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Could the asymmetrical commissure in rhynchonellide brachiopods be an adaptive trait?

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This paper presents new arguments that contribute to support the hypothesis about the functional meaning of the commissural asymmetry in the Coniacian (Upper Cretaceous) rhynchonellide *Cyclothyris cardiatelia* Berrocal-Casero. According to this hypothesis, commissural asymmetry is interpreted as an adaptation to life on soft substrates, which leads to a life position that is oblique and partially sunk in relation to the substrate. The taphonomic compression of one of the shell lobes observed in asymmetrical *C. cardiatelia* has been compared to the compression found in a symmetrical rhynchonellide in which the compression is located at the frontal part of the shell, supporting the idea of a different life position than in *C. cardiatelia*. Additionally, the fossil record shows that brachiopods exhibiting external asymmetry usually display the corresponding asymmetry in the brachidium, related to dysfunction or atrophy of one of the lophophore arms. Observations in extant rhynchonellides show they can live with one arm of the lophophore atrophied or misfunctioning, and even amputated. The applicability of this hypothesis to other cases of commissural asymmetry in rhynchonellides, such as those living in closely packed clusters, reef environments or affected by unidirectional currents, is discussed, considering that the common physiological response to these different palaeoenvironmental scenarios would be a differential use of the arms of the lophophore, in turn affecting commissure plication. This physiological response could explain the origin of obligate asymmetry in other rhynchonellide lineages besides *Cyclothyris* M´Coy, for instance in *Torquirhynchia* Childs. Continuous records of both facultative and obligate asymmetrical rhynchonellides along single phyletic lines will be necessary, in order to establish whether this interpretation is a generalized explanation for asymmetrical shells in rhynchonellides. □ *Asymmetry, rhynchonellides, taphonomy, plasticity, inactive lophophore.*

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The commissural asymmetry of fossil rhynchonellides is frequently recognized in the fossil record, but is not clearly understood. Ager (1967) associated it with reef environments and Brookfield (1973) related the asymmetry to environments conditioned by tidal water currents. However, there does not seem to be a general correlation between the occurrence of asymmetrical rhynchonellides and such kinds of environments. Fürsich & Palmer (1984) examined an exhaustive list of species with commissural asymmetry, distinguishing two possibilities: facultative (when the individuals of the same species can develop both symmetrical and asymmetrical shells; basically ecophenotypic) and obligate (all individuals of the same species display asymmetrical shells), concluding that this last feature must be a genetically driven condition, 'which possibly was selected neither particularly for nor against' (Fürsich & Palmer 1984, p. 251). Additional authors (e.g. Gaspard 1991; Motchurova-Dekova 1995) could not find adaptive traits that justify this obligate asymmetry either, considering its origin unclear.

Some authors have recognized a number of subtle distinctions for commissural asymmetry in brachiopods and given them particular names, such as 'peculiar' asymmetry (Schroeder *et al*. 2016, 2018), 'dissymmetry vs asymmetry' (Gaspard & Charbonnier 2020), or 'rotational vs. non-rotational' asymmetry (Sulser *et al*. 2022), among others. In this paper, we prefer to consider only the 'facultative' and 'obligate' type of asymmetry as stated above, since what is being discussed is whether the asymmetrical commissure in rhynchonellide brachiopods could be an adaptive trait. The facultative type includes different styles of asymmetrical commissure, basically from a laterally displaced fold to a non-centred step, while the obligate asymmetry seems to be expressed only as centrally stepped commissures.

Recently, a new hypothesis about the functional meaning of the asymmetry in the Coniacian (Upper

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Cretaceous) rhynchonellide *Cyclothyris cardiatelia* Berrocal-Casero, from Western Europe has been proposed (Berrocal-Casero *et al.* 2017; Berrocal-Casero 2020). This hypothesis is based in palaeoenvironmental and taphonomic observations suggesting that this species lay inclined in life position, partially buried, as a consequence of an important increase in fine detritus in the platform which made the substrate much softer (see Berrocal-Casero *et al.* 2017, fig. 13). This explanation has been discussed and questioned by some authors like Gaspard & Charbonnier (2020) who considered that 'such a position would lead quickly to the infilling of the shell by the sediment and consequently to the inefficiency of the lophophore or the ability to feed' (Gaspard & Charbonnier 2020, p. 17). The model of life position of *C. cardiatelia* is defended here providing additional taphonomic evidence and after contrasting more information from fossil and extant brachiopods.

Furthermore, based on this hypothesis, Berrocal-Casero *et al.* (2020b) also published the first hypothesis about the relationship between the 'facultative' and the 'obligate' type of asymmetry for Upper Cretaceous rhynchonellides of the genus *Cyclothyris* from Europe (see also Berrocal-Casero 2020). These authors proposed that the facultative asymmetry of some species with phenotypic plasticity (such as *Cyclothyris segurai*) could have been fixed in succeeding species (such as *C. cardiatelia*) and be genetically assimilated to become obligate asymmetry. Thus, other species possibly related to *C. cardiatelia*, such as *Cyclothyris globata* and *Cyclothyris vesicularis*, which may occur in various different facies, would maintain the obligate asymmetry even in palaeoenvironmental conditions different from those that induced the adaptive change (Berrocal-Casero *et al.* 2020b, fig. 6). Lister (2021) has shown how phenotypic plasticity followed by genetic assimilation is well known in the fossil record.

These hypotheses could explain the origin of the obligate asymmetry in Upper Cretaceous *Cyclothyris*, but could be generalized for other cases? In this paper, a deeper study and comparison with other asymmetrical brachiopods from different ages have provided new data to understand these issues.

