Axial increase in some early tabulate corals

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Lee, D.-J., Jun, Y.-H., Bae, B.-Y. & Elias, R.J., 2007: Axial increase in some early tabulate corals. – In: Hubmann, B. & Piller, W. E. (Eds.): Fossil Corals and Sponges. Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera. – Österr. Akad. Wiss., Schriftenr. Erdwiss. Komm. 17: 31–41, 1 Tab., 2 Pls., Wien.

Abstract: In addition to lateral increase, considered typical of tabulate corals, a total of four types of axial increase are recognized in *Saffordophyllum newcombae, Trabeculites maculatus, Manipora amicarum, Manipora* sp. A, *Catenipora rubra,* and *Catenipora* spp. B, C and D from the Upper Ordovician of southern Manitoba, Canada. In type 1 increase, the dividing wall originates in the axial area of a normal corallite and subsequently joins the corallite wall, dividing the parent into two, or rarely three or four, offsets. Type 2 is similar, but is associated with rejuvenation following sediment influx. Type 3 involves the division of a large but otherwise normal corallite into two offsets, when a dividing wall that originates from a septum on one side of the corallite lengthens to join a septum on the opposite side. In type 4 increase, the corallite beneath a foreign skeletal grain divides and grows around the object, eventually incorporating it into the corallum. Axial increase occurs more widely in tabulates than previously suspected. The interpretation that the taxa in this study are closely related to one another is supported by the presence of unique types of increase. The relationship of these taxa to other tabulate corals remains unresolved.

Key words: tabulate corals, Ordovician, corallite increase

Contents

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1. INTRODUCTION

The mode of increase of corallites or their morphologic equivalents is an important character in the recognition and taxonomic assignment of Paleozoic corals and coral-like fossils (SCRUTTON, 1997). It is generally thought that tabulate corals are characterized by lateral or coenenchymal increase; the few reports of axial increase have been questioned (SCRUTTON, 1997, 1998). In Rugosa, the other main Paleozoic coral group, lateral increase is also typical (FEDOROWSKI & JULL, 1976). Additional, multiple parricidal modes of increase, however, are considered to be uniquely rugosan (SCRUTTON, 1997, 1998). These modes include axial increase, which is rare. Among the coral-like forms are chaetetid sponges, displaying axial increase as well as intramural increase and peripheral expansion (WEST & CLARK, 1983, 1984).

Despite the importance of identifying and evaluating modes of increase, few detailed studies have been done, especially on early Paleozoic material. In the case of early tabulate corals, PANDOLFI (1989) noted that he was unable to use corallite increase as a character in phylogenetic analysis, because of insufficient information on the majority of taxa. Since our initial report of axial increase in an Ordovician tabulate (LEE & ELIAS, 1991), we have described this mode of increase in another genus (LEE & ELIAS, 2000) and have found it in additional taxa, all from the same stratigraphic unit and locality. The corals are *Catenipora rubra* SINCLAIR & BOLTON in SINCLAIR, 1955, *Catenipora* spp. B, C and D, *Manipora amicarum* SINCLAIR, 1955, *Manipora* sp. A, *Saffordophyllum newcombae* FLOWER, 1961, and *Trabeculites maculatus* FLOWER, 1961 from the Upper Ordovician of southern Manitoba, Canada. In addition to lateral increase, which is usual for tabulates, various types of axial increase are apparent in these species. The purpose of this study is to document and compare these types of axial increase, and to consider the significance of our findings. For explanations of morphologic terminology and discussions of paleobiologic concepts, refer to LEE & ELIAS (2000).

2. MATERIAL AND METHODS

This study is based on specimens from the Selkirk Member of the Red River Formation at Garson, Manitoba (for locality maps, see ELIAS, 1981, Fig. 1; WESTROP & LUDVIGSEN, 1983, Fig. 1). Our material was obtained from cut and broken quarry rubble, because collection of coralla from this massive unit is otherwise almost impossible. Quarrying has exposed about 8 m of strata; the lowest level is 6 m above the base of the Selkirk Member, which is about 50 m thick in this area (KENDALL, 1977, Fig. 1). The member is considered to be mid-Maysvillian to early Richmondian in age (ELIAS, 1991). It is lithologically homogeneous, consisting of dolomite mottled, carbonate wackestone to packstone (KENDALL, 1977). Deposition occurred in a shallow marine environment with occasional storms (ELIAS, 1981; WESTROP & LUDVIGSEN, 1983).

