Critical review of the Trochoidomeandridae family (Scleractinia; Cretaceous) and the genera *Felixigyra*, *Rhipidomeandra, Trochoidomeandra,* and *Wellsimeandra*

Hannes Löser

Abstract

The Early to early Late Cretaceous coral family Trochoidomeandridae is critically reviewed. Its systematic position is changed from the suborder Rhipidogyrina to the suborder Heterocoenina. A third species – *Axosmilia cylindrica* Prever, 1909 – is assigned to the type genus *Trochoidomeandra*. The positions of the other genera formerly assigned to the family are modified. *Rhipidomeandra* and its junior synonym *Wellsimeandra* are – together with *Felixigyra* – gathered in the informal *Felixigyra* group. The group is assigned to the suborder Meandrinina and considered a very early member of this suborder. Their members differ by smaller trabeculae and a different septal ornamentation from the Trochoidomeandridae family. The genus *Rhipidomeandra* is revisited and new, hitherto unknown material is presented: two species originally assigned to *Phyllastraea*, one species originally assigned to the genus *Columellogyra*, and two species in open nomenclature. Together these additions significantly expand the stratigraphical and palaeobiogeographical distribution of this genus.

Keywords: Corals, Cretaceous, taxonomy, Scleractinia.

1. Introduction

The family Trochoidomeandridae was established by Turnšek & Mihajlovič (1981) on the basis of *Trochoidomeandra* Morycowa, 1971. The family is poorly known because the type species of *Trochoidomeandra*, *T. problematica* Morycowa, 1971, is extremely rare and fine skeletal structures are almost unknown. Moreover, most material subsequently assigned to *Trochoidomeandra* does not belong to this genus. After the creation of the family Trochoidomeandridae, three more genera (*Bogdanovicoenia* Kumicheva, 2002, *Rhipidomeandra* Morycowa & Masse, 1998, *Wellsimeandra* Idakieva & Cheshmedzhieva, 2003) were assigned to it, probably because they simply did not fit in any other family. The critical revision of the type genus *Trochoidomeandra* both modifies the systematic position of the family and indicates that all previously assigned genera need to be separated from the Trochoidomeandridae.

Abbreviations

BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany
IGM	Instituto de Geología, Mexico City, Mexico
MB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
PU	Università degli Studi di Torino, Dipartimento di Scienze della Terra, Italy
TUM	The Tohoku University Museum, Sendai, Japan
crd	distance of calicular rows (mm)
crl	length of calicular rows (mm)
crw	width of calicular rows (mm)
s	number of septa
sd	density of septa
si	number of septa in isolated calices
n	number of measurements
min–max	range (mm)
μ	arithmetic mean (mm)
σ	standard deviation (mm)
cv	coefficient of variation according to K. Pearson (%)
μ ± σ	first interval (mm).

The abbreviations used in the synonymy lists follow Matthews (1973):

*	earliest valid publication of the specific name
p	only part of the specimen belongs to the species
v	specimen was observed by the author

Acknowledgements

I am grateful to Dieter Korn (Berlin), Elzbieta Morycowa (Kraków), Daniele Ormezzano (Torino), and Winfried Werner (München) who allowed me to examine material from their museum and university collections. Field work in Italy was covered by project FL 42/73 of the Deutsche Forschungsgemeinschaft, field work in Spain and the examination of type material was supported by a UNAM/DGAPA PASPA (Mexico) programme. Comments by an anonymous reviewer helped to improve the manuscript. Linguistic correction by Brian Hallmark (Tucson, Arizona, USA).

2. Material and methods

The material discussed here comes from localities that are commented on and provided with additional references in Löser et al. (2005).

Germany, Bavaria, Allgäuer Helvetikum, Kürental (D.2296); Schrattenkalk, Late Barremian to Early Aptian, Sartousi – Weissi zones. Specimen BSPG 1994 XI 14.

Greece, Kozani, Nea Nikopolis (GR.2090); Early Cenomanian (BSPG 2003 XX 5818, 7443).

Greece, Viotía, Arachova (GR.976); Evangelistria Schichten, Early Aptian. Specimens BSPG 2003 XX 5578, MB K524, K 542, K544.

Italy, Abruzzi, Monti d'Ocre (without exact locality; I.171); Early Aptian. Specimen PU 18291#11.

Italy, Abruzzi, Monti d'Ocre, Fossa Mezza Spada (I.1732); Early Aptian. Specimens PU 17955, 18101, 18102.

Italy, Abruzzi, Monti d'Ocre, Fossa Agnese (I.1735); Early Aptian. Specimens BSPG 2003 XX 5297, 5301, 5401.

Italy, Abruzzi, Monti d'Ocre, Fonte Cerasetti; Early Aptian. Specimen BSPG 2003 XX 5323.

Japan, Iwate-ken, Shimohei-gun, Tanohata-mura, Koikorobe (J.3326); Miyako Gr, Tanohata Fm, Moshi sandstone, Late Aptian. Specimen TUM 56501.

Mexico, Michoacán, Turitzio, Loma de San Juan; Cumburindio Fm, Early Aptian. Specimen IGM 7008.

Spain, Cantabria, Santander, Cobreces, Luaña playa (E.2213); Altamira Fm, Early Cenomanian, Dixoni Zone. Specimen BSPG 2007 V 48.

Coral slabs and thin sections were examined using a Zeiss STEMI 2000-C stereo microscope. Microphotographs for illustration purposes were obtained using an Epson Perfection V750-M Pro transparency scanner with an optical resolution of 6400 dots per inch. Scanned images were then transferred to grey scale bit maps. Their quality was amended by histogram contrast manipulation (contrast stretching) where possible.

To gain more insight into the intraspecific variation of the corals, thin sections were systematically measured. To achieve statistical significance, the largest possible number of measurements were taken (n). For each type of measurement in one thin section the lowest and highest measured values (min-max) were obtained. Based on the values, the arithmetic mean (μ), the standard deviation (σ), the coefficient of variation according to K. Pearson (cv), and the first interval ($\mu \pm \sigma$) were calculated. Thin sections were measured and values were calculated using the Palaeontological Database System PaleoTax, module PaleoTax/Measure (http://www.paleotax.de/measure).

3. Systematic palaeontology

Order Scleractinia Bourne, 1900
Suborder Heterocoeniina Beauvais, 1974
Family Trochoidomeandridae Turnšek & Mihajlovič, 1981

Genera. – Only the type genus.