Taphonomic arguments for an inclined life position in *Cyclothyris cardiatelia*

Partial infilling of the shell is common in fossil brachiopods. According to Seilacher (1973), biogenic cavities can remain empty or become partially filled with material that usually presents granulometric and textural differences with respect to the materials of the matrix, depending on the hydrodynamic conditions and the size of the openings through which the sediment could enter the cavity. The mechanical stability of the preserved elements, their orientation and inclination are also factors that influence the processes of filling. Since incomplete infilling of the shell will favour subsequent deformation during burial and compaction, the way in which shells are compressed can be used as a tool to interpret the way in which they were buried and infilled and sometimes to indicate if shells were buried in life or nonlife orientations (Manceñido & Walley 1979; Alexander & Gibson 1993; Fernández-López 1998; Berrocal-Casero *et al.* 2022).

In this work, two examples of deformation during burial and compaction are compared (Figs 1, 2). The first one involves shells of *Soaresirhynchia bouchardi* (Davidson) collected from argillaceous marls, Lower Jurassic in age, of the Iberian Range (Eastern Spain). This species presents symmetrical shells with great intraspecific variability, showing opportunistic characteristics and a very rapid occupation of numerous Western Tethys basins after the Lower Toarcian Mass Extinction Event (García Joral *et al.* 2011). The collected specimens show different sizes compatible with a paleodeme and no evidence of fragmentation or abrasion, probably having been quickly buried in situ. Partial infilling and taphonomic compression are occasionally present, in all cases affecting the anterior part of the shell (Fig. 1A).

The second example corresponds to the rhynchonellides with asymmetrical commissures belonging to *Cyclothyris cardiatelia* Berrocal-Casero, studied by Berrocal-Casero *et al.* (2017, 2022). They have been collected in argillaceous marls of Coniacian age (Upper Cretaceous) from the Northern Castilian Platform (Northern Spain). Berrocal-Casero *et al.* (2017, p. 82) have shown that this species is more abundant in the levels where the percentage of $CaCO_3$ is lower (73–75%) and the grain size is smaller (<0.7 mm), without signs of fragmentation or erosion of the shells. The palaeoenvironment in which these asymmetrical brachiopods lived was interpreted as a low-energy offshore area with low sedimentation rates, and these brachiopods likely remained in their life position after death. Partial infilling and taphonomic compression are also present in some specimens but, unlike the case of *S. bouchardi*, in all cases they show compression of one of the two lobes in which the shell is divided, always the larger one (Fig. 1B).

The explanation for the difference in the compression of the partially infilled shells in these two

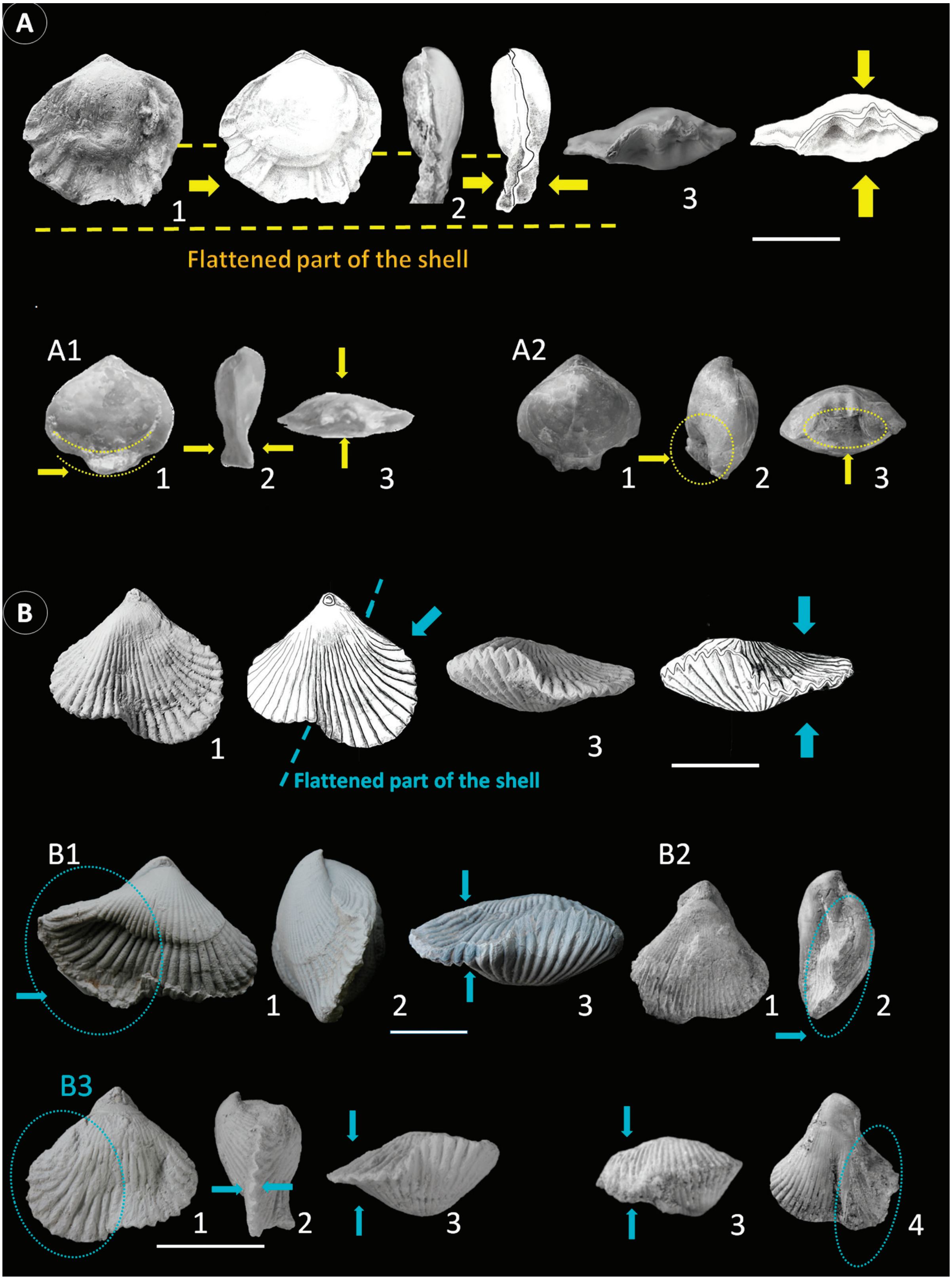

Fig. 1. A, symmetrical rhynchonellide *Soaresirhynchia bouchardi* (Davidson) from the Lower Toarcian (Jurassic) of the Iberian Range, Spain, showing the compression of the anterior part of the shell. Three examples in: dorsal (1), lateral (2) and frontal (3) views. Scale bar: 0.5 cm. B, asymmetrical rhynchonellide *Cyclothyris cardiatelia* Berrocal-Casero, from the middle Coniacian (Cretaceous) of Northern Spain, showing the compression of one lobe of the shell. Four examples in: dorsal (1), lateral (2) frontal (3) and ventral (4). views. Scale bar: 1 cm.

