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Vassiljukia, a new colonial rugose coral from the Early Visean (Mississippian) of the Donets Basin (Ukraine) and NW Turkey

Vassiljukia, *un nouveau corail rugueux colonial du Viséen inférieur (Mississippien) du bassin du Donetz (Ukraine) et du Nord-Ouest de la Turquie*

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ABSTRACT

The cerioid colonial coral previously described as *Lithostrotion columnariformis* from the Early Visean of the Donets Basin (Ukraine) is here reattributed to the new genus *Vassiljukia*. This genus is introduced for colonial amygdalophylloid developing a stable cerioid habitus. It differs from amygdalophylloid proto-colonies by its ability to produce second generation offsets. This ability is proposed here as a definition to differentiate proto-colonial stages from genuine colonies within the rugose corals. *Vassiljukia columnariformis* is also known from equivalent strata of northwestern Turkey where it occurs with the oldest cerioid *Lithostrotion* and *Ceriodotia*. The origin and affinity of *Vassiljukia columnariformis* within the Amygdalophyllidae are also discussed.

RÉSUMÉ

Les coraux cérioïdes décrits sous le nom *Lithostrotion columnariformis* du Viséen basal du bassin du Donetz sont ici réattribués au nouveau genre *Vassiljukia*. Ce genre est créé pour les formes coloniales d'*Amygdalophyllum* développant un habitus cérioïde stable. Il diffère des proto-colonies amygdalophylloïdes par son aptitude à produire une seconde génération de bourgeons. Cette aptitude est proposée comme définition pour différencier les stades proto-coloniaux des vraies colonies chez les coraux rugueux. *Vassiljukia columnariformis* est également connu dans les strates du même âge du Nord-Ouest de la Turquie, où il a été découvert avec les plus anciens *Lithostrotion* et avec *Ceriodotia*. L'origine et l'affinité de *Vassiljukia columnariformis* au sein des Amygdalophyllidés sont également discutées.

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1. Introduction

The Early Visean time was a period of deep changes in the sedimentation patterns, climate and faunal associations (Poty et al., 2013). Following the highest relative sea level in the Latest Tournaisian time (Poty, 2007), the Earliest Visean recorded a strong sea-level fall resulting of a common gap in the stratigraphical succession. Hence, the third-order sequence 5 of Hance et al. (2001) is commonly lacking in platform settings. In contrast, the following third-order sequence (6) flooded again the platforms. As a consequence of these eustatic variations, the rugose corals association underwent strong modifications. During the Avins event in the Latest Tournaisian, most genera were cosmopolitan and many typically Visean corals appeared during this time interval (e.g., *Axophyllum, Amygdalophyllum, Haplolasma, Palaeosmilia*). During the low sea-level period of the Earliest Visean, the corals became more endemic due to the isolation of the palaeobiogeographic units. After the rise of the sea-level in the Early Visean, the corals spread again and new forms become very common. At this time, the colonial genera *Siphonodendron* and *Dorlodotia* appeared and became common in the shallow-water carbonate settings throughout the European provinces. The emergence of the cerioid genera *Lithostrotion* and *Ceriodotia*, respectively evolved from the fasciculate *Siphonodendron* and *Dorlodotia* was recently documented (Denayer, 2011, 2014) in the uppermost part of the Early Visean. This event of "cerioidization" was possibly driven by environmental conditions as both genera first occured in high-energy facies in NW Turkey (Denayer, 2014). From the same area and in the same stratigraphic interval was recovered a cerioid colonial coral which was identified as "*Lithostrotion" columnariformis* Vassiljuk, 1960. This species is also present in time-equivalent levels in the Donets Basin (Ukraine). Contrary to Vassiljuk's attribution, it is not a *Lithostrotion* but a colonial amygdalophylloid taxon. The aims of the present paper are:

- to describe the species based on newly collected material from Ukraine and Turkey;
- to re-attribute *columnariformis* to a new genus;
- to discuss the affinity of this new genus within the Amygdallophyllinae subfamily and other Early Visean massive colonial corals.

