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Heba El-Desouky^{1*}, Hans-Georg Herbig² and Mahmoud Kora¹

Abstract

A strongly endemic Upper Pennsylvanian (Kasimovian) rugose coral association consisting of small, mostly non-dissepimented, simple structured and poorly diversified species is studied from the lower member of the Aheimer Formation (Western side of the Gulf of Suez, Egypt). The unit is composed of grey, silty mudstone intercalated with thin, ferruginous, silty dolostone-limestone and calcareous siltstone beds. Ten taxa from four families were identified. Four species of the Antiphyllinae are new; Actinophrentis crassithecata n. sp., Lytvolasma aheimerensis n. sp., L. paraaucta n. sp. and Monophyllum galalaensis n. sp. Besides, Rotiphyllum exile de Groot, 1963 and Bothrophyllum okense Kossovaya, 2001 were identified; four taxa remain in open nomenclature (Lytvolasma cf. canadense, Zaphrentites cf. parallela, Zaphrentites sp. and Ufimia sp.). Rejuvenation, encrustation and bioerosion phenomena are rare. Attachment structures during mature stages are not evident; attachment scars in the apical parts are also rare. Growth patterns and embedding in the muddy deposits indicates that the corals lived as mudstickers in soft substrate. Recrystallization, dolomitization and ferrugination of open pore spaces inside the corals are the most common diagenetic features. The corals from the lower Aheimer Formation represent a typical cyathaxonid fauna that was adapted to high clastic input and turbid waters in a restricted, sheltered, episodically storm-swept inner ramp environment in an embayment of the southern shelf of the Palaeotethys. A time-averaged ramp model shows a regressive development from a mixed carbonate-siliciclastic open inner ramp setting during the Moscovian to the restricted inner ramp of the lower Aheimer Formation (Kasimovian) and following peritidal to fluvial environments of the Gzhelian. General and local palaeoclimatic considerations indicate cooling. Besides relations to northern Spain that root Egypt in the western Palaeotethys, connections existed via the Donets Basin (and the southern Urals) to the Cordilleran-Arctic–Uralian realm which is a cool water province during the Lower and Middle Permian. The Egyptian fauna appears to be a precursor of the anti-tropical cyathaxonid fauna of the latter time slice and also of the Lower Permian coolwater faunas of the east Cimmerian peri-Gondwana terranes.

Keywords Rugosa, New species, Cyathaxonid facies, Restricted inner ramp, Palaeoclimate, Carboniferous (Pennsylvanian), Gulf of Suez (Egypt)

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*Correspondence: Heba El-Desouky hebaeldesoky@mans.edu.eg Full list of author information is available at the end of the article



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Fig. 1 Geological map of the eastern cliffs of the Northern Galala Plateau, modified after Abdallah and El Adindani (1965)

Introduction

Carboniferous deposits of Egypt are exposed on both sides of the Gulf of Suez as discontinuous outcrops. East of the Gulf, they are exposed in the west-central Sinai at Um Bogma, Wadi Feiran and Abu Durba, and west of the Gulf in the Northern Galala, Abu Darag, Wadi Araba and at Wadi El-Dakhel in the northern reaches of Wadi Qena (Ernst et al., 2020; Issawi and Jux, 1982; Klitzsch, 1990; Kora, 1998 [with extensive references]; Said, 1971). Pennsylvanian rugose corals are known from the exposures bordering the eastern and southern rims of the Northern Galala Plateau, on the western side of the Gulf of Suez. On the eastern cliffs of the Northern Galala, about 2 km south El Galala Resort and 3 km to the north of Porto Sukhna (29° 28′ 21″ N, 32° 27′ 38″ E) a succession of the lower Aheimer Formation predominantly made up of fossiliferous grey mudstone, was investigated for its rugose coral fauna (Fig. 1).

In spite of their importance in clarifying the palaeobiogeographic relations within the Carboniferous Palaeotethys and its extraordinary, isolated position at the southern rim of the Palaeotethys, the rugose corals from Egypt have received little attention. They were usually mentioned among diverse fossil assemblages. Some identification based only on external characters had been done in earlier work (e.g., Abdallah and El Adindani 1965; El Adindani, 1968; Schweinfurth, 1885), therefore, is mostly unreliable.

In the meanwhile, the late Moscovian rugose coral association from the Rod El Hamal Formation of the Wadi Araba area at the southern rim of the Northern Galala is quite well-known (El Desouky, 2018; El Desouky et al., 2019; Herbig and Kuss, 1988; Kora et al., 2019). In a very first account Herbig and Kuss (1988) described *Pseudozaphrentoides* ex gr. *juddi* (Thomson, 1893) and *Amygdalophylloides ivanovi* (Dobrolyubova, 1937) from the section Bir Madsus, southeastern edge of the Northern Galala/northeastern end of Wadi Araba. The taxa, recently revised in Kora et al. (2019) are now attributed to *Bothrophyllum cylindricum* Kora, Herbig and

El Desouky, 2019, respectively, to *Amygdalophylloides omarai* Kora, Herbig and El Desouky, 2019. Using serial transverse thin-sections of the corallites, El Desouky (2018) and Kora et al. (2019) in total recorded six species belong to the Bothrophyllidae and the Geyerophyllidae, including three endemic new species. In addition other three undeterminable Bothrophyllidae were left in open nomenclature.

In contrary, rugose corals from the eastern cliffs of the Galala Plateau (Aheimer Formation) are less known. They were first noticed by Abdallah and El Adindani (1965), who just mentioned the presence of corals and inappropriately named the lower member of the Aheimer Formation as Lophophyllidium bearing shale series. However, Kora and Mansour (1991) rightly rejected that name, as Lophophyllidium was not identified at all and just proposed the informal name "lower member of the Aheimer Formation". Herbig and Kuss (1988) described Bothrophyllum pseudoconicum Dobryolyubova, (1937) from the section Bir Qiseib, southeastern edge of the Northern Galala (Fig. 1); its presence was confirmed by Kora and Mansour (1991) further north in the type region of the Aheimer Formation around Bir Aheimer. Moreover, Herbig and Kuss (1988) described *Pseudozaphrentoides* ex gr. juddi (Thomson) (=Bothrophyllum cylindricum Kora, Herbig and El Desouky, 2019) from the section Ain Sukhna which is close to Bir Aheimer (not to be confused with Porto Sukhna in Fig. 1, compare Bandel and Kuss, 1987, Fig. 1). We could not identify these taxa in our study. According to the synthetic stratigraphic section and microfacies description in Herbig and Kuss (1988; see also Bandel and Kuss, 1987), both species have been found in 3–8 m thick dolomitic, strongly sandy, biosparitic limestone. Such facies is not encountered in the lower Aheimer Formation, but is typical of the upper Rod El Hamal Formation (unit 3 of Kora et al., 2019). Bandel and Kuss (1987) reported such limestone horizons in several sections along the eastern escarpment of the Northern Galala. Therefore, though not recognised in our study (Fig. 1), the Rod El Hamal Formation probably is locally present below the Aheimer Formation in the eastern cliffs of the Northern Galala. In this context it has to be stressed that already Said (1971) considered a conformable contact or interfingering of both formations.

Kora and Mansour (1991) recorded 17 solitary rugose corals from the lower member of the Aheimer Formation belonging to 5 families and 13 genera of the Stauriida. Based on El Desouky (2018), these identifications are mostly revised herein and compared with the newly collected material, although hampered by the bad preservation of the corallites and rarity of serial transverse sections. In fact, many corallites are only known by a transverse section close to the calice. El Desouky et al. (2019) also discussed the depositional environment and the palaeobiogeographic relations of the Aheimer corals.

Geological and stratigraphic setting

The faulted marine Pennsylvanian succession of the Aheimer Formation at the eastern escarpment of the Northern Galala Plateau was investigated from the south of Wadi Abu Darag, occupied now by El Galala Resort, and north of Wadi Qiseib, where the Porto Sukhna Resort was recently constructed (Fig. 1). The landscape has changed drastically in the last few years as the area is receiving many industrial, domestic and tourism projects. Consequently, several fault blocks are destroyed and partly removed. Abdallah and El Adindani (1965) who introduced the formation, measured a ca. 250 m-thick succession at its type locality, Wadi Aheimer on the eastern foot slopes of the Northern Galala massif, about 10 km SSE of Ain Sukhna. For the present study, only the lower part of the formation (about 8.5 m thick) was sampled and studied, as the strata above are devoid of corals. The formation base is not exposed, and it has been considered to rest conformably over/or to interfinger with the Abu Darag Formation (Klitzsch, 1990) or the Rod El Hamal Formation (Said, 1971). It underlies the Permo-Triassic red beds of the Qiseib Formation without visible unconformity.

Kora and Mansour (1992) subdivided the Aheimer Formation into three members; lower, middle, and upper members (Fig. 2A). Following this classification, El-Refaiy et al., (2023; Table 2) recently subdivided the Aheimer Formation into four informal units: units I, II, III and IV. Unit I, named Tisoa-bearing unit, is correlated with the lower member of Kora and Mansour (1992). Units II and III are correlated with the middle member of Kora and Mansour (1992), subsequently unit IV equals their upper member. The lower member (Lophophyllidiumbearing shale series of Abdallah and El Adindani (1965) and Tisoa-bearing unit of El-Refaiy et al., 2023) is best exposed around Wadi Abu Darag (El Galala Resort) in our study area. The lithological characteristics of the lower part of this interval are summarised in Fig. 2A, B and its appearance in the landscape is illustrated in Fig. 3. It is made up of about 34 m thick dark grey shales, intercalated with fossiliferous thin brown dolomitic beds and alternating with some reddish siltstone and sandstone beds (Fig. 3A, B). The lower part of this member is fossiliferous with small cornuted rugose corals, bryozoans, ossicles from crinoid columnals and brachiopods (Fig. 3C-H). Opposed to determinable brachiopods, bryozoans are badly preserved (A. Ernst, pers. comm.) and could not be included in the studies of Ernst et al., (2019, 2020). The overlying middle member (Crinoidal dolostone-siltstone unit of Kora and Mansour, 1992) is



Fig. 2 A Lithostratigraphic succession of the Aheimer Formation studied along the eastern cliffs of the Northern Galala Plateau after Kora and Mansour (1992). B Enlargement of the mudstone dominated basal shale part of the lower member of the Aheimer Formation studied herein (see also Fig. 3A)

best exposed at Wadi Aheimer and is composed of yellowish-brown sandstone beds intercalated with a few siltstone and calcareous sandstone beds (about 40 m thick). The upper member (Sandstone series of Abdallah and El Adindani, 1965) consists of thick-bedded sandstones with few siltstone interbeds, assuming an average thickness of 90 m at Wadi Aheimer. A late Pennsylvanian to early Permian age was suggested for the formation based on the macro- and microfaunal content (Abdallah and El Adindani, 1965; Abd-Elshafy et al., 2000; Kora and Mansour, 1991, 1992; Said and Eissa, 1969), thus its lower member is of late Pennsylvanian age. According to its relation to the late Moscovian coral fauna from the upper member (unit 3)



Fig. 3 Field aspects of the Aheimer Formation; A General view of the studied succession of the lower member exposed in a faulted block to the north of Porto Sukhna; the shales mudstones close to the base (rectangle) are interbedded with thin, hard dolomitic bands. B Close up view on of the lower fossiliferous shale mudstone beds of A. C, D Close-up view on of two rugose corals entombed in the shale mudstone beds. E Close-up view on of a rugose coral species with diagenetically compressed calyx. Note strong ferrugination of corallite and surrounding matrix within the fossiliferous shale. F Fossiliferous shales mudstone with thin bands of ferruginous dolomitic limestone and secondary evaporite veinlets; Cr=crinoidal stems. G Crinoid columnals (Cr) and rugose corals (RC) are embedded in the shale mudstone. H Close-up view on of a spiriferid valve shell within the shale (arrow). Diameter of coins in C-E, G: 25 mm



Fig. 4 Effects of diagenesis on some coral specimens: A Thin-section in the calice of the specimen RAh (44) shows a completely compressed calice filled with fossiliferous mud. B Thin-section below the calice of the *Bothrophyllum okense* (RAh 37) shows beginning of compression and breakage of septa. C Thin-section below the calice of the specimen RAh (79), shows completely broken and altered septa, probable outer dissepimentarium and axial structure, filled with ferruginous mud. D Thin-section of a completely compressed specimen RAh (200) shows high alteration, breakage and ferrugination of skeletal elements. E Thin-section in the early mature part of the *Actinophrentis crassithecata* n. sp. (RAh 11), shows ferrugination affects a large part of the interior skeleton. F Mature thin-section of *Rotiphyllum exile* (RAh 29), shows ferrugination and dolomitization of skeletal elements. G, H Thin-sections of mature part of the specimen (RAh 81) in G and the immature part of the specimen RAh (99) in H show extensive dolomitization and ferrugination of the internal skeletal elements

of the underlying Rod El Hamal Formation (Kora et al., 2019), we herein assign it to the Kasimovian.

Described materials and methods

About 200 small, solitary rugose coral specimens have been collected from the shales close to the base of the lower member of the Aheimer Formation, ranging between complete to incomplete corallites. Except for few corallites, most of the specimens are moderately to badly preserved. All sections high in the calyx are laterally compressed due to compaction of sediment inside (Figs. 3E, 4A–D). This is easily seen, as lower sections with cemented coral interiors are perfectly round. In some other coral specimens, the interior skeletal elements of the corals are partly to completely dissolved or septa are completely broken. Recrystallization, dolomitization and ferrugination of open pore spaces inside the corals are abundant, (Fig. 4D–H). About one third of the specimens do not show any internal structure in thin-sections. All the examined corallites are nondissepimented except three corallites (RA 37, RA 79, and RA 200) which show few preserved dissepiments in its wall, of them RAh 200 (Fig. 4D) is completely compressed and very badly preserved to a limit that makes its study impossible.