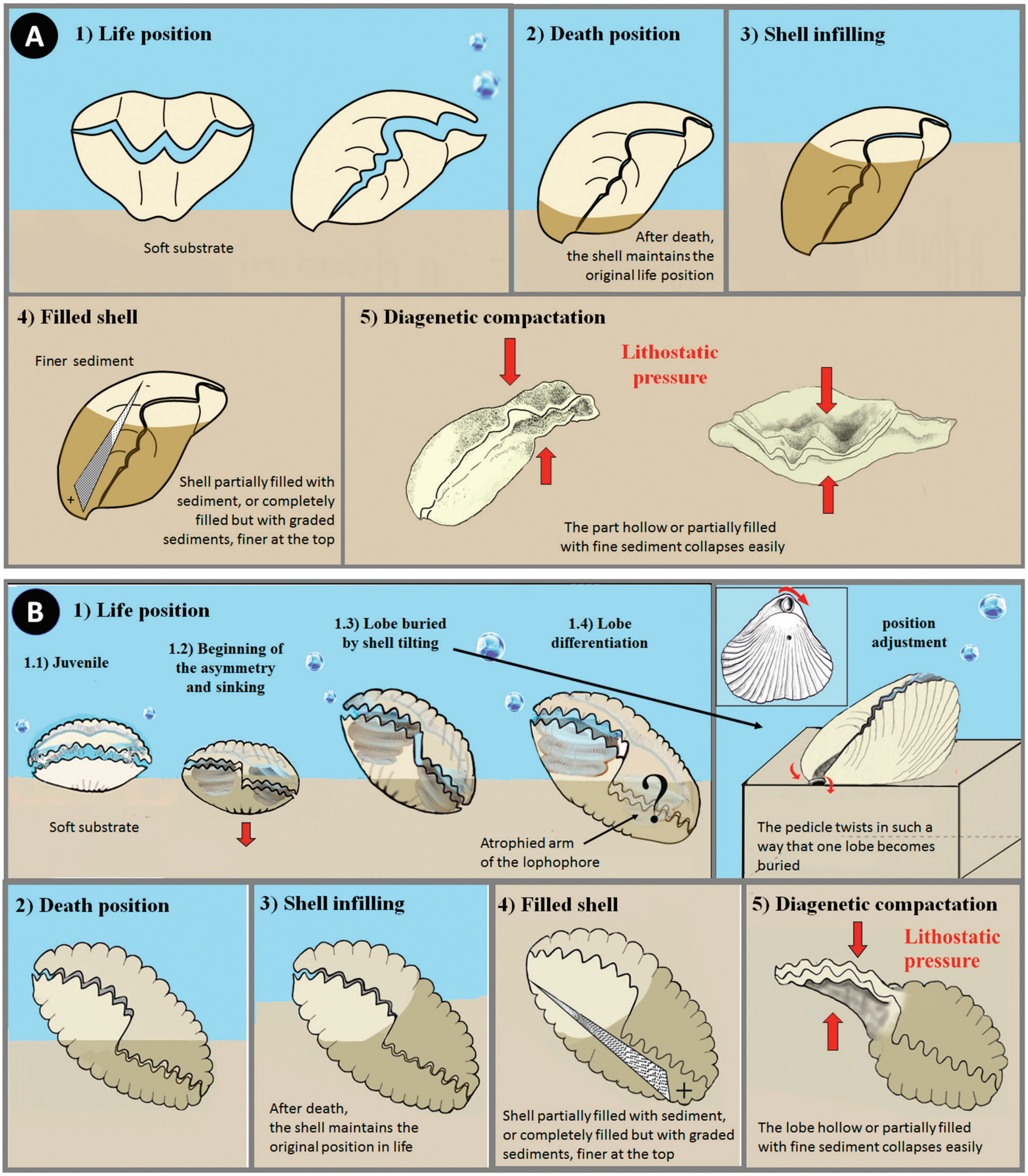

Fig. 2. A, reconstruction of the taphonomic compression in *Soaresirhynchia bouchardi* (Davidson), showing symmetrical uniplication of the frontal commissure. 1) Living brachiopods, in frontal and lateral views. 2) Death by rapid burial in low energy conditions. 3) After death, the shell in life position becomes filled with sediment. 4) The upper part of the shell (around the frontal commissure) can remain empty (or becomes filled with finer grained sediment). 5) The upper part of the shell (around the frontal commissure), which is totally or partially filled with finer sediment collapses easily. B, reconstruction of the development of commissural asymmetry in *C. cardiatelia* and of the differential taphonomic compression 1.1: Juvenile stage. 1.2: When juvenile specimens grow to a certain size, they begin to sink into the soft substrate. 1.3: The differentiation of the asymmetrical lobes increases as the sinking lobe gets further. 1.4.1: Semilateral view of the brachiopod. 1.4.2: The pedicle can adjust the shell to an inclined position to keep the non-buried lobe away from the sediment-water interface. As a consequence, the beak bends progressively sideways pointing towards the sunken lobe. The unsunken lobe grows more than the sunken lobe. 2) Death in low energy conditions below the storm wave base. 3) After death, the buried lobe becomes filled with sediment, in life position. 4) The other lobe can remain empty (or becomes filled with finer grained sediment). 5) The lobe, which is totally or partially filled with finer sediment collapses easily. (Modified after Berrocal-Casero *et al.* 2017).

cases can be related with the different life position of the individuals in either species (Fig. 2). In typical symmetrical forms in which partial infilling occurs, given that the posterior part of the shell is normally the heavier, thus closer to the substrate, it becomes filled earlier than the anterior part, which may remain partly filled or empty. Therefore, these shells will show the anterior part of the shell squashed by taphonomic compression (Fig. 2A).