Diagnosis. – Only solitary corals known. Septa compact, thick. Symmetry of septa irregularly radial. Septa not connected to each other. Septal lateral face with long and thick ornamentation comparable to apophysal septa that are connected to each other forming a loose meshwork. No pali or paliform lobes, synapticulae, or columella. Endotheca unknown.

Remarks. – The family was originally and is currently assigned to the suborder Rhipidogyrina Roniewicz, 1976, mainly because of the assumed existence of a septothecal wall. Considering the type genus a solitary coral, it contradicts the concept of this suborder in various aspects. The type of strong septal ornamentation, as the type genus show, is unknown from the Rhipidogyrina. The first septal cycle is not disproportionally stronger as in the Rhipidogyrina (based on studies on type material of *Lobophyllia flabellum* Michelin, 1843, type species of *Rhipidogyra*). The family is therefore placed in the suborder Heterocoeniina, closely related to the family Paronastraeidae Beauvais, 1974 with *Budaia* Wells, 1933, *Hexasmilia* Fromentel, 1870, *Hexasmiliopsis* Löser, 2008, *Paronastraea* Beauvais, 1977, and *Tiarasmilia* Wells, 1932 (see Löser 2006, 2008a, b, 2010b).

Kuzmicheva (2002) created for the family a new suborder and included the genera *Bogdanovicoenia* Kuzmicheva, 2002, *Tiarasmilia*, and *Trochoidomeandra*. *Bogdanovicoenia* is here considered a junior synonym of *Preverastraea*, a presumably rhipidogyrid coral (Family Aulastraeoporidae). *Tiarasmilia* belongs to the family Paronastraeidae. Indeed both – *Preverastraea* and *Tiarasmilia* – show strongly ornamented lateral septal faces (see Löser 2007, 2010b). But in *Preverastraea* spines dominate, and in *Tiarasmilia* long apophysal septa. In *Trochoidomeandra*, the septal ornamentation shows a third mode as discussed below. The three genera are then just examples of genera with strongly ornamented septal lateral faces, and there are more genera showing such patterns. This characteristic alone is insufficient to gather genera into one group because the type of ornamentation differs from genus to genus.

Genus *Trochoidomeandra* Morycowa, 1971

Type species: *Trochoidomeandra problematica* Morycowa, 1971, by original designation.

Diagnosis. – Solitary turbinate coral. Calicular outline elliptical. Septa compact. Microstructure of septa of medium sized trabeculae. Septa in cross section externally slightly thicker, becoming slightly thinner towards the centre. Septa thick (maximum thickness 700µm in the type of the type species). Symmetry of septa irregularly radial. Cycles of septa subregular. Number of septa low (ca. 24 in the type of the type species). Septal cycles differ in length and thickness. Half of all septa extended to the calicular cen-

tre. Septa not connected to each other. Septal distal margin unknown, lateral face with long and thick apophysal septa, inner margin swollen. Pali or paliform lobes absent. Costae absent (probably due to preservation). Synapticulae absent. Columella absent. Endotheca unknown. Wall absent.

Remarks. – The genus was originally and also later (Morycowa & Masse 1998) understood as a meandrinoid coral where calicular rows are growing centrally from one point, with poorly marked calices, very irregular developed septa and a septothecal wall. Later (Turnšek & Mihajlovič, 1981) considered the genus a solitary coral with extremely ornamented septal lateral faces where the ornamentation itself is similar to septa. Comparable patterns are known from *Tiarasmilia* Wells, 1932 or *Paronastrea* Beauvais, 1977, but in these genera the ornamentation (also called apophysal or secondary septa) shows a growth direction towards the calicular centre, and moreover, they are not connected to each other, whereas in *Trochoidomeandra* the septal ornamentation is not oriented in any direction, and the apophysal septa are connected to each other and form a more or less rigid meshwork.

If *Trochoidomeandra* would be a colony, the so-called septothecal walls should be fused in the centre of the calice, because the centre would be the origin of the "colony" but they aren't. What Morycowa (1971) is considering septa, is too irregular developed and moreover in places so densely connected that calices cannot be distinguished. Also the quite regular arrangement of septal cycles when considering the genus a solitary coral is a strong argument for a solitary form.

Species included: The type species, *Trochoidomeandra problematica* Morycowa, 1971, and another two species: *Trochoidomeandra ovalis* Turnšek & Mihajlovič, 1981 and *Trochoidomeandra cylindrica* (Prever, 1909). Critical synonymy lists are given below to show that all *Trochoidomeandra* material – except for the type material – belongs to other genera.

Trochoidomeandra cylindrica (Prever, 1909)
Pl. 1, Figs. 1–2

*v 1909 *Axosmilia cylindrica* Prever, p. 112, text-fig. 18, pl. 10, fig. 1.

Types: Holotype PU 17955, by monotypy.

Dimensions:

c 8.5 x 9.5mm

s 48

Occurrences: Early Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fossa Mezza Spada (PU 17955).

Trochoidomeandra problematica Morycowa, 1971

*v 1971 *Trochoidomeandra problematica* Morycowa, p. 131, text-figs. 38–39, pl. 37, figs. 1–2, pl. 38, fig. 1.

non 1988 *Trochoidomeandra problematica* Morycowa, 1971. – Kuzmicheva & Aliev, p. 180, pl. 8, fig. 3 [= *Rhipidomeandra* sp.].

non 1997 *Trochoidomeandra* cf. *problematica* Morycowa 1971. – Baron-Szabo & Fernández Mendiola, p. 48, fig. 5e [= *Tiarasmilia* sp.].

non 2002 *Trochoidomeandra problematica* Morycowa, 1971. – Kuzmicheva, pl. 11, fig. 1 [= *Paronastraea* sp.].

2004 *Trochoidomeandra problematica* Morycowa, 1971. – Stolarski et al., fig. 7c [refiguration of the type material].

Trochoidomeandra ovalis Turnšek & Mihajlovič, 1981

* 1981 *Trochoidomeandra ovalis* Turnšek & Mihajlovič, p. 26, pl. 25, figs. 1–5, pl. 26, figs. 1–2.

non 1993 *Trochoidomeandra* ? *ovalis* Turnšek 1981. – Baron-Szabo, p. 161, pl. 4, fig. 5 [= *Tiarasmilia* sp.].