Four genera are represented in this study. Research in progress on *Catenipora* from the Selkirk Member at Garson indicates that four species are present. One is identified as *Catenipora rubra,* which was originally described from the same locality (SINCLAIR, 1955, p. 99, 100, Pl. 1, Figs. 2, 6, 7, 11). The others are tentatively referred to as *Catenipora* spp. B, C and D. *Catenipora* is characterized by cateniform coralla. *Manipora* *amicarum* was originally described from the same vicinity (SINCLAIR, 1955, p. 97, 99, Pl. 1, Figs. 1, 4, 10). Research in progress suggests that a second species is also present; it is tentatively referred to as *Manipora* sp. A. *Manipora* is characterized by cateniform coralla with some multiple ranks and aggregates of corallites. *Saffordophyllum newcombae,* originally described from the Second Value Formation of the Upper Ordovician Montoya Group at El Paso, Texas (FLOWER, 1961, p. 60, 61, Pls. 24, 25), and *Trabeculites maculatus,* originally described from the Upper Ordovician on Akpatok Island in Nunavut, Arctic Canada (FLOWER, 1961, p. 62, Pl. 28, Pl. 31, Figs. 5, 6, Pl. 45, Figs. 10–12), have been identified from the Selkirk Member at Garson (LEE & ELIAS, 2000, p. 404, 405, Figs. 1–12; LEE & ELIAS, 2004). Both *Saffordophyllum* and *Trabeculites* are characterized by massive, cerioid coralla.

To document modes of corallite increase in detail, sets of transverse serial thin sections and longitudinal thin sections were prepared from relatively well preserved coralla. In the plates, all figures of transverse sections are oriented as they appear looking down from the top of the corallum toward its base. Longitudinal sections are oriented with the direction of growth toward the top of the page. Figured specimens are deposited in the Manitoba Museum (MM), Winnipeg, Canada.

3. TYPES OF AXIAL INCREASE

The axial mode of increase is recognized from both transverse serial thin sections (Pl. 1, Figs. 1–37; Pl. 2, Figs. 1–21) and longitudinal thin sections (Pl. 2, Figs. 22–31). The four types of axial increase distinguished in this study are described below. Their relative abundance in the eight tabulate species that we examined is summarized in Table 1.

3.1. Type 1

Type 1 axial increase involves a seemingly normal, undamaged parent corallite (Pl. 1, Figs. 1–10, 32–37; Pl. 2, Figs. 22–24). Based on some serial sections, it appears that the dividing wall originates in the axial area and subsequently lengthens in both directions to join the corallite wall. The dividing wall is initially relatively thin and usually crenulate or zigzaged (Pl. 1, Figs. 1–10), or rarely straight (Pl. 1, Figs. 32–37). The process of division is accomplished very rapidly, within a vertical distance of 1 mm in *Saffordophyllum newcombae* and *Trabeculites maculatus*, and 2 mm in *Manipora amicarum* and *Manipora* sp. A. The vertical distances required for an offset to attain "adult" corallite size and polygonality are variable, depending mainly on the initial polygonality; the more sides the offset starts out with, the more rapidly it attains an "adult" appearance. As a result of type 1 axial increase, the parent usually divides into two, but rarely three or even four, offsets separated by walls that usually divide the parent corallite radially. This form of increase usually occurs in low-density cyclomorphic bands (*Saffordophyllum newcombae* and both species of *Manipora*), but happens in high-density cyclomorphic bands in *Trabeculites maculatus*. In some cases, the process of axial increase is aborted temporarily (Pl. 2, Fig. 29) or permanently. Type 1 axial increase has not been observed in species of *Catenipora*.