Conversely, in the specimens with asymmetrical commissure and two differenced lobes belonging to *C. cardiatelia*, the flattened part always corresponds to the larger lobe, while the shorter lobe maintains its original volume (Fig. 1B). That this happens by chance does not seem plausible and can be reasonably interpreted because they were buried in a laterally inclined position, with the smaller lobe partially sunken in the substrate (Fig. 2B). The taphonomic compression (deformation after burial) of the larger lobe of the shell would be easily explained if the life position of these individuals were to be so, with the smaller lobe sunken obliquely into the substrate. The difference in size of the lobes can also be explained if the smaller one was partially sunken, and consequently less active, as will be explained later in this paper. The sunken lobe would be filled early, while the other would remain empty for a longer time (see Berrocal-Casero *et al.* 2017, figs 5, 13). It is not uncommon for rhynchonellides to live partially buried, as several authors have pointed out (cf. Fürsich & Palmer 1984, p. 260).

Palaeontological arguments and observations on extant brachiopods supporting the feasibility of living with part of the lophophore atrophied

To explain how *Cyclothyris cardiatelia* Berrocal-Casero could live with a part of the shell obliquely buried in the substrate, Berrocal-Casero *et al.* (2017) proposed that one arm of the lophophore could be atrophied but the other not, as implied by the different size of each shell lobe. This hypothesis has been rejected by some authors believing that a brachiopod cannot survive with one side of the lophophore atrophied (Fürsich & Palmer 1984, p. 261; Gaspard & Charbonnier 2020, p. 17). However, this is not the first time that atrophied (or inactive) arms of lophophores have been hypothesized in fossil brachiopods. As rhynchonellides lack a supporting brachidium, the atrophy of one spirolophous arm can be only presumed in fossils, but it has been recorded in other groups. Afanasjeva (2014, fig. 5) shows, for instance, one spirolophous arm atrophied, affecting the shell shape, in the atrypid *Kerpina veneta goniorhyncha* Struve, from the Middle Devonian of Germany, originally described by Copper (1967); and another specimen with asymmetry in shell shape and inner structures of the spiriferid *Orthospirifer* (formerly *Spinocyrtia*) *iowensis* (Owen) from the Devonian of United States, showing the left brachial arm longer than the right one, interpreted by Ager & Riggs (1964) as related to strong currents in the species habitat. In this last case, the internal asymmetry does not imply an external asymmetry, but these examples confirm that the two arms of the lophophore could function differently, one being less developed than the other one or possibly atrophied while the other remains active, as proposed by Berrocal-Casero *et al.* (2017).

In the specific case of rhynchonellides, it has been repeatedly argued that the spirolophe lophophore could become non-functional on one side by palaeoenvironmental conditioning (e.g. Ager 1965; Warth 1969; Brookfield 1973). This last author (Brookfield 1973, p. 254–255) proposed that the asymmetrical rhynchonellide *Torquirhynchia inconstans* (Sowerby) 'lay attached by its pedicle in a stable position resting on its side on the sediment surface with the plane of its commissure vertical'. According Brookfield, there are different possible ways in which the feeding currents were organized in *T. inconstans*. One of them maintains that the asymmetrical commissure separated the two sides of the lophophore into two independent systems, so that one side of the lophophore could be active while the other remained inactive (the side that was in contact with the sediment). If the shell had lain consistently on one side, Brookfield (1973) considered likely that growth of the side in contact with the sediment would be retarded due to retraction of the mantle edges. Although this hypothesis has been discussed by Fürsich & Palmer (1994, p. 259), the inference about the growth retardation of one side of the shell is applicable therefore to *C. cardiatelia* which shows one lobe shorter than the other one. In this case, in contrast to *T. inconstans*, *C. cardiatelia* would have been leaning and partially sunken in the soft substrate on the same side of the shell (randomly left or right).

Other point of discussion about the hypothesis of Berrocal-Casero *et al.* (2017) is the question if the sediment enters into the brachiopod shell and if the brachiopod could live with sediment inside the shell. However, as discussed in the study of Brookfield (1973) on *T. inconstans*, the posterior parts of the shell commissure, that would be mainly in contact with the sediment surface in specimens lying on its side, is much less widely open than frontal commissure, thus limiting the entry of sediment particles. In the case of *C. cardiatelia*, the growth retardation of the partially sunken lobe implies that the opening of the part of the shell in contact with the sediment would have been even smaller, perhaps preventing the entry of an unbearable amount of sediment into the shell.

From the physiological point of view, Elliott (1948) described an asymmetrical lophophore in a specimen of the recent terebratulid *Macandrevia cranium* (Müller) dwelling in coral thickets near the shores of Norway. Half of plectolophe lophophore was normally developed whereas the remaining part was rudimentary (Elliott 1948, fig. 8; Afanasjeva 2014, fig. 1), showing that a brachiopod can live with only one part of the lophophore well developed. Childs (1969, p. 9) proposed that *Torquirynchia* species with asymmetrical anterior commissure could take advantage of the physiological independence of the right and the left halves of the mantle cavity shown by Orton (1914), since at least half of the lophophore system would have a water intake well clear of the bottom. Orton (1914) does not deal specifically with brachiopods possessing asymmetrical commissures but shows little doubt that this physiological independence applies to all brachiopods (p. 296). These observations support the hypothesis of Berrocal-Casero *et al.* (2017) who considered that one arm of the lophophore can be active while the other is atrophied.

