuous) transition from the lower into the upper form seems to be present. However, the apparent junction of the two different forms is situated in a zone where the two forms (i.e., the two specimens belonging to different forms) came to touch each other and where, consequently, dissolution and subsequent recrystallization probably glued the two different specimens together, producing a picture of a seemingly normal transition between different types of pores in the same specimen (thallus). If we do not accept this interpretation, an alternative explanation – much less likely, in my opinion – would be that different parts of the thallus had a basically different morphology. In this case, the older part of the thallus would be characterized by a simpler type of morphology, atypical of *Cylindroporella lyrata*; however, the situation in the section (MASSE & LUPERTO-SINNI, 1989, pl. 1, fig. 5) is just the opposite.

Several years after the description of *C. lyrata*, I (SOKAČ, 1993) published a description of a new species, *Salpingoporella robusta*, which was based on a similar – but not wholly identical – material as the one of 'atypical' *C. lyrata*. Obviously, I have overlooked those 'atypical' sections of *C. lyrata* which, in spite of some subtle visual differences, can be compared with the sections of *S. robusta* (SOKAČ, 1993, pl. 1). The general shape of the branches in "*S. robusta*" (in spite of their visible variability), as well as their alternating position in consecutive whorls and, at that time, lacking the knowledge about the existence of the secondaries, seemed a sufficient reason for including those sections in the genus *Salpingoporella*. However, the newly collected material from the continuation of the same zone which yielded "*S. robusta*", contained abundant sections of both typical and 'atypical' *C. lyrata*, as well as numerous sections identical to those described as "*S. robusta*". Based on this material, the following conclusion emerged: both the 'atypical' sections assigned to *C. lyrata* and those described as *S. robusta*, which in this material were shown to possess branching ramifications, certainly belong to one and the same taxon, which is characterized by a broad variation in range. Based on their identity (= 'atypical' *C. lyrata* and *S. robusta*), it follows, that both viewpoints, i.e., including the 'atypical' sections into the description of *C. lyrata* and establishing *S. robusta* as a new species, were erroneous. Thus, it follows that both groups of sections (= 'atypical' *C. lyrata* and *S. robusta*) should be united into a new taxon, that, because of the main distinguishing character of this alga – having one type of bipartite branches, with a characteristic growth pattern and shape of the secondaries – justifies the establishment of a new genus, *Biokoviella*.

Based on what has been mentioned above, the valid species *Cylindroporella lyrata* MASSE & LUPERTO-SINNI should contain only those specimens that are characterized by the alternation of fertile and sterile branches, as described in the original description (MASSE & LUPERTO-SINNI, 1989, pl. 1, figs. 1–3, 5 (pars), and 6, and pl. 2, figs 2, 4, 5, 7, 9), as well as those figured in the present paper in Pl. 1, Figs. 1–8, and Pl. 2, Figs. 1–8. However, the cross-like arrangement of the secondary branches should be deleted from the description because it is highly unlikely that the section in question belongs to *C. lyrata* MASSE & LUPERTO-SINNI. According to the above, the diagnosis of *Cylindroporella lyrata* MASSE & LUPERTO-SINNI should be more restricted, as follows: cylindrical calcified thallus, with narrow axial cavity. Branches arranged in dense and clearly alternating whorls. In individual whorls, sterile and fertile branches also are in clearly alternating arrangement. Fertile branches have a narrow, shorter or longer stalk in the proximal part, and a pronounced swelling distally. In contrast, sterile branches are widened proximally, narrower in the middle part, and again slightly widened distally, thus acquiring a guitar-like shape. At their outer ends, sterile branches bear short secondaries. Some specimens, with slightly pronounced swellings of the proximal ends and evenly narrowed and somewhat elongated distal ends, may appear similar, in some parts of tangential sections, to *Cylindroporella*? *barnesii* JOHNSON.

So far, the discovery of this species within the karstic Dinarides is restricted to only one locality on Mt. Biokovo. The species occurs within the rich algal assemblage (see the descriptions of the *Biokoviella* species) from the top layers of the Upper Barremian.

Genus *Biokoviella* n. gen.

Type species: *Biokoviella robusta* (SOKAČ) n. gen., nov. comb.

Origin of the name: after Mt. Biokovo (central Dalmatia), where the taxon has been found.

Diagnosis of the genus: Cylindrical thallus, with a narrow axial cavity. Branches are divided into clearly differentiated primaries and secondaries and are arranged in whorls. Sometimes, the secondaries show a tendency to further divide into tertiaries. In consecutive whorls, primary branches show an alternating arrangement. Generally, they are phloiophorous, but may vary in shape; may be more or less swollen, almost cylindrical to rounded wineskin-shaped or club-shaped; some may only slightly widen distally, appearing similar to the acrophorous type. Therefore the pores on the outer surface may be large, polygonal or rhombic, densely packed, or else small, rounded, and set widely apart. Short secondaries occur in a dense tuft, rarely showing a cross-like arrangement, or, more rarely, irregular and unequal, arranged in a circle. The genus is cladosporous.

Biokoviella robusta (SOKAČ) nov. comb.

Pls. III–V

1989 part. *Cylindroporella lyrata* n.sp. – MASSE & LUPERTO-SINNI, p. 30–38, pl. 1, fig. 4?, 5 (upper part), 6 (transverse and oblique sections in upper right part); pl. 2, figs. 1, 3, 6, 8.

1993b part. *Cylindroporella lyrata* MASSE & LUPERTO-SINNI – LUPERTO-SINNI & MASSE, p. 295–309, pl. 5, fig. 5.

non 1993a *Cylindroporella lyrata* MASSE & LUPERTO-SINNI – LUPERTO-SINNI & MASSE, p. 411, pl. 31, fig. 5.

1993 *Salpingoporella robusta* n.sp. – SOKAČ, p. 175–180, pl. 1, figs. 1–6.

1994 *Cylindroporella*? *lyrata* MASSE & LUPERTO-SINNI – BODROGI, BONA & LOBITZER, p. 241–242, pl. 16, figs. 1–5, 8–10.

1999 *Cylindroporella* cf. *lyrata* MASSE & LUPERTO-SINNI – BUCUR, p. 58, pl. 2, figs. 14, 19.

The newly observed characteristics of this form, which had previously been assigned to *Cylindroporella lyrata* and afterwards described as a new species of *Salpingoporella*, imply that a revised more complete description, and a revised taxonomic position, are necessary.

Amended diagnosis: Comparatively large, generally phloiophorous, branches may be variously shaped: more or less strongly swollen, with a short stalk, or more club-shaped, widening gradually from the base toward the distal end. The number of branches in a whorl can also vary (Table 1). Depending on the shape of the primary branches, the consecutive whorls may be seemingly more or less densely spaced. Primary branches bear short secondaries, crowded together in a tuft, which are visible as funnel-shaped depressions on the outer surface of the skeleton. Some specimens may have irregular secondaries, some of which may even show a tertiary division.

As previously mentioned in the original description (SOKAČ, 1993), the cylindrical calcareous skeleton is characterized by a comparatively narrow, sharply delineated, axial cavity which occupies 25–30% of the total diameter. The outer surface shows either funnel-shaped pores (Pl. I, Figs. 1, 3, 8; Pl. IV, Fig. 10), through which tufts of secondary branches protrude, or the single pores of dispersed secondaries. The outer surface is frequently abraded, which may give the impression that no secondary branches are developed, and the primaries reach the outer surface (Pl. III, Fig. 5; Pl. IV, Figs. 8–10).

Bipartite to tripartite branches are arranged into regular whorls with the alternating arrangement of

		Most frequently
Maximum observed length of thallus (L)	8.2	1.20–1.35
Outer thallus diameter (D)	0.88–1.50	0.35–1.20
Inner thallus diameter (d)	0.24–0.40	0.25–0.35
Relation d/D	19–30%	24–28%
Distance between whorls (h)	0.12–0.24	0.16–0.24
Diameter of primary branches (p)	0.15–0.25	0.20–0.24
Length of primary branches (l)	0.18–0.48	0.30–0.40
Number of primary branches per whorl (w)	6–12	8–9
Angle of inclination of primary branches (α)	0–20	
Diameter of secondary branches (p’)	0.04–0.10	
Length of secondary branches (l’)	0.10–0.16	0.10–0.12
Number of secondaries per primary branch (w”)	4–6	5–6

Table 1 Main biometric parameters of *Biokoviella robusta* (SOKAČ) n.comb. Dimensions in mm.

branches in neighbouring (adjacent) whorls. Primary branches have a short, thin stalk (Pl. IV, Figs. 6, 9–10) or, more rarely, a broad base sticking to the axial cavity. In the latter case, communication with the central cavity is accomplished through a narrow pore, situated in the middle of the broad base (Pl. IV, Fig. 3). The branches are generally phloiophorous but may vary widely in shape, being distally more or less swollen and acquiring a wineskin-like, robustly bulbous, cylindrical (Pl. IV, Figs. 2, 7; Pl. IV, Figs. 5, 6), slightly club-like, or, more rarely, fusiform shape (Pl. V, Figs. 4, 6). Due to the varying diameter, their number in a whorl also varies widely (6–12, most frequently 8–9; Pl. IV, Figs. 4–7, 9, 10; Pl. V, Figs. 3–5). Primary branches may be situated perpendicularly to the outer surface or may be slightly directed upwards, forming an angle of up to 20º with the horizontal plane (Pl. III, Figs. 3, 6–8). The essential distinguishing characteristic of this species are the secondary branches of varying shape, which may grow out either from the distal or lateral surfaces of the primary branches. In general, they are very short and barely visible; most frequently, when compressed (squeezed together) into a tuft, they appear as shallow, funnel-shaped depressions on the outer surface (Pl. III, Figs. 7–9; Pl. IV, Figs. 9–10). More rarely, however, single secondaries growing out from the distal end (Pl. IV, Figs. 3, 5, 6), or even from lateral surfaces of a primary branch, may be discerned (Pl. IV, Figs. 4, 6; Pl. V, Fig. 5). The irregular manner of growth of the secondaries may be visible even on the same primary branch: first growing out in a tuft and gradually individualizing into single secondary branches (Pl. IV, Fig. 6). In some specimens, individual secondary branches may occasionally be observed growing out irregularly from the lateral surface of a primary branch and showing, distally, a tendency to further, i.e. tripartite, subdivision (Pl. IV, Fig. 4). In general, the secondaries are also of a phloiophorous shape, slightly widening outwards (Pl. IV, Figs. 3, 7). Their number on a primary branch cannot be established with certainty, but seems to vary from 5–7(?). In those specimens which have fusiform, only slightly swollen (similar to acrophorous), or generally only slightly distally narrowed (shrinking) primary branches, and in which secondary branches grow out in tufts, the secondaries may acquire a cross-like or similar arrangement. This characteristic has been stated by MASSE & LUPERTO-SINNI (1989) to be a typical arrangement of the secondaries growing out of sterile primaries in *Cylindroporella lyrata*, but an almost identical section has been figured by PRATURLON & RADOIČIĆ (1974, figs. 2b, d) as an argument for the amended description of *Acroporella*.

Cysts are seldom observable, but sometimes can be seen in the pores of the large, wineskin-shaped primary branches, which indicates that the species is (was) cladosporous.

Similarities and differences of the genus *Biokoviella* and its type species: The newly established genus, with the main characteristics as outlined above, appears visually similar to *Triploporella*, particularly to those species that have columnar and somewhat more strongly swollen primary branches, e.g. *Triploporella? uragieliformis* CONRAD & PEYBERNÈS, (N.B. according to a remark by a reviewer, M.A. CONRAD, that species possibly belongs to the genus *Supiluliumaella*, or *Montenegrella*) or else to those in which the primaries are almost acrophorous, as in *Triploporella bacilliformis* SOKAČ. However, the differences between these genera are clearly visible: in *Triploporella*, the axial cavity is, as a rule, much broader, primary branches are of a more regular shape, much more numerous per whorl, and their alternating arrangement in successive whorls is not so clearly expressed as in *Biokoviella*. There is also a difference regarding the secondary branches: in *Triploporella*, the secondaries, though short, are clearly phloiophorous, individual and visibly separated from each other, grouped into distinct tufts, and seldom number more than four. In contrast, in the type species of *Biokoviella* the secondary branches are tightly squeezed together into a tuft, not visibly separated from each other, or else they grow out individually, often from lateral surface of the primary branch, and are much more irregular in shape. They are more numerous varying between 4 and 7 depending on the species. With regard to *Acroporella*, differences in the shape of both primary and secondary branches are clearly visible. However, it should be emphasized that another form (i.e., except for the type species) figured in the emended description of *Acroporella* by PRATURLON & RADOIČIĆ (1974) and also assigned to *Acroporella radoicici* PRATURLON, does not belong to that genus, as has been previously mentioned (SOKAČ, 1996). According to the original diagnosis (PRATURLON, 1964), the genus *Acroporella* includes forms with an unsegmented, cylindrical thallus and long, simple (tubular) acrophorous branches. In contrast, in *Biokoviella*, as mentionend above, the primary branches may have a highly variable shape and bear a tuft of secondaries, some of which may even show a tripartite division.

The joint occurrence of *Biokoviella* and *Suppiluliumaella* species, as in the case of the Biokovo algal assemblage, makes a comparison between these genera necessary. According to the original diagnosis of *Suppiluliumaella* by ELLIOTT (1968), the differences concern the shape of the primary branches and the manner of how the secondaries emerge. In *Suppiluliumaella*, the primaries are long and slender, with a well-developed terminal swelling, out of which swollen and clearly individualized secondaries emerge (see SOKAČ & NIKLER, 1973). BAKALOVA (1971) also mentions the possibility of third-order branches in *S. praebalcanica* BAKALOVA; these, however, differ both in shape and the manner of growth from those sporadically developed in the type-species of *Biokoviella*. A similar difference, concerning the shape of both primary and secondary branches and the way the secondaries grow out from the distal ends of the primaries, exists between *Biokoviella* and both *Montenegrella* and *Crinella*, as represented by SOKAČ & NIKLER (1973). As the type species of *Biokoviella* was originally thought to be a representative of *Salpingoporella* (SOKAČ, 1993), obviously, the two genera may, in some instances, look similar. This similarity arises in cases when the outer surface of *Biokoviella* is eroded (abraded) and thus the traces of secondary branches are lost and primary branches seemingly open on the surface. In the original description of *Biokoviella robusta*, SOKAČ (1993) was misled by such specimens and therefore assigned these to *Salpingoporella* (see plate 1 in SOKAČ, 1993). The “*Salpingoporella*-like” appearance is strengthened by the regularly alternating arrangement of branches in neighbouring whorls. However, the existence of secondary branches, though sometimes only hinted by slight, funnel-shaped depressions, nowadays clearly distinguishes the two genera.

