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Dasycladalean alga *Furcoporella diplopora* Pia (1918) from the type-locality (upper Paleocene–Eocene, Radstadt, Austria): new remarks and taxonomic implications

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Abstract: The dasycladalean green alga *Furcoporella diplopora* Pia (1918) exhibits a peculiar structure comprising pairs of diverging and rather indistinct pores. Because of such structure, the genus *Furcoporella* has been a matter of debate. Currently, there is still no agreement on its taxonomic position within Dasycladales. This paper provides a re-description of the type-species *F. diplopora* Pia (1918), based on Pia’s type material from the upper Paleocene to Eocene reworked carbonates of Radstadt/Pongau, Austria. New observations carried out on this material allowed the acquisition of additional and more complete data on this quite neglected alga. Some morphological characteristics of the thallus, specifically of the laterals are discussed and a suite of potential taxonomic implications are evaluated. Finally, according to interpretations the genus *Furcoporella* is ascribed to the Family Triploporellaceae and more specifically it should be placed within the tribe Thyrsoporelleae.

Keywords: micropaleontology, taxonomy, green algae, Dasycladales, *Furcoporella.*

Introduction

The dasycladalean alga *Furcoporella diplopora* was introduced by Pia (in Trauth 1918), investigating the Paleocene to middle Eocene detrital limestones, exposed near Radstadt/Pongau, in Austria. Describing the species, the same author erected the genus *Furcoporella*. Currently it is still considered to be a poorly known genus (Deloffre & Génot 1982), despite its reported occurrences in many Paleocene–Eocene Tethysian shallow-water limestones. Besides the type-locality, *F. diplopora* specimens have been found in the Middle East (Elliot 1956, 1968), Libya, Egypt (Pfender & Massieux 1966; Kuss & Leppig 1989), China (Yu Jing 1976) and Anatolia (Radoičić & Özgen-Erdem 2011).

Presumably, the incomplete understanding of this taxon is a consequence of the problematic structure exhibited by *F. diplopora* that displays few pairs of diverging pores arranged in whorls around the central stem cavity.

Discussions on this dasycladalean alga started, indeed, with Pia’s original generic and specific descriptions (in Trauth 1918): these were hypothetical (see *Paleontological description*) and Pia clarified the necessity of further modifications, admitting that his generic diagnosis was only temporary. Additionally, although Pia figured two sections of *F. diplopora* (pl. 1. fig. 1–2), he did not designate a holotype.

A notable number of descriptions have followed the original study, coupled with attempts to unravel the taxonomic relationships of the genus *Furcoporella* with other dasycladalean algae (Pia, in Hirmer 1927; Pfender 1940; Elliott 1968; Bassoullet et al. 1979; Deloffre & Génot 1982, Deloffre 1988; Deloffre & Granier 1992). Consequently, this genus is central to much debate, since there is no agreement on the tribe in which it should be placed.

It is also worth mentioning that *Furcoporella,* which corresponded formerly to a monospecific genus, encloses the species *Furcoporella vasilijesimici* (Radoičić, 2005) described from the lower Valanginian detrital limestones of the Metohija Unit (Mirdita Zone, Kosovo).

Considering that the taxonomic placement of *F. diplopora* remains unresolved, this taxon deserves to be the subject of a more in-depth paleontological study. This paper provides a formalized and detailed re-description of this species, made on the basis of Pia’s type material.

Geological setting

The type-locality is situated near Radstadt (see Trauth 1918) in the Enns Valley area (47°22’48.3” N, 13°26’01.0” E), adjacent to the Tauern tectonic Window and the Northern Calcareous Alps. The whole area belongs to the Eastern Alps realm. Here, the Northern Calcareous Alps constitute part of the Austro-Alpine nappe complex and represent its most prominent tectonic unit. The Eastern Alps stacked nappes consist of sedimentary deposits of Late Permian to Eocene age and the entire succession is strongly dominated by Triassic carbonates (e.g., Wagreich & Faupl 1994; Mandl 2000).

