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Some genera and species of dissepimented solitary Rugosa (Anthozoa) from the Pennsylvanian (Carboniferous) and Cisuralian (Permian) of North America. Part 2. *Dibunophylloides* Fomichev, 1953

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ABSTRACT:

Fedorowski, J. and Chwieduk, E. 2025. Some genera and species of dissepimented solitary Rugosa (Anthozoa) from the Pennsylvanian (Carboniferous) and Cisuralian (Permian) of North America. Part 2. *Dibunophylloides* Fomichev, 1953. *Acta Geologica Polonica*, 75 (3), e53.

Species that earlier authors included in *Dibunophyllum* Thomson and Nicholson, 1876 are re-identified here as belonging to *Dibunophylloides* Fomichev, 1953 and specimens from the Missourian (Pennsylvanian) deposits of the Glass Mountains (SW Texas, USA) are described. Species described previously in adequate detail and specimens from our collection display great morphological diversity. This and the lack of data on intraspecific variability for most species described so far resulted in the introduction here of six new species (*Dibunophylloides differentialis*, *D. parcus*, *D. colligatus*, *D. similis*, *D. infirmis* and *D. complexus*). An additional species is identified as *Dibunophylloides* cf. *valeriae* (Newell, 1935) and four species are left in open nomenclature. Stressful extrinsic conditions, documented by common rejuvenations and possibly variegated micro-environmental niches on the one hand and close relationships of specimens on the other hand are suggested as responsible for the large morphological variability and repetitions of some skeletal features across species. *Dibunophylloides* supplements a group of genera suggested by Fedorowski (2023) as having originated in the Paleotethyan superprovince before migrating to the North American superprovince. Paleobiogeography, including that based on rugose corals) provides an important tool for tectonic and paleoenvironmental reconstructions. However, coral taxonomy may be hampered by the great variability displayed by many taxa.

Key words: SW Texas (USA); Dibunophylloides (Anthozoa, Rugosa); Missourian; Taxonomy; Relationships; Paleobiogeography.

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INTRODUCTION

Several former North American authors (e.g., Newell 1935; Moore and Jeffords 1945; Jeffords 1948; Ross and Ross 1962, 1963; Rowett and Sutherland 1964; Cocke 1966, 1969, 1970; Cocke and Haynes 1973; Cocke and Molinary 1973) identified some dissepimented solitary rugose corals as *Dibunophyllum* Thomson and Nicholson, 1876. We question that identification and discuss two possible options (see remarks for the genus *Dibunophylloides*): that it: (i) is congeneric with the genus *Dibunophylloides* Fomichev, 1939, or (ii) represents a new genus. Irrespective of the option, corals described in this paper are included in

the Subfamily Dibunophyllinae Wang, 1950. A third option expands on the second, i.e., they have a separate generic position within the frame of a new subfamily, comprising the North American *Dibunophyllum*-like genera.

Already Sando (1985) was conscious of a difference between European and North American *Dibunophyllum*. He suggested *Amandophyllum* Heritsch, 1941 as a temporary substitute name for the North American '*Dibunophyllum*' and '*Neokoninckophyllum*' Fomichev, 1939. Sando's (1985) idea as well as the ideas of Fedorowski (1971, 1986) and Garcia-Bellido and Rodríguez (2005) were recently analyzed and rejected by Fedorowski (2022, p. 271). Here we follow arguments of that analysis without its repetition. We recognize similarities in the mature growth stages of both early Permian *Amandophyllum* from the Carnic Alps and the Pennsylvanian to Permian North American '*Dibunophyllum*' species, but we consider them to be homeomorphic.

The indisputable *Dibunophyllum* species occurred in the upper Visean Windsor Group of Nova Scotia, Canada, i.e., at the south-eastern margin of the Euramerican continent. That area was distinguished by Sando (1975) as the North American Maritime Province. Fedorowski (1981) included that area in his Western European Province since the species described by Bell (1929), Lewis (1935) and other authors (see Bamber *et al.* 2017, p. 59 for the complete list) are the same as those occurring in Western Europe. That relationship remains unquestioned (Fedorowski 2022, 2023). However, rare representatives of *Dibunophyllum* may have occurred in various other Carboniferous strata in the western part of North America. Fedorowski *et al.* (2012) described *Dibunophyllum bipartitum craigianum* (Thomson, 1874) from the middle Bashkirian refuge area in the Sverdrup Basin, Canadian Arctic Archipelago. Also, rare occurrences of poorly studied specimens of *Dibunophyllum* were listed by Bamber *et al.* (2017, pp. 59, 60) from the upper Visean and Serpukhovian of the United States. Some of them may truly belong to that genus, but their incomplete preservation and/or incomplete description do not allow their indisputable acceptance. However, these probable occurrences may indicate a true relationship of some western North American specimens to European Dibunophyllinae and, consequently, the incorporation of the North American '*Dibunophyllum*' within that family.

Following Fedorowski (1997) we consider the cardinal and the counter septa as the only protosepta in the Rugosa.

GEOLOGICAL SETTING AND MATERIAL AND METHODS

Specimens described in this paper were derived from the same localities as those included in Part 1 of the series of our papers (Fedorowski and Chwieduk 2024). Thus, the reader is kindly directed to that paper. Also, the methods applied here are the same as those described in that paper. The number of specimens included in particular species is mentioned in the Material sections of the species descriptions.

SYSTEMATC PALEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder Aulophyllina Hill, 1981
Family Aulophyllidae Dybowski, 1873
Subfamily Dibunophyllinae Wang, 1950
Genus *Dibunophylloides* Fomichev, 1953

TYPE SPECIES: *Cyathoclisia simmetrica* Dobrolyubova, 1937; subsequently designated by Fomichev (1953, p. 393).

DIAGNOSIS: See Fedorowski (2017, p. 476).

REMARKS: The remarks that follow are based on the Donets Basin fauna (Fomichev 1953; Fedorowski 2017) with references to the specimens newly described here and to the Pennsylvanian taxa from Kansas, Oklahoma and Texas (e.g., Newell 1935; Moore and Jeffords 1945; Jeffords 1948; Rowett and Sutherland 1964; Cocke 1966, 1970; Cocke and Haynes 1973; Cocke and Molinary 1973). The rugose coral faunas of the Donets Basin, Ukraine and the south-western United States demonstrate several similarities. Also, their stratigraphic positions are comparable (Fedorowski 2019, 2022). The similarities are documented so far by the occurrence in the Donets Basin and SW Texas of genera *Barytichisma* Moore and Jeffords, 1945 (Fedorowski and Vassilyuk 2011) and *Yuanophylloides* Fomichev, 1953 (Fedorowski 2017, 2022; Fedorowski and Chwieduk 2024). The occurrence in both areas of a common species, i.e., *Dibunophyllum*? (= *Yuanophylloides) inauditum* Moore and Jeffords, 1945 (Fedorowski 2019) and of the genus *Dibunophylloides*, established in this paper, strengthen that similarity.

Derivation of *Dibunophylloides* from *Dibunophyllum* in the Donets Basin was documented al-

though not postulated *explicite* by Fedorowski (2017). He described two new species, i.e., *Dibunophyllum medium* and *Dibunophylloides paulus* from the same locality and the same beds representing lowermost Bashkirian strata (Limestone D510 = earliest Voznessenkian = earliest Chockerian). The senior author of this paper (JF) herein declares full support for that suggestion.

Re-examination by the senior author of Fomichev's (1953) original collection, the reinterpretation by him of the genus *Dibunophylloides* and his description of a few Bashkirian species of that genus (Fedorowski 2017) allow for the recognition of the most important features and distinctive characteristics of *Dibunophylloides*. An occurrence of the axial column in *Dibunophylloides* early in ontogeny documents its close relationship to *Dibunophyllum* while the disappearance of that feature in the course of *Dibunophylloides* ontogeny is a major character distinguishing the two genera. In *Dibunophyllum* the axial column is permanent.

The occurrence of *Dibunophylloides* Fomichev, 1953 in North America is adequately documented as discussed in this paper, although its first appearance is not quite certain. *Neokoninckophyllum arcuatum* Moore and Jeffords, 1945 from the Marble Falls Formation (= R2 to G1 Biozones; Fedorowski 2019, p. 82) can be temporarily considered as the oldest North American species of *Dibunophylloides*. Unfortunately, the incomplete description and illustrations of its holotype (Moore and Jeffords 1945, p. 161, figs 162–164), lack of information on its neanic growth stage, almost a total reduction of the axial structure in the advanced mature growth stage and lack of a clear distinction between the inner and outer tabularium (Moore and Jeffords 1945, fig. 164c), may put its taxonomic position in doubt. Only the early mature growth stage of the holotype and one paratype (Moore and Jeffords 1945, figs 164b and 163, respectively) resemble the same growth stages in *Dibunophylloides* adequately. A single specimen identified by Rowett and Sutherland (1964) as *Dibunophyllum* sp. A from the upper part of the Wapanucka Formation (upper Morrowan) is slightly younger than the specimen described by Moore and Jeffords (1945) discussed above. It demonstrates the axial structure in the transverse section typical for *Dibunophylloides*, but its longitudinal section was neither illustrated nor described. Thus, it can only be suspected as a member of the latter genus. All characters typical for *Dibunophylloides* are demonstrated by two new species identified by Jeffords (1948) as *Dibunophyllum moorei* from Desmoinesian deposits of Oklahoma and *D. exigum* from Virgilian deposits of Kansas. The stratigraphically younger species of those two displays an axial column developed in its younger growth stage (Jeffords 1948, text-fig. 1a). Additionally, the early occurrence of the axial column in ontogeny, disappearing in the more advanced growth stage, was demonstrated by Ross and Ross (1962, pl. 162, fig. 5) in '*Dibunophyllum*' *moorei* from Desmoinesian deposits of SW Texas. An axial column cannot be demonstrated in the longitudinal sections of '*Dibunophyllum*' species described by Cocke (1966, pl. 3, figs 1b, 3b; 1970, pl. 1, figs 1c, 3b, 8b, pl. 2, figs 1b, 2b, 3b, 4b, 8b, 12b) from Missourian deposits, perhaps because early growth stages were not sectioned by him, but all other characters of these sections are typical for *Dibunophylloides*. An occurrence of the axial column in the early growth stages and its disappearance in more advanced growth stages, typical for *Dibunophylloides,* is established in some specimens described here from a similar stratigraphic level (see below). The occurrence of the axial column in the Virgilian species cited above documents the long-term existence of that plesiomorphic character in North American *Dibunophylloides* taxa. Despite the doubts mentioned, the data suggest a very probable occurrence of *Dibunophylloides* in North America since the early Bashkirian and its continuous occurrence up to the Cisuralian (early Permian).

Only a few species introduced by the earlier North American authors as *Dibunophyllum* were illustrated adequately to establish their true intraspecific variability. Most species were based on random sections of 2–3 specimens and some on a single illustrated specimen (Newell 1935; Jeffords 1948; Ross and Ross 1962, 1963; Rowett and Sutherland 1964; Frauenfelter 1965; Cocke 1966, 1969, 1970; Cocke and Haynes 1973; Cocke and Molinary 1973). The extremely wide variability both between specimens and during the growth of particular corallites (see below) suggest a similar variability within the earlier introduced taxa. This leaves the intraspecific variation unknown in the latter and we did not have an opportunity to re-investigate the original collections. Thus, we have decided to introduce new species names for our specimens rather than include them in the previous incompletely known species concepts.

The great variability of the specimens described and characteristics of different species appearing in the course of growth of particular specimens, allows for two solutions: 1) inclusion of all specimens investigated here in a single species, with its diagnosis comprising all characteristics available for the genus; or 2) introduction of a few new species, each based on

Species	Extremal n:d values	Major septa	Minor septa	Axial structure		Dissepimentarium
				transverse	longitudinal	
D. colligatus	20:8.5 mm 22:7–9 mm 26:9–10 mm	tapering axially, several united with axial structure	commonly intersecting dissepimentarium	median lamella united with cardinal septum, lamellae short, dense	1/5–1/4 tabularium, 1–4 loose tabellae, very steeply elevated	1/4–1/3 radius wide, mostly irregular, lateral-cystose absent
D. complexus	26:11 mm 28:13 mm 30:18–14 mm 33:16 mm	thick, tapering axially, approaching axial structure	1/3 dissepimentarium width to approaching tabularium	median lamella weak, free, lamellae rotating	>1/4 tabularium, tabellae densely packed, very steeply elevated	1/4 radius wide, mostly irregular, densely packed, lateral-cystose numerous
D. differentialis	26:12–14 mm 28:9–12 mm 31:13–15 mm	free ended, tapering axially	short strips to almost reaching tabularium within same section	free, median lamella strong, lamellae straight, regular	>1/3 tabularium, fragmentary axial column, tabellae numerous, elevated moderately	1/4>1/3 radius wide, dissepiments mostly regular, lateral-cystose numerous in some
D. infirmis	23:7–10 mm 23-28:10 mm	tapering axially, most free ended	from short strips to entering tabularium within some sections	median lamella weak to reduced, lamellae dense, tending to rotate	>1/3 tabularium, tabellae densely packed, very steeply elevated	1/5–1/4 radius wide, mostly irregular, lateral-cystose rare
D. parcus	22:10 mm 26:9–14 mm 30:13–14 mm	thin, most free ended	absent to 1/3 dissepimentarium	mostly free, median lamella weak, lamellae tending to rotate	1/6–1/4 tabularium, tabellae few, very steeply elevated	1/3-1/2 radius wide, herringbone prevail, lateral-cystose and lonsdaleoid sporadic
D. similis	23:7.5 mm 26:9–10 mm 29:11 mm 30:9.5 mm	tapering axially, several approaching axial structure	commonly intersecting dissepimentarium	median lamella strong, meeting cardinal septum, lamellae regular	1/3 tabularium, tabellae densely packed, steeply elevated	1/4-1/3 radius wide, mostly irregular, lateral-cystose rare

Table 1. Distinguishing mature morphological characters of the new *Dibunophylloides* species introduced in this paper. Species described as *conformis* and species left in open nomenclature are not considered.

a holotype specimen most distinct in some features from the remaining specimens. Boundaries of such defined species are flexible. We decided to follow the second option for the reason discussed in more detail in the Considerations, supported by Table 1 comprising most characteristic features of particular species.

Dibunophylloides differentialis sp. nov.
(Text-figs 1–5)

?1970. *Dibunophyllum* sp. cf. *D. bourbonense* Cocke, n. sp.; Cocke, p. 22, pl. 2, fig. 3a, b.

ETYMOLOGY: Latin *differentialis*, *-is*, *-e* – differentiated – after its morphology differentiated in several details.

HOLOTYPE: Specimen USNM PAL 800134.

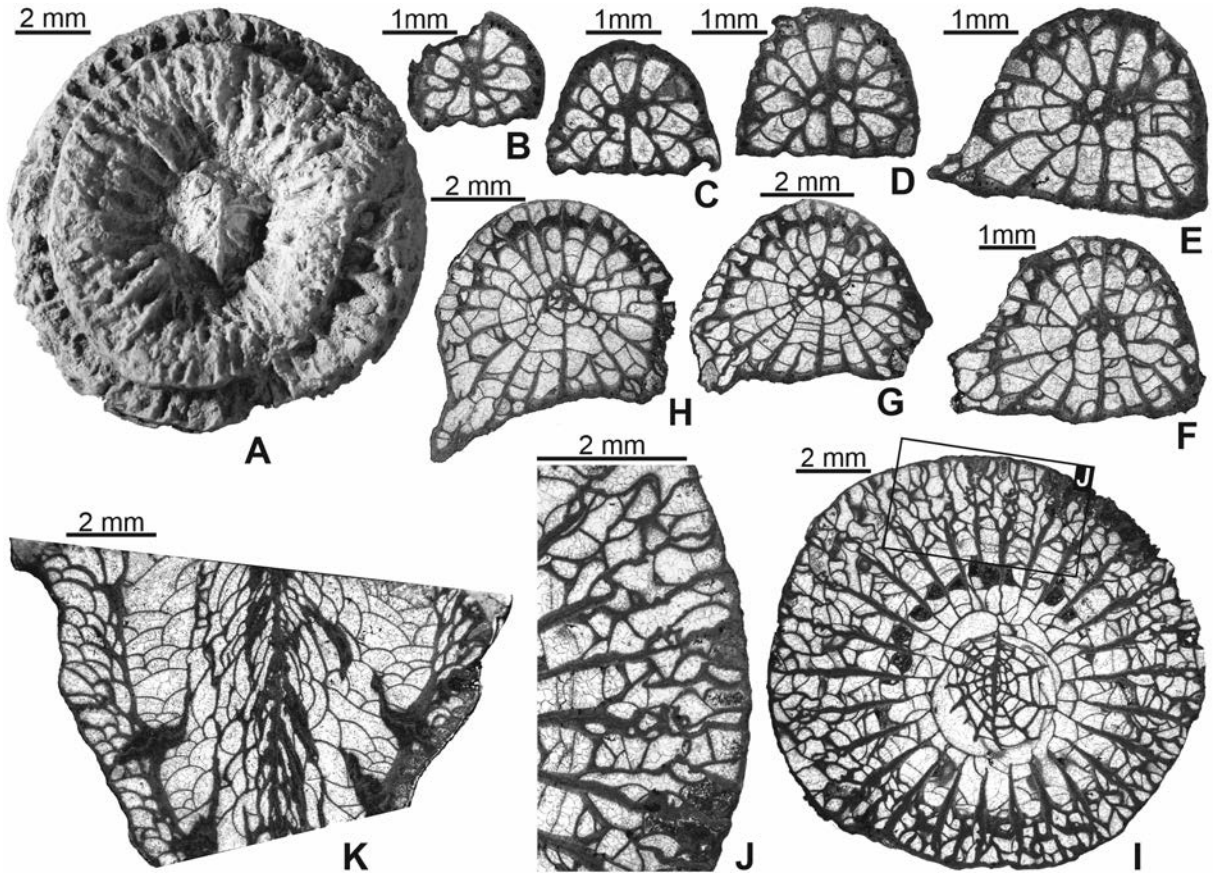
TYPE LOCALITY: USNM 700a of Cooper and Grant (1972).

TYPE STRATUM: Gaptank Formation, upper part of Bed 10 of King (1930, 1937), Missourian.

MATERIAL: Holotype USNM PAL 800134 and 28 paratypes (see Occurrence). Internal structures well-preserved. Most corallites almost complete with calices and neanic growth stage preserved. Several rejuvenated. For n:d values see Text-fig. 5. Eighteen thin sections and 156 peels available for study.

DIAGNOSIS: *Dibunophylloides* with n:d value of holotype beneath calice 26:11 mm. N:d value of paratypes inconsistent (see Text-fig. 5). Major septa in inner tabularium and outer dissepimentarium thickened, taper axially. Minor septa vary in length from very short to almost intersecting dissepimentarium within same transverse section. Axial structure in transverse section comprises distinct medial lamella and inconsistent number of septal lamellae, some joining major septa. Dissepimentarium complex, commonly differentiated in width within same transverse section, <1/4 to >1/3 corallite radius wide. Dissepiments differentiated both in particular parts of section and between specimens: herringbone, pseudoherringbone, regular, irregular and lateral-cystose in various proportions. Tabulae incomplete. Lateral tabellae bubble-like, loosely arranged. Axial tabellae densely packed, elevated steeper than peripheral tabellae. Axial column absent, except for early growth stage.

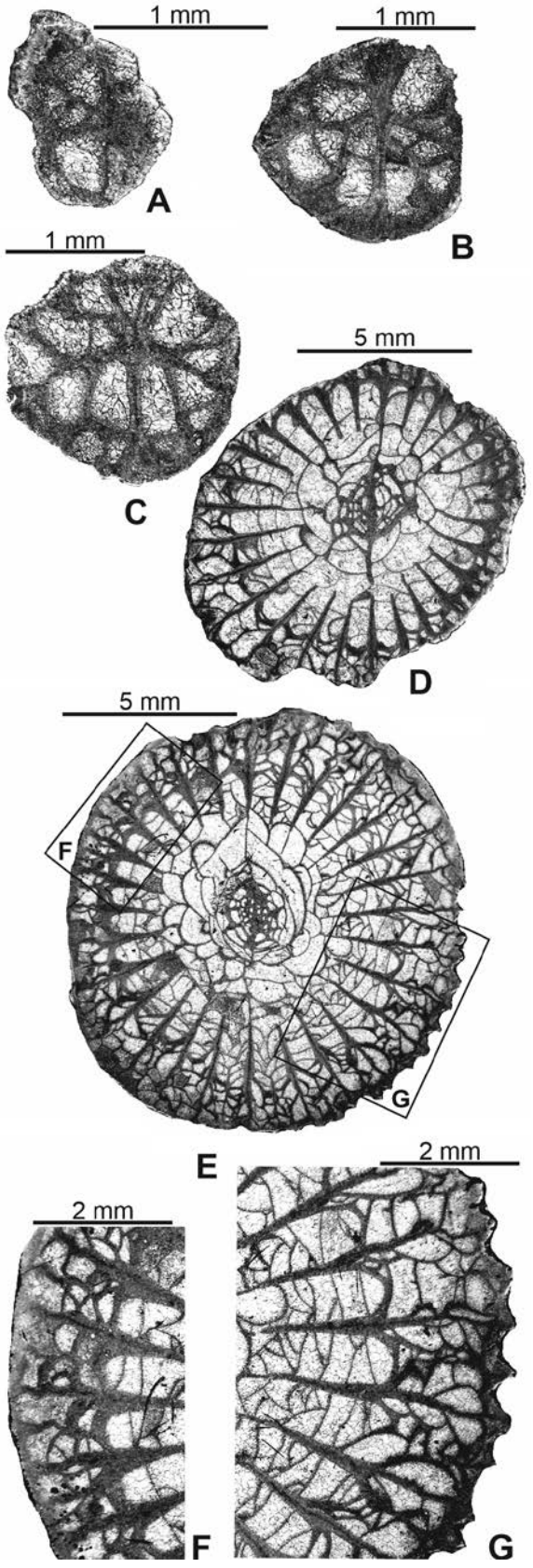
DESCRIPTION OF THE HOLOTYPE: The corallite is conical in shape, rejuvenated in the mature growth



Text-fig. 1. *Dibunophylloides differentialis* sp. nov. Specimen USNM PAL 800134, holotype. Transverse sections except when stated otherwise. A – calice; note narrow rejuvenation; B–H – early to late neanic growth stage; I – mature growth stage; J – enlarged from I to show morphology of dissepimentarium peripheral margins of major septa and minor septa; K – longitudinal section; note rudiments of axial column in ontogenetically youngest part. For stratigraphic position see text. Scale bars correspond to particular images.

stage. Both the rejuvenated and the abandoned calice (Text-fig. 1A) form almost horizontal outer rims, approximately 1 cm wide. Upper margins of major and minor septa on the rim are elevated. Minor septa are restricted to the outer rim whereas major septa turn obliquely down at the inner margin of the rim to reach the calice floor. Most turn up to participate in formation of the oval boss. The median lamella, directed towards the cardinal and counter septa, is elevated slightly above the upper limit of the axial boss.