The collected coral specimens were cleaned and photographed using ammonium chloride whitening. All samples were impregnated with resin under vacuum for preparation of transverse thin-sections. As far as possible serial sections were made to describe the internal microscopic features, including number and distribution of septa, and presence or absence of dissepiments. They are of special importance in small cornute corals to study the ontogenetic stages of the specimens and to achieve precise, reliable identifications. Up to 360 thinsections were studied and photographed using a Leica M420 microscope equipped with a Leica digital camera DFC 320. All the collected materials are deposited at the Geology Department, Faculty of Science, Mansoura University, Mansoura, Egypt. Terminology, criteria of identification, generic characters and systematic classification are mostly in accordance with Hill (1981). A thorough literature review of later taxonomic assignments of genera, widely dispersed in literature, is given to clarify the current status of the often-controversial discussed taxa that in general are difficult to identify. In the same manner, palaeobiogeographic distributions were analysed to clarify the relations of the isolated Egyptian fauna. Some important morphological terms used in the systematic description are illustrated in Fig. 5 based on Denayer and Hoşgör (2014).

The abbreviation n:d indicates the ratio of number of septa (n) vs. diameter of corallite (d).

Systematic palaeontology

Order **Stauriida** Verrill, 1865. Suborder **Stereolasmatina** Hill, 1981.

Family Antiphyllidae Ilina, 1970.

Diagnosis (Fedorowski, 2012a): Small, solitary, non-dissepimented corals with cardinal septum located on convex side of corallite; early ontogeny rotiphylloid; cardinal septum shortened late in ontogeny or only on calice wall; counter septum commonly elongated, never shortened; stereocolumn of early ontogeny often replaced by free axial area in maturity.

Remarks: Opposed to Hill (1981), Weyer (1975) and in consequence Fedorowski (1987a) did not recognise a



Fig. 5 Internal morphological characters of the non-dissepimented rugose corals referred to in the systematic descriptions, after Denayer and Hoşgör (2014). A Transverse section. B Longitudinal section

Table 1 Morphological 1928 for comparison with	comparison of genera in / n morphologically close Ly	Antiphyllinae llina, 1970 pr <i>tvolasma</i> Soshkina, (basec	esent in the Aheimer For I on Fedorowski, 1987a an	mation, western side of G Id Chwieduk, 2013)	ulf of Suez, Egypt includir	ng <i>Bradyphyllum</i> Grabau,
Genus	Cardinal septum	Cardinal fossula	Counter septum	Alar septa	Major septa	Minor septa
Actinophrentis Ivanowski, 1967	Thin, some-what short, shortened on calice floor	Narrow, its axial end reach- ing or almost reaching corallite axis, narrowing adaxially	Moderately to distinctly elongated	As long as other major septa, or slightly elongated	Thickened to contiguity in early growth stages, pinnately arranged, almost reach corallite axis, in late growth stages contiguous in peripheral stereozone and wide axial structure	Very short
<i>Bradyphyllum</i> Grabau, 1928	Long in early ontogeny, shortened in maturity below calice floor	Triangular, not reaching corallite axis	Slightly elongated, at least in early ontogeny	Equal in length to adja- cent major septa	Radially arranged, short- ened to form free axial area	Very short
<i>Lytvolasma</i> Soshkina, 1925	in early growth stages long, in late stages slightly shortened	Open, deep, key-hole, often bordered by half- aulos in counter quadrants in late growth stages, weakly marked	As other major septa or slightly elongated at least in neanic stage	As long as other major septa, slightly elongated in neanic stage	Long, thickened, laterally contiguous over much of their length, some- what curved to straight and almost reaching axis, and almost reaching axis often thicker and grouped about fossula, pseudo- radial	Very short, confined to narrow peripheral stereozone
Monophyllum Fomichev, 1953	Shortened on calice floor	Widened adaxially, reach- ing corallite axis	Elongated to form incipi- ent columella	In neanic stage slightly elongated	Pseudoradial, often thicker in cardinal quadrants, straight	Underdeveloped
Rotiphyllum Hudson, 1942	Shortened on calice wall, long on floor	Reaching corallite axis, narrowing adaxially	More or less elongated	As long as other major septa in late stages, long- est of quadrants in neanic stage	Radially arranged, dilated, with extra thickening in inner third of their length, joined to form dense axial structure	Short

family Antiphyllidae Ilina, 1970, but separated the subfamilies Hapsiphyllinae Grabau, 1928 and Antiphyllinae Ilina, 1970 within the Hapsiphyllidae Grabau, 1928. However, Fedorowski (2009a, 2009b) and in his following papers treated the Antiphyllidae as an independent family. An emended diagnosis, differing from Hill (1981) and based on the main characters of the subfamily diagnosis by Fedorowski (1987a) was finally given in Fedorowski (2012a).

Subfamily **Antiphyllinae** Ilina, 1970. emend. Fedorowski, 2012a.

Type genus: Antiphyllum Schindewolf, 1952.

Diagnosis: As for the family.

Remarks: The most important diagnostic characters of genera of the subfamily recognised in our material are displayed in Table 1. For comparison with morphologically close *Lytvolasma* Soshkina, 1925 also *Bradyphyllum* Grabau, 1928 is listed. Comparisons with further Antiphyllinae were listed by Fedorowski (1987a) and supplemented by Chwieduk (2013).

The synonymy of the type genus of the subfamily, *Antiphyllum* Schindewolf, 1952 with *Claviphyllum* Hudson, 1942, stressed by Weyer (1974, 1975) and followed by Fedorowski (1987a) was not further recommended by Fedorowski (2012a).

Genus Actinophrentis Ivanovski, 1967.

Type species: *Actinophrentis donetziana* Fomichev, 1953.

Diagnosis: Non-dissepimented, small, solitary corals with pinnately arranged major septa up to calice floor, united axially by stereocolumn; cardinal septum shortened from early maturity; counter septum distinctly or moderately permanently elongated; cardinal fossula reaches or almost reaches corallite axis; minor septa underdeveloped (after Fedorowski, 1987a, p. 36).

Remarks: Weyer (1975) unambiguously synonymised *Actinophrentis* Ivanovski, 1967 with *Rotiphyllum* Hudson, 1942. Hill (1981) accepted *Actinophrentis*, though she did not rule out synonymy with the later genus. Fedorowski (1987a) stated the validity of the genus, especially based on the development of cardinal and counter septum (see diagnosis). He also discussed questionable synonymies with other genera, which include ?p.p. *Stereolasma* Fomichev, 1953 non Simpson, 1900 and 1962 *?Longiclava* Easton, 1962. *Actinophrentis columnare* Fedorowski, 1987 from the lower Wolfcampian of Texas is known in time-equivalent strata from the northern Timan (Kossovaya, 1996); unfortunately, its presence in the Urals and the Russian Platform cannot be deduced

from this publication. However, the type species of the genus, *A. donetziana* Fomichev, 1953 is from the Donets Basin, Ukraine. One specimen described by de Groot (1963) to belong to *Zaphrentites paralleloides* de Groot, 1963 from the Sierra Corisa Limestone (Westphalian D=upper Moscovian) of northern Palencia (Cantabrian Mountains, Spain) was included by Fedorowski (2004) as *Actinophrentis* sp. In addition, Rodríguez et al., (2022, Table 1) accepted the presence of the genus in the Asturian Substage (upper Moscovian) of the Cantabrian Mountains without further discussion.

Geographic and stratigraphic range: Upper Moscovian of the Donets Basin (Fomichev, 1953; Ivanovski, 1967) and the Cantabrian Mountains (northern Palencia, Spain) (Fedorowski, 2004); Upper Pennsylvanian (Kasimovian) of Egypt (Kora and Mansour, 1991 and this paper); lowermost Permian (Asselian) of N Timan Ridge (Kossovaya, 1986); lowermost Permian (lower part of Wolfcampian Series = Nealian Stage) of Glass Mountains, western Texas (Fedorowski, 1987a).

Actinophrentis crassithecata n. sp.

(Fig. 6A1–A5, B1–B2)

Derivation of the name: From the Latin crassus—means thick, theca—F cover—after the great thickness of the external wall.

Holotype: Specimen RAh 57, illustrated in Fig. 6A1–A4. Three transverse thin-sections are available.

Material: In addition to the holotype, two moderately to badly preserved corallites (RAh 11 and RAh 42) are paratypes, with 11 transverse thin-sections. Although looking good preserved in their external form, keeping a good preserved outer epitheca with septal furrows and concentric growth lines (Fig. 6B1, B2), serial thin-sections of the specimens (RAh11, 42) are not suitable for illustrations as they suffer from either compaction or ferrugination (e.g., Fig. 4E), The proximal ends of the corallites are largely eroded. They are collected from the basal shales of the lower member of the Aheimer Formation.

Type locality: Eastern cliffs of the Northern Galala plateau (Lat. 29° 28′ 21″ N and Long. 32° 27′ 38″ E), northern Eastern Desert, western side of the Gulf of Suez, Egypt.

Type horizon: Basal shales of the lower member of the Aheimer Formation; Upper Pennsylvanian (Kasimovian).

Diagnosis: *Actinophrentis* with thick external wall (about 1.5 mm thick), having maximum n:d ratio at calice floor 24:11. Major septa are pinnately arranged. Cardinal septum shortened with maturity. Counter septum elongated from the immature stage up to calice floor.

Description: External characters: Corallites only faintly conical (see minimal increasing n:d ratios below) and



Fig. 6 A Actinophrentis crassithecata n. sp.: (Holotype specimen RAh (57). A1 External view showing a thick walled, slightly curved corallite with septal furrows ornamenting the external wall. Position of thin-sections indicated. A2 Transverse thin-section near the non-preserved apical part, shows thick major septa meeting in the centre and adaxially thinning cardinal septum. A3 Transverse thin-section in the middle part of the corallite, shows major septa meeting in the centre and noticeable fossular breaks. A4 Last adult transverse thin section just below the calice shows septa withdrawn a little from the centre. A5 Details of the external wall of A3. B1, B2 External lateral views of the specimen RAh (11) showing a thick walled, slightly curved corallite with septal furrows and concentric growth lines on the external wall. C *Lytvolasma* cf. canadense Fedorowski and Bamber, 2001, specimen RAh (66). C1, C2 Transverse thin-section in the middle mature part of the corallite, shows a short cardinal septum and a long counter septum with a rhopaloid axial end. C3 Transverse thin-section in the calice, shows a long counter septum. Scale bars: 2.5 mm, except A2–A5: 2 mm. Black dots indicate the positions of cardinal septum (below), counter septum (above) and the two alar septa

slightly curved (Fig. 6A1, B1–B2). The preserved parts are 2–2.5 cm long. Calices are deep. If preserved, they are compressed due to compaction. Apexes are not

preserved. The thick external wall (1.5 mm-thick) bears distinct furrows of major and minor septa. The latter could only be detected inside the calyx (Fig. 6A1).

Internal characters (transverse sections): the ontogenetically earliest preserved part has a n:d ratio of 22:7 mm (Fig. 6A2). Major septa are pinnately arranged. Cardinal fossula is distinguishable. Alar fossulae are also distinct, they are marked by the underdeveloped last pair of major septa in the counter quadrants. All septa meet in the corallite axis. The cardinal septum is thinner than the other major septa, whereas the counter is slightly thicker. External wall about 1.5 mm thick and internally enforced by steroplasmatic layer in the most external septal loculi. The mature morphology seen in the next transverse section (Fig. 6A3) is characterised by a pinnate arrangement of long major septa with n:d ratio of 24:8. Major septa are conspicuously acutely thickened in their peripheries and wedge-like rooted in the thick external wall (Fig. 6A5); they are also slightly thickened to contiguity in their inner ends. Cardinal septum shortens, whereas the counter is the longest. Pericardinal septa are as short as the cardinal. The cardinal fossula extends to the corallite axis, where it moderately widens. Alar septa are long and meet with the axial end of the long counter septum in the axis. The alar fossulae are still well-marked. Minor septa are absent. Peripheral interseptal loculi are filled by stereoplasma, thus apparently increasing the prominent, about 1.8 mm thick external wall (Fig. 6A5). One row of axially updomed tabulae well-developed in peripheral interseptal loculi of right cardinal and counter quadrant. Opposed, strongly horseshoe-arched, isolated and small peripheral, convex tabulae (i.e., inclined towards the external wall) are mostly confined to the left cardinal and counter quadrants. The last mature section below the calice (Fig. 6A4) has a n:d ratio of 24:11. Major septa are withdrawn from the corallite axis, leaving a free axial area, invaded by the distinctly elongated counter septum. Cardinal septum strongly shortened. Minor septa are absent. No tabulae are visible except for one in right alar fossula. Like in previous cross section (Fig. 6A3) septa are wedge-like thickened in external wall, which is 1.9 mm thick.

Discussion: Actinophrentis columnare Fedorowski, 1987 is of similar size with n:d ratios ranging from 20:8 in the holotype to 24:10 in the largest paratype. However, in contrast, it has a remarkable thick counter septum at maturity forming a weak columella in the calice. In the studied species the counter septum thins with maturity and/or has the same thickness as the other major septa or is only slightly thicker. Its wall is conspicuously thicker than the wall of the *A. columnare*. The current species differs from the smaller Actinophrentis bonespringense Fedorowski, 1987 in the wall thickness and n:d ratios. The Actinophrentis sp. (Fedorowski, 2004), previously named Zaphrentites paralleloides de Groot, 1963 differs in the radial arrangement of the major septa that extends from Page 11 of 39 32

the earliest growth stages up to the calice, vs. the pinnate arrangement in the current species. Diameter and the number of septa in the Spanish species are much smaller. In addition, the type species of the genus, *A. donetziana* Fomichev, 1953 appears to be smaller with a higher number of septa (n:d=23:8.5); its wall is conspicuously thinner (based on fig. 203, 7a, b in Hill, 1981).

Genus Lytvolasma Soshkina, 1925.

Type species: *Lytvolasma asymetrica* Soshkina, 1925 [sic!].

Diagnosis: Non dissepimented small solitary corals; cardinal fossula deep, key-hole shaped, often bordered by half aulos in counter quadrants; cardinal septum shortened late in ontogeny; counter septum slightly elongated; major septa semi-radial in arrangement; minor septa very short; microstructure of septa trabecular (Fedorowski, 1987a).

