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VARIABILITY IN *EPISTREPTOPHYLLUM* FROM THE MIDDLE JURASSIC OF KACHCHH, WESTERN INDIA: AN OPEN QUESTION FOR THE TAXONOMY OF MESOZOIC SCLERACTINIAN CORALS

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ABSTRACT—*Epistreptophyllum cornutiformis* Gregory, 1900, is the name assigned to a Middle Jurassic population of scleractinian corals from Kachchh, western India. Measurements of ten variables from 84 specimens of this population have been statistically examined by means of univariate and multivariate analyses. A wide range of variation in corallum shape, septal perforation, lateral septal surface ornamentation, nature of the endotheca, and that of the columella is observed. The great majority of specimens are solitary. The wide range of gradational variation observed in this population corresponds to and includes the morphological characters described for various scleractinian genera such as *Protethmos* Gregory, *Metethmos* Gregory, *Frechia* Gregory, and *Epistreptophyllum* Milaschewitsch. The assignment of these genera to this later senior synonym genus is supported by the description of a well-preserved topotype from Nattheim. The ornamentation of the septa in *Epistreptophyllum* is detailed and distances it from typical pennular corals.

INTRODUCTION

DESPITE THE wide use of corals in stratigraphical, biogeographical, and paleosynecological studies, their taxonomy remains poorly established. Since the systematic works by Alloiteau (1952, 1957) and Wells (1956), details of septal morphology and structure have served as a main criteria for the taxonomy of scleractinian fossil corals as exemplified in the recent work of Roniewicz and Morycowa (1993). Careful evaluation of pennular ornamentation in Mesozoic corals led Gill (1967) to propose the erection of the superfamily Pennulacae in a paper that remains fundamental to Mesozoic scleractinian coral research. In this paper on pennulae, the variability of this structure was evoked and subsequently, several authors began to detail this pennular diversity by analyzing the microarchitecture and microstructure of various corals (e.g., Gill, 1968; Cuif, 1975; Gill and Russo, 1980; Roniewicz, 1982; Lathuilière, 1990; Lathuilière and Gill, 1995; in press). The population of *Epistreptophyllum* from Kachchh described in the present paper illustrates the variability within a single species, including its near-pennular septal ornamentation. The taxonomic consequences of this variability are discussed.

MATERIAL AND METHODS

The population studied here comes from the Middle Jurassic of the pericratonic shelf basin of Kachchh, western India (Figure 1). *Epistreptophyllum* represents a small part of a large fauna studied initially by Gregory (1900) and partly by Beauvais (1978), who revised specimens from Gregory's collection deposited at the Natural History Museum, London. Pandey and Fürsich (1993) gave an overview of the taxonomy of this fauna, based on a new collection assembled over the last five years; the population selected for study here comes from this and more recent field research. Our material was collected from different outcrops at two stratigraphic levels; 189 specimens from the Patcham Formation of Jumara Dome (Upper Bathonian; Callomon, 1993) and 13 specimens from the Chari Formation of Keera Dome (Middle Callovian; Spath, 1933) (Figure 2). Only Bathonian corals have been used in statistical analyses. They can be considered autochthonous and were collected in two thin beds deposited in low energy, turbid, possibly poorly lit environments subject to moderate rates of sedimentation. The corals lived on soft lime mud and never formed reefs (Fürsich et al., 1994). The specimens are deposited at the Department of Geology, University of Rajasthan, Jaipur, India.

In addition to current techniques of coral examination (qualitative observations of polished surfaces and thin sections), 10 characters were measured by a single researcher (D.K.P.) for a set of 84 corals from Jumara Dome. These characters were (Figure 3):1) great calicular diameter (gd): the longest linear length passing across the center of the calice, measured with a vernier calliper; 2) small calicular diameter (sd): the shortest linear length passing across the center of the calice, measured with a vernier calliper; 3) height of the corallum (h) vertical distance measured with a vernier calliper between the attachment area and the uppermost part of the calice; 4) attachment area (att): maximum diameter of the attachment area, measured with a vernier calliper; 5) number of septa (ns): septa counted along the corallite periphery; 6) septal density (ds): septa counted per 2 mm at the periphery; 7) thickness of major septa (tmaj): minimum septal thickness, measured with an ocular micrometer, at the periphery of the corallite of a septum which reaches the corallite center; 8) thickness of minor septa (tmin): minimum septal thickness measured with an ocular micrometer, at the periphery of the corallite of a septum not reaching the corallite center; 9) intertrabecular distance (itd): width of septal pores or distances between the outer sides of adjacent trabeculae measured near the inner margin of the septa with an ocular micrometer; 10) calicular depth (dep): distance between the uppermost portion of the calice and the bottom of the calice (measured with the vernier calliper).

The angle between the direction of the trabeculae and the vertical was measured only within two specimens (RUC1992I 69 and RUC1992I 70). The statistical program Biomeco (developed by C.E.P.E., Montpellier, France) was used to process all measurements. Univariate analysis, principal component analysis and correspondence analysis were performed on the data matrix provided in appendix 1.

In addition to the material from Kachchh, the holotype of *E. commune,* the type species of the genus, and about 100 topotypes of this genus from the Upper Jurassic of the Nattheim area (Germany) were studied. Among them, two specimens of *E. commune* loaned by the Staatliches Museum für Naturkunde

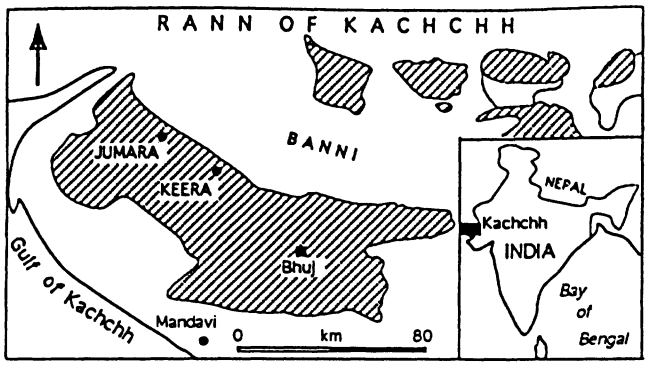


FIGURE 1—Location map showing Jumara Dome and Keera Dome localities in district Kachchh, Western India. The hatched area represents the extent of Jurassic-Tertiary outcrop in the Kachchh region.

in Stuttgart, from the White Jura, Beckeri-zone, Upper Kimmeridgian, Nattheim Margareten Wald, Germany (SMNS collection n° 62638/1 and 2) have been figured. Another specimen exhibits similarities to both *E. cylindratum,* based on the number of septa, and to *E. flabelliformis,* based on the shape of the corallum. This representative specimen, here assigned to *Epistreptophyllum* sp., comes from the private collection of F. Papier and is thoroughly described, here because of its excellent preservation.

SYSTEMATIC PALEONTOLOGY

Family uncertain

Familial affinities are treated further below under remarks, following character analysis.

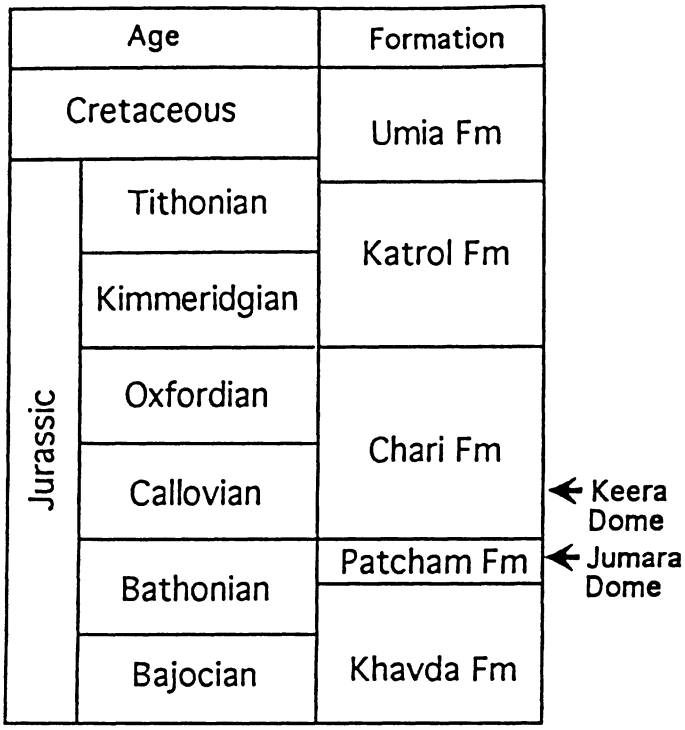


FIGURE 2—Lithostratigraphic units of Jurassic sediments of Kachchh showing the relative position of sites providing *Epistreptophyllum cornutiformis*: Jumara and Keera Domes, Kachchh, India.