Stratigraphic position: The species was originally included in the description of *Cylindroporella lyrata* MASSE & LUPERTO-SINNI and also thereafter was frequently cited under that name. Its stratigraphic position, both at the type locality and other, later mentioned localities (MASSE & LUPERTO-SINNI, 1989; LUPERTO-SINNI & MASSE, 1993a, b), has been determined as Lower Aptian. SCHLAGINTWEIT (1991) supposes its possible extension into the Upper Aptian. SOKAČ (1993), under the name of *Salpingoporella robusta* n.sp., has found this species in a rich algal–foraminiferal assemblage which was dated on the basis of the first appearance of *Palorbitolina lenticularis* (BLUMENBACH) and consequently the age was determined as Uppermost Barremian–Lower Aptian. An almost identical stratigraphic position was mentioned by BODROGI et al. (1994), who also determined as transitional, Upper Barremian–Lower Aptian levels within the *Palorbitolina lenticularis* zone in the Schrattenkalk Formation in Vorarlberg. BUCUR (1999) questioned its generic attribution and under the name *Cylindroporella* cf. *lyrata* MASSE & LUPERTO-SINNI recorded its occurrence in the Caposeni Member of the Blid Formation on Mt. Apuseni. The rich algal assemblage of the Caposeni Member makes a Barremian age more likely. The repeated occurrence of the species in sample KJ–18 at a new locality on Mt. Biokovo within an equally rich and diverse algal assemblage (see the description of *Biokoviella gusici* n.sp. in this paper), and immediately below the first finds of *Palorbitolina lenticularis*, also indicates a Late Barremian age. Summing up all data from the localities described so far, it can be concluded that the stratigraphic range of the species can be defined as Upper Barremian–Lower Aptian, with possible extension into the Upper Aptian.

Biokoviella gusici n.sp.

Pls. VI–VII

Selected synonymy

1974 *Acroporella radoicici* PRATURLON – PRATURLON & RADOIČIĆ, p. 17–20, figs. 1b, 2a–d, 3a–d.

1978 *Acroporella radoicici* PRATURLON, 1964 – BASSOULLET et al., p. 25, pl. 1, figs. 6–8.

?1989 *Cylindroporella lyrata* n.sp. – MASSE & LUPERTO-SINNI, p. 30–36, pl. 1, fig. 4.

?1993 *Cylindroporella lyrata* MASSE & LUPERTO-SINNI – LUPERTO-SINNI & MASSE, pl. 5, fig. 7.

1993b *Acroporella radoicicae* PRATURLON – LUPERTO-SINNI & MASSE, pl. 4, figs. 11–12.

Origin of the name: The species is dedicated to my colleague Ivan GUŠIĆ, who established the foraminiferal genus *Biokovina* and thus first introduced the name of Mt. Biokovo into the palaeontological literature.

Type locality: Mt. Biokovo; in a road-cut about halfway between the road branching toward the mountain hut Vošac and the peak of Sv. Jure (1762 m); see Fig. 1. Coordinates: x = 6423980, y = 4798490.

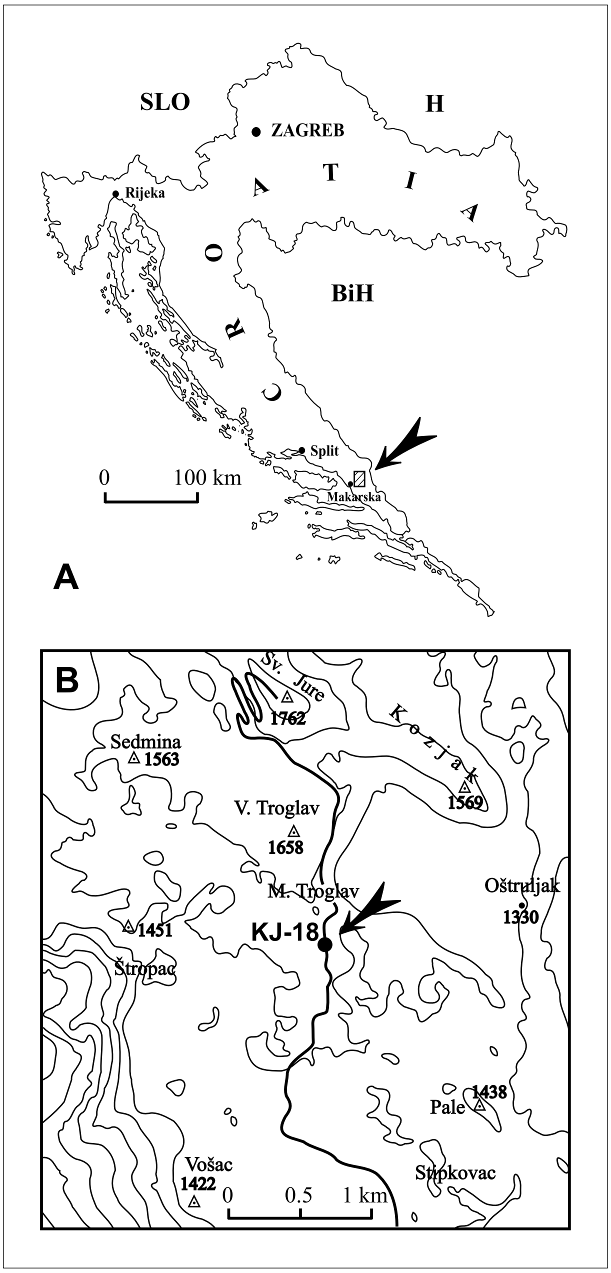

Fig. 1 (A) General position of the locality of sample KJ–18 in the territory of Croatia. (B) Simplified topographic map of the area on the central Mt. Biokovo, type locality of the sample KJ–18.

Type stratum: Well-bedded limestone, consisting of the vertical and lateral alternation of mudstones, algal and foraminiferal wackestones, and, more sporadically, skeletal–intraclastic grainstones; deposition took place in energetically varied environments in a shallow subtidal zone. The species occurs within a rich algal assemblage of Late Barremian age, immediately below the first occurrence of *Palorbitolina lenticularis* (BLUMENBACH).

Holotype: Oblique section in Pl. 7, Fig. 2; thin section KJ–18/185. Isotypes are represented by variously oriented sections, figured in Plates 6 and 7. The original material is stored in the Institute of Geology, Zagreb.

Diagnosis: Cylindrical, unsegmented, calcareous skeleton, with clearly differentiated primary and secondary branches. Primaries are arranged in whorls with a clearly alternate arrangement. In general, they are long and slender, slightly, not distinctly phloiophorous, often similar to the acrophorous shape; they bear a tuft of short, equally phloiophorous secondaries, which, if cut at their base, give a cross-like arrangement or are circularly arranged around a larger pore of the primary branch.

Description: The regular, non-branching, and unsegmented skeleton is built up of yellowish, medium-grained, mosaic calcite. The outer surface is sharply delineated toward the surrounding sediment in specimens with a uniformly abraded outer surface (Pl. VI, Figs. 5–6; Pl. VII, Figs. 8–12), or may be shallowly indented in those specimens in which the pores of secondary branches have been partly preserved (Pl. VI, Figs. 1, 2; Pl. VII, Figs. 3, 7, 14).

Specimens with a dark micritic coating are seldom observed (Pl. VI, Fig. 2). This, being a secondary feature, is of no distinguishing character. The inner, axial cavity is uninterrupted and sharply delineated; it occupies 24–35% of the total diameter (Table 2).

Branches, divided into primaries and secondaries, are situated in distinctly separated whorls and are arranged in clearly alternating position in consecutive whorls. Primary branches are long and slender, and because of a slightly developed terminal swelling may be described as indistinctly phloiophorous (Pl. VI, Figs. 2, 5–6; Pl. VII, Figs. 1–6). The same characteristic is also clearly visible in the specimens figured by PRATURLON & RADOIČIĆ (1974, figs. 2a, c, 3a–c). More frequently, the primary branches are almost acrophorous (Pl. VII, Figs. 8–9, 12). There are also fusiform branches which are intermediate between the slightly phloiophorous and the almost acrophorous ones (Pl. VII, Fig. 14). The angle of inclination of the primary branches with regard to the main axis may vary from an almost perpendicular position to an inclination of 45°. Each primary branch bears a tuft of secondary branches; in deeper tangential sections, cutting near their emerging points, they appear in a cross-shaped arrangement, which is clearly visible in sections figured by PRATURLON & RADOIČIĆ (1974, figs. 2b, d). In cases when the secondaries do not grow out from a common point of emergence but, instead, grow individually and separately from the distal surface of the primary branch, as seems to be the case in some sections in PRATURLON & RADOIČIĆ (1974, figs. 2c, 3b) as well as in some sections presented here (Pl. VII, Figs. 6, 11, 14), they appear in tangential section as a (not fully regular) ring of smaller pores surrounding the large pore of the primary branch (Pl. VII, Fig. 13). Secondary branches are very short, only seldom clearly visible, and also seem to be distally slightly widened (Pl. VII, Figs. 11, 14). Their number in a tuft varies from 4, as indicated by the cross-shaped

		Most frequently
Maximum observed length of thallus (L)	6.5	
Outer thallus diameter (D)	0.64–1.22	0.70–1.00
Inner thallus diameter (d)	0.20–0.44	0.24–0.35
Relation d/D	24–43%	24–35%
Distance between whorls (h)	0.11–0.24	0.11–0.15
Diameter of primary branches (p)	0.06–0.12	0.10–0.12
Length of primary branches (l)	0.20–0.36	0.24–0.34
Number of primary branches per whorl (w)	8–10	9
Diameter of secondary branches (p')	0.04–0.06	
Length of secondary branches (l')	0.07–0.14	0.10–0.12
Number of secondaries per primary branch (w")	4–6?	

Table 2 Main biometric parameters of *Biokoviella gusici* n.sp. Dimensions in mm.

arrangement, to probably 7 in cases of their individual growth.

The species is probably cladosporous.

Similarities and differences: *Biokoviella gusici* n.sp., as described here, was first thought to represent better preserved specimens of *Acroporella* and was, as such, treated by PRATURLON & RADOIČIĆ (1974) in their emended description of *Acroporella*. However, the two species cannot be identical, because *Biokoviella gusici* has secondary branches which are lacking in typical specimens of *Acroporella radoicici*. With the alternating arrangement of branches in neighbouring whorls and sometimes slightly curved and upwardly directed phloiophorous primary branches bearing indistinct secondary branches, it can be confused with *Salpingoporella verticillata* (SOKAČ & NIKLER). The differences with the latter species, as well as with smaller specimens of *Salpingoporella pygmaea* (PIA), to which it can also resemble in some cases, are emphasized by the existence of secondary branches in *B. gusici* and more densely spaced and more distinctly phloiophorus branches in *Salpingoporella*. With regard to *Triploporella bacilliformis* SOKAČ, which is characterized by stick-like, tubular primary branches bearing short secondaries, the difference between this and the new species is expressed by the number of branches in a whorl, which in *T. bacilliformis* amounts to 40–50, and by their poorly expressed alternating arrangement, and the larger diameter of the axial cavity.

Stratigraphic position: *Biokoviella gusici* n.sp. has been found in a sample of Upper Barremian limestone from Mt. Biokovo. The sample KJ–18 was collected from a sequence of well-bedded limestone, represented by an alternation of poorly fossiliferous mudstone, foraminiferal–algal wackestone, and sporadically vertically and laterally developed skeletal intraclastic grainstone. The latter contain, beside the new species, an abundance of algal remains, among which about 15 taxa, partly known and partly as yet undescribed, could be more or less reliably identified. The following algal species have been determined: *Biokoviella robusta* (SOKAČ), *Salpingoporella muehlbergii* (LORENZ), *S. verticillata* (SOKAČ & NIKLER), *S. patruliusi* BUCUR, *Salpingoporella* sp., *Cymopolia velici* SOKAČ & NIKLER, "*Praturlonella*" *dalmatica* SOKAČ & VELIĆ, *Cylindroporella lyrata* MASSE & LUPERTO-SINNI, *Korkyrella texana* SOKAČ & VELIĆ, *Triplopoprella*? *sarda* JAFFREZO et al., rare specimens of *Neomeris cretacea* STEINMANN, *Suppiluliumaelle polyreme* ELLIOTT, and others. Numerous specimens of *Humiella catenaeformis* (RADOIČIĆ) MASSE et al. and *Clypeina*? *solkani* CONRAD & RADOIČIĆ, indicating an Upper Hauterivian age can be found in the deeper underlying layers beneath the sample, while immediately above the algal bearing sample, in a continuous sequence, the first appearance of *Palorbitolina lenticularis* (BLUMENBACH) occurs. Therefore, the stratigraphic position of this species at its type locality can be reliably defined as Upper Barremian.

Genus *Neomeris* LAMOUROUX, 1816; emend. DELOFFRE, 1970

Neomeris cretacea STEINMANN, 1899

Pls. VIII–IX

Selected synonymy

1899 *Neomeris (Herouvalina) cretacea* n.sp. – STEINMANN, p. 149–154, figs. 14–18.

1978 *Neomeris cretacea* STEINMANN – BASSOULLET et al., p. 175–178, pl. 20, figs. 7–9.

1989 *Macroporella aptiensis* n.sp. – SOKAČ, p. 1–6, pls. 1–2.

1990 *Neomeris cretacea* STEINMANN – BARATTOLO, p. 207–218, figs. 5, 6, pls. 1–4.

1993 *Neomeris cretacea* STEINMANN – GRANIER & DELOFFRE, p. 36, 47.

1993 *Neomeris cretacea* STEINMANN – SOTÁK & MÍŠÍK, p. 402–403, pl. 12, figs. 1–4, 9.

1993 *Neomeris* cf. *cretacea* STEINMANN – SOTÁK & MÍŠÍK, pl. 12, figs. 8, 10.

2002 *Neomeris* sp. aff. *N. aptiensis* (SOKAČ) nov. comb. – RADOIČIĆ, pl. V, fig. 4.

2002 *Neomeris (Larvania*) *conradi* n.sp. – RADOIČIĆ, p. 9–10, pl. I, figs. 1–10, pl. IV, figs. 4, 6–7.

2002 *Neomeris (Larvania) decapoaae* n.sp. – RADOIČIĆ, p. 10, 12, pl. II, figs. 1–8, pl. IV, fig. 5.