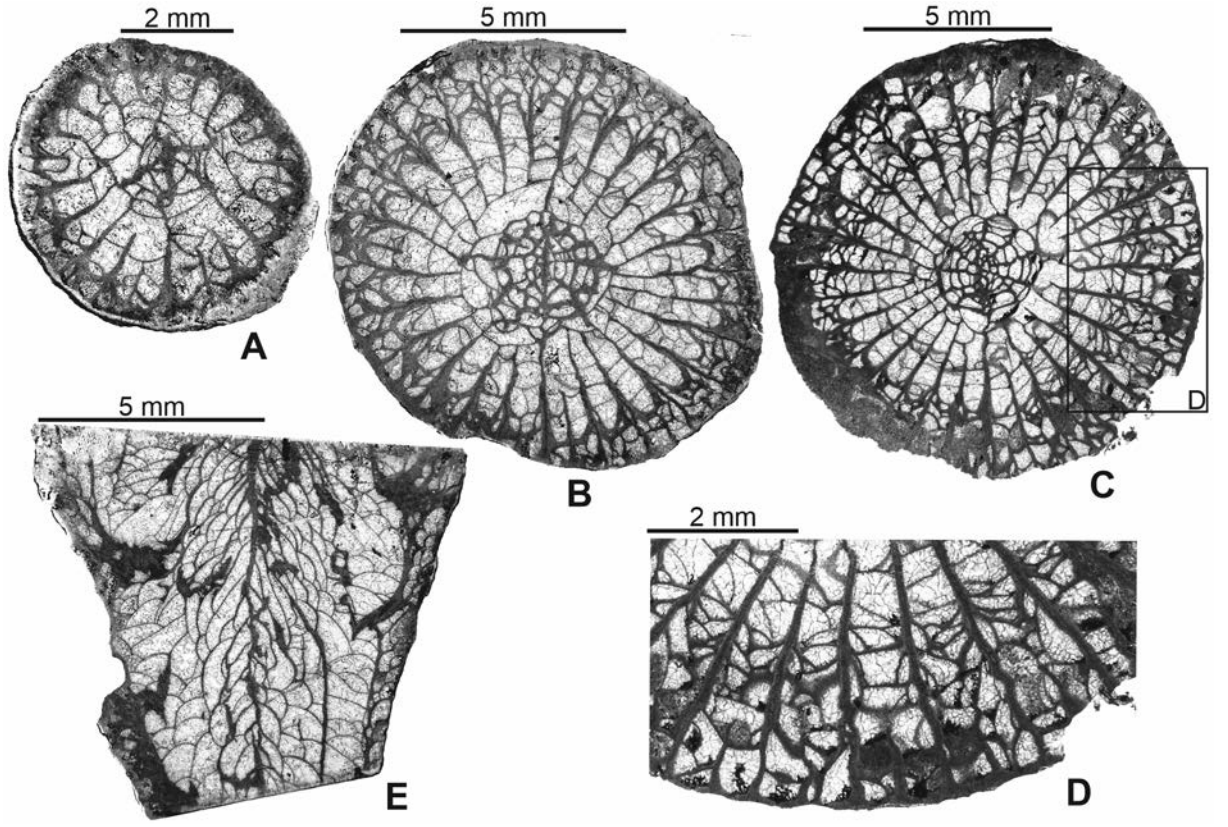
The brephic growth stage is not preserved. In the earliest neanic growth stage (Text-fig. 1B) with n:d value 11:1.6′1.8 mm major septa are zaphrentoidaly arranged with the cardinal and counter septa united to form the axial septum. Minor septa are not visible in the corallite lumen. Dissepiments are absent. First dissepiments appeared approximately 0.6 mm and 1.1 mm higher with n:d values 12:1.8′2.5 mm and 12:2.0′2.5 mm (Text-fig. 1C, D). First minor septa become visible in the corallite lumen approximately 1 mm higher, with n:d value 15:2.7′3.5 mm (Text-fig. 1E). Attachment to a hard substrate at the cardinal septum corallite side, lasting during the entire neanic growth stage, resulted in absence of dissepiments at that side (Text-fig. 1B–H). In the mature growth stage with n:d value 26:11 mm (Text-fig. 1I), major septa are radially arranged, mostly free ended, equal in length and shape, taper axially. They are thickest in the inner dissepimentarium and outer tabularium. Their peripheral parts are almost strait and moderately thickened where the dissepimentarium is narrow (Text-fig. 1I, lower). In the wide dissepimentarium (Text-fig. 1I, upper, J) peripheral parts of major septa are thin, commonly twist, with carinae-like bodies common. Minor septa are differentiated in length and shape. Most of them approach the tabularium where dissepimentarium is narrow, but cross less than 1/2 of the dissepimentarium where it is wide.



Many of them twist being hardly distinguishable from dissepiments; totally reduced from some loculi. The *Dibunophyllum*-like axial structure comprises median lamella which is long, slightly thickened, free from major septa, and four and seven septal lamellae each side of the median lamella. Sections of several loosely arranged axial tabellae supplement the axial structure. The dissepimentarium is less than 1/4 corallite diameter wide at the cardinal septum side, whereas it reaches more than 1/2 of the corallite diameter at the counter septum side. Irregular dissepiments prevail in both parts of the dissepimentarium whereas lateral-cystose dissepiments are rare (Text-fig. 1J). Herringbone dissepiments occur only in the wide dissepimentarium. The longitudinal section (Text-fig. 1K) illustrates the late neanic to late early mature growth stage. Oblique sections of some septa slightly obfuscate the image. In the ontogenetically youngest part, axial tabellae are steeply elevated, with lateral tabellae contouring the *Dibunophyllum*-like axial column higher in section, the axial tabellae become less steeply arranged and the axial column disappears; several axial tabellae anastomose with loosely arranged, mostly bubble-like peripheral tabellae. The dissepimentarium consists of 2–3 rows of dissepiments differentiated in size. A peripheral and middle row are inclined at approximately 45º down. The thickened innermost row forms the inner wall.

INTRASPECIFIC VARIABILITY: Calices of paratypes are similar to that of the holotype (e.g., Text-fig. 4K), but n:d values of paratypes differ (Text-fig. 5). The morphology of paratypes is inconsistent both during growth of particular specimens and between corallites. Several specimens are selected, described and illustrated in order to demonstrate sets of characters that frame this species on the one hand and features that point towards closely related species on the other hand: USNM PAL 800174 (n:d value 31:13 mm), USNM PAL 800158 (n:d value 30:12 mm), USNM PAL 800142 (n:d value 29:12 mm), USNM PAL 800146 (n:d value 28:12 mm) and USNM PAL 800139 (n:d value 28:10.8 mm). N:d values of selected specimens (Text-fig. 5) differ slightly from that in the holotype, being placed in the middle and upper part of the species frames.

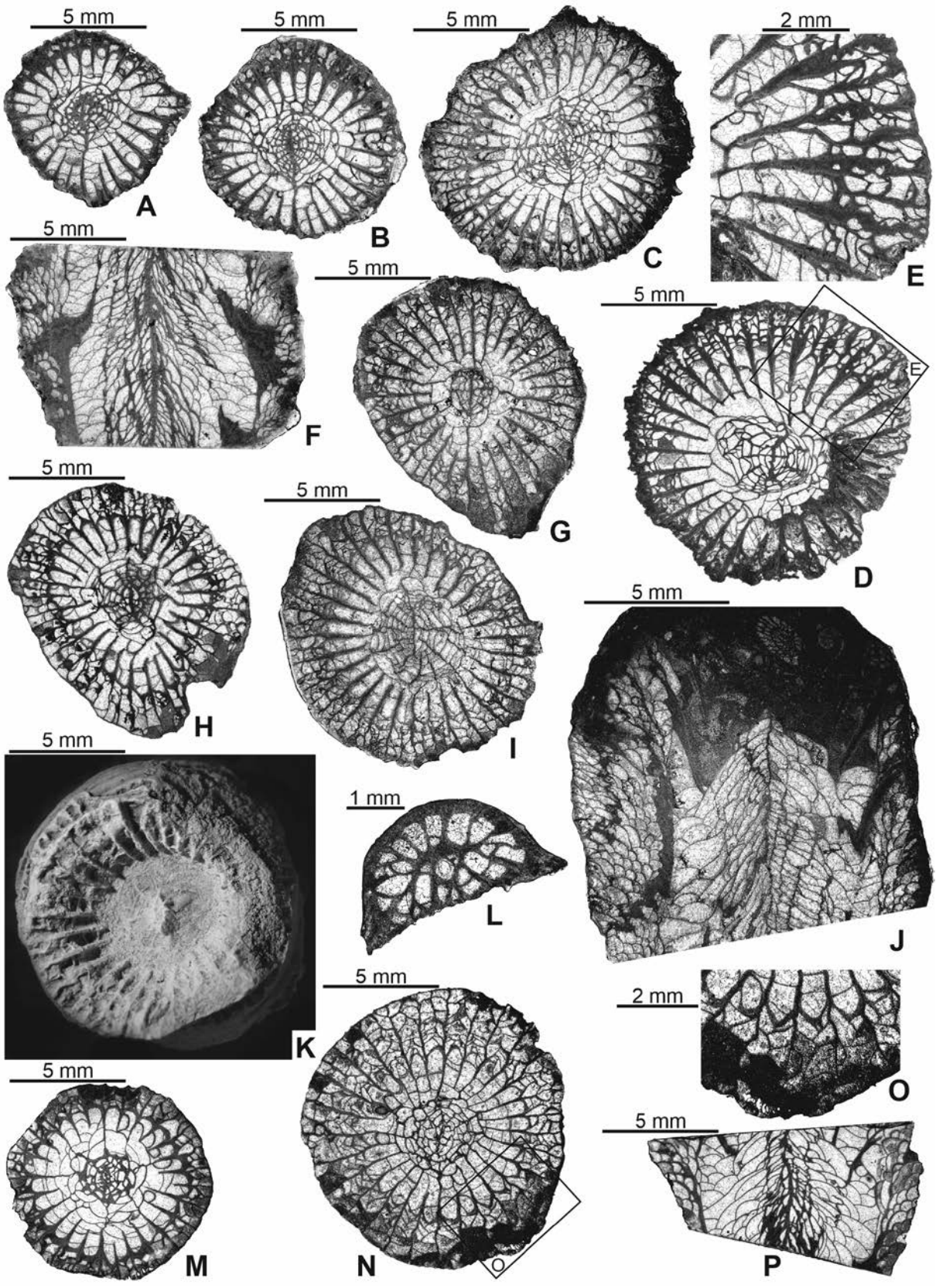
Text-fig. 2. *Dibunophylloides differentialis* sp. nov. Specimen USNM PAL 800146, paratype. Transverse sections. A – brephic growth stage; B, C – neanic growth stage; D – early mature growth stage; E – mature growth stage; F, G – enlarged from E, differentiated length of minor septa and different morphology of dissepimentarium at two opposite parts of transverse section (marked). For stratigraphic position see text. Scale bars correspond to particular images.



Text-fig. 3. *Dibunophylloides differentialis* sp. nov. Specimen USNM PAL 800142, paratype. Transverse sections except when stated otherwise. A – late neanic/early mature growth stage; B, C – mature growth stage; D – enlarged from C (marked) to show morphology of dissepimentarium; E – longitudinal section, note occurrence of axial column early in ontogeny. For stratigraphic position see text. Scale bars correspond to particular images.

The arrangement and increase of major septa early in the ontogeny, described for the holotype, is confirmed and supplemented by the study of specimen USNM PAL 190331. This is the only specimen in the collection with the brephic growth stage preserved (n:d value 6:0.8′1.0 mm; Text-fig. 2A). The dominating axial septum is straight and slightly thickened. The first four metasepta meet the axial septum irregularly. Major septa in the earliest neanic growth stage, with n:d values 9:1.0′1.3 mm are irregularly arranged. The axial septum dominates (Text-fig. 2B). Major septa became zaphrentoidaly arranged 0.7 mm higher with n:d value 11:1.8 mm (Text-fig. 2C). Despite deformation resulting from a strong attachment to the substrate, the zaphrentoid arrangement of major septa is recognizable in the early neanic growth stage of the specimen USNM PAL 800139 (Text-fig. 4L). In the late neanic/early mature growth stage of another specimen (Text-fig. 3A), with n:d value 21:5.2′6.0 mm, rudiments of the zaphrentoid arrangement of major septa remain recognizable. Their number in counter quadrants is greater, but the cardinal septum dominates in length. The axial structure, minor septa and the narrow dissepimentarium are already present. In the earliest mature growth stage illustrated from some paratypes (e.g., Text-figs 2D, 4A, B, M), the last major septa inserted in quadrants remain underdeveloped, but the arrangement of the remaining major septa become close to radial and the axial structure is well developed.

In all specimens included in *D. differentialis* sp. nov. the arrangement and morphology of tabular parts of major septa are similar and resemble those in the holotype, except for being either slightly more or slightly less thickened. Their lengths differ, either approaching the axial structure with inner margins of some united with their lamellae (Text-figs 3B, C, 4C, I, N), or leaving the axial structure free (Text-figs 2E, 4D, G). However, this character may change from section to section of the same specimen (Text-fig. 4G–I).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← Text-fig. 4. *Dibunophylloides differentialis* sp. nov. Transverse sections except when stated otherwise. A–F – Specimen USNM PAL 800141, paratype. A – late neanic/early mature growth stage; B – early mature growth stage; C, D – mature growth stage; E enlarged from D (marked) peripheral parts of major septa with carinae-like bodies and morphology of dissepimentarium; F – longitudinal section. G–J – Specimen USNM PAL 800158, paratype. G, H – early mature growth stage; I – mature growth stage; J – longitudinal section. K–P – Specimen USNM PAL 800139, paratype. K – calice, note three shallow rejuvenations in upper part; L – neanic growth stage deformed by attachment; M – early mature growth stage; N – mature growth stage; O – enlarged from N (marked) to demonstrate simplified dissepimentarium; P – longitudinal section. For stratigraphic position see text. Scale bars correspond to particular images.

The morphology of the dissepimental parts of major septa varies. For example, in specimen USNM PAL 800139 they are mostly thin and almost straight, resembling major septa in *Dibunophylloides* sp. 1 (Text-fig. 4N). In specimen USNM PAL 800146 they differ in the opposite sides of the section (Text-fig. 2E–G). In specimen USNM PAL 800142 the peripheral parts of major septa are slightly wavy with carinae-like structures either sporadic or lacking (Text-fig. 3B–D), whereas in specimen USNM PAL 800141 the peripheral parts of major septa are thick, wavy and bear several carinae-like bodies (Text-fig. 4D, E).

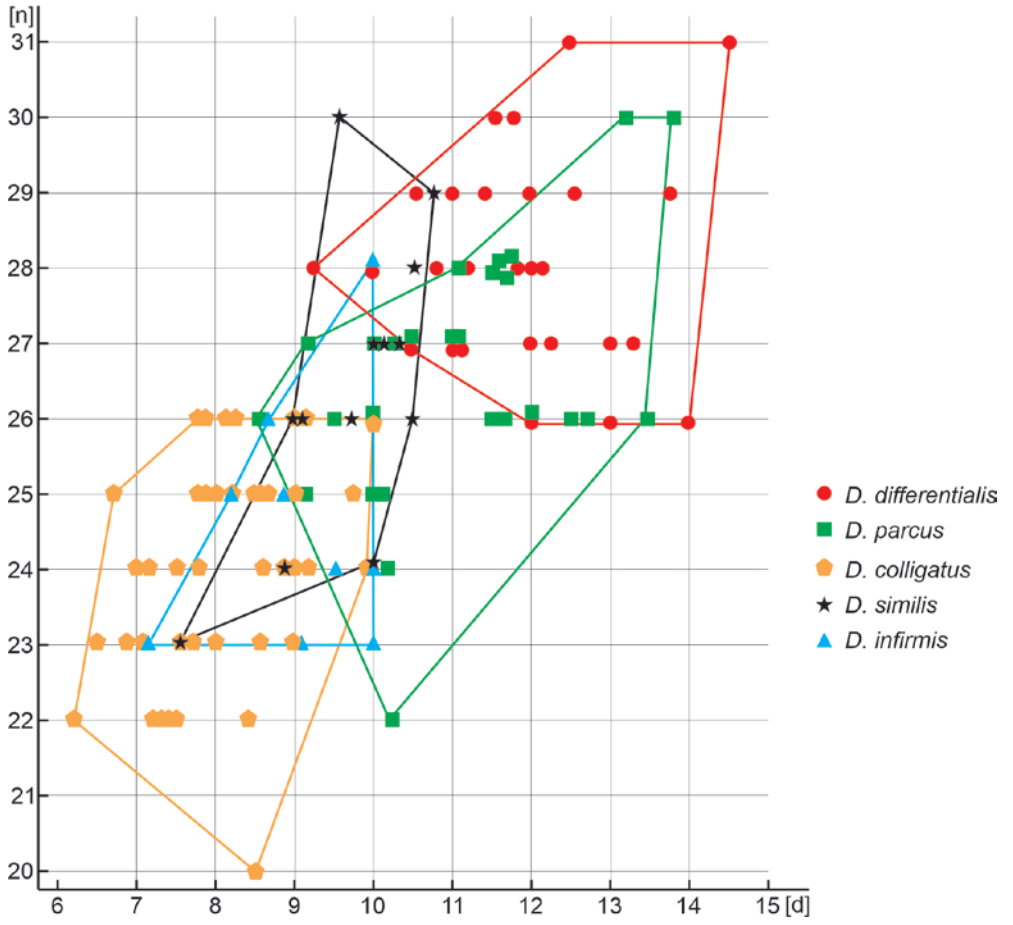
The length and morphology of minor septa differ both between specimens and in the course of growth of a given specimen. They are as a rule stronger and longer in the early mature growth stage where they may intersect a narrow dissepimentarium (Text-figs 2D, 4B, H, M). In the advanced mature growth stage, minor septa commonly resemble those in the holotype in being short, almost reduced in some loculi where the dissepimentarium is wide and much longer where the dissepimentarium narrow. Similar differences may occur within the same transverse section (Text-figs 2E–G, 3C, 4N, O).

Although small details in the morphology of the axial structure in paratypes varies greatly, some generalizations are possible. Most corallites possess the regular axial structure in the transverse sections, either narrow or moderately wide but consistent in particular growth stages. The median lamellae in such axial structures are straight, slightly thickened and septal lamellae are regular (e.g., Text-fig. 3B, C). The axial structure in some corallites varies in diameter from section to section, but remains similar in morphology (Text-fig. 4G–I). The axial structure may vary in size with the median lamella indistinct or curved (Text-fig. 4C, D, N). Also, the axial structure may be free starting from early ontogeny, comprising a strong median lamella and only a few short septal lamellae (Text-fig. 2D, E). The differences listed make the axial structure the most variable character of this species.

In most corallites investigated the width of dissepimentarium resembles the holotype. It widens during the mature growth stage from less than 1/4 in the early mature growth stage to more than 1/3 in the widest part of the advanced maturity. However, its morphology differs. In USNM PAL 800141 (Text-fig. 4D) it is most similar to the holotype, although its inner dissepiments in the wide part are more delicate. In paratype USNM PAL 800139 (Text-fig. 4N) herringbone dissepiments prevail and lateral-cystose dissepiments are sporadic. It represents a group of paratypes that differs in that character most from the holotype. The remaining paratypes display the morphology of dissepimentarium either resembling that in the holotype or intermediate between it and the most different corallites (e.g., Text-figs 2E, 3C, 4I).

Differences in the morphology of the longitudinal section result at least in part from ontogenetic growth stage of the paratypes sectioned. Two of them illustrate the ontogenetically advanced growth stage and the calice (Text-fig. 4F, J, respectively). The axial parts of their tabularia are wide, occupying more than 1/3 tabularium width; axial tabellae are steeply arranged and densely packed and lateral tabellae are bubble-like. Corallite USNM PAL 800139 (Text-fig. 4P) displays the morphology of late early to late mature growth stage. Its axial tabularium is hardly distinguishable from the peripheral tabularium. The longitudinal section of corallite USNM PAL 800142 (Text-fig. 3E) displays the ontogeny from fairly early, perhaps late neanic, to the mature growth stage. In its ontogenetically youngest part a few axial tabellae form the narrow axial column, soon after being replaced by longer and less steeply arranged axial tabellae anastomosing with the bubble-like peripheral tabellae. The inner tabellae in the upper part of the section are comparatively short and densely packed, resembling the ontogenetically most advanced part of the holotype and the paratypes described above. The peripheral tabellae of all paratypes closely resemble those in the holotype in their bubble-like morphology, size and arrangement.

REMARKS: Cocke (1970, p. 22, pl. 2, fig. 3a, b) illustrated a single specimen as conforming to his new species '*Dibunophyllum*' *bourbonense*. Its mature morphology and the longitudinal section fit the main features of *D. differentialis* sp. nov. while its n:d value (25:13.0 mm) is closer to *D. similis* sp. nov. from which it differs in possessing a strong median lamella and



Text-fig. 5. N-d values of the new species *Dibunophylloides differentialis*, *D. parcus*, *D. colligatus*, *D. similis* and *D. infirmis* distinguished by colors and frames. *Dibunophylloides complexus* sp. nov., represented by only four specimens, is not included.

narrower inner tabularium with tabellae elevated much steeper. Thus, we included that taxon in *D. differentialis* sp. nov. with doubt. It is the only species from among the existing North American *Dibunophylloides* comparable to *D. differentialis* sp. nov.