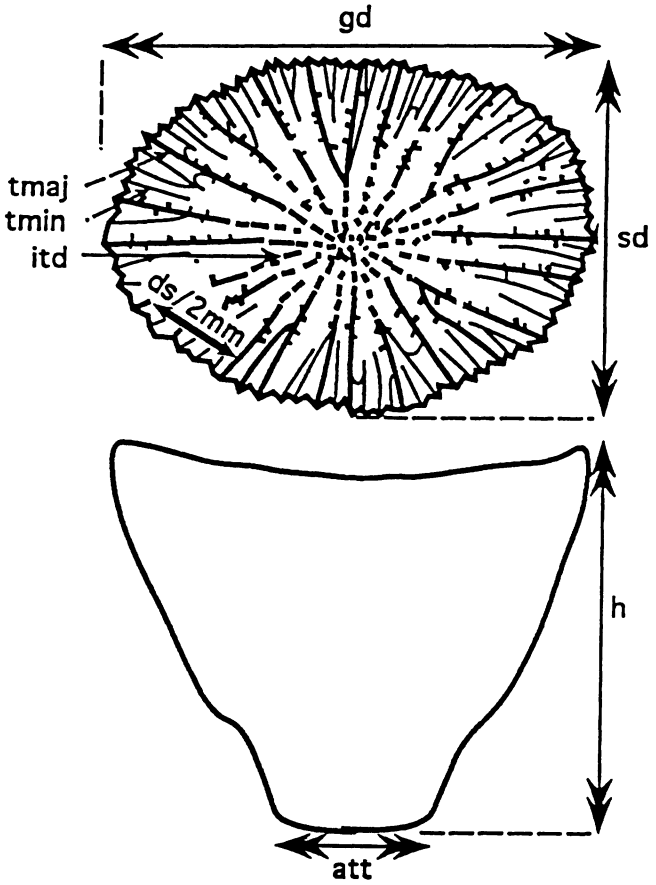


FIGURE 3—Schematic illustration of measured dimensions in *Epistreptophyllum cornutiformis.* Double arrows at both ends indicate dimensions that were directly measured; single arrows at both ends indicate counts; single arrows at one end indicate locations of measurements.

Genus EPISTREPTOPHYLLUM
Milaschewitsch 1876

Type species.—*Epistreptophyllum commune* Milaschewitsch 1876.

EPISTREPTOPHYLLUM CORNUTIFORMIS
(Gregory 1900)

Figures 7.1-7.7, 7.12-7.17, 8.7-8.12, 9.1-9.12, 10.1-10.12

Protethmos oldhami GREGORY 1900, p. 164, pl. 18, figs. 10, 12, 13.; BEAUVAIS, 1978, p. 59, pl. 4, figs. 4–5.
Protethmos duncani GREGORY 1900, p. 164, pl. 18, fig. 7.
Metethmos blanfordi GREGORY 1900, p. 165, pl. 18, figs. 4–6, 11.
Metethmos griesbachi GREGORY 1900, p. 166, pl. 18, fig. 9.; FLÜGEL, 1966, p. 59, pl. 16, figs. 5–6.
Frechia cornutiformis GREGORY 1900, p. 168, pl. 21, figs. 1–3.
Protethmos griesbachi (Gregory). BEAUVAIS, 1972, p. 57, pl. B, figs. 7–8.
Protethmos blanfordi (Gregory). BEAUVAIS, 1978, p. 60, pl. 5, figs. 1–3.; PANDEY AND FÜRSICH, 1993, p. 35, pl. 8, figs. 6, 8, 10.
non *Epistreptophyllum* cf. *oldhami* (Gregory). FLÜGEL 1966, p. 58, pl. 16, figs. 1–2.
? *Epistreptophyllum* cf. *cornutiformis* (Gregory). LIAO AND LI, 1980, p. 231, pl. 2 fig. 6.; LIAO 1982, p. 161, pl. 16, figs. 4, 5.; LIAO AND XIA, 1994, p. 118, pl. 23, fig. 12–15.
? *Epistreptophyllum* cf. *duncani* (Gregory). LIAO, 1982, p. 160, pl. 8 fig. 1.
? *Epistreptophyllum cylindratum* (Milaschevitsch). LIAO, 1982, p. 161, pl. 8, figs. 4–9.; LIAO AND XIA, 1994, p. 118, pl. 23, fig. 3–11.

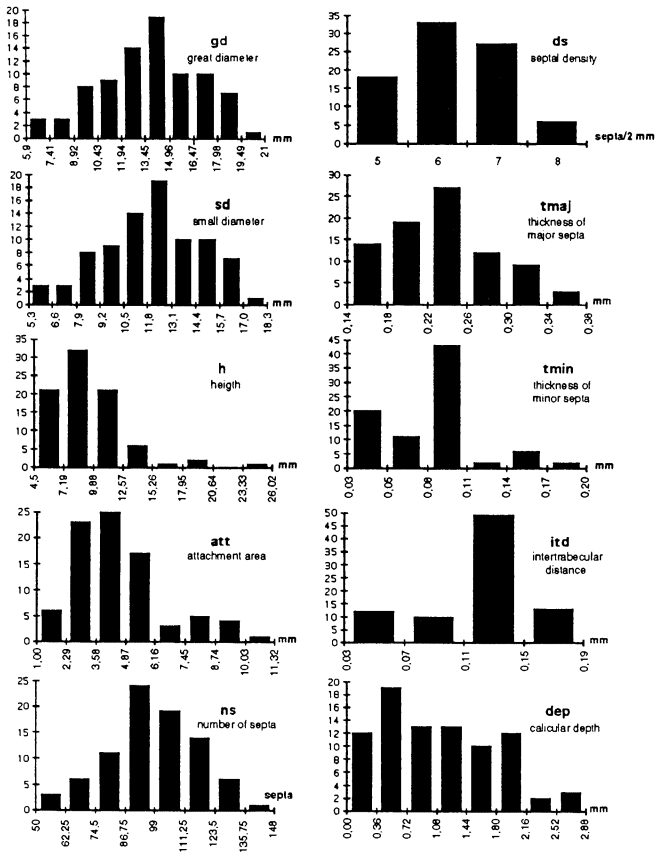


FIGURE 4—Univariate distribution of various quantitative characters in *Epistreptophyllum cornutiformis* Gregory.

Epistreptophyllum cornutiformis (Gregory). PANDEY AND FÜRSICH, 1993, p. 36, pl. 11, fig. 3.

Description.—Corallum small, occasionally curved, solitary. Only one colonial or pseudocolonial specimen was observed (RUC1994I 219); it exhibits a rejuvenescence (Figure 7.12–13). Forms vary; ceratoid, trochoid, turbinate, patellate, subcylindrical. Some flattened with large attachment area. Some specimens proximally turbinate, sharply narrowing down to peduncle, which can be curved, pointed, distally cylindrical. In one specimen (Figure 7.16), attachment area bears a cast of a probable montlivaltiid coral.

Calicular platform infundibuliform, horizontal to feebly convex; margin sharp, circular to subelongate in distal view. Costae thin, dentate (RUC1994I 146), slightly unequal, corresponding to septa, becoming inconspicuous toward the base. Some costae twisted, twisting probably related to avatars of growth (plate 8, figure 7 *in* Pandey and Fürsich, 1993; RUC1992I 71). Epitheca thin, fragile some cover costae in rings (Figure 7.16) (RUC1994I 220).

Radial elements are costosepta; costal part reduced to less than 0.7 mm (Figures 10.7,; 10.8). In the septal part, trabeculae rather vertical near the wall (range 0–20°), becoming less steeply inclined toward center (angle varies from 30° to 40° with respect to the vertical); zone of divergence almost coinciding with wall. Septa thin to moderately thick, straight, some curved, perforated at inner upper margin only. Major septa thickness rather constant beneath ornamentation; minor septa more cuneiform. General symmetry approximately radial. In elongated calices, septal curvature may produce bilateral symmetry (Figure 7.5, 7.14). Arrangement of septa not easily recognized according to the classic hexameral model. Fifteen to 29 septa reach columella (major septa). Inner edges of minor septa frequently anastomose to major septa (18, 21 and 24 such junctions were counted in three cross sections); this phenomenon emphasized toward center between major septa, forming of a spongy columella.

Septal surface ornamented with various lateral expansions, such as stout and blunt or long and curved granules, and flat, subhorizontal, irregularly distributed balconies that resemble pennulae in some aspects. In transverse or longitudinal sections perpendicular or oblique to the septal plane, some balconies display symmetry of true pennulae, show trend of alternation with those of adjacent septa (Figure 8.12). Balconies irregularly distributed, oriented, their peripheral margins never upturned or clearly ornamented. Subhorizontal ridges exist; more or less prominent, look like menianae. Ridges slightly independent of growth direction of trabeculae, can diverge at a very wide angle (130°) to growth axes (Figure 9.1). In some, lateral surface of septa smooth. Distal septal margins either denticulate or smooth (Figure 9.11). In many, distal part of septa (less than 0.5mm) smooth. In a few septa pennula-like structures can be identified near distal margins (Figure 8.8). Radial elements composed of closely and uniformly spaced trabeculae; perforation regular (three to four perforations per millimetre) or irregular, sparse, increasing toward axis (Figure 9.1, 9.5). Internal septal structure characterized by occurrence of laminar layers that are continuous with dissepiments (Figures 9.9, 10.6).

