Some genera and species of dissepimented solitary Rugosa (Anthozoa) from the Pennsylvanian (Carboniferous) and Cisuralian (Permian) of North America. Part 1. *Yuanophylloides* Fomichev, 1953

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ABSTRACT:

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Several specimens derived from the Missourian (Pennsylvanian) deposits of the Glass Mountains (SW Texas, USA) are identified as *Yuanophylloides* Fomichev, 1953. Some species that earlier authors included in the genera *Campophyllum* Milne-Edwards and Haime, 1852, *Bothrophyllum* Trautschold, 1879, and *Neokoninckophyllum* Fomichev, 1939 are re-identified as belonging to *Yuanophylloides*. In addition to the type genus, a new subgenus *Patulaxis* of *Yuanophylloides* with the type species *Y. (P.) molestus* sp. nov. and the new species *Y. (P.) parcus and Y. (P.) laxus* are introduced. Re-identification of the upper Serpukhovian *Campophyllum kansasense* Miller and Gurley, 1893 as *Yuanophylloides* renders untenable the origin of that genus in the Donets Basin. The circum-Laurussia warm current is suggested as having carried *Yuanophylloides* larvae from the North American superprovince to the Paleotethyan superprovince. This genus supplements the group of genera suggested by Fedorowski (2023) as having originated in the North American superprovince and migrating to the Paleotethyan superprovince. Together, these genera demonstrate the importance of taxonomic investigation to establish paleobiogeography as a constrain on global (i.e., tectonic scale) environmental reconstructions.

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

https://zoobank.org/References/E03EF205-5C79-4A68-AC13-E8AE154F915D

INTRODUCTION

Solitary dissepimented rugose corals with an axial structure are common in the Pennsylvanian (upper Carboniferous) and Cisuralian (lower Permian) strata of North America. Several species are represented by hundreds of specimens (Cocke 1970) and personal observations in the field by one of us (JF), which have been included in various families. Our focus is on pa-pers dealing with taxa included by authors in the families Aulophyllidae Dybowski, 1873, Cyathopsidae Dybowski, 1873, and Clisiophyllidae Thomson and Nicholson, 1876 (Newell 1935; Easton 1944; Moore and Jeffords 1945; Jeffords 1948; Ross and Ross 1962, 1963; Rowett and Sutherland 1964; Cocke 1969, 1970; Rowett 1969; Cocke and Haynes 1973; Cocke and Molinary 1973). Papers older than those cited here are not taken into consideration, since neither the de-

scriptions nor the illustrations published in them are adequate for taxa re-identification. Genera included in the cited families bear names introduced earlier for the Mississippian European taxa, an approach that has been criticized by Fedorowski (2017, 2022).

The relationships of the several genera described in this and the following papers should perhaps be treated as provisional. They illustrate our personal attitude to the taxonomy of rugose corals on the one hand, and an imprecise recent knowledge of Bashkirian paleogeography on the other. Two factors are crucial for reconstructing the ancestry of many species within genera and of genera within families: (i) the ultimate closing of the Rheic ocean, i.e., the indisputable time of Pangea formation; and (ii) a firm reconstruction of the pathways of warm oceanic currents acting at that time. The occurrence of warm currents carrying rugose coral larvae and the presence of oceanic carbonate platforms that allowed them to settle and metamorphose are the conditions *sine qua non* for the migration and spreading of the taxa, whereas the presence of both the Rheic Ocean (or an isthmus at least) and of a circum-Laurussia warm current that lasted to the early Bashkirian inclusively allows the exchange of rugose coral fauna between the Paleotethyan and North American superprovinces (Fedorowski 2023). Reconstruction of relationships, that is, the precise taxonomy of the taxa described in this and the following papers, must be considered as provisional until those conditions have been precisely established.

MATERIAL AND METHODS

In this and the papers that will follow, corals belonging to the Department of Paleobiology, Smithsonian Institution, Washington, D.C., and corals collected by JF in early 1973 during his field work in the Glass Mountains, SW Texas are described. All specimens described in this paper were collected from localities N700 and N700a. Cooper and Grant (1972) described their positions as follows:
– N700 – Gaptank Formation (middle of Bed 10 of King 1930, 1937); 3.2 km (2 miles) to the south of Gap Tank, 2 km (1.25 miles) to the east of a point on Marathon-Fort Stockton road (U.S. Highway 385), about 38 km (23.5 miles) to the north-east of Marathon.
– N700a – Gaptank Formation (upper part of Bed 10 of King 1930, 1937); 0.4 km (0.25 mile) to the east of locality N700 in a small canyon.

All specimens were sectioned either with a reg-ular cutting machine or with a machine supplied with a 0.05 mm thick wire. Several thin sections or peels were prepared from each investigated specimen. The collection with the acronym USNM PAL is housed in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

GEOLOGICAL SETTING

General remarks

The type section of the Gaptank Formation is located in the Glass Mountains, SW Texas, in Stockton Gap on the Fort Stockton-Marathon Highway (U.S. Highway 385), south of the tank called Gap Tank (Text-fig. 1). The formation was named by Udden *et al.* (1916) for exposures near Gap Tank. Udden (1917) briefly described the formation. King (1930, 1937) published the first detailed description of the type section and worked out the time of its relationship to the flysch deposits of the same age in the western part of Marathon Basin.

From the type section at Gap Tank as far west as Wolf Camp Hills, the Gaptank Formation is exposed in a set of low limestone cuestas at the base of the Glass Mountain escarpment, along the northern edge of the Marathon Basin (Ross 1967). The Gaptank Formation rests within this band on an irregular erosional surface formed on strongly folded, faulted, and structurally complex flysch deposits of the Tesnus and Dimple formations. The Haymond Formation, structurally similar to the underlying two formations, is conformably overlain by the Gaptank Formation; it generally dips at 15–30º N and lacks major structural deformation (Kier *et al.* 1979). East of Gap Tank, the upper part of the formation has been deeply eroded and overlapped by Permian and Cretaceous strata. In the subsurface north of the Glass Mountains escarpment, strata of the same age form part of a thick sequence of thin bedded black shale and fine sandstone in the buried Val Verde depositional basin. The Gaptank Formation extends westward for a distance of nearly 48 km (30 miles) from the type section to Dugout Mountain. A significant gap appears in its distribution in the 8 km (5 miles) between Iron Mountain and the east end of Lenox Hills (Cooper and Grant 1972).

At the type section about 1.6 km (1 mile) south of Stockton Gap, King (1930) recognized 21 units that aggregate in a thickness of about 548 m (1800 feet) along a broad east-west anticline. The lower 300 m (984 feet) is siliceous and has small limestone
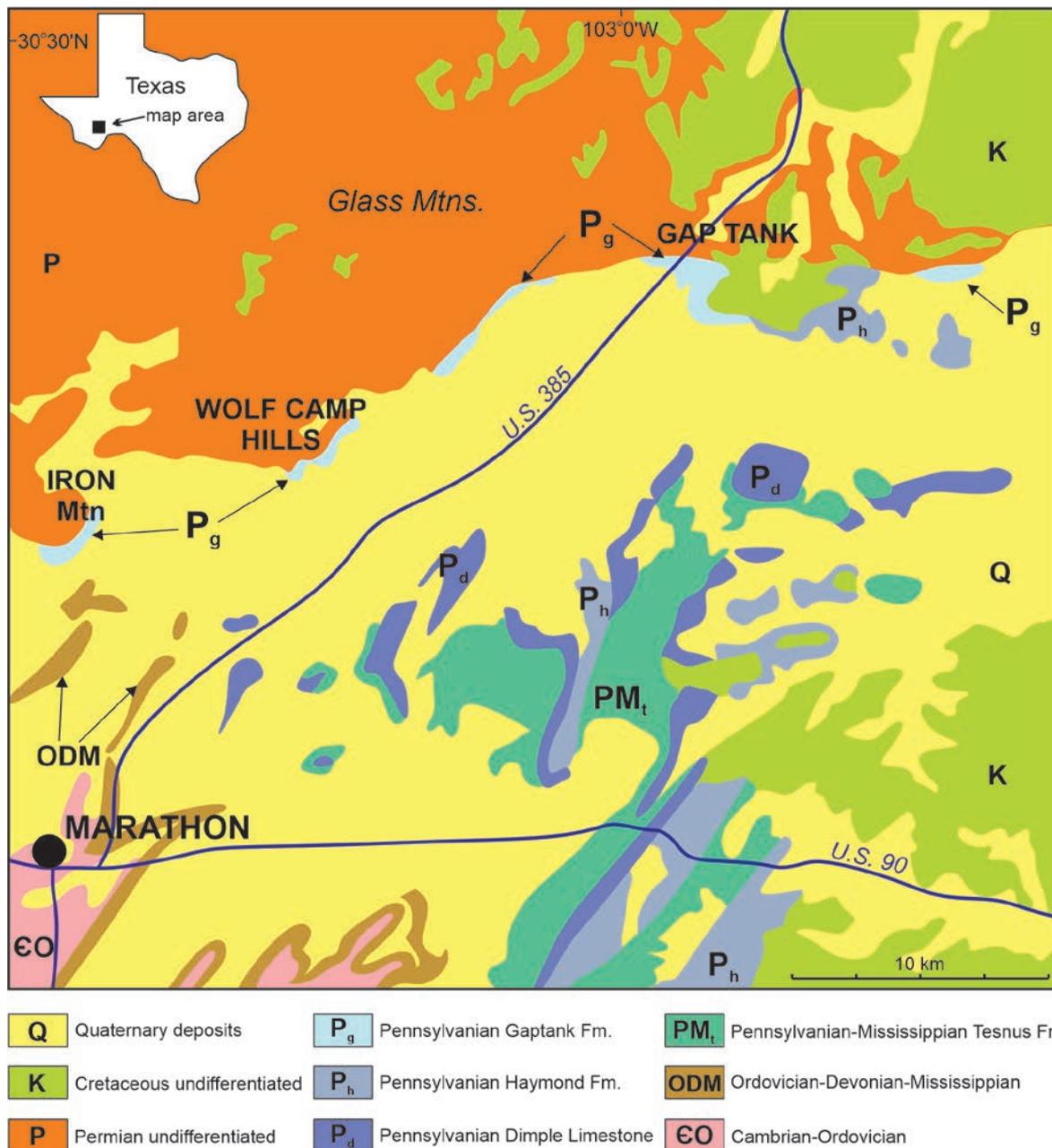
Text-fig. 1. Map of geological strata in the northern part of Marathon Basin (after Chapman and McCarty 2013, simplified). For details of the study area see Cooper and Grant (1972).

intercalations, whereas limestone beds prevail in the upper 240 m (787 feet). According to King (1930), the lower part of the sequence (beds 1–12) consists mostly of shale and sandstone in which five layers of conglomerate and rare calcareous intercalations occur. According to Moore (1944), the fifth conglomerate bed forms the base of the Cisco (Virgilian) Series. In the upper part (beds 13–21), five sets of limestone beds form conspicuous members. A few of these beds are fossiliferous, containing fauna of Pennsylvanian age. The beds above this conglomerate (beds 12–21) in the type section are poorly fossiliferous but contain thick limestone. Ross (1967) subdivided the Gaptank Formation into the Conglomerate Member (bottom) and the Limestone Member (top) that intercalates, in part, with the Sandstone and Shale Member (middle;

Udden (1917)	King (1931)	King (1937)	Ross (1963)	Ross (1967) west · east	PERMIAN / PENNSYLVANIAN	Ross (1978)	Cooper and Grant (1972)	R.&R. (2003)
Upper Shale	Upper Member	Upper Shale Member	Neal Ranch Fm.	Neal Ranch Fm.		Wolf-camp.	PERMIAN — Wolfcampian	PERM. — Virgilian
Massive Limestone	Gray Limestone Member	Gray Limestone Member	bed 2 of Gray Limestone Mbr.	hiatus		Virgilian		
Basal Shale	*Uddenites* Zone	*Uddenites* Zone	*Uddenites*-bearing Shale Member	Limestone Member				
Gaptank Formation	Upper Gaptank	Upper portion	Limestone and Shale	Sandstone and Shale Member ☆		Missourian	PENNSYLVANIAN — Missourian	Missourian
	Lower Gaptank	Lower portion	Conglomerate and Shale	Conglomerate Mbr.		Desmoinesian	Desmoinesian	Desmoinesian
	Chaetetes Limestone	*Chaetetes*-bearing Limestone Mbr.	*Chaetetes*-bearing Limestone Mbr.	younger beds / hiatus; *Chaetetes*-bearing Limestone Mbr.				
base not defined								
Haymond Fm.	Haymond Fm.	Haymond Fm.	Haymond Fm.	Haymond Fm.				

(Vertical labels: Wolfcamp Fm.; Gaptank Fm.)

Text-fig. 2. Lithological subdivisions of the Gaptank Formation (left) and its stratigraphic subdivisions (right). The subdivisions of Ross (1967, modified) are used in this paper. Abbreviation: R.&R. = Ross and Ross (2003). The star-shaped symbol indicates stratigraphic position of units containing sampled specimens.

