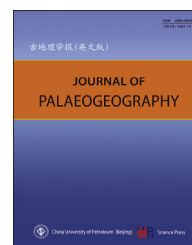




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Biopalaeogeography

Origin and evolution of the genera *Lonsdaleia* and *Actinocyathus*: Insights for the Mississippian palaeogeography from the western Palaeotethys



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Abstract Representatives of the subfamily Lonsdaleiinae Chapman, 1893 are common in the Mississippian of the western Palaeotethys. A general analysis of the origin, distribution and evolution of that subfamily has been undertaken. The most probable hypothesis for the origin of the genus *Lonsdaleia* McCoy, 1849 is to acquire colonialism via the genus *Axophyllum* Milne Edwards and Haime, 1851. *Actinocyathus* d'Orbigny, 1849 would be a descendant of *Lonsdaleia* by increasing integration in the colonies. The first occurrences of *Lonsdaleia* have been recorded in the lower Viséan from northern Britain and northern Tianshan Mountains of northwestern China, but the diversification and migration to the whole Palaeotethys only happened in the late Viséan. Three hypotheses are proposed on that matter. The Serpukhovian was also a period of migrations and diversification for these genera. Both *Lonsdaleia* and *Actinocyathus* have been recorded in Bashkirian refuges, the Sverdrup Basin in northern Laurasia and the Tindouf Basin in northern Africa, respectively. The division of the western Palaeotethys into six subprovinces based on the distribution of corals is proposed.

Keywords Carboniferous, Palaeotethys, Biogeography, Evolution, Rugosa

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1. Introduction

The subfamily Lonsdaleiinae Chapman, 1893 comprises colonial corals of the family Axophyllidae (Hill, 1981). The genera *Lonsdaleia*, *Actinocyathus* and *Seraphyllum* are included in that subfamily. The first two genera are abundant and almost cosmopolitan. The third one has been recorded only in the Montagne Noire up to now (Poty and Hecker, 2003). Some other genera have been also included in the subfamily, but they have been regarded as synonyms of the cited ones (Hill, 1981).

The Lonsdaleiinae have been cited in most areas of the world in the upper Visean and the Serpukhovian (see references below), and more rarely in the Bashkirian. However, their distribution is quite irregular for several reasons: The knowledge of the Mississippian coral record shows strong variations in different geographical areas. In addition, the name *Lonsdaleia* has been used for Pennsylvanian corals that belong to other families such as Petalaxidae or Waagenophyllidae (Dobrolyubova, 1936; Douglas, 1936; Easton, 1960; De Groot, 1963). Moreover, some citations may not be consistent, either because the identification is not clear, or because the age of the occurrence is doubtful (Grosch, 1912; Hudson, 1958). An extensive revision of the occurrences of the genera *Lonsdaleia* and *Actinocyathus* in different regions of the world provides new data that are useful to present a general view of the origin, evolution and migrations of these two genera.

The taxonomic position of the two involved genera, *Lonsdaleia* McCoy, 1849 and *Actinocyathus* d'Orbigny (1849), has been matter of discussion for a long time. Martin (1809) described and figured corals with the names *Erismatolithus Madreporites (duplicatus)* and *Erismatolithus Madreporites (floriformis)*. Both were later described and figured under different names (see Smith, 1915 for a complete review of the older literature). McCoy (1849) defined the genus *Lonsdaleia* for fasciculate corals having a complex axial structure and lonsdaleoid dissepiments. d'Orbigny (1849) introduced the genus *Actinocyathus* for corals having massive (cerioid) habit, complex axial structure and lonsdaleoid dissepiments. McCoy (1851) established the species *L. duplicata* as the genotype of *Lonsdaleia* and used the name *Strombodes* for the massive corals with identical inner features. Milne-Edwards and Haime (1850–54) included both massive and fasciculate forms in a single genus that they called *Lithostrotion* (in 1850) and later *Lonsdaleia* (in 1851 and 1854). Fromentel (1861) introduced the name *Stylidophyllum* for the massive forms. This proposal was not much followed, because most authors in the subsequent

years used the name *Lonsdaleia* for both massive and fasciculate corals (Thomson and Nicholson, 1876; Vaughan, 1905; Garwood, 1912; etc.), but some authors used that name (Chi, 1931; Gorsky, 1935).

Lang *et al.* (1940) stated that the name *Actinocyathus* is available. Kato (1966) demonstrated that it has priority over *Stylidophyllum* Fromentel (1861) that was used for cerioid Lonsdaleiinae by some authors (Gorsky, 1935; Dobrolyubova, 1936, 1958; Yamagiwa, 1961), either as a subgenus of *Lonsdaleia* or as a generic name. Kato (1966) proposed that *Actinocyathus* should substitute *Stylidophyllum* if the latter could be considered as a separate genus. Thus, Sando (1975) postulated it as a subgenus of *Lonsdaleia*. Hill (1981) proposed the use of *Actinocyathus* as a separate genus from *Lonsdaleia*. Subsequently, some authors considered it as a subgenus (Poty, 1981; Sando, 1983; Poty and Hecker, 2003; Hecker, 2012) and others as a genus (Mitchell, 1989; Wang, 1989; Rodríguez *et al.*, 2013a). The differentiation of genera based on different habits is a common feature in Paleozoic corals (e.g. *Lithostrotion* Fleming, 1828, *Siphonodendron* McCoy, 1849), but there are different opinions between the specialists on rugose corals on that matter (Hill, 1938–41, 1981; Fedorowski, 1978, 1981, 1984; Poty, 1981, 2010). In the case of *Lonsdaleia* and *Actinocyathus*, as there is no consensus, and since it is a matter of subjectivity, we will use both names as separate genera, because it simplifies the terminology.

2. Discussion

The Lonsdaleiinae from the Tindouf Basin in Morocco provide important information for the understanding of the Visean and Serpukhovian palaeogeography of the western Palaeotethys, because they complete the view of the evolution of these corals in the context of Europe and North Africa. In order to analyse the distribution of the Lonsdaleiinae, it is necessary first to revise the origin and evolution of the genus *Lonsdaleia* s.l. (including the genera/subgenera *Lonsdaleia* and *Actinocyathus*).

