

Symmetry in graptolite zooids and tubaria (Pterobranchia, Hemichordata)

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Abstract

Extant and fossil pterobranchs show distinct symmetry conditions of the individual zooids and their tubaria that are not necessarily comparable. The strict bilateral symmetry in the zooids of extant Cephalodiscida is modified to a considerable anatomical asymmetry in extant Rhabdopleurida. This type of left–right asymmetry can be recognized as antisymmetry, as dextral and sinistral developments are equally common. Antisymmetry is also recognized in the rhabdopleurid tubaria and in the proximal development and branching of planktic graptoloids. The antisymmetry of the graptoloid tubarium is modified during the Tremadocian time interval to a fixed or directional asymmetry. From the latest Tremadocian or earliest Floian onwards, proximal development in the Graptoloidea is invariably dextral and very few examples of a sinistral development have been found. The transition from antisymmetry to directional asymmetry can only be recognized in the graptolite tubaria, as the anatomy of the zooids is unknown from the fossil record. Directional asymmetry is not recognized in extant Pterobranchia.

KEYWORDS

antisymmetry, bilateral symmetry, directional symmetry, graptolites, Pterobranchia

1 | INTRODUCTION

Symmetry conditions in the Pterobranchia are not easy to understand and recognized due to the complexity of these colonial organisms. Also, preservational aspects prevent the recognition of the underlying symmetrical aspects of the colonies in the fossil record, especially when the graptolite tubaria are preserved as flattened organic films and not found in their original three-dimensional shape. Clear differentiation between the symmetry of the individual zooids, the symmetry of the colony, and the symmetry of the housing construction has to be made. The colonial organization of the

Pterobranchia is an important factor that has to be incorporated into the understanding of their symmetry, as the modules form a complex colony with quite different symmetry aspects.

Most animals show a general bilateral symmetry, but very little is known about the early evolution of symmetry in organisms and the understanding of symmetry conditions in organisms is still in flux (cf. Holló, 2014, 2015, 2017; Holló & Novák, 2012; Manuel, 2008; Matus et al., 2005; Toxvaerd, 2021; Yasui et al., 2000; and others). Bilateral symmetry is generally understood as representing an advantage of organisms for directed locomotion. More than 99% of all modern animals (e.g., Finnerty, 2005, p. 1174)

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show typical bilateral symmetry and it is also predominantly found in the fossil record, as can be seen in the explosive radiation of animals during the Cambrian explosion time interval. Finnerty (2005) expressed his belief that most animals with radial symmetry are sessile bottom dwellers or planktic drifters. The evolution of bilateral symmetry would then be advantageous for actively moving organisms and he used as an example, the development of extant Cnidaria. However, he also suggested that bilateral symmetry may be an advantage for the internal circulation in the Cnidaria as an alternative viewpoint. Holló (2015, 2017) discussed the influence of mechanical forces on the shape of the animal body and, thus to the symmetry exhibited. He did not believe that symmetry is mainly determined by genes and developmental necessities but through simple physical laws. In any way, the symmetry of an organism is one of the fundamental or basic features of the body plan. Altogether, many questions about the origin and expression of symmetry in early animals are still open to discussion.

The Pterobranchia, close to the origin of the Deuterostoma (cf. Han et al., 2017, fig. 3; and many more), possess a general bilateral symmetry of their zooids, known only from extant taxa. Larouche-Bilodeau et al. (2020, p. 13550) considered asymmetry in hemichordates (Pterobranchia and Enteropneusta) to be fairly restricted and recognized only the position of the single gonad in *Rhabdopleura* as an example of antisymmetry and mentioned the asymmetry of the coiling direction of the enteropneust *Saccoglossus*. The authors indicated that the presence of the single gonad in *Rhabdopleura* may be related to the miniature size of the zooids, which may suggest that a true bilateral symmetry may have been lost in the taxon due to the body size reduction. The idea may be supported by the larger size of the zooids of the closely related genera *Cephalodiscus* and *Atubaria* showing

bilateral symmetry of the internal organs (e.g., Komai, 1949; Schepotieff, 1905, 1907b, 1908). However, the development of symmetry in fossil pterobranchs has to be seen in a somewhat different light, as their colonial organization may incorporate other aspects that are not relevant for individuals and has largely to be inferred from their housing constructions, the tubaria.

2 | SYMMETRY IN PTEROBRANCH ZOIDS

The zooids of the pterobranchs *Cephalodiscus* (Figure 1a,b) and *Rhabdopleura* (1c) are generally bilaterally symmetric in appearance with their variable number of paired arms, reduced to a single pair in *Rhabdopleura*. Schepotieff (1905, p. 4) recognized minor asymmetry in the cephalic shield of *Cephalodiscus dodecalophus*, shown through a stronger development of the left side. His material possessed paired ovaries and paired genital pores (Schepotieff, 1905, p. 12), thus did not show more extensive asymmetry. Harmer and Ridewood (1913, p. 547) discussed the asymmetry of a single specimen of *Cephalodiscus agglutinans* in which the left testis is large and the right one undeveloped, as an individual peculiarity of the specimen. All other investigated specimens were bilateral symmetric. Harmer (1905, p. 85) reported that the left testis was smaller in some specimens of *Cephalodiscus sibogae*, but not in all. Komai (1949) described the ovary of *Atubaria* as a “conspicuous paired organ,” supporting the symmetrical anatomy of the genus. Thus, some minor asymmetry appears to be present in the cephalodiscids, but has not been investigated in detail.

