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Gregarious growth versus colonial habit in the rugose coral family Geyerophyllidae Minato, 1955

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ABSTRACT: The family Geyerophyllidae Minato, 1955 includes corals having clinotabulae, lonsdaleoid dissepiments and a variable complex axial structure formed as an extension of the cardinal septum. Included in the family are four genera originally considered to have a colonial (fasciculate) growth habit - *Carniaphyllum* Heritsch, *Carinthiaphyllum* Heritsch, *Lonsdaleoides* Heritsch, and *Darwasophyllum* Pyzhyanov. More recent studies and a review of the type specimens of *Carniaphyllum, Carinthiaphyllum* and *Lonsdaleoides* have shown them to be solitary corals with a gregarious growth habit. In its original description and in all subsequent works, *Darwasophyllum* has consistently been referred to as a fasciculate coral, but the presence of offsets has not been illustrated in the genus and a colonial growth habit has not been clearly demonstrated. Early Serpukhovian specimens of *Darwasophyllum* from the Etherington Formation (Mississippian) in Canada were initially regarded as fasciculate colonies with long, sub-parallel, closely spaced corallites. When they were studied in detail by means of serial sections, however, these corals were found to be solitary individuals grouped into gregaria, without shared structures or offsets. Thus, true colonies are unknown in the Geyerophyllidae and all genera described as colonial in that family consist of gregarious, solitary corals.

KEYWORDS: Solitary corals, Colonialism, *Darwasophyllum*, *Axolithophyllum* Carboniferous, Rugosa.

1. Introduction

Rugose corals show a large amount of variation in growth form, occurring as solitary individuals or as various types of colonies. There is a great deal of diversity in the size and shape of colonial corals, which range in morphology from incipient colonies through branching, fasciculate colonies to various types of massive colonies. Detailed descriptions of the different types of colonies and their methods of development have been published by many authors (e.g., Fedorowski, 1978; Hill, 1981; Scrutton, 1998; Poty, 2010) and are not treated further in this paper. It should be noted, however, that the formation of colonies may be confused with the development of a gregarious growth habit – i.e., the tendency for solitary corallites to grow in groups of closely spaced but separate individuals and form large populations. This is a tendency observed not only in corals, but also in many other invertebrate groups (e. g., brachiopods, rudists, etc.). Because of their contrasting growth forms, massive colonies and gregaria may easily be distinguished from each other. It may be more difficult to distinguish gregarious corals from fasciculate colonies, however, because both may have sub-parallel corallites completely or partly separated by matrix. When these corals occur in growth position and are well preserved, their growth form can be determined by checking for the presence of budding corallites, but this may be difficult if the relationship between corallites is obscured by reworking or poor preservation. Consequently, the growth habits of some taxa have not been accurately described, or colonialism has been inferred only from the presence of individuals either growing together or occurring together in reworked groups. This is especially true in the family Geyerophyllidae, where solitary corals commonly have a gregarious growth habit.

2. Gregarious growth habit *vs.* colonialism in Geyerophyllidae

The family Geyerophyllidae was erected by Minato (1955) for corals having variable, complex axial structures, lonsdaleoid dissepiments and clinotabulae. In a comprehensive review of the taxonomic history and morphology of the family, Minato & Kato (1975) presented a revised diagnosis and emphasized that the axial structures in these corals are connected to the cardinal septum. They also enlarged the list of genera assigned to the family to include 9 genera: *Kionophyllum* Chi, 1931, *Carinthiaphyllum* Heritsch, 1936, *Carniaphyllum* Heritsch, 1936, *Geyerophyllum* Heritsch, 1936 (=*Kionophyllum)*, *Lonsdaleoides* Heritsch, 1936, *Amygdalophylloides* Dobrolyubova & Kabakovich, 1948, *Axolithophyllum* Fomichev, 1953, *Paracarruthersella* Yoh, 1961 and *Darwasophyllum* Pyzhyanov, 1964. Other genera showing the basic morphology of the Geyerophyllidae have been described in later studies: *Chuanshanophyllum* Yü, 1977 (?= *Kionophyllum*), *Ramiphyllum* Wu & Zhang, 1979, *Majiaobaphyllum* Fan, 1980, *Qinglongshanophyllum* Yü, 1980, *Naoticophyllum* Shi, 1982, *Geyeronaotia* Rodríguez, 1984, *Protonaoticophyllum* Xu & Chen in Xu et al., 1987 (?= *Geyeronaotia*), and *Pseudoaxolithophyllum* Xu, Ding & Chen, *In* Lin *et al.*, 1995 (?= *Axolithophyllum*) (Table 1).