2.1. *Lonsdaleia* origin and diversification

Several hypotheses have been proposed in order to explain the origin of the genus *Lonsdaleia*. Thomson (1883) suggested that *Thysanophyllum* (a massive genus similar to *Lonsdaleia*, but without or with reduced axial structure) could be the ancestor of *Lonsdaleia*. Carruthers in Garwood (1912) followed

that hypothesis by comparing the neanic stages of *Lonsdaleia* and *Thysanophyllum*. Smith (1915), in his monograph on *Lonsdaleia*, supported it, showing the early neanic stages of these genera in his plate XVII. Vaughan (1905) proposed a different hypothesis when he suggested that *Lonsdaleia* was derived from the solitary genus *Clisiophyllum* by development of colonialism and lonsdaleoid dissepiments. Only a year later, Matley and Vaughan (1906) changed his hypothesis and proposed the genus *Carcinophyllum* as the ancestor of *Lonsdaleia*. The advantage of this genus for the ancestry is its lonsdaleoid dissepimentarium, and thus requiring only the development of colonialism for the appearance of the new genus.

Hill (1938–41) suggested that the relationship between *Lonsdaleia* and *Thysanophyllum* could be inverse, with the first being the ancestor of the latter. That hypothesis was followed by Vassiljuk (1960) and other authors, but they did not explain the ancestry of *Lonsdaleia*. Poty (1981) suggested that *Axophyllum* should be the ancestor of *Lonsdaleia*, following the hypothesis of Matley and Vaughan (1906), as Semenov-Tian-Chansky (1974) demonstrated that *Carcinophyllum* is a synonym of *Axophyllum*. That hypothesis has been followed later by most authors (Poty and Hecker, 2003; Poty, 2010; Rodríguez and Somerville, 2010; Somerville and Rodríguez, 2010). Smith (1915) also suggested that the massive forms of *Lonsdaleia* derived from the fasciculate ones. He used the name *Lonsdaleia*, but now the name *Actinocyathus* is accepted for massive forms, either as a separate genus, or as a subgenus. Also, the consideration of *Lonsdaleia* as an ancestor of *Actinocyathus* is agreed by most authors (Hecker, 1997; Poty and Hecker, 2003; etc.).

An important question for the analysis of the distribution of the genera *Lonsdaleia* and *Actinocyathus* is when and where they appeared. The oldest *Lonsdaleia* species is *L. praenuntia* Smith (1915). The type specimens were collected by Vaughan (1911) in the lower Viséan from Arnside, NW England. This species shows a reduced axial structure that resembles that of *Cystolonsdaleia* Fomichev, 1953 or *Dorlodotia* Salée, 1920. In fact, this species was not included in the biostratigraphical chart of Mitchell (1989), who considered the first appearance of *Lonsdaleia* to be much higher, in his zone H (Brigantian). The doubts on the identification of the specimens of Vaughan (1911) as *Lonsdaleia* are due to the absence of buddings that demonstrate its coloniality. Thus, they could also be regarded as representatives of *Axophyllum*. Poty (1980, 1981) suggested that this species could be the ancestor of the genus *Dorlodotia*. Hecker (2011, p. 47) indicated that “studies of variability in *Dorlodotia*

suggest that *Lonsdaleia praenuntia* is also a *Dorlodotia*”. We can't agree with this statement, because even if the axial structure of *L. praenuntia* is “loosely constructed and asymmetrical ...” as pointed out by Smith (1915, p. 243), the structure of the tabularium is typical of *Lonsdaleia* and, as noted by Smith (1915, p. 243), “the central column exhibits no marked difference from the same structure in *L. duplicata*.” Fig. 1 shows the similitudes and differences: a complex axial structure and concave periaxial tabulae in *L. praenuntia* and simple axial structure and periaxial tabulae elevated towards it in *Dorlodotia briarti*. Consequently, *Lonsdaleia praenuntia* must be regarded as an early representative of that genus.

It is a common fact in many rugose corals that colonial taxa descend from solitary corals (Fedorowski, 1978; Poty, 2010; Rodríguez and Somerville, 2010; Denayer and Webb, 2015). In many cases, there are some intermediate stages of gregarism and of solitary corals developing offsets in the calice without further growth of a true colony. It has been called quasi-colonialism (Fedorowski, 1978) or protocolonialism (Somerville and Rodríguez, 2010). As stated above, *Lonsdaleia* probably derived from a solitary species of *Axophyllum*, a genus which shares most inner features with it. A case of a gregarious and quasi-colonial axophyllid (*Howthia* Somerville and Rodríguez, 2010) was

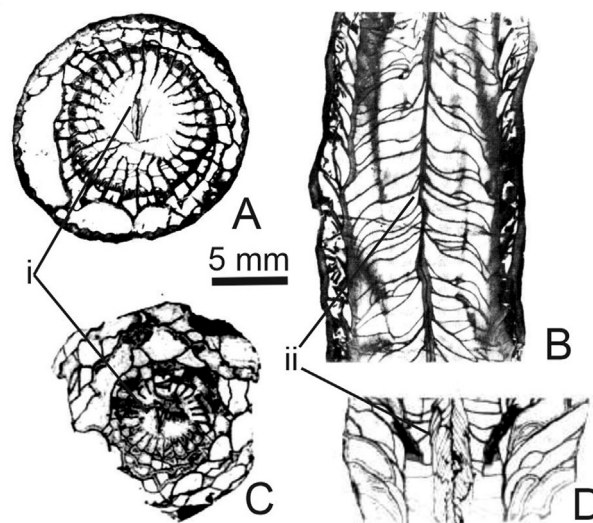


Fig. 1 Comparison between *Dorlodotia briarti* (A, B, transverse and longitudinal sections; figures taken from Poty, 1981) and *Lonsdaleia praenuntia* (C, D, transverse and longitudinal sections; figures taken from Smith, 1915). The main differences are (i) that the axial structure is more complex in *L. praenuntia*; it is joined to the counter septum in *D. briarti* and to the cardinal septum in *L. praenuntia*, and (ii) the periaxial tabulae are concave and more or less horizontal in *L. praenuntia*, but in *D. briarti* there are no axial and periaxial series of tabulae and they are elevated towards the medial plate.

described in the upper Tournaisian from Howth (Ireland). It could be an example of the way for the appearance of *Lonsdaleia* from *Axophyllum*. And it could be the ancestor of all the Lonsdaleiinae if they are not polyphyletic.

The main difficulty to accept *L. praenuntia* as the ancestor of the late Viséan species of *Lonsdaleia* is the total absence of the genus in the middle Viséan. However, several species have been recorded in the upper Viséan of the same domain (the Alston block of northern Britain) (Smith, 1915). This could be due to two different reasons (1) *L. praenuntia* is not the ancestor of the late Viséan species, and they evolved quickly during the Asbian transgression. The development of that species could be an early attempt to develop colonialism in the family, without descendants, or it could be an *Axophyllum*. (2) The presence of several species in the same area indicates a previous diversification during the middle Viséan that is not recorded, or they evolved quickly during the late Viséan.