A generally bilateral symmetrical development can be seen in the zooids of *Rhabdopleura* with their single pair

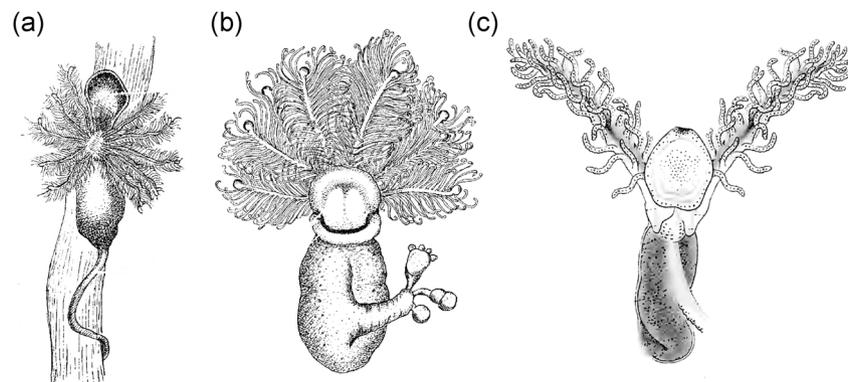


FIGURE 1 Symmetry in pterobranch zooids. (a) *Cephalodiscus hodginsoni* Ridewood, 1907, single zooid in dorsal view on a spine of the tubarium, the stalk is visible (after Dawydoff, 1948, fig. 110b). (b) *Cephalodiscus dodecalophus* M'Intosh (1887) in ventral view (after Dawydoff, 1948, fig. 76). (c) *Rhabdopleura normani* Allman in Norman, 1869, single zooid in ventral view attached to the zooidal stalk (after Sars, 1874, pl. 1)

of arms (Figure 1c), but asymmetrical development of the intestines is commonly recognized. Lankester (1884, p. 633, pl. XL, fig. 7) was the first to describe asymmetrical development in *Rhabdopleura normani* with the localization of the testes on the right side of the body. Schepotieff (1907a, p. 475) discussed the asymmetrical development of the zooids of *Rhabdopleura normani*, indicating a stronger development and the position of certain organs on the left side of the body. Lester (1988, p. 96) investigated zooids of *Rhabdopleura normani* and found a single gonad in zooids of either sex, which is displaced to the right or the left side. Sato and Holland (2008) investigated the position of the gonads in male and female specimens of *Rhabdopleura normani* and recognized that in 24 out of 55 mature females, the gonad is found on the left side (random distribution), while in 53 out of 81 mature males it is found on the left side (tendency for the left side). Comparison of the right and left side localization of the gonads in *Rhabdopleura compacta* with the tube building indicated that tube building is also affected, as zooids with right-sided localization of gonads tend to form right-coiling tubes. The left–right (LR)-asymmetry recognized by Sato and Holland (2008) in the Pterobranchia is typical for vertebrates and is found in numerous taxa across the Bilateria (Blum & Ott, 2018; Grimes & Burdine, 2017; Namigai et al., 2014).

3 | SYMMETRY IN PTEROBRANCH TUBARIA

The general bilateral symmetry of the Pterobranchia is clearly expressed in the development of the graptolite housing construction, the tubarium. Here, the individual modules (thecae) are bilateral symmetrically secreted by

the zooids, easily recognized through the dorsal and ventral zigzag sutures formed through the secretion of fusellar halfrings (Kozłowski, 1949, fig. 5) and only the prosicula does not obviously show this type of symmetry (Maletz et al., 2016). The colonial tubaria, however, do not necessarily show this exact bilateral symmetry, and especially, in benthic taxa, the symmetry of the tubaria is strongly influenced by ecological and environmental factors. Only in the planktic taxa of the Ordovician to Devonian time interval, the Graptoloidea, a more symmetrical colony shape can be observed (Maletz, 2017) and the focus is here on these taxa.