Remarks: Lytvolasma is a complex genus with unclear relations to several other taxa, as extensively discussed by Fedorowski (1987a). He modified the diagnosis by Hill (1981) who questioned the validity of Lytvolasma and considered it as a possible junior synonym of Bradyphyllum Grabau, 1928. However, due to morphological differences Fedorowski (1987a) considered both genera as valid and did not include the presence of long, slightly curved, thickened septa that are laterally contiguous over much of their length and almost reach the axis from Hill's diagnosis. However, opposed to Fedorowksi, these characteristics were confirmed by Chwieduk (2013, tab. 3). According to Fedorowski (1987a), intimate relations of the genus exist with further Antiphyllinae, as Lytvolasma specimens were attributed by authors in part to Actinophrentis Ivanovski, 1967, as well as to species of Allotropiophyllum Grabau, 1928 and Bradyphyllum. In addition, the type species of the hapsiphyllinid Parasterophrentis, P. virgata Fomichev, 1953 has to be transferred to Lytvolasma.

Opposed, *Lytvolasma* (?) cf. *L. geinitzi* (Toula, 1875) described by Flügel (1973) from the Upper Permian of eastern Greenland was included in *Tachylasma rhizoides* Soshkina, 1925 by Fedorowski (1982). He also excluded *Lytvolasma* from Northeast China figured by Guo (1980), but opposed, Fedorowski and Bamber (2001) did not rule out the possibility that some of Guo's specimens might be included. *Lytvolasma* described from Tibet (Wang and Liu, 1982; Wu, 1975) and Xingjiang (Wang and Yu, 1986) were included in *Euryphyllum* (Fedorowski, 1982). Similarities to further genera were extensively discussed by Fedorowski (1987a). According to the author, *Lytvolasma* Soshkina, 1925 shows some similarities to *Allotropiophyllum* Grabau, 1928. It is distinguished from the

latter by the elongation of counter septum and the alar septa in the early growth stage, a slightly but permanently elongated counter septum at maturity, shortening of the cardinal septum late in ontogeny, and the calice floor deeper in the cardinal quadrants. Based on the holotype of the type species of Allotropiochisma Fedorowski, 1982, Allotropiochisma longiseptata (Flügel, 1973), this genus is sufficiently different from *Lytvolasma* in having a narrow cardinal fossula, lacking an elongated counter septum, "biform reduction" of minor septa, and biform peripheral-most tabularium. In addition, Euryphyllum Hill, 1938 is similar. In fact, Lytvolasma sp. No. 2 described from the Lower Permian of the Northern Urals (Dobrolyubova, 1936) and at least some specimens described as Lytvolasma by Wu (1975) and Lin (1983) from the Lower Permian of Tibet might belong to that genus, as well as some specimens described by Guo (1980) from Northeast China (Fedorowski and Bamber, 2001).

Geographic and stratigraphic range: Lytvolasma is a spatiotemporally widespread genus. It is known from the Bashkirian of the Donets Basin and the Southern Urals/ Bashkirian Mountains (Kossovaya, 1986), but was not listed from the Bashkirian of the Donets Basin by Fedorowski (2022). According to Fedorowski (1987a), it occurs there from Kasimovian to Gzhelian $(C_2^3 - C_3^3)$. The genus is known from the Kasimovian of Egypt (Kora and Mansour, 1991 and this paper) and Donets Basin, from the Pennsylvanian-Permian transition of the Glass Mountains, western Texas (Uddenites-bearing shale member of Gaptank Formation, Fedorowski, 1987a), from the upper Artinskian and lowermost Kungirian (lower Saranian) of the Central Urals (Kossovaya et al., 2001; Kossovaya, 2007, Fig. 6; Shoshkina, 1925), the Sakmarian of Spitsbergen (Chwieduk, 2013) and from the Wordian (Middle Guadalupian) of the Canadian Arctic Archipelago (Fedorowski and Bamber, 2001). The existence of Lytvolasma in Tibet (Wu, 1975) was rejected by Fedorowski (1987a), but Fang and Fan (1994; not seen) again reported a "Lytvolasma fauna" in SW Yunnan (Baoshan-Pengchong). To us, the presence of Lytvolasma in Tibet and the Baoshan Block, southwestern Yunnan, i.e., in terranes originally bordering the northern margin of Gondwana, remains unsure and needs revaluation.

Lytvolasma cf. *canadense* Fedorowski and Bamber, 2001.

(Fig. 6C1–C3, 12A).

cf. 2001 *Lytvolasma canadense* Fedorowski and Bamber.—Text-Fig. 8, pl. 3, Fig. 2, pl. 5, Fig. 5.

Material: Only one worn specimen (RAh 66) with calice rims and a large part of the corallite not preserved, collected from the basal shales of the lower member of the Aheimer Formation. Two transverse sections are available.

Description: External characters: The preserved mature part of the corallite is 17 mm long. It does not show any furrows or ridges on the outer wall except for very delicate growth lines. The calice is not preserved, and also the apex and a large part of the immature ontogenetic stages are not preserved.

Internal characters: Only two transverse sections in the mature part of the corallite are available for study. An ontogenetically earliest section (Fig. 6C1-C2) shows sub-radial arrangement of septa, with short cardinal septum and long counter septum with a rhopaloid axial end. The axial area is free of septa, only the swollen end of the counter septum invading the centre. A typical half aulos is developed in the counter quadrants. At this stage n:d is 26:10 mm. Minor septa are underdeveloped. Biform morphology is developed. The last ephebic stage (Fig. 6C3), more or less at the calice floor, shows all septa withdrawn from the axis and the axial area becomes large. Only the counter septum is still prominently longer, and the cardinal septum is slightly shorter than the others. The n:d ratio is 26:12.8 mm. Minor septa are rudimentary. Cardinal fossula is slightly triangular, but open adaxially.

Discussion: The current species closely resembles Bradyphyllum counterseptatum described by Fedorowski (1987a). It differs from it in the n:d ratio in the ephebic stage; the current species is larger in dimensions than the former species. It also differs in the length of the counter septum; which is longer and thicker in the currently described species than the former. Lytvolasma canadense is distinguished from all other Lytvolasma species by its greater dimensions (Fig. 12A), the stronger elongation of its counter septum and in the underdevelopment of its minor septa. The shortening of the last major septa in all quadrants is not expressed herein. However, in the n:d ratio (Fig. 12A) and further morphological aspects our specimen seems to be identical to L. canadense (see Fedorowski and Bamber, 2001, Fig. 8c, d) from the Guadalupian (Wordian) of Ellesmere Island (Sverdrup Basin, Canadian Arctic). Due to the fragmentary nature of our single Egyptian specimen and considerable geographic and stratigraphic differences we did not include it into the nominate species and retained determination as "cf".

Lytvolasma aheimerensis n. sp. (Fig. 7A–I).

Derivation of the name: From the bearing rock unit "Aheimer Formation".

Holotype: Specimen RAh 2, illustrated in Fig. 7A–I. Eight transverse thin-sections are available.



Fig. 7 Lytvolasma aheimerensis n. sp. **A** External view of the specimen RA (2), showing a straight corallite with partly eroded calice and non-preserved apical part, positions of thin-sections indicated. **B–D** Successive transverse thin-sections in the early preserved growth stages, shows very thick major septa joining together near the centre. The cardinal septum is deformed in **D. E–G** Successive thin-sections in the early mature stages show the formation of a stereozone with a free axial area, shortening of the cardinal septum with maturity and the longest counter septum with a rhopaloid end. **H–I** Two transverse thin-sections below the calice, deformed due to rejuvenation in **H** and lateral compaction in **I**. Scale bars: 2.5 mm, except **A**: 5 mm. Black dots indicate the positions of cardinal septum (below), counter septum (above) and the two alar septa

Material: In addition to the holotype, two moderately preserved paratypes with compressed to crushed calices and eroded apical ends (RAh 10 and RAh 113). Five transverse thin-sections are available. They are collected from the basal shales of the lower member of the Aheimer Formation.

Type locality: Eastern cliffs of the Northern Galala plateau (Lat. 29° 28′ 21″ N and Long. 32° 27′ 38″ E), northern Eastern Desert, western side of the Gulf of Suez, Egypt. **Type horizon:** Basal shales of the lower member of the Aheimer Formation; Upper Pennsylvanian (Kasimovian). **Diagnosis:** *Lytvolasma* with thick wall, up to 2 mm thick. Cardinal septum shortened from early maturity. Counter septum elongated up to late maturity without forming a columella. It enters the free axial area with its rhopaloid end.

Description: External characters: Solitary, small, conicocylindrical corallites. The preserved parts of the three corallites ranges in length between 2 and 3 cm. Moderately preserved; their apexes and much of their early neanic stages are missing. Calices are deep. Growth lines, rugae, septal ridges and furrows are well-developed on the outer wall of the corallites. Rejuvenation is not common, only constrictions are visible (Fig. 7A).

Internal characters: The ontogenetically earliest growth stage available has 23 septa in 5.9 mm (Fig. 7B, C). Major septa are radially arranged. They are very thick and joined together in the centre forming a strong axial structure. The cardinal septum is somewhat thinner and the fossular break is noticeable. Further in the ontogeny, at a diameter of 8.8-13.3 mm with 24-26 septa (Fig. 7D-H), the septa become thinner gradually with maturity, and are more radially arranged. They are united near the axis with their rhopaloid ends, forming a stereozone with a free axial area. A strange attitude of one of the lateral cardinal septa is shown in Fig. 7G-I. It started to diminish gradually with maturity. This led to the reduction of the number of septa below the calice (Fig. 7I) to 25 septa. This attitude might be attributed to the rejuvenation took place in this part of the corallite. The cardinal fossula is slightly triangular and open adaxially. Counter septum is the longest with swollen end, invading the free axial area (Fig. 7F), and irregular in shape. Alar fossulae are not developed. The most adult stage, below the calice and the calice itself are compacted and the septa are somewhat deformed, the stereozone gradually diminishes and the septa retreat a little from the centre (Fig. 7I), the cardinal septum becomes distinctively shorter than the other major septa, whereas the counter is still long with thick rhopaloid end. The wall is thick (0.9-2 mm) in all ontogenetic stages. Minor septa are absent. A white line in the midlines of the septa may indicate their original compound trabecular growth.

Discussion: The elongation of the counter septum makes this species similar to *Monophyllum* Fomichev, 1953. It can be differentiated from *Monophyllum* in the shape of the cardinal fossula and the lack of the incipient columella formation in the calice. The current species differs from *L. aucta* Fedorowski, 1987 from the Pennsylvanian–Permian transition of southern Texas in the following:

- Number of septa are higher and diameter (n:d ratio) is larger in the present species.
- The wall of the current species is remarkably thicker.
- Minor septa are short and restricted to the corallite wall in the latest mature stages of *L. aucta*, whereas they are absent in the current species even in the last ephebic stage near the calice floor.

The type species of the genus, *L. asymetrica* Soshkina, 1925 differs by the early appearance of free axial area in the holotype (Fedorowski, 1987a, with comparisons to further similar specimens from different taxa) and the appearance of minor septa (Chwieduk, 2013), though n:d ratios are similar. *L. aucta* illustrated in Kora and Mansour (1991) (=*L. paraaucta* n. sp.) has smaller dimensions and a lower n:d ratio than the present species.

Lytvolasma paraaucta n. sp.

(Fig. 8A1–A5, B1–B5, 12A).

1991 *Lytvolasma aucta* Fedorowski, 1987.- Kora and Mansour, figs. 2 c1, c2.

1991 *Bradyphyllum* cf. *bellicostatum* Grabau, 1928.- Kora and Mansour, figs. 2 b1, b2.

2001 Lytvolasma—Fedorowski and Bamber, p 48.

Derivation of the name: From the Greek "*para*" for resemblance to the species "*aucta*".

Holotype: Specimen RAh 54, illustrated in Fig. 8A1–A5. Four transverse thin-sections are available.

Material: In addition to the holotype, four moderately preserved corallites with compressed calices and occasionally preserved apical part (RAh 19, RAh 74 and RAh 81); collected from the basal shales of the lower member of the Aheimer Formation. Eight transverse thin-sections are available. They are collected from the basal shales of the lower member of the Aheimer Formation.

Type locality: Eastern cliffs of the Northern Galala plateau (Lat. 29° 28' 21'' N and Long. 32° 27' 38'' E), northern Eastern Desert, western side of the Gulf of Suez, Egypt.

Type horizon: Basal shales of the lower member of the Aheimer Formation; Upper Pennsylvanian (Kasimovian). **Diagnosis:** *Lytvolasma* having maximum n:d ratio 26:11.5. Major septa frequently thickened in all quadrants to make a stereocolumn that opens in the cardinal quadrants, that changes to half aulos in the counter quadrants with maturity. Cardinal septum is short within the fossula.

Description: External characters: Corallites are small, up to 3 cm long. The external wall is ornamented by septal furrows and fine concentric growth lines in the holotype specimen (Fig. 8A1), in other paratypes the corallites are enclosed in mud and do not show any septal furrows (Fig. 8B1). Calices either eroded or crushed and compressed (Fig. 8A1). Two of the specimens with their apexes preserved. Two shallow constrictions are visible



Fig. 8 A Lytvolasma paraaucta n. sp. A1 Lateral external view of the holotype specimen (RAh 54). Note that, calice is compressed due to compaction. A2 Transverse thin-section in the immature part, showing major septa with irregular zaphrentoid arrangement. A3 Transverse thin section in the early mature part of the corallite, showing radially arranged major septa with rhopaloid ends. A4 Laterally compressed section in the calice base, showing a deformed fossula. A5 Transverse thin-section in the compressed calice, with calcareous mud filling. B1 Lateral external view of the paratype specimen (RAh 19). B2–B5 Successive transverse thin-sections from the immature part near the apex (B2) to the last mature part in the calice (B5)

below the calicinal part in the holotype specimen. Constrictions are also observed in the apical part.

The following description refers mostly to the holotype (RAh 54).

Internal characters: The ontogenetically earliest preserved part has 18 septa in 4 mm of corallite diameter (Fig. 8A2). At this stage major septa show irregular zaphrentoid arrangement. They are thick, among them only the cardinal is thinner, whereas the counter is thicker with rhopaloid ending. The cardinal fossula is noticeable with long cardinal septum that fuses with the other major septa making a dense stereocolumn in the centre, that opens in the cardinal quadrants. Minor septa are absent in this stage (see also Fig. 8B2). The subsequent section made at a diameter of 7 mm shows 23 septa which are radially arranged (Fig. 8A3). Their inner ends are rhopaloid and form a stereocolumn in the corallite centre. The cardinal fossula is slightly key-hole to subtriangular in shape and open adaxially (Fig. 8A3, B3–B4), with the cardinal septum thinner and slightly shortened.