The Valley of the Enns river is filled by Oligocene to Quaternary deposits (see Keil & Neubauer 2011 for a review). It corresponds to a WE-striking fault-controlled valley developed after Neogene time (Keil & Neubauer 2009). Since that period, the Eastern Alps have been affected by strike-slip movements, parallel to the Alpine orogen, accommodating lateral extrusion tectonics (Ratschbacher et al. 1991). Such strike-slip scheme produced fault-induced lowlands and intramontane basins (Dunkl et al. 2005) and modified the drainage pattern setting the stage for the modern river system (Frisch et al. 1998).

Near Radstadt, exposed fluvial conglomerates contain reworked shallow-water carbonate sediments (e.g., Trauth 1918). Reworked calcareous clasts comprise: i) platform-derived limestone components (with corals, foraminifera and calcareous algae); ii) other carbonate debris with nummulitids (Trauth 1918; Moussavian 1984). Such reworked carbonates also host *Furcoporella diplopora* specimens, and have been interpreted as late Paleocene/early Eocene in age (J. Pignatti 2018, personal communication).

In the Eastern Alps, Early Paleogene shallow-water carbonates are exposed only as small-scale outcrops or as reworked clasts and boulders within younger poorly-dated conglomerates (Nebelsick et al. 2005), as in the case of Radstadt/Pongau. These localized occurrences likely correspond to the remnants of a former shallow-water shelf environment, developed since the Middle Paleocene time on the southern edge of the Northern Calcareous Alps (e.g., Moussavian 1984; Nebelsick et al. 2005). Such limestone beds were indeed repeatedly exposed since the late Paleocene to the Eocene (Kázmér et al. 2003) and subsequently subject to block segmentation and fluvial erosion during Oligocene and Miocene times (Moussavian 1984).

Material

Furcoporella diplopora specimens in Fig. 1 represent Pia' s type material (in Trauth 1918). Such material consists of two thin sections labelled CLXXII.1 and CLXXII.2., belonging to the 'Pia Collection', stored at the Natural History Museum of Vienna. One of the authors (F. Barattolo) took the photomicrographs in 1993, during the meeting 'Alpine Algae', examining Pia's original material.

Repository and institutional abbreviation: types examined in this study are deposited in the Natural History Museum of Vienna, Department of Geology & Paleontology (NHMV-DGP), Pia collection, slides labelled CLXXII.1 and CLXXII.2.

Paleontological description

Order Dasycladales Pascher, 1931
Family Triploporellaceae (Pia, 1920) Berger & Kaever 1992
Tribe Thyrsoporelleae Pia 1927
Genus *Furcoporella* Pia in Trauth 1918
Type-species *Furcoporella diplopora* Pia in Trauth 1918

Introducing the species *F. diplopora*, Pia erected the genus *Furcoporella* (Pia in Trauth 1918). The original generic description is reported hereafter (English translation by Deloffre & Génot 1982):

"General cylindrical shape. The pores are widened towards the exterior. At the level of the verticils, they are joined 2 by 2 at the base and are few in number. Unsegmented skeleton. This definition must be considered as temporary, for it seems likely that it will have to be modified as forms related to our Eocene species will be discovered."

The same author then provided the following short description for the type-species (from Deloffre & Génot 1982):

"The thallus seems to be always straight. The calcification does not reach the axial cell."