3.2. Type 2

Type 2 axial increase is similar to type 1, but takes place in association with rejuvenation of a damaged single corallite or group of corallites following sediment influx (Pl. 1, Figs. 11–37; Pl. 2, Figs. 25–27). This process is commonly accomplished very rapidly, within a vertical distance of 1 mm in *Saffordophyllum newcombae* and *Trabeculites maculatus*, 2 mm in *Manipora amicarum* and *Manipora* sp. A, and 1.75 to 2.6 mm in *Catenipora rubra*. As a result, the damaged parent corallite is replaced by two, or rarely three or even four, corallites. This type of increase appears to be very common and is observed in all species. In several cases it occurs together with type 1 axial increase in the same astogenetic stage (Pl. 1, Figs. 32–37).

In a few cases, the process of axial increase is aborted and the corallite is restored to its original form (Pl. 2, Fig. 28). Axial increase is sometimes accompanied by the formation of a tubular structure that presumably housed a symbiont; this has been observed in *Saffordophyllum newcombae* and *Trabeculites maculatus* (Pl. 1, Figs. 26–31). Type 2 axial increase often coincides with high-density cyclomorphic bands in *Saffordophyllum newcombae* and all *Catenipora* species, but usually occurs in the low-density bands in *Trabeculites maculatus*, *Manipora amicarum* and *Manipora* sp. A.

3.3. Type 3

Type 3 axial increase involves the division of a relatively large but otherwise normal corallite into two offsets that are similar in size and nearly as large as typical "adult" corallites. This type of increase is rare, but is recognized in *Saffordophyllum newcombae*, *Trabeculites maculatus*, *Manipora* sp. A, and *Catenipora* sp. B (Pl. 2, Figs. 1–21). The dividing wall originates from a septum on one side of the parent corallite, and lengthens to join a septum on the opposite side. The vertical distance required for the offsets to attain "adult" size is approximately 1.5 mm in *Saffordophyllum newcombae* and *Trabeculites maculatus*, 4 mm in *Manipora* sp. A, and 1.4 mm in *Catenipora* sp. B.

3.4. Type 4

Type 4 axial increase is rare. It occurs in response to deposition of a relatively large foreign skeletal grain (e.g., crinoid ossicle) on the growth surface of a corallum (Pl. 2, Figs. 30, 31). The corallite beneath the grain divides and grows around the object, eventually incorporating it into the corallum. This process must have involved axial division of the affected polyp and subsequent growth of its buds around the foreign object. Polyps were evidently unable to reject relatively large grains of sediment deposited on the colony surface, but such an occasion provided an opportunity for budding. Type 4 axial increase is observed in *Saffordophyllum newcombae* and *Manipora amicarum*. This type of increase, involving deposition of relatively coarse debris on the colony surface, may indicate that these corals lived with the upper surface of the corallum at or just above the sediment-water interface (see also Lee & Elias, 1991).

4. DISCUSSION AND CONCLUSIONS

In addition to the lateral mode of increase, considered typical of tabulate corals, a total of four types of axial increase are recognized in *Saffordophyllum newcombae*, *Trabeculites maculatus*, *Manipora amicarum*, *Manipora* sp. A, *Catenipora rubra*, and *Catenipora* spp. B, C and D from the Upper Ordovician of southern Manitoba (Table 1). In type 1 increase, the dividing wall originates in the axial area of a normal corallite and subsequently joins the corallite wall, dividing the parent into two, or rarely three or four, offsets. Type 2 is similar to type 1, but is associated with rejuvenation following sediment influx. Type 3 involves the division of a large but otherwise normal corallite into two offsets, when a dividing wall that originates from a septum on one side of the corallite lengthens to join a septum on the opposite side. In type 4 increase, the corallite beneath a foreign skeletal grain divides and grows around the object, eventually incorporating it into the corallum.

This study demonstrates that the axial mode of increase occurs more widely in tabulate corals than previously suspected, and that more types of axial increase exist among corals and organisms producing coral-like skeletons than previously known. The various types of axial increase that are characteristic features of certain tabulate corals from the Upper Ordovician of southern Manitoba, are unlike those that may occur in other tabulates. The forms of axial increase reported in some alveolitids and agetolitids (SHARKOVA, 1971; HILL, 1981), involving the extension and union of septal structures, do not resemble types 1 to 4 of the present study. Type 1 axial increase is most comparable to the form that occurs in the Devonian cerioid rugose coral *Melasmaphyllum mullamuddiensis,* although increase in the latter species results in up to six offsets (see WRIGHT, 1966). Type 3 most closely resembles the form of axial increase in chaetetid sponges, although in the latter group it is the extension of a pseudoseptum or union of a pair of pseudosepta that divides a calicle into two (see WEST & CLARK, 1983, 1984).

