Shell asymmetry in Cretaceous Cyclothyrididae (Brachiopoda): variability, ontogeny and terminology

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ABSTRACT

The asymmetry observed in rhynchonellid brachiopod shells has been discussed for decades and continues to attract attention. This noteworthy modification of the anterior margin morphology during the ontogeny has evolved several times in rhynchonellids, and seems to reflect a genetic basis. First, we try to clarify the terminology regarding asymmetrical, dissymmetrical and symmetrical shells that has existed since the beginning of the 20th century. The Cretaceous populations observed clearly exhibit antisymmetry (also called random asymmetry). During the Cretaceous, some populations of *Cyclothyris* McKoy, 1844 include a mixture of truly asymmetrical specimens and others that exhibit an intermediate degree of asymmetry, herein called atypical morphologies. Shapes of specimens coming from two different locations in France were captured using geometric morphometrics. We used the range of different morphologies: 1) to test alternative hypotheses about the ontogeny of asymmetry; 2) to test for the possibility of several morphogroups; and 3) to discuss the determinism of the asymmetry.

KEY WORDS
Brachiopods,
Rhynchonellida,
Cretaceous,
asymmetry,
antisymmetry,
random asymmetry,
terminology,
geometric
morphometrics.

RÉSUMÉ

L'Asymétrie de la coquille chez des Cyclothyrididae (Brachiopoda) du Crétacé : variabilité, ontogenèse et terminologie.
L'asymétrie observée chez les coquilles de Brachiopodes rhynchonellides est discutée depuis des décennies et continue d'attirer l'attention. Cette importante modification de la morphologie de la commissure antérieure observée au cours de l'ontogenèse apparaît plusieurs fois indépendamment au cours de l'évolution et semble avoir un déterminisme génétique. Dans un premier temps, nous essayons de clarifier la terminologie concernant les coquilles asymétriques, dissymétriques et symétriques établie

MOTS CLÉS
Brachiopodes,
Rhynchonellida,
Crétacé,
asymétrie,
antisymétrie,
asymétrie aléatoire,
terminologie,
morphométrie
géométrique.

depuis le début du XXᵉ siècle. Les populations du Crétacé observées représentent d'indubitables cas d'antisymétrie (aussi appelé asymétrie aléatoire). Au cours du Crétacé, certaines populations de *Cyclothyris* McKoy, 1844 sont composées de vrais spécimens asymétriques, mais d'autres formes présentent un degré d'asymétrie intermédiaire, que nous nommons ici les morphologies atypiques. La forme de spécimens provenant de deux localités en France a été quantifiée en utilisant une approche de morphométrie géométrique. Nous utilisons l'éventail des morphologies pour : 1) tester des hypothèses concernant les patrons ontogénétiques de l'asymétrie ; 2) tester la possibilité de plusieurs morphogroupes ; et 3) discuter le déterminisme de l'asymétrie.

INTRODUCTION

Brachiopods, which first appeared in the Cambrian, are benthic marine lophophorates living attached to various substrates, both organic and inorganic. They are protected by an exoskeleton, a bivalved shell, that normally exhibits a bilateral symmetry because the valves are dorsal and ventral, in contrast to bivalved molluscs where the paired valves are left and right. After spawning, rhynchonelliform brachiopod larvae enjoy a short free-swimming period before settling on suitable substrata, followed by metamorphosis and the secretion of the calcite shell.

During shell ontogeny in Rhynchonellida Kuhn, 1949 (Williams *et al.* 1996), the anterior margin starts out as rectimarginate (has a planar commissure) at the beginning. The shape of this margin remains the same later throughout ontogeny or can be modified to become monoplicate (medial commissure elevated relative to anterolateral commissure). In the Cyclothyrididae Makridin, 1956, juveniles are nearly rectimarginate. Then, at the preadult stage, modifications occur to shape a monoplicate anterior margin. Sometimes, one of the more noteworthy modifications is the asymmetry of this anterior margin, where one side is raised and the other lowered and where the raised side is the left in roughly half the specimens and the right in the remaining half. This phenomenon, sometimes called antisymmetry or random asymmetry evolved independently in several rhynchonellid genera (e.g. *Torquirhynchia* Childs, 1969, *Lacunosella* Wisniewska, 1932, *Lamellaerhynchia* Burri, 1953, *Erymnaria* Cooper, 1959 and in *Cyclothyris* McKoy, 1844 discussed here, see Fürsich & Palmer 1984; Gaspard 1991; Gaspard & Charbonnier 2020). Apart from brachiopods, the question of left-right asymmetry has also caught attention for over a century in biology (e.g. Duncker 1904; Ludwig 1932; Palmer 1996; Addadi & Weiner 2001; Stern 2002; Várkonyi *et al.* 2006; Flamant 2016).