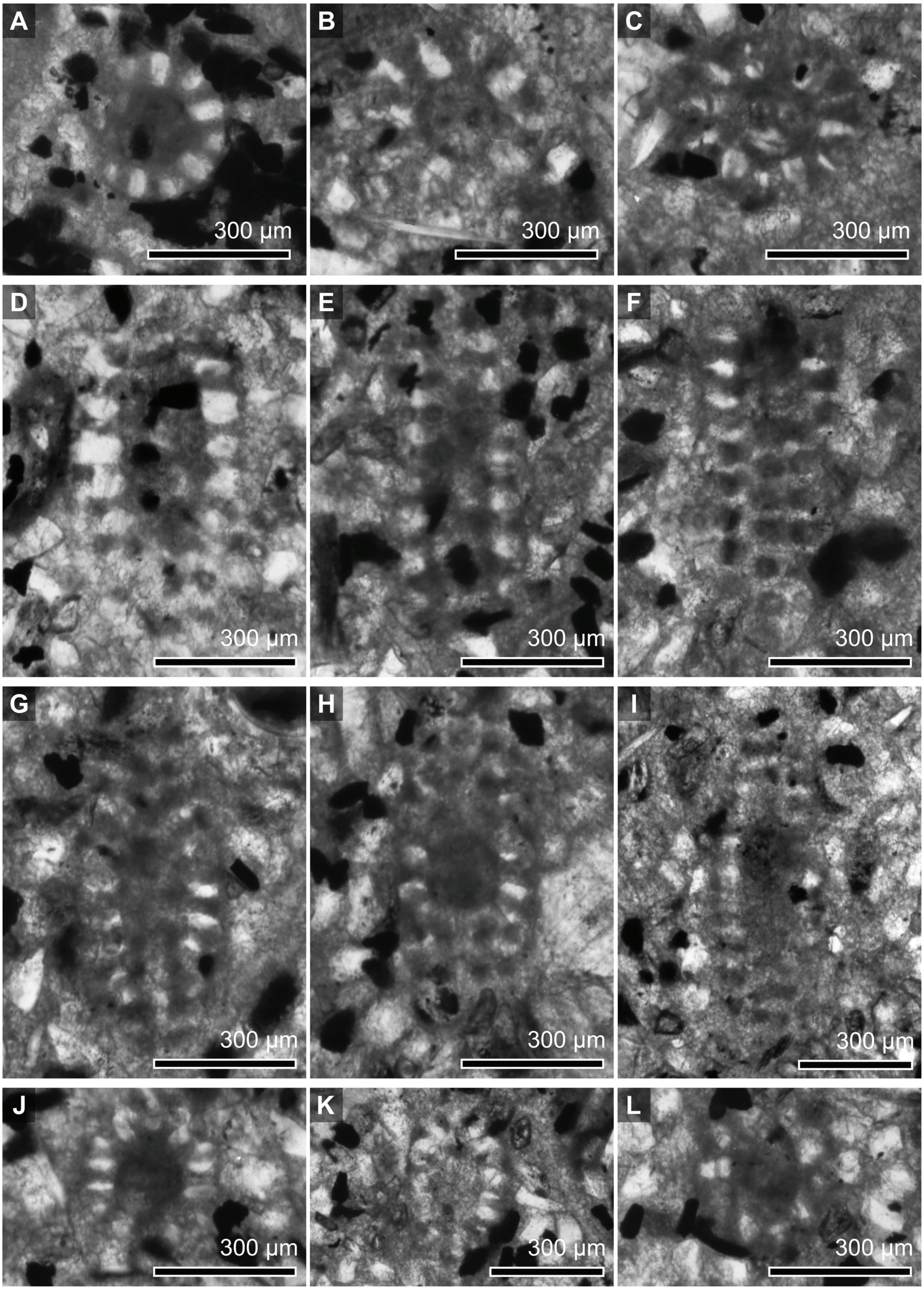
Elliott (1968) added further observations both on the genus and on the type-species after the study of larger Middle East specimens. In his revision, the author described the ramified pores, observable in transversal sections, as short primary laterals subsequently dividing into two divergent secondaries.

Deloffre & Génot (1982) supplied the following comment/remarks for the genus *Furcoporella* and the type-species:

"Furcoporella is still a little-known genus, relatively and rarely quoted. It is a hollow cylindrical calcareous tube with numerous regular horizontally-set verticils with a very short primary canal divided into two divergent secondary branches. This genus is found between the Paleocene and the Lutetian of Europe, Middle East and China"

"Furcoporella diplopora — Cylindrical dasyclad tube with numerous horizontally-set verticils. Each verticil shows a single very short and large primary branch divided almost at once into two divergent secondaries widening to the exterior […]"