It may be concluded from the description by Heritsch (1936) that he considered *Carniaphyllum* and *Carinthiaphyllum* to be solitary corals, but this growth form was later questioned by Hill (1981), who regarded *Carinthiaphyllum* as possibly fasciculate. Heritsch (1936) did not specify a solitary or colonial growth form for his new genus *Lonsdaleoides,* but from his comparisons with colonial corals (*Lonsdaleia, Waagenophyllum*) it could be inferred that he was describing a colonial coral. Minato & Rowet (1967, p. 178), re-describing *Lonsdaleoides nishikawai* Hayasaka and Minato, 1966, stated that the collected specimens were free of matrix and widely separated, and therefore could not form part of a fasciculate coral. They also noted that the three paratypes show no sign of budding, but the holotype has several small

Table 1. List of genera included in Geyerophyllidae Minato.

Genus	Author	Year	Habit
Kionophyllum	Chi	1931	Solitary
Carinthiaphyllum	Heritsch	1936	Fasciculate?
Lonsdaleoides	Heritsch	1936	Fasciculate?
Carniaphyllum	Heritsch	1936	Fasciculate?
Geyerophyllum (= Kionophyllum)	Heritsch	1936	Solitary
Koninckocarinia	Dobrolyubova	1937	Solitary
Amygdalophylloides	Dobrolyubova & Kabakovitch	1948	Solitary
Axolithophyllum	Fomichev	1953	Solitary
Paracarruthersella	Yoh	1961	Solitary
Darwasophyllum	Pyzhanov	1964	Fasciculate?
Chuanshanophyllum	Yü	1977	Solitary
Ramiphyllum	Wu & Zheng	1979	Solitary
Majiaobaphyllum	Fan	1980	Solitary
Qinglongshanophyllum	Yü	1980	Solitary
Naoticophyllum	Shi	1982	Solitary
Geyeronaotia	Rodríguez	1984	Solitary
Protonaoticophyllum	Xu & Chen	1987	Solitary
Pseudoaxolithophyllum	Xu, Ding & Chen	1995	Fasciculate?

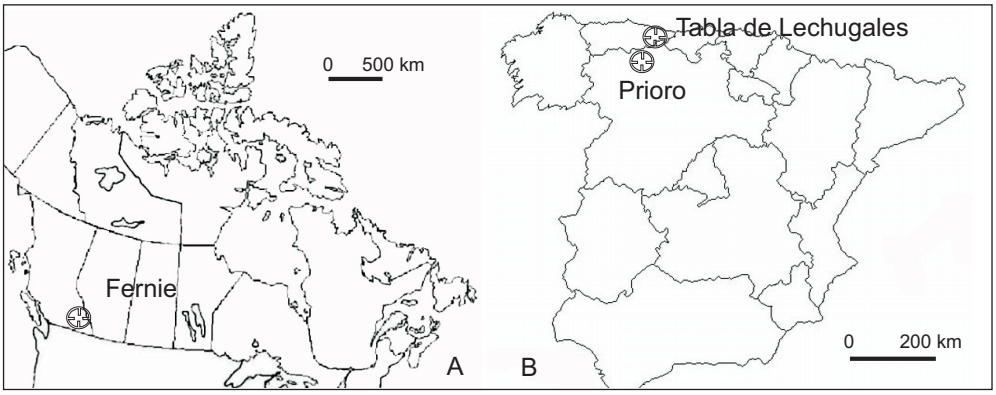

Figure 1. Localities yielding studied specimens. A. Outcrops near Fernie, British Columbia, in the southern Rocky Mountains, Canada. B. Prioro and Tabla de Lechugales outcrops in the Cantabrian Mountains, Spain.