Any considerations of brachiopod valve asymmetry must distinguish between specimens with a dissymmetrical anterior margin and those with a truly asymmetrical one (Gaspard 1991; Gaspard & Charbonnier 2020). For example, if many larvae settle on a restricted substrate, the shells can be prevented from growing normally due to crowding (e.g. Asgaard & Bromley 1991). Such crowding may interfere with growth, leading to random deformations of the shell that can even impact the brachidium and lophophore. These deformed shells are considered dissymmetric, and represent a purely developmental response coping with a confined environment. Dissymmetric valves can also arise as deformations resulting from insufficient pedicle length (e.g. shells attached too closely to the substrate), when individual shells grow between coral branches (Schrøder *et al.* 2017) or in other restricted growth environments (Schumann 1990-1991; Afanasjeva 2014; Berrocal-Casero *et al.* 2017, 2020).

As a consequence, and owing to some misinterpreted cases of mixed asymmetrical dissymmetrical specimens (Berrocal-Casero & Garcia-Joral 2023), the spectrum of observed asymmetries is more complex and requires consideration of their: 1) origin (larval or post-larval); 2) effects in a group of individuals or populations; 3) symmetry to asymmetry transition; and 4) patterns of variation (Duncker 1904; Timoféeff-Ressovsky 1934; Van Valen 1962; Palmer 1996). Relevant terminology was developed since the early 20th century, and recognizes several types of asymmetry:

– cases of sidedness, modification or greater development of a character primarily on one side (directional asymmetry (DA), Van Valen 1962; Okumura *et al.* 2008);

– cases of random asymmetry: right/left-sided mostly equally frequent in populations of a species (antisymmetry (AS), Duncker 1904; Timoféeff-Ressovsky 1934; Van Valen 1962; Palmer 2005);

– cases of fluctuating asymmetry (FA) resulting from the inability of organisms to develop precisely along determined paths due to minor developmental errors, which leads to subtle departures from symmetry (1-2%: Ludwig 1932; Van Valen 1962; Palmer & Strobeck 2003; Palmer 2005);

– cases of dissymmetry, where departures from symmetry are conspicuous but where they vary greatly in extent and direction in no predictable manner.