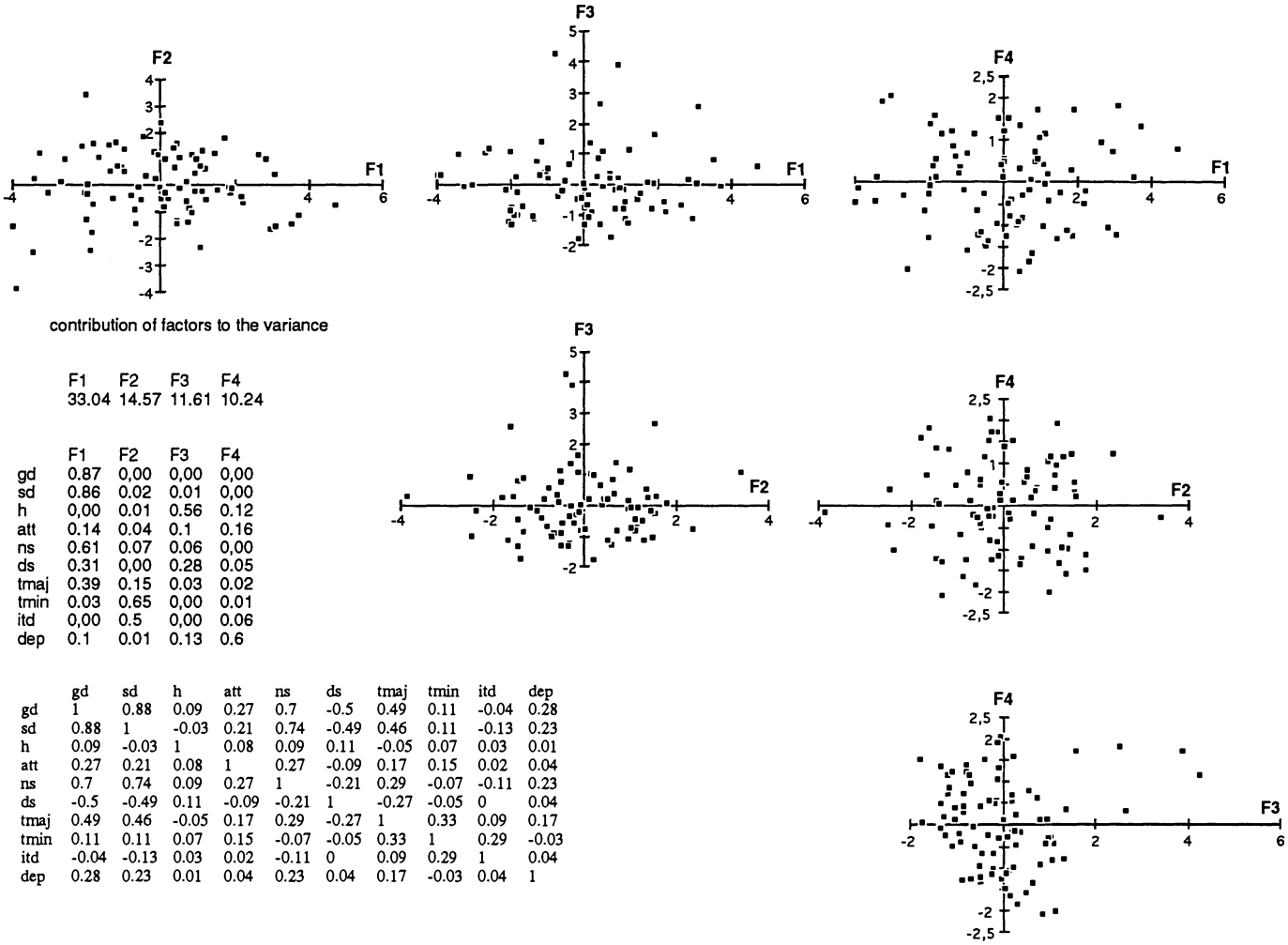
Parietal columella papillose to spongy (Figure 10.2, 10.3, 10.5). Papilla blunt or jagged (Figure 10.2, 10.5). Dissepiments vesicular to tabuloid, thick or thin, more common towards proximal part of corallum (Figure 9.3); rare along distal part, seen only along outer margin. They may form a ring around the columellar space (Figure 10.3). Synapticulae present (Figures 8.12, 9.12), seem to be common, often difficult to differentiate from anastomosing processes at the inner margins of minor septa.

Remark.—Continuity between endotheca and laminar layers and convexity of interseptal spaces at outer edge suggest that wall built in the same way by the septal and dissepimental laminar layers. The usual terms "parathecal" or "septothecal" are insufficient to describe this wall structure. Apart from laminar layers, the state of preservation does not allow further observation of septal microstructure.

Material examined.—213 specimens; 200 specimens (RUC1992I 69–71, 997-1033; RUC1994I 128–221, 376–386, 1073–1075; RUC1995I 513–559; Ju/25/30, 32, 40, 48, 123) from Patcham Formation (Upper Bathonian) of Jumara Dome and 13 specimens (RUC1994I 115–127) from Chari Formation (Middle Callovian) of Keera Dome, Kachchh, Western India.

Statistical analysis.—Results of univariate analyses of characters are given in Figure 4. For most characters, variables are unimodally distributed. Despite a few exceptions (att, tmin, dep), it is impossible to distinguish more than one population. Normality is accepted according to Lilliefors' test (confidence 80 percent) only for gd, sd, ns, and is rejected for h, att, ds, tmaj, tmin, itd, dep, with a probability of less than one percent. Among these latter characters, lognormality is acceptable only for att with a confidence of 80 percent. For this reason, we decided to perform multivariate analyses both by component analysis (Figure 5) and by correspondence analysis (Figure 6). Both analyses gave similar results. An attempt was made to exclude height and attachment area in order to avoid overwhelming other variables that are usually considered taxonomically more significant. Differences in height and attachment area are often due to substrate control and are a result of phenotypic plasticity. Exclusion of these variables did not change the results; only one cluster is apparent.

Discussion.—The results of the statistical analysis (Figures 4–



contribution of factors to the variance

F1	F2	F3	F4
33.04	14.57	11.61	10.24

	F1	F2	F3	F4
gd	0.87	0,00	0,00	0,00
sd	0.86	0.02	0.01	0,00
h	0,00	0.01	0.56	0.12
att	0.14	0.04	0.1	0.16
ns	0.61	0.07	0.06	0,00
ds	0.31	0,00	0.28	0.05
tmaj	0.39	0.15	0.03	0.02
tmin	0.03	0.65	0,00	0.01
itd	0,00	0.5	0,00	0.06
dep	0.1	0.01	0.13	0.6

	gd	sd	h	att	ns	ds	tmaj	tmin	itd	dep
gd	1	0.88	0.09	0.27	0.7	-0.5	0.49	0.11	-0.04	0.28
sd	0.88	1	-0.03	0.21	0.74	-0.49	0.46	0.11	-0.13	0.23
h	0.09	-0.03	1	0.08	0.09	0.11	-0.05	0.07	0.03	0.01
att	0.27	0.21	0.08	1	0.27	-0.09	0.17	0.15	0.02	0.04
ns	0.7	0.74	0.09	0.27	1	-0.21	0.29	-0.07	-0.11	0.23
ds	-0.5	-0.49	0.11	-0.09	-0.21	1	-0.27	-0.05	0	0.04
tmaj	0.49	0.46	-0.05	0.17	0.29	-0.27	1	0.33	0.09	0.17
tmin	0.11	0.11	0.07	0.15	-0.07	-0.05	0.33	1	0.29	-0.03
itd	-0.04	-0.13	0.03	0.02	-0.11	0	0.09	0.29	1	0.04
dep	0.28	0.23	0.01	0.04	0.23	0.04	0.17	-0.03	0.04	1

FIGURE 5—Specimen scores of first four principal components in *Epistreptophyllum cornutiformis* Gregory.

6) and the direct observation of a large number of specimens (Figures 7–9) strongly support the hypothesis that all of these specimens belong to a single taxonomic unit. We conclude that the specimens of the population studied belong to a single highly variable species. The above synonymies are based on this conclusion.

Gill (1982) interpreted Callovian corals from Israel, which he assigned to *Epistreptophyllum*, as broken branches of phaceloid colonies. In the population studied here, the morphology of coralla, the presence of an attachment area, the distribution pattern of the corals in the field do not support this interpretation.

EPISTREPTOPHYLLUM sp.
Figures 8.1–8.6

Description.—Corallum simple, 32 mm high, turbinate, with basal expansion, attachment area (13 mm). Calicular margin sharp. Calicular platform infundibuliform, moderately depressed (dep = 5 mm). Calice irregular in shape, not circular (Figure 8.1). Great diameter (gd) =25 mm, small diameter (sd) =23.5 mm. Epitheca seems absent but possibly damaged by silicification. Costae nearly equal, smooth or weakly dentate, covering basal expansion. Each costa corresponds to a septum. Costal density reaches 9 per 5 mm.

Radial elements are costosepta. Costae very short, less than 0.9 mm in transverse plane. Trabeculae vertical near wall, inclined near center, divergence between external trabeculae reaches approximately 30 to 40°. Septal perforation irregular, more abundant at inner end where trabeculae tend to dissociate. Minor septa anastomose to longer ones (but pattern is difficult to trace in distal view). Major septa join parietal papillose columella. Excluding ornamentation, septal thickness rather constant; minor septa more cuneiform. Thickness of major septa 250–750 μm; thickness of minor septa 150–750 μm. 138 septa, straight, rarely curved, arranged in radial symmetry and unequal systems. Lateral septal faces display a wide range of ornamentation patterns. Menianae and pennula-like structures dominant, simple granules also observed (Figure 8.2–6). In distal view, pennula-like structures frequently shifted on both sides of septa. Outer rims of pennula-like structures frequently occur as tiny spoons enlarged and concave at distal extremities. Distal edge of septa more or less regularly dentate, rather smooth in minor septa, inner edge characterized by dissociation of trabeculae. Distance between centers of adjacent trabeculae varies from 500 to 700 μm.

Endotheca present but difficult to observe. Similarly, synapticulae are present but rarely observed from the only available distal view. Wall very thin, 250–300 μm thick near the distal edge, concave on both internal and external sides.