Remarks

In his assessment of this species, BARATTOLO (1990) gave a more complete description of its morphological characteristics and the specific relationship that exists between the primary and secondary branches and the fertile ampoules. He also gave detailed biometric parameters and indicated, in some cases, at their mutual interdependence; he also emphasized that some fertile ampoules are more strongly pronounced than others. However, he doesn't mention that they appear to be completely absent in the sections of some specimens. It was this lack of distinctly shaped fertile ampoules, in addition to the apparent existence of only one type of indistinctly phloiophorous and irregularly distributed branches (as shown on the outer surface) that misled SOKAČ (1989, pl. 1, figs 1–3; pl. 2, fig. 2) to describe such specimens as a new species of *Macroporella*. Also in BARATTOLO's (1990) paper, some figured sections of *N. cretacea* (pl. 1, fig. 2; pl. 2, figs. 2, 4, 7) looked very similar to "*Macroporella aptiensis*". Re-examination of the sections figured as "*Macroporella aptiensis*" produced ambiguous results, in that some more distinctly phloiophorous branches that reach the outer surface may in fact represent atypically developed, elongated fertile ampoules. Therefore, new samples have been collected at the same locality. Analysis of a large number of new thin-sections has proven that most sections of this species belong to forms with slender branches of indistinctly phloiophorous or almost acrophorous type (Pl. VIII, Figs. 1, 2, 4, 8–10; Pl. IX, Figs. 4, 7), in which the existence of fertile ampoules could not be unequivocally established. However, a few sections (out of many) do show some larger and shorter pores of branches which may indicate their function as fertile ampoules (Pl. VIII, Fig. 3; Pl. IX, Figs. 5, 8), together with branches typical of the species, such as the sections figured in Pl. VIII, Fig. 5, and Pl. IX, Fig. 8).

Later, this species has been found at several more localities at Mt. Biokovo (Pl. IX, Figs. 1, 2, 9, 10), as well as in central Croatia (locality Grabrk). There are some differences, both within individual populations and between them where these are even more pronounced. Therefore the question arises, whether sterile individuals were also present in a population, or perhaps some parts of the thallus, in some specimens, were characterized by sterile branches? Still another unsolved question concerns the possible existence of sterile third-order branches, as suggested by some branches in sections figured in Pl. XIII, Fig. 7 and Pl. IX, Fig. 6 (top part). Taken together, all these variations point to the conclusion that rare specimens with indistinct sporangial ampoules as well as those with well-developed ampoules, should be regarded as belonging to the same species. Therefore the species *Macroporella aptiensis* SOKAČ, which was later, by RADOIČIĆ (2002, pl. 5, fig. 4), without further comment, given the designation *N. aptiensis* (SOKAČ), is here considered to be a younger synonym of *Neomeris cretacea* STEINMANN and thus should be treated accordingly. Species described by RADOIČIĆ (2002) should also be considered in this analysis, in which I attempted to compare specimens from different localities but from identical or close stratigraphic levels. (N.B. I am grateful to the reviewer, M.A. CONRAD, for drawing my attention to that paper). The two new species, established by RADOIČIĆ (2002) – *Neomeris* (*Larvaria*) *conradi* RADOIČIĆ and *Neomeris* (*Larvaria*) *decapoaae* RADOIČIĆ, are distinguished from one another by minimal differences in some biometric parameters: the d/D relationship and the shape of the more or less elongated gametangia. They have been compared only with Tertiary species but not with either the contemporaneous *N. cretacea* or with the form which was designated by RADOIČIĆ (2002) as *N. aptiensis* (SOKAČ) nov.comb. The similarity between the new species described by RADOIČIĆ (2002) and those specimens with variable characteristics which I included in *N. cretacea*, are indeed striking. This also applies to their biometric values, which fall within the variation range of *N. cretacea*. It would appear that all this clearly indicates that the new species established and described by RADOIČIĆ (2002) should be considered younger synonyms of *Neomeris cretacea* STEINMANN.

The stratigraphic position of the species, with regard to the hitherto known occurrences from the Middle Albian and Cenomanian in the Dinarides, can be somewhat lower (older). At two localities in Croatia, which are situated rather far apart (Mt. Biokovo in central Dalmatia versus Grabrk, southwest of Karlovac, central Croatia), the species has been found in identical levels that are characterized by the first appearance of *Palorbitolina lenticularis* (BLUMENBACH). It is accompanied by numerous dasyclad algae, e.g., *Suppiliuliumaella polyreme* ELLIOTT, *Biokoviella robusta* (SOKAČ), *Korkyrella texana* (JOHNSON), *Salpingoporella dinarica* RADOIČIĆ, etc. The first appearance of *N. cretacea* in the road-cut between Vošac and Sv. Jure in the more western part of Mt. Biokovo (in the above mentioned sample KJ–18 and in the abundant algal assemblage which also contains typical Barremian species), though represented by rare specimens, suggests that the beginning of its development took place as early as the Late Barremian. A similar stratigraphic range – Barremian to Albian – is mentioned by SOTÁK & MÍŠÍK (1993) in the Lower Cretaceous of the West Carpathians.

Genus *Korkyrella* SOKAČ & VELIĆ, 1981

Remarks

The taxonomic position of the genus Korkyrella, which was invalidly described by SOKAČ & VELIĆ (1981), has always, since the very beginning been problematic and/or contested. The reasons for this situation can be supposed to be due to the rather intricate structure (morphology), high degree of recrystallization, and generally poor state of preservation. The consequence of this situation has been the variable assignation of this alga to different genera or different species within a particular genus.

- The first description of the alga was given by JOHNSON (1965), in an invalid description, under the name *Salpingoporella texana* n.sp. In this publication, only cotypes illustrated in pl. 89, figs. 5–9 in JOHNSON (1965) have been mentioned.
- BAKALOVA (1971) assigned fragments of the stalk of this alga to the genus *Acroporella* and described *Acroporella*? *nissoviensis* n.sp. (BAKALOVA, 1971, pl. 1, figs. 1–3; pl. 2, fig. 7; holotype: slide No. 1260–1, figured in pl. 1, fig. 1).
- JAFFREZO et al. (1978) described a new species of the genus *Pseudoepimastopora*, *P. pedunculata*, based on sections of the upper, swollen, part of the thallus with visible transition into the stalk. This was illustrated by sections in JAFFREZO et al. (1978, pl. 2, figs. 1–3, 6, 9; pl. 4, fig. 2; pl. 6, fig. 3; holotype: pl. 2, fig. 2).
- PEYBERNÈS & CONRAD (1979) labelled similar sections – fragments of the bulbous head with transition into stalk, and possible stalk? (PEYBERNÈS & CONRAD, 1979, pl. 2, figs. 4, 5) – as *Cylindroporella barnesii* JOHNSON, whereas an oblique section through the head (pl. 2, fig. 6) was questionably assigned to the same species.
- SOKAČ & VELIĆ (1981) established the new genus *Korkyrella*. They, however, choose as type-species the invalidly described *Salpingoporella texana* JOHNSON, whereupon this genus also becomes invalidly described. Though invalid, the new genus, i.e. its type-species, was illustrated by numerous sections (SOKAČ & VELIĆ, 1981, pls. 1–3).
- CONRAD (1982) critically reassessed *Korkyrella texana* and regarded it as being synonymous with *Cylindroporella barnesii* JOHNSON, except for some sections, e.g., those that had been interpreted as stalks (SOKAČ & VELIĆ, 1981, pl. 2, figs. 2, 3), which he considered as possibly belonging to other species, e.g., *Salpingoporella muehlbergii* (LORENZ).
- SOKAČ (1987) analyzed and reinterpreted the genus *Korkyrella*. He supported the validity of the genus, but based it, in retrospect, on an incorrect interpretation of the arrangement and disposition of sterile and fertile branches in the fertile part of the thallus (SOKAČ, 1987, text-fig. 1). In his interpretation (and in the graphic representation), the pores of their secondary branches were considered as the fertile ampoules. The inadequately known structure (morphology) of the alga, that due to various degrees of preservation and different types of sections, may appear as belonging to different taxa, misled him again and he wrongly concluded that the original description contained heterogeneous material and thus pleaded for the complete abandonment of the invalid *Salpingoporella texana* JOHNSON, rejection of the name, and introduction of the irregular new name, "*Korkyrella ivanovici*", all of which proved, in retrospect, unnecessary and unjustified, because the type-species was invalid and wrongly used, the genus also remained invalid.
- MASSE & LUPERTO-SINNI (1989), when comparing their new species *Cylindroporella lyrata* with other species of the genus, dealt also with the renamed *Korkyrella ivanovici* and came to the conclusion that it had all the features of a *Cylindroporella*. Therefore they labelled it *Cylindroporella ivanovici*, wherewith the genus *Korkyrella* was, in fact, contested.
- GRANIER & DELOFFRE (1993) designated the genus *Korkyrella* SOKAČ & VELIĆ, 1981, nom. nud., and *Korkyrella ivanovici* SOKAČ 1987, nom. nud., as taxonomically invalid for formal reasons, without commenting on their decision.
- LUPERTO-SINNI & MASSE (1993b) reminded of their earlier (MASSE & LUPERTO-SINNI, 1989) transfer of *Korkyrella ivanovici* into the genus *Cylindroporella* also emphasize that under the name *Cylindroporella pedunculata* (JAFFREZO et al.) they now mean the form presented by SOKAČ & VELIĆ (1981) as the type species of the genus *Korkyrella*, where *Korkyrella ivanovici* should be considered as a younger synonym of *Cylindroporella pedunculata*.

This short chronological review of different taxonomic treatments of the alga illustrates a number of errors that were made in new descriptions of its detached fragments, its later determinations and assignment to different genera and their species, all of which having as a consequence, the lengthy invalidity of the genus *Korkyrella* and its originally designated type species.

According to the ICBN, before formally validating the genus *Korkyrella*, it is firstly necessary to give a taxonomically valid status to its type species, designated by SOKAČ & VELIĆ (1981). Originally, the species was invalidly described by JOHNSON (1965) as *Salpingoporella texana*, because he failed to designate the holotype but instead only illustrated the cotypes (JOHNSON, 1965, pl. 89, figs. 5–9). Therefore I propose as the lectotype of *Salpingoporella texana* JOHNSON the oblique section figured in JOHNSON, 1965, pl. 89, fig.

9, which is, together with other cotypes in thin-section USNM 42468, deposited in the U.S. National Museum.

The renewed reinterpretation of the genus *Korkyrella*

New generic diagnosis

The thallus is clearly differentiated into a more or less elongated, swollen and bulbous upper part – the head, and a lower, narrower, part – the stalk. The transition between the two parts is abrupt. The head bears both fertile and sterile branches, whereas the stalk bears only the sterile ones. In the head, fertile and sterile branches alternate in neighbouring whorls, fertile ampoules also have secondary branches. Sterile branches in the stalk are also arranged in whorls.

Remarks

The main distinguishing character of the genus *Korkyrella,* that clearly separates that genus from other similar ones, concerns the arrangement and the division of the branches (Fig. 2) and can be summarized as follows: *Korkyrella* differs from *Otternstella* and *Chinianella* by the alternating arrangement of fertile and sterile branches, and from *Cylindroporella*, which has an identical arrangement of branches, by the existence of secondary branches on the fertile ampoules.

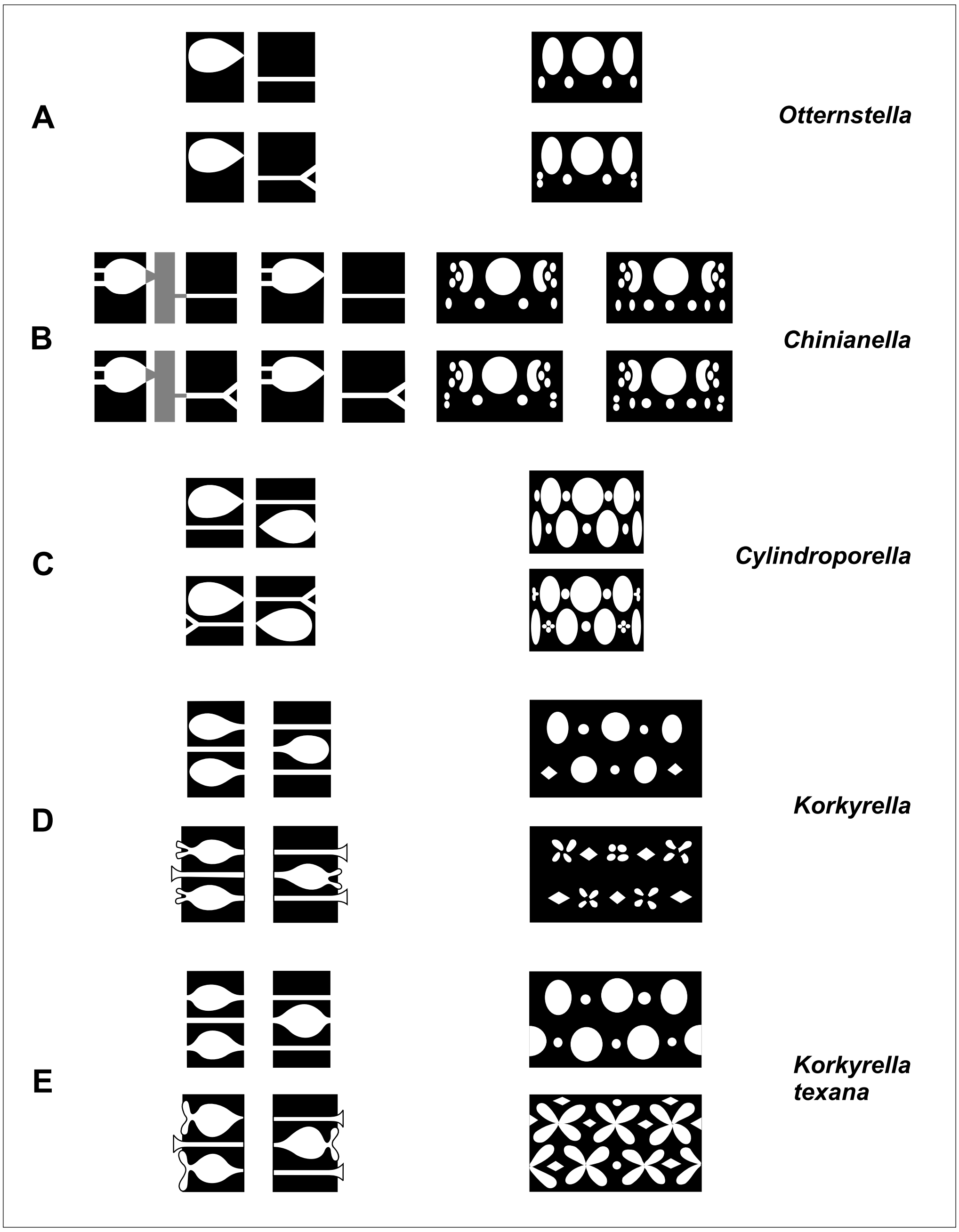

Fig. 2 Comparison of *Otternstella*, *Chinianella*, *Cylindroporella*, *Korkyrella* and *Korkyrella texana* (JOHNSON) in axial and different tangential sections of the upper fertile part of the thallus (A–C, after GRANIER et al., 1994).

Korkyrella texana (JOHNSON) nov. comb.

Pls. X–XII

Selected synonymy

1965 *Salpingoporella texana* n.sp. – JOHNSON, p. 719–720, pl. 89, figs. 5–9.

1971 *Acroporella nissovensis* n.sp. – BAKALOVA, p. 58–59, pl. 1, figs. 1–3.

1978 *Pseudoepimastopora pedunculata* n.sp. – JAFFREZO, POISSON & AKBULUT, p. 79–80, pl. 2, figs. 1–3, 6, 9; pl. 4, fig. 2 (part); pl. 6, fig. 3 (?part).