The present paper investigates a complex variety of antisymmetrical morphologies in the species *Cyclothyris difformis* (Valenciennes *in* Lamarck, 1819), which shows classical asymmetrical margin shapes but also some atypical ones that are neither truly monoplicate nor entirely asymmetrical. They appear morphologically as intermediates. Among others, Fürsich & Palmer (1984) described a possible shift of the fold during the ontogeny from monoplicate margin to asymmetrical ones.
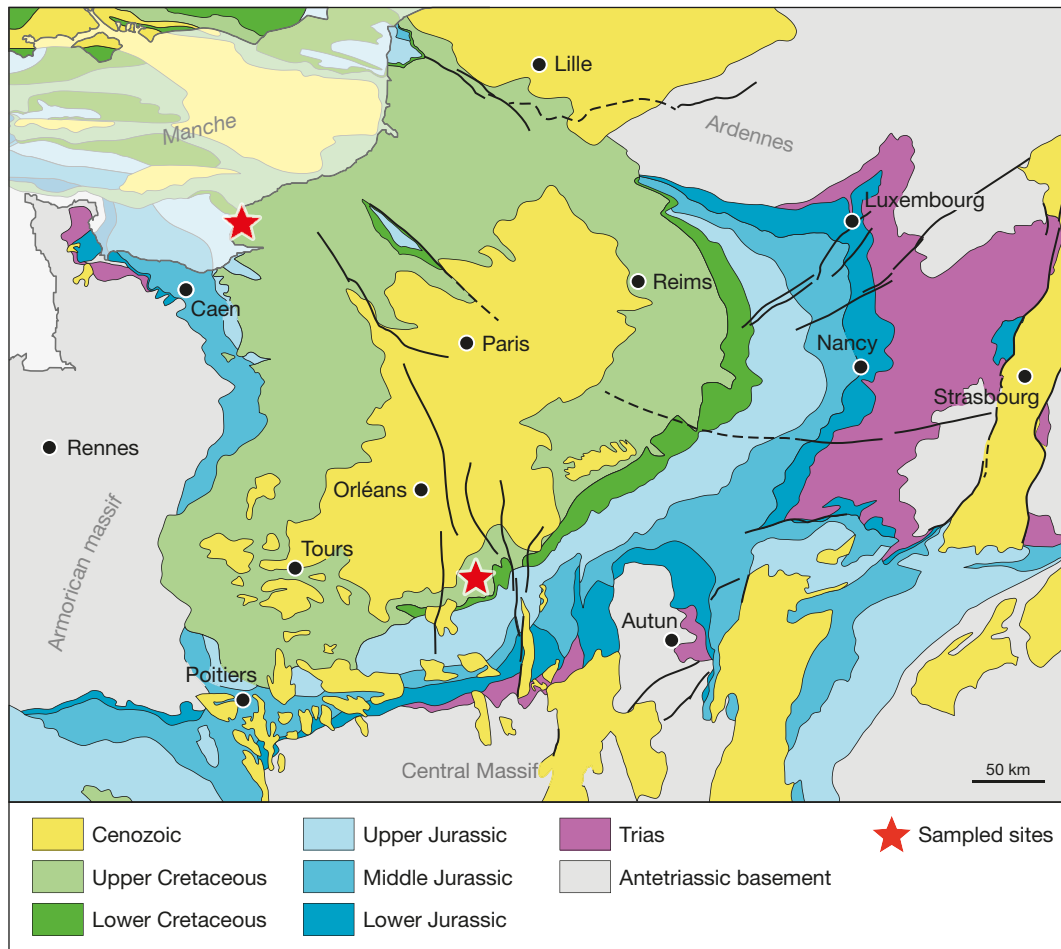
FIG. 1. — Location of the two populations of *Cyclothyris difformis* (Valenciennes *in* Lamarck, 1819) observed in the lower Cenomanian from Le Pays de Caux (Normandie) and Le Pays Fort (Cher), France. Simplified map of the Paris Basin. Modified after BRGM (1996).

An alternative possibility is that the degree of asymmetry is constant throughout ontogeny. These two hypotheses lead to very different interpretations on the nature of atypical forms. We propose to test these hypotheses by capturing anterior margin shapes using geometric morphometrics. Moreover, we also investigate if asymmetrical and atypical forms are clustered in morphospace to assess whether they might be distinct species or ecomorphs. Finally, we test whether morphologies differ between two different French localities.

MATERIAL AND METHODS

MATERIAL
Among several asymmetrical rhynchonellid populations (most of which are from the Mesozoic and a few from the Cenozoic, (partly illustrated in Gaspard 1991: pl. 1; Gaspard & Charbonnier 2020), those from the Cretaceous attract attention because of their additional atypical specimens. Populations of the family Cyclothyrididae (Manceñido *et al.* 2002) were observed from the lower Cenomanian (Lower Greensand) of Western Europe belonging to the genus *Cyclothyris*: *C. difformis* from Le Pays Fort (Cher, France; Paccard 2021) and from Cap de La Hève

(Pays de Caux, Normandie, France, stored at the MNHN, Paris) (Fig. 1) among other localities (e.g. from England: Wiltshire, South Devon (sandy layers); Belgium (Tourtia) and in Germany: Essen) highlighted by Owen (1962), with all age groups and some atypical adults (Fig. 2).

ABBREVIATIONS
AS   antisymmetry;
DA   directional asymmetry;
FA   fluctuating asymmetry;
PCA   principal component analysis.

METHODS
Capturing the shape of anterior margins
To identify atypical specimens, a multivariate analysis was applied (PCA) using semilandmarks (Bookstein 1997) positioned on the anterior margin of all specimens in each population (juveniles, preadults, asymmetrical and atypical adults). The first step was to image all specimens viewed by their anterior margin (Fig. 3A), draw a smoothed line through the interlocking costae representing the path of the anterior margin (Fig. 3B), and finally position equally spaced landmarks (semilandmarks, n = 23) along this margin (Fig. 3C).