2. Geologic and stratigraphic settings

The Lower Visean Skelevatka Suite (Zones C_1^vb-d) exposed along Mokra Volnovakha River (Fig. 1B) and in the central fluxing limestone quarry, is divided into two parts. The lower part is composed of bioclastic, foraminiferal and algal packstone and grainstone. The upper part displays similar facies but is also contains black chert nodules and lenses (Fig. 2). Brachiopods and calcareous green algae are the most common elements, together with the tabulate and rugose corals. The solitary rugose corals *Haplolasma subibicina* and *Amygdalophyllum brazhnikovae* are common (Vassiljuk, 1960), as well as colonies of *Siphonodendron affine tanaicum* (possibly *S. ondulosum*), "*Lonsdaleia" longisepta, Eolithostrotionella zhizhinae, Eolithostrotionella*

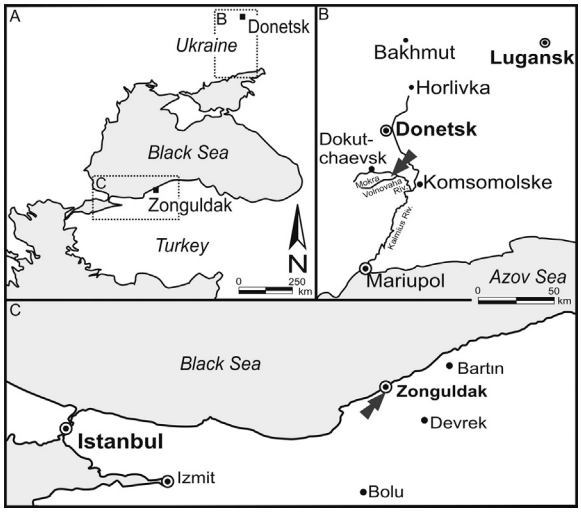

Fig. 1. Location maps. A. Schematic map with position of the studied areas. B. Close-up view of the Donets Basin, south of Donetsk and position of the sampling locality (arrow). C. Close-up view of NW Turkey, near Zonguldak and position of the sampling localities.
Fig. 1. Cartes de localisation. A. Carte schématique avec localisation des régions étudiées. B. Vue rapprochée du bassin du Donetz, au sud de Donetsk, et localisation de la localité échantillonnée (flèche). C. Vue rapprochée du la Turquie du Nord-Ouest, près de Zonguldak, et localisation de la localité échantillonnée (flèche).

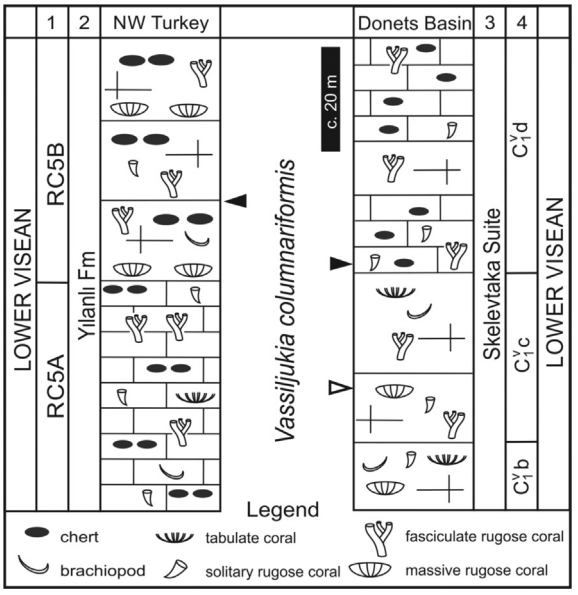

Fig. 2. Schematic lithostratigraphical succession of the Lower Visean in NW Turkey and the Donets Basin with stratigraphic position of *Vassiljukia columnariformis* (holotype: white arrow, and additional material: black arrows). Modified after Denayer (2014) and Ogar (2010). Column heads: 1: substages; 2: rugose coral zones (after Denayer, 2014); 3: formations; 4: subzones.
Fig. 2. Succession lithostratigraphique schématique du Viséen inférieur de la Turquie du Nord-Ouest et du bassin du Donetz, avec position stratigraphique de l'holotype (flèche blanche) et spécimens additionnels (flèches noires) de *Vassiljukia columnariformis*. Modifié d'après Denayer (2014) et Ogar (2010); intitulé des colonnes : 1 : Sous-étage ; 2 : zones à coraux rugueux (d'après Denayer, 2014) ; 3 : formations ; 4 : Sous-zones.

mariupoliensis (possibly *Ceriodotia*), *Siphonodendron* sp. (= *Diphyphyllum lateseptatum* in Vassiljuk, 1960), *Dorlodotia fomitschevi*, *D. briarti* and numerous colonies of the tabulate *Syringopora geniculata*. The systematic position of several corals (*Eolithostrotionella*) is still unresolved but some have been discussed by Ogar (2010), Denayer (2011) and Hecker (2012).