The subsequent mature section is made beneath the calice floor (Fig. 8A4). The corallite in this part is laterally compressed and almost half of the septa are broken and deformed. At this stage of maturity, the deformed cardinal fossula is bordered by a half aulos in counter quadrants. Major septa are almost radially arranged and are 24 in number. Cardinal septum is short within the fossula. Minor septa are rudimentary. They appear as small triangular spikes along the relatively thin epitheca. The last section within the compressed calice (Fig. 8A4) is filled with mud and shows short major septa and underdeveloped minor septa. At a diameter of 11.5 mm of the paratype specimen (RAh 19), more or less at the base of the calice (Fig. 8B5) the septal ends are free leaving a free axial area with a short cardinal septum and a relatively longer counter septum than the adjacent septa. The counter septum, always a little longer and/or slightly thicker than other major septa, a character clearly evident in the paratype specimen (Fig. 8B3-B5).

Discussion: *Lytvolasma paraaucta* n. sp. was illustrated by Kora and Mansour (1991; Fig. 2 c1, c2). Based on one transverse section in the mature part of the corallite and a longitudinal section, they assigned their specimen to *L. aucta* Fedorowski, 1987. Due to the lack of description and additional illustrations of younger ontogenetic stages Fedorowski and Bamber (2001) accepted this identification only at a generic level. We also include *Bradyphyllum* cf. *bellicostatum* Grabau, 1928 briefly described and figured by Kora and Mansour (1991, p. 599, Fig. 2 c1c2) in our new species. Additional transverse thin-sections from the youngest stages clearly confirm the difference of the Egyptian specimens from *L. aucta* by the following characters:

- *Lytvolasma paraaucta* n. sp. has higher n:d ratios than the holotype of *L. aucta* (Fig. 12A). Nevertheless, *L. aucta* paratypes can reach a higher n:d ratio up to 22:9.
- The septal ends in the Egyptian species are thickened in contiguity to form a stereocolumn that is open towards the cardinal fossula, whereas in *L. aucta*, the septal ends are free or form a half aulos only in the counter quadrants.

Lytvolasma paraaucta n. sp. differs from *L. canadense* Fedorowski and Bamber, 2001 from the Middle Permian

of the Canadian Arctic Archipelago, in having an unremarkable counter septum, which is elongated in *L. canadense* in the calice and below its bottom. It also slightly differs by its n:d ratio in the ephebic stage near the calice floor (24:12? vs. 26:12.6; Fig. 12A). The same case is for the Egyptian *Lytvolasma* cf. *canadense*.

In relation to *L. asymetrica* Soshkina, 1925, described from the Early Permian (Sakmarian) of Spitsbergen by Chwieduk (2013), the current new species has slightly similar n:d ratio in the mature stage below the calice (24:12? vs. 23–26:8–14 in *L. asymetrica;* Fig. 12A). However, in *L. asymetrica* the inner ends of major septa join to form a quite irregular, incomplete aulos that opens on the alar septum sides throughout most of ontogeny; whereas in the current species a stereocolumn is developed through most of its ontogeny and in the mature stage, the thickened inner ends of the septa form an aulos that opens on the cardinal side (Fig. 8A3, A4).

Genus Monophyllum Fomichev, 1953.

Type species: *Monophyllum sokolovi* Fomichev, 1953. *M. sokolovi* Fomichev, 1953; ? 1953 M. *parvum* Fomichev 1953; *M. cassum* Fedorowski, 1987.

Diagnosis: Non-dissepimented, small solitary corals, with major septa radially arranged, may withdraw a little from corallite axis in maturity; cardinal septum shortened from early maturity; counter septum permanently elongated to corallite axis; alar septa slightly elongated at least in some portion of growth; minor septa underdeveloped (after Fedorowski, 1987a, p. 67).

Remarks: In contrast to Hill (1956, 1981), de Groot (1963) and Weyer (1975) who listed *Monophyllum* Fomichev, 1953 as a synonym of *Rotiphyllum* Hudson, 1942, Fedorowski (1987a) considered it as a separate genus. This view was followed by Kossovaya (1996, 2001), Ogar (2012) and Wang et al. (2017). Fedorowski (1987a) mentioned the following differences to *Rotiphyllum* and further similar antiphyllinid genera (see also Table 1):

- *Monophyllum* differs from *Rotiphyllum* by: (1) the strongly and permanently elongated counter septum reaching the corallite axis, even on the calice floor, where it may form an incipient columella, (2) shortening of the cardinal septum not only on the calice wall as in *Rotiphyllum*, but also on the calice floor, (3) the triangular shape of at least peripheral parts of the cardinal fossula at maturity.
- *Monophyllum* differs from *Bradyphyllum* by the permanently elongated counter septum that reaches the corallite axis and tends to form an incipient columella. Although *Monophyllum* develops a tendency



Fig. 9 A Monophyllum galalaensis n. sp. (Holotype specimen, Rah 9). A1 Lateral external view of the corallite, positions of thin-sections indicated in A1. A2 A calice view of the paratype specimen (RAh 41), with eroded rim, shows an elongated counter septum that form a columella (arrow). A3–A5 Successive transverse thin-sections of the neanic stage, showing the pseudo-radial to pinnate arrangement of major septa, a long thin ended cardinal septum, and a longer counter septum with a swollen end in a dense stereocolumn. A6–7 Two successive mature sections, showing a short cardinal septum. A8^{1, 2} Transverse thin-section in the late mature stage below the calice, showing radially arranged major septa that retreat a little leaving a narrow free axial area occupied by the elongated part of the counter septum. Note, A8² is a redrawing of section A8¹. Paratype specimen (RAh 13). External alar view of the corallite, positions of thin-sections are indicated in white lines. B2 Nepionic stage. B3 Early neanic stage. B4–5 Two partly compressed successive mature sections (ephebic stage), show a distinctly long counter septum. B6 Last mature section—more or less in the calice—showing a detached columella that is separated from the long counter septum. Black dots indicate the positions of cardinal septum (below), counter septum (above) and the two alar septa

to form an axial area free of septa, like most of the genera included in Antiphyllinae (Illina, 1970), its counter septum remains elongated, which is not the case in *Bradyphyllum*.

• *Monophyllum* differs from *Actinophrentis* Fomichev, 1953 by (1) the radial arrangement of septa in the mature portions of *Monophyllum* vs. the pinnate arrangement of the major septa lasting up to the calice floor in *Actinophrentis* and (2) the lacking tendency of *Actinophrentis* to form a free axial area.

Species described by Fomichev (1953) to be "*Stereo-lasma*" might belong to *Rotiphyllum* (in toto, see Hill, 1956; de Groot, 1963), to *Monophyllum* and/or other Antiphyllinidae (Fedorowski, 1987a, p. 36, 68).

Geographic and stratigraphic range: Monophyllum is a long ranging but relatively rare genus. It is known from the Bashkirian of the Donets Basin (Fomichev, 1953; Kossovaya, 1986, Fig. 7; Fedorowski, 2022, Fig. 2: M. sokolovi Fomichev, 1953, M. parvum Fomichev, 1953), the Moscovian of the same region (Fomichev, 1953: original designation of the type species *M. sokolovi*; Kossovaya, 1986, Fig. 7; Ogar, 2012) and the Moscovian of Novaya Zemlya (fide Fedorowski, 1981 and Wang et al., 2022). It is also known from the Pennsylvanian-Permian transition and the Wolfcampian (Asselian-middle Artinskian) of southwest Texas (Fedorowski, 1987a: M. cassum Fedorowski, 1987). Kossovaya et al., (2001, Fig. 6) figured ?Monophyllum sp. from the late Artinskian of the Urals and/or northern Timan Ridge (not further specified). Herein, we report the genus from the Kasimovian west of the Gulf of Suez, Egypt.

Monophyllum galalaensis n. sp.

(Fig. 9A1–A8², B1–B6, 12B).

Derivation of the name: From the type locality (eastern cliffs of the Northern Galala Plateau).

Holotype: Specimen RAh 9; collected from the basal shales of the lower member of the Aheimer Formation and illustrated in Fig. 9A1–A8². Six transverse thin-sections are available.

Material: Paratypes are represented by five partly preserved corallites (RAh 13, RAh 41, RAh 52, RAh 80 and RAh 92); collected from the lower shales of the Aheimer Formation. The internal structures of these corallites are diagenetically altered. Eighteen transverse thin-sections are available, four of them belonging to RAh (13) are extremely altered by diagenesis and thus excluded from illustrations.

Type locality: Eastern cliffs of the Northern Galala plateau (Lat. 29° 28′ 01″ N and Long. 32° 27′ 38″ E),

northern Eastern Desert, western side of the Gulf of Suez, Egypt.

Type horizon: Basal shales of the lower member of the Aheimer Formation; Upper Pennsylvanian (Kasimovian). **Diagnosis:** *Monophyllum* having maximum n:d ratio 24:11. Major septa meet in the corallite axis forming a stereocolumn; they retreat near the calice floor, forming a small free axial area occupied only by the incipient columella resulting from the elongated counter septum. Cardinal septum moderately shortened from early maturity.

Description: External characters: Corallites are ceratoid, about 2.2–3 cm long. Calyx and apex are not preserved in the holotype (Fig. 9A1) but preserved in most of the paratype specimens (Fig. 9B1). When preserved, calyx is deep and laterally compressed. A remarkably long counter septum that forms an incipient columella with its end can be detected on its floor (Fig. 9A2). Delicate growth lines and distinct septal furrows are visible in the good preserved external wall (Fig. 9A1–A2).

Internal characters: The young stages of ontogeny are described from the paratype specimen (Fig. 9B2–B3), where the apical part is well-preserved. In the earliest ontogenetically preserved section (nepionic stage) of the paratype RAh (13) only 3 protosepta can be traced in about 1 mm diameter (Fig. 9B2). The subsequent section records the early neanic stage (Fig. 9B3), where there are 14 major septa in 2.5 mm diameter, all meet near the corallite axis with their thick inner ends. The subsequent neanic growth stages of the paratype have n:d of 19–22: 5–6.7 mm. These sections are not suitable for illustration as stated before.

The two earliest preserved ontogenetic sections of the holotype have 21-22 septa in 6-6.5 mm diameter (Fig. 9A3–A4). In this stage major septa are thick, except for the cardinal septum. The counter septum is slightly thicker than the others and is longer. Septa are pinnately to sub-radial arranged and meet in the centre to form a stereocolumn. Minor septa are mostly missing. In the successively youngest sections (Fig. 9A5–7, B4), major septa count 23-24 in 8-10.5 mm diameter. They are joined with their thickened axial ends to form a dense axial column, with a narrower free axial area. The counter septum is the longest and exceeds all the majors in the axial stereocolumn with a rhopaloid thickened end. Cardinal septum thins towards the axis (Fig. 9A5), immediately becoming short, situated within a triangular, adaxial open cardinal fossula, which is located on the concave side of the corallite (Fig. 9A6-7). Alar fossulae are not visible. In the last mature sections, below the calice floor (Fig. 9A8^{1, 2}, B5), and within the calice (Fig. 9B6), major septa are a little withdrawn from the axis and a narrow free axial area is developed that disappears in the lower, less mature sections. They are radially arranged. Minor

septa are underdeveloped and form small triangular spikes at the inner wall. However, the long rhopaloid counter septum, incipient columella, and the short cardinal septum in the triangular fossula are still developed. The arrangement of the major septa changes from radial to pseudo-radial and then pinnate when going down towards the successively older parts of the corallite.

Discussion: The species discussed differs from the Upper Moscovian type species *Monophyllum sokolovi* Fomichev, 1953 in the strong elongation of the counter septum up to the calice floor, forming an incipient columella. *Monophyllum parvum* Fomichev, 1953 differs in its smaller n:d ratio (Fig. 12B). The current species differs from *M. cassum* Fedorowski, 1987 by its larger n:d ratio (24:11.5 vs. 22:9.3). In addition, *M. cassum* shows withdrawing of major septa from the corallite axis already in the late neanic/early ephebic stage, while this happens in the late ephebic stage near or at the calice floor in the Egyptian species. The formation of a stereocolumn is missing in *M. cassum*.

Genus *Rotiphyllum* Hudson, 1942.

Type species: *Densiphyllum rushianum* Vaughan, 1908; Upper Viséan of Ireland.

Diagnosis: Antiphylline coral with major septa meeting near corallite axis. Cardinal septum reaching corallite axis along cardinal fossula in all growth stages, shortened on calice wall but long on floor; counter septum commonly thicker and slightly longer than adjacent major septa; major septa evenly spaced, with extra thickening in inner third of their length, forming a dense axial structure; minor septa short; tabularium normal, sometimes weakly biform in some septal loculi. (Fedorowski, 2004, slightly modified by Fedorowski, 2009a).

Remarks: Generic relations of Rotiphyllum were widely discussed by authors, among them Weyer (1975, 1977), Fedorowski (1987a), and Wang (1994) who supported Fedorowski's concept of the genus. Fedorowksi (1987a) especially discussed the relation to Bradyphyllum and stressed the difference of Rotiphyllum by its long cardinal septum along the fossula floor, though, later, Fedorowski (2004) stated the very close relationship of both genera. The synonymy of Actinophrentis, unambiguously synonymised by Weyer (1975) and also supposed by Hill (1981) was rejected by Fedorowski (1987a; see above under Actinophrentis), who also rejected the conclusion of de Groot (1963), Weyer (1975), and Hill (1981) that Monophyllum Fomichev, 1953 would be a junior synonym of Rotiphyllum Hudson, 1942 (see above under Monophyllum), (Table 1). Finally, Fedorowski (1989; updated in Fedorowski, 2009a) gave an extensive review on the synonymy, the included species and the relations of the genus. According to the extended number of species attributed by him, the very long stratigraphical range from the Tournaisian throughout the Lower Permian and even the middle Permian in Japan (fide Wang et al., 2017)—and geographical distribution from the British Isles and the westernmost Palaeotethys (northern Spain) to northeastern China and the peri-Gondwana terranes from Tibet to Yunnan (judged from Fedorowski's synonymy list and complemented by Wang et al., 2017), *Rotiphyllum* might be a waste basket of morphotypes belonging to different taxa. It appears to be absent from the Cordilleran–Arctic–Uralian realm (Wang et al., 2017).