The holotype specimen USNM PAL 800134 is one of the smallest specimens of *D. differentialis* sp. nov. However, it was selected as the holotype because it is most completely investigated, thus allowing for a comparison of other specimens to the features of its particular growth stages. The large intraspecific variation within *D. differentialis* sp. nov. with several features weakly developed in this species, but occurring in a more complete form in other species, makes it at the same time a reference species for comparison to other taxa described here.

OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). USNM PAL 800134 (holotype) and paratypes: USNM PAL 800135–800152. Locality 700 of Cooper and Grant (1972) = middle part of Bed 10 of King (1930, 1937). Paratypes: USNM PAL 800153–800158, 800160–800163. Missourian.

Dibunophylloides parcus sp. nov.
(Text-figs 5–8)

ETYMOLOGY: Latin *parcus*, *-a*, *-um* – concise, terse, brief – after the morphology of the axial structure in transverse and longitudinal section.

HOLOTYPE: USNM PAL 800164.

TYPE LOCALITY: N700a of Cooper and Grant (1972).

TYPE STRATUM: Gaptank Formation. Upper part of Bed 10 of King (1930, 1937), Missourian.

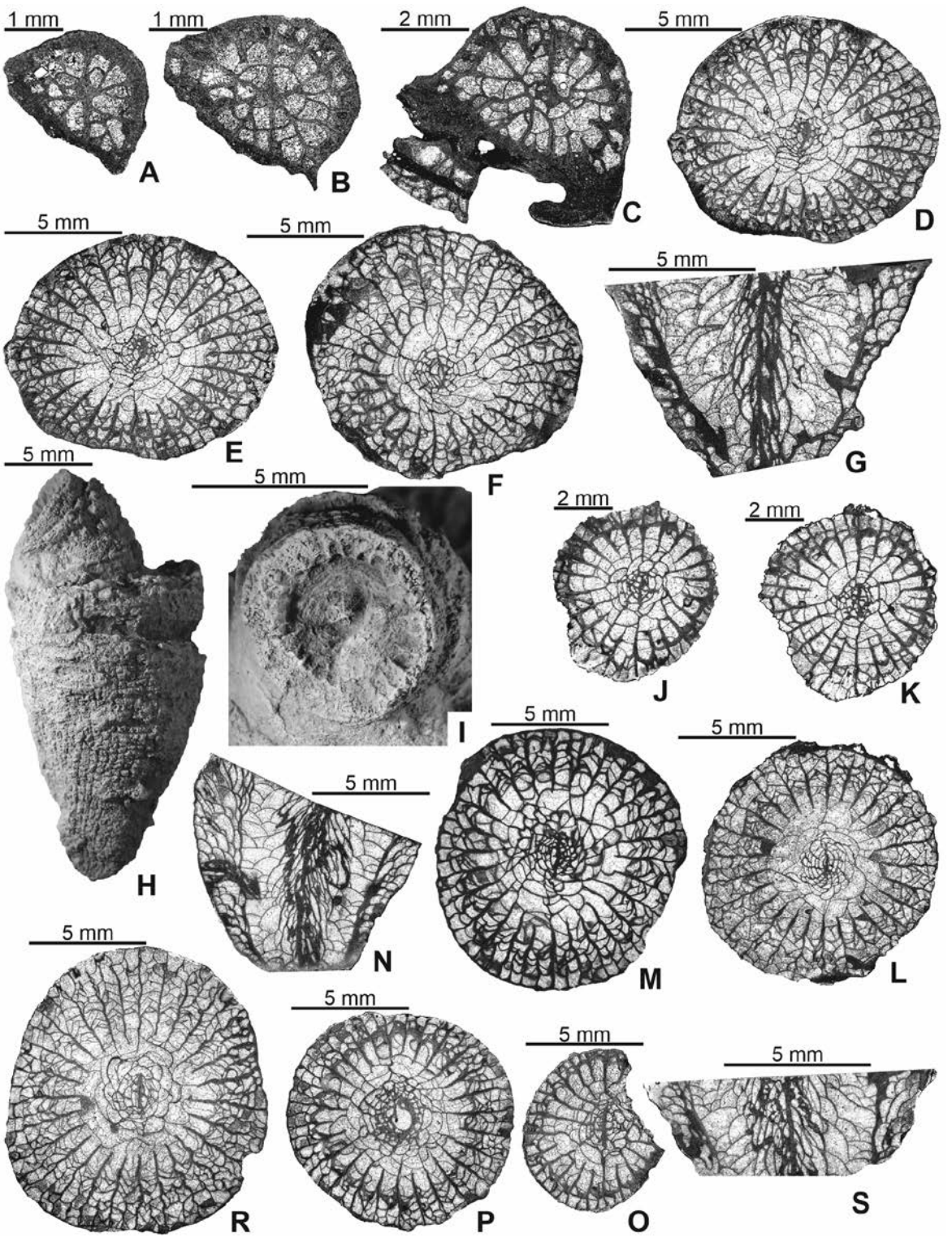
MATERIAL: Holotype USNM PAL 800164 and 28 well preserved paratypes (see Occurrence). Most corallites with calices and/or almost complete proximal ends preserved. Several rejuvenated. For n:d values see Text-fig. 5. Twenty six thin sections and 83 peels available for study.

DIAGNOSIS: *Dibunophylloides* with n:d value of holotype 26:11.6 mm and paratypes from 25:10.1 mm to 30:13.8 mm (see Text-fig. 5). Most major septa free ended, rarely meet axial structure, approximately 1/4–1/5 corallite diameter wide. Median lamella commonly short, thin. Septal lamellae weak, tend to rotate. Minor septa vary from very short strips to intersecting 1/3 dissepimentarium width within some transverse sections. Dissepimentarium 1/3 to 1/2 corallite radius wide. Herringbone dissepiments prevail; rare lonsdaleoid dissepiments. In longitudinal section axial tabellae steeply inclined towards median lamella, occupy 1/4–1/6 corallite diameter, tabellae in middle part of tabularium elongated, peripheral tabellae bubble-like.

DESCRIPTION OF THE HOLOTYPE: In the early neanic growth stage with n:d value 12:3′2 mm (Text-fig. 6A), major septa are zaphrentoidally arranged with middle part of the axial septum thickened. In the more advanced neanic growth stage, with n:d values 14:3.8′3.0 mm and 18:5.2′4.0 mm (Text-fig. 6B, C), zaphrentoid arrangement of major septa still recognizable. First dissepiments and first minor septa appeared in counter quadrants. The cardinal fossula is absent. In the mature growth stage with n:d values 26:10.5 mm to 26:11.8 mm (Text-fig. 6D–F), major septa are either thin along or are slightly thickened in the inner dissepimentarium and the outer tabularium. Most of them terminated at some distance from the axial structure. Rare major septa, the cardinal and counter septa in this number, extend to the axial structure reaching it with their very thin inner margins. Minor septa range from 1/3 to 1/5 of the dissepimentarium width; in rare loculi they may be totally reduced. The transversally sectioned axial structure occupies approximately 1/5 of the corallite diameter. The median lamella is thin and slightly wavy. Septal lamellae are very thin, weakly twisted; they change in number and length from section to section. The dissepimentarium is slightly differentiated in width, occupying 1/3 to 1/2 of the corallite radius. Irregular dissepiments prevail where minor septa are long; rare regular and lonsdaleoid dissepiments occur at the periphery; herringbone dissepiments form a belt above minor septa. In the longitudinal section, dissepiments are small, globose, arranged in steep rows. Tabulae are incomplete; inner tabellae elevate steeply towards the median lamella; several are thickened. Rare lateral lamellae border the incomplete axial column (Text-fig. 6G, middle left). In the ontogenetically youngest part illustrated, peripheral tabellae are bubble-like. In further growth, elongated, convex middle tabellae appear and anastomose with bubble-like tabellae at the periphery and with densely arranged axial tabellae. The axial column is absent from the mature growth stage.

INTRASPECIFIC VARIABILITY: Text-fig. 5 illustrates variability in the n:d values. Thus, that character is seldom if at all mentioned below. The paratype USNM PAL 800165, with maximum n:d value 26:10.5 in the mature growth stage, was selected to demonstrate several different rejuvenations with one very deep that resulted in losing 1/2 of the earlier size (Text-fig. 6H). A partly damaged calice of the rejuvenated part (Text-fig. 6I) documents an almost flat peripheral ring of dissepiments with uppermost margins of septa slightly elevated and with a narrow boss in the axial part. The mature growth stage of this corallite (Text-fig. 6L) closely resembles the holotype in most main characteristics except for the axial structure, which is more distinctly isolated from the inner margins of major septa with median lamella slightly thicker and septal lamellae that rotate more distinctly. In the very early mature growth stage of this specimen (Text-fig. 6J, K), major septa meet the very narrow axial structure, most minor septa approach the tabularium and the last inserted major septa remain slightly underdeveloped.

Several paratypes (e.g., Text-figs 6O–S, 8A–D) resemble the holotype both in transverse and longitudinal sections, although the cited ones differ slightly or distinctly in n:d value (27:12.2 mm and 23:9.0 mm, respectively). Also, median lamellae in these corallites are stronger and parts of their dissepimentaria are more complex. The late neanic/early mature growth stage of specimen USNM PAL 800181 (Text-fig. 6O) displays a wide axial structure with strong median lamella while its early mature growth stage (Text-fig. 6P) shows a peculiar deformation of the axial structure being empty in the middle. The mature morphology in both transverse and longitudinal sections resemble those of the holotype (Text-fig. 6R, S, respectively). The morphology of specimen USNM PAL 800167 (Text-fig. 8A–D), closely resembles the holotype of *D. parcus* sp. nov. whereas its n:d value corresponds to *D. infirmis* sp. nov. suggesting a relationship between these two species. Specimen USNM

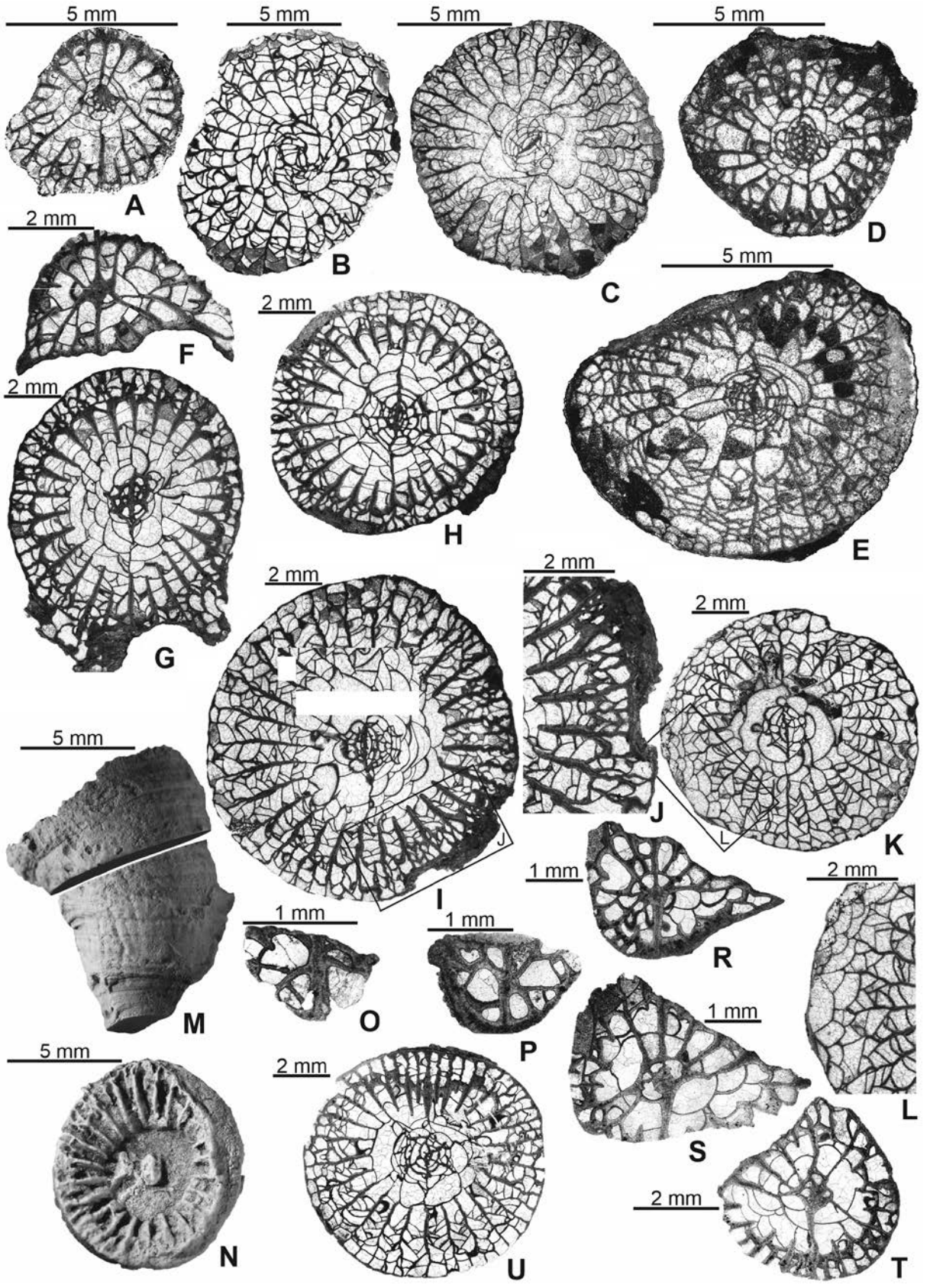


Text-fig. 6. *Dibunophylloides parcus* sp. nov. Transverse sections except when stated otherwise. A–G – Specimen USNM PAL 800164, holotype. A–C – neanic growth stage; D–F – mature growth stage; G – longitudinal section. H–L – Specimen USNM PAL 800165, paratype. H – side view, shallow rejuvenation (arrow) and deep rejuvenation (upper); I – rejuvenated calice; J, K – very early mature growth stage; L – mature growth stage. M, N – Specimen USNM PAL 800166, paratype. M – mature growth stage; N – longitudinal section. O–S – specimen USNM PAL 800181, paratype. O – late neanic/early mature growth stage; P – early mature growth stage, note peculiarity in axial structure; R – mature growth stage; S – longitudinal section. For stratigraphic position see text. Scale bars correspond to particular images.

PAL 800182 (Text-fig. 7A–C) closely resembles the holotype in most details of the late neanic/early mature and mature growth stages, but in the early mature growth stage it temporarily loses the median lamella from the axial structure that comprises only a wire of inner margins of major septa. The morphology in the longitudinal section of specimen USNM PAL 800166 closely resembles that in the holotype, whereas its axial structure in transverse section, similar to that in the holotype in the morphology, is united with the inner margins of major septa (Text-fig. 6M, N). The very early mature growth stage of paratype USNM PAL 800183 closely resembles a comparable growth stage of paratype USNM PAL 800165 (Text-figs 7D, 6K respectively), while its mature growth stage (Text-fig. 7E) displays some similarity to the holotype in morphology of the axial structure and width of the dissepimentarium, but differs from it in developing a few lonsdaleoid dissepiments at the periphery and in disappearance of the minor septa from most loculi.

Some specimens are conditionally included in *D. parcus* sp. nov. as either exposing extremely variable characters, or resembling other species. Inclusion in *D. parcus* sp. nov. of specimen USNM PAL 800185 (Text-fig. 7M–U) is provisional. Its external shape and calice morphology (Text-fig. 7M, N) are typical for the species as is its early neanic ontogeny (Text-fig. 7O–R), while its late neanic and late neanic/earliest mature growth stages (Text-fig. 7S, T) are not. The shortened major septa and thick axial part of its axial septum resembles those in *D. colligatus* sp. nov. (see below). The mature n:d value of the specimen (26:9.0 mm) is slightly below the limit for *D. parcus* sp. nov., being located at the uppermost limit of *D. colligatus* sp. nov., but its remaining characters disagree with the diagnosis of the latter species. It resembles *D. parcus* sp. nov. in the morphology and width of the dissepimentarium, length of minor septa, occurrence of rare carinae-like bodies in dissepimental parts of some major septa, but its axial structure closely resembles that in *D. differentialis* sp. nov. Elongation and thickening of its minor septa adjacent to the counter septum is atypical for *Dibunophylloides* and defies explanation. We illustrated that specimen to demonstrate the enormous morphological variability of the North American *Dibunophylloides*. Specimen USNM PAL 800167 (Text-fig. 8A–D) closely resembles the holotype in the width and morphology of the dissepimentarium, in lacking lateral-cystose dissepiments, and in the morphology of the axial structure in longitudinal section, but its mature n:d value (23:9.0 mm) exceeds the limit accepted here for *D. parcus* sp. nov., resembling in that respect *D. colligatus* sp. nov. and *D. infirmis* sp. nov. The specimen also resembles the latter species in the morphology of the axial structure in transverse section, but not in longitudinal section. We consider such a close similarity as evidence of relationship between these two species. The morphologies of particular growth stages of specimen USNM PAL 800184 differ considerably from each other (Text-fig. 7F–L). Its neanic growth stage (Text-fig. 7F) corresponds to that of the holotype and typically built paratypes in the zaphrentoid arrangement of the major septa; only its thickened middle part of the axial septum differs. Its very early mature growth stage (Text-fig. 7G) can hardly be compared to any species of North American *Dibunophylloides* described so far, while the next transverse section of the early mature growth stage (Text-fig. 7H) resembles *D. differentialis* sp. nov. in the morphology of the axial structure and the dissepimentarium with some lateral-cystose dissepiments present. Only its narrow dissepimentarium differs from that species. In the transverse section made at a distance of approximately 1.5 mm higher, both width of the dissepimentarium and occurrence of lateral-cystose dissepiments in some septal loculi closely resembles *D. differentialis* sp. nov., but its axial structure is that of the *D. parcus* sp. nov. type (Text-fig. 7I, J). The most advanced growth stage of this specimen (Text-fig. 7K, L) resembles the holotype of *D. parcus* sp. nov. both in the morphology of the axial structure and width of the dissepimentarium, but the lonsdaleoid dissepiments present in the lateral part of its dissepimentarium are absent from the holotype of this species, but occur in paratype USNM PAL 800183 (Text-fig. 7E). The almost total reduction of the minor septa in the two paratypes mentioned is also observed in several other paratypes (e.g., Text-figs 6L, 7C). Morphological differences in particular growth stages of specimen USNM PAL 800184 puts in doubt some criteria accepted here as diagnostic for the particular species of *Dibunophylloides* (see Table 1).

REMARKS: The holotypes of both *D. differentialis* sp. nov. and *D. parcus* sp. nov. were purposely selected from among the smallest specimens of the species they represent, with their n:d values almost identical (Text-fig. 5). By doing so we intended to express both the close relationship of those species and the diagnostic morphological differences that they display (Text-figs 1A–K *vs* 6A–G). Also, several characters of one of these species occur temporarily and in a primitive form in the other (see descriptions). However, the axial structure in *D. differentialis* sp. nov. is strong with the median lamella distinct and the septal lamellae comparatively thick and arranged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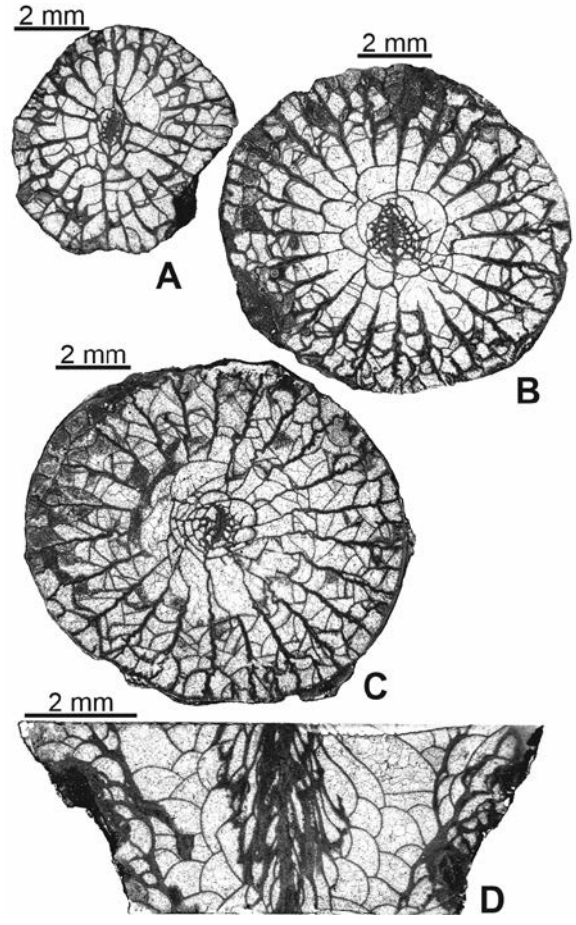
← Text-fig. 7. *Dibunophylloides parcus* sp. nov. Transverse sections except when stated otherwise. A–C – Specimen USNM PAL 800182, paratype. A – late neanic/early mature growth stage; B – early mature growth stage, note peculiarity in axial structure; C – mature growth stage. D, E – Specimen USNM PAL 800183, paratype. D – late neanic/early mature growth stage; E – mature growth stage. F–L – Specimen USNM PAL 800184, paratype. F – neanic growth stage; G – late neanic/early mature growth stage; H – early mature growth stage; I – mature growth stage; J – enlarged from I (marked), major septa bearing carinae-like bodies and complex dissepimentarium contrasting with simple dissepimentarium at opposite side of section; K – mature growth stage, diameter reduced by rejuvenation; L – enlarged from K (marked), lonsdaleoid dissepiments. M–U – Specimen USNM PAL 800185, paratype. M – side view; N – calice; O – brephic growth stage; P–S – early to late neanic growth stage; T – ? late neanic/early mature growth stage; U – mature growth stage, note long minor septa next to counter septum. For stratigraphic position see text. Scale bars correspond to particular images.

radially, while the axial structure in *D. parcus* sp. nov. is weak and narrow with the median lamella reduced to a thin body accompanied by few septal lamellae that are thin and rotating. The dissepimentarium of most specimens included in *D. parcus* sp. nov. lacks lateral cystose dissepiments, comprising mostly herringbone dissepiments, while lateral-cystose dissepiments are common in *D. differentialis* sp. nov. The morphology of the longitudinal section shows the main difference between the two species. In *D. parcus* sp. nov. it comprises inner tabellae that are very steeply inclined towards the axis, occupying approximately 1/6 of the corallite radius in the mature growth stage, while in *D. differentialis* sp. nov. the inner tabellae are less steeply arranged and occupy approximately 1/3 of the corallite diameter. Only the earliest parts of the inner tabularia are similar in the two species (Text-figs 1K, 3E *vs* 6G, 8D).