offsets in the peripheral part of its lonsdaleoid dissepimentarium. Lower Permian specimens of *Carinthiaphyllum* from the Glass Mountains of Texas were shown to be solitary corals with gregarious growth habit by Fedorowski (1980, p. 435, pl. 26, fig. 2). Rodríguez (1985) analysed the relationships between various solitary geyerophyllids and questioned the colonialism of some of the genera described by Heritsch (1936). A review of the type material of *Carniaphyllum*, *Carinthiaphyllum* and *Lonsdaleoides* during the IX Symposium on Fossil Cnidaria by one of the authors (S. R.) confirmed that they are solitary corals with gregarious growth habit. Consequently, *Darwasophyllum* is the only remaining genus within the family Geyerophyllidae that may still be regarded as a colonial coral.

3. Growth habit in *Darwasophyllum*

Authors dealing with *Darwasophyllum* have consistently described it as a colonial coral, using such terms as "branching" (Pyzhyanov, 1964, p. 170; type species, *D. irregulare*), "loosely fasciculate" (Rowett and Kato, 1968, p. 39) and, most commonly,

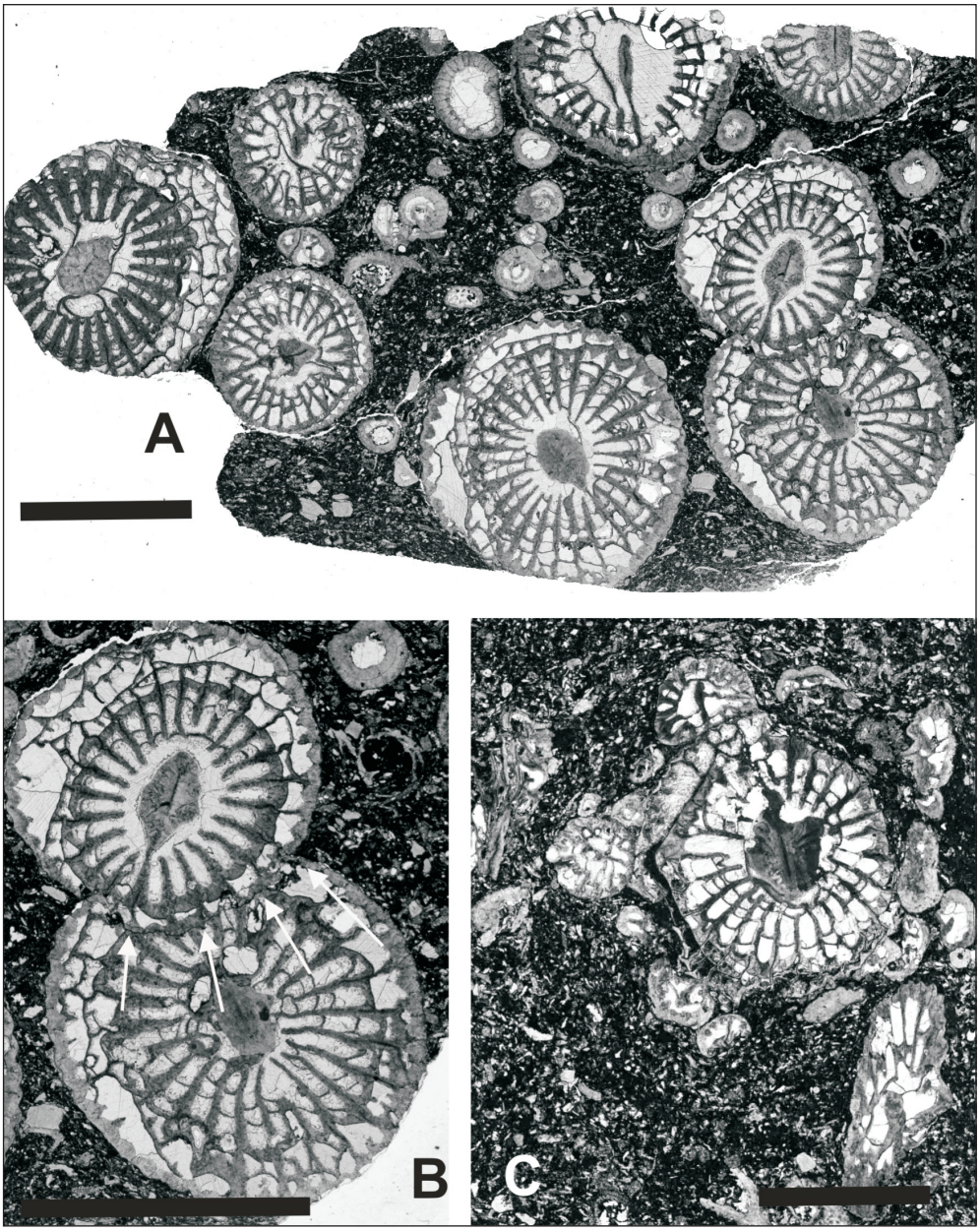

Figure 2. Gregarious growth form in *Darwasophyllum* sp. from the Etherington Formation. A. Several individuals growing together (hypotype GSC 133206; Geological Survey of Canada (GSC) locality C-409092, specimen 7). Note that the corallites in the lower right appear to share some structures. B. Close-up of figure A, showing a stylolite producing the false impression of structures common to adjacent corallites. C. Numerous young corallites surrounding an adult corallite (hypotype GSC 133207; GSC locality C-409092, specimen 15); some are attached to the wall of the adult, but none of them is an offset.
Locality information: Both specimens collected from GSC locality C-409092; Latitude 49°27'57"N, Longitude 115°07'45"W; Cedar Bowl section, Lizard Range, near Fernie, southeastern British Columbia, Canada (Fig 1A) ; 56.91-57.59 m. below stratigraphic top of inverted section. Scale bars = 5 mm.

"fasciculate" [e.g., Fan (1978, p. 180), Hill (1981, p. F407), Yu & Wang (1987, p. 83), Lin et al. (1995, p. 536)]. In no instance, however, has a colonial growth habit been clearly demonstrated for the genus. The descriptions of Rowett & Kato (1968, p. 40) and Wu & Zhao (1989, p. 158) are each based on a single corallite, and all published illustrations, including those of the type species, show separate corallites, none of which appear as definite offsets or share internal structures with other corallites.