Locality.—Gerstetten, near Nattheim, Germany. n°GER 1 coll. Univ. Nancy.

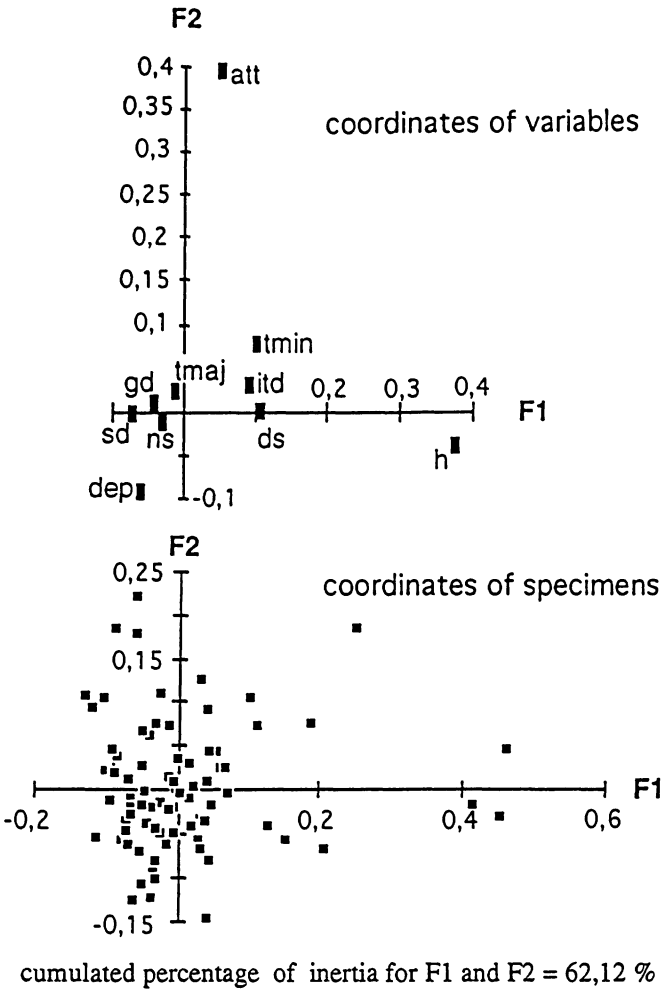


FIGURE 6—Specimen scores and correlation of variables of two first factorial axes of correspondences analysis.

Comparison.—This sample from Nattheim shares many common characters with the population from Kachchh. Nevertheless, its dimensions are bigger and therefore recognition of a different species is justified. It is also noteworthy that the pennular pattern is clearer in the sample described from Germany. This difference is tempered by other topotypes of *Epistreptophyllum* from the Stuttgart collections in which all transitional steps exist between horizontal menianae and sharp granules more or less vertically aligned. Compared to the topotypic *Epistreptophyllum* from Nattheim, the Indian specimens display a similar range of variation in septal structure and ornamentation, and other generic characters. In accordance with this study and the overview of the ratio "Number of septa/diameter" of the different species given by Löser (1994, figure 23), we can expect similar intraspecific variability in German *Epistreptophyllum* of the Upper Jurassic.

Remark.—Milaschewitsch (1876) has described this variability in the original diagnosis but subsequent authors have more or less emphasized the importance of sharp granulations (Geyer 1954, Beauvais 1964, Roniewicz 1966).

DISCUSSION

The variable fauna of Kachchh was described by Gregory as being composed of five different nominal species belonging to three different new genera of his family Ethmotidae: *Protethmos*, *Metethmos*, *Frechia*. Following Vaughan and Wells (1943), we confirm that these three genera are synonyms of *Epistreptophyllum*. Gregory (1900, p 163) distinguished *Epistreptophyllum* from *Protethmos* and *Metethmos* on the basis of his incorrect assumption that the former had imperforate septa and the latter had perforate septa near the inner and distal margin. The shape of the corallum, another distinguishing character suggested by Gregory displays a wide range of gradational variation and therefore is not significant.

Over the past century and a half, the genera *Epistreptophyllum* and *Protethmos* have been referred to numerous families (Table 1). This situation, is a consequence of the poor knowledge of the morphology of *Epistreptophyllum* and *Protethmos* as well as imprecise definition of families. Through the description of topotypes from Nattheim, the morphology of *Epistreptophyllum* is now more precisely known, although families remain poorly defined. Among the families cited in Table 1, Plesiofungidae and Ethmotidae are nomenclaturally incorrect (art. 63 of the code). Fungiidae and its type-genus have a completely different septal structure. The family Calamophyllidae has been based on *Calamophyllia* whose Burdigalian name-bearing type of the type-species is lost. The type genus is now considered as incertae sedis (Alloiteau, 1957, p. 176). This family should therefore be dropped. The assignment of *Epistreptophyllum* to the Dermosmiliidae is still possible. Unfortunately, we know very little about *Dermosmilia*, the type genus of the Dermosmilidae, and a revision of the type species is needed. We can only note that the figures of septal lateral faces within *Dermosmilia*, as illustrated in the pioneering work by Koby, 1889 (see pl. 129, figure 11 and not 2 as indicated in the text p. 547), are quite compatible with our description of *Epistreptophyllum*. The assignment of this genus to the Haplaraeidae can be rejected. The holotype of *Haplaraea elegans*, the type species of the type genus has been observed. The absence of a wall, the regularity in the distribution of synapticulae and in septal ornamentation preclude this option. The assignment of the genus to the Acrosmiliidae, to the

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FIGURE 7—*1–7—Epistreptophyllum cornutiformis* Gregory. *1–2*, RUC1994I 128, Patcham Formation (Bathonian) of Jumara Dome, *1*, side view, *2*, view of upper surface, ×4. *3*, RUC1994I 120, Chari Formation (Callovian) of Keera Dome, side view, ×4. *4*, RUC1994I 215, Patcham Formation (Bathonian) of Jumara Dome, view of upper surface, ×3. *5–6*, RUC1994I 133, Patcham Formation (Bathonian) of Jumara Dome, *5*, view of upper surface, see bilateral symmetry, *6*, side view, ×4. *7*, RUC1994I 130, Patcham Formation (Bathonian) of Jumara Dome, view of upper surface, ×3. *8–11 Epistreptophyllum commune* Milaschewitsch, Upper Jurassic (Beckeri Zone Upper Kimmeridgian) of Margareten Wald, Nattheim; collection G. Pistl 1972, *8–9*, Collection no. SMNS 62638/2, *8*, view of upper surface, *9*, side view; *10–11*, Collection no. SMNS 62638/1, *10*, view of upper surface, *11*, side view, all natural size. *12–17 Epistreptophyllum cornutiformis*, *12–13*, RIJC1994I 219 colonial or pseudocolonial form, Patcham Formation (Bathonian) of Jumara Dome, *12*, view of upper surface exhibiting a rejuvenescence pattern, *13*, side view, ×4. *14*, RUC1994I 214, Patcham Formation (Bathonian) of Jumara Dome, view of upper surface, see the pinched outline of the calice ×3, *15*, RUC1994I 197, Patcham Formation (Bathonian) of Jumara Dome, polished upper surface, ×4, *16*, RUC1994I 220, Patcham Formation (Bathonian) of Jumara Dome, side view showing thin epithecal ring, note the attachment area which exhibits a mould of a coral with quite different type of septa (probably montlivaltid), ×4, *17*, RUC1994I 117, Chari Formation (Callovian) of Keera Dome, side view, ×4.