However, the development of colonialism could have occurred more than one time in the Axophyllidae and *Lonsdaleia* could be polyphyletic. In many species of *Lonsdaleia*, the axial structure is closer to that of the genus *Dibunophyllum* than to that of *Axophyllum*. In *Dibunophyllum* and many species of *Lonsdaleia*, the axial structure is composed of a median lamella, a small number of radial lamellae and tabulae inclined to the periphery. The lamellae are usually anastomosed or winding. On the contrary, in *Axophyllum*, the axial structure is composed of thickened, more irregular and anastomosing radial lamellae, crossed by a median plate. This was the reason why Smith (1915) also suggested the possibility of that genus as the ancestor of *Lonsdaleia*. He rejected that possibility, but the similarities are conspicuous, because in many species of the *Lonsdaleia duplicata* and *Actinocyathus floriformis* groups, the axial structure is mainly dibunophylloid. We checked many specimens of *Lonsdaleia* from different provenances (Tindouf, Betic Cordillera, Britain, Carnic Alps, Moscow Basin, etc.) and all of them show a consistent homogeneity in the microstructure that fit with the Axophyllidae family (lamellar wall, tabulae, dissepiments and septal stereoplasm), but not with *Dibunophyllum* (granulofibrous mesoplasm and fibrous stereoplasm).

Actinocyathus and *Lonsdaleia* can be divided into several groups of species, with different features, and probably with different ecological constraints that conditioned their palaeogeographic distribution. Hecker (1997, 2010) gave a complete view of the species groups of *Actinocyathus*; the species group of *A. floriformis* Martin with short minor septa and the

species group of *A. crassiconus* with long minor septa (Fig. 2). As she explained in detail their geographic and ecological distribution, we will not develop this matter here. Some species belonging to the *A. floriformis* group are *A. borealis*, *A. bronni* and *A. rossica* (Hecker, 1997). Typical representatives of the *A. crassiconus* group are *A. gorskyi*, *A. latevesiculosus*, *A. mariae*, *A. sarytschevae*, and *A. subtilis*.

In *Lonsdaleia*, the type species *Lonsdaleia duplicata* and most species show a dibunophylloid axial structure and thin structures and lived mainly in stable carbonate platforms. Some of the species included in this group are *L. alstonensis* Smith (1915), *L. arctica* Gorsky (1935), *L. caledonia* Smith (1915), *L. crassigemata* Dobrolyubova (1958), *L. duplicata* Martin (1809), *L. grandicaspia* Degtiarev (1965), *L. majobaensis* Fan (1978), *L. melmerbiensis* Smith (1915), *L. multiseptata* Dobrolyubova (1958), *L. permanoseptata* Vassiljuk (1960), *L. siblyi* Smith (1915), *L. singularis* Dobrolyubova (1958), and others. In contrast, some other species that we will name the *Lonsdaleia corbariensis* group, show smaller corallites, thick structures and more irregular axophylloid axial structure. The species that we include in this group are *L. agapoviensis* Kachanov, 1964, *L. corbariensis* Semenoff-Tian-Chansky and Ovtracht (1965), *Lonsdaleia carnica* Rodríguez et al., 2019, *L. redondensis* Poty and Hecker

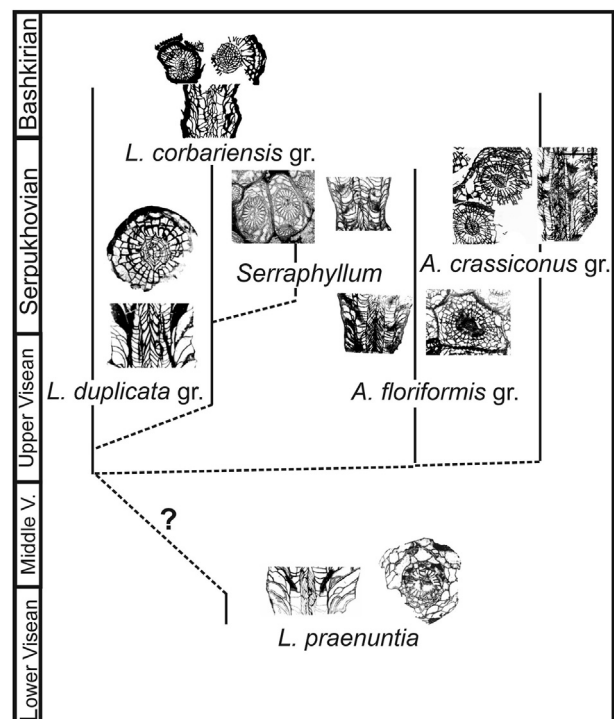


Fig. 2 Inferred phylogenetic relationships between the different species groups in Lonsdaleiinae. Abbreviations: A. = *Actinocyathus*; L. = *Lonsdaleia*; gr. = Group.

(2003), *L. reutheri* Boll (1985), *L. taveli* Altmark (1963) and *L. tichyi* Dobrolyubova (1958). Most of these species lived in more unstable environments, associated to microbial communities, and their geographical distribution differs greatly from those of the *Lonsdaleia duplicata* group. Poty and Hecker (2003) demonstrated the presence of a biform tabularium and periaxial cones in several species of *Lonsdaleia*. We checked all our specimens and many in the literature to analyse the presence of these features in the mentioned groups. In many cases we couldn't find proofs of their presence because the published figures don't show these features, but they seem to be present in several species of both groups of *Lonsdaleia* and in *Actinocyathus* (Table 1).