1979 *Cylindroporella barnesii* JOHNSON – PEYBERNÈS & CONRAD, pl. 2, figs. 4, 6, 5?

1981 *Korkyrella texana* (JOHNSON) – SOKAČ & VELIĆ, p. 1–12, text-fig. 1, pls. 1–3.

1982 *Cylindroporella barnesii* JOHNSON – CONRAD, p. 1–4, pl. 1, figs. 3, 5, 6, 4?

1987 *Korkyrella ivanovici* n.sp. – SOKAČ, p. 11–16, pls. 1–2.

1989 *Cylindroporella ivanovici* (SOKAČ) – MASSE & LUPERTO-SINNI, p. 30–38.

1993b *Cylindroporella pedunculata* (JAFFREZO et al.). – LUPERTO-SINNI & MASSE, p. 295–309, pl. 2, figs. 12–15.

?1993 *Cylindroporella pedunculata* (SOKAČ, 1987) – SOTÁK & MÍŠÍK, p. 383–404, pl. 5, figs. 5–7.

1994 *Cylindroporella pedunculata* (JAFFREZO, DELOFFRE & AKBULUT) – BODROGI, BONA & LOBITZER, pl. 10, figs. 1, 3.

1999 *Cylindroporella pedunculata* (JAFFREZO, POISSON & AKBULUT) – BUCUR, p. 53–72, pl. 2, figs. 15, 18, 21.

A a thorough re-description appears necessary after visible contradictions concerning the taxonomic assignment and the validity of this alga, due to its unclear morphology, strong recrystallization, frequent finds of detached fragments of different parts of the thallus, and, generally, the poor state of preservation resulted in different individual interpretations. In addition to the already mentioned characteristically shaped thallus, this alga is distinguished by the rather complex structure of the outer part of the calcareous envelope in the bulbous (“head“) part. The proposed lectotype (JOHNSON, 1965, pl. 89, fig. 9), selected among several cotypes, is represented by an oblique section with heavily recrystallized inner structure, poorly delineated outer surface, and visible alternating arrangement of pores, belonging to two types of branches, in the wall of the axial cavity. On the outer side of the inner wall there are arcuate protrusions directed towards the centre which mark the proximal parts of large fertile branches, with narrow channels of thin sterile branches situated in between them. Arcuate protrusions on the inner side of the outer part of the skeleton correspond to the distal ends of the fertile ampoules, as indicated by their more or less wineskin-shaped form. The traces of sterile branches in the lectotype section can only be partially seen in its middle part as tiny pores that alternate in position with larger fertile branches. In other parts of the skeleton they are obliterated by recrystallization. The lectotype section fully corresponds to the oblique sections figured by SOKAČ & VELIĆ (1981, pl. 1, fig. 7; pl. 3, figs. 3, 5, 6), which is a strong indication of the taxonomic identity of both materials. The same thing also applies to the sections accompanying the description of *Pseudoepimastopora pedunculata* JAFFREZO et al. (1978, pl. 2, figs. 1, 3–6), that also correspond – fully or partially, depending on the state of preservation – to the sections illustrated in SOKAČ & VELIĆ (1981, pl. 1, figs. 1–6) and SOKAČ (1987, pl. 1, figs. 1, 4; pl. 2, figs. 1–3), as well as to those in this paper, Pl. XI, Fig. 6 and Pl. XII, Figs. 2, 3. Also, the sections figured by LUPERTO-SINNI & MASSE (1993b, pl. 2, figs. 12–15) correspond well to those in SOKAČ & VELIĆ (1981, pl. 1, fig. 6; pl. 3, figs. 1, 5, 6) or, partly, to those in SOKAČ (1987). All these facts unequivocally indicate that all the above mentioned illustrations, deriving from various periods and localities and differently interpreted by various authors, belong to the same algal species, the characteristics of which may be summarized as follows (see Fig. 3, Table 3).

As has already been emphasized in earlier descriptions, *Korkyrella texana* (JOHNSON) has a thallus that is clearly differentiated into two distinct parts: the upper, bulbous, “head”, and the lower, narrow, stalk, that abruptly passes into the “head” via a short “neck”. The central cavity, stretching from the stalk with a constant diameter, continues into the upper part, where the inner wall is seldom observed, only in rare transverse and oblique sections (Pl. XII, Figs. 4–8). In the upper, bulbous, part of the thallus (“head”) there are both fertile and sterile branches developed. Very weak calcification of the walls of fertile branches and the lack of calcification in the intervening space leads to their almost complete destruction. This results in the apparent existence of two envelopes, an inner one surrounding the axial cavity and an outer one, which forms the outer surface. The stalk bears only sterile branches; thus the “head” can be considered to be the fertile part of the thallus. The distinguishing characteristics of the species within the genus *Korkyrella*, of which it is a typical representative, are the disposition of the branches and the existence of secondary branches on the fertile ampoules. The branches are arranged into very dense whorls. Within a whorl, in the upper part of the thallus, sterile and fertile branches alternate. The disposition of sterile and fertile branches in neighbouring whorls is also clearly alternating, as has been graphically shown for the genus *Cylindroporella* by OTT (1967) and GRANIER et al. (1994).

Fertile branches, often called “ampoules” because of their wineskin-like shape, are large, constricted at the base and rounded at the distal end. Sometimes they acquire a plump-elongated or irregularly elliptical

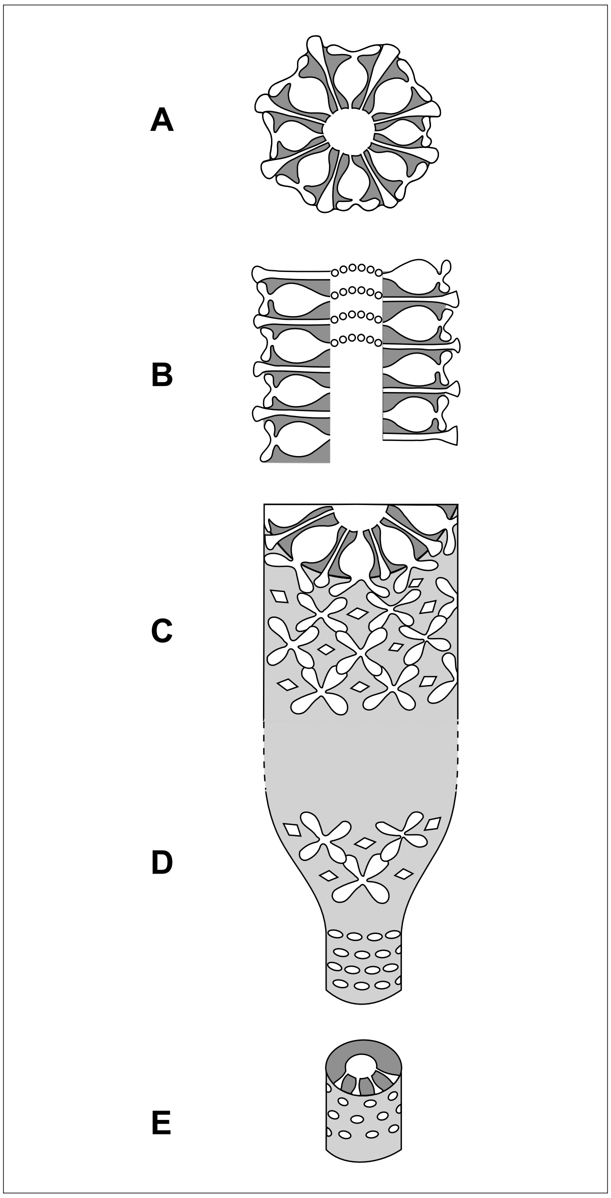

Fig. 3 Schematic reconstruction of *Korkyrella texana* (JOHNSON). (A) cross section; (B) longitudinal section; (C) outer thalus surface; (D) head passing into the handle; (E) handle.

shape. They communicate with the main cell through a narrow and short channel, situated in the middle of the base. From the top of the distal surface of each fertile branch ("ampoule"), four secondaries emerge from the same starting point. They are comparatively massive, strongly bent, and thus almost subparallel to the outer surface (Pl. XI, Figs. 1, 7). Viewed in the vertical plane, the angle of their divergence amounts to 50–60º ("below" and "above"), whereas in the horizontal plane (viewed "laterally") it is smaller, amounting to 30–40º. Therefore they often appear like an Andrew's cross (Pl. XI, Figs. 1, 7). The dense arrangement of fertile branches results in their being tightly pressed against each other, so that their walls are very thin and weakly micritized, which results, in turn, in being frequently destroyed and only rarely can they be visually traced by a thin, dark, micritic layer (Pl. X, Fig. 1; Pl. XI, Fig. 1). The spaces that are formed by the rounding of their distal ends and by the constrictions at their bases are somewhat more strongly calcified, which appears as if there is one outer and one inner calcareous envelope (Pl. XII, Figs. 6, 7). A similar situation exists with the secondary branches of the fertile ampoules, that seem to be immersed in the calcareous mass with their lower parts only, appearing exceptionally as micritized petals in a cross-shaped arrangement (Pl. X, Fig. 2; Pl. XI, Figs. 1, 4, 7). The small number of branches in a whorl (8–9) and their large size makes it impossible to see, in shallow tangential (cortical) sections, more than one or, exceptionally, two sections of the cross-shaped arrangement of secondary branches of neighbouring, alternately situated sporangia (Pl. XI, Fig. 7, central part of the picture, arrow; Pl. XI, Fig. 4, top part of the picture, arrow) and weak micritization of the surface membrane. Sterile branches, in their proximal parts up to a half or two thirds of their length, are very thin and squeezed between the fertile ampoules, with weakly calcified envelopes. Therefore they appear, in sections, as tiny circular pores with micritized margins (Pl. XI, Fig. 1). Toward their distal ends they gradually broaden and are somewhat more heavily calcified (Pl. XI, Fig. 1, going up and down from the centre of the picture). At their very distal ends, they seem to extend above the upper surface of the secondary branches (on the fertile ampoules), they appear rhombic in section, with more or less stretched sides. Some very distal sections of the secondary branches (Pl. XI, Fig. 1) may indicate their further branching, but this cannot be unequivocally ascertained.

Similarities and differences

From the chronological review of various determinations given above, it can be seen that this alga was most frequently assigned to the genus *Cylindroporella*. This was due to the occasional and not very clearly visible alternating arrangement of two types of pores, of different dimensions, in neighbouring whorls. Of these, the larger ones were thought to represent fertile, and the smaller ones sterile branches. However, the newly observed morphological characteristics – well developed secondary branches, in a cross-shaped disposition, growing out of fertile ampoules – gave this alga a new qualitative feature, by which it can be, in appropriate sections (i.e., those cutting the "head"), clearly and unequivocally distinguished from otherwise similar *Cylindroporella* species. The identification is more difficult if only sections of the stalk are available, which may appear similar to some *Salpingoporella* species with which they often jointly occur in the same sample; in such cases, the acrophorous type of branches may be taken as an indication suggesting a probable assignment of such sections to *Korkyrella*.

Stratigraphic position

In order to assess the stratigraphic range of *Korkyrella texana,* one must take into account all its

Dimensions of head in mm:	
Maximum observed length (L)	10
Outer diameter (D)	0.52–1.46
Inner diameter (d)	0.08–0.33
Relation d/D	0.18–0.24
Distance between sporangial whorls (h)	0.14–0.30
Diameter of sporangia (p)	0.10–0.24
Length of sporangia (l)	0.20–0.45
Number of sporangia per whorl (w)	8–9
Diameter of secondary branches (p’)	0.12–0.16
Length of secondary branches (l’)	0.20–0.30
Number of secondary branches on a sporangium (w”)	4
Diameter of sterile branches (p”)	0.07–0.14
Length of sterile branches (l”)	0.58
Number of sterile branches per whorl (w”)	8–9
Number of secondaries on a sterile branch (w”’)	?(4)
Dimensions of stalk in mm:	
Maximum observed length (L)	2.4
Outer diameter (D)	0.40–0.48
Inner diameter (d)	0.10–0.20
Relation d/D	0.25–0.45
Distance between whorls (h)	0.06–0.10
Diameter of branches (p)	0.04–0.06
Length of branches (l)	0.12–0.18
Number of branches per whorl (w)	?

Table 3 Main biometric parameters of *Korkyrella texana* (JOHNSON).

occurrences, dispersed at numerous localities all over the Mediterranean realm, as well as the material illustrated by JOHNSON (1965), which is said to derive from the upper part of the Edwards Formation (Albian). In contrast, the great majority of later finds, (disregarding the different taxonomic assignments by various authors – see above), seem to be of a more or less identical age, corresponding to the Barremian–Lower Aptian. However, some sections which are said to be of Cenomanian age (CONRAD, 1982, pl. 1, figs. 4–6) and which could possibly be assigned to that species (but are very poorly preserved), or perhaps to some other species of that genus (which is, for the time being, uncertain), indicate the possibility of a broader stratigraphic range. Therefore I will restrict my comments here only to those localities in the Dinarides at which the stratigraphic position of the species is well documented by rich microfossil assemblages and I will leave aside all uncertain identifications, which also need a re-examination of their stratigraphic position. In the original description of the genus *Korkyrella*, at the type locality (Brna, Korčula Island), SOKAČ & VELIĆ (1981) mention the following accompanying assemblage: *Praturlonella dalmatica* (SOKAČ & VELIĆ), *Triploporella marsicana* PRATURLON, later supplemented by *Triploporella baciliformis* SOKAČ and *Salpingoporella heraldica* SOKAČ, and the first appearance of *Palorbitolina lenticularis* (BLUMENBACH). At another locality, on the west bank of the Neretva River, upstream of Mostar, it is accompanied by *Falsolikanella danilovae* (RADOIČIĆ), *Falsolikanella nerae* (DRAGASTAN et al.), *Salpingoporella* cf. *genevensis* (CONRAD), *Salpingoporella dinarica* RADOIČIĆ, *Cylindroporella elliptica* BAKALOVA, and others. On Mt. Biokovo, there are several localities with *Korkyrella texana*. Among those, the richest microfossil assemblage has been found on the road between the Vošac mountain hut and the Sv. Jure peak. A bed lying immediately below the first appearance of *Palorbitolina lenticularis* is full with deposited algal remains: particularly frequent sections of *Salpingoporella muehlbergii* (LORENZ), *Salpingoporella verticillata* (SOKAČ & NIKLER), *Salpingoporella patruliusi* BUCUR, *Biokoviella robusta* (SOKAČ), *Cymopolia velici* SOKAČ & NIKLER, *Cylindroporella lyrata* MASSE & LUPERTO-SINNI, *Triploporella*? *sarda* JAFFREZO et al., *Neomeris cretacea* STEINMANN, *Suppiluliumaella polyreme* ELLIOTT, and others. In western Istria, well-preserved, partly isolated (washed out) specimens of this species (SOKAČ, 1987, pl. 15, figs. 5–8) have been found in platy limestone, almost immediately below the thick-bedded limestone known commercially as ‘Giallo d’Istria’ (Istrian Yellow, that, in addition to abundant *Bacinella irregularis*, contain rare sections of *Palorbitolina lenticularis*, with, in the lowest levels, the pachyodont bivalve *Toucasia* sp. The best preserved specimens, which, indeed, enabled the emendation of the genus *Korkyrella* (Pl. X, Figs. 1, 2; Pl. XI, Figs. 1, 4, 7), have been found at the locality of Grabrk, near the town of Ogulin (central Croatia), where they have been found together with *Neomeris cretacea* STEINMANN, *Ciptocampylodon fontis* (PATRULIUS), rare *Salpingoporella dinarica* RADOIČIĆ, more or less abundant *Palorbitolina lenticularis*, and numerous pachyodont bivalve debris.