Trochoidomeandra sp.

non 1977 *Trochoidomeandra* sp. – Sikharulidze, p. 97, pl. 18, fig. 2 [= *Rhipidomeandra* sp.].

non 1998 *Trochoidomeandra* sp. – Yamagiwa et al., p. 62, pl. 4, fig. 3 [= *Tiarasmilia casteri*].

non 1985 *Trochoidomeandra* sp. – Sikharulidze, pl. 29, fig. 1 [= *Rhipidomeandra* sp.]

Suborder Meandrinina Alloiteau, 1952
Felixigyra group

Genera included: *Felixigyra* Prever, 1909, *Rhipidomeandra* Morycowa & Masse, 1998, *Wellsimeandra* Idakieva & Cheshmedzhieva, 2003. The genera *Rhipidomeandra* and *Wellsimeandra* were originally assigned to the family Trochoidomeandridae, but they differ by their almost smooth septal faces.

Diagnosis. – Hydnophoroid and meandrinoid colonies known. Septa compact, thick. No septal symmetry, but distinct septal generations that differ in length and thickness. Septa generally not connected to each other, in places by the means of dissepiments. Septal lateral face rarely with medium size thorns, inner margin swollen or T-shaped. Lonsdaleoid septa present in places. No pali or paliform lobes, synapticulae, columella. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, septothecal. Budding intracalicinal, polystomodeal.

Remarks on systematic position. – It is here assumed that the *Felixigyra* group are early so-called meandrininid corals. The genus *Meandrina* sensu stricto is very probably a faviid coral and the name cannot be applied to Cretaceous corals. The Cretaceous corals currently assigned to the suborder Meandrinina (sensu Alloiteau 1952) are characterised by having very small trabeculae (often only marked as a dark line), and therefore smooth or only finely ornamented septal distal margins, and finely dentated septal lateral faces. The most prominent group is the Phyllosmiliidae family that counts with almost 50 genera, most of them having their first occurrence during the Late Turonian or Coniacian (see Löser 2013b for more de-

tails). The genera of the *Felixigyra* group are comparable to the Phyllosmiliidae but differ by almost smooth lateral septal faces, the occasional existence of lonsdaleoid septa, and the absence of a columella. One specimen depicted here (BSPG 2003 XX 5578) shows remains of microstructure comparable to those of the Phyllosmiliidae. Only the wall formation (see PU 18291#11) differs remarkably from all members of the Meandrinina suborder and appears more like that found in Amphiastreid corals.

There was no explanation for the original systematic position for *Rhipidomeandra* by Morycowa & Masse (1998). The new genus was considered closely related to *Trochoidomeandra* that was still understood a colonial coral ignoring the revision carried out by Turnšek & Mihajlovič (1981).

Felixigyra was until recently (Löser 2010a) misinterpreted as a genus synonymous with *Eohydnophora* and therefore assigned to other families such as Eugyridae, Faviidae or Stylinidae. The systematic position proposed in Löser (2010a) as Eugyridae was preliminary.

Range: Barremian to Early Cenomanian.

Genus *Felixigyra* Prever, 1909

Type species: *Felixigyra deangelisi* Prever (1909), by subsequent designation in Wells (1936).

Species included: *Felixigyra deangelisi* Prever, 1909 (including all species established by Prever 1909) and some questionable material in open nomenclature from the Albian of Sonora (Mexico) and the Early Cenomanian of Kozani (Greece).

Remarks. – The genus was revised by Löser (2010a) in greater detail. All *Felixigyra* species from the Early Aptian of the Monti d'Ocre were found synonymous. Unfortunately the type material of the type species is poorly preserved and thin sections are not available. The type material of other, subjectively synonymous species, is better preserved and includes thin sections. The genus was assigned to the family Eugyridae in Löser (2010a), but it differs by the very thick septa and their inner swollen margins. Lacking microstructural details of the septa do not allow one to define the size of the trabeculae that would be decisive for the systematic position.

Range: Aptian to Early Cenomanian.

Genus *Rhipidomeandra* Morycowa & Masse, 1998

Type species: *Rhipidomeandra bugrovae* Morycowa & Masse (1998), by original designation.

Species included: The genus counts up to the present with only the type species of *Rhipidomeandra* and *Wellsimeandra*. Prever (1909) established two species in the extant coral genus *Phyllastraea* Dana, 1846 (non *Phyllastraea* Fromentel, 1879): *P. schnarrenbergeri* and *P. stoliczkai*. Neither species have ever been cited in the literature, with the exception of catalogues of Cretaceous coral species (Felix 1914; Löser et al. 2002). The material described by Prever (1909) is completely different from *Phyllastraea* and was found, together with topotypical material from the type locality, to belong to *Rhipidomeandra*. *Columellogyra maeandra* Sikharulidze, 1985 is considered *Rhipidomeandra* as well.

Diagnosis. – Cerioid to meandroid colony. Calicular rows – if present – short or medium-long and curved. Calices in rows partly distinct. No neighbouring calices in one row. Valley septa absent. Septa compact. Septa in cross section externally slightly thicker, getting slightly thinner towards the centre. No septal symmetry, but size orders can be distinguished. Septal generations differ in length and thickness. Half of all septa reach close to the centre of the calicular rows, all others are shorter. Septa occasionally connected to each other, only by the means of dissepiments. Septal distal margin unknown, lateral face with occasional thorns, inner margin T-shaped and swollen. Lonsdaleoid septa present in places. Endotheca consists of numerous tabulae and dissepiments. Wall compact, formation unknown. Inner face of the wall with thorns. Collines tectiform in the type species. Pali or paliform lobes, costae, synapticulae, columella, coenosteum absent. Budding intracalicinal, polystomodeal, or septal.

Remarks. – Closely related to *Rhipidomeandra* is *Wellsimeandra* Idakieva & Cheshmedzhieva, 2003, that differs according to its authors by tectiform collines and shorter calicular rows. The type material of *Rhipidomeandra* shows, indeed, very long and regular calicular rows, whereas, in the type material of *Wellsimeandra* the calicular rows are very short, giving the colony a more hydnophoroid appearance. Other material shows in the same colony a cerioid calicular arrangement and calicular rows as in *Rhipidomeandra*. *Wellsimeandra* is therefore included in the synonymy of *Rhipidomeandra*.