Fig. 1. *Furcoporella diplopora* Pia (1918), upper Paleocene–lower Eocene of Radstadt/Pongau (Enns Valley, Austria). **A** – **Lectotype**; transversal section. It corresponds to the specimen figured by Pia (in Trauth 1918, pl. 1, fig. 2). Notice the evident and wide diverging pores, NHMV-DGP Pia CLXXII.1. **B** – Transversal sections, NHMV-DGP Pia CLXXII.1. **C** – Transversal slightly oblique section, NHMV-DGP Pia CLXXII.1. **D** – Oblique section. Notice the vertical section of the pores and the quite indistinct inner surface of the calcification, NHMV-DGP Pia CLXXII.1. **E** – Longitudinal section of a specimen showing the vertical section of the pores. Notice their overall hourglass shape resulting from the cut of the swollen secondary laterals (the section does not cut axially the primary laterals), NHMV-DGP Pia CLXXII.1. **F** – Oblique section showing ordered doubled pores resulting from the divergent secondary lateral. Notice that they are arranged in continuity in simple subsequent whorls, NHMV-DGP Pia CLXXII.2. **G** – Oblique section, NHMV-DGP Pia CLXXII.2. **H** – Oblique section, NHMV-DGP Pia CLXXII.2. **I** – Oblique section, NHMV-DGP Pia CLXXII.2. **J** – Slightly oblique transversal section. The section transversally cuts two subsequent whorls, NHMV-DGP Pia CLXXII.1. **K** – Oblique-transversal section, NHMV-DGP Pia CLXXII.2. **L** – Oblique-transversal section, NHMV-DGP Pia CLXXII.2.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Description in this study of *F. diplopora* expands Pia's first description and includes the observations added by Elliott (1968), interpreting diverging pores as first and second order laterals. Furthermore, it supplies additional data to the remarks provided by Deloffre & Génot (1982).

Furcoporella diplopora PIA (in Trauth) 1918
Fig. 1A–L

1918 *Furcoporella diplopora* n. gen., n. sp. – PIA, plate 1, fig. 1, 2, text-fig. 4b.
1927 *Furcoporella diplopora* – PIA, p.86.
1940 *Furcoporella diplopora* – PFENDER, p. 242–243.
1956 *Furcoporella diplopora* – ELLIOT, plate 2, fig. 5–6.
1966 *Furcoporella diplopora* – PFENDER & MASSIEUX, text-fig. 4, plate 4, fig. 8–9.
1968 *Furcoporella diplopora* – ELLIOT, plate 11, fig. 7–9.
1976 *Furcoporella diplopora* – YU-JING, plate 9, fig. 7–8.
1982 *Furcoporella diplopora* – DELOFFRE & GÉNOT, plate 8, fig. 2–4.
1989 *Furcoporella diplopora* – KUSS & LEPPIG, fig. 9, g–h; fig. 10a.
2011 *Furcoporella diplopora* – RADOIČIĆ & ÖZGEN-ERDEM, fig. 11, f–i.

Lectotype

Pia (1918) did not designate a holotype for *F. diplopora*. Among photomicrographs, one of the original specimens figured by Pia (in Trauth 1918, pl. 1, fig. 2) is reported and selected as the lectotype. It corresponds to the transversal section A of Figure 1 (NHMV-DGP Pia CLXXII.1).

Description

The investigated dasycladalean alga is characterized by a simple, cylindrical, non-segmented thallus with a relatively large central stem. Large diverging pores are interpreted as results of a short primary lateral splitting horizontally into two divergent second-order laterals, swollen outwards (phloiophorous). Laterals are arranged in a closely packed configuration and are set in continuity in subsequent whorls (euspondyl). Whorls are set orthogonally to the stem axis since both the short, thick primary laterals and the secondary ones are generally horizontal. The latter flare out distally to make a quadrangular cortex. Reproduction is supposed syringosporate, less probably endosporate.

Remarks

General features of the calcareous skeleton

The calcification corresponds to a simple massive calcareous sleeve. It preferentially envelops the laterals up to their distally widened ends, approaching the cortical zone. The central cavity is filled either by micritic matrix or blocky sparite. The pores, remnants of the former laterals, are commonly filled by matrix. Pores are connected to the central cavity by relatively wide openings (Fig. 1C,D) and the inner surface of the skeleton does not display sharp edges (Fig. 1C,E,I). This suggests that the innermost part of the calcification was not directly in contact with the central stem outer wall. Therefore, the actual central cavity diameter is slightly larger than the former axial stem diameter. Such a characteristic is presumably a primary, morphological feature (i.e., calcification does not envelop laterals base).