The Upper Devonian to Upper Visean Yılanlı Formation crops out in the Bartın and Zonguldak areas in northwestern Turkey (Fig. 1). The Lower Visean part is dominated by bioclastic grainstone to rudstone, commonly silicified in the Kokaksu section (suburbs of Zonguldak, Fig. 1C), from where the Turkish material originates (Fig. 2). The macrofossils are abundant in this stratigraphic unit: brachiopods (mainly productids), bellerophontids, syringoporid tabulate corals and numerous colonial rugose corals (*Dorlodotia euxinensis, Ceriodotia bartinensis, C. petalaxoides, Siphonodendron ondulosum, S. martini*) and the solitary rugosans *Palaeosmilia murchisoni* and *Clisiophyllum multiseptatum*. To date, no *Amygdalophyllum* is known form the Lower Visean of NW Turkey. This assemblage is typical of the upper part of the Lower Visean of northwestern Turkey and defined the rugose coral biozone RC5B of Denayer (2014), an equivalent of RC5β-γ of Poty et al. (2006). The foraminiferal content, notably numerous primitive *Pojarkovella*, indicates the biozone MFZ11B of Hance et al. (2011).

3. Systematic palaeontology

The type specimen, labelled 1405/11 is deposited in the National Museum of Natural History at the National Academy of Science of Ukraine in Kyiv; other Ukrainian material is housed in the University of Kiev; the Turkish specimen is housed in the collections of animal and human palaeontology of the University of Liege (Belgium). Nomenclature follows Hill (1981) unless specifically noted.

Family Amygdalophyllidae Grabau *in* Chi, 1935.

Vassiljukia gen. nov.

Etymology. This genus is dedicated to Prof. Dr. N. P. Vassiljuk who described the type species.

Type species. *Lithostrotion columnariformis* Vassiljuk, 1960 from the Lower Visean of the Donets Basin.

Diagnosis. Cerioid or sub-cerioid coral showing a variably thickened amygdalophylloid axial structure. Long major septa reaching the axis of the coral. Minor septa long, entering into the tabularium. Minor septa usually less thickened than the major septa. Dissepimentarium composed of concentric interseptal dissepiments and occasional second order lonsdaleoid dissepiments. Tabulae incomplete, conical, commonly thickened near the axial structure. Increase lateral and non-parricidal.

Discussion. The corallites show the characters of the solitary genus *Amygdalophyllum* Dun and Benson, 1920. The axial structure is a typically amygdalophylloid thickened spindle-shape structure, the major septa are thickened in the tabularium in the same way as in various species of *Amygdalophyllum*, and the dissepimentarium is composed of thickened concentric interseptal dissepiments. However, the colonial habitus is unusual in *Amygdalophyllum*. *Amygdalophyllum* Dun and Benson, 1920 is defined as a solitary coral (See Poty, 2007 for a recent emendation of the diagnosis) but several species can develop a limited increase with few offsets. The type specimen of *A. dianthoides* (McCoy, 1851) from the Lower Visean of England shows several offsets developed in the outer part of the calyx in a peripheral parricidal increase. Material recently collected in the type area also shows occasionally a limited increase (Boland, 2002). In these English corals, the offsets form a sub-cerioid proto-colony but no true colony is known in *A. dianthoides*. Similarly, *A. minimum* Webb, 1990 from the Upper Tournaisian–Lower Visean of eastern Australia develops non-parricidal lateral increase. The latter possibly gave rise to the genus *Cionodendron* Benson and Smith (1923) and the other Australian lithostrotionids (Denayer and Webb, 2015). However, *A. minimum* shows fasciculate proto-colonies rather than cerioid ones. Massive colonies of Australian lithostrotionids (*Australastraea*) are typically characterized by thamnasterioid, asteroid and aphroid habitus. Their internal characters are however very similar to those of *Amygdalophyllum*. *Vassiljukia* differs from these *Australastraea* by a true cerioid habitus (complete and continuous wall between neighbouring corallites), a less robust but more complex columella with distinct septal lamellae and higher diameter and number of septa. Rodríguez and Hernando (2005) described from the Late Visean of South Spain the genus *Espielia* which is either a colonial *Amygdalophyllum* or, as suggested by these authors, *Rylstonia*. *Guadiatia* Gómez-Herguedas and Rodríguez (2005) is another amygdalophyllid coral developing a colonial habitus by peripheral increase. *Espielia*, *Cionodendron* and *Guadiatia* differ from *Vassiljukia* by their fasciculate habitus. The attribution of the proto-colonies and limited increase of *A. dianthoides* to a distinct genus is debatable but we preferred to keep the species in *Amygdalophyllum* since individuals without offsets are clearly *Amygdalophyllum*. On the other hand, the Ukrainian and Turkish specimens are worth classifying in a new genus since their cerioid habitus is stable and means a further step in the corallite integration into the colony. From slightly older strata (C_1^v b), Vassiljuk (1960) figured another cerioid colony under the name *Lonsdaleia longiseptata* Lissitzin, 1925. This species does not belong to *Lonsdaleia* because the axial structure is not axophyllid but rather amygdalophylloid, with a thickened axial plate and gently upturned axial tabellae. It is very similar to *Vassiljukia columnariformis* but differs from the latter by its conspicuous lonsdaleoid dissepimentarium and possibly by a parricidal increase (see two juvenile corallites in the figured specimen). Unfortunately, there is only one colony available and without additional material it is not possible to decide whether "*L.*" *longiseptata* belongs to *Vassiljukia* (*V. columnariformis* or a distinct species) or to another distinct genus.