Corallite increase provides a record of polyp budding, which is a fundamental biologic process. Do the types of axial increase that we have found in certain tabulate corals from the Upper Ordovician of southern Manitoba, but which are unknown in other tabulates, reflect evolutionary relationships? FLOWER (1961) and FLOWER & DUNCAN (1975) proposed that a common ancestor gave rise to *Catenipora* (via *Quepora*) and

SPECIES	TYPE 1	TYPE 2	TYPE 3	TYPE 4
Saffordophyllum newcombae	C	A	R	R
Trabeculites maculatus	C	A	R	N
Manipora amicarum	R	A	R	R
Manipora sp. A	C	A	N	N
Catenipora rubra	N	A	N	N
Catenipora sp. B	N	A	R	N
Catenipora sp. C	N	A	N	N
Catenipora sp. D	N	A	N	N

Table 1: Relative abundance of the four types of axial increase in eight tabulate coral species from the Selkirk Member, Red River Formation (Upper Ordovician), southern Manitoba, Canada. A, abundant; C, common; R, rare; N, not observed.

to *Saffordophyllum*, from which both *Manipora* and *Trabeculites* arose. Others, however, have placed these genera far apart. Hill (1981) included *Catenipora* in Heliolitida, *Saffordophyllum* and *Manipora* in Favositida, and *Trabeculites* in Sarcinulida. Scrutton (1984) differed in placing *Catenipora* in Halysitida, and *Saffordophyllum* and *Manipora* in Lichenariida, whereas Lin et al. (1988) included both *Catenipora* and *Manipora* in Halysitida, and put *Saffordophyllum* with *Trabeculites* in Sarcinulida.

It seems reasonable to suggest that the presence of unique types of axial increase supports the interpretation that the taxa in our study are closely related to one another. The direct evolutionary lines proposed by Flower (1961) and Flower & Duncan (1975), however, are unconfirmed. The relationship of these taxa to other tabulate corals remains unresolved, due to the critical need for detailed paleobiologic studies of other early tabulates.

Acknowledgements: This project was supported by the Korea Research Foundation grant 2002-070-C00087 to DJL, and grants from the Natural Sciences and Engineering Research Council of Canada to RJE. We thank J. Hladil and B. Hubmann for reviewing the manuscript.

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Plate 1

Axial increase types 1 and 2 in tabulate corals from the Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba.

Figs. 1–6: Normal corallite A undergoes type 1 axial increase, resulting in three corallites Aa, Ab and Ac: transverse serial sections spaced 0.55, 0.40, 0.45, 0.45, 0.60 mm apart, respectively; x 4.2; MM I-2918, *Saffordophyllum newcombae*.

Figs. 7–10: Normal corallite A undergoes type 1 axial increase, resulting in two corallites Aa and Ab: transverse serial sections spaced 0.45, 0.75, 0.65 mm apart, respectively; x 7.8; MM I-3469, *Manipora* sp. A.