2.2. *Lonsdaleia* and *Actinocyathus* distribution

Any palaeogeographic analysis needs to take into account the plate tectonics, and the areas to be

compared should be consistent with the different terranes that are known in each period of geological history. We tried to follow this axiom in the analysis of the distribution of the genera *Lonsdaleia* and *Actinocyathus*, but sometimes, the record itself or the studies in some areas are scarce. For example, in Germany, three palaeogeographic domains are recognised for the Carboniferous: the Rhenohercynian, the Saxothuringian and the Moldanubian, from north to south (Weyer, 2000), but records in those domains are very scarce and in most cases they occur in allochthonous blocks or in reworked facies (olistostromes or culm). Thus, for this study, these three domains will be amalgamated as one single area (Germany). The same has been done with other areas, such as the three main Austrian outcrops yielding Mississippian corals (Carnic Alps, Nötsch and the Greywacke Zone; Hubmann, 2002) that will be considered as one unit. We also use the name Poland for several palaeogeographic units in that country (Sudetes, Upper Silesian Basin, Lublin Basin, and also the prolongation southeastwards

Table 1 Comparison of biometric data for species of *Lonsdaleia* and *Actinocyathus* mentioned in this paper. Abbreviations: N = Number of major septa; Dt = Diameter of tabularium; Das/Dt = Ratio of diameter of axial structure to tabularium diameter; RL = Number of radial lamellae; B.T. = Biform tabularium; ? = Not determined.

Species	N	Dt	Das/Dt	RL	B.T.	Minor septa
<i>Lonsdaleia</i>						
<i>L. duplicata</i> Martin	25–27	4.5–6	1/3–1/2	10–20	Present	Short
<i>L. agapoviensis</i> Kachanov	25–27	9.0–11.0	1/4	5–10	No	None
<i>L. alstonensis</i> Smith	26–28	4.0–5.0	1/2	15–30	?	Short
<i>L. arctica</i> Gorsky	22–24	3.0–5.0	1/3–1/2	20–30	?	Short
<i>L. caledonia</i> Smith	28–30	7.0–9.0	1/2	15–25	No	Long
<i>L. corbariensis</i> Semenoff-Tian-Chansky	20–25	5.0–7.0	1/2	15–20	?	Long
<i>L. crassigemmata</i> Vassiljuk	25–30	7.0–9.0	1/5–1/4	6–10	No	Short
<i>L. grandicaspia</i> Degtiarev	30–35	10.0–12.0	1/3–1/2	25–30	?	Long
<i>L. majiobaensis</i> Fan	36–37	10.0–12.0	1/4	20–25	Present	Short
<i>L. melmerbiensis</i> Smith	26–28	6.0–8.0	1/3	5–10	Present	Short
<i>L. multiseptata</i> Dobrolyubova	27–28	9.0–10	1/3	15–25	Present	Long
<i>L. permanoseptata</i> Vassiljuk	18–21	5.0–7.0	1/3	13–15	?	Short
<i>L. praenuntia</i> Smith	26–28	5.0–6.0	1/3	5–10	?	None
<i>L. redondensis</i> Poty and Hecker	15–18	3–4.2	1/3	5–10	Present	Long
<i>L. reutheri</i> Boll	24	7.0–10.0	1/3	5–10	Present	Short
<i>L. siblyi</i> Smith	22–24	5.5–6.5	1/3–1/2	10–15	No	Short
<i>L. singularis</i> Dobrolyubova	27–29	9.0–10.0	1/3–1/2	15–25	?	Short
<i>L. taveli</i> Altmark	27–28	6.0–9.0	1/3	8–10	?	Long
<i>L. tichyi</i> Dobrolyubova	20–23	5.0–7.0	1/3	5–10	?	None
<i>L. carnica</i> Rodríguez	22–25	4.3–5.2	1/4–1/3	5–20	No	Long
<i>Actinocyathus</i>						
<i>A. borealis</i> (Dobrolyubova)	19–23	5.0–6.5	1/4–1/2	10–20	Present	Short
<i>A. bronni</i> (Milne-Edwards and Haime)	30–34	7.0–10.0	1/3	10–15	No	Short
<i>A. crassiconus</i> (McCoy)	22–27	4.8–6.5	1/2	15–30	Present	Long
<i>A. floriformis</i> (Martin)	20–25	4.0–6.0	1/3	5–10	Present	Short
<i>A. gorskyi</i> (Dobrolyubova)	26–33	5–7.5	1/2	15–24	Present	Long
<i>A. latevesiculosus</i> (Dobrolyubova)	22–27	6–8.5	1/3	7–12	Present	Long
<i>A. mariae</i> Rodríguez <i>et al.</i>	23–28	6–9	1/3–1/2	10–30	Present	Long
<i>A. rossicus</i> (Stuckenberg)	19–24	5.0–6.0	1/3–1/2	15–25	No	Short
<i>A. sarytschevae</i> (Dobrolyubova)	34–40	7.5–10.3	2/3	10–30	Present	Long
<i>A. sp.</i> A Hecker	21–26	4.8–6.5	1/3–1/2	8–20	Present	Long
<i>A. subtilis</i> (Dobrolyubova)	21–30	4–6.3	1/3–1/2	10–24	Present	Long

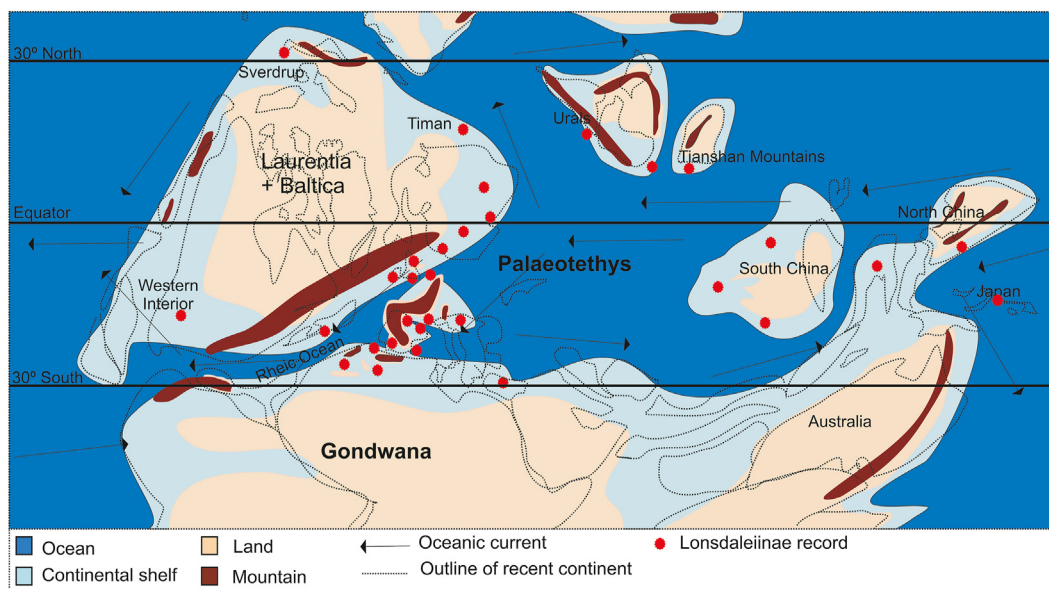


Fig. 3 Global palaeogeography during the late Mississippian with location of occurrences of the Lonsdaleiinae. The geographical areas that are not labelled are listed in Fig. 4 (modified from Webb, 2002 and Somerville *et al.*, 2020).