Our specimens of *Darwasophyllum*, collected from the middle part of the Etherington Formation (Upper Viséan-Lower Serpukhovian, Canada), were also first regarded as colonial, with a close relationship between corallites. They occur in a single, laterally extensive, packstone bed that was traced over a considerable distance at the Fernie Alpine Resort in the Lizard Range of south-eastern British Columbia (Fig. 1A). The corallites are located in the upper part of this bed and appear to have been concentrated, in part, by re-working. Most of them occur as separate coral fragments, but locally they form groups of closely spaced, sub-parallel individuals, which resemble colonies but show no evidence of offsetting or shared structures. We have interpreted these groups as gregaria, based on observed relationships between immature specimens and associated, larger corallites of *Darwasophyllum* and other taxa.

The most convincing evidence for a solitary, gregarious growth habit was derived from serial transverse acetate peels and thin sections through a small specimen from our collection (Fig. 2C; hypotype GSC 133207). It consists of a mature corallite surrounded by numerous, closely spaced, immature corallites in various stages of development. New corallites appear at several levels within the growth interval studied. For the most part they lie very near or are in contact with the central mature corallite or other larger immature corallites. The new corallites are consistently oriented with their cardinal quadrants facing the corallites to which they are attached. Along the contacts between attached corallites, their external walls and other peripheral skeletal elements may show local damage caused by compaction and pressure solution. Where they have not been affected by this process, however, their external walls are distinct and well developed at all observed stages of development, and are commonly separated from each other by a thin layer of limestone matrix or crystalline calcite. These contact relationships persist over significant growth intervals with no evidence for sharing of walls or internal skeletal elements to indicate that the younger corallites originated as offsets from their neighbouring, more mature specimens.