Text-fig. 2). Gaptank strata display a cyclic repetition and illustrate differences in deposition arising from differences in subaqueous topography (Ross 1967). The uppermost part of the Gaptank Formation, the *Uddenites*-bearing Shale Member, is not present in the type section, but it is well displayed in Wolf Camp Hills (Cooper and Grant 1972).

The Gaptank Formation, in contrast to the underlying flysch deposits of the Tesnus, Dimple and Haymond formations, consists of a cyclical series of interfingering regressive shallow water carbonates and upper slope clastics. This formation illustrates the differences in deposition that arise from differences in subaqueous topography. Conspicuous grainstones, packstones, and wackestones occur, and local bioherms rich in dasycladacean algae developed in a shallow setting. Shallow-water environments extended progressively basinward while the formation was being deposited with many limestone beds being traced laterally from a shallow-shelf facies through a shelf-edge facies into an upper-slope facies (Ross 1967). The Gaptank Formation carbonate facies separate shallow-water clastic deposits to the southeast from deep-water clastic deposits to the northwest (Ross 1967). Powell (1958) studied ostracodes and fusuline foraminifera from the Pennsylvanian Gaptank Formation (Desmoinesian–Missourian) in Pecos County, suggesting that the lower Gaptank Formation strata underwent deposition in a nearshore, hyposaline sea that received sediments rapidly as a result of diastrophic movements.

The shallow-water sediments of the upper Pennsylvanian Gaptank Formation represent the formation of a new shelf as a result of the Variscan orogeny (yellow dot in Text-fig. 3). The lower (Desmoinesian) part of the formation was interpreted by Ross and Ross (2003) as a foreland of coarse-grained fluvial and deltaic basinal deposits. Lithologically, bed 2 of King's (1930) Gray Limestone Member is a shelf margin carbonate bank and a continuation of the depositional pattern of the Gaptank Formation. In Wolf Camp Hills, the bank crops out as a thick, 30 to 40 m (98–130 feet), massive lens in Hill 5060, and also in an outlier just to the west (Ross and Ross 2003).

As deposition continued to the north, the older Gaptank sediments were folded, thrusted, and overridden by the Marathon allochthon (Hickman *et al.* 2009). By the earliest Permian time, the allochthon had overridden the Gaptank basin, and thrusting had ended. The leading edge of the thrust belt was buried by younger Wolfcampian sediments.

Starting near the end of the late Pennsylvanian and
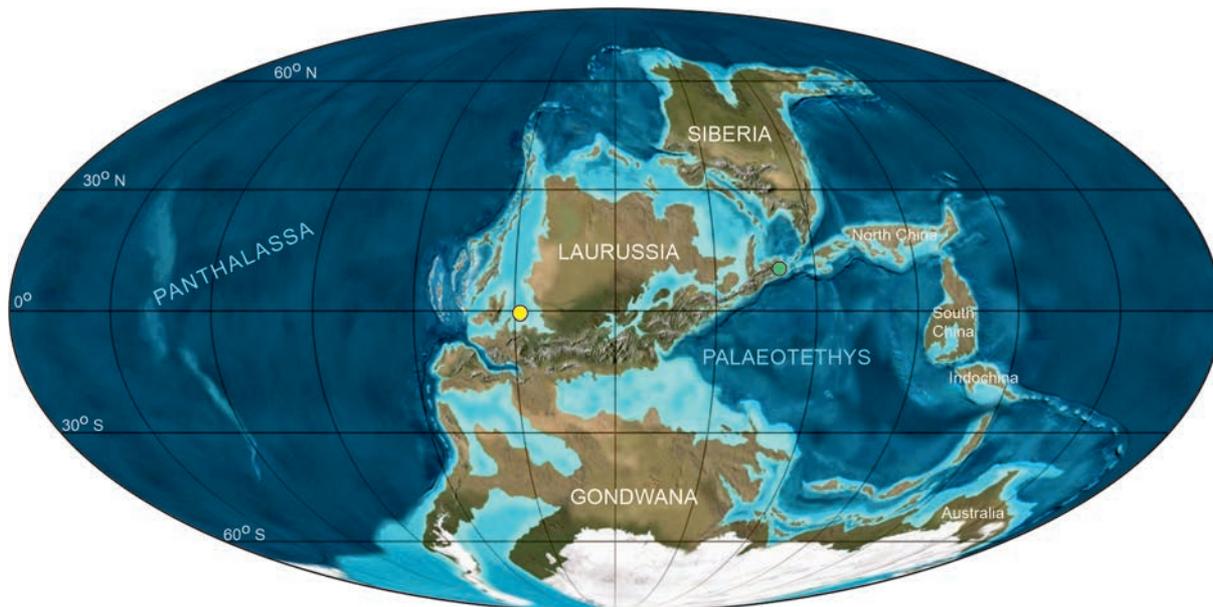
Text-fig. 3. Late Pennsylvanian paleogeography (map by Ron Blakey *via* Wikipedia under CC-BY-SA & GFDL); yellow dot marks the position of the study area in Texas, USA; green dot marks the approximate position of the Donets Basin in Ukraine.

extending into the middle part of the Wolfcampian Epoch (Permian, i.e., the Neal Ranch Formation), folding and finally major thrust faulting (Ross 1963, 1978) again thrust the southern craton and its wedge farther northwest on the southwestern edge of the Laurasian craton. Although some relatively minor warping and structural adjustments occurred on the northern edge of the Marathon basin in post-middle Wolfcampian time, this final thrusting completed the collision between the two cratonic masses (Ross 1978).

Stratigraphy

Although exposures of the Gaptank Formation are relatively small, its stratigraphic subdivisions have been the subject of controversy. Text-fig. 2 illustrates the history of its classification in the northern part of the Marathon uplift. The Gaptank Formation in the eastern Glass Mountains represents late Pennsylvanian age, being formerly described by King (1930) as consisting of late middle (Desmoinesian) to late Pennsylvanian rocks with the type area in the Gap Tank area. The Gaptank Formation was revised by Ross (1963, 1965, 1967), and then by Ross and Ross (2003) to exclude the Desmoinesian part, which was found to be part of the strongly folded underlying stratigraphic succession (Haymond Formation) and to lie within the thrust sheet below a major late Desmoinesian to early Missourian tectonic uncon-

formity (Ross and Ross 2003). At the type locality near the eastern end of the outcrop belt, the highest carbonate banks below the sub-Permian unconformity are latest Missourian and early Virgilian in age (Ross and Ross 2003). Westward across Allison, Moore, and Brooks Ranches, the marginal carbonate banks prograded in a series of depositional sequences during the Virgilian. Deposited on this middle-to-late Virgilian unconformity was a carbonate bank (or possibly several closely spaced banks) characterized by mainly sublithographic limestones (*sensu* Ross 1967). In the Wolf Camp Hills, King (1930), called this unit 'bed 2' of his Gray Limestone Member, together with the underlying *Uddenites*-bearing Shale Member, and the overlying shale, i.e., his 'bed 3', and conglomerate, 'bed 4'. The prograding Virgilian carbonate banks located eastward, as far as Gap Tank, were also included by King (1930) in the lower part of his Permian Wolfcampian Formation.

The *Uddenites*-bearing Shale Member of the Gaptank Formation is the most controversial as far as its stratigraphic position is concerned. Although generally accepted by fusulinid scholars as uppermost Virgilian, it contains brachiopods that suggest a lowermost Permian age (Cooper and Grant 1972). The corals of this member are mixed in their stratigraphic implications. Carboniferous taxa dominate in the fauna, but there are several species that occur both in that member and in the Neal Ranch Formation (e.g.,

Allotropiochisma (*Alligia*) *flabellum*, *Actinophrentis columnare*, *Bradyphyllum counterseptatum*, and several specimens of *Monophyllum cassum*, all documented in Fedorowski (1987). The most primitive representative of the very common Permian genus, *Assimulia* (*Assimulia*) *uddenitense* Fedorowski, 1987, also occurs at this stratigraphic level. Fedorowski (1987) accepted the *Uddenites*-bearing Shale Member of the Gaptank Formation as the beginning of the Permian phase of evolution of the rugose corals.

A definition of the Carboniferous–Permian boundary (Davydov *et al.* 1995; Chernykh and Ritter 1997), valid till present, is based on the first appearance of the conodont *Streptognathodus isolatus* Chernykh, Ritter and Wardlaw, 1997, established in successions in the southern Urals. Wardlaw and Davydov (2000) suggested that this conodont boundary should lie somewhere within bed 2 of King's (1930) Gray Limestone Member, but that conodont species was not found in the samples they studied. The conodont Carboniferous–Permian boundary thus remains undefined in the Glass Mountain succession. This uncertainty allowed Ross and Ross (2003) to place the Gray Limestone Member within the Gaptank Formation (Text-fig. 2).

A second controversy concerns the lower limit of the Gaptank Formation: the *Chaetetes*-bearing Limestone Member. The 15 m (50 feet) thick limestone layer of this member is interbedded with lower Desmoinesian limestone and sandstone (Ross 1963), whereas the overlying lenticular conglomerate member, about 200 m (650 feet) thick, is thought to represent the Missourian. Later, Ross (1967) redefined the base of the Gaptank Formation as the base of the conglomerate member and transferred the underlying *Chaetetes*-bearing Limestone Member to the Haymond Formation. This suggestion gives the Gaptank Formation a more distinctive lithologic base with greater areal continuity but lacks a biostratigraphic marker. Thus, both the base and the top of the Gaptank Formation lack biostratigraphic markers.

The corals described in this paper were derived from localities N700 and N700a, which have been described by Cooper and Grant (1972) as belonging to the middle (N700) and upper (N700a) part of Bed 10 of King (1930, 1937). This latter author mentioned *Triticites irregularis* from the lower part of that bed, whereas Merchant and Keroher (1939, p. 594) wrote that: "*Triticites irregularis sensu stricto,* appeared to be confined to the Dennis limestone in the lower part of the Missouri series and is replaced at higher horizons by other easily distinguished forms." However, they considered the species to be Missourian. This,

as well as two species treated in this paper, first described by Cocke (1970) from the Missourian deposits, allows us to consider the corals described here as Missourian in age, but their more precise stratigraphic position cannot be indicated.

SYSTEMATIC PALEONTOLOGY

Subclass Rugosa Milne Edwards and Haime, 1850
Order Stauriida Verrill, 1865
Suborder Aulophyllina Hill, 1981
Family Neokoninckophyllidae Fomichev, 1953

Genus *Yuanophylloides* Fomichev, 1953

TYPE SPECIES: *Yuanophylloides gorskyi* Fomichev, 1953, OD.

EMENDED DIAGNOSIS: Mostly solitary dissepimented corals, but protocolonies may occur rarely. Neanic growth stage zaphrentoid with axial septum lasting at least to the end of that stage. In maturity, axial septum either persistent or divided into cardinal and counter-septa temporarily or permanently. Both protosepta either equal in length and thickness to remaining major septa when axial septum divided, or counter-septum remains long whereas cardinal septum may be slightly shortened. Loose axial structure may temporarily or permanently occur. Axial parts of tabulae elevated slightly when axial septum present, flat and horizontal or slightly sagging in axial parts when axial septum reduced; peripheral parts of tabularium may contain bubble-like tabellae. Dissepimentarium consists of several kinds of dissepiments, commonly appearing irrespective of remaining skeletal characteristics.

REMARKS: The diagnoses of both the Neokoninckophyllidae family and genus *Yuanophylloides* were recently emended (Fedorowski 2019). We follow here the diagnosis of the family. However, the present collection requires a reinterpretation of some North American taxa described by earlier authors. This and the species assigned to *Patulaxis* subgen. nov. requires the diagnosis of the genus *Yuanophylloides* to be emended. Some characters in the emended diagnosis of *Yuanophylloides*, such as the zaphrentoid neanic growth stage or greater variability of the dissepimentarium, are common with several other genera. However, we consider their inclusion in this diagnosis as necessary for understanding the entire morphology of the specimens included in that genus.

Subgenus *Yuanophylloides* Fomichev, 1953

TYPE SPECIES: As for genus.

POSSIBLE SYNONYMY: See Fedorowski (2019, p. 66) and:

　　1893. *Campophyllum* Miller and Gurley, non Milne Edward and Haime, 1850.
　　1944. *Bothrophyllum* Easton, 1944, non Trautschold, 1879.
e.p. 1962. *Neokoninckophyllum* Ross and Ross, non Fomichev, 1939.
e.p. 1970. *Neokoninckophyllum* Cocke, non Fomichev, 1939.

PROVISIONAL SPECIES CONTENT: See Fedorowski (2019, p. 67) and (in alphabetic order by species names): *Neokoninckophyllum cooperi* Ross and Ross, 1962; *Neokoninckophyllum dunbari* Ross and Ross, 1962; *Campophyllum kansasense* Miller and Gurley, 1893 [= *Bothrophyllum kansasense* (Miller and Gurley, 1893) of Easton, 1944 = *Neokoninckophyllum kansasense* (Miller and Gurley, 1893), variant 1 of Cocke, 1970]; *Neokoninckophyllum perplexum* Cocke, 1970; *Neokoninckophyllum petilum* Cocke, 1970; *Neokoninckophyllum variabile* Cocke, 1970.