A closer view at the initial development of tubaria, the proximal development (cf., Cooper & Fortey, 1983; Mitchell, 1987), indicates some interesting aspects concerning the symmetry of the construction. The proximal development has been described in great detail for numerous planktic species but is largely unknown for benthic forms. The sicula, the housing of the only zooid formed through sexual reproduction, is placed in the center of the colony and further development is formed in a general bilateral symmetry around it. However, dextral and sinistral proximal developments (Figure 2) can be differentiated in well-preserved material of the Graptoloidea (cf. Cooper & Fortey, 1982, p. 174, 1983, table 1). Thecae are successively secreted in the graptolites, in which usually one theca can generate a single further theca to form a stipe. Branching is produced through the secretion of two thecae from the mother theca, called a dicalycal theca, at slightly different positions. The first branching division of the colony is formed by $th1^2$ in many taxa and can be used as a reference here. $Th1^2$ is the second theca generated by the growing colony, while $th1^1$ is the first theca (see Figure 2). The dicalycal theca $th1^2$ forms the first two stipes of a branching colony. With the sicula in the center of the

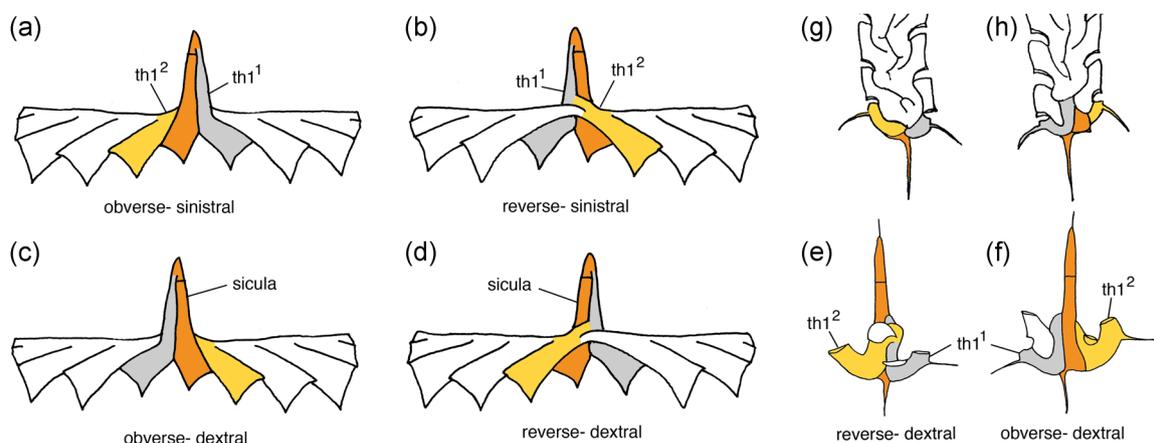


FIGURE 2 Dextral and sinistral development in *Expansograptus* sp., Dichograptina (a–d) and in *Archiclimacograptus* sp., Axonophora (e–h) for comparison. The first three thecae are color-coded

colony, $th1^1$ and $th1^2$ form a more or less symmetrical pair around it.

The obverse and reverse sides of the proximal ends of the graptoloids can easily be differentiated (Figure 2) through the visibility of the crossing canals, the initial thecal parts of $th1^1$ and $th1^2$, growing across the sicula on the reverse side, but not on the obverse side. Thus, both sides look quite differently in relief material. These differences may not be recognizable in the more common flattened shale material, however.

A simple example to explain the symmetry of the proximal development is seen in the genus *Expansograptus* (Figure 2a–d), in which the sicula is fully exposed on the obverse side (Figure 2a,c), but partially covered by the crossing canals on the reverse side (Figure 2b,d). Dextral and sinistral development can be separated by the side on which the first theca ($th1^1$) originates (shown in gray in Figure 1a–d) from the sicula (shown in brown) and, and by the growth direction of $th1^2$ (shown in orange). A dextral development is seen when $th1^2$ originates on the right side of $th1^1$ and grows dextrally across the sicula (Figure 2d). In sinistral development, $th1^2$ originates on the left side of $th1^1$ and grows in a sinistral direction (Figure 2b). The development does not differ much in biserial axonophoran colonies as is seen in specimens of *Archiclimacograptus* (Figure 2e–h) in which also $th1^1$ and $th1^2$ form a symmetrical pair, but in the distal part of the colony, the sicula and the early thecal origins are covered by the upward growing stipes (Figure 2g,h).

4 | HANDEDNESS AND THE GROWTH OF THECAE AND BRANCHES

Branching of pterobranch colonies appears to be lateral, as can be seen in extant *Rhabdopleura*, where zooidal stalks develop laterally on the stolon system (Maletz & Beli, 2018, fig. 2). Thus, the origin of new zooids can be on the right or left side of the stolon, shown also in the development of the tubarium (Maletz & Cameron, 2016; Ridewood, 1907). Similarly, the origin of the thecae in the tubarium of planktic graptolites can be on the right or left side of the previous theca. All thecae originate laterally on their parent thecae in benthic taxa and in most Anisograptidae, in early Dichograptina and Sinograptina. In younger taxa, the origin of new thecae universally is on the dorsal side of the previous theca, a pattern that differs considerably from the development in the Rhabdopleuridae, the Dendroidea, and the Anisograptidae.

Stubblefield (1929, p. 274) originally introduced the terms “right-” and “left-handed” for the proximal

development of *Adelograptus tenellus* (Linnarsson, 1871). The terms initially were used to describe the origin and growth direction of the first theca ($th1^1$) on the reverse side of the proximal end. The term ‘dextral’ was introduced to describe a growth of $th1^1$ from the left side (actually the dorsal side) of the sicula to the right side (ventral side of the sicula) on the reverse side of the proximal end, where the crossing canal covers part of the sicula in its wake. It implied an origin of $th1^1$ on the left side of the sicula but did not state this directly. It has to be noted that the left side of the sicula in Stubblefield (1929) actually describes the dorsal side and the right side is now interpreted as the ventral side of the sicula, following Maletz’ (1992, p. 298) identification of the dorsal and ventral sides of the sicula in the Anisograptidae.