We used the tools developed by Deregnaucourt *et al.* (2021) to automate sampling of semilandmarks on vectored drawings. Information on specimens, and coordinates of semilandmarks for all specimens, are in Appendices 1 and 2. We did a generalized Procrustes superimposition that optimizes translation, rotation and scaling by minimizing distances between semilandmarks. Then a principal component analysis (PCA) was performed. These two last steps were conducted with the R package *geomorph* (Adams *et al.* 2022). We used as shape variables the coordinates of specimens from the two first axes of the PCA (Appendix 3). This morphospace shows both left- and right-sided specimens. To explore the deviations in shape from typical asymmetry, we digitally inverted all right-sided images to be left-sided, realigned all left-sided and inverted right-sided images and conducted another PCA of these realigned semilandmarks (Fig. 4).

Testing ontogenetic role in atypical forms
The shells of asymmetrical rhynchonellids illustrate an example of antisymmetry (AS), starting from a bilateral symmetry at a belated post-larval stage (after the juveniles and preadult stages), the population is mainly composed of a roughly equal number of left and right-sided distorted adult specimens (Appendix 3).

The tendency for a species or a clade to develop and maintain antisymmetrical features (AS) has been recognized as hereditary and likely genetic (Palmer 2016); however, for each individual, the tendency to be left- or right-sided is generally not genetic. In the specific case of brachiopods, Fürsich & Palmer (1984) and Gaspard (1991) concluded that brachiopods asymmetry is a genetic condition. Fürsich & Palmer (1984) proposed that the asymmetry appears through a lateral shift of the sulcus during the ontogeny. Hereafter, we refer to this later proposition as the FP model (Fig. 5). They propose that the degree of lateral shift can result from weak to strong asymmetries. This model implies that strongly asymmetric adults should pass through weakly asymmetric stages of ontogeny.

In the asymmetric species *Cyclothyris difformis*, some specimens show an anterior margin neither rectimarginate nor truly monoplicate or clearly asymmetrical. These specimens appear as intermediate between monoplicate and truly asymmetrical forms (Fig. 5A). Several hypotheses could explain this pattern. First, the FP model can explain these atypical forms through two potential heterochronies (Alberch *et al.* 1979) (Fig. 5B). Atypical specimens may occur through progenesis, hypermorphosis, neoteny or acceleration depending on the definitive size and plesiomorphic state (Fig. 5C). Our second hypothesis is that atypical forms are not intermediate ontogenetic forms (Fig. 5D). This would reject the FP model and implies that the lateral shift of asymmetrical specimens appears in its definitive degree (i.e., the same of the adult) early during ontogeny. This behaviour of a feature that is unchanging during ontogeny has been described as static by Webster & Zelditch (2005), and we use this terminology to apply to this second hypothesis. While conducting the morphometric analysis, the centroid size (i.e., the square root of the sum of squared distances of a set of landmarks from their centroid) can be extracted and is here used as a proxy of the ontogeny.

Testing the homogeneity of specimens' morphology and differences between localities
We also investigated the clustering of these different forms with different degree of asymmetry to answer the presence or not of several morphogroups that could be interpreted as distinct species. Based on the same shape variables, we performed a Gaussian Mixture analysis (Everitt & Dunn 2001) to detect eventual morphological clusters with functions from the R package mclust (Scrucca *et al.* 2016). Finally, the difference of morphologies between the two localities was tested with a series of Hotelling tests with the package Hotelling (Curran & Hersh 2021).

Repeatability of the measurement protocol
We estimated the variance introduced by our protocol (i.e., from specimen positioning to computation of shape variables) to test whether this could influence our conclusions by including too much noise in shapes. Three randomly chosen specimens were used to quantify the repeatability of our protocol. Each was photographed at the beginning of each photography session. The replicates of these three specimens were used to estimate the variance linked to the protocol. We compared these variances to the variance of 1000 sets of three others randomly selected specimens. For two of the three specimens the variance of the random sets is never smaller. Their proportions can be interpreted as the p-value of a one-tailed test on variance (both $p < 0.001$). The third specimen has a slightly higher variance on PC1 ($p = 0.13$, Appendix 4). This is the consequence of very slight differences of the positioning of specimens on a piece of modelling clay used to hold specimen under the camera. However, its magnitude is low and we consider it negligible.