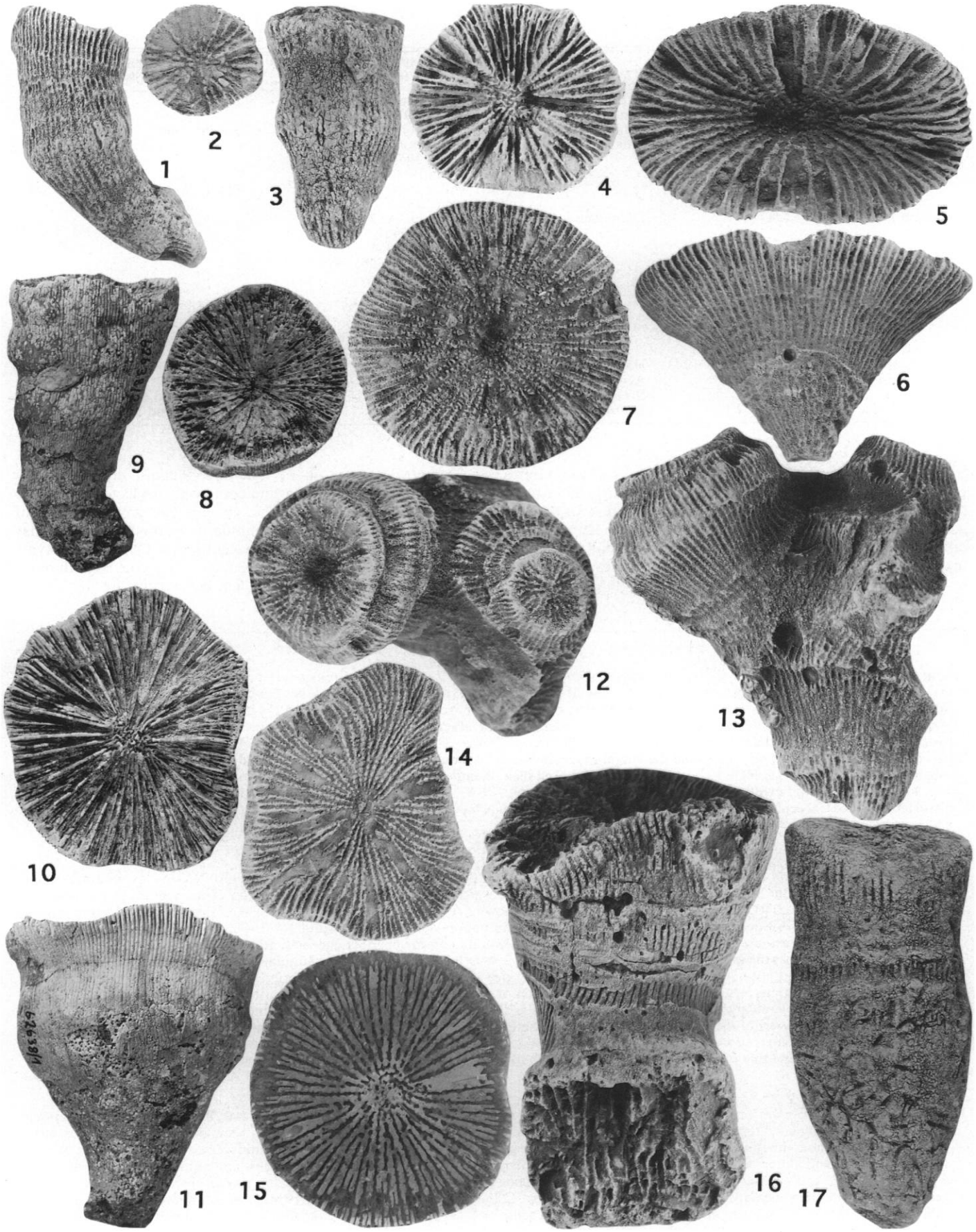
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TABLE 1—Familial assignment of *Epistreptophyllum* and *Protethmos* (here established as a junior synonym) in the literature. *Metethmos, Sematethmos,* and *Frechia* are usually classified in the same way as *Protethmos.*

Family	Author	Type genus	Nomenclature	*Epistreptophyllum* referred to this family by	*Protethmos* referred to this family by
Fungiidae	Dana 1846	Fungia	valid	Milaschewitsch 1876	
Plesiofungidae	Duncan 1885	none	unvalid	Duncan 1885	
Ethmotidae	Gregory 1900	none	unvalid	Gregory 1900	Gregory 1900
Calamophyllidae	Vaughan and Wells 1943	Calamophyllia	valid	Vaughan and Wells 1943	Vaughan and Wells 1943
				Geyer 1954	
				Wells 1956	Wells 1956
				Flügel 1966	Flügel 1966
				Liao 1982	
Dermosmiliidae	Koby 1887	Dermosmilia	valid	Alloiteau 1952	
				Sokolov 1962	
				Beauvais 1964	
				Roniewicz 1966, 1976	
				Turnsek 1972	
				Beauvais 1980	
				Liao and Xia 1985	Liao and Xia 1985
				Rosendhal 1985	
				Chevalier and Beauvais 1987	
				Errenst 1990	
Haplaraeidae	Vaughan and Wells 1943	Haplaraea	valid	Löser 1994	
Acrosmiliidae	Alloiteau 1952	Acrosmilia	valid		Beauvais 1978
Synastraeidae	Alloiteau 1952	Synastraea	valid		Chevalier and Beauvais 1987
Latomeandridae	Alloiteau 1952	Latomeandra	valid		Morycowa and Roniewicz 1995

Synastraeidae or to the Latomeandridae is difficult to establish because a revision taking into account a thorough description of pennular arrangement and morphology is needed for the type genera of these families. Even a synonymy with *Acrosmilia* is not to be excluded. We believe that it is more useful to describe taxa precisely than to propose a new and groundless assignment of a genus to a family.

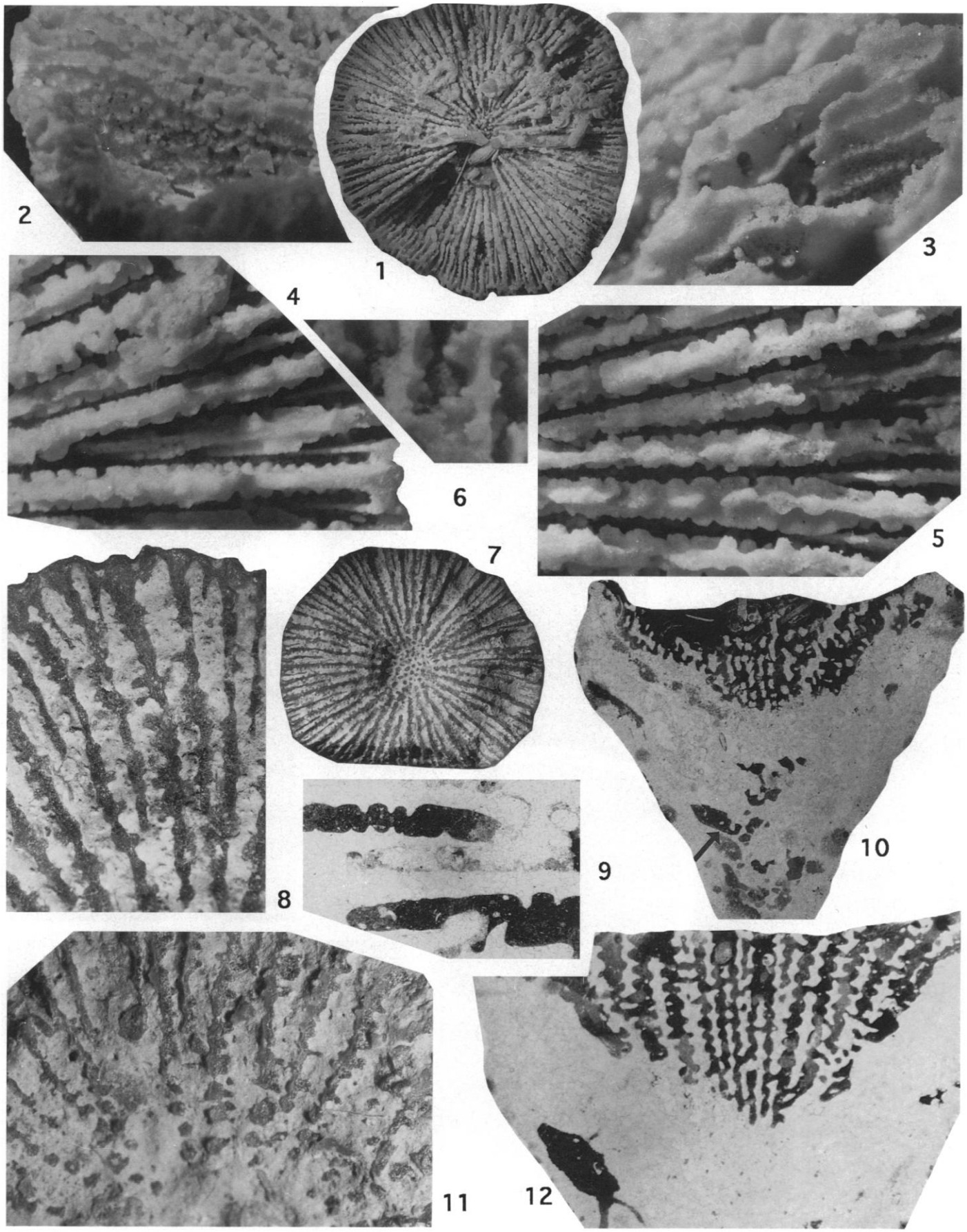
The new description of *Epistreptophyllum* presented here points out some distinctive and commonly neglected characters that should be sought for other genera. The ornamentation of septa is highly variable. The pennula-like structures lack regular vertical alternation between adjacent septa. They are not symmetrically arranged around trabeculae. They coexist with other kind of granules (Figure 11). Their outer rims are neither di-

→

FIGURE 8—*1–6*—*Epistreptophyllum* sp. Upper Jurassic of collection F. Papier, *1–6*, *1*, view of upper surface, ×2.5, *2*, lateral view of a septum exhibiting granules and balconies, ×6.8, *3*, lateral view of septa from back to front, exhibiting subhorizontal ridges and pores, subhorizontal ridges without pores, granules, ×27.5, *4–5*, enlarged part of the corallite from upper view showing a similar variability, ×22 and ×14, *6*, perpendicular view to the previous one, along the outer edge, showing alternating pennulae like structures, ×16.7. *7–12 Epistreptophyllum cornutiformis* Gregory, Patcham Formation (Bathonian) of Jumara Dome, *7–8*, RUC1994I 162, *7*, view of upper surface, ×3.7, *8*, enlarged part of the corallite from upper view, note the lateral expansions such as stout and blunt or long and curved granules, and flat, subhorizontal, irregular balconies, ×14.7, *9*, RUC1992I 1011, septa exhibiting sharp granules in a transverse section, skeleton in white. ×24.3, *10*, RUC1994I 173, longitudinal section exhibiting vesicular dissepiments (arrow), ×6.8, *11*, RUC1994I 177, enlarged part of the upper surface exhibiting dissociation of the trabeculae, ×30.6, *12*, RUC1992I 1032, longitudinal section between periphery and the axis showing pennular-like structure and anastomosed septa, ×6.5.