Diverging laterals

Transversal sections of the calcareous skeleton (Fig. 1A–C) offer the opportunity to clearly observe the pores splitting into two divergent canals. In geometrical terms and in the case of an even number of laterals, if the axial section of the skeleton cuts the primary laterals axially, it will not cut the divergent secondaries at the same time. The longitudinal and oblique sections (Fig. 1D,F), however, display elongated pores with an overall hourglass shape. The hourglass-shaped pores result from a cut passing longitudinally along the primary pore and just one of the two divergent secondary laterals. Such elongated hourglass shape of the pores may be also produced by the relative high thickness of the thin sections.

The number of primary laterals per whorl can be simply obtained from transversal sections (Fig. 1A–C). It corresponds to 5–6, a number markedly lower than that observed by Radoičić & Özgen-Erdem (2011, fig. 11g), i.e., 10–12.

According to the geometry observed in the oblique sections of the calcareous skeleton (Fig. 1F,H), the phloiophorous secondary laterals are arranged horizontally, appearing elongated and relatively thick at the same time. Their angle of divergence has been obtained from the transversal sections and corresponds to 43° (average value, see Table 1 for other main biometrical parameters). At the far end, each secondary lateral flares out and comes in touch with the others alongside, making a cortex.

Since the calcification does not envelop the central stem and the most proximal part of the laterals, the morphology of their junction with the stem is still debated. Additionally, there is no trace of narrowing between the large inner pore and the diverging ones.

Reproduction

No evidence of reproductive organs has been observed within the calcareous skeleton, neither within the central cavity nor in the primary laterals. There is also no trace of reproductive structures such as ampullae. According to the current state of knowledge, the reproduction type of *F. diplopora* remains unknown.

Reconstruction in this study (see *Conclusions*) proposes large openings connecting both the laterals and with the central stem. This kind of large connection is here considered to be a primary, morphological characteristic. Presumably, these wide portions hosted gametophores (cysts), thus, the reproduction type is herein supposed syringosporate (Granier 2010;

Table 1: Main biometrical parameters of *Furcoporella diplopora* Pia. All size parameters are given in µm, with the exception of *α*, given in degrees. **d** — inner diameter of the central cavity; **D** — outer diameter of the calcareous skeleton; **w** — number of primary laterals per whorl; **h** — height between subsequent whorls; **p** — width of primary laterals; **p'** — width of secondary laterals (measured at the base); ***α*** — average angle of divergence of the secondary laterals.

Specimen	Thin Section	d	D	w	h	p	p'	*α* (°)	d/D
a	CLXXII.1	175.3	317.6	6		69.2	35.1	43	0.55
b	CLXXII.1	174.7	383.7	5		81.6	44.3	43	0.46
c	CLXXII.1	195.2	370.5	*6*		68.9	33.8	38	0.53
d	CLXXII.1	186.9	350.6						0.53
e	CLXXII.1	138.9	254.7		86.7				0.55
f	CLXXII.2	152.2	258.1	5	68.3				0.59
g	CLXXII.2	167.1	284.5		68.2				0.59
h	CLXXII.2	161.3	287.8	*6*	88.4				0.56
i	CLXXII.2	173.2	285.9		78.7				0.61
j	CLXXII.1	147.6	274.6	6		60.9	31.8	46	0.54
k	CLXXII.2	147.5	256.4						0.58
l	CLXXII.2	154.8	291.1			67.0	34.9		0.53
Min		138.9	254.7	5	68.2	60.9	31.8	38	0.46
Max		195.2	383.7	6	88.4	81.6	44.3	46	0.61
N. of measures		12	12	8	5	5	5	4	12
Average		164.6	301.3	6	78.1	69.5	36.0	43	0.55
St. deviation		17.14359	44.56555	0.51640	9.66737	7.52627	4.81697	3.31662	0.03947

Mathieu et al. 2011; Granier & Bucur in Granier et al. 2013) (see *Interpretation of the diverging pores and attribution to higher rank*).

Interpretation of the diverging pores and attribution to higher rank

Studies of fossil dasycladalean algae are frequently met by problems connected to the calcification. Since the calcification degree is indeed strongly variable, it produces highly different kinds of skeleton (e.g., extensive, scattered or largely absent calcification). The structure of fossil dasycladaleans must be interpreted principally on the basis of the pores left by calcified parts. Consequently, the development of algal reconstructions may be hard and challenging in the case of scattered or even largely absent calcification.