RESULTS

A PCA was performed on the above data, after: 1) the positioning of the semilandmarks on the pathway of all the anterior margins; and 2) Procrustes superposition. We scrutinized the distribution of the left and right-sided specimens on the first two components. This first PCA revealed a continuum from juveniles to adults along PC2 and the left-sided specimens on one side of PC1 and right-sided specimens on the opposite side (Appendix 3). The distribution of the two directions of shifting is conspicuously regular and homogeneous.

The second PCA was conducted after symmetrisation of the margins. The 1st principal component revealed an apparent gradient from the truly asymmetrical shapes to the atypical ones (hereafter called lateral shift of fold) and the 2nd principal component depicts the juvenile-adult continuum (hereafter called vertical amplitude of fold) (Fig. 4A). The whole set of specimens seems at first sight homogeneous.

We also investigated how margin shapes varied with centroid size. The result strengthens the previous observations that PC2 (vertical amplitude of fold) was related to ontogeny, which was revealed by the highly significant regression ($R^2 = 0.15$,
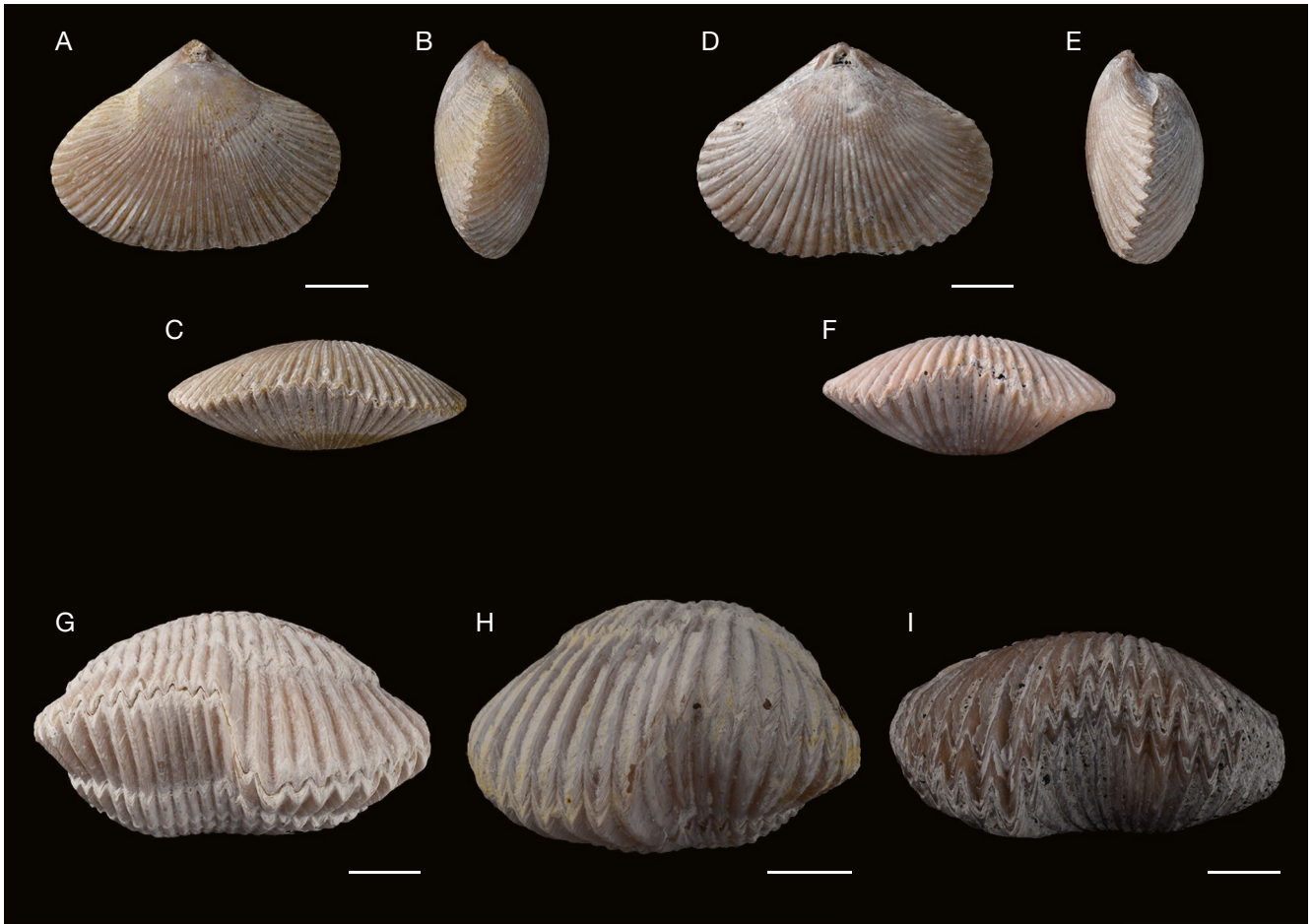
Fig. 2. — Differentiated specimens in the populations from the lower Cenomanian of Le Pays Fort and Le Pays de Caux: **A-C**, dorsal, lateral and anterior views of a juvenile specimen; **D-F**, dorsal, lateral and anterior views of a monoplicate preadult specimen; **G**, anterior view of a right-sided adult specimen, dorsal valve above; **H**, anterior view of a left-sided specimen; **I**, anterior view of an atypical specimen. **A-F, I**, specimens from Le Pays de Caux; **G, H**, specimen from Le Pays Fort. Scale bars: 5 mm.