In this sense, one frequently argued advantage that some extant rhynchonellide brachiopods possess over other suspension-feeding organisms is their ability to uncoil and extend the lophophore beyond their shells. This ability is known since the 19th century (e.g. in *Hemithyris psittacea* Gmelin, described by Morse 1869) and it has been also demonstrated in *Notosaria nigricans* (Sowerby). Hoverd (1985) observed the capacity of this species to uncoil, extending an arm or both out beyond the valves in *in situ* populations as well as under controlled laboratory conditions. This is probably favoured by the detachment of the lophophore axis from the mantle cavity, contrarily to what is observed in other types of lophophores, as shown by Kuzmina & Malakhov (2006). Hoverd (1985) also demonstrated that, occasionally, sudden shell closure without complete retraction of spiralium amputates part of the uncoiled distal whorls of the lophophore and regeneration subsequently occurs. Hoverd figured a specimen of *N. nigricans* in which three-quarters of one spirolophous lophophore arm had been amputated and the regeneration process had commenced (Fig. 3). This image demonstrates that rhynchonellides do not need the entire lophophore system working, being able to live with only part of an arm. Moreover, in this image it can be seen that the side of the shell with the well-developed arm of the lophophore seems to be more developed (bigger) than the side with the amputated arm. This supports the hypothesis that rhynchonellides like *C. cardiatelia*, which have one (supposedly sunken) lobe of the shell underdeveloped in relation to the other, were able to live and grow with one arm of the lophophore active while the other was atrophied. Fürsich & Palmer (1984) considered that it seems unlikely that most brachiopods could have thrived when their feeding system was severely impaired, but the particular ability of rhynchonellides to extend the lophophore beyond the shell should be taken into account, which represents a great advantage because it allows enlarging the food particle trapping area (cf. Ager 1987), thus minimizing the loss of part of the filtering cavity.

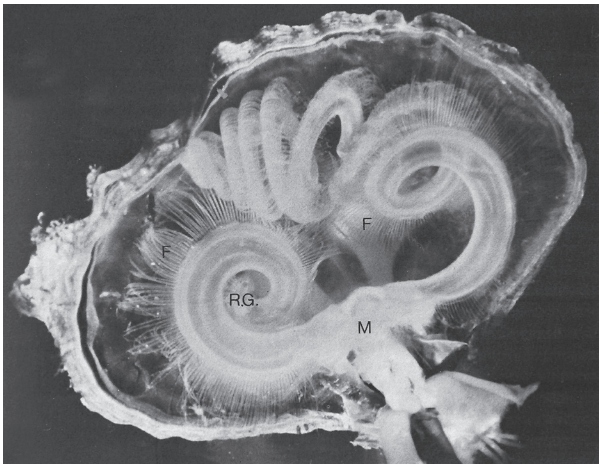

Fig. 3. Notosaria nigricans (Sowerby) (shell length 16 mm, breadth 20 mm). Zeiss Tessovar photomicrograph of live specimen. Brachial view showing fully developed spirolophous lophophore. Note: three-quarters of one arm have been amputated and regeneration (R.G.) of the damaged stump has commenced. F, filaments; M, mouth. (Modified from Hoverd 1985).

Relation between commissural asymmetry and lophophore asymmetry

Berrocal-Casero *et al.* (2017, 2020a, 2020b) observed that the development of asymmetry in *Cyclothyris cardiatelia* Berrocal-Casero, begins when the shell grows to a certain size. This observation has been also perceived in other rhynchonellides with obligate asymmetry, such as in *Torquirhynchia inconstans* (Sowerby) (cf. Childs 1969; Brookfield 1973; Fürsich & Palmer 1984) or in *Cyclothyris globata* (Arnaud) (cf. Gaspard 1991). In asymmetrical brachiopods, the beginning of the asymmetry may be correlated with a change in the lophophore from a schizolophe to a spirolophe (Rudwick 1970). In the schizolophe, a median inhalant aperture is flanked by two lateral exhalant apertures, whereas in the spirolophe, the inhalant currents are lateral and the exhalant currents are median. According to Brookfield (1973, p. 253), during growth, as can be seen in the extant *Notosaria*, the schizolophe lophophore changes to spirolophe (thus passing to a laterally incurrent and centrally excurrent condition). This is commonly marked by a median deflection in the commissure, allowing better separation of inhalant and exhalant water currents according to Rudwick (1970, p. 135).

The spirolophe type of lophophore is characteristic of all living rhynchonellides, and reasonably it is the same in fossil members of this group. In this sense, possibly the onset of the asymmetry in *T. inconstans*, *C. cardiatelia* and other asymmetrical rhynchonellides also coincide with the ontogenetic change in the lophophore. It is logical to assume that, if there are conditions that lead to a different development of the spirolophe arms, this would in turn condition the development of the folding.

Ager (1965), Warth (1969) and Brookfield (1973) have argued that in a crowded reef environment the spirolophe of the rhynchonellides may become non-functional on one side, so that only one half of the lophophore system would be functional, either alternately or permanently. This could be due either to obstacles or to a position on the lee side of a unidirectional current, resulting in similar deformations of the commissure which were allowed by a remarkable plasticity in the ontogenetic development of rhynchonellides. This plasticity was explored by Fürsich & Palmer (1984, fig. 6) who explained the ontogenetic development of the commissural asymmetry as a progressive widening of the sulcus on one side of the median axis. This development may be only partially completed; many species with facultative asymmetry show only a deformation of the median fold, which seems to be slanted to one side, as in the intermediate stage of their scheme (Fürsich & Palmer 1984, fig. 5). Several examples of this 'commissural deformation' are known in the rhynchonellide fossil record, as can be seen in *Cyclothyris difformis* (Lamarck) form the Cenomanian of South England or in *Rhynchonelloidea goyi* García Joral, from the Toarcian of Eastern Spain (Fig. 4). The explanation for such deformations should surely be sought in the specificities of the inhalant/exhalant currents pattern. The mantle cavity of extant rhynchonellides is always divided by the lophophore into inhalant and exhalant chambers with separate apertures (Rudwick 1962, 1970). These apertures correspond to the lateral commissure for the inhalant currents and the frontal commissure for the exhalant. If the morphology or size of a lophophore arm changes, this should condition the shape of the mantle edges and, in turn, the position of the apertures.