of it in Ukraine, the Lviv-Volynsk Basin). The same problem exists with the Balkans, where there are some important studies (Kolosvary, 1951; Kostic-Podgorska, 1957, 1958), but the knowledge is scarce and incomplete. In other cases, the palaeogeographic domains do not fit completely with the recent political divisions. In order to avoid unnecessary terminology, we will use a generic geographic name as an approximation. Thus, Scotland, northern England, NW England, Derbyshire and North Wales can all be included in northern Britain, with South Wales, Bristol district and Mendips in southern Britain. Although two distinct palaeogeographic regions can be distinguished in Belgium, the Campine and the Franco-Belgian basins, we will consider both under the common name of Belgium, because the data in the Campine Basin are relatively scarce (Poty, 1981; Aretz and Chevalier, 2007) and because the two genera involved are respectively in the Franco-Belgian Basin and in the Campine Basin (Poty, 1981; Denayer *et al.*, 2011). Finally, Turkey comprises several terranes that were clearly separated during the Mississippian; in at least four of them there are records of Mississippian corals. In the Istanbul-Zonguldak terrane, whose position in the Visean is not clear (Okay and Tüysüz, 1999), there is no record of *Lonsdaleia* or *Actinocyathus* and it will not be considered here as a separate unit. The Tauride block is related to the north border of Gondwana (Denayer, 2015).

If the oldest known occurrence of *Lonsdaleia* is that of *L. praenuntia* in the lower Visean from north-western England, we can assume that the genus

appeared in that area of the British Isles during the early Visean. The maximum development of *Lonsdaleia* occurred in the late Visean. The great transgression that took place in that period (Conil and Lys, 1977; Ramsbottom, 1979; Herbig, 1998) facilitated the distribution of the coral planulae transported by currents for large distances, because they easily found marine areas to attach themselves to. *Actinocyathus* first appeared also in the late Visean and quickly reached a large area of distribution.

We summarize the occurrences of both genera in Figs. 3 and 4. A general view of their distribution in the Palaeotethys is given in Fig. 3 and a more detailed one with data on each genus is presented in Fig. 4. Only data for the western Palaeotethys are included in the latter, because considering larger areas would impede a precise recognition of the details. Going from south to north and from west to east, the occurrences are as follows.

In the Tindouf Basin of southern Morocco (1), *Lonsdaleia* first occurs in the uppermost Visean, and reaches the maximum abundance and diversity during the Serpukhovian. *Actinocyathus* first occurs in the Serpukhovian, and is still recorded in the lower Bashkirian (Rodríguez *et al.*, 2013a, 2013b). In the Béchar and Reggan areas of Algeria (2), the only record of *Lonsdaleia* is from the Serpukhovian and *Actinocyathus* hasn't been recorded there (Semenoff-Tian-Chansky, 1985). We included here the eastern Tafilalt (near Erfoud, eastern Morocco) where neither *Lonsdaleia* nor *Actinocyathus* have been recorded (Aretz *et al.*, 2013). The same situation happens in Jerada (3) and

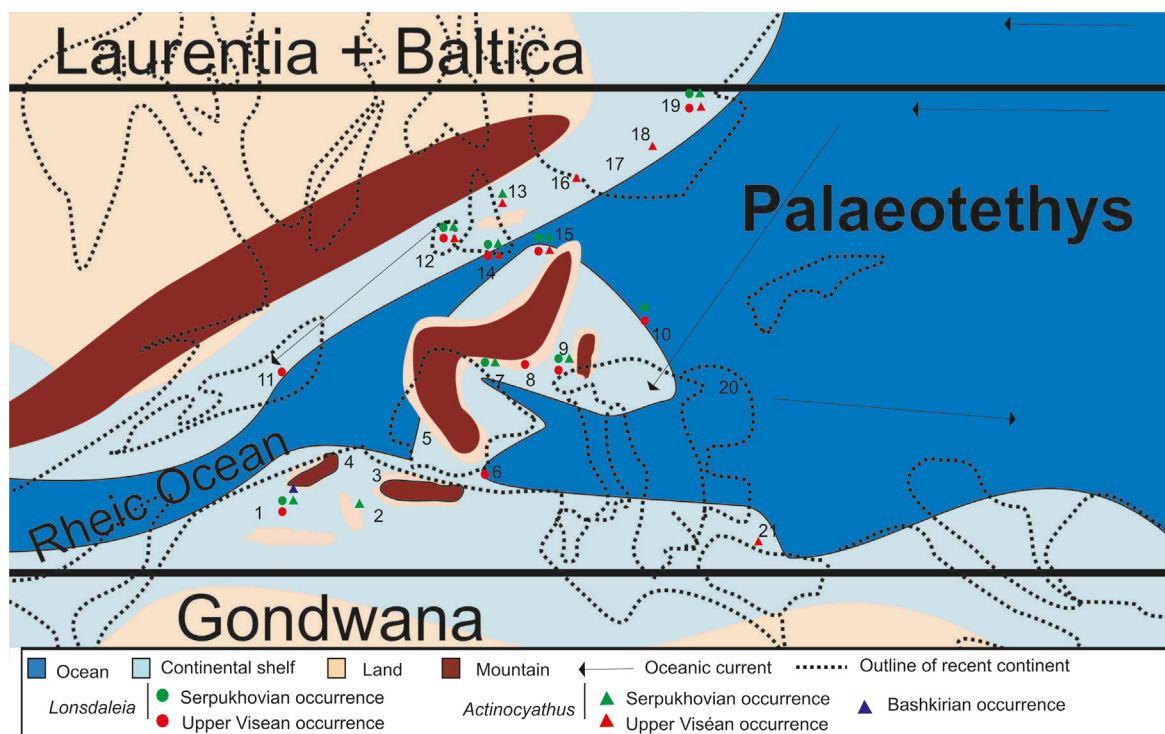


Fig. 4 Palaeogeography of the western Palaeotethys with location of occurrences of the Lonsdaleiinae in the Viséan, Serpukhovian and Bashkirian (modified from Webb, 2002 and Somerville *et al.*, 2020). 1 – Tindouf Basin; 2 – Béchar-Reggan; 3 – Jerada; 4 – Azrou-Khenifra Basin; 5 – Ossa-Morena; 6 – Betic Cordillera; 7 – Cantabrian Mountains; 8 – Pyrenean Mountains; 9 – Montagne Noire; 10 – Carnic Alps (+Nötsch); 11 – Nova Scotia; 12 – Ireland; 13 – Northern Britain; 14 – Southern Britain; 15 – Southern Belgium; 16 – Germany; 17 – Poland; 18 – Donetz Basin; 19 – Moscow Basin; 20 – Balkans; 21 – Tauride.