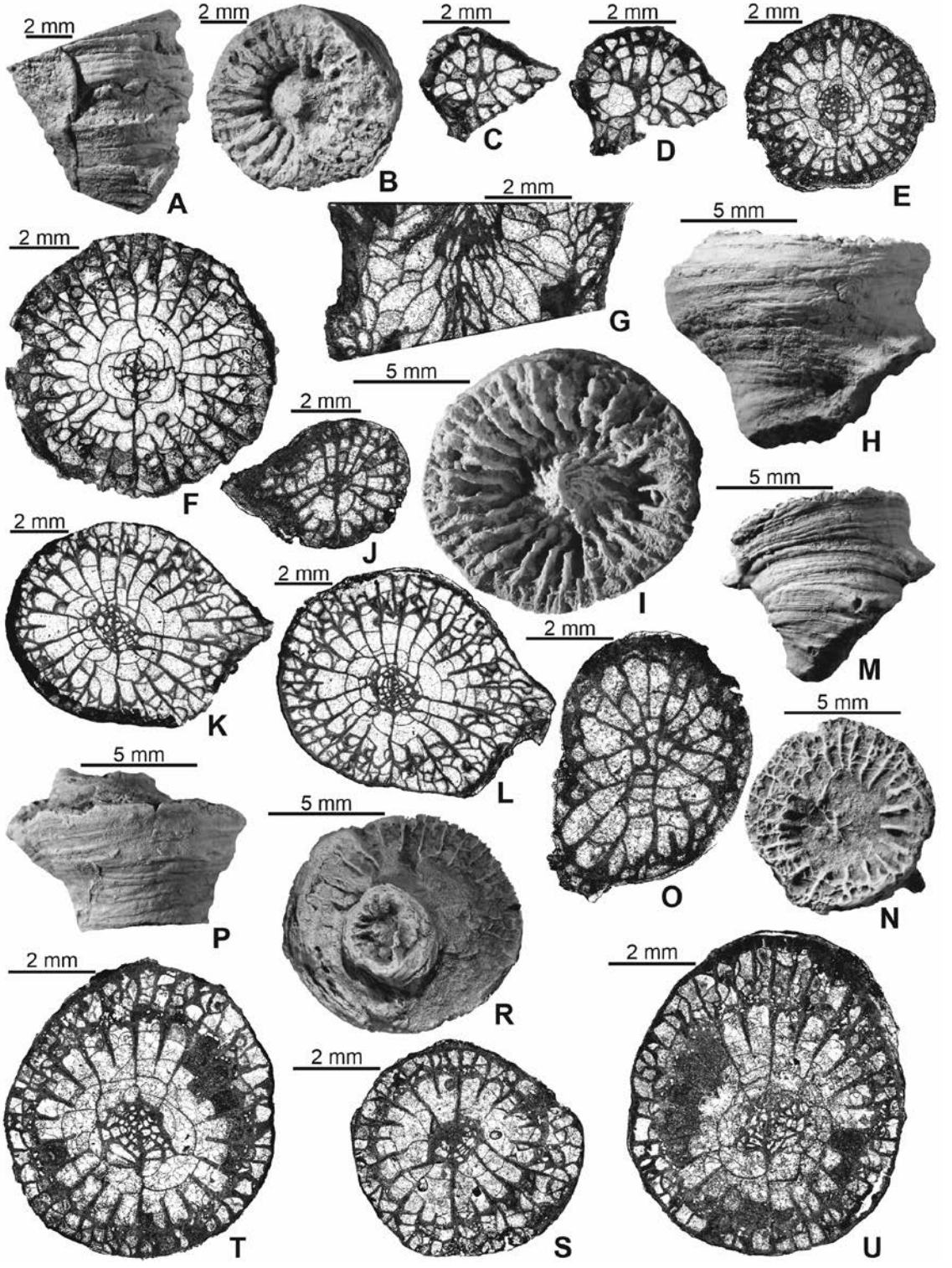
Text-fig. 8. *Dibunophylloides parcus* sp. nov. Specimen USNM PAL 800167, paratype. A – late neanic/early mature growth stage; B, C – mature growth stage; D – longitudinal section. For stratigraphic position see text. Scale bars correspond to particular images.

Dibunophylloides parcus sp. nov. displays close similarity to '*Dibunophyllum*' *hansoni* Cocke and Haynes, 1973 in the morphology and width of the dissepimentarium with herringbone dissepiments prevailing. It differs from that species in the morphology of the longitudinal section. Its similarity to *D. similis* is discussed with the latter species. It is difficult to compare *D. parcus* sp. nov. to '*Dibunophyllum*' *valeriae* Newell, 1935 for the reasons discussed below with *D.* cf. *valeriae*. However, a larger diameter and number of septa, longer minor septa and probably the morphology in the longitudinal section in '*D.*' *valeriae* are differences that can be mentioned here. We temporarily accept with doubt a wide approach to '*Dibunophyllum*' *valeriae* by Cocke (1970, pl. 1, figs 1, 8–13), from which only the specimen illustrated by him in pl. 1, fig. 9 adequately resembles *D. parcus* sp. nov. to be considered its relative.

OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). USNM PAL 800164 (holotype) and paratypes: USNM PAL 800165–800180. Locality N700 of Cooper and Grant (1972) = middle part of Bed 10 of King (1930, 1937). Paratypes: USNM PAL 800181–800192. Locality N705i of Cooper and Grant (1972), Gaptank Formation, undivided. Paratype USNM PAL 800193. Missourian.

Dibunophylloides colligatus sp. nov.
(Text-figs 5, 9, 10)

ETYMOLOGY: Latin *colligatus*, *-a*, *-um* – connected – after its similarity, perhaps close relationship to '*Dibunophyllum*' *clathrum* Cocke, 1970 and '*D.*' *elegante* Cocke, 1970.



Text-fig. 9. *Dibunophylloides colligatus* sp. nov. Transverse sections except when stated otherwise. A–G – Specimen USNM PAL 800194, holotype. A – side view; B – calice; C, D – late neanic growth stage; E – early mature growth stage; F – mature growth stage; G – longitudinal section. H–L – Specimen USNM PAL 800195, paratype. H – side view; I – calice; J – late neanic growth stage; K – early mature growth stage; L – mature growth stage. M–O – Specimen USNM PAL 800244, paratype. M – side view; N – calice; O – late neanic growth stage. P–U – Specimen USNM PAL 800196, paratype. P – side view; R – calice, note deep rejuvenation; S – late neanic/early mature growth stage; T – early mature growth stage; U – mature growth stage. For stratigraphic position see text. Scale bars correspond to particular images.

HOLOTYPE: USNM PAL 800194.

TYPE LOCALITY: 700 of Cooper and Grant (1972).

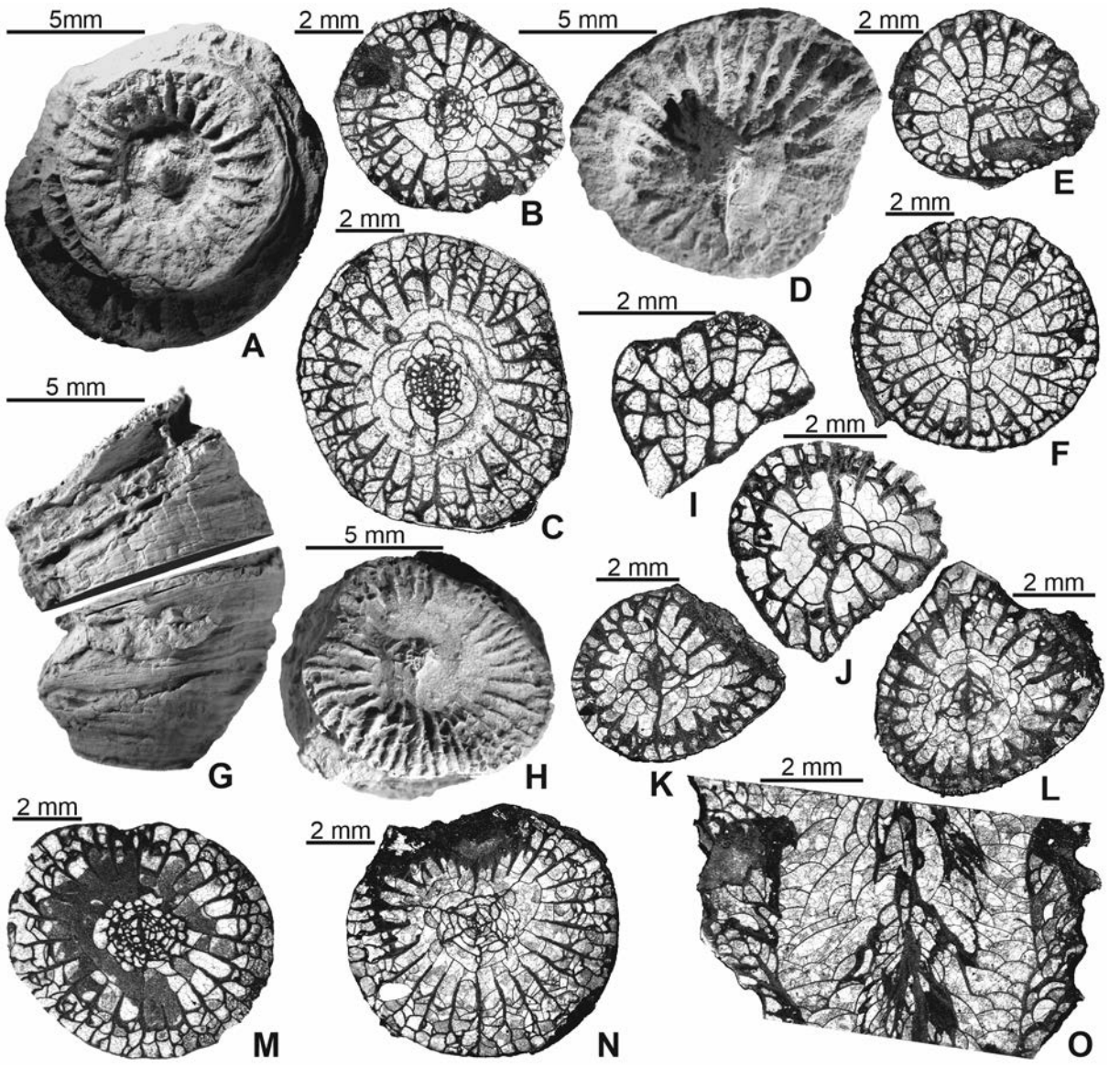
TYPE STRATUM: Gaptank Formation. Middle part of Bed 10 of King (1930, 1937), Missourian.

MATERIAL: Holotype USNM PAL 800194 and sixty paratypes (see Occurrence), mostly well preserved. Many corallites with calices and/or almost complete proximal ends present. Several rejuvenated. For n:d values see Text-fig. 5. Fourteen thin sections and 89 peels available for study.

DIAGNOSIS: *Dibunophylloides* with n:d value 22:6.5 mm to 26:10 mm. Cardinal septum invariably, and counter septum commonly, meet median lamella. Axial structure narrow, commonly simple with weak median lamella. Major septa either free-ended or some participate in forming the axial structure. Last pairs in cardinal quadrants shortened. Cardinal fossula absent. Minor septa differentiated in length within a given transverse section. Dissepimentarium occupies 1/4 to almost 1/3 corallite radius. Dissepiments regular and irregular, herringbone where minor septa shortened. In longitudinal section peripheral tabellae loosely distributed, long and/or bubble-like; one to four axial tabellae steeply inclined towards median lamella.

DESCRIPTION OF THE HOLOTYPE: The holotype is conical with the external wall thin, covered by fine growth striae. Septal furrows are hardly recognizable. Two rejuvenations are well marked while the third one, located in the lower part of the specimen is shallow (Text-fig. 9A). The calice (Text-fig. 9B) is partly filled with matrix. Thus, a complete description of calices is found in the intraspecific variability section below. The brephic and early neanic growth stages are not preserved. In the neanic growth stage (Text-fig. 9C), the zaphrentoid arrangement of major septa is irregular with the axial septum wavy and thickened in the corallite axis. First minor septa and dissepiments appeared at the counter septum corallite side. The irregularity increases in the more advanced neanic growth stage (Text-fig. 9D). It is stronger in the cardinal quadrants, with some major septa shortened. Also, the waviness of the axial septum increases. In the early mature growth stage (Text-fig. 9E), free ended major septa are radially arranged, thickened in the tabularium, mostly equal in length. Only the protosepta are elongated so as to meet the median lamella and the major septa adjacent to the cardinal septum are shortened. A cardinal fossula is absent. Most minor septa cross the dissepimentarium, 1/4 of the corallite radius wide. The dense, narrow axial structure comprises the median lamella, slightly thickened, accompanied by several short septal lamellae on both sides. Most dissepiments are regular, arranged in 1–3 rows. In the fully mature growth stage (Text-fig. 9F), major septa are thin, free ended, equal in length, except for the cardinal and counter septa that join the weak median lamella. Two septal lamellae each side of the median lamella and few sections of axial tabellae complete the weak axial structure. Minor septa cross approximately 1/2 of the dissepimentarium that occupies slightly less than 1/3 of the corallite radius. In the longitudinal section (Text-fig. 9G), dissepiments are mostly small, generally uniform in size, and inclined steeply down. The loose outer tabularium occupies slightly less than 2/3 of tabularium width. It consists of bubble-like and elongated tabellae that pass gently into the narrow inner tabularium. Rare inner tabellae, one to four each side of the thin median lamella, are steeply elevated.

INTRASPECIFIC VARIABILITY: All corallites are conical in most part of growth with strong attachments to the sediment during the neanic growth stage, prolonged up to the early mature growth stage in several. Their external walls closely resemble that of the holotype (Text-figs 9H, M, P, 10G). Calices (Text-figs 9I, N, R, 10A, D, H) are deep as compared to the length of the specimens. Their peripheral parts, occupying approximately 1/4 of the corallite radius, form a platform slightly inclined inwards with well exposed upper margins of both major and minor septa. Most minor septa terminate at the inner margin of the platform. Major septa turn down at the platform edge at approximately 50º to reach the calice floor. In the holotype and some paratypes (Text-figs 9B, 10A, respectively) most major septa terminate on the calice floor, with only the cardinal septum, less clearly the counter septum and some major septa elongated towards the median lamella. Such calices correspond to specimens with shortened major septa (Text-figs 9F, 10C, respectively). In the specimens with major septa reaching the axial structure, inner parts of major septa turn at the corallite floor upward to meet the median lamella and form a prominent axial boss (Text-figs 9I, ?N, 10D). Axial bosses in the latter are elongated slightly more than in those with short major septa. The protosepta may remain connected to the median lamella up to a calice floor inclusively (Text-figs 9B, I, 10A, D, H). A cardinal fossula is absent from calices in all specimens. Many



Text-fig. 10. *Dibunophylloides colligatus* sp. nov. Transverse sections except when stated otherwise. A–C – Specimen USNM PAL 800245, paratype. A – calice, note three subsequent rejuvenations; B – late neanic/early mature growth stage; C – mature growth stage. D–F – Specimen USNM PAL 800246, paratype. D – incomplete calice; E – late neanic/early mature growth stage; F – mature growth stage. G–O – Specimen USNM PAL 800197, paratype. G – side view, note rejuvenation in upper and lower part; H – rejuvenated calice; I – neanic growth stage; J – late neanic growth stage; K, L – late neanic/early mature growth stage; M – mature growth stage immediately above rejuvenation; N – mature growth stage slightly above M; O – longitudinal section. For stratigraphic position see text. Scale bars correspond to particular images.

specimens were rejuvenated. The rejuvenation may be rather shallow as in the holotype (Text-fig. 9A, middle, 9B, right side), moderate, repeated several times (Text-fig. 10A, G, H) or very deep (9P, R).

In the neanic growth stage, the zaphrentoid arrangement of major septa is hardly recognizable in the holotype and paratypes (Text-fig. 10I). In the advanced neanic growth stage that arrangement may be either more or less clearly camouflaged by shortening of the major septa (Text-figs 9J, 10J, K), may be unrecognizable (Text-fig. 10F), or is obvious (Text-fig. 9O). Shortening of the major septa lasts up to the late neanic/early mature growth stage inclusively (Text-figs 9S, 10B, L). Thus, it may be a species feature, while the irregularity in the arrangement may be environmentally caused.

In the mature growth stage, n:d values vary from 22:6.4 mm to 26:10 mm with n:d value of a single specimen 20:8.6 mm (Text-fig. 5) exceeding the species frame. Major septa are all comparatively thin and arranged radially with the last pair adjacent to the cardinal septum slightly underdeveloped in most. A cardinal fossula is absent. Two trends in length of major septa were observed: (i) reaching slightly more than 2/3 corallite radius like in the holotype and leaving the axial structure free (Text-figs 9T, U, 10C), and (ii) mostly approaching the axial structure and/or forming its part (Text-figs 9K, L, 10F, M. N). The cardinal septum as a rule and the counter septum commonly join the short, thin median lamella, hardly recognizable in some corallites (Text-figs 9L, 10C). The axial structure occupies 1/6 to 1/4 of the corallite diameter. Its morphology changes both in the course of growth of specimens (Text-fig. 9E, F, S–U, 10B, C, L–N) and between fully mature corallites (Text-figs 9F, L, U, 10C, F). A group of eleven corallites, represented by specimen USNM PAL 800197 (Text-fig. 10M, N), developed a more complex axial structure than the remaining corallites. They may represent a separate subspecies. Minor septa are thin and slightly wavy. They are commonly differentiated in length within a given transverse section from intersecting the dissepimentarium without penetrating the tabularium to slightly or distinctly reduced in length within particular septal loculi (Text-figs 9L, T, U, 10C, F, M, N). The dissepimentarium occupies approximately 1/4 of the corallite radius. It contains some regular dissepiments at the periphery, irregular dissepiments in most part and herringbone dissepiments where minor septa are shortened. Rare lateral-cystose dissepiments may occur.

REMARKS: The species discussed resembles '*Dibunophyllum*' (= *Dibunophylloides*) *elegante* Cocke, 1970 in the morphology of the long-septa specimens. Cocke (1970, p. 24) mentioned 19 to 21 major septa and 8–10 mm corallite diameter as being counted for his specimens while 22:6.5 mm in the smallest, 26:10 mm in the largest and 23–25:7–9 mm most commonly, occur in *D. colligatus* sp. nov. Thus n:d values of specimens from the collections differ considerably. Also, the intraspecific variability of. *D. elegante* remains unknown, excluding a comparison between that species and *D. colligatus* sp. nov. '*Dibunophyllum*' (= *Dibunophylloides*) *clathrum* Cocke, 1970 is another species that we consider related to *D. colligatus* sp. nov. It differs from the latter in possessing longer major septa, and more regular dissepimentarium. Also, a character as important as the longitudinal section is either eccentric and uncertain in *D. clathrus*, or incomparable to any species of *Dibunophylloides* (Cocke 1970, p. 2, figs 4b, 5b respectively). Additionally, the intraspecific variability of Cocke's (1970) species remains unknown, making its close comparisons to our specimens impossible. Accepting the morphological similarities of our specimens to two of Cocke's (1970) species mentioned, we decided to introduce a new species name for our collection rather than to include them in any of these two incompletely known taxa. The variant of *D. colligatus* sp. nov. with a dense axial structure and weak medial lamella resembles *D. parcus* sp. nov. in these characters as well as in the morphology of the longitudinal section (Text-fig. 10O) and in the n:d value of its largest corallites, but it differs from that species in the majority of much smaller corallite diameters and numbers of septa (Text-fig. 5), in a much narrower dissepimentarium and longer length of the minor septa when compared to the major septa. *Dibunophylloides similis* sp. nov., a species displaying an n:d value similar to both *D. clathrus* and *D. colligatus* sp. nov. differs from both in the longitudinal section and the axial structure. *Dibunophylloides colligatus* sp. nov. differs considerably from *D. differentialis* sp. nov. in the n:d value, width and morphology of the axial structure, both in transverse and longitudinal section, and in the width and morphology of the dissepimentarium.

OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700 of Cooper and Grant (1972) = middle part of Bed 10 of King (1930, 1937). USNM PAL 800194 (holotype) and paratypes: USNM PAL 800195–800243. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Paratypes: USNM PAL 800244–800254. Missourian.