Vassiljukia columnariformis (Vassiljuk, 1960)

Fig. 3

* 1960 *Lithostrotion columnariformis* Vassiljuk, p. 90, pl. 22, figs. 4-4a.

Holotype. Specimen 1405/11, from the Lower Visean (C_1^vc) of the Mokra Volnovakha River valley, Donets Basin.

Additional material. One colony from the type locality (Ukraine) and one colony is known from Kokaksu (Zonguldak, NW Turkey).

Description.

Habitus and external character. The colonies are subcerioid to cerioid and count less than 10 polygonal corallites. The colonies are up to 5 cm in diameter and less than 3 cm high.

Internal characters in transverse section. The corallites are polygonal to sub-circular in transverse section (Fig. 3: 1a, 3a). Their width is 13.3 mm on average (maximum 22 mm) and their tabularium is 8.5 mm-wide (maximum: 10 mm). There are, in average 31 septa of each order (maximum 35). The major septa are long and reach the axial structure. They are spindle-shaped and slightly wavy in the dissepimentarium, straighter in the tabularium, except their axial ends that curve near the axial structure. Their width is greatest (0.8 mm) in the outer part of the tabularium. Their axial ends are sharp or rounded. The minor septa enter into the tabularium on 1 mm, their length varies between one-half and two-thirds of the major (Fig. 3: 3c). The cardinal and counter septa are connected to the axial plate but the cardinal one can also be shorter than the other septa. The axial structure is symmetrical and composed of 2.5-3 mm-long axial plate spindle-shaped or elongated, bearing about 20 septal lamellae, usually short and thick. The latter are confluent with the axial ends of the major septa (Fig. 3: 1b, 3b) or are intercepted by upturned axial tabellae (Fig. 3: 1c). The dissepimentarium is composed of 5 to 11 rows of concentric or rarely herringbone interseptal dissepiments. The inner row is thickened in continuity with the septa (Fig. 3: 1a) and closely spaced to the next row. Lonsdaleoid dissepiments are occasional in the outer zone (Fig. 3: 1a). The external wall is 0.4–0.5 mm-thick, wavy or festooned.

Internal characters in longitudinal section. The axial structure is continuous vertically and its axial plate is slightly sinuous (Fig. 3: 1b). The tabularium is slightly divided in Vassiljuk's holotype. The axial tabellae are cone- to tent-shape, upturned towards the axial structure. The periaxial tabellae are vesicular and sub-parallel to the axial ones. The dissepiments are vesicular and relatively flat but show an abrupt change in the orientation from gently inclined in the outer part of the dissepimentarium to steeply inclined near the tabularium (Fig. 3: 1b). There are c. 22 tabellae and 18 dissepiments per vertical centimetre.