The type species of *Rhipidomeandra* shows no coenosteum, the calicular rows share one wall, and the calicular rows are long. There exists additional material that has an extended coenosteum, double walls and very short calicular rows giving a cerioid appearance. All this material is for the moment included into *Rhipidomeandra*.

Species distinction. – Species are distinguished on the basis of their calicular width. The septal density shows a high variation within one colony. The length of calicular rows is not taken into account, because it is either not possible to measure this value (e.g. in the specimens with long calicular rows) or it varies too much in one colony.

Range: Barremian to Early Cenomanian.

Rhipidomeandra maeandra (Sikharulidze, 1985)
Pl. 2, Figs. 7–9

*1985 *Columellogyra maeandra* Sikharulidze, p. 64, text-fig. 10, pl. 29, fig. 3.

Dimensions:
(TUM 56501)

	n	min–max	μ	σ	cv	μ±σ
crw	10	0.94–1.59	1.22	0.18	14.7	1.04–1.40
crd	10	2.13–2.66	2.33	0.16	7.0	2.16–2.49
sd	4/2mm					

Remarks. – The type material of the species and the present specimen is the only known material. It shows very small dimensions.

Occurrences: Early Aptian of Georgia (Kartli) Ali. Late Aptian of Japan (Iwate-ken, Shimohei-gun) Tanohata-mura, Koikorobe (TUM 56501).

Rhipidomeandra morycowae (Idakieva & Cheshmedzhieva, 2003)
Pl. 1, Figs. 4–6

*2003 *Wellsimeandra morycowa*. – Idakieva & Cheshmedzhieva, p. 64, pls. 1–2.

Dimensions:
(BSPG 2003 XX 5578)

	n	min–max	μ	σ	cv	μ±σ
crw	10	4.50–6.61	5.53	0.65	11.7	4.88–6.18
crd	10	4.63–7.32	5.75	0.88	15.3	4.86–6.64
sd	11/5mm					

Remarks. – It was not possible to observe the type material because the staff of Sofia University did not reply to various inquiries. The sample presented here differs from the type material by longer calicular rows and thinner septa. It presents remains of microstructure that are comparable to that of *Phyllosmilia*. The wall formation is the same as that observed in other *Rhipidomeandra* species.

Occurrences: Early Barremian of Bulgaria (Veliko Tarnovska oblast) Novo selo. Early Aptian of Greece (Viotía) Arachova (BSPG 2003 XX 5578).

Rhipidomeandra schnarrenbergeri (Prever, 1909)
Pl. 1, Figs. 7–9

v*1909 *Phyllastraea Schnarrenbergeri* Prever, p. 77, pl. 3, fig. 4.
v 1998 *Rhipidomeandra bugrovae* Morycowa & Masse, p. 735, figs. 9.1-3, 10.6, 10.7, 11.

Type: Holotype PU 18101, by monotypy.

Dimensions:
(PU 18101)

	n	min–max	μ	σ	cv	μ±σ
crw	20	2.00–3.07	2.49	0.33	13.3	2.15–2.82
crl	25	4.34–6.56	5.31	0.69	13.0	4.62–6.00
crd	20	3.31–5.13	4.10	0.59	14.4	3.50–4.69
si	20–30mm					
sd	10/5mm					

(BSPG 2003 XX 5323)

	n	min–max	μ	σ	cv	μ±σ
crw	20	2.04–3.20	2.72	0.35	13.0	2.36–3.08
crl	20	3.76–9.26	5.75	1.38	23.9	4.37–7.13
crd	20	3.04–4.62	3.76	0.43	11.6	3.32–4.20
si	20–26					
sd	10/5mm					

Remarks. – The holotype is a small colony without any polished surface. The type as well as the topotypical specimen show numerous isolated calices and short calicular rows.

Occurrences: Late Barremian of France (Bouches-de-Rhône) Orgon, (Vaucluse) Les Gardettes. Early Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fonte Cerasetti (BSPG 2003 XX 5323); Fossa Mezza Spada (PU 18101).

Rhipidomeandra stoliczkai (Prever, 1909)
Pl. 1, Fig. 3

v* 1909 *Phyllastraea Stoliczkai* Prever, p. 77, pl. 3, fig. 3.

Type: Holotype PU 18102, by monotypy.

Dimensions:
(PU 18102)

	n	min–max	μ	σ	cv	μ±σ
crw	10	3.21–4.79	3.79	0.57	15.2	3.21–4.37
crl	10	4.82–6.44	5.38	0.52	9.7	4.86–5.91
crd	10	3.95–5.68	4.72	0.52	11.1	4.19–5.24
si	12–15					
sd	8/5mm					

Remarks. – The holotype is the only available specimen. It has a polished surface. It mainly has isolated calices. It differs from most other species by its large calicular dimensions.

Occurrences: Early Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fossa Mezza Spada (PU 18102).

Rhipidomeandra sp. 1
Pl. 2, Figs. 1–6

v 1996 *Microphyllia densecostata* Sikharulidze, 1979 – Baron-Szabo & Steuber, p. 26, pl. 15, figs. 4–5.
vp 1996 *Pleurostylina corallina* Fromentel, 1856. – Baron-Szabo & Steuber, p. 23, pl. 11, fig. 5.

Dimensions:
(BSPG 1994 XI 14)

	n	min–max	μ	σ	cv	μ±σ
crw	20	1.22–2.12	1.72	0.27	15.7	1.45–1.99
crd	15	2.71–4.47	3.74	0.44	11.7	3.30–4.18
sd	11/5mm					

(BSPG 2003 XX 5401)

	n	min–max	μ	σ	cv	μ±σ
crw	40	1.27–2.51	1.82	0.31	17.4	1.51–2.14
crl	25	2.37–7.33	4.60	1.28	27.9	3.31–5.88
crd	15	3.12–4.42	3.65	0.40	11.0	3.25–4.05
si	16–24					
sd	4/2mm					

(MB K544)

	n	min–max	μ	σ	cv	μ±σ
crw	20	1.68–2.28	1.89	0.16	8.4	1.73–2.05
crd	20	1.85–2.59	2.26	0.25	11.3	2.01–2.52
crl	20	2.49–7.91	4.57	1.56	34.2	3.00–6.13
sd	9/2.5mm					

(PU 18291#11)

	n	min–max	μ	σ	cv	μ±σ
crw	30	1.31–2.09	1.65	0.20	12.6	1.44–1.86
crl	25	1.93–6.27	3.96	1.26	31.8	2.70–5.23
crd	20	2.29–3.40	2.95	0.36	12.4	2.58–3.32
s	16–24					
sd	10/5					

R e m a r k s . – The material of this species has isolated calices and calicular rows, as well as both forms with and without a coenosteum. Within the material from Italy, it shows the longest and most pronounced calicular rows and has the most affinities to the type material of *Rhipidomeandra bugrovae*, the type species of the genus.