Rotiphyllum exile de Groot 1963

(Fig. 10A1–A4, B1–B4, C1–C2, D1–D2, 12C).

1963 Rotiphyllum exile de Groot, p. 8, Text-fig. 1, Pl. 1, figs. 1–2.

1963 *Rotiphyllum equabilae* de Groot, p. 9, Text-figs. 2–3, Pl. 1, Figs. 3–4.

? 1984b *Rotiphyllum exile*: Rodríguez, p. 122, Text-figs. 33–34, Pl. 1, figs. 1–2.

1991 *Rotiphyllum equabilae* de Groot.—Kora and Mansour, Fig. 2d.

1991 *Rotiphyllum exile* de Groot.- Kora and Mansour, Fig. 2g.

1999 *Rotiphyllum exile*: Rodríguezand Kullmann, p. 80, Text-figs. 37–40, Pl. 8, Figs. 1–12.

2004 *Rotiphyllum exile* de Groot.- Fedorowski, p. 80–82, Pl. 1, Figs. 2–4; Pl. 4, Figs. 1–4.

Material: Ten corallites; RAh 21, RAh 26, RAh 29, RAh 46, RAh 56, RAh 69, RAh 116 and RAh 117, collected from the basal shales of the lower member of the Aheimer Formation. Twenty-one transverse thin-sections are available.

Description: External characters: Small, straight conical to slightly curved corallites. The preserved parts of the corallites range in length between about 1.5 cm and 2.5 cm. Fairly good preserved specimens, with either eroded or compressed and crushed calices. Calices are very deep (up to 10 mm). Apexes are eroded. Septal furrows are developed on the external wall of the corallites (Fig. 10A1, B1).

Internal characters: *Rotiphyllum* with maximum n:d value below the calice 27:9 mm (Fig. 10B4, 12C). Counter septum is slightly thicker and longer than counterlateral septa. Cardinal septum is long up to late maturity, thinning with maturity (Fig. 10C2). Inner margins of major septa join at the axis to form a stereocolumn. In few cases a small axial tube is developed in mature stages (Fig. 10B3–B4). In addition, the majors of one of the specimens (Fig. 10A3–A4) do not form a dense



Fig. 10 Rotiphyllum exile de Groot, 1963. A1 External lateral view of the corallite RAh (116), showing a slightly curved corallite with a calice largely preserved but compressed. Positions of thin-sections indicated. A2 Transverse thin section at the immature part of the corallite, showing a stereocolumn in the centre. A3–A4 Two successive transverse thin-sections at the early and latest mature stages, showing a long cardinal septum with thin axial end (diagenetically broken in A4). B1 External lateral view of the corallite RAh (117), with partly eroded calice. B2–B4 Successive transverse thin-sections marked in B1, showing the radial to sub-radial arrangement of major septa, the central stereocolumn and the long cardinal septum with a thin axial end. C1–C2 Two successive transverse thin-sections in the mature part of the corallite RAh (21). D1 Transverse thin-section in the immature part of the specimen RAh (46) showing a zaphrentoid arrangement of major septa. D2 Transverse thin-section in the mature part of the corallite, showing a deformed long cardinal septum in a triangular fossula. Black dots indicate the positions of cardinal septum (below), counter septum (above) and the two alar septa

stereocolumn in mature stages like in the other individuals of this species. This is due to the irregular manner of the last major septa in quadrants and the formation of the alar fossulae. Major septa are radially arranged in adult stage and pinnately arranged in early ontogenetic stages (Fig. 10D1). In some specimens, major septa preserve a white middle line. Minor septa are rudimentary developed mostly in late mature stages, below the calice (Fig. 10A4, B4, C2). Tabulae are common and form at least one incomplete concentric circle around central stereocolumn (Fig. 10A3–A4, B3–B4, C1–2). The cardinal fossula is rectangular to slightly triangular in shape and narrows adaxially. The alar fossulae are occasionally wellmarked by the thin and irregular last major septa in the counter quadrants (Fig. 10A3–A4, B4). The thin to moderately thick wall is formed or at least enforced by the peripheral thickened septa.

Discussion: In their morphology the Egyptian specimens are almost identical to the species described from the type region in the Cantabrian Mountains, northern Spain (de Groot, 1963; Rodríguez and Kullmann, 1999). Tabulae appear to be less and slightly more irregularly developed, although similar transverse sections were figured by Rodríguez and Kullmann (1999, text-Fig. 37 c1–c2, d). This might be related to the less mature position of our transverse sections (compare Figs. 10A1 and 12A2), and is not sufficient for specific differentiation. Concerning n:d ratio, our specimens (Fig. 12C) plot into the upper range of the individuals of Rodríguez and Kullmann (1999, text. Fig. 40). The white middle line seen in the major septa of some specimens might correspond to the relict of the trabecular microstructure described by Fedorowski (2004).

Geographic and stratigraphic range: *Rotiphyllum exile* de Groot, 1963 was described from the Westphalian D (Asturian, upper Moscovian) of the Cantabrian Mountains (see Rodríguez et al., 2022 and references in the synonymies listed herein). According to Fedorowski (2004), its occurrence in the Westphalian C of the Escalada Formation (Rodríguez, 1984b; Podolskian according to Rodríguez, 1985) is questionable. The species was previously reported from the western side of the Gulf of Suez by Kora and Mansour (1991).

Family Hapsiphyllidae Grabau, 1928. Subfamily **Hapsiphyllinae** Grabau, 1928. Genus **Zaphrentites** Hudson, 1941.

Type-species: Zaphrentis parallela Carruthers, 1910. Diagnosis: Small, conical to slightly curved with wellmarked longitudinal ribbing. Cardinal fossula is on the concave side. In early growth stages it is closed and expands adaxially, and major septa are pinnately arranged. In late growth stages cardinal septum is shortened and septa are withdrawn from the fossula, first in cardinal quadrants, then in counter quadrants and thus a radial arrangement of the septa supersedes pinnate arrangement. Minor septa are very short or immersed in the wall. Tabulae are incomplete (after Hill, 1981; p. F316).

Remarks: Hill (1981) included *Zaphrentites* into Hapsiphyllidae, but Fedorowski (2012b) insisted on the validity of the family Stereophrentidae Fomichev, 1953 according to IRZN, although the genus *Stereophrentis* is not valid, as it is an objective younger synonym of *Zaphrentites*. Herein, we did not follow this proposal. *Zaphrentites* shares its simple morphology with many zaphrentoid-like taxa. The position of the cardinal fossula on the concave side of the corallite distinguishes it from the other zaphrentoid corals, where it is located on the convex side. It differs from *Amplexizaphrentis* Vaughan, 1906 by its smaller dimensions, missing minor septa and major septa never withdrawn from the axis. Similarities to *Rotiphyllum* Hudson, 1942 are evident and Fedorowski (2009a) moved several species described under "*Zaphrentis*" and *Zaphentites* to the first genus. The main distinctive feature of *Zaphrentites* is the morphology of the axial stereocolumn. Fedorowski (2012b) also moved several species from *Zaphrentites* to *Zaphrufimia* Fedorowski, 2012, based on the septal development.

Geographic and stratigraphic range: Zaphrentites is a common genus through the Mississippian (Tournaisian-Viséan-Serpukhovian) of the Palaeotethys and adjoining epicontinental seas from Northwest Europe to East Asia (Denayer and Hoşgör, 2014, cum lit.; Rodríguez et al., 2016; Wang et al., 2022). It is also known from the Mississippian of the conterminous USA (fide Wang et al., 2022). From the Sinai Peninsula, Egypt, it was previously reported from the late Viséan Um Bogma Formation (Kora and Jux, 1986). Zaphrentites is rare in the Pennsylvanian, reported to our knowledge only from northern Spain ("Westphalian D"=Asturian, late Moscovian, de Groot, 1963; Rodríguez and Kullmann, 1990; Kullmann and Rodríguez, 1994 and Rodríguez et al., 2022), but both species known (Z. clithria de Groot, 1963, Z. paralleloides de Groot, 1963) were moved to Rotiphyllum paralloides (de Groot, 1963) by Fedorowski (2004). Rodríguez et al., (2022, tab. 1) listed Zaphrentites also from the late Moscovian (Asturian) of North America (Ellesmere Island, Arctic Canada-not supported by our literature review) and from the Uralian-Arctic realm). Herein, we describe Zaphrentites from the Kasimovian West of the Gulf of Suez, Egypt. The genus was also described from the Lower and Middle Permian of China (fide Wang et al., 2017).

Zaphrentites cf. parallela (Carruthers, 1910).

(Fig. 11A1–A3, B1–B4, 12D).

cf. 1910 Zaphrentis parallela Carruthers.- p. 533, Pl. 37, Fig. 4.

cf. 2014 *Zaphrentites parallela* (Carruthers).- Denayer and Hoşgör, p. 350, Fig. 4: 6a–d, 14 (cum syn.).

Material: Three corallites (RAh 109, RAh 111 and RAh 118); collected from the basal shales of the lower member of the Aheimer Formation. Nine transverse thin-sections are available.



Fig. 11 A, B Zaphrentites cf. parallela (Carruthers, 1910). A1–A3 Successive transverse sections in the specimen RAh (118), starting from the early immature stage with zaphrentoid arrangement of the septa in A1 to the last mature stage below the calice in A3. B1 External lateral view of the specimen RAh (109), showing strong longitudinal ribbing on the corallite wall. Positions of thin-sections indicated. B2–B4 Successive transverse sections represent the ontogenetic development, starting from the immature section in the apical part in B2 to the last mature section below the calice floor in B4. C Zaphrentites sp. C1 External view of the specimen RAh (84). C2–C4 Successive transverse sections; from the immature section in C2 to the last mature section below the calice floor in C4. Black dots indicate the positions of cardinal septum (below), counter septum (above) and the two alar septa



Fig. 12 Relation between number of major septa and coralla alar diameters for: A *Lytvolasma paraaucta* n. sp., *L aucta* Fedorowski, 1987, *L. asymetrica* Soshkina, 1925 described by Chwieduk (2013), *L. canadense* Fedorowski and Bamber, 2001 and the current studied *L. cf. canadense* Fedorowski and Bamber, 2001. B *Monophyllum galalaensis* n. sp. and *M. parvum* Fomichev, 1953. C *Rotiphyllum exile* de Groot, 1963. D *Zaphrentites* cf. *parallela* (Carruthers, 1910) and *Zaphrentites* sp

Description: External characters: Straight, conical corallites, about 1.5 cm long, slightly curved in the immature stage. Calyx is largely eroded, apex not preserved. Septal furrows and delicate growth lines are distinctly marked on the external wall (Fig. 11B1). An attachment scar is visible in one corallite near the apical part.

Internal characters: In the earliest ontogenetic preserved stage (Fig. 11A1), septa are very thick, reaching the corallite axis. There are 16 septa at a corallite diameter of about 3 mm; of them the counter septum is the thickest. At diameter of 3.7 mm (Fig. 11B2), major septa are still thick, they join in the centre forming a thick stereocolumn; a parallel sided cardinal fossula can be recognised. In the subsequent early mature growth stage at a diameter of 5 mm, there are 20 major septa (Fig. 11A2). Minor septa are absent. The axial ends of major septa join to form an axial stereocolumn slightly staggered towards the counter quadrants. Septa of the counter quadrants are radially arranged, the counter septum is slightly thicker and has the same length as the adjacent septa. Those in the cardinal quadrants are grouped pinnately around a long parallel sided cardinal fossula. The thin cardinal septum is straight, long and reaches beyond the corallite axis to join the stereocolumn at the upper end of the cardinal fossula in the counter quadrants. It further thins towards the axis. Further mature, at a diameter of 6.5 mm, there are 21 septa (Fig. 11B3); the cardinal septum becomes slightly shorter.

The uppermost mature transverse section near the calice floor (Fig. 11A3, B4) is slightly deformed due to compaction and some of the septa are broken. In this stage there are maximum 26 septa in 8.6 mm (Fig. 11B4). Axial ends of the major septa in cardinal quadrants are bent to sides with the two pericardinal septa, curved most distinctly. Such septal morphology makes the cardinal fossula opens towards the free axial area. The cardinal fossula is slightly deformed. The cardinal septum is short, and the counter is slightly longer and thicker than the adjacent septa. All major septa are thick at the base, join at their rhopaloid ends around the well-developed cardinal fossula, which invades the counterpart, being longer than the radius of the corallite. Pseudoalar fossulae are not markedly developed. Minor septa are absent from the corallite lumen, they are visible in the stereoplasm of the wall.

Discussion: According to the septal arrangement and the axial stereocolumn, the current species clearly belongs to the genus *Zaphrentites*. It is closely similar to *Z. parallela* (Carruthers, 1910) in the septal arrangement and more or less in the shape of the cardinal fossula, with the cardinal septum withdrawn in late stages. However, our specimens reach larger n:d ratios (Fig. 12D) in the last mature stage near the calice (26:8.6 vs. 20:5.6). *Z. delanouei* (Milne-Edwards and Haime, 1851) and *Z. crassus* Hudson, 1944 are both larger and have more septa than the herein described species. It is quite similar to *Z. parallela* of Denayer and Hoşgör (2014) from the Lower Carboniferous of Turkey. It differs in the n:d ratio of the last mature stage (21:8.5) and in general counts more septa at the same diameter.

Zaphrentites sp.

(Fig. 11C1–C4).

Material: One corallite (RAh 84), collected from the basal shales of the lower member of the Aheimer Formation. Three transverse thin-sections are available.

Description: External characters: Straight, conical, small (about 1.5 cm long) corallite. Calice is very deep, partly eroded. Septal furrows are marked on the external wall (Fig. 11C1).

Internal characters: Near the apex, in the earliest ontogenetic preserved stage, at diameter of 4 mm septa are 16 (Fig. 11C2). Major septa are sub-radial to pinnately arranged. They show a distinct white middle line. The cardinal fossula is well-developed with parallel sides and long, thin cardinal septum. Later with maturity, at a diameter of 6.4 mm there are 20 major septa (Fig. 11C3). These are radially arranged in the counter quadrants, curve towards the counter septum, and join to form a stereocolumn. The cardinal fossula has parallel sides with somewhat short cardinal septum. Alar fossulae are not developed. The uppermost mature section below calice floor (Fig. 11C4), displays 23 septa in 7.2 mm diameter. Septa are altered, and their ends are free, leaving a narrow free axial area. Cardinal septum is short. Minor septa are absent.