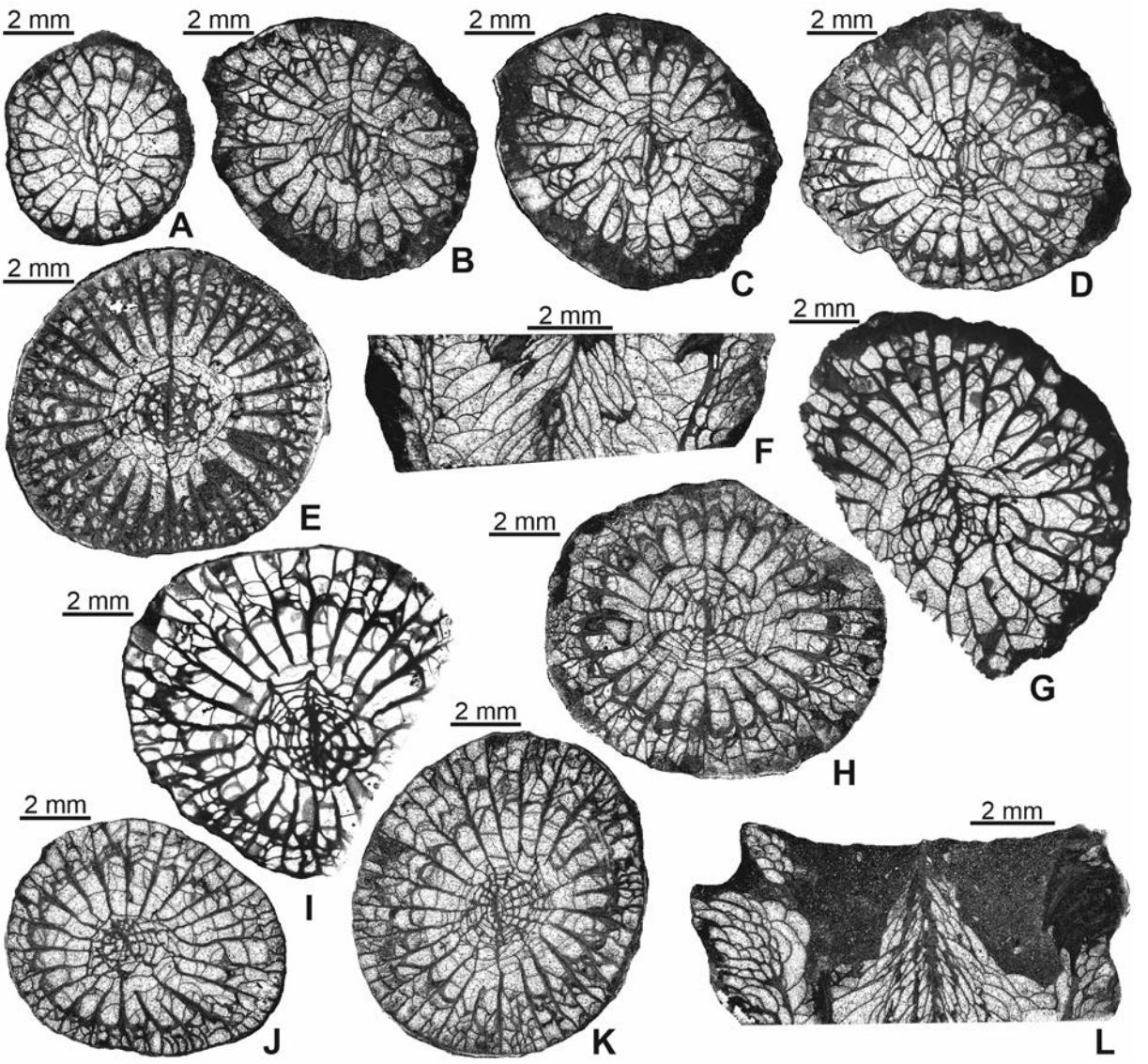
Dibunophylloides similis sp. nov.
(Text-figs 5, 11, 12)

ETYMOLOGY: Latin *similis*, *-is*, *-e* – similar – after its similarity or relationship to '*Dibunophyllum*' *elegante* Cocke, 1970, '*D.*' *clathrum* Cocke, 1970 and *D. colligatus* sp. nov.

HOLOTYPE: Specimen USNM PAL 800255.

TYPE LOCALITY: N700a of Cooper and Grant (1972).

TYPE STRATUM: Gaptank Formation, upper part of Bed 10 of King (1930, 1937), Missourian.



Text-fig. 11. *Dibunophylloides similis* sp. nov. Transverse sections except when stated otherwise. A–F – Specimen USNM PAL 800255, holotype. A – late neanic/early mature growth stage; B–E – successive sections from early to advanced mature growth stage; F – longitudinal section. G, H – Specimen USNM PAL 800265, paratype. G – early mature growth stage; H – mature growth stage. I – Specimen USNM PAL 800263, paratype, mature growth stage. J–L – Specimen USNM PAL 800266, paratype. J – early mature growth stage; K – mature growth stage; L – longitudinal section. For stratigraphic position see text. Scale bars correspond to particular images.

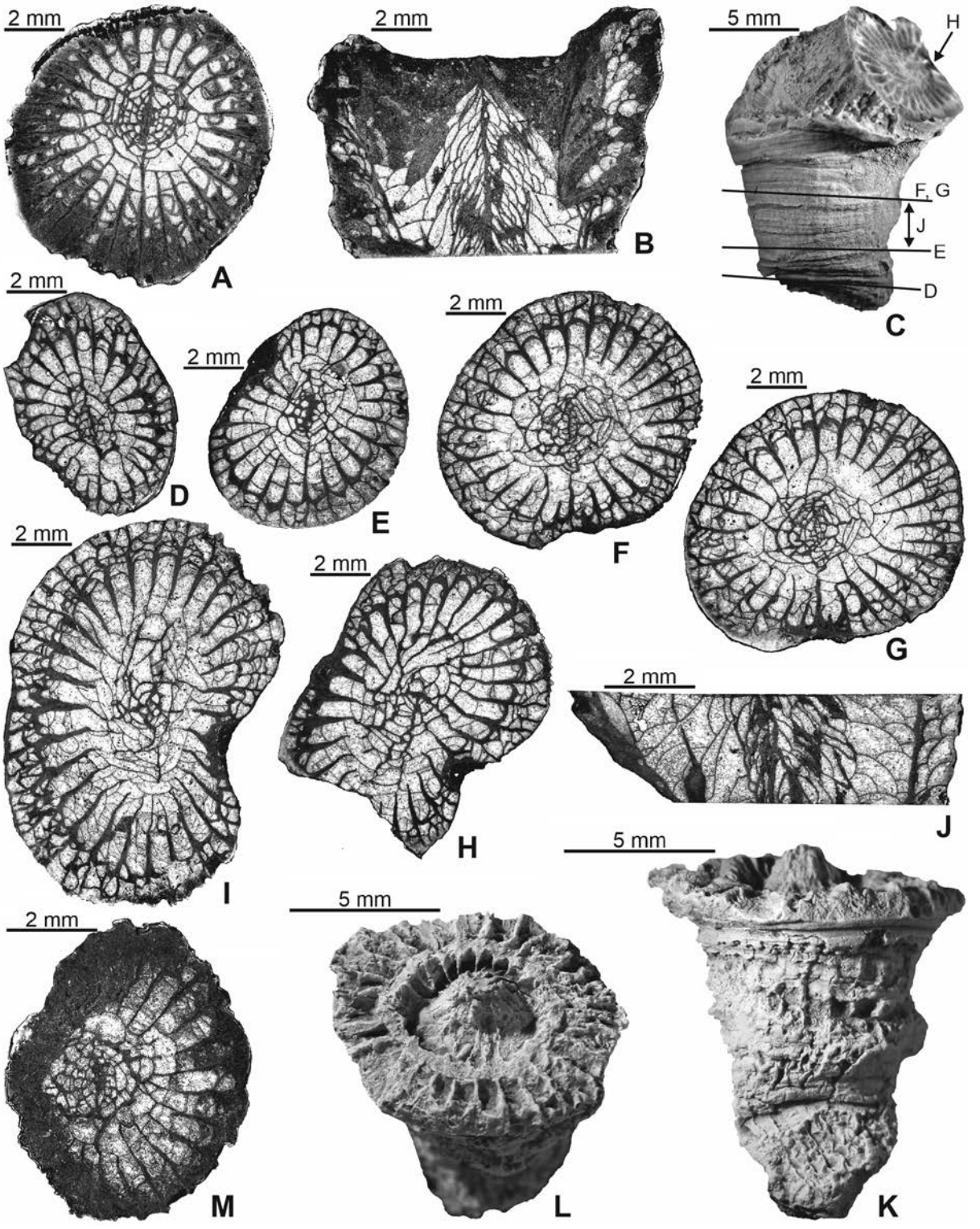
MATERIAL: Holotype USNM PAL 800255 and eighteen paratypes (see Occurrence). Most specimens well preserved. Several corallites with calices and/or almost complete proximal ends present. Some rejuvenated. For n:d values see Text-fig. 5. Two thin sections and 58 peels available for study.

DIAGNOSIS: *Dibunophylloides* with n:d value of holotype 26:9.8 mm and paratypes from 23:7.7 mm to 30:9.6 mm; 26–27:9.0–10.4 mm prevailing. Major septa commonly meet regular axial structure with median lamella distinct. Minor septa approach tabularium. Dissepimentarium occupies approximately 1/3 corallite radius or less. Dissepiments mostly irregular; lateral-cystose inconsistent. In longitudinal section tabulae incomplete; inner tabellae densely arranged, steeply elevated towards median lamella, occupy more than 1/3 tabularium width.

DESCRIPTION OF THE HOLOTYPE: Early ontogeny lacking. In the late neanic/early mature growth stage (Text-fig. 11A) with n:d value 21:6.0′5.2 mm major septa are thin, semi-bilaterally arranged, stop short of the thin, wavy median lamella. Minor septa are hardly recognizable within the narrow dissepimentarium comprising 1–3 rows of irregular dissepiments. First short septal lamellae appear in the axial structure with n:d value 22:7.2 mm (Text-fig. 11B, C). Minor septa remain thin and hardly recognizable. We consider this part as the early mature corallite growth. The mature growth stage is morphologically inconsistent. In the earlier maturity with n:d value 25:9.0–8.4 mm (Text-fig. 11D) major septa are radially arranged, slightly thickened in the inner dissepimentarium and outer tabularium. Most meet the regular axial structure occupying 1/3 of the corallite diameter. Only the pair of major septa adjacent to the cardinal septum is shortened and the protosepta are elongated to join the median lamella. Minor septa either approach the inner margin of the dissepimentarium or are slightly shortened. The axial structure comprises the median lamella and three to five septal lamellae on each side; all slightly thickened. They and the densely packed sections of inner tabellae form a regular 'cobweb' design. In the advanced mature growth stage with n:d value 26:9.8′8.5 mm (Text-fig. 11E), the major septa become strongly thickened. Most of them leave the axial structure free. Only the protosepta remain connected to the thickened median lamella. Septal lamellae are regularly arranged and thickened, but the axial structure is less regular and narrower than in the earlier growth stage. Minor septa are thickened; most extend to the inner limit of the dissepimentarium, but do not penetrate the tabularium. The dissepimentarium occupies slightly more than 1/4 corallite radius and consists of irregular dissepiments. Lateral-cystose dissepiments are sporadic. In longitudinal section (Text-fig. 11F) dissepiments are differentiated in size, steeply sloping down with the inner row vertical. The tabularium occupies approximately 3/4 of the corallite diameter. Tabulae are incomplete. Peripheral and some median tabellae are bubble-like. Other median tabellae are long, arranged steeper than bubble-like tabellae, some meet median lamella. Axial tabellae are densely packed, steeply elevated towards the median lamella.

INTRASPECIFIC VARIABILITY: Most specimens display the mature morphology closely comparable to the mature, but not the most advanced growth stage of the holotype (Text-figs 11D *vs* 11G, H, I) and do not require a detailed description. Paratype USNM PAL 800256 (Text-fig. 12A) resembles the most advanced growth stage of the holotype in the arrangement and thickening of the major septa, but its dissepimentarium is narrower. Paratype USNM PAL 800266 (Text-fig. 11J, K) resembles the mature growth stage of the holotype in all characters except for density of the axial structure comprising a thin median lamella and numerous septal lamellae. Also, the late neanic/early mature growth stage in the investigated paratypes is similar to that of the holotype (Text-figs 11A–C *vs* 12D, E). The longitudinal section of paratype USNM PAL 800257 (Text-fig. 12J) resembles the holotype most closely while slight differences in the longitudinal sections of the other two specimens illustrated (Text-figs 11L, 12B) may result from their more advanced growth stage. Both are cut through calices. The inner tabellae in these two specimens are slightly more steeply elevated and more densely arranged than those in the holotype. The similarities in morphology mentioned allow acceptance of a large intraspecific variability in n:d values of this species (Text-fig. 5). One specimen requires separate comments. It was removed from its living position but continued its growth at approximately 45º to its preceding position (Text-fig. 12C). Its shape and morphology below (Text-fig. 12D–G) and above (Text-fig. 12H, I) the turning point differ. The early morphology resembles the holotype except for the axial structure being less regular and almost free from major septa, and the dissepimentarium is narrower and more regular. The specimen becomes elongated in its new growth direction and its axial structure is deformed with the median lamella indistinguishable. However, the number of its major septa remain constant although the mean diameter differs slightly (29:9.8′8.0 mm and 29:13.0′8.6 mm). We illustrated it as an example of ability to survive in contrast to another specimen whose deep rejuvenation (Text-fig. 12M–L) did not rescue its life in the stressful conditions both lived in.

REMARKS: *Dibunophylloides similis* sp. nov. closely resembles in its n:d value the three species mentioned in the etymology. However, its separate features resemble not all, but only a single character in a given compared species and its complete morphology differs from all those species as discussed above with remarks about *D. colligatus* sp. nov. It clearly differs from *D. valeriae*, *D. differentialis* sp. nov. and *D. parcus* sp. nov. in n:d value and from each of these species by its particular features. Its difference from the remaining species of *Dibunophylloides* is large enough to be omitted.



Text-fig. 12. *Dibunophylloides similis* sp. nov. Transverse sections except when stated otherwise. A, B – Specimen USNM PAL 800256, paratype. A – early mature growth stage; B – longitudinal section. C–J – Specimen USNM PAL 800257, paratype. C – side view of rejuvenated corallite; D–G – successive sections of early mature to advanced mature growth stage; H, I – successive sections of rejuvenated part of corallite; J – longitudinal section. K–M – Specimen USNM PAL 800267, paratype. K – side view; L – calice, deep, unsuccessful rejuvenation; M – early mature growth stage. For stratigraphic position see text. Scale bars correspond to particular images.

OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). USNM PAL 800255 (holotype) and paratypes: USNM PAL 800250–800265. Locality N700 of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Paratypes: USNM PAL 800266–800273. Missourian.

Dibunophylloides infirmis sp. nov.
(Text-figs 5, 13–15)

ETYMOLOGY: Latin *infirmis*, *-is*, *-e* – weak – after weak septal lamella, broken within some specimens.

HOLOTYPE: Specimen USNM PAL 800274.

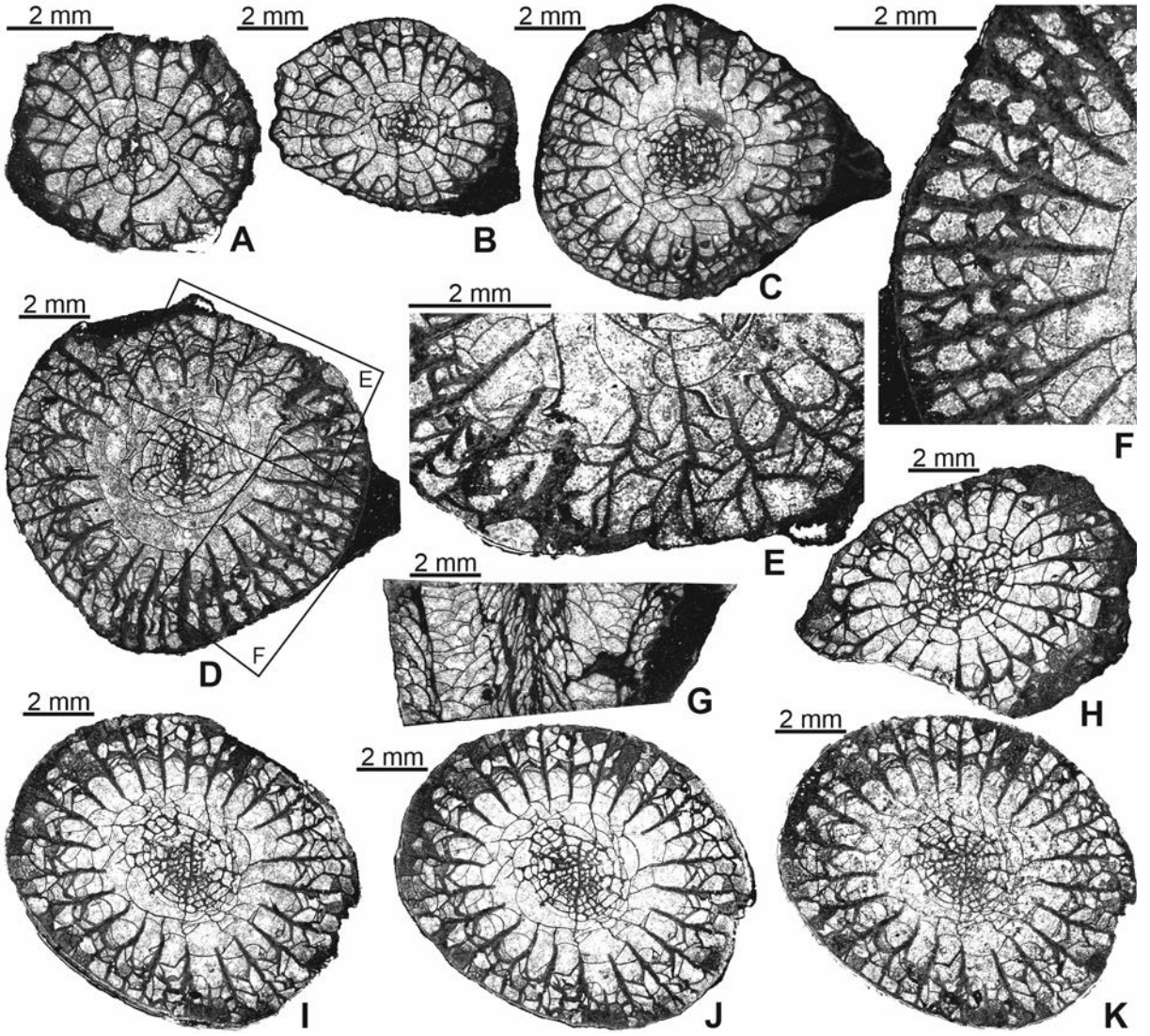
TYPE LOCALITY: N700a of Cooper and Grant (1972).

TYPE STRATUM: Gaptank Formation, upper part of Bed 10 of King (1930, 1937), Missourian.

MATERIAL: Holotype USNM PAL 800274 and nine well preserved paratypes (see Occurrence). Some calices preserved, but filled with matrix. Tips almost complete; only brephic and earliest neanic growth stage destroyed. Six thin sections and 29 peels available for study.

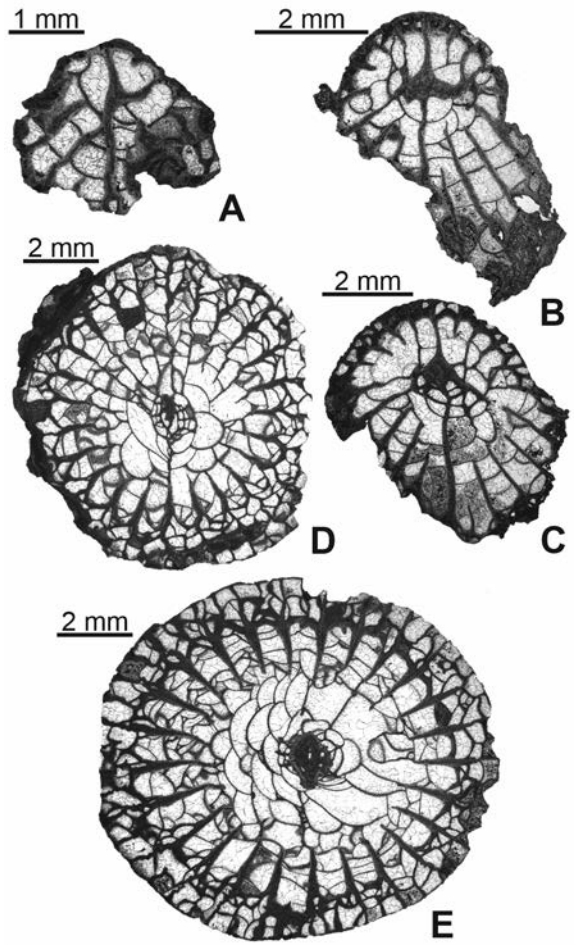
DIAGNOSIS: *Dibunophylloides* with major septa slightly thickened in inner dissepimentarium and outer tabularium, approximately 1/3 corallite radius long, rarely extend to axial structure, free in most. Minor septa variable, most approach tabularium. Median lamella weak, hardly recognizable or lacking from some transverse sections. Septal lamellae numerous, thin. Dissepimentarium approximately 1/4 of the corallite radius wide. Dissepiments variable; rare lateral cystose dissepiments occur. In longitudinal section tabulae incomplete. Peripheral tabellae horizontal and bubble-like, anastomose. Inner tabellae densely packed, steeply arranged, occupy 1/3 of the tabularium width.