O c c u r r e n c e s : Late Barremian of Germany (Bavaria) Kürental (BSPG 1994 XI 14). Early Aptian of Greece (Viotía) Arachova (MB K544); Italy (Abruzzi, L'Aquila) Monti d'Ocre (PU 18291#11); Fossa Agnese (ERNO L-5401); Mexico (Michoacán) Turitzio, Loma de San Juan.

Rhipidomeandra sp. 2
Fig. 1

D i m e n s i o n s :
(BSPG 2003 XX 5818)

	n	min–max	μ	σ	cv	μ±σ
crw	25	0.55–0.85	0.7	0.08	11.5	0.61-0.77
crd	20	1.16–1.87	1.55	0.19	12.4	1.35-1.74
sd	7/2mm					

(BSPG 2007 V 48)

	n	min–max	μ	σ	cv	μ±σ
crw	10	0.73–1.10	0.88	0.11	13.1	0.76–0.99
crd	10	2.43–3.64	3.13	0.38	12.2	2.74–3.51
sd	4/1mm					

R e m a r k s . – The three specimens have the smallest dimensions of all known specimens and an extensive coenosteum. The Greek material has smaller dimensions than the material from Spain, but preliminarily all specimens are kept together in one species.

O c c u r r e n c e s : Early Cenomanian of Spain (Cantabria, Santander) Cobreces, Luaña playa (BSPG 2007 V 48); Greece (Kozani) Nea Nikopolis (BSPG 2003 XX 5818, 7443).

4. Discussion

The family Trochoidomeandridae with its only genus *Trochoidomeandra* is quite an isolated family. Its ancestors or closely related families are unknown. Its systematic position is preliminary. The new position of the family in the suborder Heterocoeniina is mainly supposed by the strongly ornamented lateral septal faces. The ornamentation of the septal lateral faces with apophysal septa is considered a convergent characteristic that occurs in some families more commonly than in others. Generally, this type of ornamentation is restricted to Heterocoeniids.

The present study has increased the number of known *Rhipidomeandra* species as well as data about their distribution in time and space. With the exception of one species that occurred in the Early Cenomanian, the genus had its principal stratigraphical distribution in the Barremian and Aptian, with most species in the Early Aptian (Fig. 2). This distribution pattern corresponds with the general diversity patterns of Cretaceous corals that have a notable diversity peak during the Early Aptian (Löser et al. accepted, fig. 1). The distribution of *Rhipidomeandra* is comparable to that of the similar *Felixigyra*, which has its highest abundance during the Early Aptian and few records during the Albian and Cenomanian. *Rhipidomeandra* shows a particular distribution pattern (Fig. 3) with four different distribution areas that can be distinguished; the Late Barremian to Early Aptian of the Central Tethys, the Cenomanian of the Tethys, the Barremian and Aptian of the Eastern Tethys and the Western Pacific, and an unspecific area combining the Guerrero Terrane with one locality in the Central Tethys.

The here applied informal group with the genera *Felixigyra* and *Rhipidomeandra* combines characteristics of several suborders. The wall structure and lonsdaleoid septa is reminiscent of Amphiastreids, the thickened inner margins of the septa and microstructural features are closer to Meandrininids (sensu lato), and the poorly ornamented septa place the genera closer to the Eugyridae in the suborder Fa-

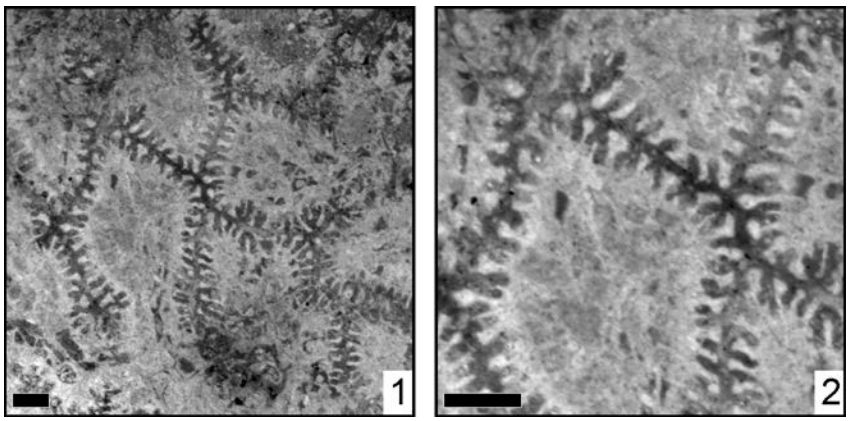


Fig. 1. *Rhipidomeandra* sp. 2, BSPG 2007 V 48, transversal thin section. Scale bar 1 mm.

Stratigraphy / Species	Barremian		Aptian		Albian			Cenomanian		
	Early	Late	Early	Late	Early	Middle	Late	Early	M.	L.
R. meandra										
R. morycowae										
R. schnarrenbergeri										
R. stoliczkai										
R. sp. 1										
R. sp. 2										

Fig. 2. Stratigraphic distribution and commonness of species of the *Rhipidomeandra* species. The thickness of the bars indicates the number of localities (multiples localities within the same lithostratigraphic unit are counted as one) in which the concerned species was found.