Discussion. As stated earlier, the species shows corallites very similar to individual specimens of the solitary genus *Amygdalophyllum*. *A. dianthoides* (McCoy, 1851) which sometimes develops a limited increase shows larger corallites and has more septa (up to 40 septa for c. 20 mm in diameter) than *Vassiljukia columnariformis*. The proto-colonial *A. minimum* Webb (1990) differs from the present species by smaller corallites (less than 8 mm) and a fasciculate habitus. The largest species of massive Australian lithostrotionid, *Australastraea parvicolumnare* (Pickett, 1966) has similar dimension (15 mm wide) but has less septa (24-27 versus 31-35 for *V. columnariformis*). Moreover, the Australian species shows a discontinuous wall that produces a thamnastreoid habitus rather than a cerioid one.

Distribution. Vassiljuk's (1960) specimens come from the C_1^v c-d levels of the Donets Basin which corresponds to the Early Visean (Fig. 2). The Turkish specimen was collected at Kokaksu, in a horizon attributed to the Uppermost Moliniacian (Lower Visean) RC5B coral subzone (Denayer, 2014), together with *Dorlodotia briarti, D. euxinensis, Ceriodotia bartinensis and Lithostrotion potii*). Associated foraminifers indicate the MFZ11B zone of Hance et al. (2011).

4. Discussion

As discussed above, *Vassiljukia columnariformis* differs from *Amygdalophyllum dianthoides* by a stable colonial habitus. But what is a stable colonial habitus? How can we distinguish a small colony from a solitary coral with a limited increase? Where does the coloniality begin? It is commonly admitted that all the colonial genera originated from solitary corals that developed, for any reason, an increase at different moment of their evolution. Examples are numerous (see Rodríguez and Somerville, 2010): *Corwenia* evolved from *Dibunophyllum, Lonsdaleia* evolved from *Axophyllum, Palastraea* evolved from *Palaeosmilia*, the latter producing a massive habitus while the others are fasciculate.

In theory, the first specimens of a colonial genus are those who produce one or several buds which have the ability to produce themselves other clonal buds and thus initiating a third generation of individuals. This ability is supposed to be genetically controlled (Fedorowski, 1978; Fedorowski and Ogar, 2013). Nevertheless, before reaching this true colonial stage, the solitary coral can develop proto-colonies in which the second generation of individuals is unable to produce any buds (limited increase, see example in Table 1). These offspring-less individuals are the "lost structures" of Fedorowski (1978) and form, together with the initial corallite, a protocolony in the sense of Fedorowski and Ogar (2013). After these authors, the lost structures are characterized by a small diameter and morphological features different from those observed in the mature parent. Several proto-colonies have been documented in the fossil record and described either under a new generic name, or as a special case of the solitary taxa. *Palaeosmilia murchisoni* showing few offsets occurs in the Lower Visean of Belgium (Poty, 2010) whereas the true *Palastraea* (i.e. with a stable colonial habitus) appeared only in the Upper Visean. Obviously, the Lower Visean specimens are protocolonies and consequently, being still *Palaeosmilia*, they should not be classified within the genus *Palastraea*. Similarly, *Amygdalophyllum minimum* from the Tournaisian of eastern Australia (Webb, 1990) shows occasional offsets but the true coloniality is not acquired at this stage. Following this rule, the Lower Visean *Amygdalophyllum dianthoides*, producing only limited offsets, is a proto-colony and differs from *Vassiljukia*. Moreover, in the Donets Basin, the proto-colonial forms commonly co-occur with true solitary specimens of the same species in the same beds. They thus share a stratigraphic and geographic distribution and exemplify a sympatric evolution. On the other hand, the Givetian genus *Heliophyllum* of North America includes solitary, proto-colonial and true