Cooper and Fortey (1982, p. 173) revised the terms right- and left-handed to the modern use and restricted the terms to the point of origin of a theca and do not refer to the growth direction, which, according to them is an independently changing character of the proximal development of graptolites. They used the terms differently and the right-handed mode of Stubblefield (1929) became the left-handed mode of Cooper and Fortey (1982) and vice versa. Cooper and Fortey (1982) stated that a right-handed origin means an origin on the biologically right side of a theca when seen from the dorsal side of the stipe. This is the way in which Maletz et al. (2014) used the terms also for the Treatise. Thus, right-handed and left-handed just means the origin of a theca on the left or right side of the parent theca, but does not describe the independent character of growth direction (cf. Cooper & Fortey, 1982, p. 173).

The terms left-handed and right-handed cannot be used for the origin of $th1^1$ on the sicula. The origin of $th1^1$ is invariably on the ventral side of the sicula as defined by Maletz (1992, p. 298) and not laterally. Riva (1994, p. 3) mistakenly identified the dorsal side of the sicula in *Xiphograptus* as the side on which $th1^1$ originates. Maletz (2010) discussed the dorsal and ventral virgellar spines and, thus, the identification of the dorsal and ventral sides of the sicula in the Graptoloidea.

In the development of later thecae, a differentiation of right-handed and left-handed origin and dextral and sinistral growth is easily made in well-preserved material. The development has been investigated in a single specimen of *Dichograptus logani* (Hall, 1858) from Västergötland, preserved in partial relief and showing the development at 13 dicalycal thecae, forming 14 stipes (Figure 3). All dicalycal thecae (in red) are separated by a single monocalycal theca. There are six dextral and seven sinistral branching divisions present in the specimen. The distribution of dextral and sinistral branching

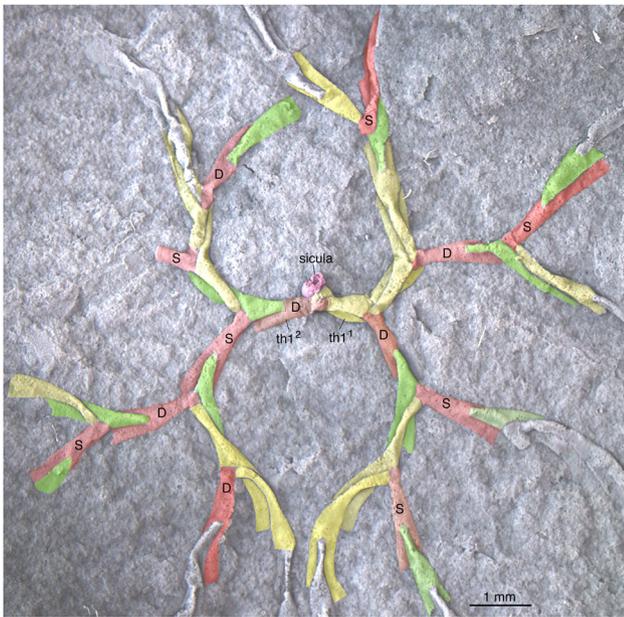


FIGURE 3 *Dichograptus logani* (Hall, 1858). LO 1732t, latex cast of specimen, Mossebo, Hunneberg (Törnquist, 1904, pl. 2, fig. 18). Dicalycal thecae in red, others in yellow. (D) indicates dextral growth, (S) indicates sinistral growth of dicalycal thecae. Thecae with dorsal origin in green

divisions is somewhat regular. After a dextral branching, usually, but not invariably, a sinistral one is following. As there is only one specimen available, nothing can be said about a consistent pattern of branching in the dichograptids and data from other species are not available. The dicalycal thecae and their first offspring originate laterally from their parent thecae, but other thecal origins (thecae shown in green in Figure 3) are dorsal in this species.

In dendroids and in most anisograptids, the origin of all thecae on the stipes is laterally on the right and left sides of the parent theca (Figure 4g,h). In taxa with bithecae, two thecae (an autotheca and a bitheca) originate at the same point on the sides of their parent theca. Usually, the origins of autothecae and bithecae alternate, and for example, on one side, each second autotheca appears associated with a bitheca, while the bithecae on the other side are hidden. The autothecae initially grow upwards to the dorsal side of their parent thecae and the bithecae grow laterally towards their parent autotheca's aperture (Figures 4g and 5a). This development is identified as the “triad budding” or the “Wiman rule” (cf. Kozłowski, 1949; Maletz et al., 2016).