Fig. 3. — **A**, View of a specimen from the anterior margin; **B**, illustration of the smoothed anterior margin path; **C**, localization of the equally-spaced semilandmarks along the smoothed anterior margin path. Scale bar: 5 mm.

p = 7e-06) versus centroid size (Fig. 4B). No association was found between PC1 (lateral shift of fold) and centroid size (Fig. 4C, regression: R² = 0.006, p = 0.39).

Because PC1 (degree of lateral shift of the marginal fold) was not correlated to centroid size, we prefer the second hypothesis (Fig. 5). Indeed, if the degree of lateral shift had been acquired by heterochrony we would have expected a correlation between these shapes and size. The plot depicting size and lateral shifts (Fig. 4C) shows that all degrees of asymmetry

can be observed at any size, and thus developmental stages. Therefore, the primary shape variation with increasing size was an increase of the dorso-ventral amplitude of the fold (PC2). Therefore, at least in *Cyclothyris difformis*, the hypothesis of Fürsich & Palmer (1984) is the least supported.

Although we observed what appeared to be homogeneity within the lateral shift of the fold (PC1), is it truly homogenous or not? We therefore used a Gaussian mixture analysis (Everitt & Dunn 2001) to test whether there were distinct
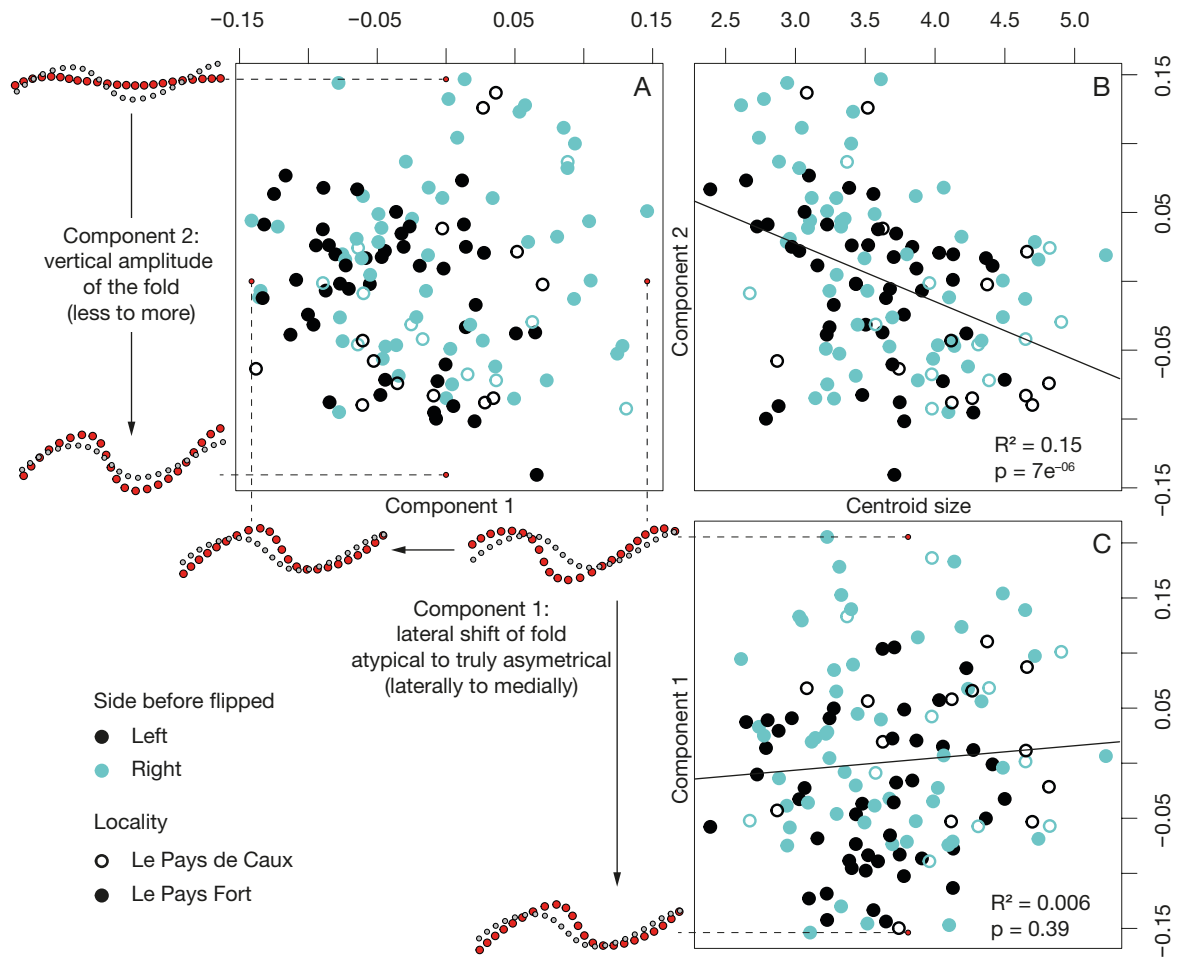
FIG. 4. — Distribution of the specimens along the two first principal components and versus the centroid size. The first PC axis (72.3%) mainly represents the lateral shift of the fold corresponding to the difference between asymmetrical and atypical specimens while the second PC axis (21.1%) represents the vertical amplitude of fold correlated to centroid size: **A**, first and second principal components; **B**, second component versus centroid size; **C**, first component versus centroid size. Colours of dots represent original sides of specimens before flipping specimens: **blue**, right; **black**, left. Full **circles** represent specimens from Le Pays Fort and empty circles from Le Pays de Caux. **Grey dots** along the margin represent the mean shape of the morphospace and red dots the shapes of the minimum and maximum of each PC axis. **Lines** inside **B** and **C** represent regression lines, R² and p-values are indicated.