In the specific case of *Furcoporella*, though it exhibits an evident calcareous skeleton, the calcification of the divergent pores remains indistinct. Indeed, the absence of clear narrowing at the pore junctions opens the field to ample speculation regarding the order of the laterals (i.e., first+second-order laterals vs. first-order only). A suite of junction combinations and potential arrangements of the laterals is reported in Fig. 2. The first two solutions (Fig. 2A, B) show two orders of laterals and consequently an euspondyl arrangement. Both are geometrically consistent with the thin section observations. The only difference between these first two solutions lies in the width of the connections. The other solutions (Fig. 2C, D) are instead representative of a metaspondyl arrangement. In solution C, two first-order laterals are directly connected to the stem axis, while the last solution (Fig. 2D) is characterized by a vestibule supporting the tuft of laterals. Among the reported morphologies, however, the euspondyl arrangement is considered to be the most probable configuration. It is worth mentioning that each of the four alternative solutions provided in Fig. 2 may fit well the geometry of the pores of *Furcoporella*. Of course, the choice of one among the four-reported hypotheses leads to relevant taxonomic consequences. According to the features observed in thin section, the "channelled primary lateral" option (Fig. 2A) is selected as the most probable one, since it requires fewer assumptions.

A metaspondyl arrangement (with or without a vestibule) would cause the shifting of the genus *Furcoporella* to the Family Diploporaceae. In his first description, Pia actually pointed out the morphological affinity of *F. diplopora* with the genus *Diplopora* (in Trauth 1918): the specific name he has chosen is certainly a clear reference to this similarity. Anyway, the elements and the geometries figured in Fig. 2C, D are typical of Upper Paleozoic and Triassic genera. Given the remarkable time gap between these older genera and the Eocene age of *F. diplopora*, it is considered these two solutions less probable than the first two. Because of the euspondyl configuration, the genus *Furcoporella* should be placed in the Family Triploporellaceae: this attribution is indeed in agreement with the one already proposed by Radoičić (2005). The same author (Radoičić 2005) and Radoičić & Özgen-Erdem (2011) assigned *Furcoporella diplopora* to the tribe Salpingoporellae, which includes verticillated genera sharing the occurrence of only primary laterals. Here, the occurrence of two orders of laterals prompts us to exclude such attribution.

Lastly, excluding the assignment of the genus to the subtribe Macroporellinae initially proposed by Pfender (1940): actually, this subtribe formerly included both euspondyl and aspondyl forms (Pia 1927), but now is restricted to grouping only some aspondyl genera (Deloffre 1988).

Among the Triploporellaceae, *Furcoporella diplopora* shows a remarkable resemblance to some other Paleocene–Eocene species belonging to the tribes Dissocladelleae and Thyrsoporelleae. The occurrence of two orders of strong laterals allows comparison of *Furcoporella* with *Dissocladella*. The latter genus shows indeed a short, globose primary lateral and phloiophorous secondaries similar to those of *Furcoporella*, but in the case of *Dissocladella* the primary lateral is attached to the central stem through a small pore and the number of secondary laterals is always more than two.

Differently, the short and strong primary lateral of *Furcoporella* exhibits a wide opening with the central cavity. Such a wide junction closely resembles that of *Thyrsoporella* and *Belzungia*. However, these two genera can still be differentiated since they display four to five orders of laterals fining outwards (e.g., Radoičić & Özgen-Erdem 2011).

It is suggested that the genus *Furcoporella* seems to be strictly related to the genus *Anatolia* Radoičić & Özgen-Erdem 2011. According to the authors (p. 231), in *Anatolia* "*the thallus consists of cylindrical articles with rather spaced whorls. The whorl consists of three orders of horizontal to sub-horizontal laterals arranged in vertical rows. The primary laterals divide into two divergent, strong and stocky secondaries. Each secondary lateral gives rise to 4–5 slender tertiaries, distally enlarged. Reproductive organs are unknown.*" Apart from the shape of the thallus (presumably not articulated vs. articulated), the two genera share similar features of the primary and secondary laterals. The only remarkable difference consists of the absence and presence of tertiary phloiophorous laterals respectively. In *Anatolia* the sites of reproduction were seemingly located within the primary and secondary laterals and the relatively thin phloiophorous tertiary laterals functioned as assimilators. In *Furcoporella* secondary laterals alone probably performed both reproduction and assimilation. Such hypothesis coupled with the previously listed morphological similarities lead us to assign the genus *Furcoporella* to tribe Thyrsoporelleae.