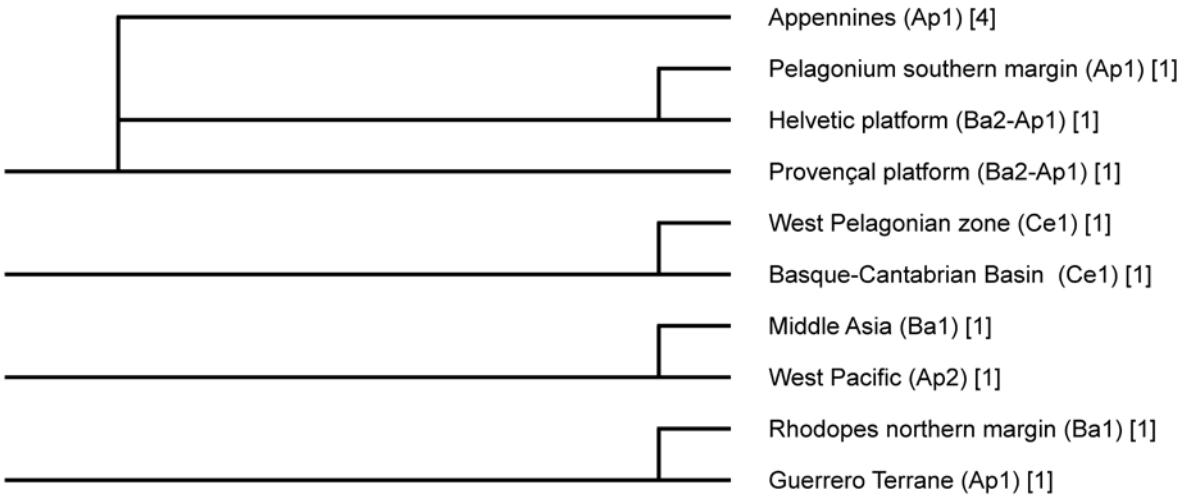


Fig. 3. Correlation of provinces with joint species of the study area. The correlation ratio coefficient was applied.

viina. The preliminary position within the Meandrinina is guided by the microstructural details and the striking feature of the swollen inner septal margins. This character is shared by two suborders, the Rhipidogyrina (family Rhipidogyridae) and the Meandrinina (family Phyllosmiliidae). The latest Rhipidogyridae are known from the Late Aptian (*Ogilvinella* sp. in Tomás et al. 2008), whereas the earliest Phyllosmiliidae are known from the Aptian on (*Pachyphyllia*; Löser 2013a). Both families share the characteristic that the first septal cycle or generation is disproportionally thicker than younger cycles (generations). This feature is not shared by the members of the *Felixigyra* group. Rhipidogyrids later than Aptian do not belong to this family: *Barysmilia* Milne-Edwards & Haime, 1848 (for instance Eliášová 1991) belongs to the Phyllosmiliidae; the type of the type species of *Placohelia* Počta, 1887 (see Eliášová 1991) lacks microstructure and the genus probably belongs to the Hemiporitidae; *Rhipidastraea* Eliášová, 1991 is – based on the observation of thin sections from the type of the type specimen – a penular coral that belongs to the family Leptophylliidae. The genus *Paracanthogyra* Morycowa & Marcopoulou-Diacantoni, 2002, originally assigned to the Rhipidogyridae, was later assigned the family Aulastraeoporidae (Löser 2011).

5. References

Alloiteau, J. (1952): Embranchement des coelentérés. – In: Piveteau, J. (Ed.): Traité de Paléontologie (1): 376–684; Paris (Masson).

Baron-Szabo, R. C. (1993): Korallen der höheren Unterkreide („Urgon“) von Nordspanien (Playa de Laga, Prov. Guernica). – Berliner geowissenschaftliche Abhandlungen, (E), **9**: 147–181.

Baron-Szabo, R. C. & Fernández Mendiola, P. A. (1997): Cretaceous scleractinian corals from the Albian of Cabo de Ajo (Cantabria Province, N-Spain). – Paläontologische Zeitschrift, **71**: 35–50.

Baron-Szabo, R. C. & Steuber, T. (1996): Korallen und Rudisten aus dem Apt im tertiären Flysch des Parnass-Gebirges bei Delphi-Arachowa. – Berliner geowissenschaftliche Abhandlungen, (E), **18**: 3–75.

Eliášová, H. (1991): Rhipidogyridés (Scléractiniaires) du Crétacé de Bohême (Cénomanien supérieur – Turonien inférieur, Tchécoslovaquie). – Vestnik Ustredního ústavu geologického, **66** (3): 163–172.

Felix, J. (1914): Anthozoa Cretacea. – Fossilium Catalogus, (1: Animalia), **5**–**7**: 1–273.

Idakieva, V. & Cheshmedzhieva, V. L. (2003): *Wellsimeandra* gen. n. du Barrèmien de la région de Veliko Tirnovo (Prébalkan central). – Doklady Bolgarskoj Akademiy Nauk, **56**: 61–55.

Kuzmicheva, E. I. (2002): [Skeletal morphology, systematics and evolution of the Scleractinia.] – Trudy Paleontologicheskogo instituta, **286**: 1–211.

Kuzmicheva, E. I. & Aliev, O. B. (1988): [Corals.] – In: Ali-Zade, A. A., Aliev, G. A. & Aliev, M. M. (eds.): Cretaceous fauna of Azerbaijan: 153–184; Baku (Elm).

Löser, H. (2006): Morphology, taxonomy and distribution of the Cretaceous coral genus Paronastraea (Barremian-Cenomanian; Scleractinia). – Rivista Italiana di Paleontologia e Stratigrafia, **112** (1): 121–131.

Löser, H. (2007): Morphology, taxonomy and distribution of the Cretaceous coral genus *Preverastraea* (Late Barremian-Cenomanian; Scleractinia). – Rivista Italiana di Paleontologia e Stratigrafia, **113** (1): 3–19.

Löser, H. (2008a): A new solitary coral genus of the suborder Heterocoeniina (Scleractinia) from the Aptian (Cretaceous) of Spain. – Paläontologische Zeitschrift, **82** (3): 279–284.

Löser, H. (2008b): Remarks on the genus *Hexasmilia* (Scleractinia; Cretaceous) and description of a new species from the Aptian of Spain. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **250** (1): 45–52.

Löser, H. (2010a): Revision of the Early Cretaceous coral genus *Felixigyra* and general remarks on the faviid hydnophoroid coral genera. – Rivista Italiana di Paleontologia e Stratigrafia, **116**: 177–188.

Löser, H. (2010b): Revision of the Cretaceous coral genus *Tiarasmilia* Wells, 1932 (Scleractinia). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **258** (2): 157–165.

Löser, H. (2011): The Cretaceous corals from the Bisbee Group (Sonora; Late Barremian – Early Albian): introduction and family Aulastraeoporidae. – Revista Mexicana de Ciencias geológicas, **28** (2): 254–261.

Löser, H. (2013a): Late Aptian (Cretaceous) corals from Central Greece. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **267** (1): 89–116.