The above review of fossil occurrences of this species at several widely dispersed localities in the Karst Dinarides, reliably indicate that the stratigraphic range of *Korkyrella texana* in the Dinaric Mountains corresponds to the Barremian–Lower Aptian. It remains, however, an open question whether its occurrence at new localities, provided a secure identification and well documented stratigraphic position are available, will perhaps necessitate a revision, i.e. broadening, of the stratigraphic range as given above.

Acknowledgements

This paper is based on samples that were collected by several colleagues who participated in the field work, i.e. in the mapping of the Lower Cretaceous deposits, to all of whom I am greatly indebted. They are: Đuro BENČEK, Josip BUKOVAC, Ivan GALOVIĆ, and Ivo VELIĆ. I am particularly grateful to Ivo VELIĆ for his determination and stratigraphic interpretation of the accompanying foraminiferal assemblages. I also thank Tonći GRGASOVIĆ for lengthy discussions and his critical remarks on earlier drafts of this paper. I am grateful to the reviewers, Ivan GUŠIĆ and Marc A. CONRAD, who critically read the manuscript, indicated some errors, and gave several useful remarks that clearly improved the presentation.

I must emphasize that my discussion concerning the *Neomeris* species described by RADOIČIĆ (2002) and my conclusion that they should be considered younger synonyms of *N. cretacea* has been added to the text after the suggestion of M.A. CONRAD and the reviewers did not have the opportunity to see, and to comment on, it. I must also emphasize the difference in opinions between M.A. CONRAD and myself concerning the form which served as the basis for the emendation of the genus *Acroporella* PRATURLON & RADOIČIĆ (1974); in my opinion, it is a new species, i.e., *Biokoviella gusici.* In his review, M.A. CONRAD expressed the opinion that *B. gusici* is a younger synonym of *Acroporella radoicici.* In spite of this reviewer's remark, I decided to stick to my opinion. It may be debatable whether my arguments are conclusive, but it seems unacceptable to me to unite forms which, in spite of being superficially similar, show some obvious differences. I hope that this question will be the subject of further research, and more arguments will be put forward which will support either opinion.

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Manuscript received June 09, 2003.

Revised manuscript accepted May 04, 2004.

PLATE I

1–8 *Cylindroporella lyrata* MASSE & LUPERTO-SINNI

1 Longitudinal section, KJ–18/54, x17.

2 Oblique–tangential section, KJ–18/29, x22.

3 Oblique section, KJ–18, x22.

4 Oblique–tangential section, KJ–18/22, x17.

5–6 Oblique sections; Fig. 5, KJ–18/224; Fig. 6, KJ–18/111, x34.

7–8 Transverse sections; Fig. 7, KJ–18/32; Fig. 8, KJ–18/212, x34.

Mt. Biokovo, Upper Barremian.

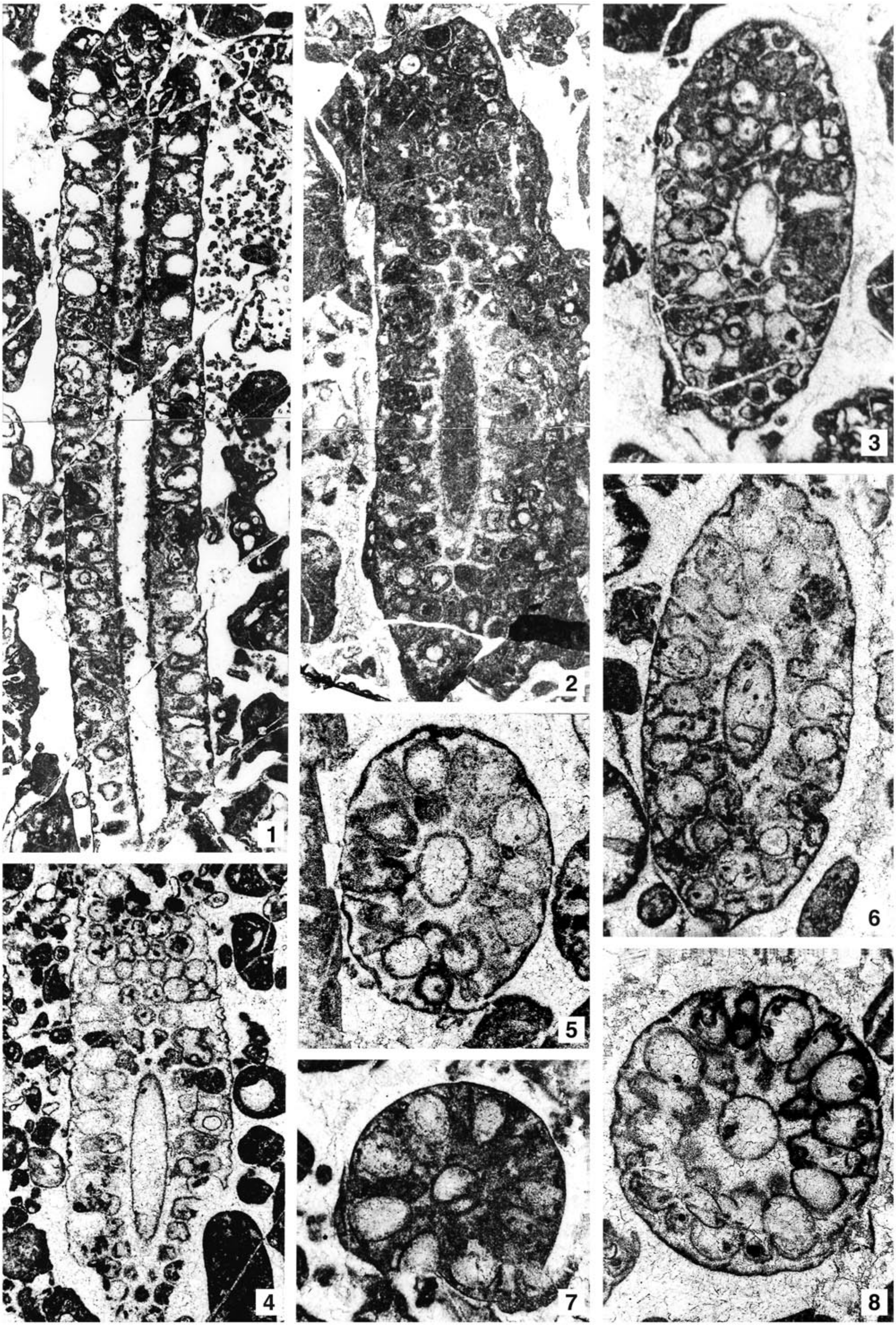
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PLATE II

1–8 *Cylindroporella lyrata* MASSE & LUPERTO-SINNI

1 Oblique section, KJ–18/208, x22.

2 Oblique section; groups of cysts are visible in the pores of fertile ampoules; KJ–18/124, x34.

3 Oblique section of the lower part of the thalus, near the stalk; KJ–18/25, x22.

4–5, 8 Oblique sections; Fig. 4, KJ–18/172; Fig. 5, KJ–18; Fig. 8, KJ–18/194, x22.

6 Oblique section, KJ–18/230, x22.

7 Transverse section, KJ–18/223, x34.

Mt. Biokovo, Upper Barremian.

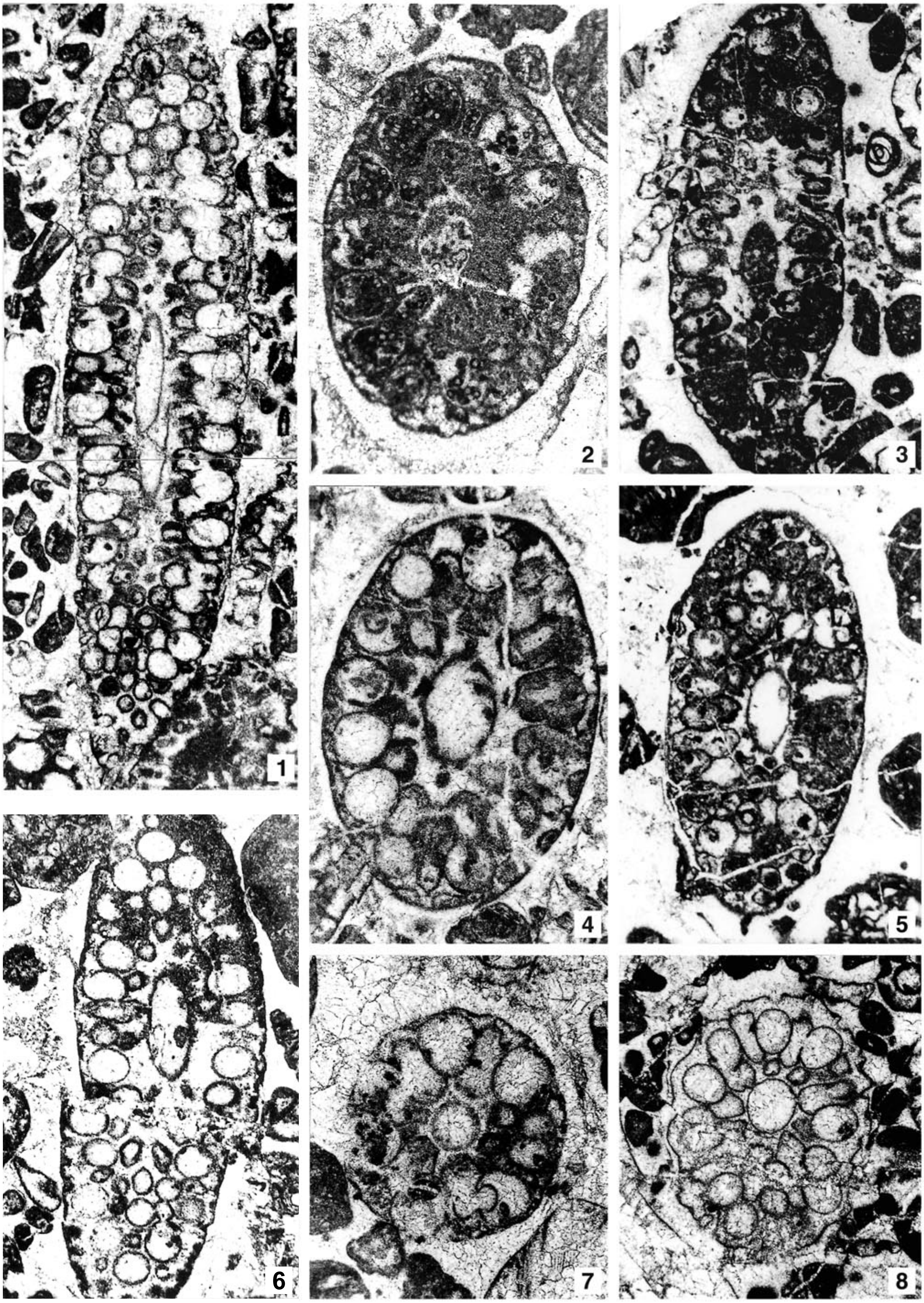
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PLATE III

1–8 *Biokoviella robusta* (SOKAČ) nov.comb.

1, 3–4 Oblique–tangential sections, Fig. 1, KJ–18/241; Fig. 3, KJ–18/245; Fig. 4, KJ–18/55; x22.

2 Tangential section, KJ–18/28, x22.

5–7 Oblique sections; Fig. 5, KJ–18/58; Fig. 6, KJ–18/18; Fig. 7, KJ–18/107; x22.

8 Longitudinal section, KJ–18/210, x22.

Mt. Biokovo, Upper Barremian.

PLATE III

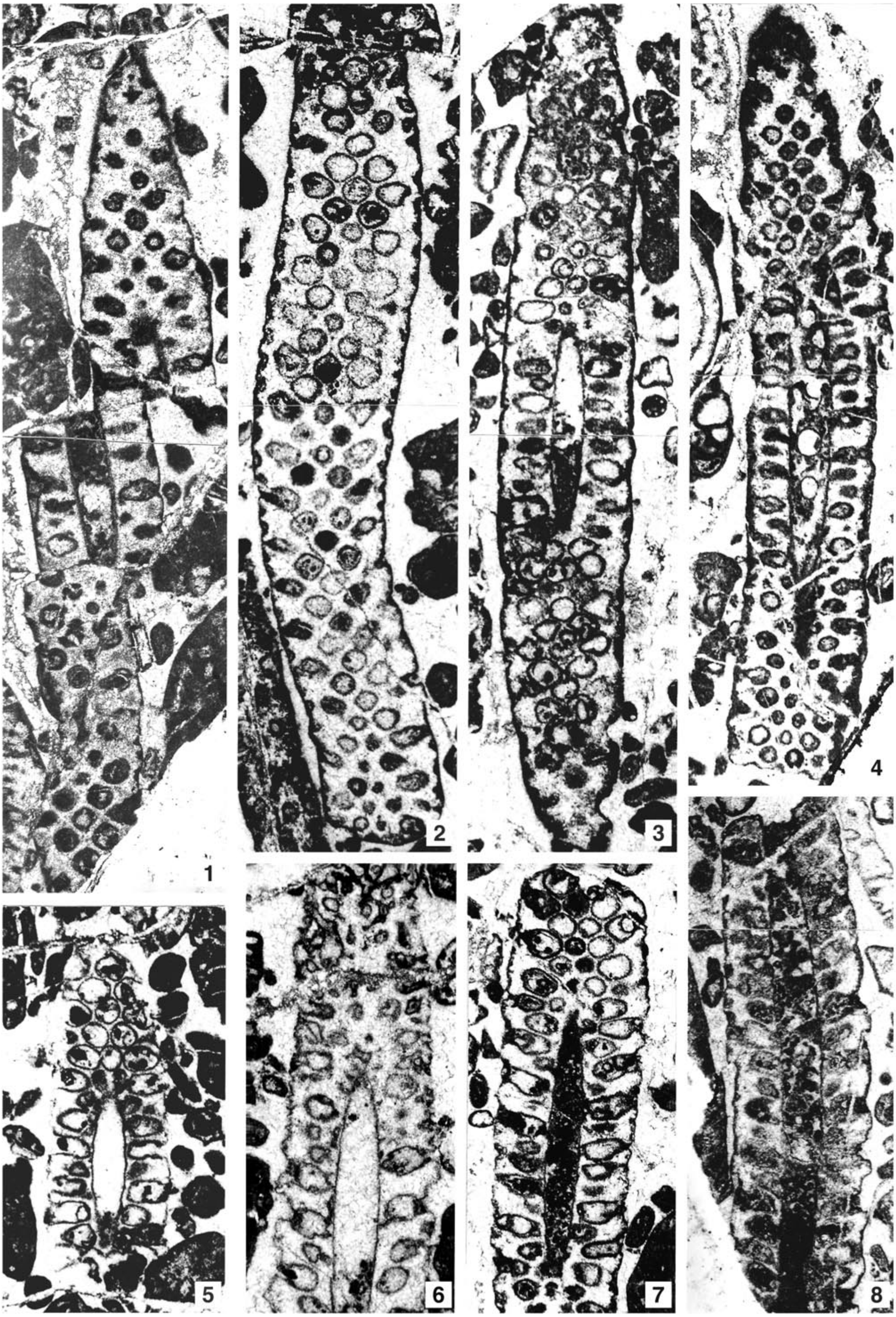

PLATE IV

1–8 *Biokoviella robusta* (SOKAČ) nov.comb.