FIGURE 9—*Epistreptophyllum cornutiformis* Gregory, Patcham Formation (Bathonian) of Jumara Dome. *1*, RUC1994I 169, longitudinal section, note the angles between the subhorizontal ridges and the trabeculae which change from upper inner margin of the septum to outer margin, skeleton in white, ×12.6, *2*, RUC1994I 134, view of upper surface showing rejuvenescence, ×5, *3*, RUC1994I 175, longitudinal section showing vesicular dissepiments, relationship between subhorizontal ridges and trabeculae, skeleton in white, ×8.2, *4–5*, RUC1994I 221, *4*, view of the upper surface showing anastomosed septa, ×3, *5*, enlarged part of the corallite from upper oblique view, note the evenly spaced pores, trabeculae and subhorizontal ridges at the inner upper part of the septum, ×15, *6–7*, RUC1995I 558, *6*, longitudinal section exhibiting slightly curved to almost straight spines and pores, ×4; *7*, enlarged longitudinal oblique view of a part of a single septum showing slightly curved spine, ×60, *8–9*, RUC1994I 196, *8*, transverse section exhibiting dissociation of trabeculae towards the center, anastomosed septa at the inner edge and papillose columella, ×4, *9*, enlarged part of the transverse section showing dissepiments and their continuity with a laminar layer, ×60, *10–11*, RUC1994I 217, *10*, view of the upper surface showing ornamented, anastomosed septa, ×3, *11*, enlarged part of the corallite from upper oblique view, note the demarcation of the trabeculae along the distal part of the septa and opening of pores, ×15, *12*, RUC1994I 174, part of the transverse section, note that one side of the septum shows horizontal "pennular-like" structure and other side sharp granules, ×18.6.

FIGURE 10—*Epistreptophyllum cornutiformis* Gregory, Patcham Formation (Bathonian) of Jumara Dome. *1–2*, RUC1994I 172, *1*, transverse section, note the granulated, anastomosed septa, wall, costae and papillose columella, ×4.7, *2*, enlarged view of the papillose columella in transverse section, note the subangular to angular outline of the papilla, ×17.9, *3–4*, RUC1994I 153, *3*, transverse section exhibiting papillose spongy columella and almost a ring of dissepiments, ×9.3, *4*, enlarged part of same showing dissepiments and septal ornamentation, ×25.3, *5–8*, RUC1994I 171, *5*, enlarged part of the transverse section showing spongy columella, ×14.2, *6*, laminar layer in septa, ×34.7, *7*, costae and exotheca, note the concavity of the dissepiments outwards, ×22, *8*, costae, ×22, *9–12*, RUC1994I 170, *9*, transverse section, ×7.1, *10*, enlarged part of the same showing irregular zig-zag pattern in septa, ×18.9, *11*, pennular like structure and other lateral expansions, ×18.8, *12*, pennular like structure, no visible teeth along the outer margin of the balcony, ×50.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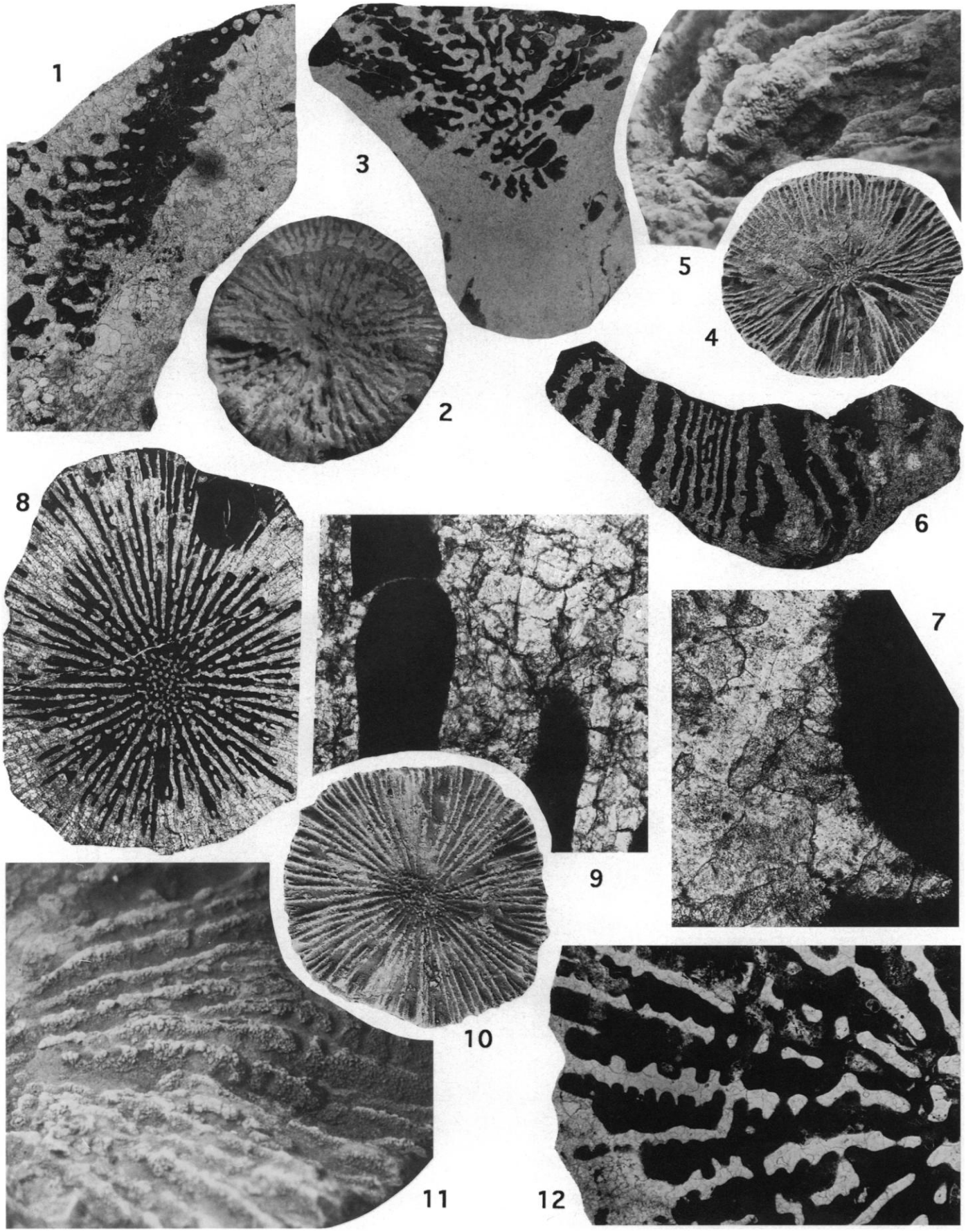
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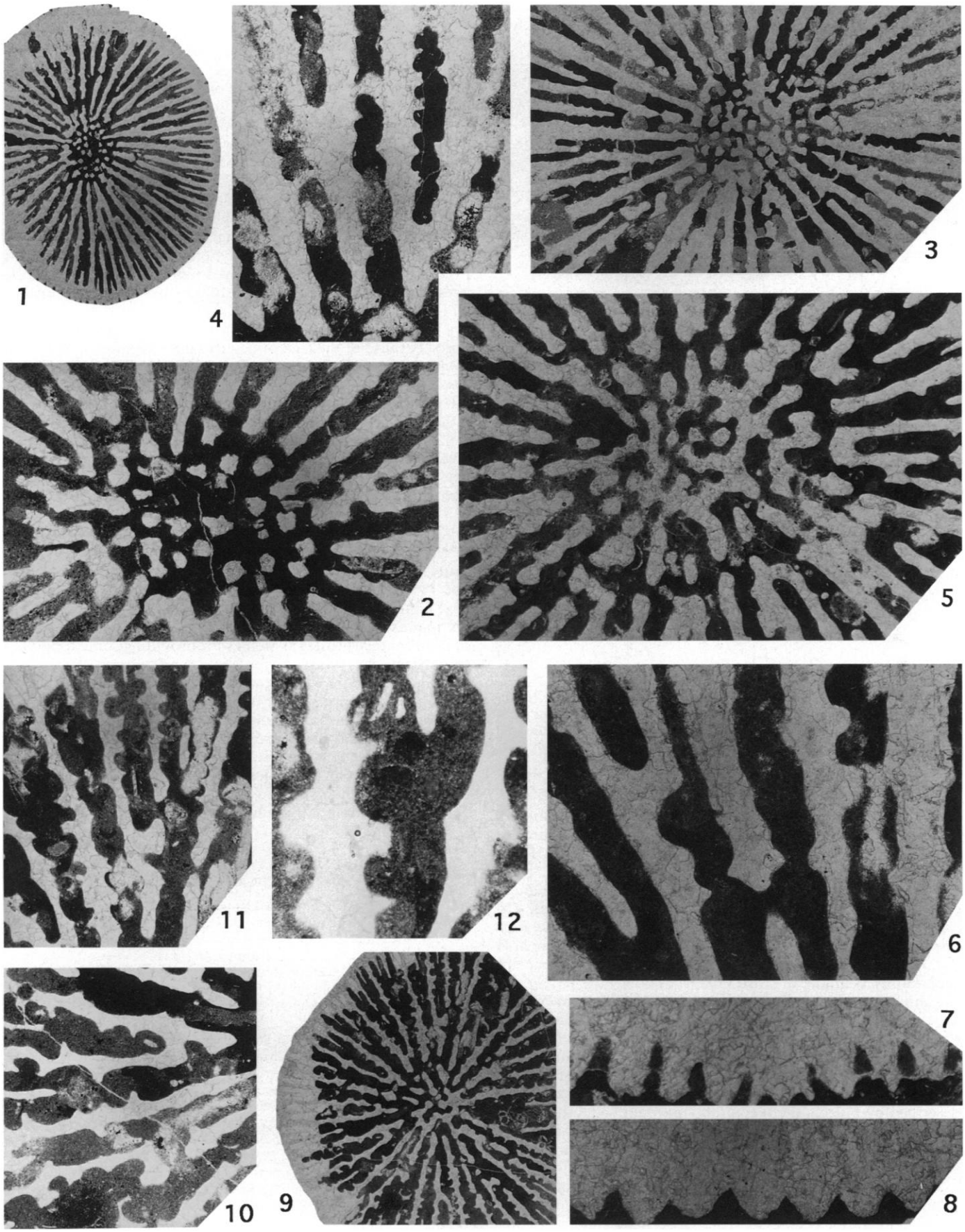
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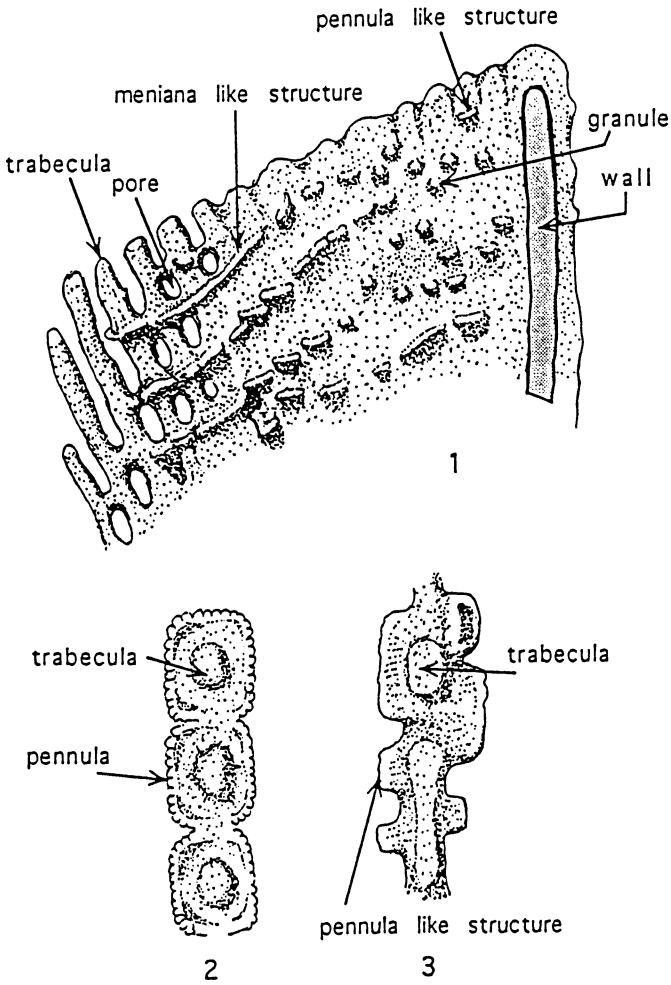