Löser, H. (2013b): An Early Albian shallow marine coral fauna from Southern France – insight into evolution and palaeobiogeography of Cretaceous corals. – Palaeobiodiversity and Palaeoenvironments, **93**: 1–43.

Löser, H., Castro, J. M. & Nieto, L. M. (in press): Late Albian Scleractinian corals from the Prebetic zone (SE Spain). – Palaeontographica, (A).

Löser, H. et al. (2002): List of Citations. – Catalogue of Cretaceous Corals, **2**: 1–784.

Löser, H. et al. (2005): List of Localities. – Catalogue of Cretaceous Corals, **3**: 1–366.

Matthews, S. C. (1973): Notes on open nomenclature and on synonymy lists. – Palaeontology, **16**: 713–719.

Morycowa, E. (1971): Hexacorallia et Octocorallia du Crétacé inférieur de Rarau (Carpathes orientales roumaines). – Acta Palaeontologica Polonica, **16**: 1–149.

Morycowa, E. & Marcopoulou-Diacantoni, A. (2002): Albian corals from the Subpelagonian zone of Central Greece (Agrostylia, Parnassos region). – Annales Societatis Geologorum Poloniae, **72**: 1–65.

Morycowa, E. & Masse, J. P. (1998): Les Scléractiniaires du Barrémien-Aptien inférieur de Provence (SE de la France). – Geobios, **31**: 725–766.

Prever, P. L. (1909): Anthozoa. – In: Parona, C. F. (Ed.): La fauna coralligena del Cretaceo dei Monti d'Ocre nell'Abruzzo Aquilano. – Memorie descrittive della Carta geologica d'Italia, **5**: 51–147.

Sikharulidze, G. Y. (1977): [Lower Cretaceous hexacorals from the Georgia.] – Paleontologiya i stratigrafiya mezozojskikh otlozhenij Gruzii, **3**: 66–109.

Sikharulidze, G. Y. (1985): [Hexacorals from the Urgonian facies of the Dzirul Massif and its northern frame.] – Trudy Akademija Nauk Gruzinskoj SSR, Geologiceskij Institut, **59**: 1–110.

Stolarski, J., Roniewicz, E. & Grycuk, T. (2004): A model for furcate septal increase in a Triassic scleractiniamorph. – Acta Palaeontologica Polonica, **49**: 529–542.

Tomás, S., Löser, H. & Salas Roig, R. (2008): Low-light and nutrient-rich coral assemblages in an Upper Aptian carbonate platform of the southern Maestrat Basin (Iberian Chain, eastern Spain). – Cretaceous Research, **29**: 509–534.

Turnšek, D. & Mihajlovič, M. (1981): Lower Cretaceous Cnidarians from eastern Serbia. – Razprave Slovenska Akademija Znanosti in Umetnosti, (4), **23**: 1–54.

Wells, J. W. (1936): The nomenclature and type species of some genera of recent and fossil corals. – American Journal of Science, (5), **31**: 97–134.

Yamagiwa, N., Hisada, K.-I. & Tamura, M. (1998): Early Cretaceous Hexacorals from the Western Part of the Sanchu Area, Kanto Mountains. – Bulletins of the National Science Museum Tokyo, (C), **24**: 51–66.

Address of the author:

Hannes Löser, Estación Regional del Noroeste, Instituto de Geología, Universidad Nacional Autónoma de México, L.D. Colosio y Madrid s/n, Col. Los Arcos, 83200 Hermosillo, Sonora, México.

E-mail: loeser@paleotax.de

Manuscript received: 22 May 2013, revised version accepted: 2 August 2013.

Plate 1

Figs. 1–2. *Trochoidomeandra cylindrica* (Prever, 1909), holotype of *Axosmilia cylindrica*, PU 17955, transversal thin section.

Fig. 3. *Rhipidomeandra stoliczkai* (Prever, 1909), holotype of *Phyllastraea stoliczkai*, PU 18102, transversal slab.

Figs. 4–6. *Rhipidomeandra morycowae* (Idakieva & Cheshmedzhieva, 2003), BSPG 2003 XX 5578, transversal thin section. Fig. 6 with remians of microstructure.

Figs. 7–8. *Rhipidomeandra schnarrenbergeri* (Prever, 1909), ERNO L-5323, transversal and longitudinal thin section.

Fig. 9. Holotype of *Phyllastraea schnarrenbergeri*, PU 18101, coral surface.
Scale bars 1 mm.