1 Oblique section, KJ–18/141, x34.

2 Oblique section; a tuft with 6 pores of secondary branches is visible in the upper part, KJ–18/141, x34.

3 Oblique section; specimen with very large cylindrical pores of primary branches, each bearing relatively large, separately grown, secondary branches; KJ–18/108, x34.

4 Transverse section; specimen with irregular (deformed) primary branch, possibly triple divided; KJ–18/117, x34.

5 Transverse–oblique section; specimen with large primary branches bearing both tufts and separately grown secondary branches; KJ–18/57, x34.

6 Transverse section; specimen with large primary branches bearing both tufts and separately grown secondary branches; KJ–18/203, x34.

7 Transverse section; specimen with large primary branches, bearing separately grown secondary branches and possible tertiary branches; KJ–18/240, x34.

8 Oblique–tangential section; possible club-shaped primary branches; KJ–18/58, x22.

9–10 Transverse sections; possible tuft-growing of secondary branches; Fig. 9, KJ–18/244; Fig. 10, KJ–18/90, x34.

Mt. Biokovo, Upper Barremian.

PLATE IV

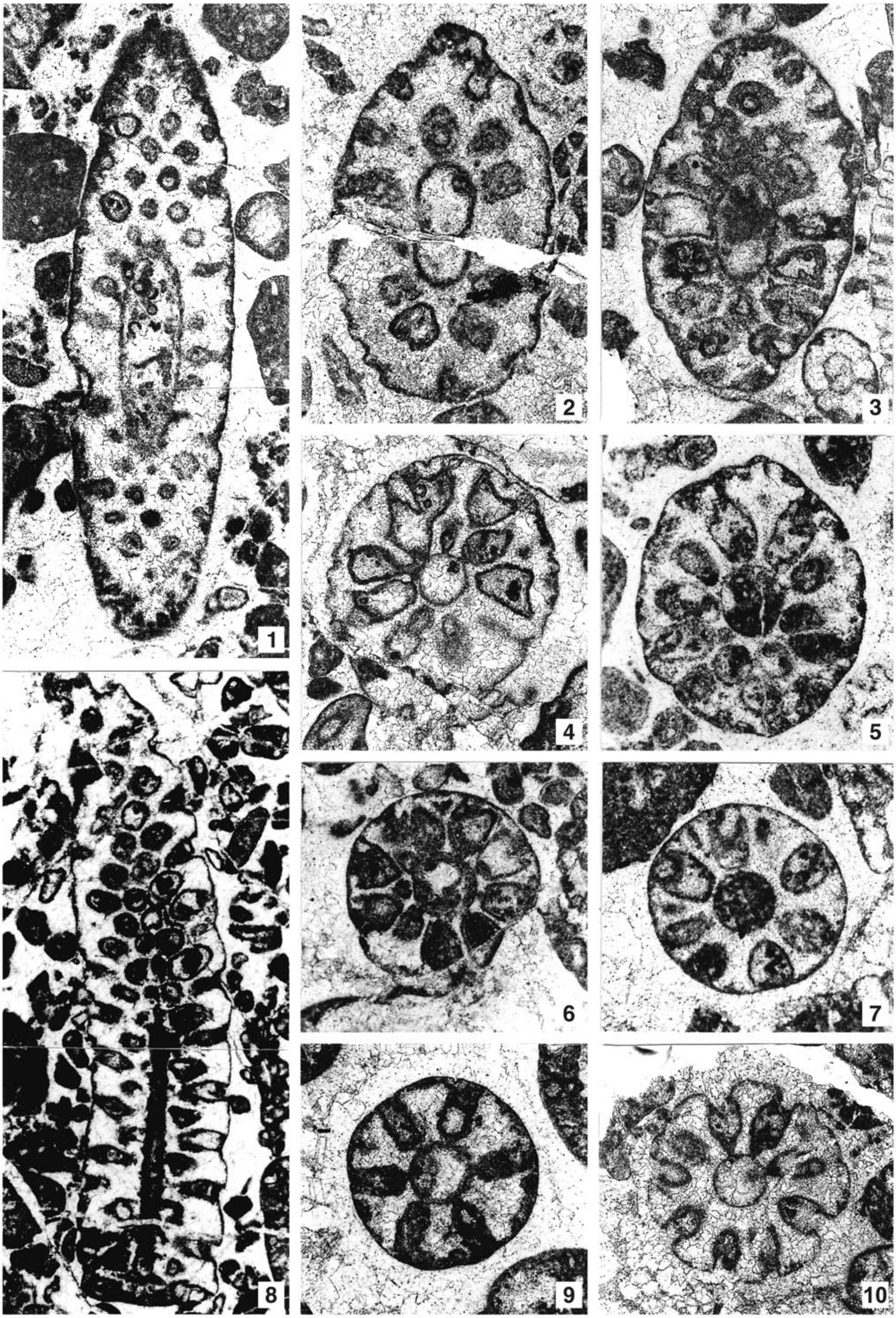

PLATE V

1–8 *Biokoviella robusta* (SOKAČ) nov.comb.

1 Oblique, partly tangential section; specimen with fusiform to club-shaped primary branches; KJ–18/67, x22.

2 Oblique, partly tangential section; specimen with phloiophorous primary branches, approaching the similar species *Biokoviella gusici* n.sp.; KJ–18/146, x34.

3 Transverse and transverse–oblique sections; specimens with variously shaped primary branches, and with a variable number of branches per whorl; KJ–18/247, x34.

4–5 Transverse sections; irregular growth of the secondary branches is visible on Fig. 5; Fig. 4, KJ–18/244; Fig. 5, KJ–18/170, x34.

6 Oblique sections; showing differences between specimens, both in dimensions and in the density of branches; KJ–18/15, x22.

7 Transverse sections; showing the pronounced variability, both in the shape of the primary branches, and in the number of the branches per whorl; KJ–18/247, x14.

8 Fragment of the oblique section; tuft-growing secondary branches on the right side of the specimen; KJ–18/215, x34.

Mt. Biokovo, Upper Barremian.

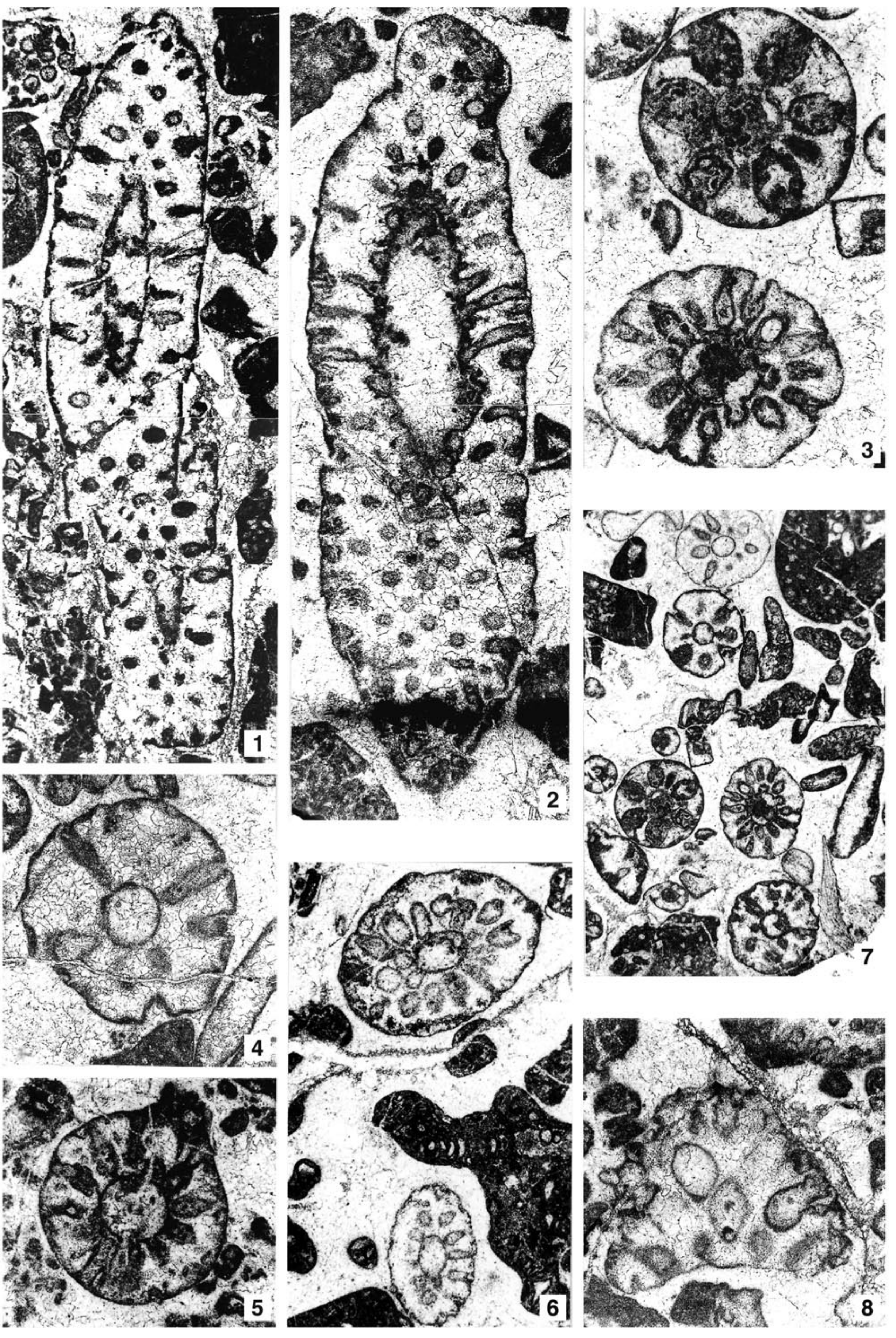
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PLATE VI

1–7 *Biokoviella gusici* n.sp

1–2 Oblique–tangential sections; Fig. 1, KJ–18/30; Fig. 2, KJ–18/5, x22.

3 Tangential section, KJ–18/28, x22.

4–6 Oblique sections; Fig. 4, KJ–18/139; Fig. 5, KJ–18/33; Fig. 6, KJ–18/91; x34.

7 Oblique section, KJ–18/22, x22.

Mt. Biokovo, Upper Barremian.

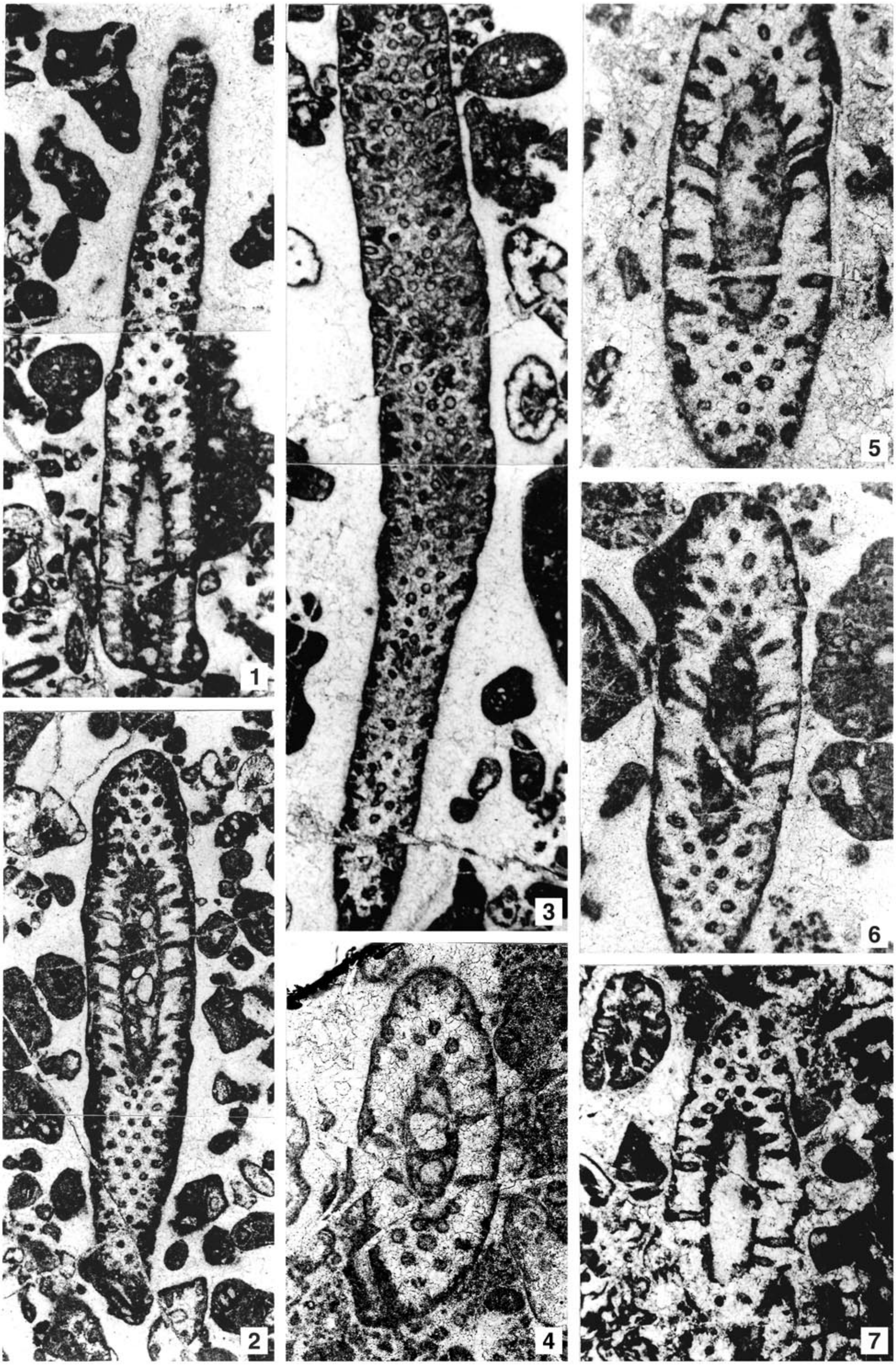
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PLATE VII

1–7 *Biokoviella gusici* n.sp

1–6 Oblique sections; Fig. 2 = Holotype; clearly visible secondary branches in Figs. 2–4; Fig. 1, KJ–18/124; Fig. 2, KJ–18/185; Fig. 3, KJ–18/98; Fig. 4, KJ–18/138; Fig. 5, KJ–18/159; Fig. 6, KJ–18/193, x34.