Discussion: Zaphrentites sp. and Zaphrentites cf. parallela (Carruthers, 1910) show almost no differences in the morphology of the earlier growth stages. Nevertheless, the studied Zaphrentites sp. shows n:d ratio in the last mature stage near the calice smaller than that of the Zaphrentites cf. parallela (Carruthers, 1910); (23: 7.2 vs. 26: 8.6; Fig. 12).

Suborder **Plerophyllina** Sokolov, 1960. Family **Plerophyllidae** Koker, 1924. Subfamily **Plerophyllinae** Koker, 1924. Genus *Ufimia* Stuckenberg, 1895.

Type-species: Ufimia carbonaria Stuckenberg, 1895.

Diagnosis: Small solitary corals with zaphrentoid early stages. Alar and counter lateral septa dominating in late stages becoming longer, taller, thicker, and more rhopaloid. Rhopaloid axial ends of major septa commonly conjunct in axial region in middle stages of development, withdrawing and becoming free axially in late stages. Longest and strongest metasepta are commonly midquadrant. Cardinal and counter protosepta shorten progressively. Minor septa rudimentary to short. Tabular floors tall and axially depressed; dissepiments missing. Septa trabecular, uniseriate (after Hill, 1981 and Fedorowski, 2004).

Remarks: Schindewolf (1942) discussed the genus and gave earlier synonymies. Like following authors (e.g., de Groot, 1963; Kullmann, 1965, 1968), he considered Ufimia as subgenus of Plerophyllum Hinde, 1890, only differing by the shortened cardinal septum in adult stages. Fedorowski (1973), like in the original designation of Stuckenberg (1895), as well as Hill (1956, 1981) and later authors again considered Ufimia as valid on the genus level. Rhopalolasma Hudson, 1936 like the most probably misspelled *Rhopalelasma* Lang et al., 1940, as well as ?Plerophyllum (Meniscophylloides) Kullmann, 1966, are younger synonyms of Ufimia (e.g., Hill, 1981; Fedorowski and Bamber, 2001). The strong similarity of the genus with Tachylasma Grabau, 1922 was stressed by Rodríguez (1984b). In the adult stage, the genera are virtually not distinguishable, but in juvenile stages, the septa in Tachylasma are not conjunct axially. Moreover, though in cases difficult to see, Ufimia has zaphrentoid septal development in earlier ontogenetic stages, opposed to the pentaphyllid development in Tachylasma (see discussion in Fedorowski and Bamber, 2001).



Fig. 13 A Ufimia sp. A1 External view of the specimen RAh (101), showing a straight conical corallite with eroded calice rim and apex. Positions of thin-sections indicated. A2–A3 Two successive transverse thin-sections in the mature part of the corallite show the thick, rhopaloid major septa meet in the corallite centre. Scale bars: A1: 5 mm; A2, A3: 2 mm. B Bothrophyllum okense Kossovaya, 2001. B1 External view of the partly preserved corallite (RAh 37), with partly eroded wall. Positions of thin-sections indicated. Successive transverse thin-sections from the lower less mature part in B2 up to the more mature section below the calice in B4, the transverse sections show the axial septum and a very narrow dissepimentarium. Scale bars: 5mm

The diagnosis of the *Ufimia* was slightly emended by inclusion of septal microstructure (Fedorowski, 2004).

Geographic and stratigraphic range: *Ufimia* is a complex, wide-spread genus—probably a group of intimately related, mostly homeomorphic genera, as indicated by stratigraphic gaps between occurrences. It is recorded from Lower Devonian (Upper Emsian) to Upper Permian strata throughout the Palaeotethys, adjoining epicontinental seas, and the Ural and Franklinian seaways (fide Hill, 1981, and Fedorowski and Bamber, 2001). It is absent from Canada south of the Arctic realm and the conterminous USA. (Wang et al., 2017, 2022). A detailed review is out of scope from the present paper, but we present the distribution patterns from the Pennsylvanian to the Permian. Flügel (1991) described a rich fauna

consisting of several species known from lower Carboniferous and the new species U. biforma Flügel, 1991 from Namurian (Serpukhovian-Bashkirian) strata of central-eastern Iran. From the westernmost Palaeotethys Ufimia was recorded from Asturian strata (=Westphalian D, Kasimovian) of the Cantabrian Mountains, northern Spain (de Groot, 1963; Fedorowski, 2004; Rodríguez, 1984b; Rodríguez and Kullmann, 1990; Rodríguez et al., 2022). The genus is known from the Middle and Upper Pennsylvanian of the Donets Basin (Fomichev, 1953). It is an important faunal element of the Upper Artinskian strata from the central to subpolar Urals; also the type species, Ufimia carbonaria Stuckenberg, 1895 is from the Late Artinskian of the Urals (Kossovaya et al., 2001; Kossovaya, 2007; see also Ilina, 1984 who redescribed the type species). In the Kungurian to Capitanian interval, Ufimia

was a common faunal element in South China and Indochina, but persisted into the latest Permian; in Inner Mongolia and North China block as well as in the peri-Gondwana terranes the genus also was widespread from the Asselian to Lopingian, appearing also in the Guadalupian of Japan (fide Wang et al., 2017); Fedorowski and Bamber (2001) described *Ufimia* from the Wordian (Middle Guadalupian) of the Sverdrup Basin (Canadian Arctic) and the Upper Permian of eastern Greenland, where it was first described by Flügel (1973: "*Cryptophyllum (Tachylasma?*) sp.?"). It is also known from the Kungurian (probably Guadalupian according to Wang et al., 2017) in Spitsbergen (Ezaki, 1997).

Ufimia sp.

(Fig. 13A1-A3).

Material: Two corallites (RAh 101 and RAh 114), with four transverse thin-sections; collected from the basal shales of lower member of the Aheimer Formation.

Description: External characters: Straight, conical corallites, the preserved part of both range in length from 1.5 to 2 cm. The calices are eroded, and the apical parts are not preserved. The external wall does not show any septal furrows (Fig. 13A1).

Internal characters: There are 20 major septa in a diameter of 5.5 mm (Fig. 13A2), they are all very thick, the longest of them reach the corallite axis with rhopaloid ends. The corallite lumen is filled with stereoplasm. Below the calice there are still 20 major septa in a diameter of 7 mm (Fig. 13A3). Major septa are thick, rhopaloid, withdrawn a little from the centre which is largely filled with stereoplasm. At this stage of maturity, the cardinal septum becomes shorter and thinner towards the centre within indistinct fossula in contrast to the other major septa. The counter septum also becomes shorter than the counter-laterals. The alar septa exceed the major septa in length and in thickness. Septa are strongly accelerated in number in counter quadrants. Tabulae are not observed in transverse sections. Minor septa are underdeveloped.

Discussion: *Ufimia alternans* from the upper Moscovian of Spain differs from the current species in the following:

- *Ufimia alternans* de Groot, 1963 is larger than the current species; The Spanish species reaches max. 24:13 mm vs. 20:7 mm in the Egyptian species.
- The biform tabularium of the Spanish species is not expressed in the current species.
- The Spanish species is characterised by the alternation of long and short major septa, a feature that is not found in the Egyptian *Ufimia*.

Suborder Caniniina Wang, 1950.

Family Bothrophyllidae Fomichev, 1953.

Genus Bothrophyllum Trautschold, 1879.

Type species: *Turbinolia conica* Fischer von Waldheim, 1837.

Diagnosis: see Kora et al. (2019).

Geographic and stratigraphic range: *Bothrophyllum* is known from the Viséan to the lower Permian, being typical of the Pennsylvanian (Chwieduk, 2013). It is recorded from the British Isles, Northern Spain, North Africa, Donets and Moscow basins, Ural Mountains, China, Australia, and North America.

Bothrophyllum okense Kossovaya, 2001

(Fig. 13B1–B4).

Material: One preserved corallite (RAh 37), collected from the basal shales of lower member of the Aheimer Formation. Three transverse thin-sections are available.

Description: External characters: The corallite is ca. 20 mm in length. Calyx and apical end parts of are largely eroded. The external wall is partly damaged, eroded and enclosed in fossiliferous mud (Fig. 13B1). The outer wall of the corallite in cross section is irregular.

Internal characters: The early preserved growth stage (Fig. 13B2), in a diameter of 14 mm there are 30 major septa. All major septa are long, some reach more than 2/3 of the corallite radius, leaving a small axial area which is filled with a diagenetically altered axial structure formed from the axial ends of the major septa and axial tabellae. Septa are strongly thickened in the tabularium, but thin in the very narrow dissepimentarium that consists of two rows of dissepiments. In the following higher section (Fig. 13B3) cardinal and counter septa are long and meet in the corallite center forming an axial septum that contributes with other septal axial ends in making a loose axial structure. At this stage, there are 31 septa for about 14 mm. In the higher mature thin-section near the eroded calice (Fig. 13B4), all septa are broken due to the compaction of the calicular part. There are about 34 septa in 13.5 mm compressed diameter. The counter septum is still long and reach the corallite centre, in contrast to the cardinal septum that seems to be shorten (Fig. 13B4). The axial structure that formed of the axial tabellae and inner ends of the longest major sept is still present. In a fairly good-preserved part of the corallite wall, a narrow dissepimentarium composed of 2 rows of simple concentric inter-septal dissepiments is present (Fig. 13B4). Cardinal fossula is poorly developed. Minor septa are very short, confined to the dissepimentarium in the mature section (Fig. 13B4), enter the tabularium as thick pegs.

Discussion: The specimen shows greatest similarity to *Bothrophyllum okense* Kossovaya, 2001 from the Moscovian of the Moscow Basin in Russia, despite the incomplete preservation and the diagenetic alteration of the skeleton of the current species. It was compared with the Egyptian slightly older bothrophyllids (Rod EL Hamal Formation) and with other Moscovian and Kasimovian *Bothrophyllum* spp. from the type region of the Moscow Basin have been discussed by Kora et al. (2019; Table 1).

Palaeoecological aspects

Taphonomy

Δ

The corals derived from the lower muddy part of the Aheimer Formation do not show any evidence of reworking. In part, they are recorded in upright life position (Fig. 3C), in part they are tumbled aside (Fig. 3D, E). Most suffered from a destructive physical alteration of their skeletons, such as crushing and flattening. All calices are laterally compressed (Fig. 3E). Subcalicular zones are more resistant than calices because of cementation

В

during diagenesis and the density of skeletal structures. This is obvious in the thin-sections prepared in the calicinal part, whereas the lower sections made in the cemented coral interiors are perfectly round. Compression began soon after burial due to the weight of overlying sediments. In some specimens, the interior skeletal elements of the corals are partly to completely dissolved or septa are completely broken. Recrystallization, dolomitization and ferrugination of open pore spaces inside the corals are the most common diagenetic features.

Palaeoecology

С

The association of the small, solitary mostly non-dissepimented rugose corals of the Aheimer Formation is analogous to the first gradational facies fauna of Hill (1938, 1981) that had been variably called a zaphrentid, *Cyathaxonia*, xyringaxonid, or polycoeliid fauna or

D



Fig. 14 Palaeoecology of the Aheimer rugose coral association. A–D External photographs of antiphyllid corals, showing constrictions and rejuvenations (arrows; axial rejuvenation in **B**; lateral rejuvenation in **C–D**); samples RAh 78, 85, 64, 89, respectively. **E**, **F** *Cladochonus* (?) encrusting the outer wall of the corallites RAh 95, 115 (arrows). **G** External view of the *Monophyllum galalaensis* n. sp. (RAh 80), showing a borehole in the lower part of the corallite RAh 60 (arrow). **H** External lateral view of an antiphyllid coral (RAh 106), showing an attachment scar at the apex (arrow). All scale bars: 5 mm

facies (Hill, 1981, cum lit.), or Lytvolasma fauna (Wu, 1975 [fide Wang et al., 2010]). Its members occurred in calcareous shales with thin-bedded argillaceous limestone/dolostone and crinoidal limestone/dolostone. In the scarcity of large dissepimented solitary and colonial corals, they are regarded as adapted to the muddier, darker, quieter, and, therefore, deeper parts of epicontinental seas or shelf sea floors (Hill, 1981), with water depth of 50-300 m and a poor water circulation (Wang et al., 2010). Though water depth is difficult to access, generally restricted living conditions, such as a high quantity of mostly fine-grained clastics, turbidity of water, in cases dysoxic and/or aphotic environments, or low temperature are postulated, thus characterising an ahermatypic fauna (Rodríguez, 2001; Rodríguez and Kullmann, 1999; Rodríguez et al., 1986; Sando, 1980; Wang et al., 2010; Webb, 1990). Cyathaxonia faunas are also typical elements of pelagic ammonoid limestones (e.g., Bandel, 1974; Kullmann, 1965, 1968, 1975; Weyer, 1981, 1984, 2016). Especially Permian Cyathaxonia faunas from peri-Gondwana terranes in China and elsewhere in Southeast Asia are evidently related to cool-or cold shallow-water environments (Wang et al., 2010, cum lit.; Wang et al., 2013), but also Artinskian cyathaxonids from the Polar Urals to the Central Urals were interpreted to be of cool to temperate-water origin (Kossovaya, 2007). Finally, it has to be stressed that the general assignment to deeper water was criticised by Fedorowski (1979), who noted cyathaxonid corals also in shallow water, an observation underpinned by cyathaxonid faunas from lower Westphalian and upper Westphalian D (upper Moscovian) shallow-water deposits in the Cantabrian Mountains, northern Spain (Kullmann and Rodríguez, 1986; Rodríguez and Kullmann, 1990) as well as from Moscovian high-energetic shallow-water deposits of the same region (Kullmann and Rodríguez, 1994; Rodríguez and Kullmann, 1999).

In summary, the "Cyathaxonia Fauna" in general has to be regarded as eurytopic and more detailed studies are necessary to interpret the depositional environment of specific occurrences.