DIAGNOSIS: As for the genus (Fedorowski 2019, p. 67), but: In maturity axial septum commonly enduring or divided into cardinal and counter-septa with the latter elongated. Cardinal septum slightly shortened in rare specimens. Loose axial structure consisting chiefly of inner margins of major septa may occur. Axial tabellae indistinctly elevated. Rare lonsdaleoid dissepiments may appear.

REMARKS: In addition to the discussion of Fedorowski (2019, p. 67), some additional remarks are necessary, concerning first of all *Campophyllum kansasense*. That species was omitted by Fedorowski (2019) from the discussion on the relationships of *Yuanophylloides*, putting part of the conclusion in doubt. Miller and Gurley (1893) described the species on the basis of external characters only. Easton (1944, p. 123, pl. 22, figs 8–10) selected the specimen illustrated by Miller and Gurley (1893, pl. 7, figs 19, 22) as the holotype, made three thin sections from it, and redescribed *C. kansasense* on their basis and questionably included it in *Bothrophyllum*? Trautschold, 1879. Describing the neanic growth stage, Easton (1944, p. 123) wrote: "two septa (cardinal-counter?) form a median septum or plate", i.e., he elevated the character typical of *Yuanophylloides*, as is also

demonstrated in his illustration. Additionally, his description of the transverse mature thin section and the illustration of the longitudinal section (Easton, 1944, p. 123, pl. 22, figs 8–10 respectively) correspond to the diagnosis of *Yuanophylloides*. Here we have thus transferred that species to the latter subgenus.

　　The occurrence of *Campophyllum* (= *Yuanophylloides*) *kansasense* in the upper Serpukhovian of Kansas reverses the mutual relationships and ways of migration of the North American and Eastern European representatives of the genus *Yuanophylloides*, suggested by Fedorowski (2019, p. 82). *Yuanophylloides kansasense* points to the North American superprovince as the site of *Yuanophylloides* origin. That genus supplements a group of genera discussed by Fedorowski (2023, p. 4) that appeared in the North American superprovince earlier than in the Paleotethyan superprovince. The occurrence of circum-Laurussia warm sea currents in the late Serpukhovian and the early Bashkirian (Fedorowski 2023, fig. 1) supports this idea. Such a current could have carried *Yuanophylloides* larvae along the northern shelves of Laurussia eastwards and then southwards to reach the Donets Basin in the Paleotethyan superprovince. The great distance and difference in timing of occurrence between *Y. kansasense* (Genozone E_2 in Kansas), and *Y. inauditus* (Moore and Jeffords, 1945) and *Y. rectus* Vassilyuk, 1983 (Genozone R_1 in the Donets Basin) allows for the hypothetical suggestion of evolutionary changes within the genus during that time. The appearance in SW Texas of *Y. inauditus* in Genozone R_2 may confirm the suggestion by Fedorowski (2019) that this species migrated from the Donets Basin westward. This in turn suggests the occurrence of an isthmus connecting both superprovinces at least to the *Reticuloceras* Genozone inclusively. However, another possibility is that while *Yuanophylloides* originated in the North American superprovince and migrated to the Paleotethyan superprovince as suggested above, the appearance of Pangea in the *Homoceras–Hudsonoceras* Genozone or in the *Reticuloceras* Genozone, rather than in *Billinguites–Cancelloceras* Genozone, may have resulted in its independent evolution in both superprovinces (i.e., parallelism). Common roots, nevertheless, allow both branches to be placed in the same family. This option would render incorrect the cospecific status of specimens from SW Texas and the Donets Basin, included by Fedorowski (2019) in *Y. inauditus*. None of the options can be firmly rejected, but we consider the first one to be more probable since *Yuanophylloides* is absent from the North American superprovince until Genozone R_2.
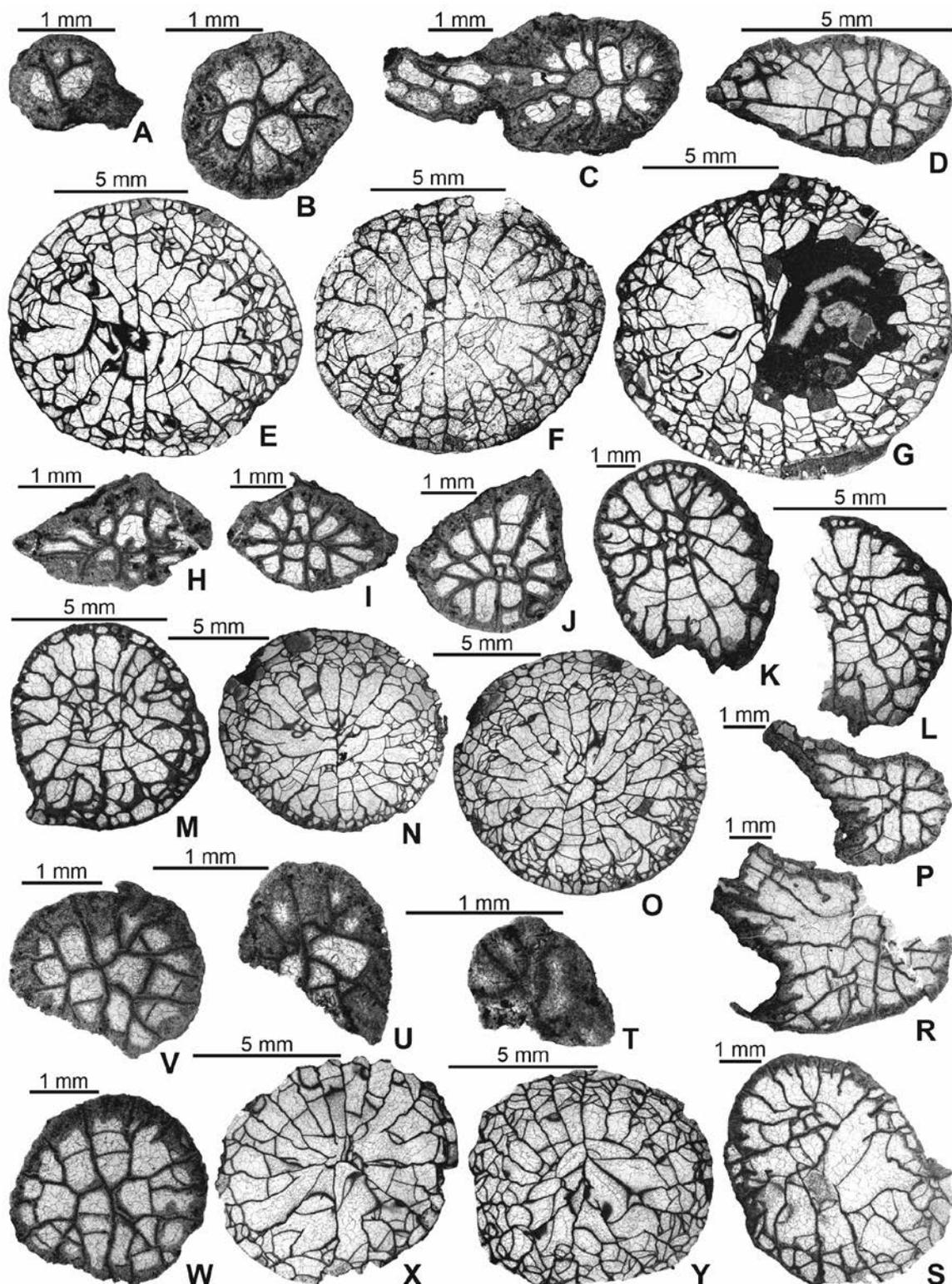
Text-fig. 4. *Yuanophylloides* (*Yuanophylloides*) *petilus* (Cocke, 1970). Transverse sections. A–G – USNM PAL 795328; A – brephic or early neanic growth stage, B–D – neanic growth stage, E–G – mature growth stage. H–O – USNM PAL 795329; H–L – neanic growth stage, M – late neanic early mature growth stage, N, O – mature growth stage. P–S – USNM PAL 795330; P, R – neanic growth stage, S – late neanic/early mature growth stage. T–Y – USNM PAL 795331; T–W – neanic growth stage, X – late neanic/early mature growth stage, Y – mature growth stage. For stratigraphic positions see text.

Additionally, the following points should be considered:

1. Fedorowski (2019, p. 66) conditionally included some specimens described by Rowett and Sutherland (1964) as *Koninckophyllum* in the synonymy of *Yuanophylloides*. We consider these here as likely belonging to a new genus or subgenus related to *Yuanophylloides*.

2. The specimens described and illustrated by Cocke (1970, p. 29, pl. 3, figs 6–10) under the name *Neokoninckophyllum kansasense* variant 1 are late Missourian in age, whereas the type material of that species is much older (late Mississippian). That difference, and the long time interval from the representatives of *Y. kansasense*, raises the question of the conspecificity *vs* homeomorphy of specimens from the two collections. The close similarity in all the main skeleton features and inadequate knowledge of corals occurring in the intervening time allow us to provisionally accept Cocke's (1970) approach. *Neokoninckophyllum kansasense* variant 2 of Cocke (1970) is included here in the subgenus *Patulaxis* subgen. nov. (see below).

3. *Neokoninckophyllum variabile* Cocke, 1970 may represent either an extremely variable species, as Cocke (1970) suggested, or a few taxa may be covered by this species name. The longitudinal section of one specimen suggests the first option, whereas another of his specimens (Cocke 1970, pl. 4, figs 4b, 3 respectively) may represent a new genus that will be introduced by us later.

4. The specimens described by Cocke (1970) as colonial forms are protocolonies, since a third or later generations of offsets were not produced by any of them.

5. The morphology of the dissepimentarium, emphasized by Fedorowski (2019) in the previous diagnosis of *Yuanophylloides*, is emended here. Species of *Yuanophylloides* (*Yuanophylloides*) with moderately wide dissepimentarium (3–4 rows), have prevailing herringbone dissepimets, e.g., *Yuanophylloides* (*Y.*) *petilus*. Also, this is a key feature of the holotype of *Yuanophylloides gorskyi* and *Yuanophylloides gorskyi* forma *b*, respectively, as illustrated by Fedorowski (2019, text-fig. 8A and 8F). The same is also true for *Yuanophylloides* (*Patulaxis*) *parcus* sp. nov. Species with narrow dissepimentarium in mature growth stage (1–2 rows) have regular, pseudoherringbone or irregular dissepiments. The appearances of various kinds of dissepiments, commonly occurring within a single transverse section, are independent from the morphology of other skeletal structures.
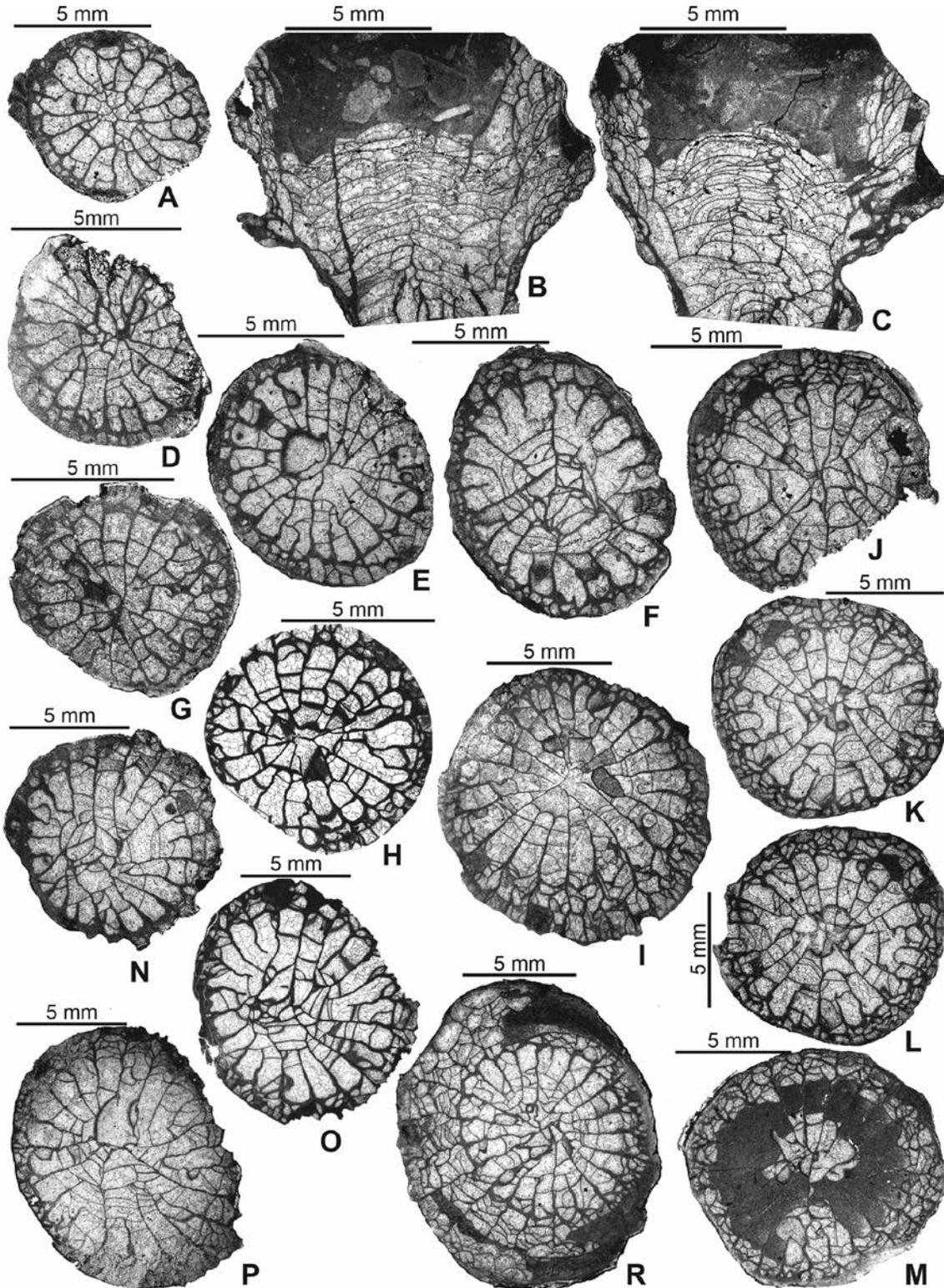
Yuanophylloides (*Yuanophylloides*) *petilus*
(Cocke, 1970)
(Text-figs 4–6)

1970. *Neokoninckophyllum petilum* Cocke, p. 28, pl. 2, figs 14–17.