the Azrou-Khenifra Basin (4) of northeastern and north central Morocco, respectively (Said *et al.*, 2007, 2013; Aretz, 2010). In the Guadiato area and the Los Santos de Maimona Basin (Ossa Morena, SW Spain) (5) both genera are also absent in the Viséan and Serpukhovian rocks (Rodríguez and Falces, 1994; Rodríguez *et al.*, 2016). On the contrary, in the Betic Cordillera (S. Spain, 6), *Lonsdaleia* and *Actinocyathus* were recorded in the uppermost Viséan and lowermost Serpukhovian (Herbig and Mamet, 1985).

In the Cantabrian Mountains of North Spain (7) both genera are absent in the Viséan, but they have been recorded in the Serpukhovian (Boll, 1985). In the Pyrenean Mountains (8), Perret and Semenov-Tian-Chansky (1971) recorded *L. duplicata*, and in the Hautes Corbières, a massif located somewhat further north, Semenov-Tian-Chansky and Ovtracht (1965) recorded *L. corbariensis*, in both cases in the upper Viséan. *Actinocyathus* was not recorded in that region. In the Montagne Noire of south central France (9), *Lonsdaleia* was recorded both in the upper Viséan and in the Serpukhovian. On the contrary, *Actinocyathus* was only recorded in the Serpukhovian (Aretz and Herbig, 2003; Poty *et al.*, 2019). In addition, Poty

and Hecker (2003) described there the subgenus *L. Serraphyllum*, with intermediate features between *Lonsdaleia* and *Actinocyathus* (Fig. 2). In the southern Austrian outcrops (Greywacke zone, Nötsch and Carnic Alps) (10), only the fasciculate genus *Lonsdaleia* has been recorded, both in the upper Viséan from the Greywacke zone (Heritsch, 1933) and in the Serpukhovian of the Carnic Alps (Rodríguez *et al.*, 2019).

In Nova Scotia (11), *Lonsdaleia* has been also recorded in the upper Viséan, but not in the Serpukhovian (Lewis, 1935; Poty, 2002). In Ireland (12), both genera, *Lonsdaleia* and *Actinocyathus* have been recorded (Caldwell and Charlesworth, 1962; Gallagher and Somerville, 1997; Somerville *et al.*, 2007), including transitional forms between them (Cózar and Somerville, 2005). A similar occurrence is recorded in the north of England and Scotland (northern Britain, 13), where both genera occur in the upper Viséan, but only *Actinocyathus* has been verified in the Serpukhovian (Hill, 1938–41; Jackson, 1958; Mitchell, 1989; Riley, 1995). In southern Britain (14), the record is like that in Ireland, with the two genera occurring both in the upper Viséan and Serpukhovian (Mitchell, 1989; Riley 1995). In southern Belgium (15) the detailed

studies by Poty (1985, 1989) indicate the presence of *Actinocyathus* in the coral zone RC8, i.e., uppermost Viséan. Poty *et al.* (2006) showed also the presence of *Lonsdaleia* in that zone. As stated previously, the record in Germany is scarce and derived mainly from allochthonous rocks. *Actinocyathus* has only been recorded in the Brigantian from the Rhenohercynian domain (16), and there is no record of *Lonsdaleia*. Similarly, only *Actinocyathus* has been recorded in the upper Viséan from the Lublin Basin (Poland) (Khoa, 1977) (17) and its southeastern prolongation in the Lviv-Volynsk Basin (Ukraine) (Shul'ga and Ogar, 2009). The record in the Serpukhovian from Poland is very poor and composed mainly of undissected corals, and neither *Lonsdaleia* nor *Actinocyathus* have been reported there. Both *Lonsdaleia* and *Actinocyathus* have been recorded in the Donetz Basin (18) (Vassiljuk, 1960; Fedorowski, 2022). In the Moscow Basin (19), the *Lonsdaleiinae* flourished, with *Lonsdaleia* and *Actinocyathus*, both being present in the upper Viséan and in the Serpukhovian (Dobrolyubova, 1958; Hecker, 1997, 2001, 2010; Somerville *et al.*, 2020).

None of the *Lonsdaleiinae* genera have been cited in the Balkans (20). As stated previously, the record there is scarce, and that region seems to be a mélange of terranes that were piled up against the Variscan Cordillera during the orogeny. The Tauride (21) represent a terrane closely related with northern Gondwana.

The Urals and Timan provided occurrences of *Lonsdaleia* and *Actinocyathus*, both in the upper Viséan and Serpukhovian (Gorsky, 1949; Degtiarev, 1965; Sayutina, 1973; Kossovaya, 1996, 1997). Gorsky (1935, 1938) described several species of *Lonsdaleia* and *Actinocyathus* in the upper Viséan from Novaya Zemlya, but only the latter in the Serpukhovian.

China and the surrounding areas have usually been divided into four or five areas regarded as different terranes with different sedimentation and coral assemblages during the Carboniferous (Wu and Zhao, 1979; Yang *et al.*, 1985; Wang, 1989): In Tianshan Mountains, Wang *et al.* (1994) cited *Lonsdaleia* in the lower Viséan. It is a very important recording, because the only other mention to lower Viséan *Lonsdaleia* is that of *L. praenuntia* in northern England. In the same region, *Lonsdaleia* has been recorded in the upper Viséan (more precisely in the Jilin area, Yang *et al.*, 1985). In Kunlun Mountains, northwestern China, Wu *et al.* (1982) described *Lonsdaleia* in the upper Viséan. *Lonsdaleia* and *Actinocyathus* have been mentioned and/or described in the upper Viséan and Serpukhovian from Sichuan, Guizhou, and Hunan provinces of South China (Yu, 1937; Jia, 1977; Fan, 1978; Jiang, 1982; Wang *et al.*, 2006), but there are no mentions of these genera in North China.