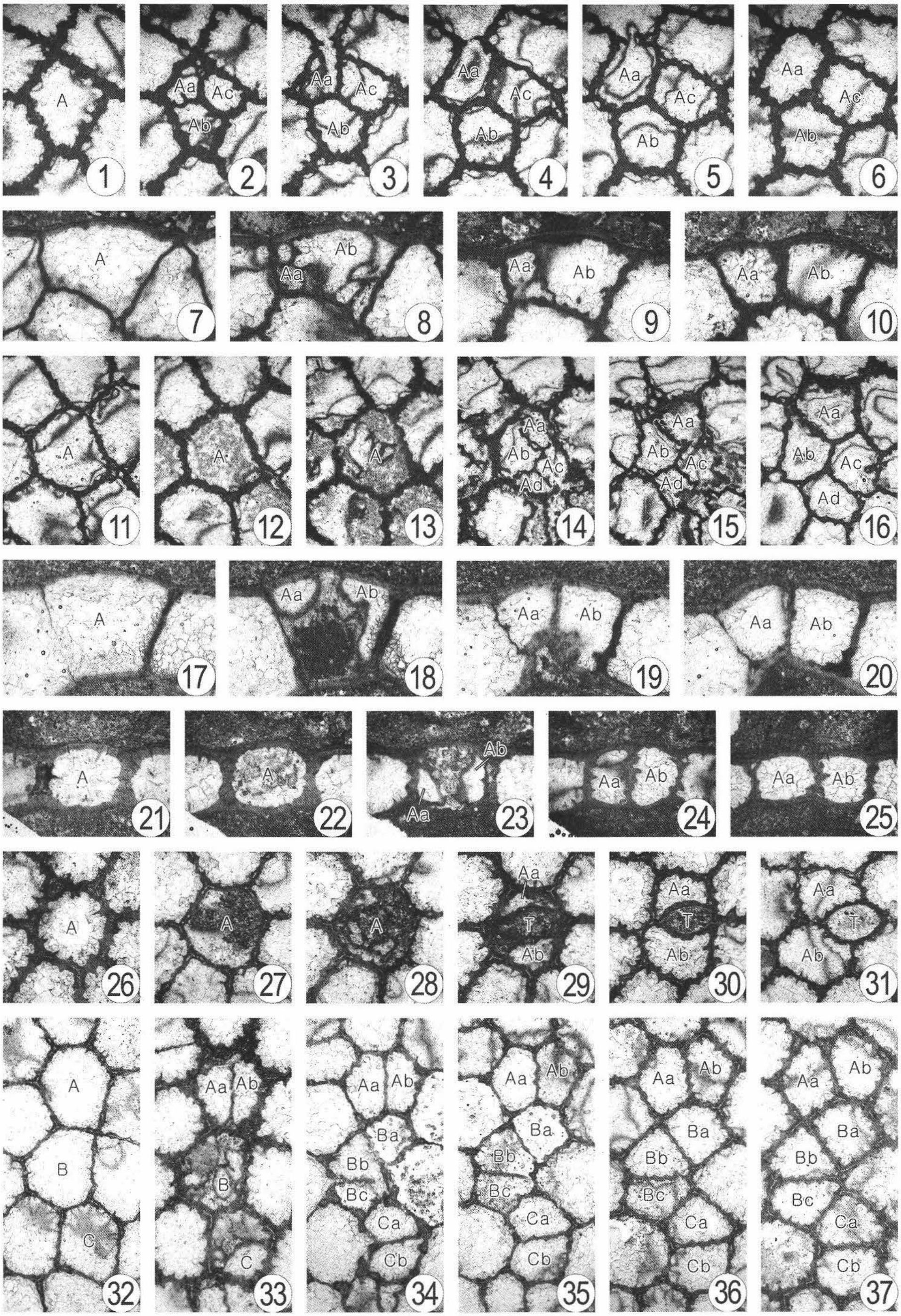
Figs. 11–16: Damage to corallite A followed by rejuvenation involving type 2 axial increase, resulting in four corallites Aa, Ab, Ac and Ad: transverse serial sections spaced 0.50, 0.40, 0.45, 0.50, 0.40 mm apart, respectively; x 4.2; MM I-2920, *Saffordophyllum newcombae*.

Figs. 17–20: Damage to corallite A followed by rejuvenation involving type 2 axial increase, resulting in two corallites Aa and Ab of approximately equal size; note that surviving soft parts expanded from opposite sides of corallite toward the centre, forming a dividing wall: transverse serial sections spaced 0.90, 0.85, 0.55 mm apart, respectively; x 8.4; MM I-3467, *Manipora amicarum*.

Figs. 21–25: Damage to corallite A followed by rejuvenation involving type 2 axial increase, resulting in two corallites Aa and Ab of approximately equal size; note that surviving soft parts expanded from opposite sides of corallite toward the centre, forming a dividing wall: transverse serial sections spaced 1.40, 0.40, 1.35, 3.35 mm apart, respectively; x 5.4; MM I-3470, *Catenipora rubra*.