In other gregaria of *Darwasophyllum* used for this study (Fig. 2A, B; hypotype GSC 133206), the contact relationships between corallites are consistent with those described above. No evidence of offsetting was found in our entire collection, which comprises more than 100 specimens. It is interesting to note that our collection contains two specimens in which the initial stages of young corallites are attached to taxa other than *Darwasophyllum*. These include a tabulate coral to which a small, doubly curved corallite is attached by its proximal end, and an incomplete cyathopsid coral bearing two very young, attached corallites of *Darwasophyllum* with diameters of 1.5 and 2 mm and no septa developed other than the cardinal septum. Thus, it appears that the preferred attachment sites for larvae of the Etherington corals were not entirely restricted to corallites of *Darwasophyllum*, but also included those of completely unrelated coral taxa.

4. Growth habit in *Axolithophyllum*

Although the genus *Axolithophyllum* has generally been regarded as solitary, some occurrences of Pennsylvanian specimens from the Cantabrian Mountains suggest the possibility of a colonial habit (Fig. 1B). These specimens show corallites that are in contact and share some septa in at least two different outcrops: close to Prioro village (Upper Moscovian, Figs 3 C, D) (De Groot in Van Loon, 1971) and Tabla de Lechugales peak (Lower

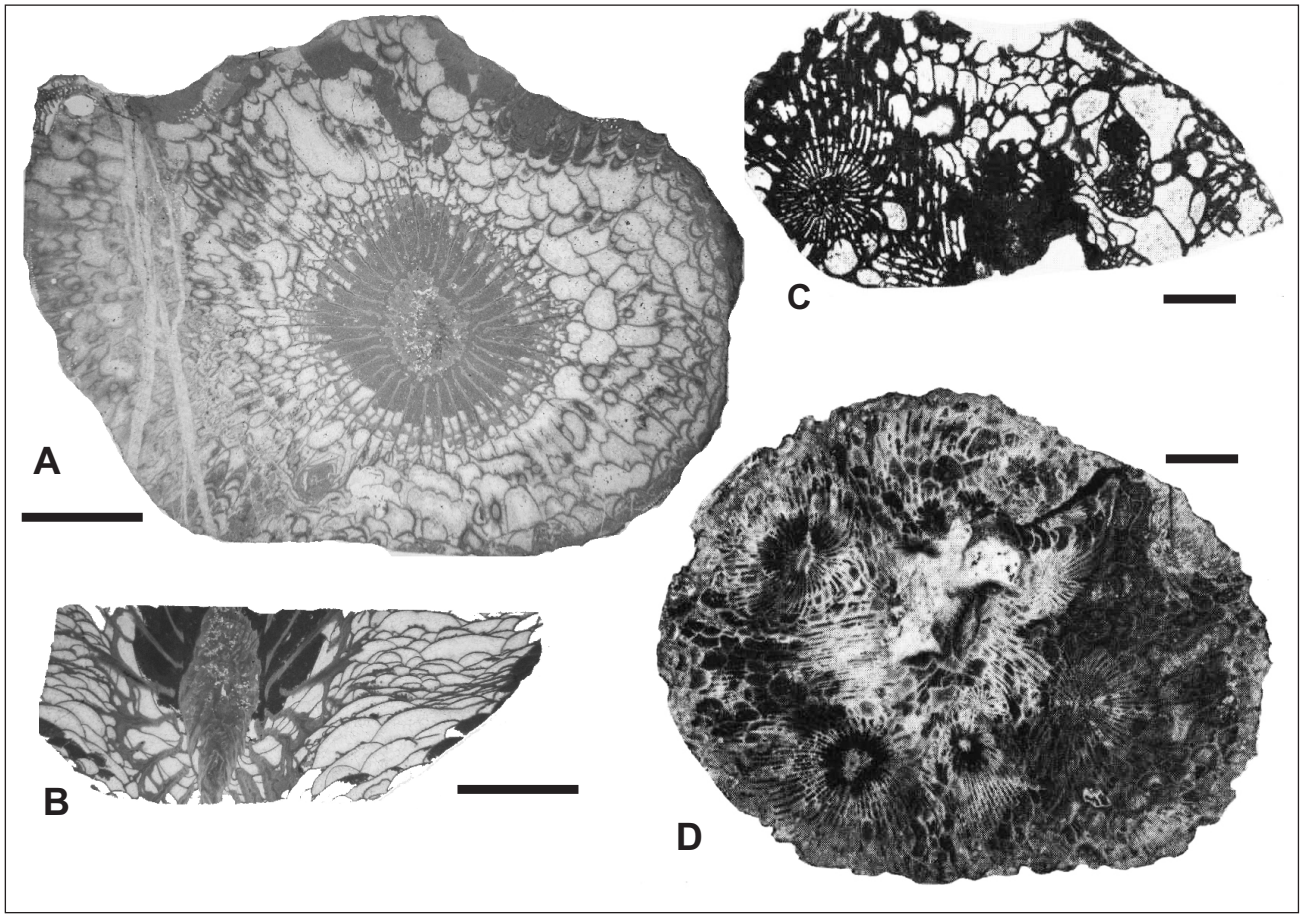

Figure 3. Protocolonialism in *Axolithophyllum*. A. *Axolithophyllum quiringui* from Tabla de Lechugales, specimen TLE1/73. Transverse section, showing contact between two adjacent corallites (upper right and left). B. Longitudinal section of the same specimen, showing it to be a solitary coral. C. cf. *Axolithophyllum* from Prioro (Escalada Formation), taken from Van Loon (1971, plate 6, fig. 4); two solitary corallites in contact. D. cf. *Axolithophyllum* from Prioro (Escalada Formation), take from Van Loon (1971, plate 6, fig. 6); solitary coral showing several offsets in calice. Scale bars = 5 mm.