Fontaine *et al.* (1991, 2003, 2005) cited or described *Lonsdaleia* and *Actinocyathus* in the upper Viséan and Serpukhovian from Thailand and Malaysia.

In Japan, there are several citations and descriptions of both *Lonsdaleia* and *Actinocyathus* in the upper Viséan and Serpukhovian from different areas, such as Akiyoshi terrane, Ichinotani Mountains, Fukuji, Onimaru and Omi Limestone (Kato, 1966; Niikawa, 1979; Kato *et al.*, 1987; Igo and Adachi, 2001).

The only citing in Australia of *Lonsdaleia* (Hill and Woods, 1964) seems to be a misinterpretation and consequently the *Lonsdaleiinae* are not present on that continent.

In North America, Webb (1987) described both *Lonsdaleia* and *Actinocyathus* from the upper Chesterian (Serpukhovian) in Oklahoma and Arkansas. Fedorowski *et al.* (2012) described *Lonsdaleia* in the Bashkirian from Sverdrup Basin (Arctic Canada).

2.3. Insights for the evolution of the subfamily *Lonsdaleiinae* from the western palaeotethys

Lonsdaleia and *Actinocyathus* are present in all continents except in Australia and South America during the Viséan and Serpukhovian. So, they can be considered as cosmopolitan genera. The configuration of their occurrences can be used for illustrating the coral migration patterns in the late Mississippian. The major factors controlling those patterns are.

- 1) The coral reproductive cycle; being sessile epibenthic organisms, their only way for migration and colonization of new habitats is the transport of the larvae (planulae).
- 2) The oceanic regime of currents; applying what we know on the system of currents in our planet, Earth's rotation causes a main equatorial current that flows from east to west, and other currents flow polarwards towards high latitudes conditioned by the distribution of the land masses. We can apply actualism here, because the Earth's rotation did not change during its history.
- 3) The distribution of land masses; we have an approximate view of the position of continents because of the many studies that have been carried out from different perspectives (tectonic, palaeomagnetic, biogeographic, etc.). But still, there are different models and reconstructions that do not agree on this matter (see Golonka, 2002; Blakey, 2008; Metcalfe, 2013; Scotese, 2021). The main reason is that the Viséan and Serpukhovian are synorogenic periods and the land masses were changing at that time.

In order to identify the migration paths of the studied genera, the first step is determining where they appeared. The main distribution of *Lonsdaleia* and *Actinocyathus* occurred during the late Viséan, but there are at least two earlier records. The two places where *Lonsdaleia* has been mentioned in the early Viséan are NW England and Tianshan Mountains (NW China). It is not possible that it migrated between the Tianshan terrane and the UK during the early Viséan without leaving occurrences in geographically intermediate areas, many of which are quite well studied. This implies that either one or both of these references may not be correct or that the genus could be polyphyletic.

Consequently, three hypotheses can be proposed on the origin of the genus.

1. *Lonsdaleia praenuntia* appeared in Arnside, NW England, near the western end of the Palaeotethys in the early Viséan. It had a certain period without main changes and without expanding its distribution. But in the late Viséan a major transgression took place and *Lonsdaleia* developed some structural changes diverging in several species in the same geographical area (*L. alstonensis*, *L. caledonia*, *L. melmerbiensis*, *L. siblyi*, etc.). It also evolved into the massive forms of the genus *Actinocyathus* (Smith, 1915). Both genera, also favoured by the transgression, migrated quickly. Theoretically, the main current in the Rheic Ocean, which was near to its final closure, should flow south-westwards (Fig. 4). Thus, the planulae could reach quickly the Nova Scotia territory (Poty, 2002). This hypothesis is also supported by foraminiferal data (cf. Cózar and Somerville, 2021). In a different way, the planulae could use local currents in the shallow platforms that bordered the continent of Laurentia plus Baltica towards Scotland, southern England, Belgium, Poland, Donetz and the Russian Platform. The migration was very quick, and both genera reached the Urals, the Tianshan Mountains, North and South China, and Japan, along the northern margin of the Palaeotethys (Fig. 3). The maximum area of development was the Russian Platform (Hecker, 1997, 2010; Poty and Hecker, 2003). A notable diversification took place there, with the development of two evolutionary lines in *Actinocyathus* and the appearance of the species group of *L. corbariensis* in *Lonsdaleia*, adapted to less favourable environments, and related to microbial communities. That line is represented in the Russian Platform by *L. tichyi*.

In all the cited areas, *Lonsdaleia* and *Actinocyathus* flourished during the late Viséan and Serpukhovian.

The local absence of them can be due more to problems of preservation and the destruction of the original habitats during the Variscan Orogeny. But their presence illustrates the quick evolutive and ecologic success of both genera in so many and distant geographic areas.

Also, during the late Viséan, a migration took place towards the southeast, probably from the Moscow or Donetz Basin. The migration in this way was represented mainly by the *L. corbariensis* group of species, which has been recorded in the southern terranes of Europe, and mainly in the border of the Armorica-Iberian Massif (Montagne Noire, Pyrenees, Cantabrian Mountains and Betic Cordillera). Most occurrences of these species are related to allochthonous blocks in flyschoid facies or in olistostromes and related to microbial communities (Boll, 1985; Herbig and Mamet, 1985; Aretz and Herbig, 2003; Poty and Hecker, 2003; Rodríguez *et al.*, 2019). But the migration towards southwest reached longer, far away to the epicontinental platforms in North Africa (Legrand-Blain *et al.*, 1989). There, the represented species group of *Lonsdaleia* is the *L. duplicata* group that reached the region during the late Viséan and *Actinocyathus*, which reached the region during the Serpukhovian (Rodríguez *et al.*, 2013b and above). The stable conditions in that region, far from the main tectonic movements occurring in the northern part of the western Palaeotethys, allowed some representatives of the genus to survive into the lower Bashkirian. A possible way of migration along the southern border of the Palaeotethys is discarded, because neither *Lonsdaleia*, nor *Actinocyathus* have been recorded in eastern terranes such as the Tauride Alborz etc. The reasons could be excessive amounts of terrigenous material or too high latitudes (see Denayer, 2015).

An additional route of migration took place from the Russian Platform towards the north, reaching Timan (Kossovaya, 1997) and Novaya Zemlya (Gorsky, 1935, 1938). This migration was directed to the west and reached the Sverdrup Basin in northern Canada (Fig. 3), where *Lonsdaleia* has been recorded in the Bashkirian (Fedorowski and Bamber, 2012; Fedorowski *et al.*, 2012).