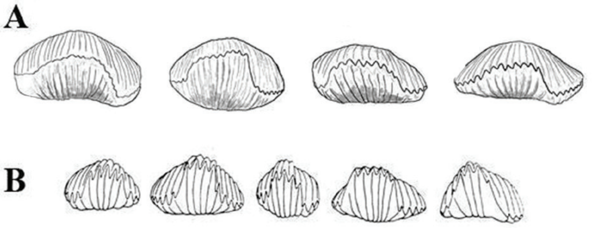

Fig. 4. Frequent commissural deformations in *Cyclothyris difformis* (Lamarck) form the Cenomanian of South England (A) and in *Rhynchonelloidea goyi* García Joral, from the Upper Toarcian of the Iberian Range of Eastern Spain (B). The explanation for these deformations should be surely sought in peculiarities of the inhalant/exhalant currents pattern.

According to the scheme of Rudwick (1962) of water circulation in *Notosaria*, the inhalant currents enter through the lateral commissure and the exhalant currents exit through the frontal commissure (Fig. 5A). However, in crowded or reef environments, with a prevailing unidirectional current or other factor preventing the uniform circulation of water in the inhalant chamber, water would preferentially enter through one side of the shell (Fig. 5B). The exhalant aperture should possibly be oriented in the same direction as the current, thus provoking a misfunctioning of the inhalant aperture and of the lophophore arm located in the half of the shell opposite to the main inhalant aperture. This misfunctioning should affect the folding, which would become slanted or twisted in the direction of the current. This is the type of asymmetry identified as intermediate in Fürsich & Palmer (1984, fig. 6).

In the case of rhynchonellides living obliquely-sunken in the substrate, the water would enter only through one side of the shell (Fig. 5C) leading to a morphological response like in the previous case. The dysfunction and atrophy of the lophophore arm in contact with the sediment would cause a similar drift in the median fold but, since there is no water income in the sunken part of the commissure. This drift would be more important, giving rise to the stepped commissure.

Adaptability of asymmetrical commissures in rhynchonellides

Commissural asymmetry could have been adaptive in *Cyclothyris cardiatelia* Berrocal-Casero, according

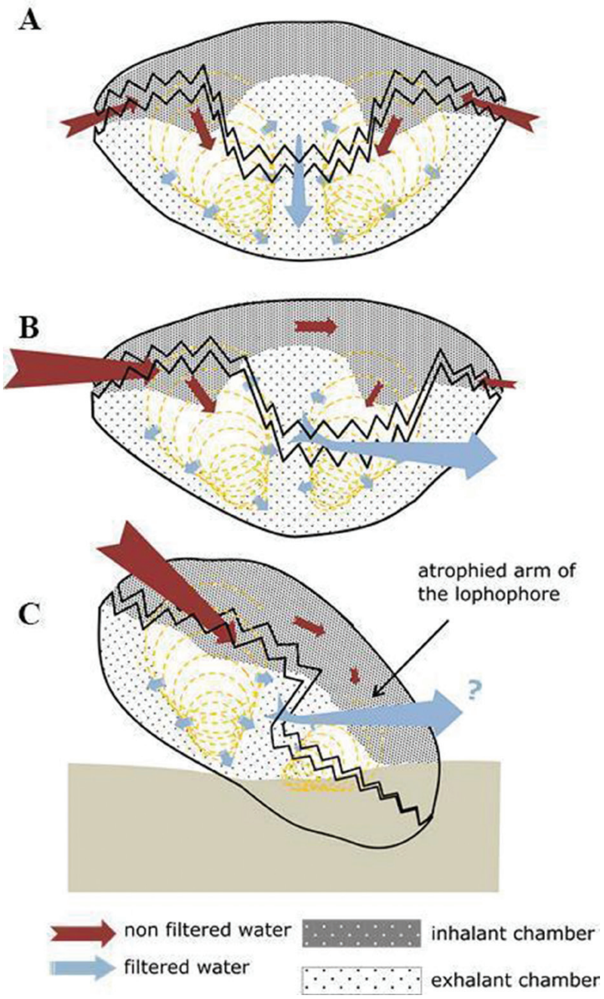

Fig. 5. A, scheme of water circulation in symmetrical rhynchonellides after Rudwick (1962, modified). B, C, how the circulation pattern may be affected in a situation of crowded packing or reef environments with water entering preferentially from one side of the shell (B), and to shells living obliquely sunken (C). With water entering mainly from one side, one inhalant aperture will capture much more water that the opposite and the exhalant aperture should possibly be oriented in the same sense of the current, thus provoking a misfunctioning of the lophophore arm situated in the half of the shell opposite to the main inhalant aperture.

to the arguments exposed in the previous paragraphs, but will it also be in other cases? This type of asymmetry in rhynchonellides has been related to different scenarios: 1) The response to problems in vital space as living in closely packed clusters (e.g. Brookfield 1973; Laurin 1984); 2) the response to prevalent or unidirectional currents such as those usual in reef or perireefal environments (e.g. Ager 1967; Asgaard 1968); and 3) the response to living in soft substrates (Berrocal-Casero 2020; Berrocal-Casero *et al.* 2017, 2022).

For the first scenario, there are numerous examples. Brookfield (1973, p. 257) observed that the facultative type of asymmetry in *Septaliphoria hudlestoni* Rollier, from the Lower Kimmeridgian of Dorset (United Kingdom) seems to be an ecophenotypic adaptation of the relatively large brachiopods (with high plasticity) to living in closely packed clusters, where interference with one another, and their respective inhalant currents, is likely. These asymmetries or 'commissural deformations' are frequent (e.g. McCammon 1970, Laurin 1984, Fürsich & Palmer 1984, Sulser *et al.* 2022). Another example is the extant *Notosaria nigricans* from New Zealand, that sometimes show asymmetry in adults due to the crowded mode of life where most specimens cluster on other members of the same species (Lee 1978).