Most specimens from the Aheimer Formation are straight conical in shape and/or slightly curved in their early mature stages. Thus, they were not secondary recliners that had adjust growth during ontogeny after tumbling of the corallites. Obviously, they were mudsticker with most of the corallites except the calicinal parts buried in the muddy sediment. This also might explain quite uncommon **rejuvenation** in a generally calm environment. Episodic instability, however, is proved in few cases by axial and lateral rejuvenations (Fig. 14A–D). **Encrustation** is scarce and only two specimens in the current association exhibit probable *Cladochonus* sp. encrusting the outer wall of the corallites (Fig. 14E, F).

Bioerosion (borings) is extremely rare; only one elliptical pore was found in the lower part of an antiphylline corallite (about 1.25 mm for longer diameter). The unhealed borehole occurs on the external wall of the corallite indicating that the coral was bored post-mortem by an unknown endobiont (Fig. 14G).

Attachment structures to the substrate during mature stages, such as roots or talons, are missing, but in well-preserved corallites slightly well-developed attachment scars can be detected in immature stages, i.e., in their apical part (Fig. 14H, I). They are located on the alar or lateral sides of the corallites. A long groove-like attachment scar on the apical part of one corallite (Fig. 14C) might have resulted from the attachment to a crinoidal stem or bryozoan.

The rarity of encrustation and bioerosion underlines the sheltered mud-sticking mode of life—both only took place post-mortem after reworking by episodic turbulence. Interestingly, Rodríguez (2001) noted that ceratoid to subcylindrical individuals of *Rotiphyllum exile*, which is also present in the Aheimer fauna, tolerated higher sedimentation rates and was mostly buried in the sediment. Finally, missing roots and talons indicate a liberosessile life (Neumann, 1988) for most of our fauna. In combination with the taphonomic observations described above—growth style, attachment structures, encrustation and bioerosion—the corals were mud-sticking organisms with corallites mostly embedded in the sediment except for the calicinal parts.

Depositional environments

The coral bearing lower member of the Aheimer Formation is composed of calcareous silty mudstone (Fig. 15A) intercalated with strongly ferruginous, thin, silty dolostone-limestone and/or thin beds of calcareous siltstone (Fig. 15B–D). It is characterised by many badly preserved fossils. Among those are small rugose corals, bryozoans, disarticulated crinoidal columnals, brachiopods and agglutinated foraminifers (Fig. 15B-D), reflecting shallow normal marine conditions inhabited by a heterotrophic filter-feeding faunal community. Corals are generally better preserved than strongly disarticulated crinoidal stems and bryozoans (Figs. 3B-D, F-G, 15A-D) which means less transportation. Opposed to the latter, the corals were not transported outside of their original habitat, but according to the mostly tumbled corallites and the strongly disarticulated crinoid ossicles, bryozoans, and shells, redeposition by storms above wave base has to be assumed. Kora and Mansour (1991) compared the

(See figure on next page.)

Fig. 15 Depositional environments of the Aheimer Formation (lower member). A Microphotograph of calcareous silty mudstone; disarticulated crinoid ossicles (Cr), tiny shell fragments (in part ostracods) and indeterminable microbioclasts associated with silt-sized quartz grains, all set in a ferruginous calcareous cement. B Microphotograph of silty dolostone; large brachiopod shell (B), crinoid ossicles (Cr) and other undifferentiated fossil fragments, all altered and dolomitized, associated with silt-sized quartz grains. Brownish-black ferruginous oxides are filling the pore spaces. C, D Microphotographs of calcareous siltstone bearing crinoids (Cr), bryozoa (Br) and other altered fossil fragments. All components set in ferruginous-calcareous cement. E, F Vertical, elongated burrows of the *Tisoa siphonalis* in mudstone in the uppermost part of the lower member of the Aheimer Formation

depositional setting to that proposed by Sando (1980) for the Mississippian in Northern America; where light to dark coloured, fissile to medium bedded mudstone was deposited in shallow, poorly circulated water in basins marginal to shoreline with a depth varying from 0 to 100 m.

The uppermost part of the coral-bearing unit is highly burrowed by simple vertical and deep burrows of the Glossifungites (Fig. 15E, F), see El-Refaiy et al., 2023 for more details. These imply deposition in a very shallow marginal marine intertidal environment, where ecological conditions were not suitable for epibenthic organisms, which, therefore, had to withdraw into the substrate for protection. Therefore, Kora and Mansour (1991) correctly assumed a sheltered, poorly circulated shallow marine environment in the lower part of the lower member of the Aheimer Formation that changed to intertidal conditions in its upper part (see also El Desouky et al., 2019). Recently, El-Refaiy et al. (2023) concluded an environment ranging from intertidal to shallow subtidal settings through a more detailed investigation of the depositional setting of the Aheimer Formation in its type locality.

Herein, we refine these interpretations implying a time-averaged ramp model for the upper Rod El Hamal and Aheimer formations (Fig. 16). In general, ramps typify passive margins and epeiric seas (Read, 1982, 1985; Wright and Burchette, 1992), i.e., a structural setting as seen in the Carboniferous of the present Gulf of Suez region that formed an embayment on a very broad, extended shallow shelf during Pennsylvanian times (the Carboniferous Proto-Clysmic Basin of Reynolds et al., (1997a, 1997b) and in Guiraud et al., 2001, who completely relied on the previous authors; see also Torsvik and Cocks, 2011, Fig. 11). Our model is very close to that established by Herbig and Weber (1996) for the mixed carbonate-siliciclastic uppermost Famennian ("Strunian") Condroz shelf in Northwest Europe, whereas references above refer to pure carbonate ramps. Herbig and Weber (1996) reconstructed a homoclinal shallow inner ramp from strongly terrigenous influenced tidal flats and an inner, marl- and siltstone dominated lagoon with carbonate nodules that was inhabited by brachiopods and mud-sticking rugose corals. It graded into a stenohaline carbonate belt consisting of an outer, carbonate-rich lagoon and seaward adjoining carbonate bar inhabited among others by foraminifers, calcareous algae, echinoderms and ostracods; large, dissepimented rugose corals occur mostly in the carbonate-rich lagoon and are mostly reworked and broken in sediments of the carbonate bar. Facies of the deeper ramp were not observed. Thus, the model is equivalent to the "ramp with barrier-bank complexes" of Read (1985), where the shoal-water complex is bordered by lagoonal carbonate muds or siliciclastic prodelta muds landward, respectively, by deep-ramp muds further seaward. The Strunian succession of the Condroz shelf consists of a stacked sequence of transgressive small cycles that in its lower part resemble the ideal cycle reconstructed for the Rod El Hamal and lower Aheimer Formation by Bandel and Kuss, 1987 (see also Herbig and Kuss, 1988).

Transferring the model to the late Moscovian upper Rod El Hamal and Kasimovian to Gzhelian (early Permian?) Aheimer formations, a generally regressive succession is seen, composed of mostly incomplete smaller transgressive cycles as idealised by Bandel and Kuss (1987). In Fig. 16 the ramp model shows the palaeogeographic situation during deposition of the Upper Rod El Hamal Formation with a hypothetical southern position of the near-shore Aheimer Formation. During regression the facies of the Aheimer Formation moved northwards on top of the Rod El Hamal Formation according to Walther's law. This mirrors the present-day outcrop situation with the Aheimer Formation exposed along the Northern Galala Plateau, north of the Rod El Hamal that is predominantly exposed in the Wadi Araba.

Kora et al. (2019) described the depositional environment of the coral-bearing upper Rod El Hamal Formation as storm-influenced inner ramp environment. Bioclastic rudstone consists of diverse, often worn organisms embedded within peloidal, more or less sandy grainstone matrix. The facies is characteristic of the low mature ramp microfacies type RMF 7 of Flügel (2004). It typifies shoals above fair-weather wave-base mostly heaped up by tempestites at the seaward border of the open inner ramp. On the shoals, small phylloid algal-microbial mounds developed (Abd Elhameed et al., 2021).



Fig. 15 (See legend on previous page.)



Fig. 16 Time-averaged mixed carbonate-siliciclastic ramp model for the late Moscovian–Gzhelian (Early Permian?) Rod El Hamal and Aheimer formations of the Proto-Clysmic Basin of Reynolds et al. (1997a, 1997b), western side of the Gulf of Suez. Hypothetical position of the Aheimer Formation south of the Rod El Hamal Formation during late Moscovian deposition of the latter to show a seaward–landward transect at the southern margin of the Palaeotethys. During continued regression the facies belts moved northwards; the Aheimer Formation overlaps the Rod El Hamal and in present outcrop is exposed north of it at the eastern rim of the Northern Galala Plateau. Phylloid algal–microbial mounds according to Abd-Elhameed et al. (2021) and terrigenous facies of the middle-upper Aheimer Formation based on Abou Khadra et al. (2012)

Most bioclasts have been derived from bryozoan-echinoderm meadows further seawards that developed between storm-wave-base and fair-weather wave-base. They are not recorded in the Egyptian sections but are well-documented in the brachiopod and bryozoan faunas described by El-Shazly (2011), Ernst et al. (2020), and Abd-Elhameed et al. (2020). Stenohaline conditions and frequent redeposition of sediment is seen by the large, dissepimented rugose corals of the typical shallow-water caniniid-clisiophyllid fauna (Hill, 1938) which show frequent constrictions (growth interruptions), rejuvenations, talons, and rootlets and which grew either as secondary recliners or mudstickers (El Desouky et al., 2019; Kora et al., 2019). After regression with onset of the Aheimer Formation presumably in the early Kasimovian, a lagoonal environment of the restricted inner ramp was established. The open marine carbonate deposition was substituted by silty mudstone with occasional thin tempestite beds washing in few bioclasts from the crinoid-bryozoan meadows across the shoal. The caniniid-clisiophyllid fauna vanished and was completely substituted by the *Cyathaxonia* fauna which consisted of mostly liberosessile mud-sticking individuals.

Further regression close to the top of the lower Aheimer Formation led to sandy intertidal deposits with vertical Glossifungites-type burrows and caused extinction of the coral fauna. Above, the sandy middle and upper members of the Aheimer Formation consist mostly of landwards adjoining mudstones, sandstones and minor carbonate intercalations deposited in peritidal environments, floodplains, in fluviatile environments and paleosols (Abou Khadra et al., 2012). The succession contains a latest Carboniferous (Stephanian, respectively, Gzhelian) to early Permian(?) flora. It consists of abundant branches of Coniferophyta that were adapted to a more temperate climate and less common leaves of Pteridophylla, that indicated a warm and humid climate (Bandel and Kuss, 1987, p. 9; Lejal-Nicol, 1987) Moreover, Abou Khadra et al. (2012) reported fissile shales rich in plant remains and trunks of Lepidodendron. Still further south the terrigenous lowlands of the Nubian shield delivered not only the siliciclastics of the middle and upper Aheimer Formation, but also the mostly fine-sandy to silt-sized detrital

quartz and clay minerals dominated the lagoon of the restricted inner ramp of the lower Aheimer Formation.

Testing a cool-water relation for the Aheimer cyathaxonid coral fauna on a first sight remains somewhat ambiguous due to the meagre knowledge concerning time-equivalent glaciogenic deposits in Northeast Africa. The depositional area was about 25° S, i.e., well in the tropical realm and also associated crinoids and brachiopods apparently testify warm waters. However, Reynolds et al. (1987b) mentioned supposedly late Carboniferous tillites and varve-type periglacial sediments some ten degrees further south in the Uweinat area (Gilf Kebir, Abu Ras) of NW Sudan. Furthermore, Bussert and Schrank (2007) described late Carboniferous glacigenic sediments from northernmost Ethiopia and adjacent Eritrea, well below 40° S, and concluded the existence of glacial uplands further north in Eritrea and/or in Saudi Arabia, i.e., far away from the South Pole. In this context, it has to be stressed that Montañez et al. (2016) identified intense glaciations in the greater part of the Kasimovian based on pedogenic carbonate- and fossil plant-based CO₂ estimates, North American Mid-Continent cyclothems and exaggerated offlaps including incised valley fills in the Donets Basin. A particularly intense, about two Myr long period with glaciations in the lower part of the Missourian, 306.5-304.5 Ma, respectively, in the middle part of the Kasimovian was identified by the authors. Obviously, this correlates with the North American Glacials C and D, depicted in the upper part of the Kasimovian by Aretz et al. (2020, Fig. 23.6). The onset of these glacial maxima might coincide with the onset of the sandy middle and upper members of the Aheimer Formation and the preceding extinction of the cyathaxonid coral fauna described herein. In this context, the development of three "incised valleys" in the middle and upper part of the Aheimer Formation has to be stressed (Abou Khadra et al., 2012), that point to prominent eustatic sea level variations. Already the phylloid algal-microbial mounds described from the underlying upper Rod El Hamal Formation (Abd-Elhameed et al., 2021) were considered to be of subtropical origin due to the important role of microbes that distinguish them from time-equivalent phylloid algal mounds of the tropical realm of the Palaeotethys and the conterminous USA.

In summary, in spite of its tropical palaeolatitude, water temperatures might be envisaged for the depositional realm of the Aheimer corals preceding a late Kasimovian temperature drop. This interpretation is supported by the coniferophyte dominated flora shortly described by Bandel and Kuss (1987, p. 9) and Lejal-Nicol (1987).

Palaeobiogeography and palaeoclimatology

The studied Late Pennsylvanian (Kasimovian) rugose coral fauna from the Aheimer Formation is poorly diversified and strongly endemic. It consists of ten taxa, among those four new species (Actinophrentis crassithecata n. sp., Lytvolasma aheimerensis n. sp., L. paraaucta n. sp., Monophyllum galalaensis n. sp.), and four species in open nomenclature (Lytvolasma cf. canadense, Zaphrentites cf. parallela, Zaphrentites sp., Ufimia sp.). Bothrophyllum okense Kossovaya, 2001 was previously described from the Moscovian Moscow Basin and the Gzhelian of Spitsbergen. Rotiphyllum exile was described from the late Moscovian (Asturian) of northern Spain. Except for the species *R. exile* the identified genera are long ranging from the Carboniferous to the Guadalupian, Ufimia even from the lower Devonian to the Upper Permian and, therefore, they are of little biostratigraphic value. However, in spite the fauna is important to clarify palaeobiogeographic and palaeoclimatic relations within the late Carboniferous western Palaeotethys.