DESCRIPTION OF THE HOLOTYPE: Corallite conical. Calice present, but filled by matrix. In the late neanic/early mature growth stage (Text-fig. 13A), with n:d value 19:4.5′4.0 mm, major septa slightly thickened in the tabularium, several meet the axial structure; these adjacent to shortened protosepta. Protosepta connected slightly aside to the median lamella. The axial structure approximately 1/6 corallite diameter wide, comprises median lamella weak, short, hardly recognizable and four septal lamellae short, thin, approaching the median lamella on both sides. A cardinal fossula is absent. Minor septa are differentiated in length, restricted to the dissepimentarium that comprises 1–3 rows of irregular dissepiments. The inner wall is slightly thickened. In the very early mature growth stage (Text-fig. 13B) with n:d value 21:7.0′5.2 mm, most major septa stay off the axial structure comprising nine septal lamellae rotated with the median lamella unrecognizable. Protosepta meet the axial structure. Minor septa differentiated in length, enter the tabularium where dissepimentarium narrow, restricted to 3/4 of its width when wide (Text-fig. 13B right and left, respectively). In more advanced growth stage (Text-fig. 13C), major septa are only approximately 1/2 corallite radius long, slightly thickened, most equal in length. The cardinal septum is recognizable only by the underdevelopment of the last pair of septa in the cardinal quadrants. Minor septa remain restricted to the dissepimentarium. The axial structure, slightly less than 1/3 corallite radius wide, comprises the thin median lamella, intersecting the entire structure, and 7 thin septal lamellae either attached to it on both sides or free. The dissepimentarium comprising irregular dissepiments reaches approximately 1/4 corallite radius. In the fully mature growth stage (Text-fig. 13D), with n:d value 24:10.1 mm, major septa remain approximately 1/2 corallite radius long, all are equal in length but differentiated in thickness with the boundary between these two kinds sharp (Text-fig. 13E, F). Minor septa are thin, strongly differentiated in length, but restricted to the dissepimentarium where the major septa are thin, but they are thick, some penetrating the tabularium where the major septa are thickened. The axial structure comprises short and indistinct median lamella and the septal lamellae differentiated in length; some long, some hardly recognizable. The dissepimentarium comprises irregular and herringbone dissepiments where major septa are thin and irregular and lateral-cystose dissepiments where the major septa are thick. It occupies approximately 1/4 corallite radius at both sides. In the longitudinal section dissepiments are elongated, steeply sloping down. Tabulae are incomplete. Peripheral tabellae are differentiated in shape. In the neighborhood of the dissepimentarium the bubble-like and horizontal tabellae anastomose. In the middle part of tabularium tabellae are long, slightly steeper elevated to the inner tabularium. Axial tabellae are dissepiment-like, densely packed, steeply elevated towards the median lamella.



Text-fig. 13. *Dibunophylloides infirmis* sp. nov. Transverse sections except when stated otherwise. A–G – Specimen USNM PAL 800274, holotype. A – late neanic/early mature growth stage; B–C – early mature growth stage; D – advanced mature growth stage; E – enlarged from D, rapid change in morphology of dissepimentarium and length of minor septa; F – enlarged from D, minor septa long and thick; G – longitudinal section. H–K – Specimen USNM PAL 800275, paratype; successive sections from early to advanced mature growth stage. For stratigraphic position see text. Scale bars correspond to particular images.

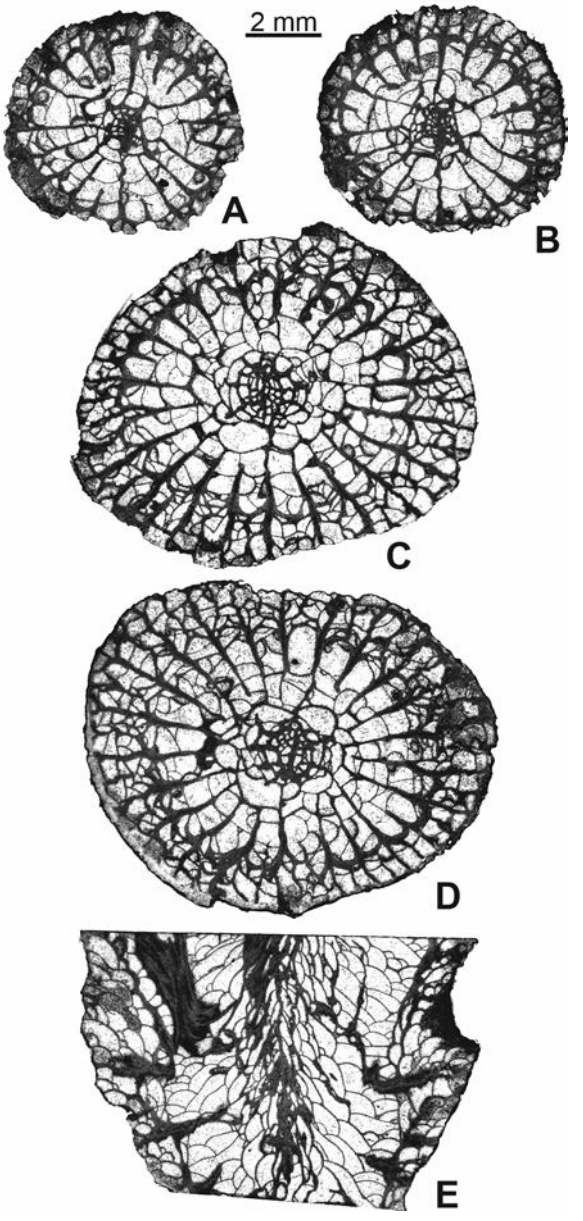
INTRASPECIFIC VARIABILITY: Paratype USNM PAL 800275 (Text-fig. 13H–K) resembles the holotype most closely in almost all aspects including the n:d value (24:9.6 mm). Main differences are: (i) all major septa are equally thin, and (ii) the median lamella is totally reduced in some parts of its growth. Two other paratypes are described and illustrated as examples of the morphology most distant from the holotype. The mature growth stage of coralite USNM PAL 800280 (Text-fig. 14A–E) differs from the comparable growth stage of the holotype in the morphology of the axial structure, which is very narrow, comprises a short, but distinct, median lamella and only a few short septal lamellae. The cardinal septum joins the median lamella up to the early mature growth stage, but the latter is free in advanced maturity (Text-fig. 14D, E, respectively). This specimen resembles the holotype in length and arrangement of major septa, which are thickened as in a part of the holotype, in length and morphology of minor septa and the dissepimentarium comprising several lateral-cystose dissepiments. Morphology of



Text-fig. 14. *Dibunophylloides infirmis* sp. nov. Transverse sections. A–E – Specimen USNM PAL 800280, paratype. A–C – early to late neanic growth stage; D – early mature growth stage; E – advanced mature growth stage. For stratigraphic position see text. Scale bars correspond to particular images.

its early growth stage (Text-fig. 14A–C) is typical for the genus in all main aspects when deformations resulting from a strong attachment to the surface are not considered. Corallite USNM PAL 800276 (Text-fig. 15A–E) is intermediate between the holotype and the afore described paratype in some characters but differs from both in its mature n:d value (23:11′9 mm). Its very early mature growth stage (Text-fig. 15A, B) resembles that of the holotype except for the longer major septa, and the cardinal septum is directed to the indistinct median lamella. Its fully mature growth stage (Text-fig. 15C, D) differs from the holotype in the longer major septa and the axial structure being narrower comprising the median lamella disrupt temporarily (Text-fig. 15C). The morphology of its longitudinal section differs from that in the holotype most. Its dissepiments are more differentiated in arrangement with the inner row being vertical. The tabularium comprises mostly bubble-like tabellae, gradually changing into densely packed, steeply arranged axial tabellae.

REMARKS: The holotype and most similar paratypes resemble *D. parcus* sp. nov. in the morphology of the axial structure in transverse section, but differ from the latter in the longitudinal section with



Text-fig. 15. *Dibunophylloides infirmis* sp. nov. Transverse sections except when stated otherwise. A–E – Specimen USNM PAL 800276, paratype. A, B – late neanic/early mature growth stage; C, D – mature growth stage; E – longitudinal section. For stratigraphic position see text. Scale bar correspond to all images.

the more steeply elevated inner tabellae occupying a wider part of the tabularium. Also, its major septa are shorter and minor septa are longer. Its dissepimentarium is narrower with more numerous lateral cystose dissepiments. Its n:d value is smaller except for specimen USNM PAL 800167 with n:d value 23:9.0 mm, which is included in *D. parcus* sp. nov. on the basis of its overwhelming morphological similarity to the holotype of that species (see above). We treat that specimen as intermediate between those two species. The n:d value of *D. infirmis* sp. nov. closely corresponds to those of *D. colligatus* sp. nov. and *D. similis* sp. nov. but it differs from both those species in the morphology of the axial structure, length of major and minor septa and the morphology in longitudinal section.

OCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). USNM PAL 800274 (holotype) and paratypes: USNM PAL 800275–800279. Locality N700 of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Paratypes USNM PAL 800280–800283. Missourian.

Dibunophylloides complexus sp. nov.
(Text-fig. 16)

ETYMOLOGY: Latin *complexus*, *-a*, *-um* – complex – after a complex morphology, of the dissepimentarium in particular.

HOLOTYPE: USNM PAL 800284.

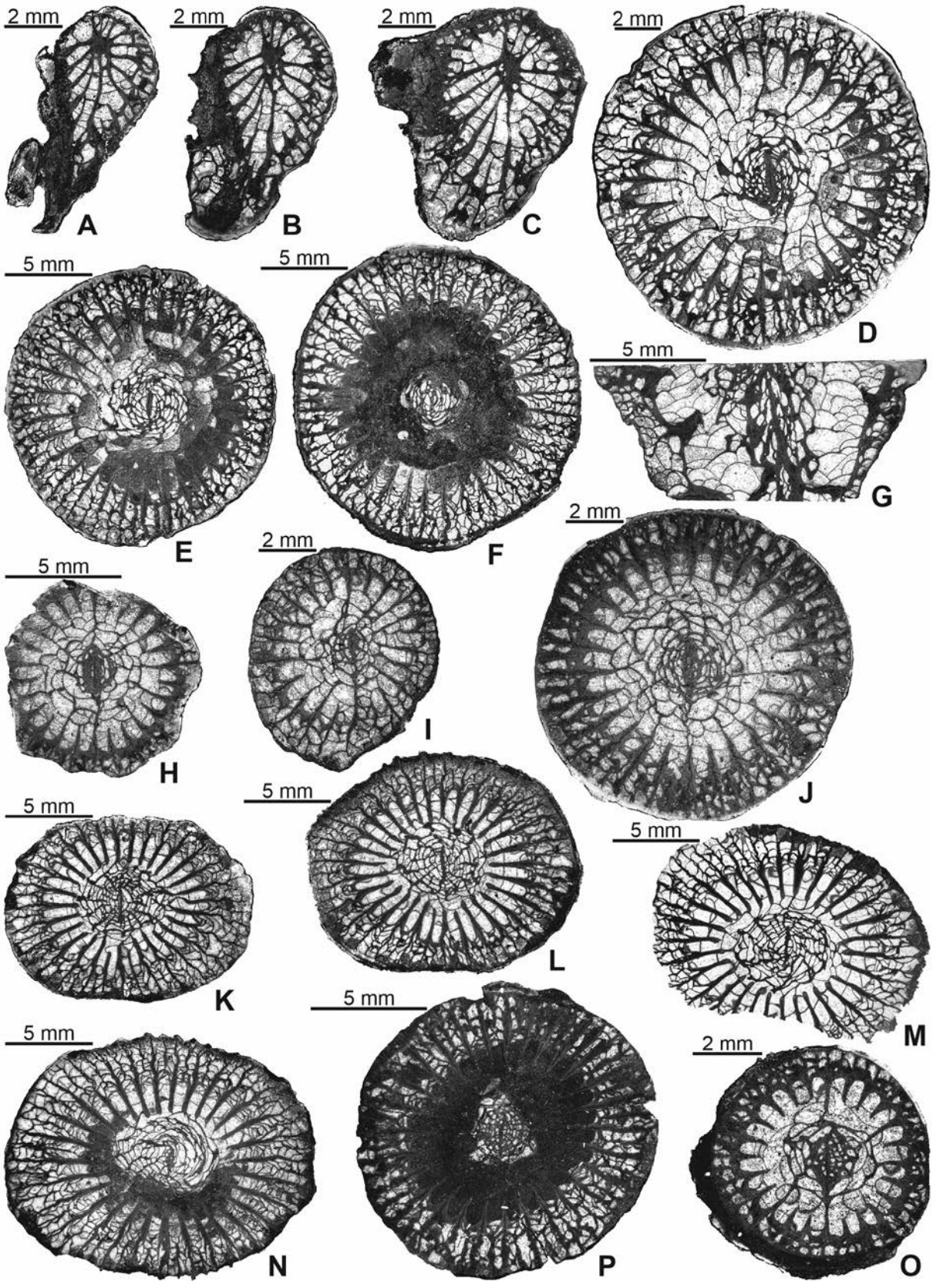
TYPE LOCALITY: N700a of Cooper and Grant (1972).

TYPE STRATUM: Gaptank Formation. Upper part of Bed 10 of King (1930, 1937), Missourian.

MATERIAL: The holotype USNM PAL 800284, and three well preserved specimens USNM PAL 800285–800287; all sectioned. Two thin sections and 22 peels available for study.

DESCRIPTION OF THE HOLOTYPE: The neanic growth stage is deformed at the left alar septum side by strong attachment to a surface (Text-fig. 16A–C). The n:d values: 19:6.0′4.6 mm, 22:7′5 mm and 23:8′6 mm. The zaphrentoid arrangement of major septa although disturbed by the attachment, is recognizable. The axial septum is thickest in its axial part through the entire neanic growth stage, being thickest in the latest part. A cardinal fossula is developed. First minor septa and irregular dissepiments already appeared in the youngest section studied, but they are absent from the part of the corallite adjacent to the attachment scar in this and in the following two transverse sections of the neanic growth stage. Most of the thin and wavy minor septa reach the inner limit of the dissepimentarium. In the mature part of corallite its n:d value increases as follows: immediately below the calice 31:14 mm, at the calice floor 32:15 mm, in the lower part of calice 33:16 mm (Text-fig. 16D–F respectively). Major septa below the calice are thickest in the thickened inner wall, whereas their inner margins are very thin and twisted. Several of them meet the axial structure. In the dissepimentarium, major septa are thin and wavy; many bear carinae-like bodies. The last pair of major septa adjacent to the cardinal septum is slightly shortened. In the calice, thin inner parts of major septa are reduced step by step. Peripheral parts of major septa become thickest and wavy in the inner dissepimentarium, bearing numerous carinae-like bodies. Minor septa are thin wavy and differentiated in length from approaching the tabularium to restricted to approximately 1/3 of the dissepimentarium width. The axial structure comprises thickened median lamella disconnected from the protosepta, septal lamellae are few, short and thickened. They rotate around the median lamella but leave it free. Numerous sections of inner tabellae supplement the dense axial structure. The dissepimentarium occupies approximately 1/4 corallite radius, comprises small, densely packed, irregular dissepiments and numerous lateral-cystose dissepiments. In longitudinal section dissepiments are differentiated in size and arrangement. The tabularium occupies approximately 2/3 of the corallite diameter. Tabulae are incomplete. Peripheral tabellae are bubble-like, those adjacent to the axial structure are larger. The axial structure occupies approximately 1/4 of the tabularium diameter. Inner tabellae are short, densely packed, steeply elevated towards the median lamella. Several sections of

Text-fig. 16. *Dibunophylloides complexus* sp. nov. Transverse sections except when stated otherwise. A–G – Specimen USNM PAL 800284, holotype. A–C – early to late neanic growth stage; D – mature growth stage immediately below calice; E – mature growth stage, above calice floor lower right; F – mature growth stage, lower part of calice; G – longitudinal section. H–J – Specimen USNM PAL 800285, paratype. H, I – early mature growth stage; J – mature growth stage. K–N – Specimen USNM PAL 800286, paratype. K–M – successive sections from early to advanced mature growth stage; N – mature growth stage, partly above calice floor (lower). O, P – Specimen USNM PAL 800287, paratype. O – early mature growth stage; P – mature growth stage, middle part of calice. For stratigraphic position see text. Scale bars correspond to particular images. →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thick septal lamellae are attached to the inner tabulae, making that part of the tabularium very dense.

INTRASPECIFIC VARIABILITY: Paratype USNM PAL 800285 (Text-fig. 16H–J) with n:d value of the mature growth stage 26:11.0 mm, is the smallest of the specimens included in this species, but displays a close similarity to the holotype in morphology. Small differences of the mature growth of this specimen from that of the holotype comprise: (i) major septa thicker, (ii) minor septa thick and commonly reaching the thick inner wall, (iii) thin septal lamellae in the axial structure, (iv) the cardinal septum meets the axial lamella with its very thin inner margin. The earliest mature or late neanic/early mature growth stage of this and another paratype specimen (Text-fig. 16H, I, O) document the morphology, not investigated in the holotype. Main characters of that growth stage are: (i) major septa are already radially arranged and thickest in the thick inner wall, (ii) the cardinal septum is united with the thickened median lamella, (iii) septal lamellae in the narrow axial structure are radially arranged, (iv) most or all minor septa approach the inner wall, (v) lateral-cystose dissepiments do not occur yet. Paratype USNM PAL 800286 (Text-fig. 16K–N), sectioned only in the mature growth stage, resembles the holotype in n:d value (30:14′11 mm, 30:15.6′12.4 mm, 30:17.6′14 mm, respectively) and in the morphology of the dissepimentarium, although it differs in possessing thicker major septa that are not lanceolate in the tabularium, slightly longer minor septa, but very thin and wavy, hardly distinguishable from irregular dissepiments, the weak median lamella in the axial structure, thin, more numerous septal lamellae that are radially arranged in early maturity and rotating in the late mature growth stage, most distinctly at the calice floor (Text-fig. 16N). Paratype USNM PAL 800287 (Text-fig. 16O, P) is sectioned only in the early growth stage (described above) and in the calice (n:d value 28:12.8 mm). The morphology of its calice resembles the holotype except for the axial structure that comprises a thin middle lamella and numerous thin septal lamellae, almost radial in the arrangement.

REMARKS: We decided to name the small group of four specimens because of the striking similarity in their morphology and a clear distinction from all species of *Dibunophylloides* described so far. Only rare parts of the dissepimentarium in *D. differentialis* sp. nov. and rotating lamellae in *D. parcus* sp. nov. and *Dibunophylloides* sp. weakly resemble those characters in *D. complexus* sp. nov.

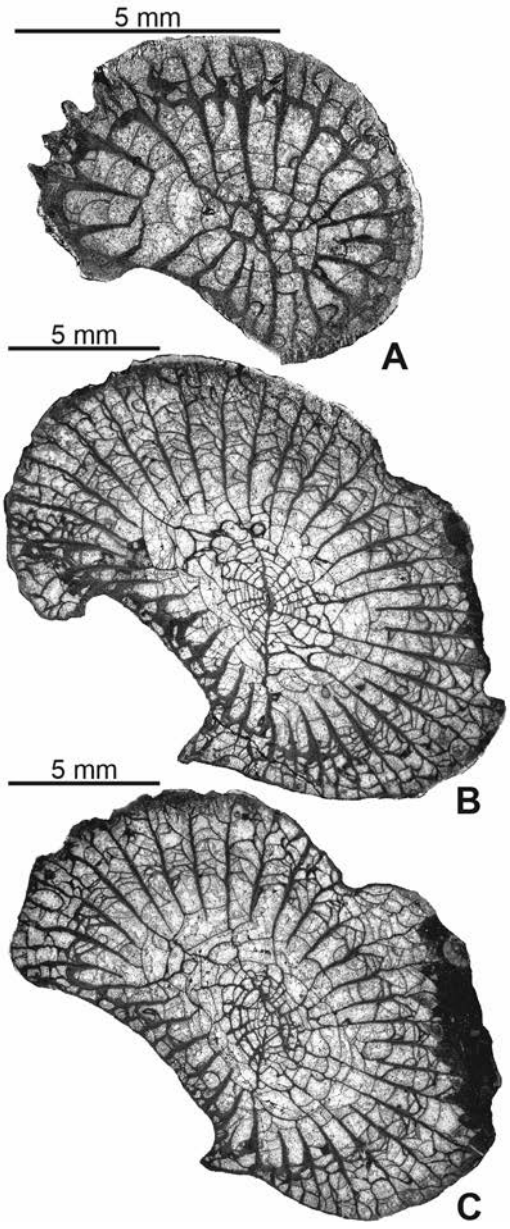
OCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). USNM PAL 800284 (holotype), paratype: USNM PAL 800285. Locality N700 of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Paratypes: USNM PAL 800286, 800287. Missourian.

Dibunophylloides cf. *valeriae* (Newell, 1935)
(Text-fig. 17)

MATERIAL: One specimen sectioned transversally in early and mature growth stages. Its irregularly oval shape resulted from permanent attachment to a hard object. Three peels available for study.

REMARKS: ‘*Dibunophyllum*’ *valeriae* Newell, 1935 was the first *Dibunophylloides* species described from North America. Unfortunately, illustrations provided by Newell (1935, pl. 33, figs 1–3) do not fit recent standards. Only two transverse thin sections taken from the unknown but probably mature part of the holotype and the paratype were illustrated (Newell 1935, pl. 33, figs 2a, 3a, respectively). Illustrations of the longitudinal section of the second paratype (Newell 1935, pl. 33, figs 1a, b) are off center. Thus, the morphology of the early mature and neanic growth stages of the holotype and its longitudinal section remain unknown. Moreover, the type material “may be presumed to be lost” (Cocke 1970, p. 21) and Cocke’s attempt to re-collect topotypes was unsuccessful. Thus, interpretation of the intraspecific variability of this species is left to the taxonomic approach of a given scientist. Cocke (1970, pp. 20, 21, pl. 1, figs 1, 8–13), who sectioned 52 specimens transversally and nine specimens longitudinally, suggested a very wide intraspecific variability in all features of this species. For instance: (i) major septa meeting the axial structure, that is either wide and loose or narrow and dense and major septa free ended (Cocke 1970, pl. 1, figs 1a, 11–13 *vs* 8a, 9); (ii) minor septa either hardly recognizable within the wide dissepimentarium, comprising mostly herringbone dissepiments, or minor septa moderate to long, some crossing the narrow dissepimentarium (Cocke 1970, pl. 1, figs 9, 10a, 11 *vs* 1b, 8a, 12); (iii) the n:d values vary (Cocke 1970, pl. 1, figs 9 *vs* 10a, 13). Lack of the median lamella in a very loose axial structure of one specimen (Cocke 1970, pl. 1, fig. 10a) may be interpreted as temporary and environmentally caused.