When the bithecae are lost, the lateral origin and initial upward growth of the autothecae may still be recognizable (Figures 4h and 5b). Lindholm (1991, p. 289) termed this construction with and without bithecae the

“plaited overlap” and found it to be common in Tremadocian planktic graptoloids. The strict regularity of the development is broken in younger taxa in which often more than a single successive theca has its origin on the same side of the stipe. The origin of the thecae slowly moves upwards to the dorsal side of the stipes and the exact origin may be difficult to observe (Figure 4h). All traces of the presence of bithecae are erased in the Floian and thecal origins are generally on the dorsal side of the stipes (Figures 4d–f and 5c), except for the lateral origins of dicalycal thecae.

5 | FREQUENCY OF DEXTRAL AND SINISTRAL PROXIMAL DEVELOPMENT

Very little is known about the frequency and consistency that dextral and sinistral proximal developments can be found in graptolites, as well preserved relief specimens or isolated material is needed to identify these patterns. A specimen of *Expansograptus urbanus* (Monsen, 1937) with a sinistral development (Figure 4a,b,d), found at Diabasbrottet, Hunneberg, Sweden among hundreds of specimens with dextral development (Figure 4c) led to the question on the frequency of dextral and sinistral proximal developments. Both sides of the tubarium of the specimen are present as external molds and latex casts have been produced to show the relief. On the obverse side (Figure 4a), the origin of $th1^1$ is visible at ca. 0.3 mm below the apex of the sicula. It grows downwards along the ventral side of the sicula, showing a wiggly form for the next 0.6 mm, before widening and growing as a normal theca downwards and outwards on the right side of the sicula. The sicula is fully visible in the specimen and the origin of $th1^2$ is not seen. On the reverse side (Figure 4b,d), the early part of $th1^1$ appears to be damaged and only the growth of $th1^2$ is full visible. The crossing canal is ca. 0.5 mm wide, growing obliquely downward across the sicula, which is largely covered. The dorsal origin of $th2^2$ is clearly visible in the distal part of $th1^2$. Further development of the tubarium is normal, but the proximal development clearly is sinistral.

Cooper and Fortey (1983, table 1) provided the only information available so far for dextral/sinistral proximal developments in early Ordovician graptoloids. They listed 55 taxa from the Floian to Dapingian, belonging to the Dichograptina and Sinograptina of which most taxa possess dextral development of the proximal end, but did not consider the Tremadocian Anisograptidae. In a few taxa, the development was quoted as uncertain. The possibly sinistral development in *Oncograptus* sp. was based on serial sections in Bulman (1936) that may have