The rugose coral fauna from the western side of the Gulf of Suez, i.e., from the Carboniferous Proto-Clysmic Basin of Reynolds et al. (1997a, 1997b) from the and the previously studied Rod El Hamal Formation (Kora et al., 2019) and the herein studied Aheimer Formation are the only documented examples of a Moscovian-Kasimovian coral fauna at the southern margin of the western Palaeotethys, respectively, along the northern margin of western Gondwana. Post-Bashkirian (=post-Lower Pennsylvanian) corals are not known in the extended Carboniferous epicontinental Saharan basins (Semenoff-Tian-Chansky, 1985; El Desouky et al., 2019; Wang et al., 2022), along the Gondwanan margin in northern Africa. Contemporaneous marine deposits from the Levant and Arabia are missing. Faunas from comparable palaeobiogeographic settings have to be seeked as distant as in the peri-Gondwana terranes from Turkey and Iran. However, no Pennsylvanian non-dissepimented corals are known to us from the latter regions except for the descriptions of Flügel (1991). According to Fedorowski (2022), this late Serpukhovian, tentatively into the Bashkirian reaching fauna needs revision. It is a mixture of Far Eastern Asian and western European coral morphotypes with slight dominance of the latter (Fedorowski, 2022, p. 38). Except for the long-ranging genus Rotiphyllum there is no genus in common with our Egyptian fauna. Neither the Bashkirian colonial corals described from east-central Iran (Badpa et al., 2016) nor a latest Pennsylvanian (late Gzhelian) coral fauna from central Iran that consists of dissepimented and compound rugose corals (Wang et al., 2018) does show any relation to Egypt. The remote and isolated occurrence of the latter region well explains the high degree of endemism, but also causes greater problems to elucidate the palaeogeographic affinities of the studied corals.

Concerning the dissepimented corals of the underlying upper Rod El Hamal Formation, Kora et al. (2019) concluded a general attribution to the Palaeotethys realm due to similarities with northern Spain (Cantabrian Mountains), the Donets and Moscow basins. In more detail, they showed that genera are characteristic of the southern subprovince of the Mediterranean Province of Fedorowski (1978, 1981), but also pointed out relations to the Uralo-Arctic Province. In this context it has to be mentioned that Dubatolov and Vassiljuk (1981) attributed the Moscow Basin to the latter. Kora et al. (2019) attributed the endemism of the coral fauna to the restricted facies in an embayment in the present-day Gulf of Suez region shown on the palaeogeographic map of Torsvik and Cocks, 2016: Figs. 9.1c, 9.3), though future research in Turkey and Iran might reduce it. In that semi-enclosed embayment, the specially adapted, low diversity coral fauna of the Rod El Hamal Formation developed in a carbonate-poor mixed siliciclastic-carbonate environment.

For the cyathaxonid corals of the Aheimer Formation, Kora and Mansour (1991) claimed stronger connections with North America, but Kora et al. (2019) and El Desouky et al. (2019) strongly doubted this, as Davydov and Cózar (2017), based on warm-water benthic foraminifera, proved that the final closure of the Rheic-Palaeotethys gateway in the early Bashkirian coincided with the onset of the Bashkirian glaciation. This implies that the equatorial connection between North America and Western Tethys was cut off at the base of the Bashkirian and the only connection would have been possible via the Arctic Franklinian corridor (Davydov and Cózar, 2017, Fig. 1B). This was illustrated before in the palaeogeographic maps of Torsvik and Cocks (2016) that show the sutured northwestern Africa and eastern North America and a definitely closed West-East marine gateway after the early Bashkirian. Already Rodríguez (1984a) claimed the disappearance of American faunal influences in northern Spain during the early Bashkirian and Legrand-Blain et al. (1989) stated no more palaeobiogeographic connections between Northern American and Northern Africa from the Bashkirian onwards. Based on these results we reject the reconstruction of Wang et al. (2022) with a narrow Rheic-Tethys gateway still open in the Late Pennsylvanian. The division of the Carboniferous coral faunas into a cool-water Gondwana realm and a tropical to subtropical Euramerican realm composed of the three main regions Asia, Europe, and North American appears to be oversimplified.

Kora et al. (2019) and El Desouky et al. (2019) doubted a palaeogeographic connection of the Egyptian corals with North America via the Uralian-Arctic seaway due to distance, palaeoclimatic differences and missing common taxa in the intermediate Donets Basin. Therefore, they advocated probable homeomorphy of the simple structured North American and Eurasian cyathaxonid corals. In fact, homeomorphy seems to be a relatively widespread feature in rugose corals, as expressed, for example, by Fedorowski (1981, 2010, 2022), Webb (1993), and Denayer and Webb (2015). However, taxonomic reevaluation of the Aheimer corals and thorough literature review on the distribution of the genera presented herein as well as additional data on regional fauna and facies along the western side of the Gulf of Suez need to modify our previous concepts. Surprisingly, the coral fauna shows strong relations to the boreal cool-water realm of the Cordilleran-Arctic-Uralian realm (CAU realm) defined by Fedorowski (1987b), which was generally accepted for the Permian by following authors. This realm includes the central and northern Urals, the Arctic and along the western margin of Northern America included the Glass Mountains of western Texas (e.g., Kossovaya, 2009: boreal realm; Wang et al., 2017). However, it has to be stressed that Somerville (1997) based on a review of previous authors (e.g. Fedorowski, 1981; Hill, 1981) stated the presence of a still warm-water Uralo-Arctic Province including the Moscow Basin, the Urals, northern Timan, Novaya Zemlya, Spitsbergen, and Arctic Canada already for the late Moscovian. Corals from the Donets Basin, although broadly comparable with those of the Uralo-Arctic Province were attributed by him to the Mediterranean Province, i.e., to the Palaeotethys realm.

According to the occurrence of *Rotiphyllum exile* and the genus *Actinophrentis* in the Aheimer Formation at the western side of the Gulf of Suez, Egypt and in time-equivalent strata of northern Spain, palaeobiogeographic relations are without doubt (Fig. 17) and underline the relations already established for the coral fauna of the underlying Rod El Hamal Formation (Kora et al., 2019). In addition, the genera *Rotiphyllum* and *Ufimia*, though widespread in time and space and, therefore, of little value for palaeobiogeographic considerations, are in common. *Zaphrentites* is part of our fauna; its species described from the Cantabrian Mountains were moved to *Rotiphyllum* and *Actinophrentis* (Fedorowski, 2004).

As mentioned above, the Egyptian genera show strong relations to the Lower and Middle Permian cold-water fauna of the Cordilleran–Arctic–Uralian realm (Fig. 17). Wang et al. (2017) identified *Actinophrentis* and *Lytvol-asma* as typical representatives. We stress the occurrence of *Lytvolasma* cf. *canadense* in Egypt, which as



Fig. 17 Palaeobiogeographic relations of the cyathaxonid coral fauna of the Aheimer Formation (asterisk) showing its rooting in the western Palaeotethys (red dots) and the strong relations to the cool-water Cordilleran–Arctic–Uralian realm (yellow dots). The fauna is a precursor of the Lower Permian cyathaxonid cool-water fauna of the eastern Cimmerian peri-Gondwana terranes (E'pGT). Base map from Abd-Elhameed et al. (2021) as modified from Kiessling et al. (1999)

nominate species was described from the Guadalupian of Ellesmere Island (Canadian Arctic). According to our literature review, *Monophyllum* has to be added as well as *Ufimia*, which constitutes a major part of the Uralian faunas in the late Artinskian (Kossovaya, 2007). From the intermediate Donets Basin, *Actinophrentis, Lytvolasma, Monophyllum, Rotiphyllum,* and *Ufimia* are known from different Pennsylvanian stages and thus testify migration routes. In addition, the dissepimented coral *Bothrophyllum okense* of the Kasimovian lower part of the Aheimer Formation and other *Bothrophyllum* spp. and *Amygdalophylloides* from the upper Moscovian Rod El Hamal Formation that underlies the Aheimer show relations to the Donets and Moscow basins and into the CAU realm (Kora et al., 2019).

Although the relations to northern Spain unequivocally testify the attribution of the middle Pennsylvanian Egyptian corals to the western Palaeotethys, the Kasimovian fauna of the Aheimer Formation thus strongly suggests influence of cool water. This is underlined by facies development, associated phylloid algal–microbial mounds, floristic elements, glaciation in northern Ethiopia and Eritrea and general palaeoclimatic considerations (see chapter 5.3, Depositional environments). The fauna, therefore, can be interpreted as a precursor of the Artinskian-Wordian anti-tropical cool-water association of cyathaxonid rugose corals (Kossovaya, 2009). On a broader frame, it also can be regarded as a precursor of the Early Permian cool-water fauna from the peri-Gondwana terranes of the eastern Cimmerides that stretch from the Himalayas (Tibet) to Southeast Asia (Fig. 17). This fauna was termed "Lytvolasma fauna" by many authors (first Wu, 1975, see also Wang et al., 2010), though Fedorowski (1982) later included the described specimens in Euryphyllum. These terranes occupy similar paleogeographic positions than Egypt close to the northern margin of Gondwana (e.g., Wang et al., 2013, 2017), but unfortunately Pennsylvanian faunas are not known due to hiatus or missing calcareous strata (Wang et al., 2017), thus preventing more detailed comparisons.

Conclusions

The coral-bearing, in part slightly calcareous mudstones of the Kasimovian lower member of the Aheimer Fm. from the eastern cliffs of the Northern Galala, western side of the Gulf of Suez (Egypt) yielded a low diverse, strongly endemic association of solitary, non-dissepimented, simple structured rugose corals. It is the youngest Carboniferous coral fauna from the southern margin of the western Palaeotethys, respectively, from northern Gondwana. All together ten taxa belonging to four families (Antiphyllidae, Hapsiphyllidae, Plerophyllidae and Bothrophyllidae), respectively, to the defining subfamilies were identified. Besides four new species (Actinophrentis crassithecata n. sp., Lytvolasma aheimerensis n. sp., L. paraaucta n. sp. and Monophyllum galalaensis n. sp.), four taxa in open nomenclature (Lytvolasma cf. canadense, Zaphrentites cf. parallela, Zaphrentites sp. and Ufimia sp.), Bothrophyllum okense and Rotiphyllum exile were identified. Further genera determined by Kora and Mansour (1991: Allotropiochisma, Allotropiophyllum, Amplexizaphrentis, Assimulina, Bradypyllum=most probably our Monophyllum, Meniscophyllum, Paraduplophyllum, Pseudowannerophyllum and Pseudozaphrentoides) remained without proof. We also stress the absence of Lophophyllidium mentioned by Abdallah and El Adindani (1965) and correct rejection of the name "Lophophyllidium bearing shale series" in favour of the informal name "lower member of the Aheimer Formation" by Kora and Mansour (1991). The strong dominance of taxa belonging to the subfamily Antiphyllinae (Actinophrentis crassithecata n. sp., Lytvolasma aheimerensis n. sp., L. paraaucta n. sp., Monophyllum galalaensis n. sp. and Rotiphyllum exile) is remarkable.

The corals suffered from a destructive physical alteration of their skeletons, such as crushing and flattening. Recrystallization, dolomitization and ferrugination of open pore spaces inside the corals are the most common diagenetic features. Rejuvenations, encrustations and bioerosions of the mostly straight conical to slightly curved specimens are extremely rare. In consequence, they lived as liberosessile mudstickers in a soft bottomencrustation and bioerosion occurred post-mortem after reworking by episodic turbulence.

Lithologically, the Kasimovian lower member of the Aheimer Fm. is composed of about 34 m thick, dark green and grey calcareous silty mudstone intercalated with some calcareous siltstone/sandstone and thin, strongly ferruginous fossiliferous, silty dolostone/limestone beds. The facies of this succession records a depositional setting in a sheltered shoreface shallow marine environment, changing to firm ground foreshore "intertidal" conditions during the deposition of the upper beds, based on the occurrence of *Glossifungites*-type trace fossils in the latter. In general, the Pennsylvanian succession from the western side of the Gulf of Suez was deposited in an embayment at the southern margin of a broad shelf of the southern Palaeotethys that was termed Proto-Clysmic Basin by Reynolds et al. (1997a, 1997b).

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A time-averaged ramp model (Fig. 16) shows a regressive development from a mixed carbonate-siliciclastic open inner ramp during deposition of the late Moscovian upper Rod El Hamal Formation to a restricted inner ramp during deposition of the lower Aheimer Formation. Further regression led to peritidal to fluvial environments within the Late Pennsylvanian (Kasimovian?-to Gzhelian) middle and upper Aheimer Formation. General palaeoclimatic considerations and a late Pennsylvanian glaciation in northern Ethiopia and Eritrea (Bussert and Schrank, 2007), supported by local facies development, the existence of phylloid algal-microbial mounds in the upper Rod El Hamal Formation (Abd-Elhameed et al., 2021) that differ from typical tropical phylloid algal mounds, and associated fauna and floristic elements show cooling from the upper Rod El Hamal Formation to the middle-upper Aheimer Formation. This is mirrored by the general regressive trend of the succession.

Palaeobiogegraphic analysis of the coral fauna underlines a temperate to cool-water environment. Besides unequivocal relations to the Cantabrian Mountains (northern Spain) that root Egypt in the western Palaeotethys, connections existed via the Donets Basin (and the southern Urals) to the Cordilleran-Arctic-Uralian realm which is a cool water province during the Lower and Middle Permian. This province stretches along the western side of North America as far as to the Glass Mountains in western Texas (Kossovaya, 2009). It explains the strong relations of the Egyptian fauna to that latter region along the Uralian and Franklinian seaways. Such a connection that was doubted by El Desouky et al. (2019) and Kora et al. (2019) and suspected to result from homeomorph taxa. Therefore, in a more general way, the Egyptian coral fauna is a precursor of the anti-tropical cool-water fauna of Kossovaya (2009) and lower Permian cool-water faunas from the eastern Cimmerian peri-Gondwana terranes (e.g., Wang et al., 2013, 2017).

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Author contributions

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Availability of data and materials

The reference fossil coral specimens and thin sections of this study will be available at the Geology Department, Faculty of Science, Mansoura University, Mansoura, Egypt.

Declarations

Competing interests

The authors declare that they have no competing interests.

Author details

¹Department of Geology, Faculty of Science, Mansoura University, Mansoura 35516, Egypt. ²Institut für Geologie und Mineralogie, Universität Zu Köln, Zülpicher Straße 49a, 50674 Cologne, Germany.

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