MATERIAL: 21 well-preserved specimens, USNM PAL 795328–795348. Several with almost complete proximal ends and/or parts of calices preserved. 30 thin sections and 63 peels available for study.

EMENDED DIAGNOSIS: *Yuanophylloides* with 19–23 major septa and 7.7–12 mm corallite diameter. N:d value inconsistent (see description). Several major septa approach corallite axis. Axial septum may be divided into cardinal and counter-septa, both long, closely approaching one another. Minor septa commonly very short; some absent from corallite lumen. Dissepimentarium most commonly narrow. Herringbone dissepiments prevail, but pseudoherringbone, incipient grape-like and lonsdaleoid locally occur.

DESCRIPTION OF MATERIAL STUDIED HERE: Both the brephic (Text-fig. 4A) and the neanic growth stage, investigated in four specimens (Text-fig. 4B–D, H–L, P, R, T–W), are very irregular. In some thin sections the axial septum is hardly recognizable, and the increase in major septa and their length varies, making recognition of individual quadrants of septa uncertain. In the late neanic/early mature growth stage (e.g., Text-figs 4M, S, 5A, D, G, H, N, O), several major septa reach or approach a corallite axis, but the irregularity in their length and the lack of underdeveloped major septa adjacent to the cardinal septum makes recognition of the protosepta intuitive rather than firmly documented. Minor septa appear in some septal loculi at this growth stage, but are absent from other loculi in the same transverse section. The narrow, incomplete ring of dissepimentarium consists of regular, irregular, and pseudoherringbone dissepiments in various proportions, both between specimens and within a given transverse section. The arrangement of major septa in the mature growth stage continue to vary both within particular transverse sections of one specimen and between specimens. They are slightly thickened in the outer tabularium and taper axially. The boundary between the dissepimentarium and tabularium is also slightly thickened. Radial septal arrangement and the absence of the cardinal fossula are characters common to all specimens investigated. In most spec-

Text-fig. 5. *Yuanophylloides* (*Yuanophylloides*) *petilus* (Cocke, 1970). Transverse sections, except when stated otherwise. A–C – USNM PAL 795332; A – late neanic/early mature growth stage, B, C – longitudinal sections through mature growth stage and calice. D–F – USNM PAL 795333; D – late neanic/early mature growth stage, E, F – mature growth stage. G–I – USNM PAL 795334; G, H – late neanic/early mature growth stage, I – mature growth stage. J–M – USNM PAL 795335, mature growth stage. N–P – USNM PAL 795336; N, O – late neanic/early mature growth stage, P – early mature growth stage. R – USNM PAL 795337, mature growth stage; rejuvenated in part. For stratigraphic positions see text.
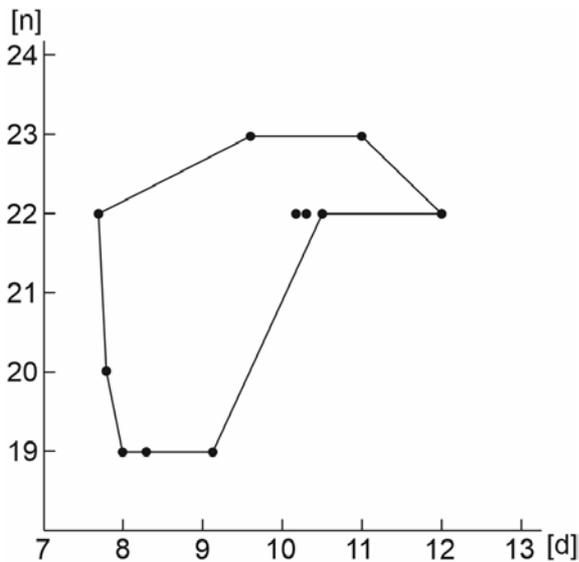
Text-fig. 6. *Yuanophylloides* (*Yuanophylloides*) *petilus* (Cocke, 1970); n:d values of selected specimens. Abbreviations: d – diameter, n – number of septa.

imens (e.g., Text-figs 4E–G, N, O, X, Y, 5E, F, I–M, P, R), some major septa are irregularly differentiated in length; some reach, while others only approach, a corallite axis, and some are slightly shortened. The protosepta may be united to form an axial septum in some sections of a given specimen, but they are disconnected in the adjacent section. These disconnected protosepta are easily recognizable when the last major septa inserted are shortened, but not when they are long. In one specimen, this shortening allows the elongation of the counter-septum and the slight shortening of the cardinal septum to be established (Text-fig. 5N, O). In most specimens the cardinal septum is longer than most major septa in the cardinal quadrants. Thus, the length of the major septa, including protosepta, is highly variable. The same is true for the minor septa. Their length is to some extent correlated to the morphology of the dissepimentarium in a given part of a corallite. They are commonly better developed when the dissepimentarium is complex, while they are shortened and in some cases reduced when the dissepiments are herringbone or lonsdaleoid. The dissepimentarium is differentiated in width and in the content of dissepiments, both within a given transverse section and between corallites. Herringbone dissepiments prevail, but pseudoherringbone, irregular, incipient grape-like, and rare lonsdaleoid dissepiments may occur. In general, the dissepimentarium width increases in the course of corallite growth, but does

not exceed a quarter of the corallite radius, and is commonly narrower. It is wider only where the specimen rejuvenated (Text-fig. 5R). The calice (Text-fig. 5B, C) is surrounded by an almost vertical wall formed of the inner row of dissepiments. Most of its floor is formed of a wide inner tabularium consisting of long, slightly convex tabellae – that is, it is hemispherical without a boss. The narrow peripheral tabularium consists of dissepiment-like peripheral tabellae. The border between the inner and the outer tabularium is not sharp. Some inner tabellae may reach the dissepimentarium. The n:d values of particular specimens vary considerably (Text-fig. 6). This variation may to some extent result from the slightly differentiated parts of the mature growth stage being sectioned and measured. However, it is also possible that a too wide frame is accepted here for the species.

REMARKS: According to Cocke's (1970) description and illustration, the morphology of 'Neokoninckophyllum' petilum is inconsistent. Some specimens included by Cocke (1970, pl. 4, fig. 4) in 'N.' variabilis also may belong to *Y. petilum*. The specimens here included in that species increase the inconsistency both in morphology and n:d value and are commonly slightly larger than those described by Cocke (1970), possessing dissepimentaria comparable to the paratypes rather than to the holotype of the species. The morphology in the longitudinal sections (Cocke 1970, pl. 2, figs 14b, 16, 17a vs text-fig. 50) also differs, and these differences make our identification disputable. However, the impossibility of reinvestigating Cocke's (1970) collection, that is probably lost, makes widening the frame of this species more reasonable than introducing a new species.

OCCURRENCE: USNM PAL 795328, 795331, 795334–795336, 795338–795342, locality N700 of Cooper and Grant (1972) = middle part of Bed 10 of King (1930–1937); USNM PAL 795329, 795330, 795332, 795333, 795337, 795343–795348, locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930–1937).

Yuanophylloides (*Yuanophylloides*) *perplexus*
(Cocke, 1970)
(Text-fig. 7)

1970. *Neokoninckophyllum perplexum* Cocke; Cocke, p. 34, pl. 4, figs 8–11.

MATERIAL: Three almost complete specimens,
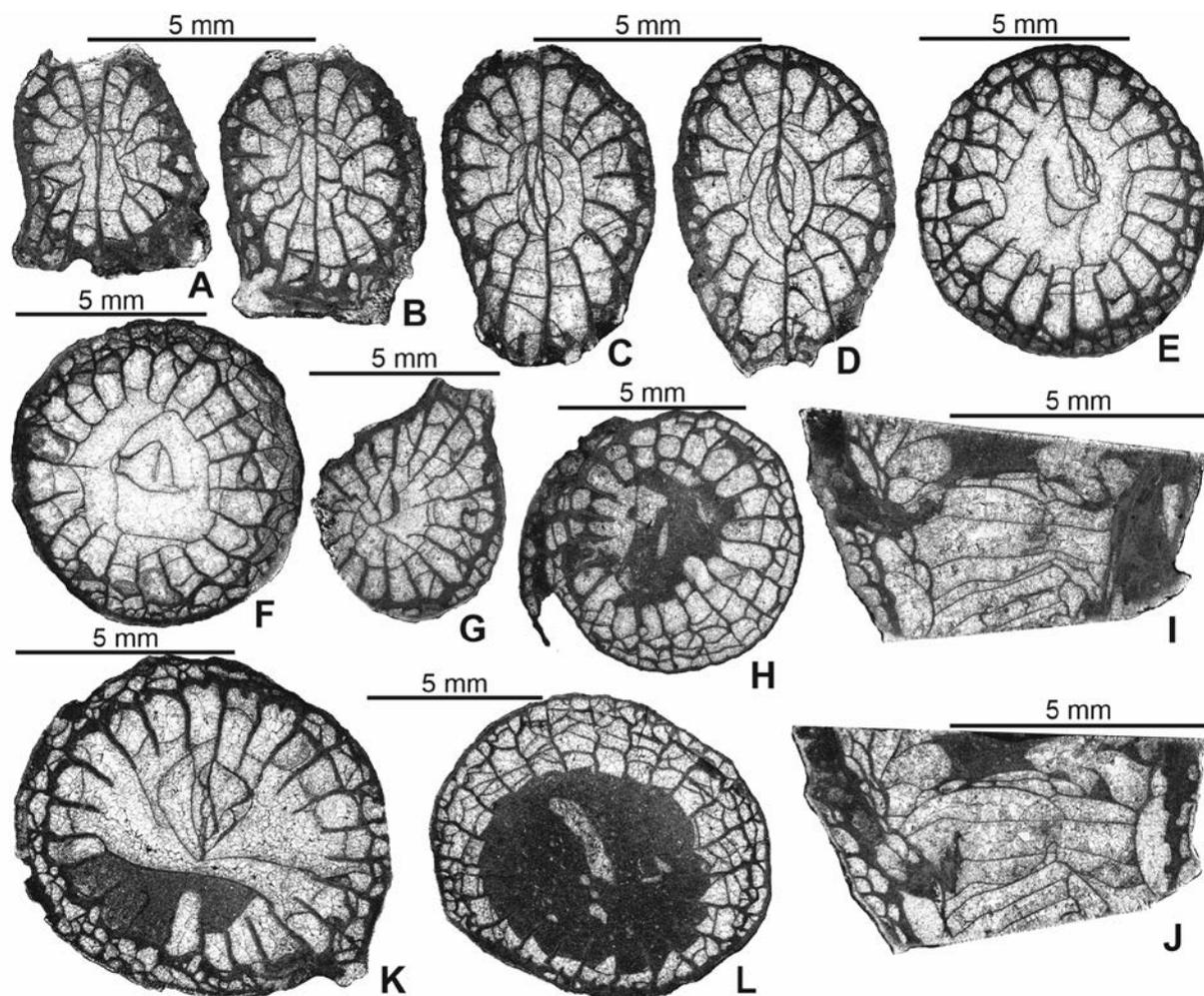
Text-fig. 7. *Yuanophylloides* (*Yuanophylloides*) *perplexus* (Cocke, 1970). Transverse sections, except when stated otherwise. A–F – USNM PAL 795349; A–C – neanic growth stage, D – late neanic/early mature growth stage, E, F – mature growth stage. G–J – USNM PAL 795350; G – neanic growth stage, H – mature growth stage, I, J – longitudinal sections; I – centric, J – slightly eccentric. K, L – USNM PAL 795351; K – mature growth stage, L – calice reduced in size. For stratigraphic positions see text.

USNM PAL 795349–795351. Mature growth stage of two specimens damaged in axial parts. 27 peels available for study.

EMENDED DIAGNOSIS: *Yuanophylloides* with major septa short, radially arranged, equal in length except for elongated counter-septum which equals the remaining major septa when free pseudocolumella temporarily occurs. Cardinal fossula absent. Minor septa differentiated in length, in advanced maturity absent from some septal loculi. Dissepimentarium narrow.