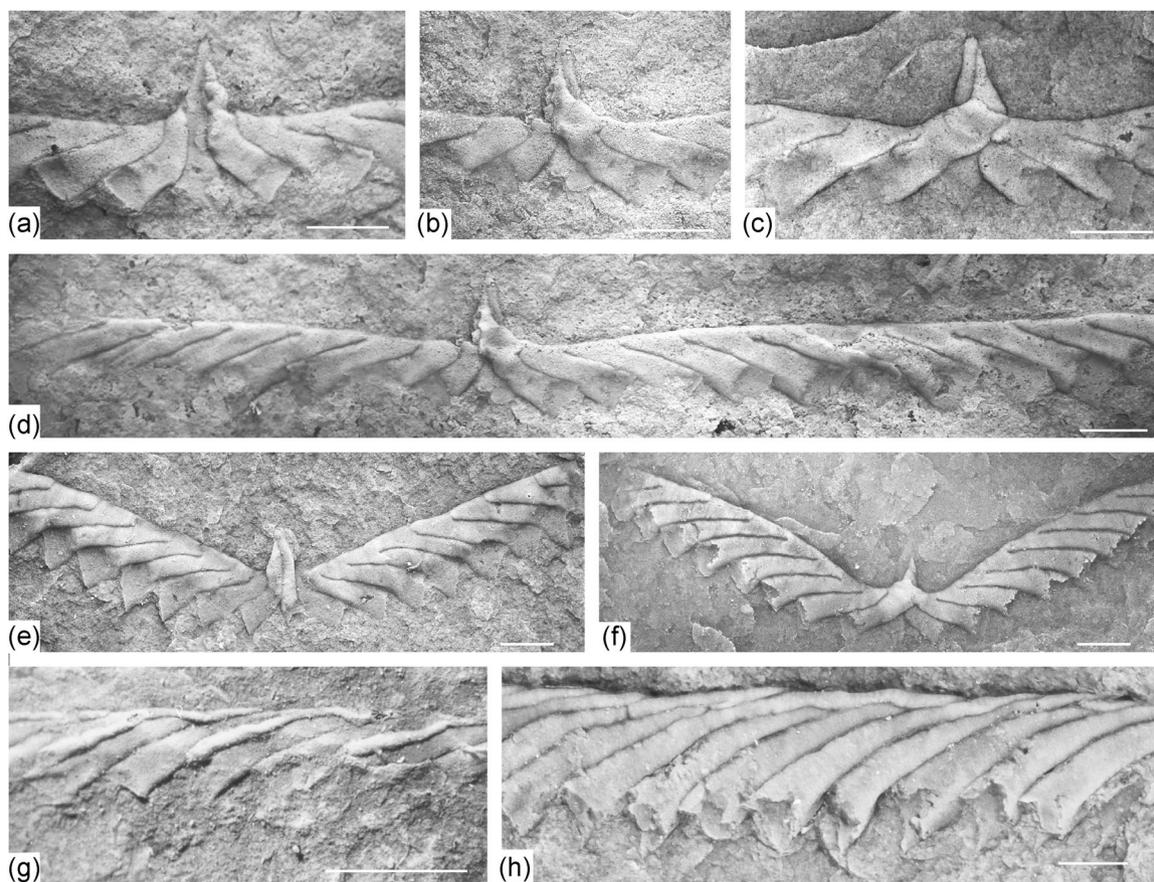


FIGURE 4 *Expansograptus urbanus* (Monsen, 1937) specimens in dextral and sinistral development. (a, b, d) PMU 38356 A, B, Di 48/1 and Di 48/2, Diabasbrottet at 6.7–6.8 m, sinistral development in obverse (a) and reverse (b, d) views. (c) PMU 38357, Di 46/1, Diabasbrottet at 6.2–6.3 m, dextral specimen in reverse view, showing robust crossing canals. (e) PMU 38358 A, B, Di 739/178B, Diabasbrottet at 4.0–4.1 m, obverse view. (f) PMU 23152.2B, reverse view, Diabasbrottet at 4.0–4.1 m. (g) *Kiaerograptus kiaeri* (Monsen, 1925), PMO 72833, Slemmestad, Norway, lateral view of stipe with plaited overlap and long bithecae associated with each second autotheca. (h) *Paratemnograptus* sp., Fezouata, Morocco, stipe fragment with plaited overlap, lacking bithecae. All photos are based on latex casts of the original molds. The scale bar is 1 mm in each photo

been erroneous as further relief material invariably indicated a dextral development (see Maletz & Zhang, 2016). They also indicated both, dextral and sinistral development in *Isograptus caduceus imitatus*, *Kinnegraptus kinnekullensis*, and *Kinnegraptus multiramosus*.

The presence of a dextral and sinistral proximal development can be followed very vaguely through the early Ordovician (Tremadocian to Floian), but little precise information is available (Figure 5). A list of known Tremadocian examples with known dextral and sinistral development is found in Appendix A. Bulman (1950) illustrated a single specimen of *Rhabdinopora rusticum* (Bulman, 1950) with a dextral development, but the development in other Anisograptidae is largely unknown. Maletz (1992) introduced a model for the proximal development of the Anisograptidae and stated that dextral and sinistral development is present. His model, however, illustrates only the dextral development.

Rickards and Stait (1984, fig. 4) illustrated dextral and sinistral specimens of *Psigraptus jacksoni* Rickards & Stait, 1984. A comparable development can be seen in the closely related *Ancoragraptus* (Maletz, 1992 fig. 2c,d) (Figure 5). The dextral and sinistral development is known for *Adelograptus tenellus*, based on chemically isolated material (Hutt, 1974) and relief specimens (Westergård, 1909), but there is no information on the frequency of dextral and sinistral forms. The only further available material of *Adelograptus* showing the development is *Adelograptus messaoudi* Legrand, 1964b (Figure 5). Dextral and sinistral development is present in *Hunnegraptus copiosus* (Figure 5) and *Kiaerograptus? supremus* from the late Tremadocian. Lindholm (1991) described the coexistence of sinistral and dextral forms of species as a “common feature in early Hunneberg time.” Due to the preservation of most specimens as flattened films of organic material and the presence of only a few