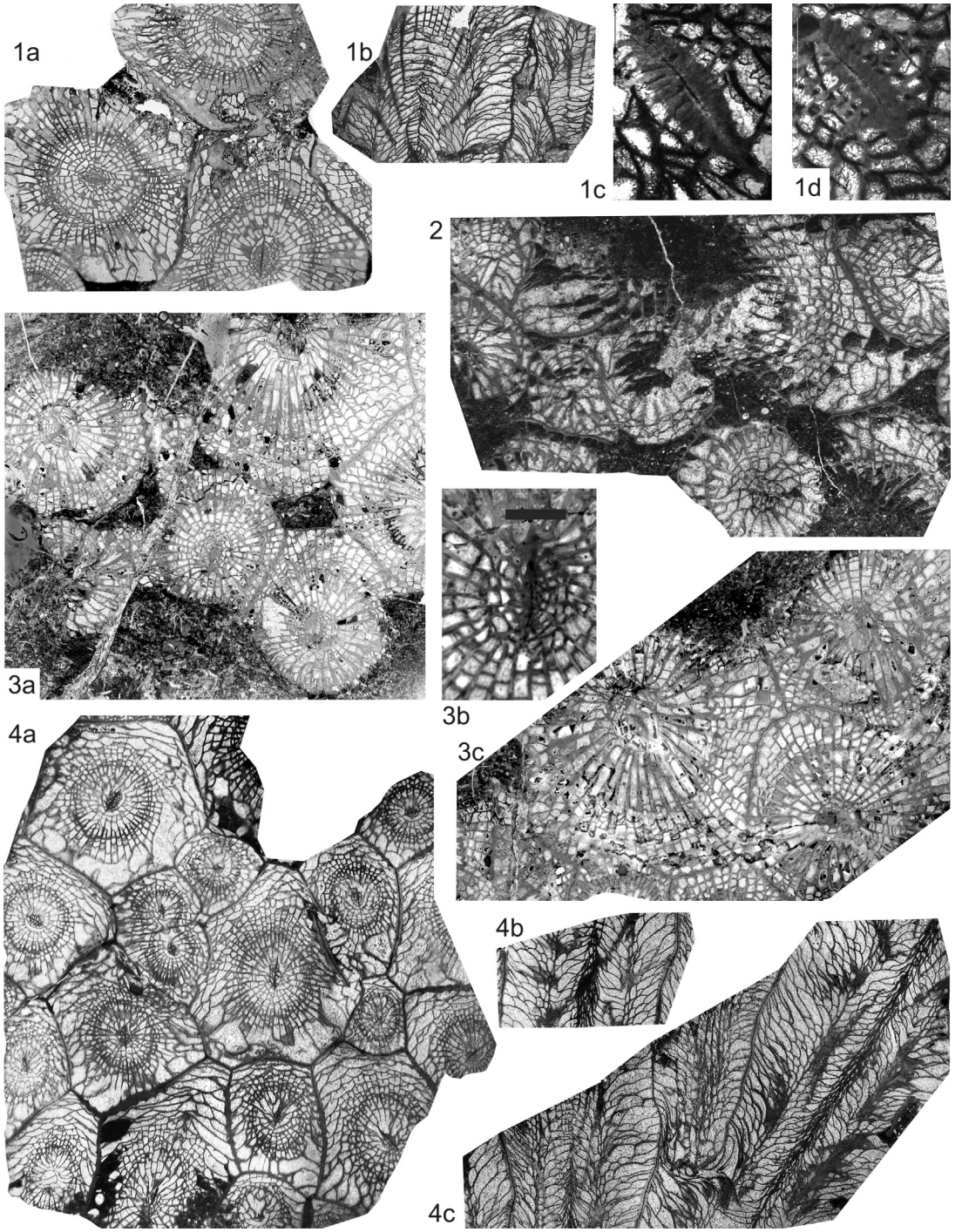

Fig. 3. *Vassiljukia columnariformis* (Vassiljuk, 1960) and *"Lonsdaleia" longiseptata* Lissitzin, 1925 from the Lower Visean of Ukraine and Turkey. 1a–b: Holotype (specimen 1405/11) figured by Vassiljuk (1960) as Plate 22, Figure 4-4a under the name *Lithostrotion columnariformis*; 1a: transverse section (TS); 1b: longitudinal section (LS); 1c–d: close-up views of the axial structure in TS. 2: Specimen 2P264-A/7-2 from the Mokra Volnovakha river valley (Donets Basin, Ukraine), TS. 3: Specimen ULg.PA.K.4.9 from the Kokaksu river valley (NW Turkey), 3a–c: TS; 3b: close-up view of the axial structure in TS. 4a–c: Specimen 1405/79, figured by Vassiljuk (1960) as Plate 30, Figure 2-2a under the name *Lonsdaleia longisepta*, 4a: TS, note the development of the lonsdaleoid dissepimentarium, 4b–c: LS, compare to 1b.