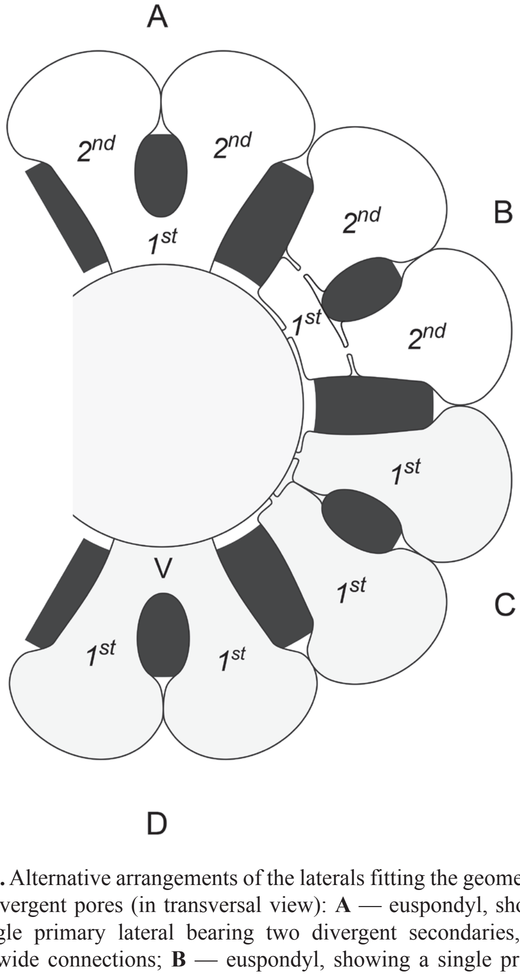

Fig. 2. Alternative arrangements of the laterals fitting the geometry of the divergent pores (in transversal view): **A** — euspondyl, showing a single primary lateral bearing two divergent secondaries, both with wide connections; **B** — euspondyl, showing a single primary lateral bearing two divergent secondaries with narrow connections; **C** — metaspondyl arrangement, showing a tuft of two primary laterals directly attached to the central cylindrical stem; **D** — metaspondyl vestibulated, showing primary lateral set in a tuft of two, sustained by a vestibule.

Concerning the issue of family level attribution, recently Granier & Bucur in Granier et al. (2013) proposed the erection of the new family Thyrsoporellaceae to include syringosporate genera. This clade is directly derived from the family Triploporellaceae that consequently becomes paraphyletic. Actually, all Dasycladales clades at family level (Berger & Kaever 1992: Granier & Bucur in Granier et al. 2013) except Seletonellaceae and Dasycladaceae, must be considered paraphyletic if not polyphyletic and need a general re-examination that takes into account DNA data from extant forms (Berger et al. 2003; Verbruggen et al. 2009). For this reason, instead of following the classification proposed by Granier & Bucur in Granier et al. (2013), we prefer the classic Berger & Kaever (1992) classification, assigning the tribe Thyrsoporelleae to the family Triploporellaceae.

Conclusions

This paper presents a detailed revision of *Furcoporella diplopora* Pia and new paleontological data on the genus *Furcoporella*. Overall, the re-description reported herein expands Pia's first description and matches the observations added by Elliott (1968) on the laterals. A comprehensive reconstruction of *Furcoporella diplopora* was provided as a result in which all the previously examined features are coherently represented (Fig. 3).

This study focused on this problematic and neglected alga, with the aim of facilitating a complete taxonomic assignment of the genus *Furcoporella* in Dasycladalean systematics. Besides simply modelling the thallus in this reconstruction, we have taken into account a suite of diverse lateral arrangements, evaluating potential taxonomic implications. Finally, according to this interpretation the genus *Furcoporella* was assigned to the Family Triploporellaceae, also suggesting that this taxon should be placed within the tribe Thyrsoporellae.