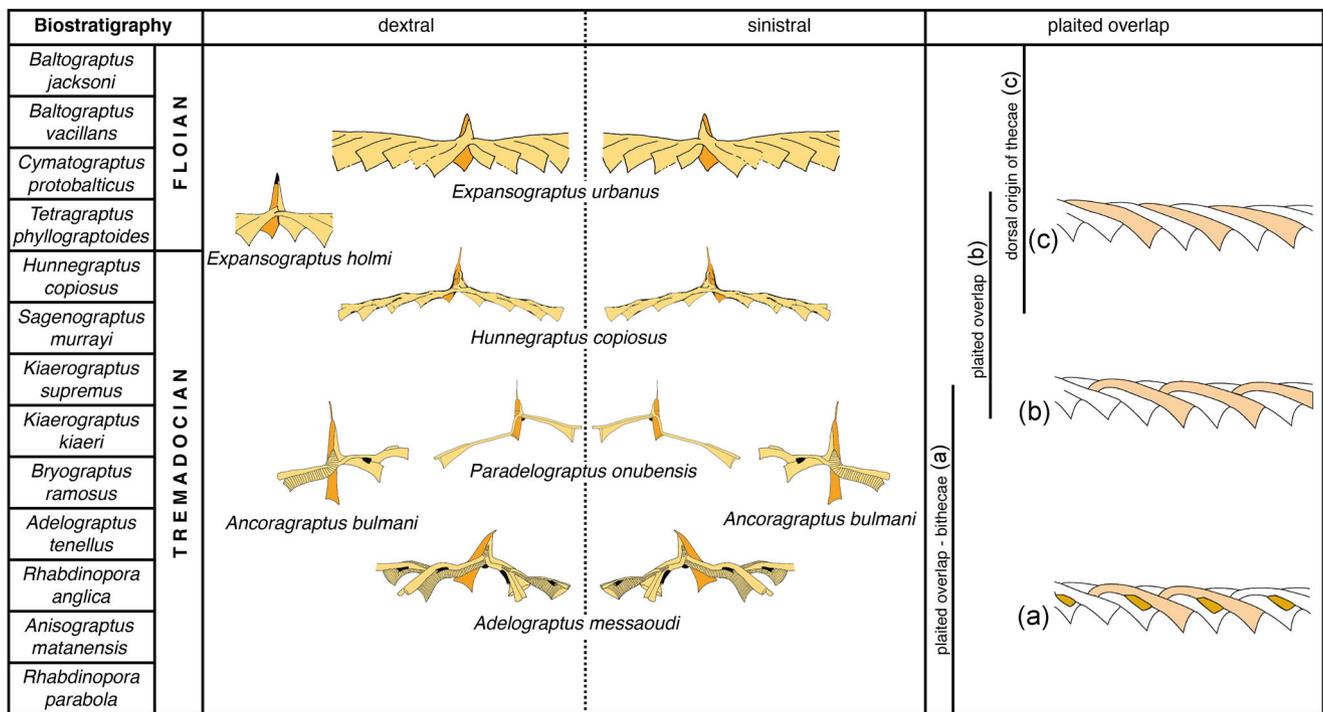


FIGURE 5 Dextral and sinistral development and plaited thecal overlap in the Lower Ordovician. Reconstructions (left side) show hypothetical dextral and sinistral developments. Thecal development. (a) Regular development of plaited overlap with bithecae. (b) Regular development of plaited overlap, no bithecae. (c) Dorsal origin of thecae (a–c after Maletz et al., 2016, fig. 16)

relief specimens no frequency information was available for her material.

From the Floian onwards, a dextral proximal development appears to be fixed in the development of nearly all graptoloids and very few specimens with a sinistral proximal development are known, a condition that may be called directional asymmetry. Cooper and Fortey (1982, fig. 54c,d) illustrated a single specimen of *Isograptus caduceus imitatus* Harris, 1933 with a sinistral development. Toro and Maletz (2008) recognized the presence of dextral and sinistral forms in *Cymatograptus bidextro* Toro & Maletz, 2008 from the Floian of Argentina. The authors stated that the number of dextral and sinistral specimens was approximately equal in this species. The sinistral example of *Expansograptus urbanus* (Monsen, 1937) (Figure 5) is based on the only available specimen showing this development and is the only known sinistral specimen of the Dichograptina. The only sinistral specimen of the Glossograptina is *Isograptus caduceus imitatus*, illustrated by Cooper and Fortey (1982).

Nothing has been stated in detail on the dextral or sinistral development in biserial Axonophora (Figure 2e–h). Even though numerous relief specimens of biserial axonophorans exist (e.g., Melchin, 1998; Mitchell, 1987, and many more), sinistral development has never been described or illustrated. Thus, it has to be

assumed that it does not exist or is extremely rare. Therefore, it is not considered here.

Dextral and sinistral development are not recognizable in the proximal ends of the Monograptidae, but a few taxa show torsion of the thecal apertures. Dextral torsion of the apertural parts of thecae may be present in some species of the genera *Spirograptus* and *Oktavites*, but details are unclear (Maletz & Loydell, 2021). Loydell (1993) described the consistent dextral torsion of the thecal apertures in the colonies of the genus *Torquigraptus*. Asymmetrical development of the thecal apertures is common in the Monograptidae, probably evolving independently in several groups (see Maletz & Loydell, 2021). Any consistency in these patterns of asymmetrical development has not been stated.

Coiling of the stipes without the torsion of the individual thecae is typical of the Dicranograptidae (see Maletz, 2020), but the direction of this coiling has not been investigated. Only Williams (1981) stated the presence of dextral and sinistral coiling in species of the genus *Dicellograptus*. Coiling of monograptid tubaria is common (see Maletz & Loydell, 2021) and appears to be dextral in illustrated chemically isolated examples of *Spirograptus turriculatus* (see Loydell et al., 1993, fig. 3b) and in *Oktavites spiralis* (see Lenz & Melchin, 1989, fig. 4). The direction of coiling has, however, never been

a character used in the descriptions of the cyrtograptids (see Lenz et al., 2012) or in other genera showing distinct coiling of their stipes. It is thus unknown for most taxa.

6 | ANTISYMMETRY IN PTEROBRANCHS

The random distribution of left- and right-handed origins or LR-asymmetry in early graptoloid (pterobranch) proximal development can be identified as antisymmetry, while fixed or directional asymmetry indicates that a certain species bears only right-handed or left-handed forms (cf. Palmer, 2005, 2016). Sato and Holland (2008, p. 3637) listed a few cases of asymmetry in enteropneusts, but concluded that the body of enteropneusts “is almost symmetrical.” Data on their variation are not available to confirm the development as antisymmetry, however.