DESCRIPTION OF MATERIAL STUDIED HERE: Brephic growth stage not preserved. In the nea-

nic growth stage with n:d values 16:4.3×5.0 mm, 16:4.7×5.8 mm, and 18:4.9×6.1 mm (Text-fig. 7A–C), the specimen is elongated due to its attachment to the substrate on the cardinal septum side. Its axial septum forms an axis of symmetry. One ring of dissepiments has already been secreted and the minor septa are recognized within several septal loculi. The last major septa inserted in the counter quadrants are shortened. New major septa in the cardinal quadrants appear at the end of that growth stage. In the late neanic/early mature growth stage (Text-fig. 7D), the corallite remains elongated but its axial septum is replaced by a long thin counter-septum that almost reaches the cardinal septum, which is equal to the remaining major septa. The morphology of the late neanic/early mature

growth stage in the other specimen (Text-fig. 7G) is similar, except for the inner margin of the counter-septum, which is slightly thickened and more clearly separated from the cardinal septum.

In the early mature growth stage with n:d values 20:8.0×7.4 mm and 23:9.2×8.2 mm respectively (Text-fig. 7E, K), the major septa are shortened to slightly less thanone-half the corallite radius and form a regular circle. The counter septum is elongated so as to reach the corallite axis, whereas the cardinal septum is equal to the remaining major septa. A cardinal fossula is absent. The minor septa remain differentiated in length; some reach the tabularium where the dissepimentarium narrows, whereas some other are hardly recognizable. The dissepimentarium occupies approximately 1/6 of the corallite radius, and consists of regular and pseudoherringbone dissepiments.

In the more advanced mature growth stage, major septa are thin, equal in length, and radially arranged with the cardinal fossula lacking. A thin, short, free pseudocolumella is cut off from the axial part of the counter-septum (Text-fig. 7F, H, L). minor septa remain differentiated in length, but many are very short; some are completely reduced. The dissepimentarium comprises mostly regular dissepiments. The morphology in the longitudinal section (Text-fig. 7I, J) closely resembles that illustrated by Cocke (1970, pl. 4, fig. 10b). Dissepiments in a narrow dissepimentarium are arranged in one-two vertical rows. The wide tabularium comprises some bubble-like peripheral tabellae and widely spaced, slightly convex, or flat inner tabellae. Some of the latter may extend to the dissepimentarium.

REMARKS: The specimens described here are very similar to the specimens described by Cocke (1970) in all morphological characters, but they are slightly smaller and their major septa are less numerous – that is, their n:d values differ slightly. *Yuanophylloides perplexum* differs from all other North American species of *Yuanophylloides* in having a free pseudocolumella established both here and in at least one specimen illustrated by Cocke (1970, pl. 4, fig. 11a). This character is typical of *Neokoninckophyllum*, but the remaining characters of all studied specimens studied, including Cocke (1970), resemble the type species of *Yuanophylloides*. We thus include all of them in the latter subgenus.

OCCURRENCE: Locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930–1937). Missourian.

Subgenus *Patulaxis* subgen. nov.

TYPE SPECIES: *Yuanophylloides* (*Patulaxis*) *molestus* sp. nov.

SYNONYMY:
e.p. 1970. *Neokoninckophyllum* Cocke, non Fomichev, 1939.
e.p. 1973. *Neokoninckophyllum* Cocke and Haynes, non Fomichev, 1939.

DERIVATION OF THE NAME: Latin *patulus* – open, extensive (shortened) and *axis* – axis – after division of axial septum into cardinal and counter septa equal to remaining major septa and lack of pseudocolumella.

SPECIES ASSIGNED: *Neokoninckophyllum acolumellatum* Cocke, 1970; *Yuanophylloides* (*Patulaxis*) *laxus* sp. nov., *Y.* (*P.*) *molestus* sp. nov., *Y.* (*P.*) *parcus* sp. nov.; *Neokoninckophyllum tushanense* (Chi, 1931) of Cocke (1970); *Neokoninckophyllum tushanense* (Chi, 1931) of Cocke and Haynes (1973); *Yuanophylloides* (*Patulaxis*) sp. nov. = *Neokoninckophyllum kansasense* variant 2 of Cocke (1970).

DIAGNOSIS: As for the genus, but: Weak axial structure without median lamella, occurring in early mature growth stage, either remains permanent or disappears from advanced maturity totally, or temporarily. Cardinal and counter-septa commonly indistinguishable from other major septa by length and thickness. Counter septum may be slightly elongated. Cardinal fossula absent. Dissepimentarium may comprise regular, herringbone, pseudoherringbone, lateral and grape-like dissepiments in various proportions. Tabularium bipartite; in axial part tabellae commonly elevated, rarely horizontal, densely packed, in peripheral part bubble-like.

REMARKS: *Patulaxis* subgen. nov. closely resembles the subgenus *Yuanophylloides* in several characters (see diagnosis for the genus), suggesting their relationship at a subgenus level. The axial septum, present invariably in the neanic growth stage in all species of the genus studied in detail, is the most important character common to both subgenera, whereas the transition from the neanic to the early mature growth stage is critical for the distinction between them. In *Yuanophylloides*, the axial septum is either permanently present during the entire ontogeny, or the counter-septum dominates in length when the axial septum is divided. The axial struc-

ture is built around that septum, where it occurs. In *Patulaxis* subgen. nov., the axial septum invariably occurs in the neanic growth stage and may be thickened in some specimens (Fig. 10B, C). In some specimens its occurrence may be prolonged up to earliest maturity. However, it becomes invariably divided in the early mature growth stage into the cardinal and the counter-septa without leaving a pseudocolumella in a corallite axis. Both protosepta become shortened to the length of the remaining major septa. The loose axial structure, comprising sections of axial tabellae accompanied by twisted inner margins of some major septa, appears at early maturity and lasts during the differentiated period of the corallite's mature growth stage. It may eventually leave the circumaxial area of corallites empty. Neither of the septa in the axial structure dominates in length. In several of the studied specimens, the loose axial structure is permanent.

Cocke (1970) studied several specimens identified by him as *Neokoninckophyllum kansasense* (Miller and Gurley, 1893) and divided them into two variants that differ considerably. His variant 1, comprising the originals of Miller and Gurley (1893), revised by Easton (1944), as well as Cocke's own specimens included in that variant, are transferred here to the genus *Yuanophylloides* (see above). His variant 2 and the specimen described by Cocke (1970) as intermediate between the two variants are distinguished here as a new unnamed species of *Patulaxis* subgen. nov. We consider this the morphologically most advanced species of the genus, as suggested by the very complex morphology of the dissepimentarium, but we do not offer a species name for this variant, which is known to us only from the literature.

Yuanophylloides (*Patulaxis*) *molestus* sp. nov.
(Text-figs 8–11)

ETYMOLOGY: Latin *molestus*, -*a*, -*um* – troublesome – after variability in several characters so advanced as to make identification of particular specimens uncertain.

HOLOTYPE: USNM PAL 795352.

TYPE LOCALITY: N700 of Cooper and Grant (1972).

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

MATERIAL: 33 specimens, USNM PAL 795352–795384. Internal structures well preserved. Some comprising proximal ends and/or calices. 25 thin sections and 153 peels available for study.

DIAGNOSIS: *Patulaxis* subgen nov. with n:d value 25:11.2 mm to 30:19.2 mm; 27–28:14–17 mm prevail. Major septa either stop short of corallite axis or inner margins of some elongated and included in the axial structure. Minor septa vary in length from very short to intersecting dissepimentarium within same transverse section. Loose axial structure either permanent or interrupted, comprises axial tabellae and inner margins of septa. Dissepimentarium narrow; dissepiments differentiated both in particular parts of sections and between specimens. Axial tabellae in mature parts of corallites densely packed, flat, or slightly elevated. Lateral tabellae bubble-like.