Kasimovian, Figs 3A, B). In longitudinal section, however, it can be seen that they are separate individuals that are joined as a result of crowding caused by diameter increase during growth. This indicates a high degree of affinity between these individual corallites, but they do not form part of a colony formed by asexual budding. Elsewhere in the Upper Moscovian of the Cantabrian Mountains (Escalada Formation; De Groot in Van Loon, 1971), *Axolithophyllum* has been found with several corallites budding from the calice of a single corallum, but without further development. These specimens do not form true colonies, but only protocolonies or pseudocolonies. The original description by De Groot indicates: "obvious budding in solitary forms" (De Groot in Van Loon, 1981, p.247). They display the maximum degree of colonialism observed in the Geyerophyllidae.

The genus *Pseudoaxolithophyllum* was erected by Xu, Ding & Chen in Lin et al. (1995) for corals identical to *Axolithophyllum*, but developing small colonies. However, the original figures show only several closely spaced corallites with no evident budding.

5. Conclusions

The geyerophyllid genera *Carniaphyllum* and *Carinthiaphyllum*, described by Heritsch (1936) as solitary corals, but later regarded as colonial, are now known to be solitary corals having a gregarious growth habit. The same gregarious habit is shown in *Lonsdaleoides*, described by Heritsch (1936) as being colonial.

The genus *Darwasophyllum* has been consistently described as colonial (fasciculate), but our review of the original illustrations and our detailed study of a large, Early Serpukhovian population from the Etherington Formation of British Columbia have shown it to be solitary with a gregarious growth habit.

With the possible exceptions of the genera *Axolithophyllum* and *Lonsdaleoides*, which show a minor tendency to form protocolonies, it can be demonstrated that all geyerophyllid corals are solitary, with a strong tendency in some taxa toward the formation of gregaria.

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