Lack of adequate original data and doubts about Cocke’s (1970) ‘lumping’ approach to *D. valeriae* led us to identify our specimen as *conformis*



Text-fig. 17. *Dibunophylloides* cf. *valeriae* (Newell, 1935). Specimen USNM PAL 800288. Transverse sections. A – late neanic growth stage; B, C – mature growth stage. For stratigraphic position see text. Scale bars correspond to particular images.

to that species. The maximum measured n:d value 35:18.0′12.8 mm of our specimen resembles that of the holotype adequately to be accepted. The earliest growth stage investigated, with n:d value 23:7.2′5.8 mm, represents the latest neanic/earliest mature growth stage (Text-fig. 17A). The axial septum forms a clear axis of symmetry and rudiments of the zaphrentoid arrangement of major septa remain, but the longest of them already form the beginning of the axial structure. Minor septa adjacent to the counter septum enter the tabularium, whereas the remaining minor septa are restricted to the dissepimentarium that comprises one or two rows of regular dissepiments. The inner wall is thickened. In the ontogenetically younger part of the mature growth stage (Text-fig. 17B), protosepta meet the median lamella, slightly thickened in the middle. Remaining major septa are semi-radially arranged, slightly differentiated in length, with some of the longest entering the regular axial structure, slightly more than 1/4 corallite diameter wide. Minor septa cross the dissepimentarium where narrow, but are restricted to its periphery where wide, i.e., reaching approximately 1/3 corallite radius in width and mostly among herringbone dissepiments. The strongly thinning, almost disappearing median lamella (Text-fig. 17C) forms the main difference of the ontogenetically most advanced growth stage compared to the younger one.

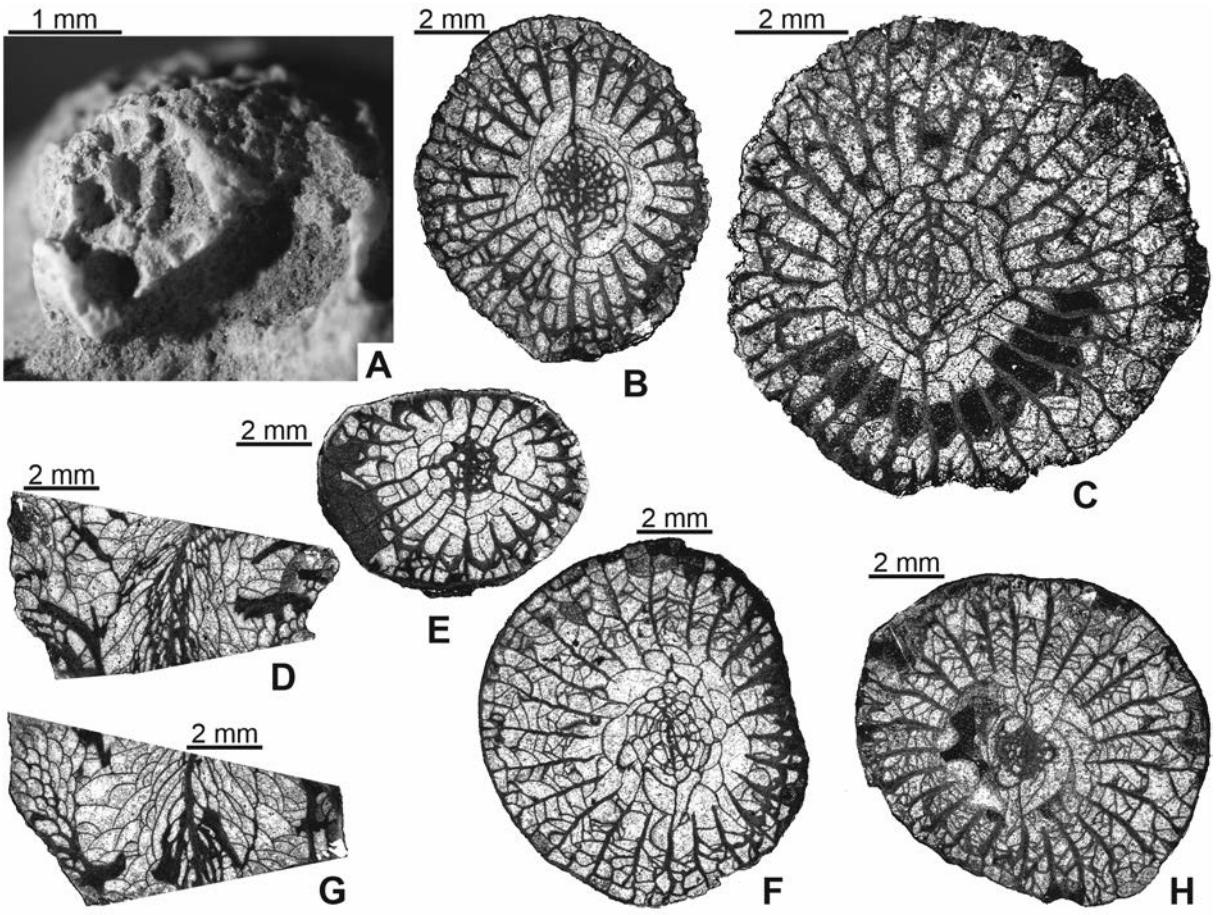
REMARKS: The specimen differs from the holotype in an almost total disappearance of the median lamella in the advanced mature growth stage and in having shortened minor septa. These characters are common to one corallite illustrated by Cocke (1970, pl. 1, fig. 11) and are comparable to *D. parcus* sp. nov. from which the specimen discussed differs most of all by its n:d value.

OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Specimen USNM PAL 800288. Missourian.

Dibunophylloides sp. 1
(Text-fig. 18)

MATERIAL: Four well preserved specimens all sectioned. Nine peels available for study.

DESCRIPTION: In specimen USNM PAL 800289 the brephic growth stage with n:d value 6(?7):1.0′0.8 mm, was exposed thanks to weathering and silicification of septa (Text-fig. 18A). Its cardinal septum side is flattened by the attachment and its external wall is thick. In the early mature growth stage (Text-fig. 18B), with n:d value 26:8.2′7.0 mm, most major septa are equal in length, except for the protosepta connected to the median lamella and slightly shortened last septa secreted in quadrants. They are approximately 2/3 corallite radius long, thickened in the inner dissepimentarium and the tabularium. The axial structure, free from



Text-fig. 18. *Dibunophylloides* sp. 1. Transverse sections except when stated otherwise. A–D – Specimen USNM PAL 800289. A – broken and weathered tip, brephic growth stage; B – early mature growth stage; C – advanced mature growth stage; D – longitudinal section. E–G – Specimen USNM PAL 800290. E – late neanic/early mature growth stage; F – mature growth stage; G – longitudinal section. H – Specimen USNM PAL 800292, mature growth stage. For stratigraphic position see text. Scale bars correspond to particular images.

most major septa, comprises distinct median lamellae and several densely packed septal lamellae attached on both sides. Minor septa, present in all septal loculi, are thin and differentiated in length. In the advanced mature growth stage (Text-fig. 18C), with n:d value 28:8.4 mm, sectioned in part immediately above the calice floor (black infillings), thin major septa reach the axial structure beneath the calice floor and are mostly free ended above it, except for the cardinal septum that reaches the median lamella with its curved inner margin. The axial structure is approximately 1/3 corallite diameter wide, comprising thin, long median lamella and rare septal lamellae. Minor septa are very short in the wide part of the dissepimentarium, which contains mostly herringbone dissepiments, but remain well developed in the narrow dissepimentarium with irregular dissepiments. In the longitudinal section (Text-fig. 18D), the dissepimentarium differs in width in opposite corallite sides. Dissepiments steeply slope down, are small, slightly differentiated in length. Tabulae are incomplete, bubble-like and loosely arranged in the peripheral part of the tabularium, transfer gradually into the inner tabularium, occupying approximately 1/3 tabularium diameter and comprising axial tabellae, elongated and steeply elevated towards the median lamella.

The mature growth stage of corallite USNM PAL 800291 (Text-fig. 18F) with n:d value 25:9.8′8.8 mm, differs from the specimen described above in its smaller n:d value. Also, its morphology both in transverse and longitudinal sections (Text-fig. 18G) is similar except for slightly thinner skeletons and rapid widening of its dissepimentarium on the left side. The late neanic/early mature growth stage of this specimen (Text-fig. 18E), with n:d value 22:7′6 mm, displays a bilateral arrangement of major septa with the

protosepta united with the median lamella and some major septa elongated so as to participate in formation of the narrow, dense axial structure. The minor septa intersect the narrow dissepimentarium, which has one to three rows of irregular dissepiments. The mature growth stage of corallite USNM PAL 800292 (Text-fig. 18H) with n:d value 25:9.8′8.6 mm, differs from the other two in the dense and narrow axial structure and in the dissepimentarium reaching almost 2/3 corallite radius in its widest part. The sectioned but not illustrated corallite USNM PAL 800290 (n:d value 25:10.0′8.2 mm) closely resembles the last described one in all main morphological characteristics.

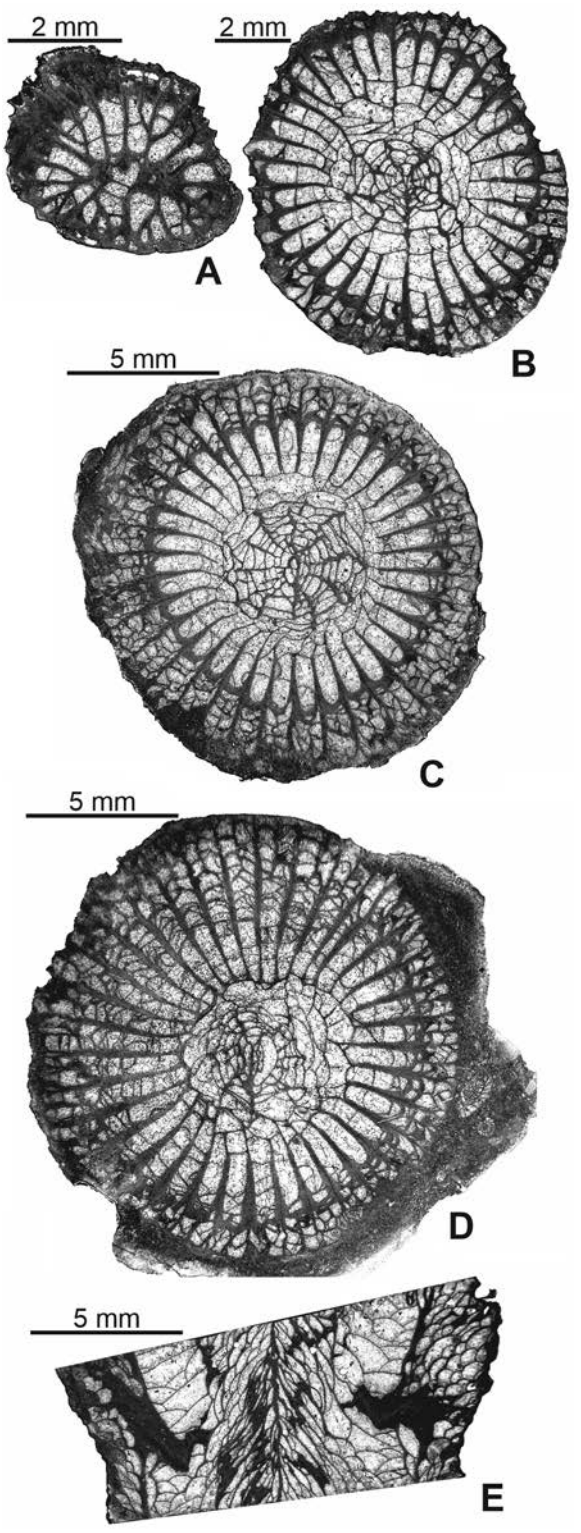
REMARKS: Specimens included in this unnamed species differ from one another in some details, but were placed together to avoid multiplication of unnamed taxa. Their main characters in common are: (i) radial arrangement of major septa with the protosepta connected to the median lamella up to the early mature growth stage or permanently; (ii) minor septa well developed in early growth stages, but very short, absent from several septal loculi in the advanced mature growth stage; (iii) axial structure free from the major septa, regular, comprising distinct median lamella and some septal lamellae attached to both sides; (iv) the dissepimentarium in advanced mature growth stage differentiated in width within a given section, comprising mostly herringbone dissepiments; its widest part occupying 1/2 to 2/3 corallite radius; and (v) similar n:d value of three specimens, with one possessing slightly more numerous major septa. Particular characters listed occur in other species described so far, but not in this combination. For instance, the axial structure resembles that of *D. differentialis* sp. nov., the morphology and differentiated width of the dissepimentarium resembles that of *D. parcus* sp. nov., and the n:d value of most specimens closely corresponds to those in *D. clathrum* Cocke, 1970, *D. colligatus*, and *D. infirmis* sp. nov.

OCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). USNM PAL 800289, 800290. Locality N700 of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). USNM PAL 800291, 800292. Missourian.

Dibunophylloides sp. 2
(Text-fig. 19)

MATERIAL: One well preserved specimen with seven peels from transverse sections, representing various growth stages and two peels from longitudinal section.

DESCRIPTION: The neanic growth stage (Text-fig. 19A) with n:d value 24:4.6′3.6 mm displays zaphrentoid arrangement of major septa, but its axial part is deformed. The axial septum is replaced by the long cardinal septum attached to one major septum in counter quadrants whereas the long counter septum is free ended in the corallite axis with its inner margin thickened. First minor septa and an incomplete row of regular dissepiments already occur. In the early mature growth stage (Text-fig. 19B) with n:d value 35:14.0′13.2 mm, major septa are radially arranged, slightly lanceolate, taper axially, meet or approach the axial structure. Those adjacent to both protosepta are shortened. The cardinal septum extends far through the corallite axis with its thin inner margin turning slightly left near its end. Thus, the distinct median lamella is absent. The counter septum is long, but does not extend to the inner margin of the cardinal septum. Minor septa are thin, almost intersect the narrow dissepimentarium that contains regular and irregular dissepiments. The inner wall is slightly thickened. The axial structure comprises three and four septal lamellae each side of the inner margin of the cardinal septum. Two transverse sections of the mature growth stage (Text-fig. 19C, D) with n:d value 35:14.2′13.2 mm and 35:15.0′14.2 mm have radially arranged major septa, equal in length, lanceolate, and tapering axially. They rarely meet the axial structure in younger stages, and all are free in the more advanced growth stage. Also, the septal lamellae in the axial structure of the younger growth stage are longer and radially arranged whereas they are short and tend to rotate with axial tabellae begin to dominate in the more advanced growth stage. A thin median lamella, intersecting the axial structure, occurs in both transverse sections. Most minor septa reach the slightly thickened inner wall, but none enter the tabularium. The dissepimentarium is differentiated in width and content, 1/4 and 1/3 or 1/2 corallite radius wide in particular sections or their fragments. It comprises rare regular dissepiments at the periphery, common irregular dissepiments through the dissepimentarium width and some herringbone dissepiments in the more advanced growth stage where minor septa slightly shorten. Lateral cystose dissepiments are only sporadic. In longitudinal section (Text-fig. 19E), the dissepimentarium differs in width both sides of the section. Dissepiments are small, steeply arranged. The inner wall is thickened. The tabularium occupies more than 2/3 of corallite



Text-fig. 19. *Dibunophylloides* sp. 2. Transverse sections except when stated otherwise. Specimen USNM PAL 800293. A – late neanic growth stage; B–D – early to advanced mature growth stage; E – longitudinal section. For stratigraphic position see text. Scale bars correspond to particular images.

diameter and is distinctly divided into an inner and a peripheral part. Peripheral tabularium contains short, bubble-like tabellae next to the dissepimentarium, anastomosing with elongated tabellae most of which extend to the inner tabularium. The inner tabularium comprises elongated tabellae, densely packed, steeply elevated towards the median lamella. Some peripheral axial tabellae resemble lateral tabellae bordering the inner tabularium to form an incomplete axial column.

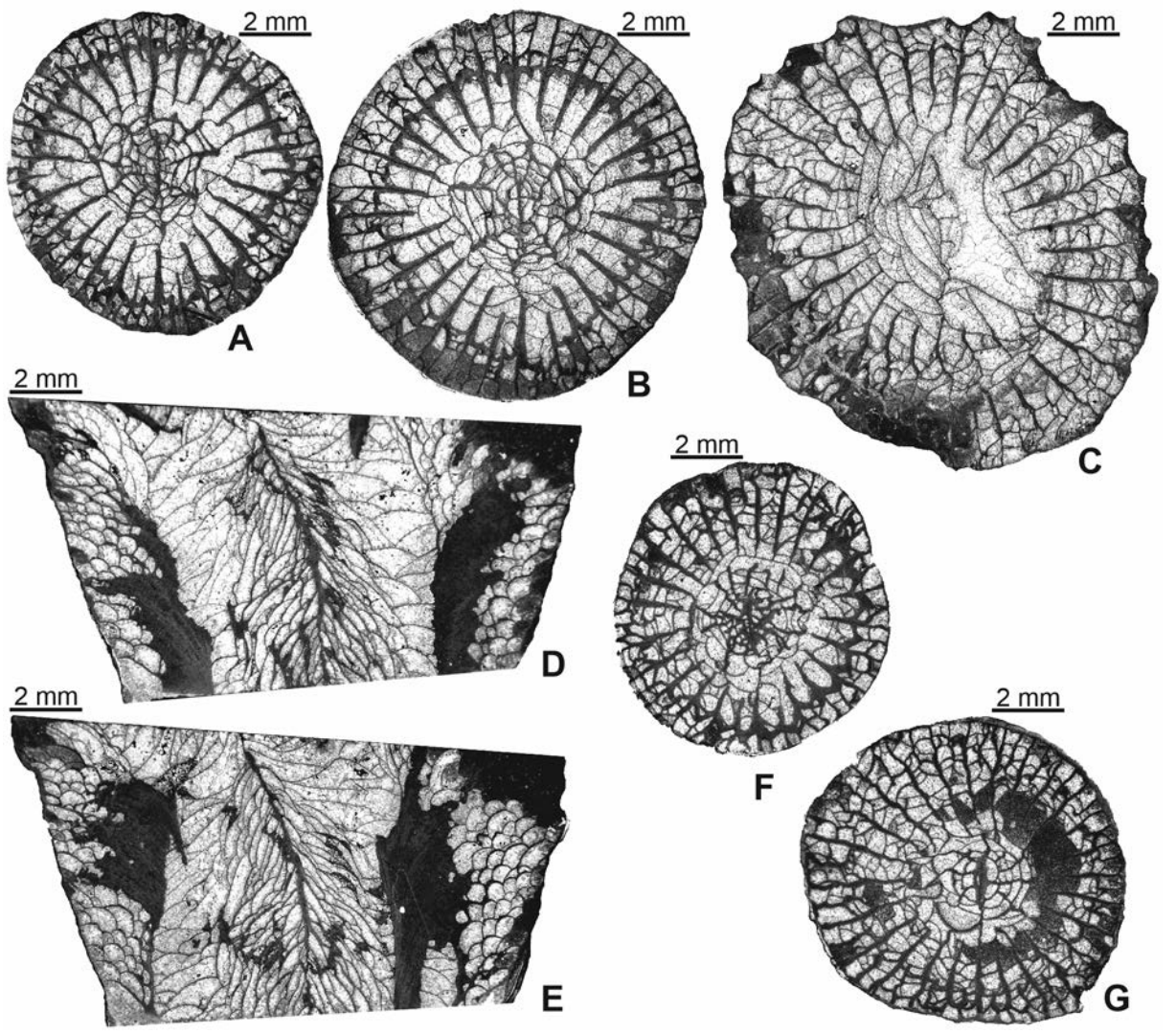
REMARKS: The specimen described weakly resembles *D. differentialis* sp. nov. in the morphology of its dissepimentarium. The morphology of its axial structure weakly resembles *D. parcus* sp. nov. The length of its long minor septa differs from both species compared as is its n:d value. The axial structure in one specimen described by Ross and Ross (1962, pl. 162, fig. 11) as *Dibunophyllum moorei* Jeffords, 1948 displays a morphology of the axial structure similar to that of *Dibunophylloides* sp. 2, but that is the only resemblance between those two. *Dibunophylloides* sp. 2 resembles '*Dibunophyllum*' *brucei* Cocke, 1966 in the morphology of the axial structure, but differ from it in the morphology and width of the dissepimentarium and in the n:d value.

OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Specimen USNM PAL 800293. Missourian.

Dibunophylloides sp. 3
(Text-fig. 20)

MATERIAL: Two slightly incomplete corallites USNM PAL 800294 and 800295 are described separately. However, we have placed them together in order to avoid a multiplication of unnamed species. Twelve peels were available for study.

DESCRIPTION: In the early and middle mature growth stage of corallite USNM PAL 800294 with n:d value 28:9.1 mm and 28:11 mm (Text-fig. 20A, B, respectively), the major septa are radially arranged, slightly lanceolate. Most are approximately equal in length either approaching the axial structure or meeting their lamellae. Only the last major septa secreted in quadrants are slightly shortened and the protosepta extend to the median lamella, meeting it with their very thin inner margins. The axial structure occupies slightly more than 1/3 corallite diameter, with a distinct median lamella, four and five septal lamellae



Text-fig. 20. *Dibunophylloides* sp. 3. A–E – Specimen USNM PAL 800294. A–C – early to late mature growth stage; D, E – longitudinal section. F, G – Specimen USNM PAL 800295. F – early mature growth stage; G – advanced mature growth stage. For stratigraphic position see text. Scale bars correspond to particular images.

attached to each side and numerous sections on inner tabellae. Minor septa penetrate the tabularium with their thickened inner margins. The dissepimentarium occupies approximately 1/5 corallite radius, with regular and irregular dissepiments. The inner wall is thickened. In advanced maturity (Text-fig. 20C) with n:d value 31:13 mm, the corallite started rejuvenation as is demonstrated next to its cardinal septum. A strange matrix appears between the rudiments of its skeleton at the periphery and some major septa inside the corallite are divided by lonsdaleoid dissepiments into inner and outer parts. Major septa are thin and radially arranged. Most are equal in length, extending 2/3 of corallite radius from the external wall. The cardinal septum is elongated and major septa adjacent to it are slightly shortened. A very thin inner part of the cardinal septum extends far beyond the corallite axis, replacing its median lamella. Four very short septal lamella are attached to the axial part of the cardinal septum at its left side and one at its right side forming an extremely weak axial structure that resembles the axial structure in *Yuanophylloides*. All minor septa are shortened; some are totally reduced. The dissepimentarium occupies almost 1/2 corallite radius at one corallite side and 1/3 radius at the opposite side, with mostly herringbone dissepiments

with irregular and/or regular dissepiments appearing between major and minor septa. In the longitudinal section (Text-fig. 20D, E), the dissepimentarium widens distinctly upwards; dissepiments in this part are larger than in the ontogenetically younger part of the section whereas the tabularium remains similar in width but not in morphology. In the younger part the inner tabularium occupies more than 2/3 of its width, comprising many small tabellae elevated at approximately 50º towards the median lamella. Width of the inner tabularium decreases upwards up to its replacement by the unified tabularium near the upper limit of the section. The bubble-like peripheral tabellae present in the ontogenetically younger part of the section were gradually replaced by increasingly longer peripheral tabellae up to the appearance of almost complete tabulae in the uppermost part of the section. The described changes in morphology started long before the process of rejuvenation started. Thus, they cannot be interpreted as its result.