With respect to the reef environments, commissural asymmetry has been repeatedly related to them. An example of that is the asymmetrical specimen of *Lacunosella arolica* (Oppel) from the Middle Oxfordian of the Iberian Range (Spain) (Fig. 6), which was growing attached to a sponge (Colás 2015). Many of these examples can also be interpreted as ecophenotypic modifications. However, Asgaard (1968) suggested that *Obliquorhynchia flustracea* (von Buch) from the Danian of Fakse (Denmark) became specialized for attachment to the coral branches in a fixed position. According to Asgaard (1968, pp. 111–112) the position of these brachiopods, relative to the branches, rendered a current system of one inhalant and one exhalant current more adequate than the normal system of two lateral inhalant currents and one median exhalant. In this case, an abnormal current system could be established through a constant atrophy of one arm of the spirolophous lophophore and an enlargement and eventual torsion of the other.

Fig. 6. Lacunosella arolica (Oppel) from the Middle Oxfordian of the Iberian Range (E. Spain), growing attached to a sponge (from Colás 2015, with permission).

That is, a similar pattern as the exposed in Figure 5B. This same case has been studied by Schroeder *et al.* (2018) who consider that *O. flustracea* could become asymmetrical, if necessary, due to limitation of space between the coral branches during the ontogenetic development. The development of asymmetry, facilitated by phenotypic plasticity, would be an advantage under these circumstances. The atrophy of one side of the filtering system would possibly allow the individual to remain attached in an otherwise uninhabitable part of the coral colony.

The third scenario is the one proposed by Berrocal-Casero *et al.* (2017, 2022), in which asymmetry is interpreted in *Cyclothyris cardiatelia* Berrocal-Casero, from the Coniacian of the Northern Castilian Platform (Northern Spain) as an adaptation to sinking in soft substrates taking place as a response to changes in palaeoenvironmental conditions. According to this hypothesis, *C. cardiatelia* would have lain obliquely in life position, partially buried in soft substrates.

The common physiological response in these different scenarios seems to be the differential use of the lophophore arms. Being caused by living in closely packed gregarious populations, by unidirectional currents or to by living obliquely sunken in soft substrates, if the water currents enter in the shell preferentially by only one of the two sides, this could cause misfunction of the lophophore arm in the opposite side and, ultimately, its atrophy. The asymmetry should be related to this fact.

Thus, in the different scenarios exposed due to external factors one arm of the lophophore would become inactive, and this internal change would lead to external asymmetry. In this sense, the key to understanding the functionality of the commissural asymmetry in rhynchonellides is not related with a concrete adaptation to a unique environment or type of substrate, but a question already known (but scarcely cited) since more than 100 years. As indicated by Orton (1914), and later Childs (1966, 1969), and Brookfield (1973) among others, in brachiopods the right and left halves of the mantle cavity can be physiologically independent. In this sense, one side (one arm) of the lophophore could function while the other not. The evidence that brachiopods are able to live with only one arm of the lophophore was demonstrated by Hoverd (1985, fig. 1) in present-day living rhynchonellides and has been valued here (Fig. 3).

The question, now, is if this physiological response (and its morphological consequence) can be selected and fixed in the genome. It is not easy to answer this question only with palaeontological data, but the records of obligate commissural asymmetry in *Cyclothyris* indicates that this has possibly occurred in the evolution of this genus, as hypothesized by Berrocal-Casero *et al.* (2020b).

Brookfield (1973) could not find the origin of the asymmetry in the Jurassic rhynchonellide with obligate asymmetry *T. inconstans*. To explain it, this author speculated that asymmetrical variants could become separated from the parent populations and form an inter-breeding group, so the asymmetry could thus become genetically fixed, instead of forming part of a variable population. In fact, even though at that moment the terms obligate and facultative were not yet proposed, this author was already suggesting that the obligate type of asymmetry observed in *T. inconstans* should have its origin in precursor species with facultative type of asymmetry, being the asymmetry genetically fixed in *T. inconstans* (see Brookfield 1973, p. 256–257). In the case of *O. flustracea*, since not all the specimens of this species show commissural asymmetry according to Schroeder *et al.* (2018), it could have been an example of such kind of 'precursor' species, but a subsequent species with obligate asymmetry is not known.

Berrocal-Casero *et al.* (2020b) exposed the first case of relationship between the facultative and the obligate type of asymmetry in rhynchonellides, from the continuous record of *Cyclothyris* species with facultative and obligate type of asymmetry in the Coniacian of Northern Spain. In the Cenomanian–Turonian, asymmetrical *Cyclothyris* show facultative asymmetry elsewhere. This feature is also present in the lower Coniacian *Cyclothyris segurai* Berrocal-Casero, which seems to be phylogenetically related to the middle–upper Coniacian *C. cardiatelia* (cf. Berrocal-Casero *et al.* 2020a). Symmetrical forms of *C. segurai* occur where lithology is mainly calcareous, whereas *C. cardiatelia* appears when it changes to marly (Berrocal-Casero *et al.* 2017, fig. 2; 2020a, figs 2, 6). However, at the uppermost stratigraphical levels where *C. segurai* appears, a few intermediate forms (uniplicate, but with certain degree of asymmetry) are occasionally found (Berrocal-Casero *et al.* 2017, figs 2, 12), suggesting that asymmetry was correlated with living in a palaeoenvironment changing to deeper and softer sea floors. When soft bottoms were generalized in upper levels, asymmetry was selected and became obligate (genetically fixed) in *C. cardiatelia*. Some subsequent species as *C. globata* and *C. vesicularis* show the same type of commissural asymmetry (cf. Berrocal-Casero *et al.* 2020b, fig. 2) but have been recorded in different palaeoenvironments and do not show different sizes of the two lobes of the shell (indicating that there would be no atrophy of one of the arms of the lophophore). Thus, its asymmetry should not have an ecophenotypic origin, but it can be explained if it is due to genetic assimilation of the obligate asymmetry.