Figs. 26–31: Rejuvenation of corallite A involving type 2 axial increase, resulting in two corallites Aa and Ab and formation of tubular structure T, which presumably housed a symbiont: transverse serial sections spaced 0.90, 0.55, 0.60, 1.15, 3.45 mm apart, respectively; x 5.5; MM I-3460, *Trabeculites maculatus*.

Figs. 32–37: Normal corallite A undergoes type 1 axial increase yielding two offsets Aa and Ab, while corallites B and C undergo type 2 axial increase during rejuvenation, yielding three (Ba, Bb and Bc) and two offsets (Ca and Cb), respectively: transverse serial sections spaced 0.90, 0.70, 0.80, 0.75, 0.90 mm apart, respectively; x 5.2; MM I-3463, *Trabeculites maculatus*.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Aa T Ab 29
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A B C 32
Aa Ab B C 33
Aa Ab Ba Bb Bc Ca Cb 34
Aa Ab Ba Bb Bc Ca Cb 35
Aa Ab Ba Bb Bc Ca Cb 36
Aa Ab Ba Bb Bc Ca Cb 37

Plate 2

Axial increase types 1–4 in tabulate corals from the Selkirk Member, Red River Formation (Upper Ordovician), Garson, Manitoba.

Figs. 1–6 Corallite A undergoes type 3 axial increase, resulting in two corallites Aa and Ab of approximately equal size: transverse serial sections spaced 0.55, 0.40, 0.45, 0.45, 0.60 mm apart, respectively; x 4.7; MMMN I-2918, *Saffordophyllum newcombae.*

Figs. 7–11: Corallite A expands in size and undergoes type 3 axial increase, yielding two offsets Aa and Ab of typical "adult" size: transverse serial sections spaced 0.60, 0.65, 0.55, 0.55 mm apart, respectively; x 6.9; MM I-3463, *Trabeculites maculatus.*

Figs. 12–15: Corallite A expands in size and undergoes type 3 axial increase, yielding two offsets Aa and Ab of typical "adult" size: transverse serial sections spaced 1.05, 0.70, 1.45 mm apart, respectively; x 7.6; MM I-3471, *Manipora* sp. A.

Figs. 16–21: Corallite A undergoes type 3 axial increase, yielding two offsets Aa and Ab: transverse serial sections spaced 1.45, 0.40, 0.50, 0.80, 1.55 mm apart, respectively; X4.9; MM I-3472, *Catenipora* sp. B.

Fig. 22: Normal corallite A undergoes type 1 axial increase, resulting in offsets Aa and Ab: longitudinal section; x 4.9; MMMN I-2918, *Saffordophyllum newcombae.*

Fig. 23: Normal corallite A undergoes type 1 axial increase, resulting in offsets Aa and Ab: longitudinal section, x 4.9; MM I-3473, *Manipora amicarum.*

Fig. 24: Normal corallite A undergoes type 1 axial increase, resulting in offsets Aa and Ab: longitudinal section; x 8.0; MM I-3460, *Trabeculites maculatus.*

Fig. 25: Damage to corallite A followed by rejuvenation involving type 2 axial increase, resulting in offsets Aa and Ab: longitudinal section; x 4.9; MM I-3476, *Manipora amicarum.*

Fig. 26: Damage to corallite A followed by rejuvenation involving type 2 axial increase, resulting in offsets Aa and Ab: longitudinal section; x 4.9; MM I-3459, *Trabeculites maculatus.*