FIGURE 11—Model of septal morphology in *Epistreptophyllum*. *1*, lateral view. *2*, upper view of true pennulae in microsolenids for comparison. *3*, homologous upper view of pennulae like structure and their relationship with trabeculae in *Epistreptophyllum*.

rected upward nor clearly dentate. The distal edge is often smooth or devoid of pennula-like structures. Laminar layers are present and are connected with dissepiments producing the kind of wall observed within montlivaltids (Lathuilière, 1996). All these characters move *Epistreptophyllum* away from typical pennular corals assigned to different families such as *Chomatoseris*, *Microsolena*, *Dimorpharaea*, *Periseris*, *Kobya*, *Astreomorpha Leptoseris*, and so on. The following alternatives are clear: restrict the wide use of the morphological term "pennula", or split the superfamily Pennulacae sensu Gill (1967).

Similar structures to those observed in *Epistreptophyllum* are expected to be found in colonial genera. It seems that *Sematethmos*, described by Gregory (1900) on the basis of a single specimen, could be rather close or even an extreme morphotype of the same specific population of *Epistreptophyllum cornutiformis* (no new specimen has been found recently). *Sematethmos* described by Flügel (1966) could be misidentified, especially if we consider the differences in gemmation, corallum shape and pattern of anastomoses of septa according to his figure. In the same way, the phaceloid form described as *Epistreptophyllum* by Gill (1982) displays different septal ornamentation as well as a different endotheca, and it is presumably misidentified.

CONCLUSIONS

1. The corals from Kachchh described by Gregory under the generic names of *Protethmos*, *Metethmos* and *Frechia* belong to a single highly variable species: *Epistreptophyllum cornutiformis*. This provides more proof of the excess of the typological approach.

2. A new kind of septal ornamentation is described (Figure 11) with its own variability. We would call attention of authors to the necessity of looking for these particular characters in other genera in order to test their taxonomic value. This indicates too that septal ornamentation, like other characters, might be observed as far as possible for variability.

3. Among the elements of septal ornamentation we describe "pennula like structures" which are in many regards different from typical pennular coral septal ornamentation. This may be a result of the polyphyletic nature of the superfamily Pennulacae Gill, 1967.

4. A familial assignment of *Epistreptophyllum* cannot be proposed because of the lack of detailed data for most type genera of named families, including *Dermosmilia*, *Synastraea*, *Latomeandra*, and *Acrosmilia*. The ritual of taxonomic publication often results in classifications that are taken as absolute truth rather than provisory hypotheses based on present knowledge. We support greater use of open nomenclature at the familial level for corals and suggest that it is more useful to provide detailed descriptions of genera awaiting further systematic analyses at the family level.

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ACCEPTED 5 NOVEMBER 1996

APPENDIX 1—Original measurements of Epistreptophyllum cornutiformis used for statistical analyses.