The occurrence of *Lonsdaleia* and *Actinocyathus* in the Midcontinent and Western Interior of USA (Webb, 1987) is less easy to explain. The northern route is discarded because these genera have not been recorded in the upper Viséan and Serpukhovian in the Rockies. The southern route along the Rheic Ocean is also difficult to accept, because most palaeogeographic reconstructions close the Rheic Ocean before the Viséan (Blakey, 2008; Cao *et al.*, 2017; Scotese, 2021). However, the coral data (as well as

foraminiferal data; see Cózar and Somerville, 2021) show that the Rheic Ocean didn't close before the Bashkirian, because there are typical components of the western Palaeotethys assemblages in the Mid-continent and Western Interior domains (García-Bellido and Rodríguez, 2005; Rodríguez and Kopaska-Merkel, 2014). However, the percentage of western Palaeotethys species in North America is very low, indicating a low level of communication.

A particular case is that of the domains of south-western Spain, the Jerada Basin and the Azrou-Khenifra Basin, where *Lonsdaleia* has not been recorded (localities 3–5, Fig. 4), despite the fact that there have been intense studies on the coral assemblages (Aretz, 2010; Said *et al.*, 2013; Rodríguez *et al.*, 2016). The explanation may be that both the Iberian Massif and the Anti-Atlas formed important barriers for this genus. On the other hand, these domains could be separated from Nova Scotia and Western European domains by a narrow but a deep remnant of the Rheic Ocean, before its final closing. It is remarkable, because in most other aspects, the assemblages of these areas have a high level of similarity with other domains from North Africa and Western Europe.

2. The second hypothesis only changes the origin of the genus to the northern Tianshan Mountains, if *Lonsdaleia praenuntia* is really an *Axophyllum*. From this area, it migrated to the east and southeast to the North China, South China and Japan terranes and at the same time to the west along the coastal platforms of the terranes bordering the northern Palaeotethys, and/or along the equator, taken advantage of the equatorial current and possible islands in the Palaeotethys, reaching first the Eastern European Platform and later (always in the late Visean) the Western European region and the northern Gondwana epicontinental seas. This second hypothesis has the advantage that it could explain better the late arrival to the latter and the scarcity of occurrences in the Midcontinent and Western Interior from North America. It also would explain better the absence in the basins of the South Iberian Massif and in the most northern basins of Gondwana and the refuge in Sverdrup, one of the most distant domains in which *Lonsdaleia* has been recorded.
3. The appearance of *Lonsdaleia* and *Actinocyathus* almost simultaneously in the whole Palaeotethys during the late Visean and two doubtful occurrences in the early Visean allow the validity of a third hypothesis: these genera could be polyphyletic, and originating in different regions at the same time (South China, northern Tianshan Mountains of northwestern China, Russian Platform, and

northern Britain). The homogeneity of structures and microstructures reduces the possibilities of this last hypothesis, but it is not completely discarded. The appearance in different domains could be favoured by the creation of conducive environments for colonial corals associated with the Asbian transgression, which covered with epicontinental seas many previous coastal plains. It also explains the quick diversification. All the routes described in the first hypothesis are valid also in this one.

The distribution of the occurrences of *Lonsdaleia* and *Actinocyathus* in the western Palaeotethys (Fig. 4) confirm the proposal of Somerville *et al.* (2013) on their division into four palaeogeographical sub-provinces that we augment to six: (1) The Atlantic Subprovince (West European countries and Nova Scotia) shows a consistent abundance of both genera in the Visean. In some areas of this subprovince, the Variscan Orogeny activity implied increase of terrigenous sediments and reduction of coral habitats, with the subsequent extinction of these genera during the Serpukhovian. (2) The Mediterranean Subprovince (Pyrenees, Montagne Noire, Betic cordillera, Rif, Balearic Islands, Nötsch, and Carnic Alps) shows similar occurrences of the *L. corbariensis* group in the upper Visean and/or the Serpukhovian. (3) The Saharan Subprovince (Béchar, Reggan, Ahnet-Mouydir, and Tindouf Basin) shows irregular occurrences of both genera, but it was a refuge for the genus *Actinocyathus* in the Bashkirian. (4) The West peri-Gondwanan Subprovince (SW Spain and Moroccan Meseta) shows a total absence of both genera. (5) The Eastern European Subprovince (Moscow Basin, Donetz Basin, and Voronezh) shows also abundance of both genera in the Visean and Serpukhovian. (6) Finally, the Central Europe Subprovince (Germany and Poland) shows an irregular record due to the effects of the Variscan Orogeny that produced a structural mélange of domains and occurrences, mainly in allochthonous facies.

3. Conclusions

The most likely ancestor of the genus *Lonsdaleia* is the solitary genus *Axophyllum*, which would acquire colonialism in favourable environments. *Actinocyathus* descends from *Lonsdaleia* by acquiring the massive habit by increasing the degree of integration in the colonies.

Two records of *Lonsdaleia* have been cited in the lower Visean from northern Britain and northern Tianshan Mountains of northwestern China. But none of these records have continuity in the middle Visean.

The diversification and migration of *Lonsdaleia* and *Actinocyathus* only occurred in the late Viséan and continued during the Serpukhovian. Three hypotheses are proposed on the origin and migration of these genera: (1) Origin in northern Britain and first migration along the epicontinental seas bordering the Palaeotethys; (2) Origin in northern Tianshan Mountains and first migration using the equatorial current and later the epicontinental seas; (3) Simultaneous appearance in several domains of the Palaeotethys and migrations using the previously mentioned routes (polyphyletic hypothesis). In all cases, the migration was quick, because these two genera are recorded in the upper Viséan from the whole Palaeotethys and North America.

Lonsdaleia and *Actinocyathus* became extinguished in most regions at the end of the Mississippian. However, *Lonsdaleia* has been recorded in the Bashkirian of the Sverdrup Basin in northern Laurasia and *Actinocyathus* has been recorded in the Bashkirian of the Tindouf Basin in northern Africa. They both could represent refuges in tropical areas far from the zones affected by the Variscan Orogeny during the early Pennsylvanian.

The western Palaeotethys is divided into six sub-provinces with different distribution of the *Lonsdaleiinae* and other rugose corals.

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Authors' contributions

All the authors participate in the planning of the study, in the review of the taxa, in the design of the manuscript, and wrote parts of it. All authors read the manuscript and approved it.

Conflict of interest

The authors declare that they have not conflict of interest.

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