DESCRIPTION: The majority of corallites are conico-cylindrical, rarely conical. External walls bear delicate growth striae. Septal furrows hardly distinguishable, and very shallow where present. Brephic growth stage was not studied; in one specimen being diagenetically destroyed (Text-fig. 8E), while remaining specimens broken apart. In the earliest neanic growth stage (n:d value ?7:1.1 mm) of the specimen described in detail (Text-fig. 8F, G), the axial septum is slightly curved. Its irregularity increases through growth (Text-fig. 8H–M), being easily recognizable only in some transverse sections (Text-fig. 8H, I, J, M) up to its probable division into the cardinal and the counter-septum (Text-fig. 8N). Insertion of the major septa is irregular and its sequence is difficult to recognize. The morphology of the neanic growth stage in another specimen (Text-fig. 9G–N) is similar to the previously described one in both the irregularity of the axial septum and in the insertion of the major septa. The disconnections of the axial septum in the latest neanic/earliest mature growth stage in both specimens are also similar (Text-figs 8N and 9N, respectively). In contrast to the two specimens described here, the arrangement of major septa in the neanic growth stage of the third specimen studied in detail is more regular. Also, the axial septum in that specimen is easily recognizable and its axial part is slightly thickened (Text-fig. 10A–C). However, the axial septum is rapidly divided into the cardinal and the counter-septum at the latest neanic/earliest mature growth stage (Text-fig. 10D). In all three specimens studied in detail, the first minor septa, accompanied by first dissepiments, become visible in the slightly differentiated parts of the neanic growth stage (Text-figs 8N, 9K, P, 10B). In these three specimens as well as in all other specimens studied, the
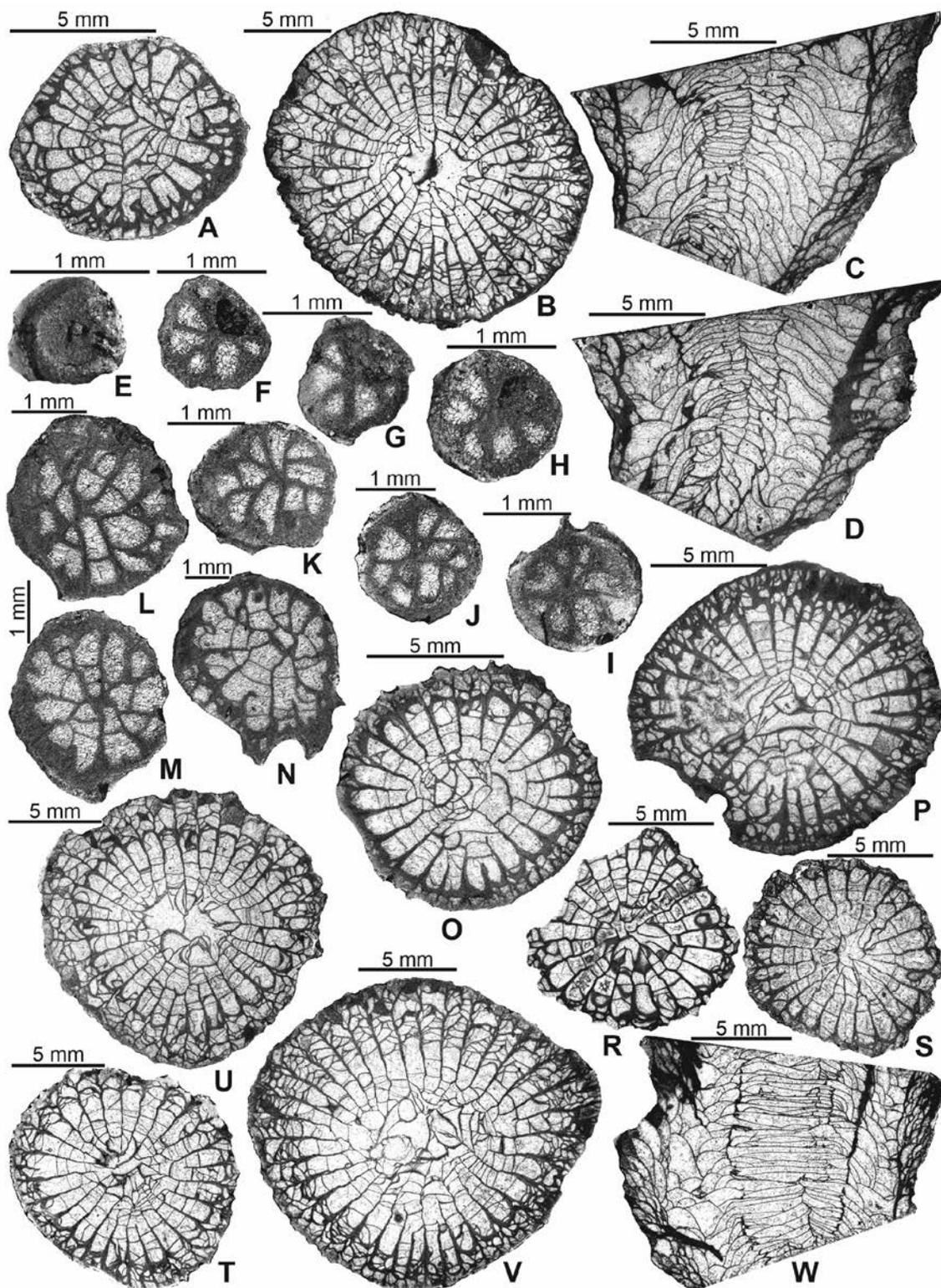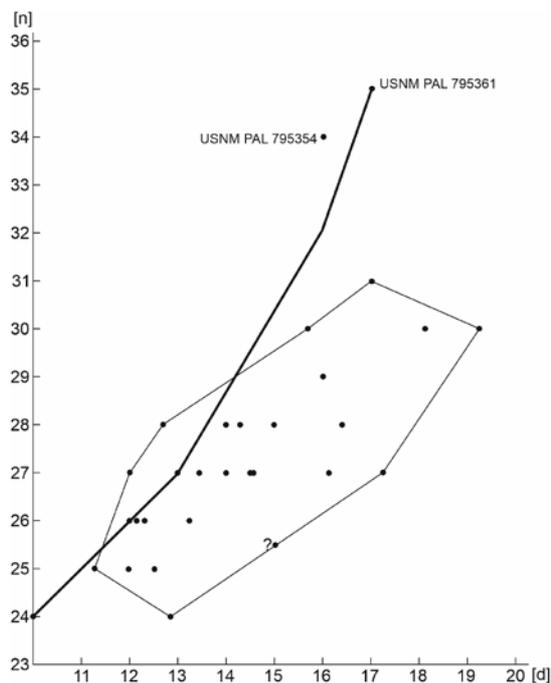
Text-fig. 8. *Yuanophylloides* (*Patulaxis*) *molestus* sp. nov. Transverse sections, except when stated otherwise. A–D – USNM PAL 795352, holotype; A – late neanic/early mature growth stage, B – mature growth stage, C, D – longitudinal sections; C – centric, D – slightly eccentric. E–P – USNM PAL 795353; E – brephic growth stage, F–N – neanic growth stage, O – early mature growth stage, P – mature growth stage. R–W – USNM PAL 795354. R, S – late neanic/early mature growth stage, T – early mature growth stage, U, V – mature growth stage, W – centric longitudinal section. For stratigraphic positions see text.
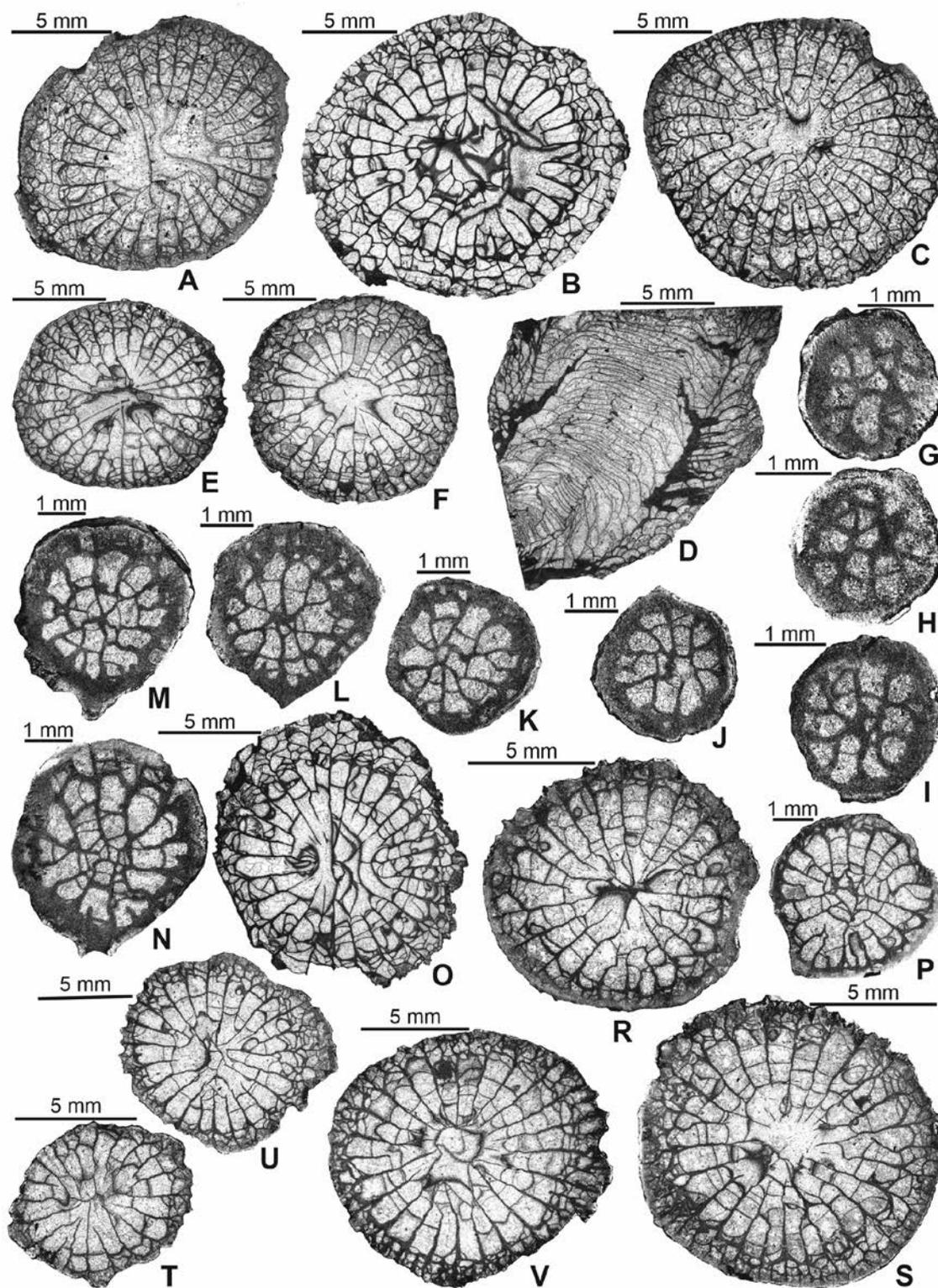
Text-fig. 9. *Yuanophylloides* (*Patulaxis*) *molestus* sp. nov. Transverse sections, except when stated otherwise. A–D – USNM PAL 795355; A–D – mature growth stage, D – centric longitudinal section. E, F – USNM PAL 795356, mature growth stage. G–O – USNM PAL 795357; G–N – neanic growth stage, O – mature growth stage. P–S – USNM PAL 795358; P – late neanic/early mature growth stage, R, S – mature growth stage. T–V – USNM PAL 795359; T – late neanic/early mature growth stage, U – early mature growth stage, V – mature growth stage. For stratigraphic positions see text.
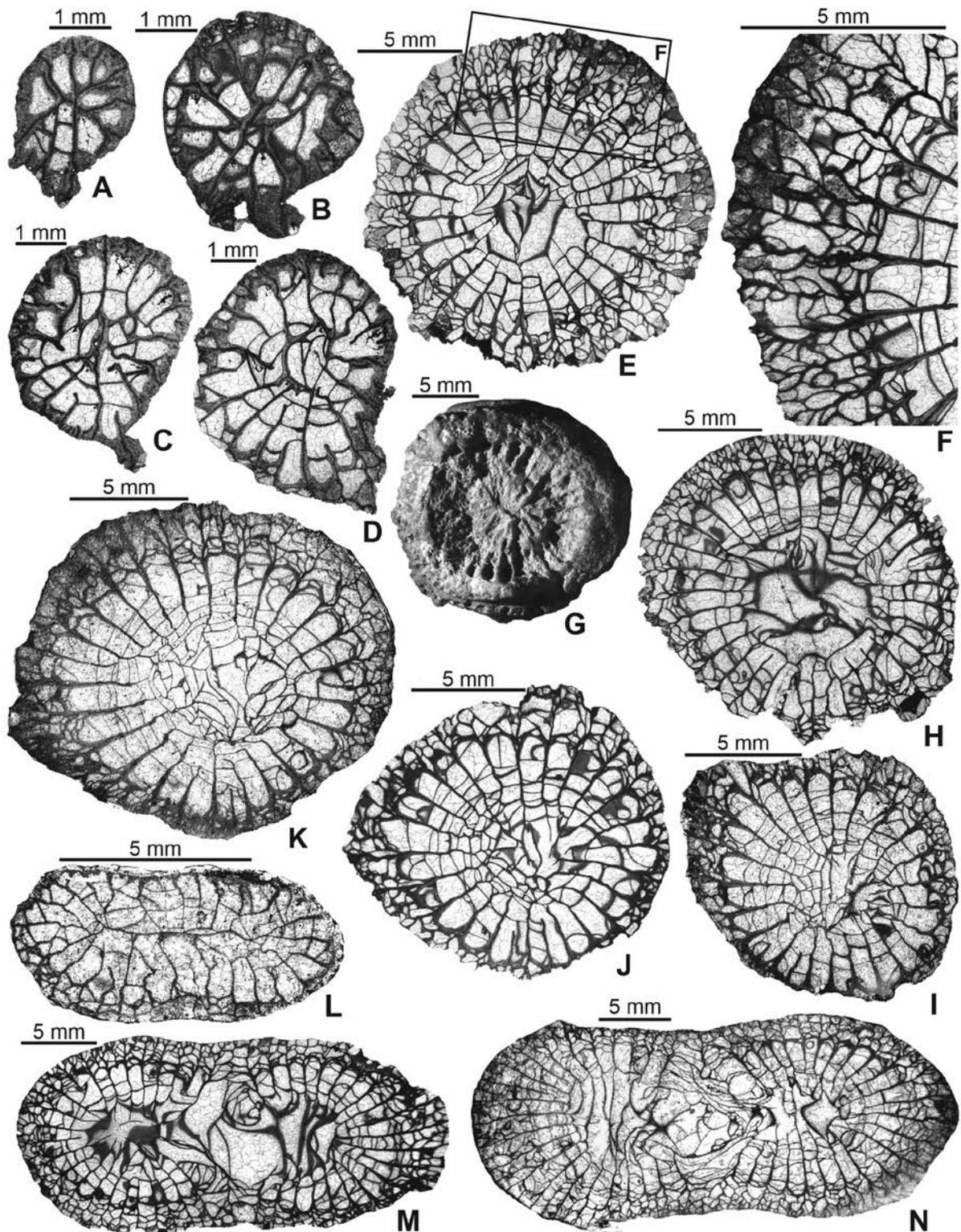
Text-fig. 10. *Yuanophylloides* (*Patulaxis*) *molestus* sp. nov. Transverse sections. A–G – USNM PAL 795360; A–C – neanic growth stage, D – late neanic/early mature growth stage, E – mature growth stage, F – complex dissepimentarium and differentiated length of minor septa; enlarged from E. G – calice. H – USNM PAL 795361, mature growth stage. I–K – USNM PAL 795362, successive sections of mature growth stage. L–N – USNM PAL 795363, composed of two calices surrounded by common external wall. L – late neanic/early mature growth stage, M, N – mature growth stage. For stratigraphic positions see text.

Text-fig. 11. *Yuanophylloides* (*Patulaxis*) *molestus* sp. nov. N:d values of selected specimens. Typical values contoured. Values of two specimens that show typical morphology of species differ. Values of one of them, starting from neanic and ending with mature growth stage connected by bold line. Abbreviations: d – diameter, n – number of septa.

neanic growth stage ends, or the mature growth stage started with the following features: (i) disconnection of the axial septum and formation of the cardinal and counter-septa, both either shortened to the length of the remaining major septa or being slightly longer; (ii) formation of a complete set of minor septa; (iii) appearance of complete circle of dissepiments; and (iv) lack of pseudocolumella or elongation of the counter-septum.

The mature growth stage of the specimens included in this species display only the following characters in common: (i) major septa slightly differentiated in length, but all long, leaving the axial area narrow; (ii) cardinal septa and the counter-septa indistinguishable from remaining major septa in most, but may be slightly elongated in some specimens; (iii) cardinal fossula absent. All remaining characters, including n:d value, vary. Differences in the n:d values of some specimens (e.g., Text-fig. 11) that show the typical morphology of the species restrict the taxonomic value of the n:d value in this species.

Two morphological variants or trends can be recognized, and their extreme representatives could be

characterized as follows: A trend towards simplified morphology (Text-fig. 9E, F, O) displayed by the major septa thinning the axial area permanently empty from any kind of axial structure, the minor septa very short, commonly restricted to peripheral-most part of the corallite, and the dissepimentarium narrow, comprising mostly herringbone and pseudo-herringbone dissepiments with grape-like and lateral dissepiments absent. A trend towards complex morphology (Text-fig. 8O, P) is displayed by the major septa slightly thickened at dissepimentarium/tabularium boundaries, tapering towards the corallite axis and forming a low boss in the calice (Text-fig. 10G), the weak axial structure permanent, the minor septa long, most approaching and some penetrating a tabularium, and the dissepimentarium narrow but complex with incipient grape-like dissepiments at the periphery and with rare lateral dissepiments. The most extreme specimens display features that allow for their distinction at the species level, but a continuous chain of intermediate morphologies confirm their inclusion in one species for the time being. These intermediate specimens (Text-figs 8A, B, T–V, 9A–C, R–V, 10E, F, I–K) display an axial structure that is either permanent, or interrupted in some specimens, but rather long lasting, with the minor septa differentiated in length within some transverse sections and the dissepimentarium comprising different dissepiments in particular parts of a given transverse sections.