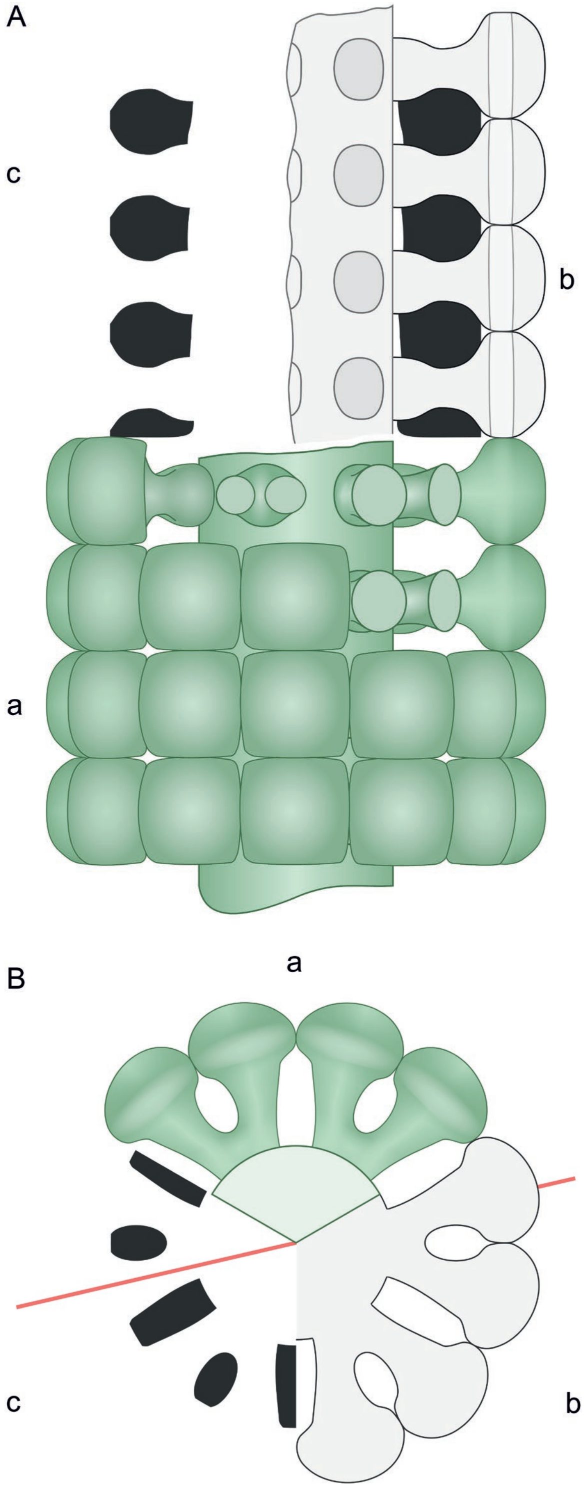

Fig. 3. *Furcoporella diplopora* Pia (1918): Reconstruction of thallus. **A** — Longitudinal (axial) view: a — perspective view of the alga, showing the cortex geometry and the splitting of the laterals; b — laterals and calcification (black-coloured); c — calcareous skeleton only (black-coloured). **B** — Transversal view: a — central stem and 3-D view of the laterals; b – former organic parts, i.e., central stem, primary and divergent secondary laterals; c — calcareous skeleton only (black-coloured) with the pores (white-coloured). Notice the trace of the axial section (A): it does not cut axially the primary laterals.

In sum, our observations confirm the presence of two orders of laterals: the wide divergent pores are interpreted as the result of short primary laterals bearing two divergent phloiophorous secondaries. These are connected to the primary lateral by large openings (Fig. 2A). Accordingly, laterals with no tapered bases were reproduced. The laterals and the subsequent cortical meshes are arranged in ordered repetitive rows. The cortical meshes, corresponding to the uncalcified outer ends or edges of secondary laterals, have been drawn as sub-rectangles set horizontally; this solution is geometrically consistent given the number of secondary laterals and the arrangement in tangential and oblique section (Fig. 1F). Additionally, according to the evidence observed in thin section (see *General features of the calcareous skeleton*), the calcification has been reproduced without directly touching the central stem wall.

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