In a recent paper on phenotypic plasticity in the fossil record, Lister (2021) has proposed different models of phenotypic plasticity followed by genetic assimilation. In one of these models, phenotypic plasticity appears as part of a reaction norm (changes ligated to an environmental variable); the stabilization of this variable at one of its extremes leads to the adaptive selection of a specific phenotype, which becomes fixed and is then the only one appearing even when the environmental conditions are different to those that induced the adaptation (Lister 2021, fig. 11.6).

This model fits very well with what was observed in Late Cretaceous species of *Cyclothyris*. The variation in the phenotypic expression of commissural asymmetry in this genus can be related to a reaction norm, since it has been observed in response to a gradient of laterality of the inhalant currents into the shell (from bilateral to predominantly unilateral), such as stated in previous paragraphs. The generalization of soft bottoms in the middle Coniacian of the northern Castilian platform and other nearby basins would have been the trigger for the selection and fixation of an extreme phenotype within this reaction norm, adapted to a partially buried lifestyle. Once genetically fixed, this phenotype would have been maintained for a certain time in the phyletic line.

As indicated above, Brookfield (1973) considered that the obligate asymmetry in *T. inconstans* should has its origin in the precursors with high plasticity leaving to the facultative type of asymmetry, that could be later genetically fixed in the subsequent species of the phyletic line. In the case of *T. insconstans*, there is no record of precursors adapting to a concrete palaeoenvironment or substrate, as in the case of *C. cardiatelia*. In the case of *O. flustracea* described by Asgaard (1968) and Schroeder *et al.* (2018), there is no record of successor species which could fix the adaptation. However, it seems likely that should be different scenarios in which a group with facultative commissural asymmetry could have evolved into taxa with obligate asymmetry (Fig. 7). It will be necessary to study further cases with a continuous record of facultative and obligate asymmetrical rhynchonellides in the same phyletic line to confirm this process. Currently, only one of these scenarios is documented (Berrocal-Casero *et al.* 2020b).

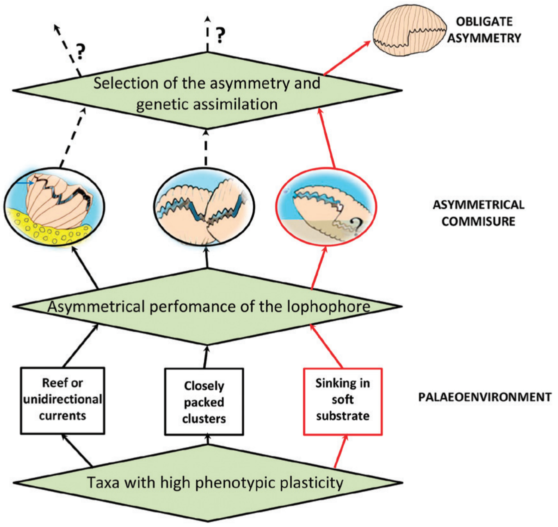

Fig. 7. Proposed scheme for the evolution of commissural asymmetry in rhynchonellides. Arising from the morphogenetic plasticity of anterior commissure shown by several lineages, factors related to the palaeoenvironment would result in a mode of life in which the lophophore functions in an asymmetrical way and this provokes the asymmetry of the commissure. If the environmental factor persists, the asymmetry can be adaptively selected and fixed by genetic assimilation. This would lead to an obligate type of asymmetry in the subsequent species of the phyletic line, even in palaeoenvironmental conditions different from those were adaptation occurred. The red arrows indicate a known scenario (Berrocal-Casero *et al.* 2020b), while the discontinuous arrows assume other possible scenarios. Discontinuous lines are used to denote yet undescribed cases.

Conclusions

Taphonomic and palaeontological arguments and observations on living brachiopods support the hypothesis that the asymmetrical rhynchonellide *Cyclothyris cardiatelia* Berrocal-Casero, from the Coniacian of Western Europe would have lived obliquely sunken in soft substrate, with one arm of the lophophore atrophied. The comparison here realized between this species and other symmetrical rhynchonellide, *Soaresrynchia bouchardi* (Davidson), considering the way in which shells are compressed as a tool to interpret their life position, reinforce the previously mentioned model. When shells show symmetrical commissure, taphonomic compression led to the collapse of the anterior part of the shell, whereas in the asymmetrical *C. cardiatelia* this compression is always presents in one lobe of the shell. Additionally, palaeontological evidence supports that brachiopods have often displayed asymmetrical brachidia, and observations on extant rhynchonellides demonstrate that they are able to live without a significant part of the lophophore being active.

Observations on the development of the lophophore of the rhynchonellides and their ability to live using it only partially allow us to relate the asymmetry of the frontal commissure in this group with the asymmetrical functioning of the lophophore, which in turn should be a consequence of changes in the pattern of water circulation inside the shell. In the case of *C. cardiateli*a, the asymmetry would be caused by the atrophy of one arm of the lophophore resulting from partial burial in soft sediments that would prevent the entry of water through one of the lateral commissures. In other scenarios that assume that water enters mainly from one side of the shell, there is not necessarily atrophy, but at least the misfunction of one side of the lophophore that would also lead to frontal commissure asymmetry.

Recent models to explain how phenotypic plasticity can be fixed by adaptive selection and genetic assimilation reinforce the hypothesis about the origin of the obligate asymmetry in *Cyclothyris* exposed in previous works. To extend this hypothesis to other rhynchonellide lineages, or to better understand how ecophenotypically selected asymmetry can lead to obligate asymmetry, it seems necessary to study this process through continuous records of species showing facultative and obligate asymmetry in the same phyletic line.

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