7–12 Transverse sections; phloiophorous primary branches with tufts of secondary branches are clearly visible in Figs. 8–11; Fig. 7, KJ–18/152; Fig. 8, KJ–18/83; Fig. 9, KJ–18/220; Fig. 10, KJ–18/182; Fig. 11, KJ–18/106; Fig. 12, KJ–18/15, x34.

13 Tangential section; tiny pores of secondary branches dispersed around large pores of primary branches; KJ–18/182, x34.

14 Oblique section; specimen with fusiform primary branches and short phloiophorous secondary branches; KJ–18/8, x22.

Mt. Biokovo, Upper Barremian.

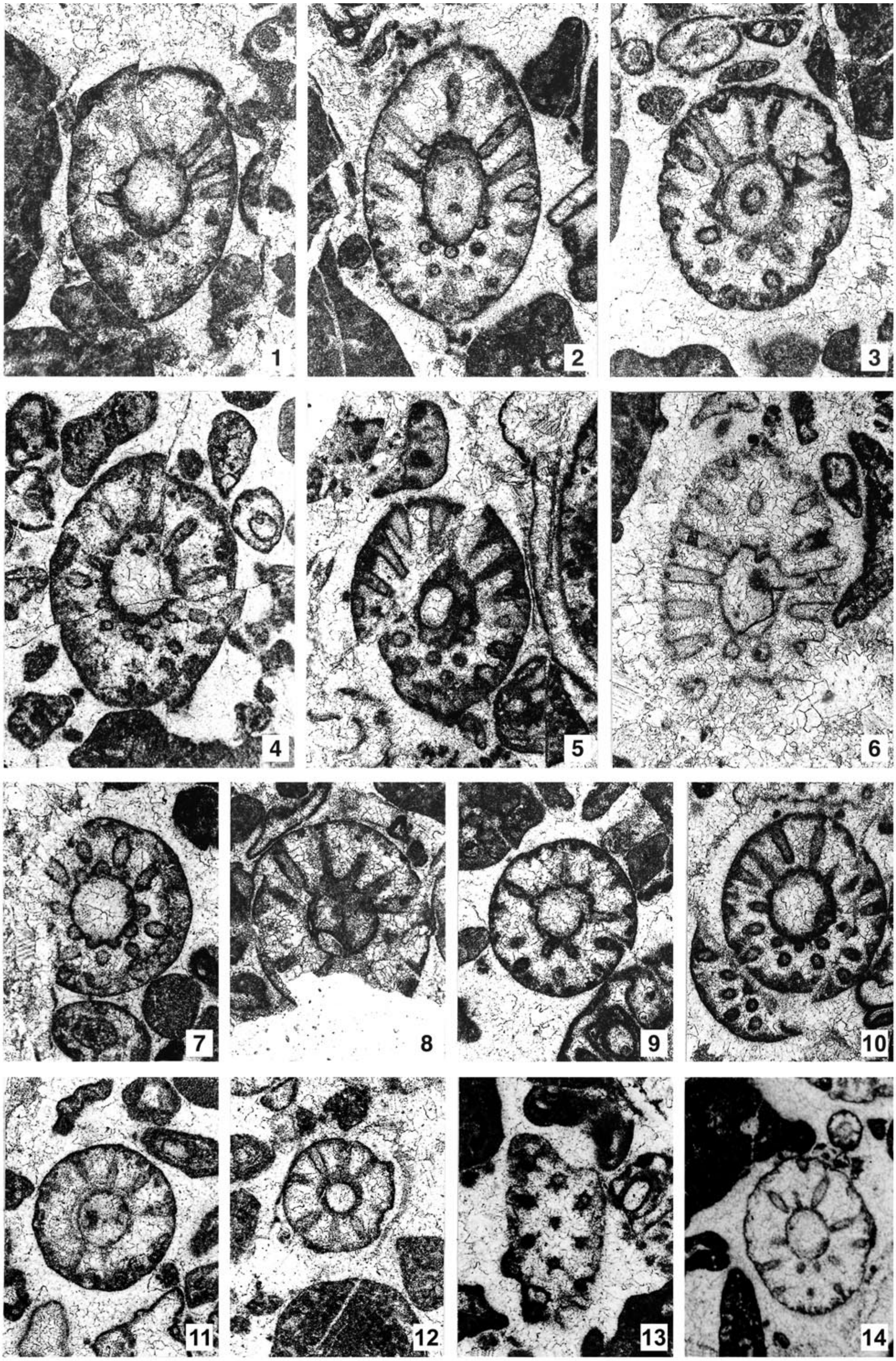
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PLATE VIII

1–10 *Neomeris cretacea* STEINMANN

1 Longitudinal section; fertile ampoules might be recognised at the lower right part of the thalus; GD 22/1, x22.

2, 4 Oblique sections; no fertile ampoules visible; Fig. 2, GD–23/5, x22; Fig. 4, GD–23/1, x17.

3 Oblique section; separate fertile ampoules are visible; GD–23/8, x22.

5–6 Oblique sections; specimens with well developed fertile ampoules; Fig. 5, GD–23/25, x 17; Fig. 6, GD–23/28, x22.

7 Transverse section; no fertile ampoules visible; there are indications of third-order branches on some sterile branches; GD–23/23, x34.

8 Oblique section; no fertile ampoules visible; GD–23/14, x22.

9–10 Transverse sections; no fertile ampoules visible; very thin secondary branches; Fig. 9, GD–23/9; Fig. 10, GD–23/8; x22.

Near Grabrk village, Lower Aptian.

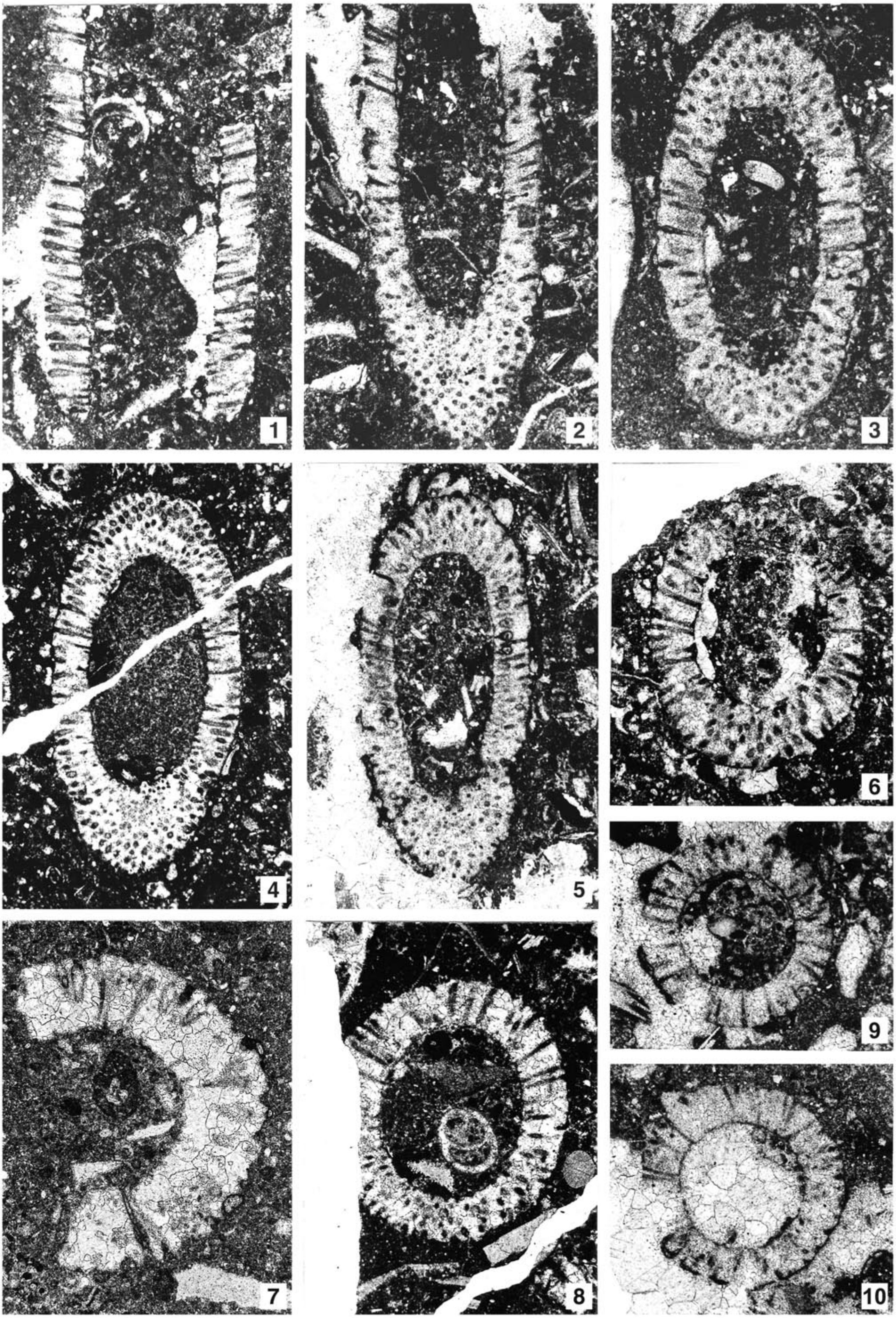
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PLATE IX

1–10 *Neomeris cretacea* STEINMANN

1 Longitudinal section; fertile ampoules are clearly visible in the thalus walls; B–127/4, x17.

2–3 Oblique sections; fertile ampoules are visible; Fig. 2, B–127/7; Fig. 3, B–127/5; x17.

4–5 Oblique sections; fertile ampoules are visible in some parts of the calcareous thallus; Fig. 4, GD–23/19, x 14; Fig. 5, GD–23/20, x17.

6 Tangential section; arrangement of the pairs of sterile branches are visible; indication of the third-order branches on the top of the figure; GD–23/33, x34.

7–8 Oblique sections; specimens with thin sterile branches and poorly visible fertile ampoules; Fig. 7, GD–23/15, x17; Fig. 8, GD–23/13, x22.

9 Transverse, slightly oblique section; fertile ampoules are clearly visible; B–127/6, x22.

10 Transverse section; the phloiophorous shape of the sterile branches is clearly visible; B–127/1, x22.

Sample B–127: central Mt. Biokovo near Saranč, boundary level Barremian–Lower Aptian.
Samples GD–22, 23: near Grabrk village, Lower Aptian.

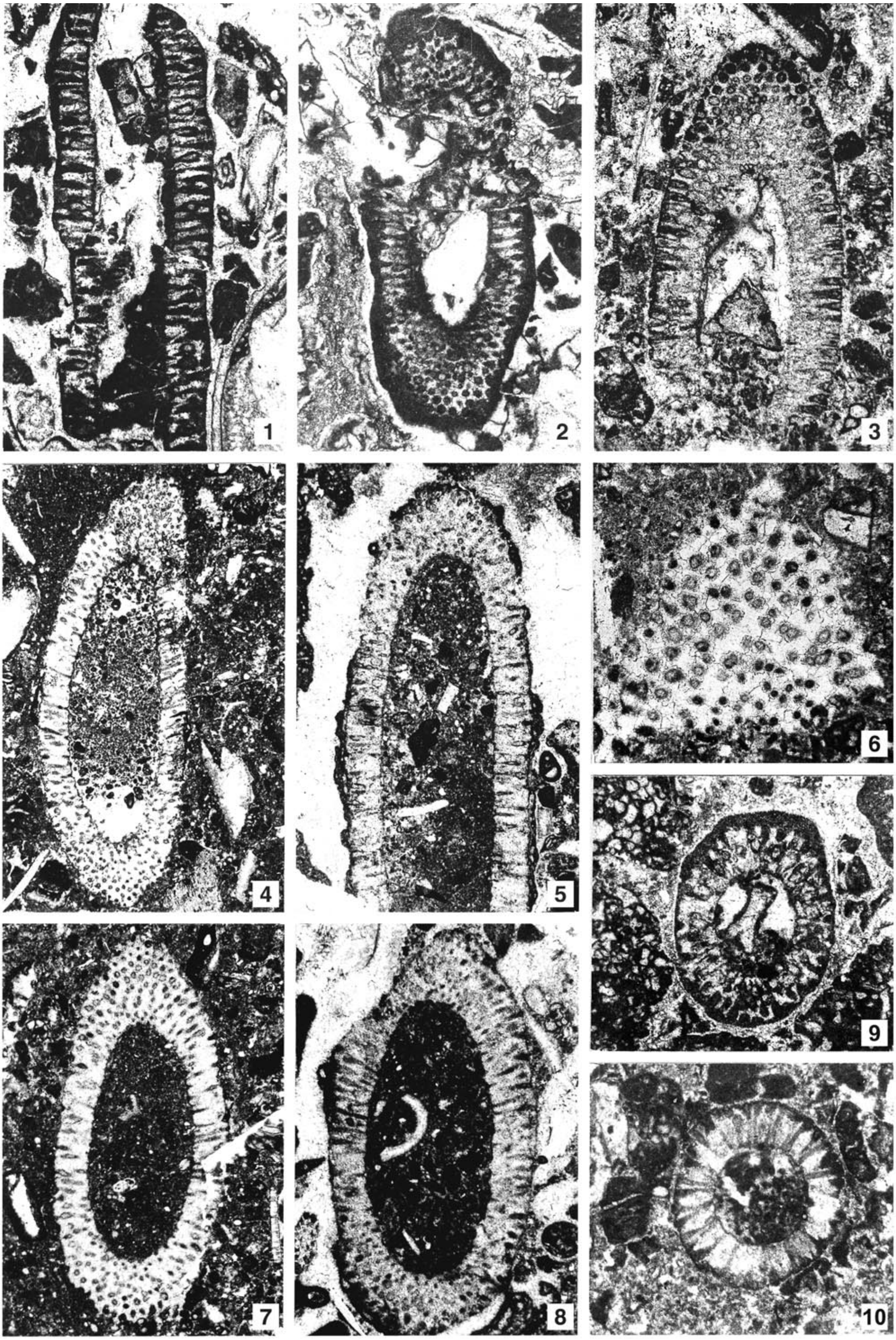

PLATE X

1–7 *Korkyrella texana* (JOHNSON)

1 Deeper tangential section; see alternating arrangement of the sporangia and sterile branches in the neighbouring whorls; GD–24A, x17.