Specimen n°	n°	gd	sd	h	att	Ns	ds	Tmaj	Tmin	itd	dep
RUC1994l 128	1	5.9	5.3	14.2	2.8	50	7	0.14	0.1	0.1	0.4
RUC1994l 181	2	7.3	6.8	6.8	5	73	6	0.2	0.1	0.15	0
RUC1994l 203	3	7.3	6	10	6	55	7	0.2	0.1	0.1	0
RUC1994l 219	4	7.7	7	20.5	5.7	70	7	0.14	0.14	0.1	0.7
RUC1994l 129	5	7.9	6.8	8.5	5.8	76	8	0.15	0.1	0.15	0.5
RUC1992l 997	6	8.5	8	7.5	2	75	8	0.25	0.05	0.1	1
RUC1992l 1006	7	9	7	7	3	87	7	0.15	0.05	0.1	1.5
RUC1994l 218	8	9.4	6.8	8.7	2.7	92	6	0.14	0.07	0.07	0.2
RUC1994l 134	9	9.5	9	9.5	1	89	7	0.25	0.1	0.1	1.4
RUC1994l 135	10	9.7	7.7	10	28	70	6	0.3	0.1	0.05	0.8
RUC1994l 204	11	9.8	9.5	6.7	3	70	7	0.25	0.1	0.1	0.5
RUC1994l 200	12	9.9	9	7.8	4	92	7	0.35	0.1	0.1	2
RUC1992l 1021	13	10	10	17.3	3.5	101	7	0.15	0.1	0.1	0
RUC1994l 177	14	10.3	9.8	5	3.9	91	6	0.15	0.05	0.1	2
RUC1994l 138	15	10.6	10	5.7	10	98	6	0.3	0.05	0.1	1.1
RUC1992l 1007	16	10.9	9.3	5	3	82	8	0.25	0.1	0.1	0.4
RUC1994l 178	17	11	10	6	4.5	88	7	0.2	0.1	0.1	0.9
RUC1995l 519	18	11	10	14.4	8	110	7	0.2	0.05	0.05	2.1
RUC1994l 210	19	11.1	10.8	5.3	4.8	92	6	0.17	0.1	0.03	0.4
RUC1994l 137	20	11.2	1 1	10	5	89	8	0.25	0.1	0.1	1.2
RUC1994l 180	21	1 1.3	11.2	7.5	2.2	93	7	0.15	0.025	0.1	1.4
RUC1995l 517	22	1 1.6	11	8	2.8	112	6	0.2	0.05	0.1	0
RUC1994l 176	23	11.9	9.8	6.8	3	90	6	0.25	0.05	0.1	0.3
RUC1994l 156	24	12	11.8	8	2	106	7	0.2	0.1	0.15	1.8
RUC1994l 201	25	12	10	7	4.1	82	7	0.25	0.15	0.15	1.3
RUC1992l 1019	26	12	11.9	8.5	3.5	106	7	0.2	0.1	0.1	0.9
RUC1995l 520	27	12	11.5	8	4	99	7	0.2	0.15	0.1	0.4
RUC1994l 150	28	1 2.3	10	9.2	2.7	86	6	0.25	0.07	0.07	0.5
RUC1992l 1029	29	12.4	11.4	8	3	91	6	0.3	0.1	0.1	1
RUC1994l 169	30	12.8	10.3	8.7	4.4	82	7	0.25	0.15	0.1	2.9
RUC1994l 198	31	12.9	11.3	10.5	4.7	84	6	0.17	0.07	0.07	0.6
RUC1994l 136	32	13	12	5.6	3	105	6	0.25	0.05	0.1	0.9
RUC1994l 211	33	13	12.9	5.8	2.8	90	8	0.25	0.1	0.1	0
RUC1992l 1002	34	13	11.4	5.5	3	75	6	0.25	0.15	0.1	0.5
RUC1994l 199	35	13.1	11.9	5.7	5.3	104	7	0.21	0.03	0.1	1.6
RUC1994l 179	36	13.2	12	6.7	3.8	97	7	0.2	0.1	0.05	1.3
RUC1992l 1013	37	13.4	10.4	9.4	5.5	95	7	0.2	0.1	0.1	2
RUC1994l 158	38	13.5	12.5	6	5.5	93	5	0.15	0.05	0.1	2.3
RUC1992l 71	39	13.7	10	11.5	4.7	103	7	0.25	0.1	0.1	1.9
RUC1994l 152	40	13.9	13.2	9.5	3.6	107	5	0.14	0.03	0.07	0.4
RUC1994l 163	41	13.9	12	5.5	7	74	5	0.25	0.1	0.05	0.4
RUC1994l 132	42	14	8.9	26	5.5	92	7	0.21	0.07	0.1	1
RUC1994l 161	43	14	12.8	10.7	4.8	117	6	0.3	0.05	0.1	1.3
RUC1994l 162	44	14	13	8.3	4	58	6	0.3	0.1	0.1	2
RUC1994l 166	45	14	12	10.4	3.6	86	5	0.3	0.1	0.15	2
RUC1994l 168	46	14	13.2	8	4	90	6	0.25	0.05	0.05	2.6
RUC1992l 1025	47	14	13.5	10	9	125	6	0.35	0.1	0.15	0
RUC1992l 1030	48	14	11.5	8.2	4.5	79	5	0.25	0.1	0.1	0.8
RUC1994l 155	49	14	12	8.5	6	73	5	0.2	0.1	0.15	0
RUC1994l 215	50	14.1	12.7	7.8	4	108	6	0.28	0.1	0.14	1.2
RUC1992l 1022	51	14.2	9.8	10	4.5	93	7	0.25	0.05	0.1	0.3
RUC1994l 148	52	14.3	12.5	14.5	3.2	80	5	0.28	0.1	0.1	1.8
RUC1994l 159	53	14.5	12.5	10.4	3.5	112	6	0.2	0.05	0.15	2
RUC1992l 1028	54	14.6	12.8	9.6	3	105	7	0.25	0.1	0.1	0.5
RUC1994l 157	55	14.8	13	7.7	4	93	6	0.25	0.1	0.1	2
RUC1994l 164	56	14.8	14.5	4.5	7	98	6	0.35	0.15	0.05	1.3
RUC1994l 151	57	15	14.7	11.8	2.8	96	5	0.35	0.07	0.07	0.4
RUC1994l 207	58	15.2	14.5	6.9	5.4	111	5	0.21	0.1	0.03	0.8
RUC1994l 167	59	15.3	8.6	9	4.8	101	7	0.25	0.05	0.1	1.7
RUC1994l 147	60	15.4	14.3	12.1	4	111	6	0.25	0.07	0.1	0.6
JU/25/30	61	15.6	14.5	8.3	3.3	112	5	0.35	0.1	0.1	1.1
RUC1994l 154	62	15.6	13.2	13.8	5.2	107	6	0.3	0.1	0.1	1
RUC1995l 518	63	15.6	12.7	10	7.6	115	7	0.25	0.1	0.05	1.6
RUC1994l 220	64	15.7	12.4	20	9	118	8	0.21	0.1	0.1	1.5
RUC1994l 206	65	15.9	14.9	9.6	3.6	126	5	0.21	0.1	0.07	0.5
RUC1994l 221	66	16.1	13.5	6.1	7.5	108	5	0.28	0.14	0.17	0.8
RUC1994l 133	67	16.5	11.5	1 0	2.4	112	6	0.25	0.07	0.07	2.5
RUC1995l 516	68	16.5	14	8.5	3	109	5	0.35	0.1	0.1	0.9
RUC1995l 514	69	16.6	16.5	11.4	2	148	7	0.25	0.03	0.03	1.3
RUC1994l 209	70	16.7	15.8	8.9	3.8	118	6	0.25	0.1	0.03	1
RUC1994l 149	71	16.8	14.2	8.3	5.5	115	6	0.17	0.07	0.07	1.4
RUC1992l 1033	72	16.8	11.4	10.4	5	87	6	0.2	0.1	0.1	0
RUC1995l 521	73	16.8	15	10.8	4.5	103	6	0.4	0.1	0.05	0
RUC1992l 1012	74	17.4	14	9.8	2.5	100	5	0.35	0.1	0.15	1.7
RUC1994l 208	75	17.5	1 1	7.4	5.5	91	6	0.21	0.03	0.1	0.7

APPENDIX 1—Continued.

Specimen n°	n°	gd	sd	h	att	NS	ds	Tmaj	Tmin	itd	dep
RUC19941 216	76	17.9	14.5	10.2	8	118	6	0.32	0.07	0.1	2
RUC19941 165	77	18	16	6.6	8.9	130	6	0.4	0.15	0.1	2
RUC19941 130	78	18.3	17.3	11	6	130	6	0.28	0.2	0.14	1.9
RUC19941 214	79	18.3	15	7.5	11.3	124	5	0.25	0.1	0.1	0.6
RUC19941 160	80	18.3	17	7.9	6	115	7	0.3	0.05	0.1	2.8
RUC19951 513	81	18.6	17.9	11.3	1.6	112	5	0.17	0.07	0.1	1.8
RUC19951 515	82	18.6	18.3	10.5	7.8	124	5	0.25	0.07	0.07	0.5
RUC19941 217	83	18.7	16.9	12.6	6.2	123	6	0.35	0.1	0.07	1.7
RUC19941 131	84	21	15.3	14.6	4.5	116	5	0.4	0.2	0.17	1.4

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EARLY CAMBRIAN *LINGULELLOTRETA* (LINGULATA, BRACHIOPODA) FROM SOUTH KAZAKHSTAN (MALYI KARATAU RANGE) AND SOUTH CHINA (EASTERN YUNNAN)

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ABSTRACT—"*Lingulepis*" *malongensis* Rong from the upper part of the Lower Cambrian Chiungchussu Formation of Yunnan is referred to *Lingulellotreta* Koneva; *L. malongensis* (=*Lingulellotreta ergalievi* Koneva) is redescribed on the basis of new material from the Lower Cambrian of south Kazakhstan. It is the earliest known taxon of the Lingulellotretidae, which is unique within the Linguloidea in having an elongate pedicle foramen and internal pedicle tube. The occurrence of *Lingulellotreta malongensis* in south China is considered usually to be of Atdabanian age, but brachiopod based correlation with south Kazakhstan suggests that a possible Botomian or younger age, for both the upper part of Chiungchussu Formation in Yunnan and the lowermost part of Shabakty Group in the Malyi Karatau Range, is equally plausible.

INTRODUCTION

THE FAMILY Lingulellotretidae is represented by some of the most distinctive Cambrian lingulates in of the Malyi Karatau Range, southern Kazakhstan. In Kazakhstan, this family has a lowermost occurrence in the early Botomian (*Ushbaspis limbata* trilobite Zone) and ranges into the Tremadocian. Although there has been a large number of recent articles documenting the Early and early Middle Cambrian lingulate brachiopod faunas from the western USA (Rowell, 1977; 1980), Siberia (Pelman, 1977; Aksarina and Pelman, 1978; Ushatinskaya, 1992) and Australia (Roberts and Jell, 1990; Kruse, 1990; Laurie, 1986; Brock and Cooper, 1993), there is no record of lingulellotretids from these areas. The unusually well-preserved specimens of "*Lingulepis*" *malongensis* redescribed recently by Jin et al. (1993) from the upper part of the Chiungchussu Formation (Lower Cambrian) of Yunnan, is reassigned to *Lingulellotreta*, the earliest known taxon of the family. Moreover, there are no significant morphological differences between specimens of *Lingulellotreta* from the Malyi Karatau Range and Eastern Yunnan; they are here regarded as conspecific. The type, and only known species, *Lingulellotreta ergalievi* Koneva, 1983, is regarded as a junior synonym of *Lingulellotreta malongensis* (Rong, 1974). The new, well-preserved *Lingulellotreta* from Kazakhstan allows precise reconstruction of the musculature and other interior characters.

GEOLOGICAL SETTING AND CORRELATION

Kazakhstan.—The brachiopods from the Malyi Karatau Range were etched (by means of 10 percent acetic acid) from the lower part of the Shabakty Group (Lower Cambrian), exposed on the east bank of the Ushbas River (sample 1233) and in the Baba-Ata River valley (sample 5/26), northwest of Zhanatas (Figures 1, 2). The Lower Cambrian stratigraphy and geology of this area was described in detail by Ergaliev and Pokrovskaya (1977, p. 8–12, figs. 1–4); the associated trilobites, lingulate brachiopods, and small shelly fossils have been described by Ergaliev and Pokrovskaya (1977), Gorjansky and Koneva (1983), and Missarzhevsky and Mambetov (1981).

The lingulate brachiopod *Linnarssonia constans* appears in the *Microcornus parvulus–Adyshevitheca* Zone (sample 1235, section VI of Ergaliev and Pokrovskaya, 1977, fig. 4), which is the lower unit of the Shabakty Group (0–4.5 m above the lower