Two specimens, both belonging to the group of intermediate morphology (Text-figs 8R–W, 10H), display n:d values extending beyond the frames established here for the species (Text-fig. 11). Despite those differences, both are included in *Y.* (*P.*) *molestus* sp. nov. as another extreme of this species.

The specimen composed of two calices surrounded by the common external wall (Text-fig. 10L–N) is interpreted here as a potential for the species to form protocolonies. Its morphology resembles specimens of a simplified trend mentioned above.

In longitudinal section (Text-figs 8C, D, W, 9D), the dissepiments are differentiated in size and arrangement; smaller at the periphery, longer near the tabularium, and sloping down more steeply. Some large dissepiments transect almost the entire dissepimentarium. The tabularium occupies two thirds of the corallite diameter or slightly more. The inner tabularium occupies approximately ½ of the tabularium width or slightly less. Both the morphology of the inner and its connection with the peripheral part of the tabularium are differentiated. This differentiation may depend to some extent on the precision of the longitudinal section. The inner tabularium transfers

gently into the peripheral tabularium where the longitudinal section is perfectly oriented, but it seems isolated from the peripheral tabularium where sectioned slightly off-center (Text-fig. 8C, D, respectively). The axial tabellae are also irregularly and loosely located in the early mature growth stage, whereas in the advanced mature growth stage they intersect the entire inner tabularium and are rather densely packed, horizontal, slightly elevated or sagging axially, with their marginal parts curved down. The peripheral tabellae are commonly bubble-like. Those adjacent to the dissepimentarium slope down, whereas those adjacent to inner tabularium are elevated towards the inner tabellae.

REMARKS: For differences from *Y.* (*P.*) *molests* sp. nov. see remaining species of the subgenus.

OCCURRENCE: USNM PAL 795353 and 795364, locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930–1937). All remaining ones, i.e., USNM PAL 795352 (holotype), 795354–795363 and 795365–795384, locality N700 of Cooper and Grant (1972) = middle part of Bed 10 of King (1930–1937). Missourian.

Yuanophylloides (*Patulaxis*) *parcus* sp. nov.
(Text-figs 12–14)

ETYMOLOGY: Latin *parcus*, *-a*, *-um* – sparing, brief – after simpler morphology by comparison to the type species.

HOLOTYPE: USNM PAL 795385.

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

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

MATERIAL: Sixteen internally well-preserved specimens, USNM PAL 795385–795400. Some specimens with parts of immature growth stage preserved. 22 thin sections and 23 peels were available for study.

DIAGNOSIS: *Patulaxis* subgen. nov. with n:d value inconsistent (see Text-fig. 14). Axial septum occurs up to earliest mature growth stage. In fully mature corallites, axial area permanently free. Minor septa very short; from several loculi absent. Dissepimentarium approximately 1/3 corallite radius wide; herringbone dissepiments prevail, but incipient grape-like and

very rare lateral dissepiments may occur. In the longitudinal section dissepiments arranged steeply. Tabularium bipartite. Peripheral part narrow, occupied by dissepiment-like tabellae. Inner tabellae long, densely spaced, horizontal, or slightly sagging axially.

DESCRIPTION: The neanic growth stage, investigated in a single specimen (Text-fig. 12I–L), displays a strong irregularity in both increase and arrangement of major septa. The axial septum is permanently present although its position is not invariably obvious due to this irregularity. The late neanic/early mature growth stage studied in the holotype and some other specimens (Text-fig. 12A–C, N, P) exhibits a morphology closely comparable to that of the type species for the subgenus. The long-lasting occurrence of the axial septum constitutes the most important difference; it continues to occur when all minor septa and a complete ring of dissepiments, doubled and tripled in some loculi, have been already inserted. Two specific characters of the late neanic/early mature growth stage should be pointed out: (i) the axial septum is perhaps disintegrated in the earliest growth stage of the holotype studied (Text-fig. 12A), (ii) the inner part of the axial septum is slightly thickened in one corallite (Text-fig. 12P). Also, the maximum n:d value of the latter specimen (23:14.3 mm) differs distinctly from the remaining specimens of this species, whereas its morphology in that growth stage resembles that of the holotype and most other specimens.

The morphology of the mature growth stage differs slightly when its early and advanced periods are compared. In the early period, the major septa are longer and slightly thicker than in the more advanced period, while the dissepimentarium is narrower and rudiments of the very weak axial structure may remain (Text-figs 13F, I, 19D, O). In advanced maturity the major septa are very thin, radially arranged, and approximately ½ of the corallite radius length. Protosepta indistinguishable. Cardinal fossula absent. The axial area is permanently free from axial structure. Minor septa very short, from several septal loculi totally reduced (Text-figs 12E, F, M, S, 13A–C, H); in rare instances well developed where dissepimentarium complex (Text-fig. 13F, I). Dissepimentarium increases in width through corallite growth, eventually occupying large parts of the major septa length and leaving only thin, short strips of their inner margins free (Text-figs 12M, S, 13A). Herringbone and interseptal dissepiments prevail in all specimens studied, being the only kinds of dissepiments present in the holotype and some other specimens (Text-figs 12E, F, O, R, S, 13A, B,
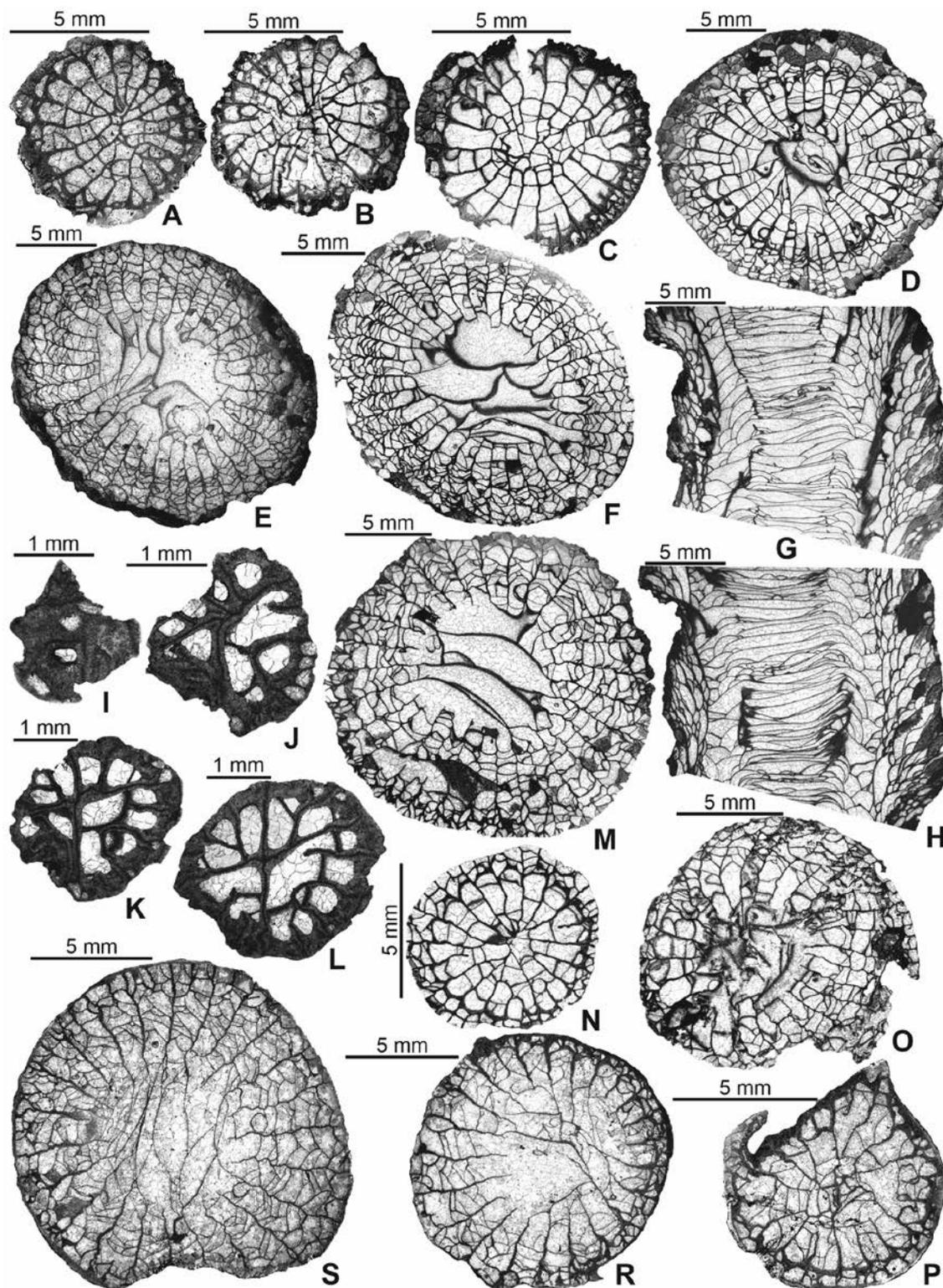
Text-fig. 12. *Yuanophylloides* (*Patulaxis*) *parcus* sp. nov. Transverse sections, except when stated otherwise. A–H – USNM PAL 795385, holotype; A, B – late neanic growth stage, C – late neanic/early mature growth stage, D–F – successive sections of mature growth stage, G, H – longitudinal sections; G – slightly eccentric, H – centric. I–M – USNM PAL 795386; I–L – neanic growth stage, M – mature growth stage. N, O – USNM PAL 795387; N – late neanic/early mature growth stage, O – mature growth stage. P–S – USNM PAL 795388; P – late neanic/ early mature growth stage, R – early mature growth stage, S – mature growth stage. For stratigraphic positions see text.
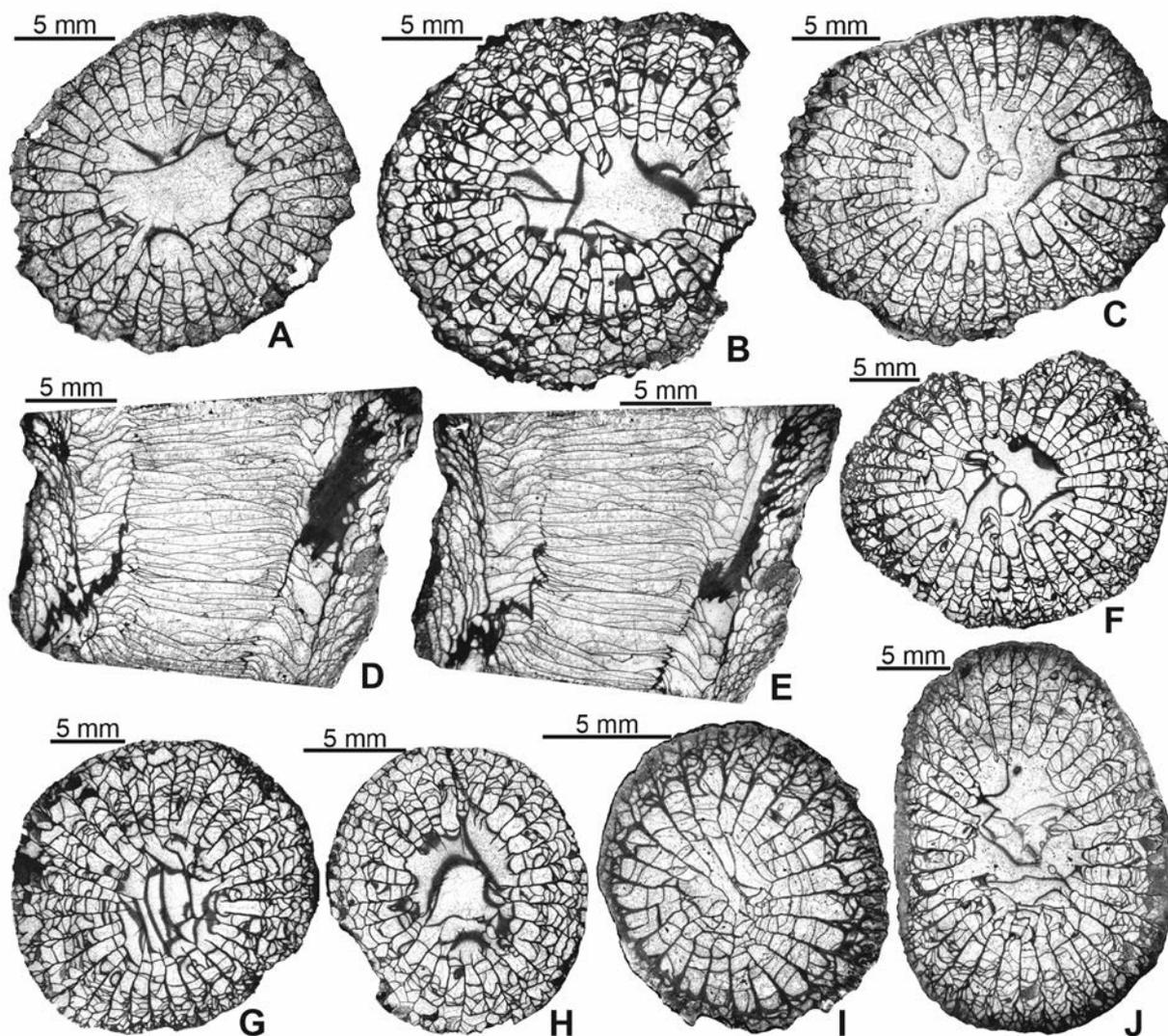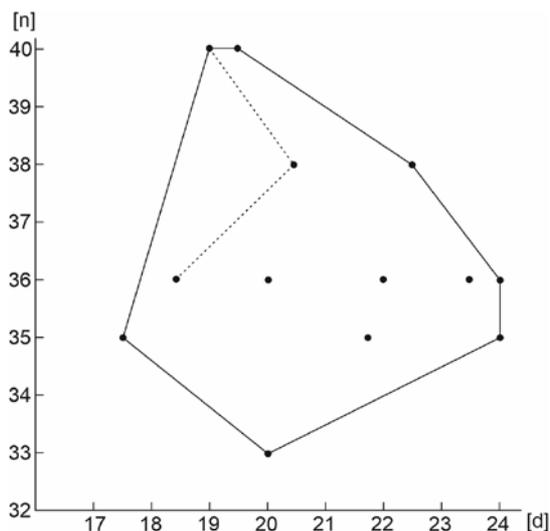
Text-fig. 13. *Yuanophylloides* (*Patulaxis*) *parcus* sp. nov. Transverse sections, except when stated otherwise. A–E – USNM PAL 795389; A–C – successive mature growth stage, D, E – longitudinal sections. F – USNM PAL 795390, mature growth stage. G – USNM PAL 795391, mature growth stage. H – USNM PAL 795392, mature growth stage. I, J – USNM PAL 795393, mature growth stage. For stratigraphic positions see text.