Two thin sections of the mature growth stage of corallite USNM PAL 800295 display small morphological differences in characters other than the axial structure. In the ontogenetically younger growth stage (Text-fig. 20F), major septa are slightly thickened in the inner dissepimentarium and outer tabularium, and equal in length including the protosepta. All extend approximately at 2/3 of the corallite radius from the external wall. Only major septa adjacent to the cardinal septum are shortened. Minor septa reach the thickened inner wall where the dissepimentarium is narrow, extending to 1/2 its width where wide. The axial structure is free from major septa, comprising the thin and hardly recognizable median lamella and 18 septal lamellae, differentiated in length and slightly rotating. The morphology of the ontogenetically more advanced growth stage (Text-fig. 20G), i.e., immediately beneath and partly above the calice floor (black infillings), differs from the afore described growth stage in displaying some major septa extending to the axial structure, the protosepta meeting the median lamella and the dissepimentarium very wide, extending at one corallite side from the outer wall to almost reaching inner margins of major septa. The axial structure is loose, comprising thick median lamella accompanied by 4 and 3 thin septal lamellae on each side.

REMARKS: The ontogenetically younger part of the corallite USNM PAL 800294 resembles *D. differentialis* sp. nov. in the morphology of the axial structure and length of the major septa. The middle part of its longitudinal section also displays some similarity to the longitudinal section of *D. differentialis* sp. nov. and its n:d value corresponds to the largest specimens of the latter. However, the long minor septa differentiates it from all species of *Dibunophylloides* described so far from North America, being comparable in this character only to *Dibunophylloides longiseptatus* Fomichev, 1953 from the late Moscovian of the Donets Basin, Ukraine. The peculiarity both in the advanced mature growth and in its longitudinal section cannot be explained.

The n:d value of the corallite USNM PAL 800295 corresponds to that of '*Dibunophyllum*' *clathrum* Cocke, 1970, *Dibunophylloides colligatus* sp. nov. and *D. infirmis* sp. nov. Most of its morphological features are comparable to *D. parcus* sp. nov., but differences in the morphology of its axial structure are unique. Both of these specimens are described as examples of the enormous morphological plasticity of the North American *Dibunophylloides*.

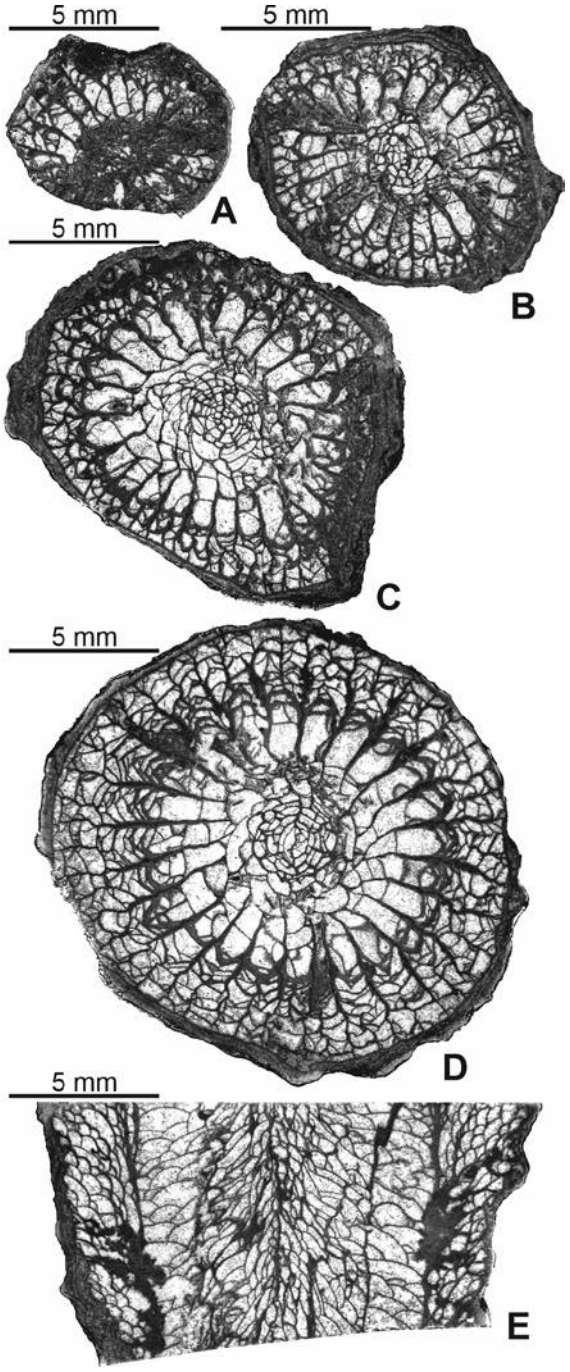
OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Specimens USNM PAL 800294 and 800295. Missourian.

?*Dibunophylloides* sp.4
(Text-fig. 21)

MATERIAL: Single, slightly incomplete specimen USNM PAL 800296, lacking calice and ontogenetically earliest part with late neanic/early mature part compressed. One thin section and twelve peels were available for study.

DESCRIPTION: The ontogenetically youngest part is compressed (Text-fig. 21A). In the earliest reasonably preserved part (Text-fig. 21B), with n:d value 26:10.8′9.0 mm, major septa are radially arranged, slightly thickened in the tabularium. Their thin inner margins tend to rotate and meet the axial structure that consists of a weak median lamella with slightly wavy and rare, indistinct septal lamellae. Minor septa cross the dissepimentarium at approximately 1/4 of the corallite radius, among regular and irregular dissepiments. In the more advanced ontogeny, perhaps early mature (Text-fig. 21C), with n:d value 26:11.4′10.2 mm, dissepimentarial parts of major septa became thin and wavy resembling minor septa most of which cross the dissepimentarium and reach its slightly thickened inner wall. The arrangement and thickness of tabularial parts of major seta remain similar to the younger growth stage except for their

inner margins that are long, very thin, and rotating around the axial structure to form its peripheral part. Inner part of the axial structure comprises 14 septal lamellae, rotating and differentiated in length from



Text-fig. 21. ? *Dibunophylloides* sp. 4. Transverse sections except when stated otherwise. Specimen USNM PAL 800296. A – late neanic/early mature growth stage; B – very early mature growth stage; C, D – early and advanced mature growth stage; E – longitudinal section. For stratigraphic position see text. Scale bars correspond to particular images.

crossing 1/2 of the axial structure to hardly recognizable. The median lamella is not recognizable or is lacking. The dissepimentarium occupies approximately 1/5–1/4 of the corallite radius, with mostly irregular dissepiments, but some regular and rarely lateral-cystose. In the advanced mature growth stage (Text-fig. 21D), with n:d values 26:16′15 mm, major septa remain similar to the earlier mature growth stage, except for being commonly free from the axial structure. Minor septa are thin and wavy but vary in length from reaching the inner limit of the dissepimentarium to penetrating less than 1/2 of its width. The axial structure becomes narrow, occupying slightly less than 1/4 of the corallite diameter. Only a few major septa meet it with thin, rotating inner margins. A thin, wavy body crossing the axial structure may be a median lamella. It is accompanied by a few short, free septal lamellae on each side. The dissepimentarium is approximately 1/4 to 1/3 of the corallite radius wide. It comprises mostly irregular and pseudo herringbone dissepiments and herringbone dissepiments where minor septa are shortened. Lateral cystose dissepiments are sporadic. In the longitudinal section (Text-fig. 21F), the dissepimentarium contains mostly small dissepiments, arranged in steeply down turning rows, the inner row is vertical with its inner margin thickened. The tabularium contains incomplete tabulae, bubble-like at the periphery, elevated at approximately 20–30º and passing gently into the inner tabularium that occupies slightly more than 1/2 of tabularium width. Inner tabellae are dissepiment-like, densely packed, elevated steeper than peripheral tabellae, steepest and most densely arranged next to the thin median lamella.

REMARKS: The specimen described is so distinct from the species of *Dibunophylloides* described in this paper and known from the literature that its comparison to them is unnecessary. It probably represents a new genus. '*Dibunophyllum*' sp. B of Ross and Ross (1962, pl. 163, figs 4, 5, 8) from the Lenox Hills Formation, Wolfcampian of the Glass Mountains, SW Texas is the only taxon known to us as being probably related to this specimen. Unfortunately, the single transverse section, the side view and the calice illustrated for '*Dibunophyllum*' B are inadequate for a closer comparison.

OCCURRENCE: Texas, Glass Mountains, Gaptank Formation. Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930, 1937). Specimen USNM PAL 800296. Missourian.

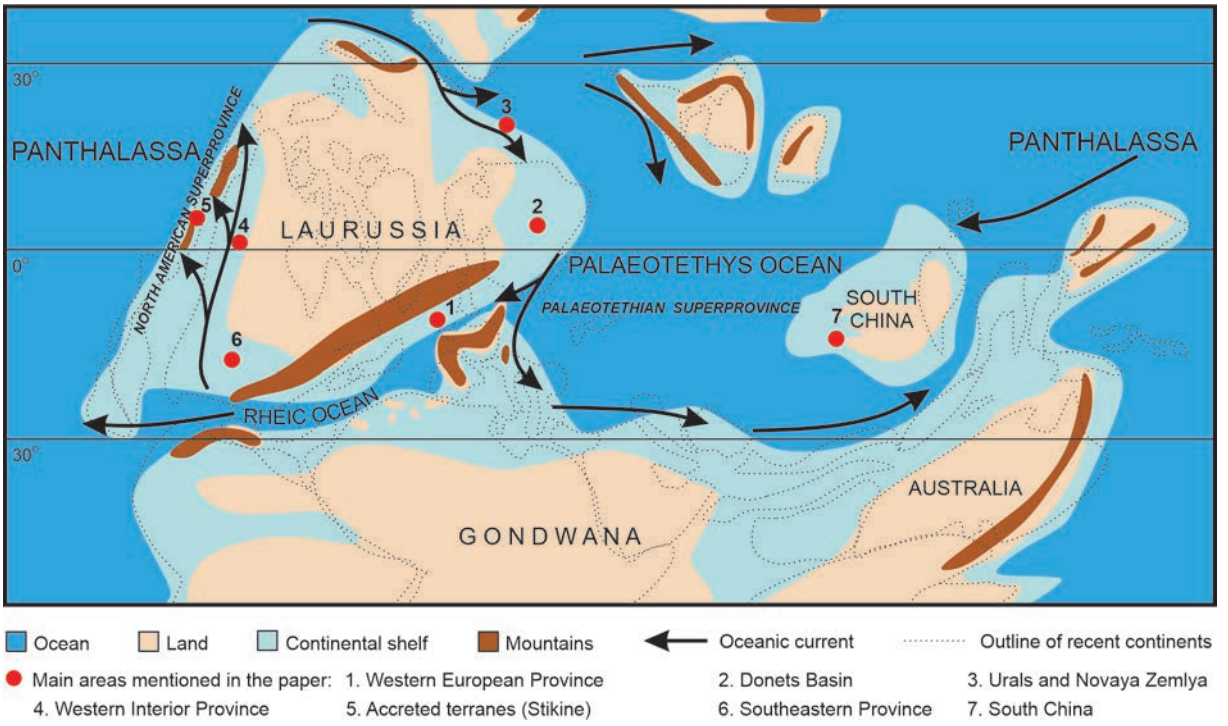
CONSIDERATIONS

Identifications of specimens described in this paper brought a lot of difficulties and little satisfaction. This results from the appearance of some identical morphological features in specimens displaying other distinctly different characteristics. Most of those features in common are sporadic in some specimens, but dominating in others. Several specimens are also morphologically intermediate between two or three groups of specimens distinguished by us as separate species. Summing up the similarities, the following should be mentioned: (i) All specimens are widely conical with strong attachment scars lasting in some corallites up to 2/3 of their length. (ii) External walls are thin, bearing numerous, shallow growth striae and hardly recognizable septal furrows. (iii) Calices are deep when compared to corallite lengths. All possess peripheral platforms almost horizontal with upper margins of both major and minor septa exposed, but only major septa turn down at the inner margin of the platform to reach calice floors. All calices have prominent axial bosses. (iv) Almost all specimens are nearly complete with delicate external walls, calices and most parts of early growth stages preserved. However, the brephic and earliest ontogenetic growth stages are broken apart from the great majority of them. Such preservation suggests sudden and shortly acting, but powerful events that broke specimens free from their sites and deposited them after being transported in suspension. Thus, their original living environment had been stressful but variable to some extent. (v) The major septa are radially arranged since the early mature growth stage. (vi) The cardinal fossula is absent. (vii) In the neanic growth stage, the arrangement and increase of the major septa is zaphrentoid in all specimens with environmental modifications in some.

Transverse sections of the mature growth stage display several morphological variants with particular characteristics differentially accentuated. Moreover, many specimens differ at the early mature growth stage being similar to each other in the advanced maturity and *vice versa*. The following main variants should be mentioned: (i) The n:d value differs from 22:6.0 mm to 35:16.0 mm. (ii) Major septa are smooth in most specimens (taxa), but bear carinae-like bodies in the dissepimentarium of some. Their length may differ both in the course of growth and between particular specimens. (iii) Minor septa differ from approaching, seldom penetrating the outermost tabularium to almost totally reduced. Such a differentiation may occur within the same transverse section. (iv) The axial structures in transverse section are narrow to wide, with septal lamellae dense to loose, connected to major septa or separated from them, with the median lamella strong, variable or absent. (v) The dissepimentarium is narrow and simple to wide and complex with or without lateral-cystose dissepiments. The latter may appear sporadically in some species but are common in others. (vi) In longitudinal section, the inner tabularium may be wide, with particular tabellae moderately elevated towards the median lamella to narrow with inner tabellae not numerous and steeply elevated, but intermediate morphologies also occur. The main characters of the particular named species are assembled in Table 1.

Common characters, as well as variable features with their proportions varying both in particular species and within specimens as well as presence of corallites displaying an intermediate morphology, allows for two taxonomic conclusions: (i) One could 'lump' and include all specimens here investigated in a single, extremely variable species. Moreover, the morphological and numerical features of these specimens can be established in almost all North American species so far described under the name '*Dibunophyllum*'. In that case, *Dibunophylloides valeriae* (Newell, 1935), i.e., the species possessing priority, could eventually be the only species of that genus present in North America. However, we reject that option as unrealistic. (ii) Thus, one could group and name the specimens described here in accordance to their prevailing characteristics, bearing in mind their possible relationship to the existing North American species we have included here in *Dibunophylloides*. Unfortunately, the exact relationships are difficult to establish because the knowledge of the intraspecific variability of most North American '*Dibunophyllum*' species is either inadequate or absent (e.g., Newell 1935; Cocke 1966). This may lead to an unacceptable overinterpretation of a species concept as that by Ross and Ross (1962, pl. 162, figs 1, 4–11, 13, 14). Thus, we have introduced mostly new species as mentioned in the remarks to the genus.

Considering all pros and cons listed, we suggest the following: Exterior characteristics of specimens, their very strong attachment scars and common rejuvenations, in some cases deep, suggest dynamic, commonly stressful extrinsic conditions with scattered micro-niches. Such conditions allow both the closely comparable shape and size of specimens and the genetic diversifications leading to the appearance of new, but hardly distinguishable species. A close relationship is suggested by repetitions of particular morphological features appearing in most species, but differently accentuated in particular taxa. The



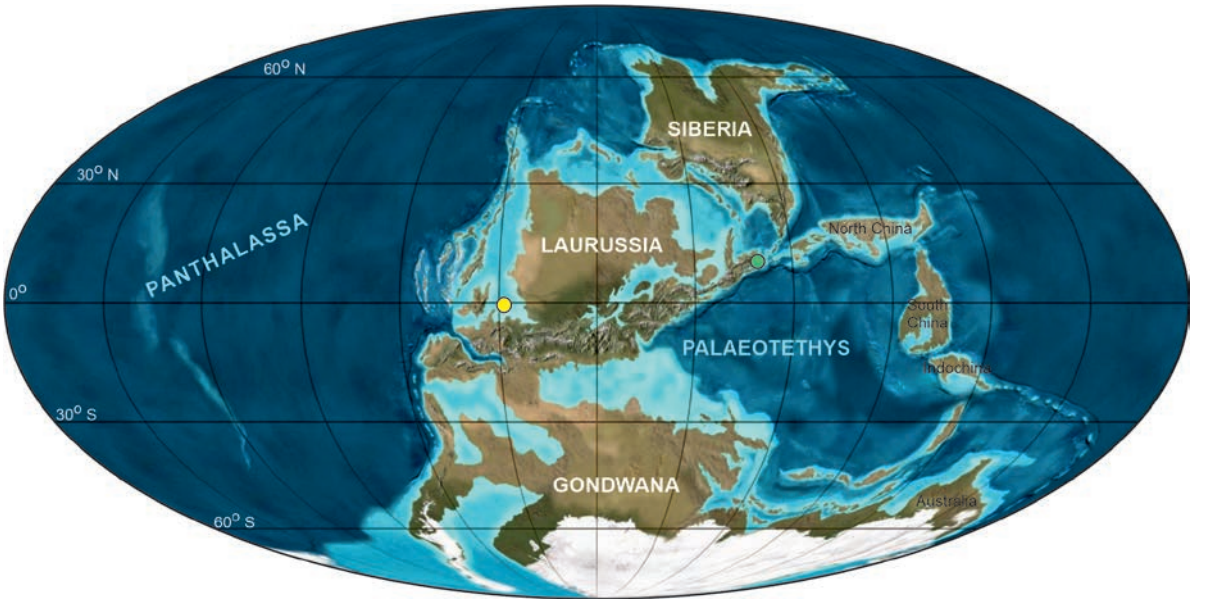
Text-fig. 22. Paleogeographic distribution of the most important Mississippian rugose corals sites. Possible directions of most important oceanic currents indicated by arrows (from Somerville *et al.* 2020, modified by Fedorowski 2023).

specimens left by us in open nomenclature additionally support that conclusion. They are represented by one to a few specimens that either bear intermediate characteristics or extend beyond the concept of all species described, or both.

Recognition of *Dibunophylloides* in the North American superprovince poses the question of its migration routes. Its derivation from *Dibunophyllum* and its earliest appearance in the Donets Basin (earliest Voznessenkian = earliest Chokierian) in the Paleotethyan superprovince was documented by Fedorowski (2017). The earliest *Dibunophylloides* (= '*Dibunophyllum*') in North America was described by Moore and Jeffords (1945) and Rowett and Sutherland (1964) from the Marble Falls Limestone (= lower Kinderscoutian) in SW Texas. The appearances mentioned and a close similarity in all main morphological features between the Ukrainian and Texan specimens (Text-fig. 22), supports two conclusions: (i) the true relationship between these taxa, with (ii) the continuous occurrence of the Iberian isthmus at least until the Kinderscoutian. *Dibunophylloides* supplements the group of genera suggested by Fedorowski (2023) as having originated in the Paleotethyan superprovince and migrating to the North American superprovince. As noted already (Fedorowski and Chwieduk 2024, p. 1): "Together, these genera demonstrate the importance of taxonomic investigation to establish the paleobiogeography as a constraint on global (i.e., tectonic scale) environmental reconstructions." The Iberian isthmus became closed either in the late Bashkirian or in the Moscovian (Text-fig. 23). The appearance of Pangea resulted in the independent development of the European and the North American aulophyllids during the late Pennsylvanian and the Cisuralian times, by the common roots proves their relationship.

CONCLUSIONS

- Most Pennsylvanian specimens identified by American scientists so far as *Dibunophyllum* Thomson and Nicholson, 1876 were transferred by us to the genus *Dibunophylloides* Fomichev, 1953. Close similarity in morphology of all growth stages of the Ukrainian and North American specimens, supported by the paleogeography, support our decision. The suggestion by Sando (1985) to include the North American '*Dibunophyllum*'



Text-fig. 23. Late Pennsylvanian paleogeography (map by Ron Blakey *via* Wikipedia under CC-BY-SA & GFDL); yellow dot marks the position of the study area in Texas; green dot marks the approximate position of the Donets Basin in Ukraine.

and '*Neokoninckophyllum*' into *Amandophyllum* Heritsch, 1941 was rejected as contradicting the first appearances of these genera in the Carnic Alps (lower Permian) and North America (Morrowan) with formation of Pangea in the meantime.

- Proportions of morphological characters diagnostic for the genus *Dibunophylloides* are either similar or variously differentiated within the specimens from our collection and species described so far from North America. Thus, a simple approach, i.e., the presence or absence of a given character as a species distinguishing method cannot be applied. Therefore, either a total generalization, leading to the acknowledgement of a single species occurring in North America, equal in fact to the diagnosis for the whole genus *Dibunophylloides*, or arbitrary taxonomic decisions are necessary. We have accepted the second method being conscious of possible mistakes. Thus, 6 variable, but discretely so, new species are distinguished, one species is identified as conformis and 4 species are left in open nomenclature.
- Close relationships, stressful extrinsic conditions that the corals lived in and possibly differentiated ecological micro-habitats present in the study area during the Missourian resulted in a multidirectional and fast adaptive radiation, here suggested to be responsible for the morphological diversification observed.
- The occurrence of *Dibunophylloides* in both rugose coral superprovinces existing in the Serpukhovian and early Pennsylvanian times and its earlier appearance in the Paleotethyan superprovince, support a long-lasting connection between them and a westward route for the migration.

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