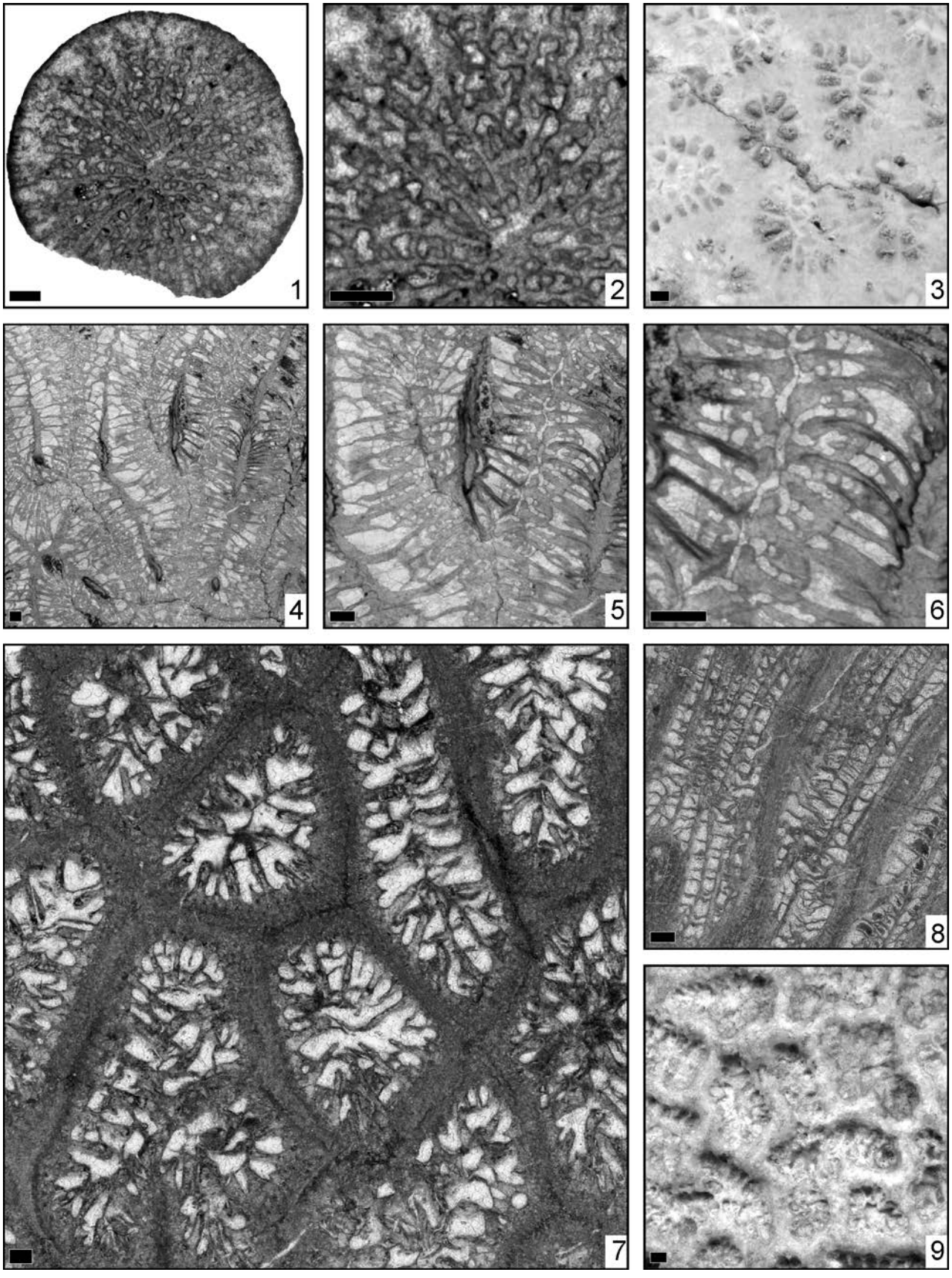

1
2
3
4
5
6
7
8
9

Plate 2

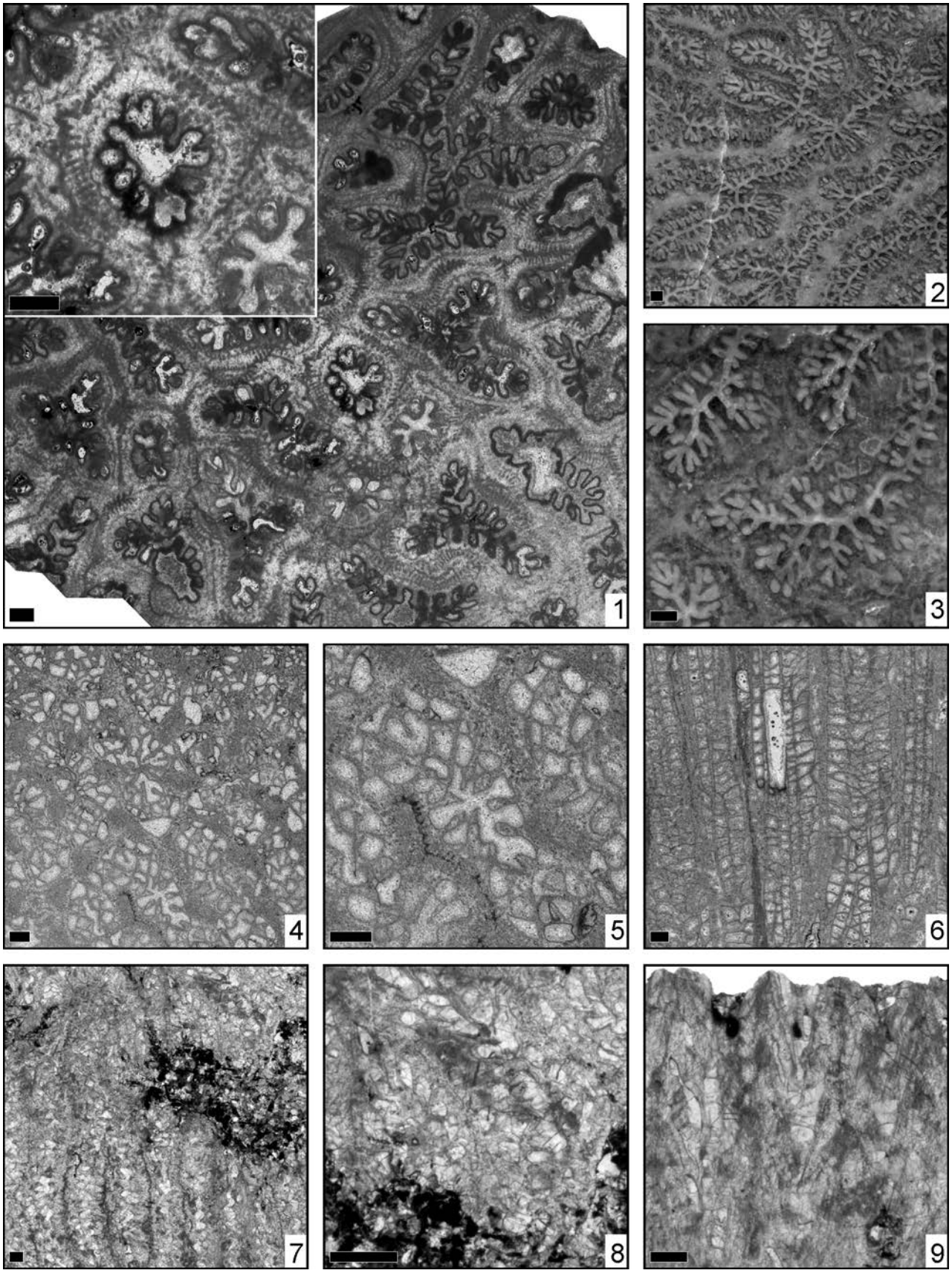
Fig. 1. *Rhipidomeandra* sp. 1, PU 18291#11, transversal thin section.

Figs. 2–3. *Rhipidomeandra* sp. 1, BSPG 1994 XI 14, transversal slab.

Figs. 4–6. *Rhipidomeandra* sp. 1, ERNO L-5401, transversal and longitudinal thin section.

Figs. 7–9. *Rhipidomeandra maeandra* (Sikharulidze, 1985), TUM 56501, transversal and longitudinal thin section.

Scale bars 1 mm.


1
2
3
4
5
6
7
8
9