G, H). More complex dissepimentaria, with incipient grape-like and/or lateral dissepiments occurring within some septal loculi in the late maturity of rare specimens (Text-fig. 12M, S). A complex dissepimentarium is better developed in the early mature growth stage of these specimens, and remains only in a few septal loculi soon after (Text-fig. 12M, 13C, F, I, J). Some peculiarities in n:d values, such as that marked by the dashed line in Text-fig. 14, were perhaps of environmental origin, whereas some other irregularities are difficult to explain.

In the longitudinal section (Text-figs 12G, H, 13D, E) dissepiments are differentiated in length. Mostly small, arranged in steep rows. Tabularium bi-partite in general, with the axial part, occupying two-thirds of its width or slightly more. Axial tabellae long, densely packed horizontally or slightly sagging axially. Their peripheral parts turned mostly down to meet peripheral tabellae, but some may extend up to the dissepimentarium. Peripheral tabellae either bubble-like in the entire narrow peripheral tabularium, or the peripheral-most tabellae horizontal. The boundary between the inner and peripheral parts of the tabularium is not sharp.

REMARKS: *Yuanophylloides* (*P.*) *parcus* sp. nov.

Text-fig. 14. *Yuanophylloides* (*Patulaxis*) *parcus* sp. nov.; n:d values of selected specimens. Different n:d values of mature growth stage in one specimen shown by dotted lines. Abbreviations: d – diameter, n – number of septa.

closely resembles *Y.* (*P.*) *molestus* sp. nov. in the morphology of the neanic and the intermediate late neanic/early mature growth stage and in the morphology of the longitudinal sections of advanced mature growth stages. It differs from the type species in the n:d value, in the wider axial area free from major septa, permanent lack of an axial structure in maturity, reduction in the length of the minor septa up to their partial disappearance from the corallite lumen, and in the larger width and less complex morphology of the dissepimentarium.

OCCURRENCE: USNM PAL 795385, 795394 and 795395, locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930–1937). All remaining, i.e., USNM PAL 795386–795393 and 795396–795400, locality N700 of Cooper and Grant (1972) = middle part of Bed 10 of King (1930–1937). Missourian.

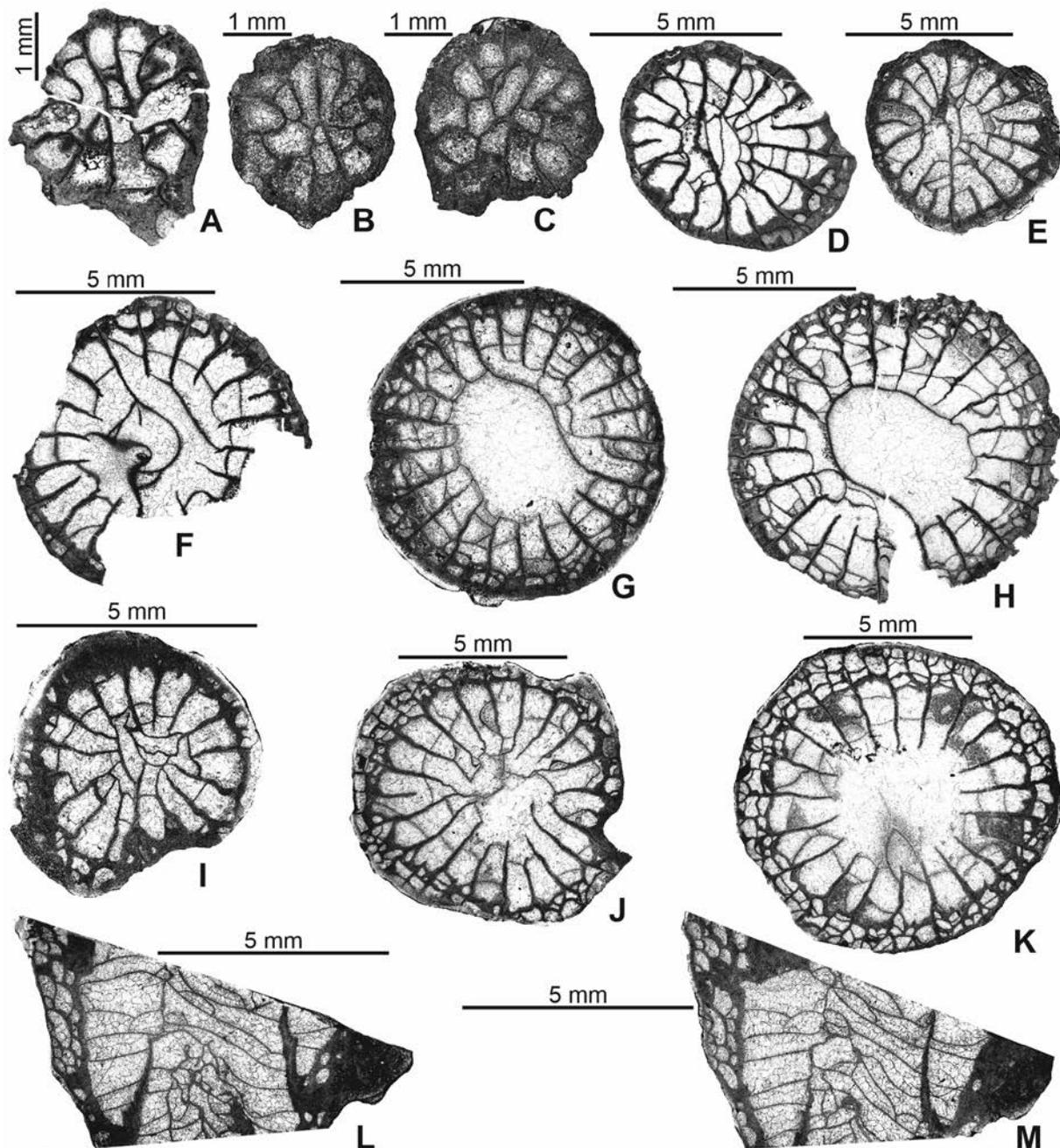### *Yuanophylloides* (*Patulaxis*) sp.
(Text-fig. 15)

MATERIAL: Two specimens with well-preserved internal structures, partly preserved calices and proximal parts, USNM PAL 795401 and 795402. 4 thin sections and 30 peels available for study.

DIAGNOSIS: *Patulaxis* with n:d ratio 20–22:8–12 mm; major septa reach 1/2 to 2/3 of the corallite

radius; minor septa commonly intersect narrow dissepimentarium; axial area permanently free of septa since early mature growth stage.

DESCRIPTION: The arrangement of major septa in the neanic growth stage, with n:d values: 11:2.7×2.4 mm and 13:2.6×2.6 mm, is irregular, but the axial septum is recognizable (Text-fig. 15A–C). In the late neanic/early mature growth stage (Text-fig. 15D, E, I) the axial septum becomes divided into the cardinal and the counter-septa with the former dominating in length. The first minor septa become recognizable and the first dissepiments appear within some septal loculi. In the early mature growth stage, the ring of dissepiments doubled in some septal loculi. The protosepta either remain elongated or become shortened to the length of remaining major septa (Text-fig. 15F, J, respectively). The lack of cardinal fossula and the shortened last pairs of the major septa inserted precludes recognition of the protosepta in the second instance. In the advanced mature growth stage (Text-fig. 15G, H, K) all major septa, including the protosepta, are equal in length, slightly thickened near the dissepimentarium/tabularium boundary and taper axially. The axial area is free of septa and occupies approximately one half of the corallite diameter. Minor septa either penetrate the peripheral-most part of the tabularium or are shortened to various extent. The dissepimentarium is 0.6–1.0 mm wide and consists of 2–4 rows of pseudo-herringbone and regular dissepiments. In the longitudinal section (Text-fig. 15L, M), dissepiments are small, globose, slightly thickened, and sloped steeply, arranged in one to three rows. The tabularium occupies approximately four-fifths of the corallite diameter. Widely spaced tabulae comprise either long or complete tabellae. In the younger part of the corallite the tabulae rise slightly upwards to reach very irregular, curved sections of the inner margins of the major septa that form a weak axial structure. They remain slightly elevated in the mature part of the corallite.

REMARKS: The diagnostic characters of the specimens described differ distinctly from all the species designated here as *Y.* (*Patulaxis*) subgen. nov. in their n:d values in the morphology and the width of the tabularium in both transverse and the longitudinal sections and in the width and morphology of the dissepimentarium. We have thus decided to describe them as most probably a new species but leave it in the open nomenclature due to the very restricted number of specimens. *Yuanophylloides* (*P.*) *acolumellatus* Cocke, 1970, another species with a

Text-fig. 15. *Yuanophylloides* (*Patulaxis*) sp. Transverse sections, except when stated otherwise. A–H – USNM PAL 795401; A–C – neanic growth stage, D, E – late neanic/early mature growth stage, F–H – mature growth stage; I–M – USNM PAL 795402; I – late neanic/early mature growth stage, J, K – mature growth stage, L, M – longitudinal sections; L – eccentric, M – almost centric. For stratigraphic positions see text.

completely reduced axial structure, possesses thin and wavy major septa, very short minor septa, and development of lonsdaleoid dissepiments.

OCCURRENCE: USNM PAL 795401 and 795402, locality N700a of Cooper and Grant (1972) = upper part of Bed 10 of King (1930–1937). Missourian.

CONCLUSIONS

1. Suggestion of a relationship between the Dibunophyllinae and Neokoninckophyllidae (Fedorowski 2019, text-fig. 4) is acceptable only when taxa from the Paleotethyan superprovince are considered. However, the inclusion here of *Campophyllum kansa-*

sense in *Yuanophylloides* puts this suggestion in some doubt. The indisputable *Dibunophyllum* Thomson and Nicholson, 1876 is extremely rare, if present at all in the Mississippian strata of the North American superprovince, whereas the Dibunophyllinae/Neokoninckophyllidae split must have taken place in late Mississippian time if *C. kansasense* is to be accepted as the oldest species of *Yuanophylloides*. We leave this question open for the time being.

2. The appearance of *Y. kansasense* in the North American superprovince earlier than in the Paleotethyan superprovince increases the possibility of the former as a center of origin of the Pennsylvanian Rugosa and supplements an idea of the presence of a circum-Laurussia current.

3. Reconstruction of relationships, i.e., the precise taxonomy of taxa, depends to a large extent on the paleooceanography. However, it works both ways. The problem of homeomorphy and especially parallelism has to be balanced against tectonic constrains whereas the precise taxonomy and good paleobiogeography can help establishing the tectonic setting.

4. The individual variation observed in many North American dissepimented solitary Rugosa makes their indisputable species identification doubtful. The extraordinary intraspecific variability in *Caninostrotion variabile* Easton, 1943 suggested by Webb (1987), and the variability in *Yuanophylloides* (*Patulaxis*) *molestus* subgen et sp. nov., can be pointed out as notable examples. Thus, the identification of the species included here in both subgenera, as well as their content, should be treated as provisional.

5. Apparently long-lasting species, such as *Y. kansasense* (late Mississippian–late Missourian), may in fact be only morphotypes, despite displaying similar morphology. Neither this nor the question raised in point three above can be solved without comprehensive studies of the large collections of specimens derived not only from the stratigraphic levels and areas they apparently occur in, but also from intermediate stratigraphic levels.

Acknowledgements

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