Fig. 3. *Vassiljukia columnariformis* (Vassiljuk, 1960) et *"Lonsdaleia" longiseptata* Lissitzin, 1925 du Viséen basal d'Ukraine et de Turquie. 1a–b : Holotype (spécimen 1405/11) figuré par Vassiljuk (1960), planche 22, figure 4-4a sous le nom *Lithostrotion columnariformis* ; 1a : coupe transversale (CT) ; 1b : coupe longitudinale (CL) ; 1c–d : vue rapprochée de la structure axiale en CT. 2 : Spécimen 2P264-A/7-2 de la vallée de la rivière Mokra Volnovakha (bassin du Donets, Ukraine), CT. 3 : Spécimen ULg.PA.K.4.9 de la vallée de la rivière Kokaksu (Nord-Ouest de la Turquie), 3a, c : CT ; 3b : vue rapprochée de la structure axiale en CT. 4a–c : Spécimen 1405/79, figuré par Vassiljuk (1960), planche 30, figure 2-2a sous le nom *Lonsdaleia longisepta*, 4a : CT, notez le développement du dissépimentarium transeptal ; 4b–c : LS, comparez à 1b.

Table 1
Examples of solitary corals and their colonial equivalent with the inferred proto-colonial stage. Data are from Barbour (1911), Denayer (2011), Denayer and Webb (2015), Fedorowski (1970), Fedorowski and Ogar (2013), McCoy (1849), Oliver and Sorauf (2002), Poty (2010), Somerville and Rodríguez (2010) and Webb (1990).
Tableau 1
Exemples de coraux solitaires et de leurs formes coloniales ainsi que leur stade proto-colonial. Données issues de Barbour (1911), Denayer (2011), Denayer et Webb (2015), Fedorowski (1970), Fedorowski and Ogar (2013), McCoy (1849), Oliver and Sorauf (2002), Poty (2010), Somerville and Rodríguez (2010) and Webb (1990).

Solitary	Age	Proto-colonial	Age	Colonial	Age	Reference
Craterophyllum verticilum	Silurian	*Craterophyllum verticilum*	Silurian	Not known with certainty		Barbour (1911)
Heliophyllum	Givetian	*Heliophyllum*	Givetian	*Heliophyllum*	Givetian	Oliver and Sorauf (2002)
Corphalia	Tournaisian	*? Corphalia*	Late Tournaisian	? *Dorlodotia*	Early Viséan	Denayer (2011)
Amygdalophyllum dianthoides	Early Viséan	*Amygdalophyllum dianthoides*	Early Viséan			McCoy (1849)
Amygdalophyllum	Early Viséan	*?A. dianthoides*	Early Viséan	*Vassiljukia*	Early Viséan	This paper
Axophyllum	Viséan	*Howthia*	Early Viséan	*Lonsdaleia*	Late Viséan	Rodríguez and Somerville (2010)
Palaeosmilia murchisoni	Viséan	*Palaeosmilia*	Early Viséan	*Palastraea*	Late Viséan	Poty (2010)
Spirophyllum geminum	Viséan	*Spirophyllum geminum*	Late Viséan			Fedorowski 1970
Amygdalophyllum minimum	Tournaisian	*Amygdalophyllum minimum*	Tournaisian	*Cionodendron*	Late Tournaisian	Webb (1990) and Denayer and Webb (2015)
Dibunophyllum	Late Viséan	*Cordibia*	Bashkirian	? *Protodurhamina*	Bashkirian	Fedorowski and Ogar (2013)

colonial forms, the latter displaying both fasciculate and massive habitus (e.g., various sub-species of *H. halli*, Oliver and Sorauf, 2002). This variability in the growth form is possibly the phenotypic expression of a genetic diversity as both habitus are found in the same beds.

5. Conclusion

The Lower Visean of the Donets Basin yielded many species of amygdalophyllid corals variously named and figured by Vassiljuk (1960). The re-investigation of her collection led to the identification of a new colonial genus. *Vassiljukia columnariformis*, originally described as a *Lithostrotion* but displays the diagnostic characters of the Amygdalophyllidae. Its cerioid habitus is interpreted as a genuine colonial facies and not just a "lost structure". Interestingly, in NW Turkey, *Vassiljukia columnariformis* first appears in the same bed as *Ceriodotia bartinensis* (a cerioid *Dorlodotia*) and *Lithostrotion potii* (the oldest of the genus, cerioid form derived from *Siphonodendron*). The Lower Visean of the Donets Basin also yielded "*Lonsdaleia" longiseptata*, another cerioid massive coral similar and questionably synonym to *V. columnariformis*. Similarly, in South China, the first Visean cerioid corals ("*Lithostrotionella*") derived from the fasciculate genus *Heterostrotion* (Poty et al., 2011) also appear at approximately the same time. The Lower Visean was hence a period of "ceriodization" of corals but no explanation is proposed so far for this observation.

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