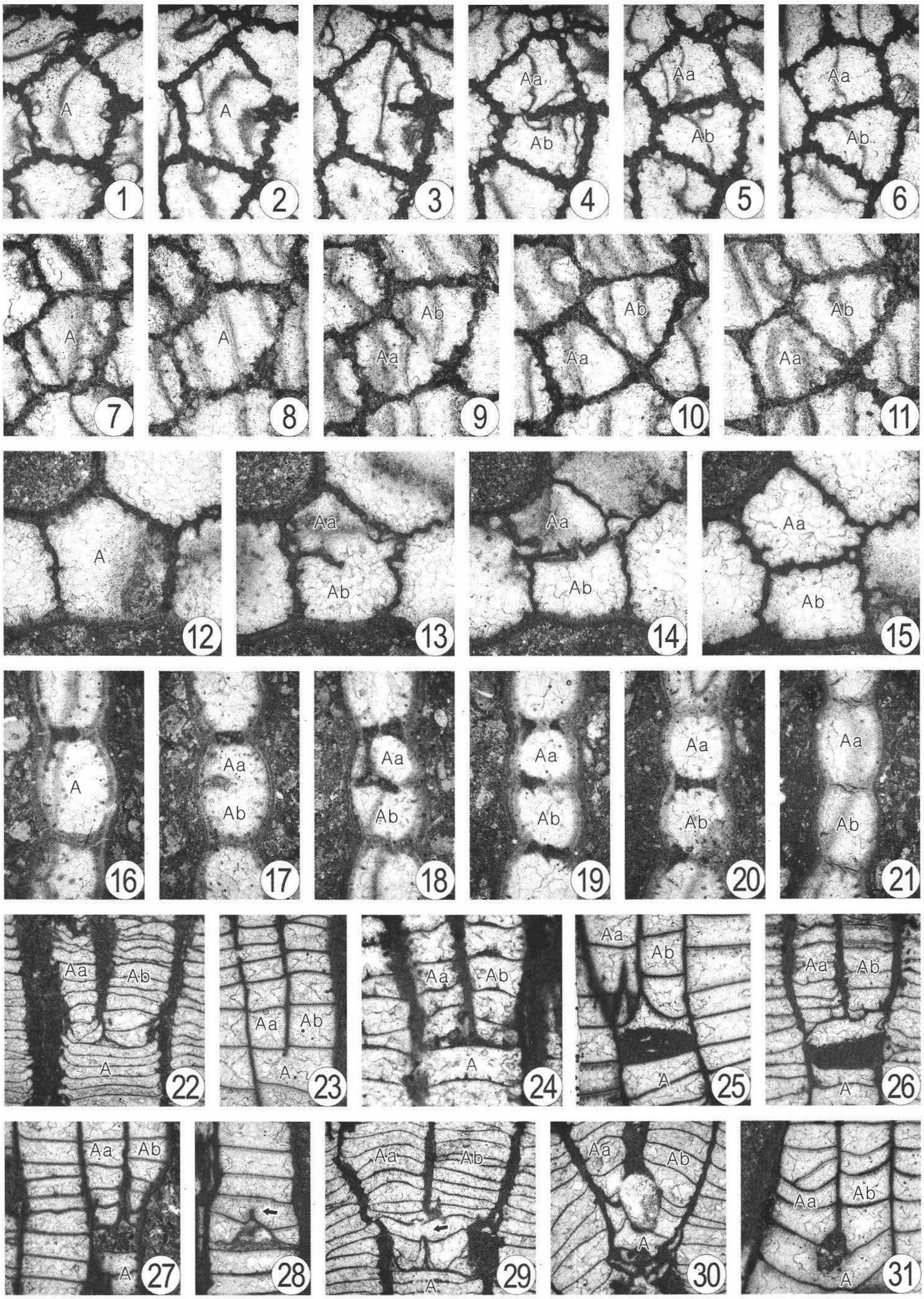
Fig. 27: Damage to corallite A followed by rejuvenation involving type 2 axial increase, resulting in offsets Aa and Ab: longitudinal section; x 4.9; MM I-3475, *Manipora amicarum.*

Fig. 28: Type 2 axial increase is aborted (arrow): longitudinal section; x 4.9; MM I-3474, *Manipora* sp. A.

Fig. 29: Type 1 axial increase is temporarily aborted (arrow): longitudinal section; x 4.9; MM I-2920, *Saffordophyllum newcombae.*

Fig. 30: Type 4 axial increase of corallite A in response to deposition of a foreign object, resulting in corallites Aa and Ab: longitudinal section; x 4.9; MM I-2920, *Saffordophyllum newcombae.*

Fig. 31: Type 4 axial increase of corallite A in response to deposition of a foreign object, resulting in corallites Aa and Ab: longitudinal section; x 4.9; MM I-3476, *Manipora amicarum.*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