Actually, LR-asymmetry is common in many organisms (cf. Levin et al., 2016) and is also typical for the development of the pterobranch tubaria. It is expressed by the variable lateral origin of thecal tubes on the left or right side of the parent tube. Sato and Holland (2008) discussed the distinct antisymmetry found in the development of the pterobranch zooids and compared it with the development in chordates. The antisymmetry in extant *Rhabdopleura* zooids might indicate an ancestral state, as it appears not to be typical of all (fossil) Pterobranchia.

Antisymmetry can be recognized in fossil pterobranchs only in the development of the tubaria due to the lack of preservation of zooids in the fossil record. These indicate distinct antisymmetry in early planktic graptolites, but the evolution leads to a change and derived taxa appear to show exclusively dextral development. Thus, the original antisymmetry is lost during the evolutionary changes in the Pterobranchia. The development in the Palaeozoic planktic pterobranchs indicates a fixation of a dextral development over time, thus a directed asymmetry, at least for their tubaria. The presence of antisymmetry in extant *Rhabdopleura* and *Cephalodiscus* is retained as an ancestral state but was transformed into directional asymmetry in the now extinct planktic Graptoloidea.

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CONFLICT OF INTERESTS

The author declares that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

Data available on request from the author.

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APPENDIX A: DEXTRAL AND SINISTRAL DEVELOPMENT IN TREMADOCIAN ANISOGRAPTIDAE

Adelograptus tenellus (Linnarsson, 1871). Hutt (1974, p. 80) stated that the fusellum of the prosicula (cauda and conus) is coiled indifferently in a clockwise or anticlockwise direction, but does not provide information on frequency. Hutt (1974) illustrated specimens with dextral and sinistral development but did not provide frequencies. Dextral and sinistral development has been illustrated by Westergård (1909) and Maletz (2020, fig. 5h). **Adelograptus sp.** GSC 123228, illustrated as *Adelograptus tenellus* by Jackson and Lenz (2003, fig. 9m). The slab bears dextral and sinistral specimens of a species with plaited overlap, but lacking bithecae.

Adelograptus bagueli Legrand, 1964b. The only illustrated proximal end is sinistral.

Adelograptus messaoudi Legrand, 1964b. The only illustrated specimen is sinistral.

Ancoragraptus bulmani (Spjeldnaes, 1963). Spjeldnaes (1963) illustrated dextral and sinistral specimens. Jackson and Lenz (2003, fig. 7a-f) illustrated dextral and sinistral specimens. Maletz et al. (2017, fig. 9b) illustrated a sinistral specimen.

Ancoragraptus sp. Maletz et al. (2017, fig. 9c,d) illustrated two dextral specimens.

Aorograptus victoriae (Hall, 1899) in Williams & Stevens, 1991. The illustrations show dextral and sinistral development of the proximal end, but this was not described.

Bryograptus ramosus Brogger, 1882. Maletz et al. (2017, fig. 1a, 9a) illustrated two dextral specimens preserved in relief.

Choristograptus louhai Legrand, 1964a. The Legrand (1964a, diagram in fig. 1) illustrated the species as a dextral one, but the illustrations are too poor for verification and consist of fragments only.

Hunnegraptus copiosus Lindholm, 1991. Dextral and sinistral specimens are available by Lindholm (1991) and Maletz (2006). The frequency is unknown.

Kiaerograptus supremus Lindholm, 1991. Lindholm (1991, fig. 5) illustrated a dextral and a sinistral specimen. Maletz (2020, fig. 13) illustrated a dextral specimen from the Fezouata Biota.

Kiaerograptus sp., cf. K. supremus Lindholm, 1991. Maletz et al. (2017, fig. 9g) illustrated a sinistral specimen.

Paradelograptus elongatus Lindholm, 1991. Dextral and sinistral specimens occur. Frequency unknown.

Paradelograptus onubensis (Erdtmann et al., 1987). Jackson and Lenz (2000, fig. 11a–e) illustrated dextral and sinistral specimens as *Kiaerograptus onubensis*.

Paratemnograptus isolatus Williams & Stevens, 1991. The illustrations show dextral and sinistral development of the proximal end, but this was not described.

Psigraptus jacksoni Rickards & Stait, 1984. Rickards and Stait (1984, fig. 4) illustrated dextral and sinistral specimens in reverse view but did not discuss this feature.

Rhabdinopora rusticum (Bulman, 1950). Bulman (1950, fig. 2) illustrated the species with a dextral development.

Staurograptus dichotomus Emmons, 1855. NYSM 6011, one of the types is a juvenile specimen, showing dextral development. Bulman (1950, fig. 9) illustrated two interpretations with dextral development.

Staurograptus mojotorensis (Monteros & Moya, 2011). Dextral development is shown in two specimens, but the material is flattened and interpretations are questionable. The material was originally identified as *Anisograptus mojotorensis*.