2 Shallow tangential section; note large pores of secondary branches in cross-shaped arrangement (“Andrews cross”); their alternating arrangement is visible in the lower part of the figure; GD–23, x17.

3 Longitudinal–tangential section; alternating arrangement of sterile branches is visible in the tangential part of the section (lower part of the figure), as well as alternating cross-shaped arrangement of secondary branches; GD–24B/1; x17.

4 Oblique section; cross-shaped arrangement of secondary branches is visible at the top and at the bottom of the figure; GD–23/2x14.

5 Longitudinal section; see transition between the “head” and the “stalk” in the lower part of the figure; KJ–18/1, x17.

6–7 Oblique sections; Fig. 6, GD–23/2, x34; Fig. 7, KJ–18/104, x17.

Samples GD–23, 24A–B: near Grabrk village, Lower Aptian.
Sample KJ–18: Mt. Biokovo, Upper Barremian.

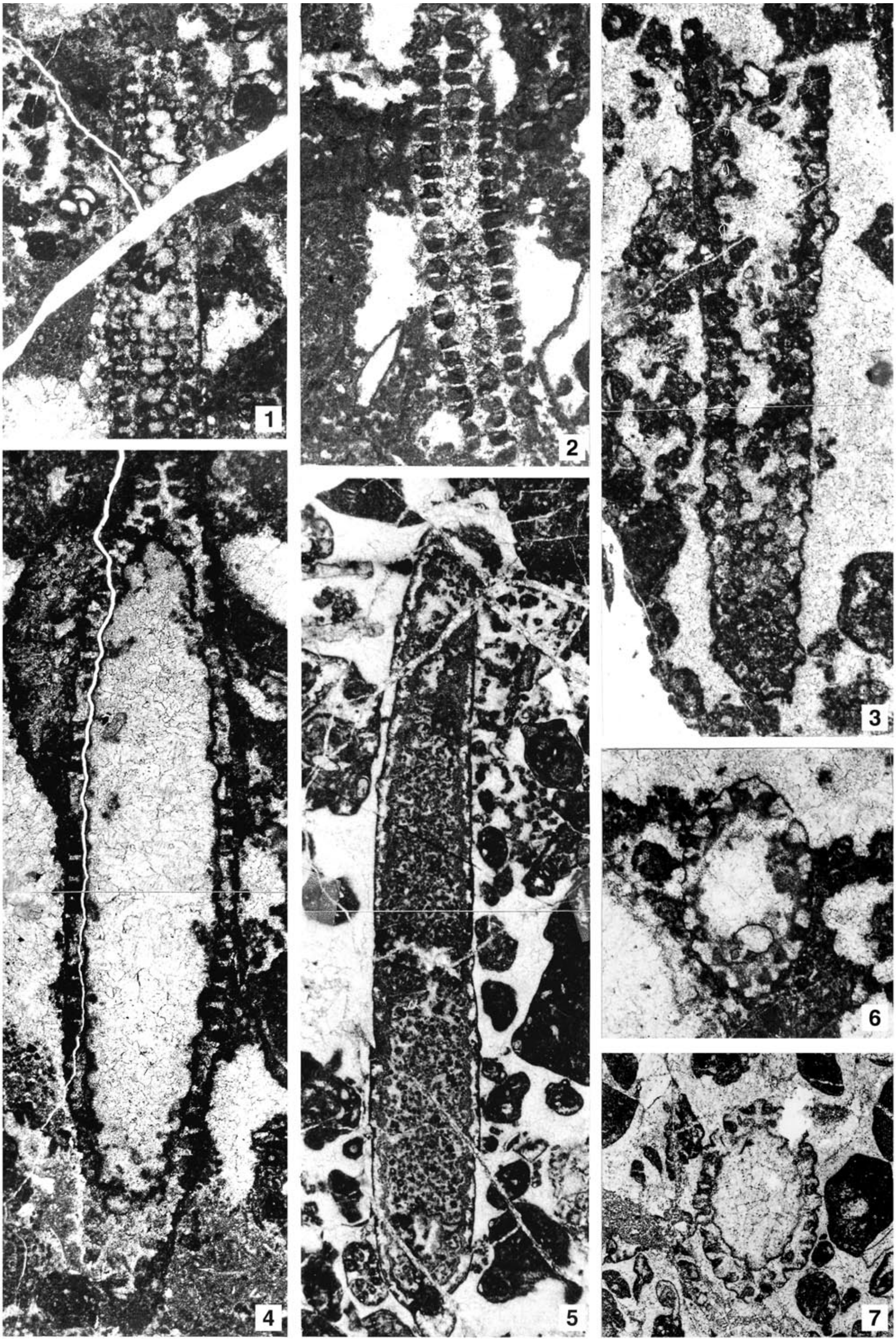
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PLATE XI

1–7 *Korkyrella texana* (JOHNSON)

1 Tangential section; see the alternation of sterile and fertile branches in the whorl, as well as their alternating position in the neighbouring whorls; note also the alternating position of the cross-shaped arrangement of the secondary branches in the outer tangential part of the section (lower part of the figure); and the rhombic shape of the distal end of sterile branches at the top and at the bottom of the figure; GD–24B/2, x22.

2 Oblique section; GD–23, x22.

3 Oblique section passing to the tangential section; KJ–18/56, x22.

4 Outer tangential section; note the alternation of sterile and cross-shaped arranged secondary branches in the neighbouring whorls; also poorly visible partial overlapping of some secondary branches at the top of the figure; GD–24B/2, x22.

5 Tangential section; SAL–372, x22.

6 Oblique section; note the transition between the “head” and the “stalk” in the lower part of the figure SAL–372/25, x22.

7 Tangential section passing to the longitudinal section; clearly visible arrangement of sterile and secondary branches in the central part of the figure, as well as their alternating position in the neighbouring whorls; GD–24B/1, x22.

Samples GD–23, 24B: near Grabrk village, Lower Aptian.
Sample SAL–372: near Salakovac village, north from Mostar (Bosnia and Herzegovina), Upper Barremian.

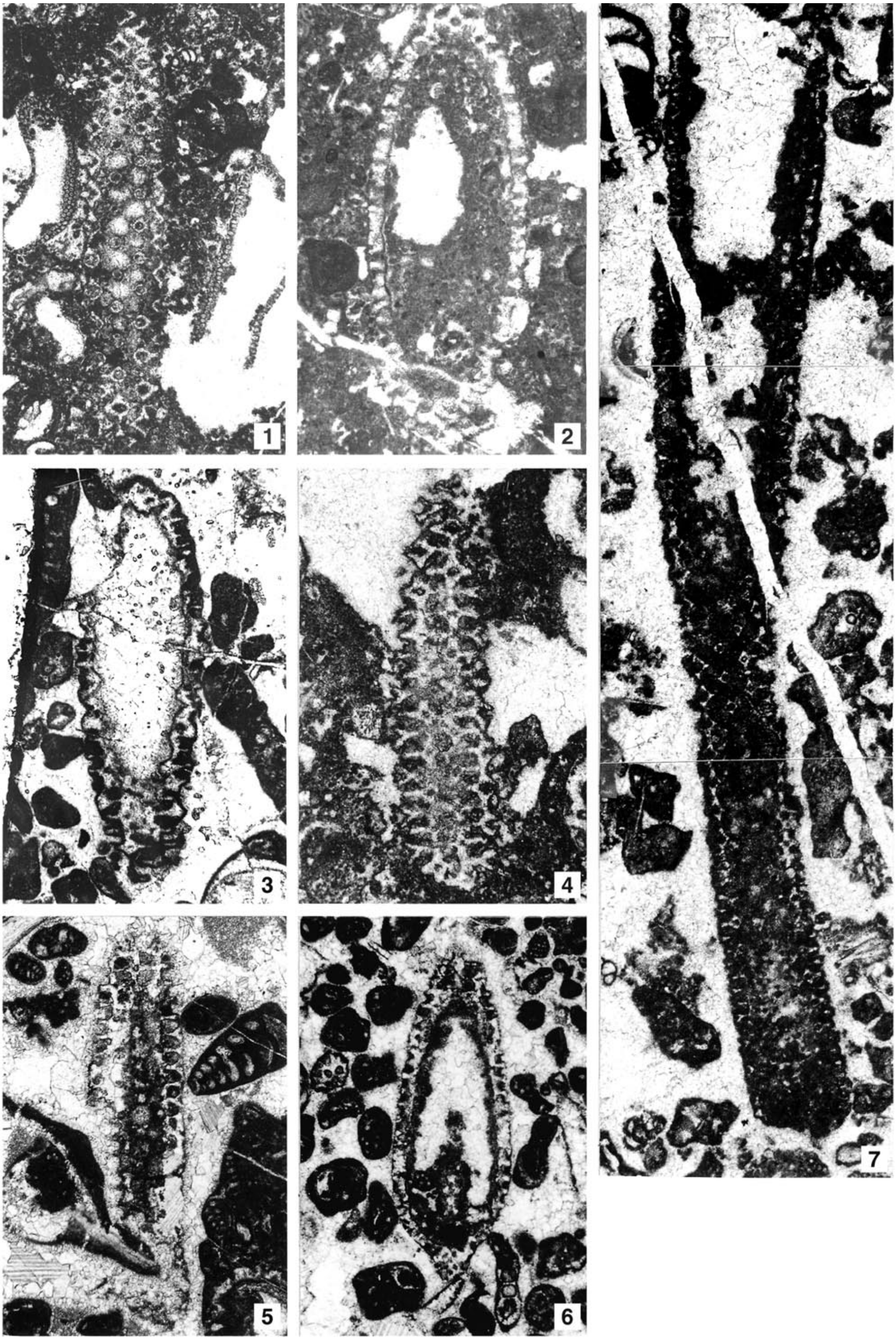
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PLATE XII

1–7 *Korkyrella texana* (JOHNSON)

1 Oblique section; KJ–18/201, x22.

2 Oblique section; see the transition between the “head” and the “stalk” in the lower part of the figure SAL–372/2, x 17.

3 Various sections; GD–24A, x14.

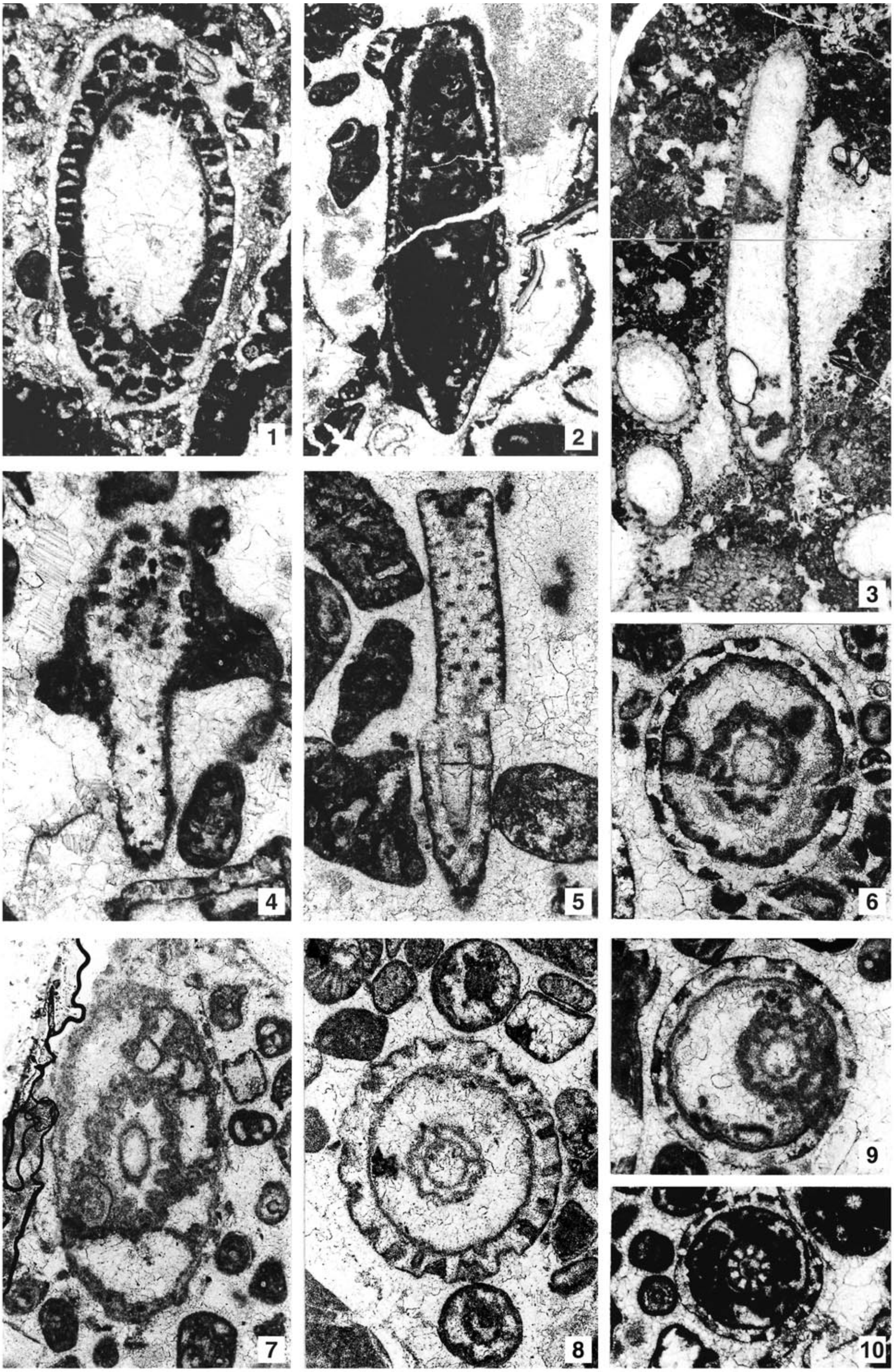
4 Tangential section; clearly visible transition between the “head” and the “stalk”; in the upper part (head) sterile and secondary branches are visible; in the lower part (stalk) only sterile branches are visible; SAL–372/2, x 34.

5 Oblique and tangential section of the stalk (= *Acroporella nisovensis* BAKALOVA); only sterile branches are visible; KJ–18/1, x34.

6, 8–10 Transverse sections; inner and outer calcareous “envelopes” are separated due the absence of calcification in the middle part of the thalus; note pores of fertile and sterile branches in the inner envelopes; Fig. 6, SAL–372/25, x34; Fig. 8, KJ–18/116, x34; Fig. 9, SAL–372/2, x34; Fig. 10, SAL–372/2, x22.

7 Oblique section; SAL–372/16, x34.

Sample KJ–18: Mt. Biokovo, Upper Barremian
Samples GD–24: near Grabrk village, Lower Aptian.
Sample SAL–372: near Salakovac village, north from Mostar (Bosnia and Herzegovina), Upper Barremian.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