groups. This method tries to find multivariate normal distributions among the data by varying the number of clusters and their characteristics (e.g. varying volume or not, orientations). If populations are well-separated we expect to find several multinormal Gaussian distributions. However, our best model, quantified by the Bayesian Information Criterion, revealed only one group, implying that atypical and asymmetrical specimens belong to a single morpho-group with no evidence of distinct species or ecomorphs.

We also asked whether differences existed between the two populations sampled: Le Pays Fort (Cher, France) and Le Pays de Caux (Normandie, France). Scatterplots of both populations (Fig. 4; Appendices 5) and density distributions of PC coordinates (Appendix 6) revealed no difference between them. A Hotelling test performed on all PCA coordinates showed no significant difference between the populations from the two localities (p = 0.62). A further test of PC2 loadings alone revealed a nearly significant difference (Appendix 6B, p = 0.07), but this difference was small. This result is certainly due to the correlation between the vertical amplitude of fold (PC2) and centroid size and because juveniles were under-represented in Le Pays de Caux sample (Fig. 4B, C; Appendices 5; 6C). This relatively low number of juveniles could have been due to biaises during sampling, but we think this unlikely because all specimens found were sampled. Alternatively, postmortem transport might account for the difference because juvenile shells are lighter than adult shells when they are no longer attached to the substrate after death.

Additionally, a video of the external surface reveals the successive modifications of the anterior margin throughout the life of a specimen (Appendix 7). The growth lines allow one to easily reconstruct all the stages by which the external shell shape progresses during ontogeny via accretion of new material at the valve edges. These growth lines show that the position of the shift is conserved throughout the ontogeny. As we only scanned one specimen, no general conclusion could be drawn on the entire population, but it supports our conclusion that atypical forms are not heterochronic variants of asymmetrical ones.
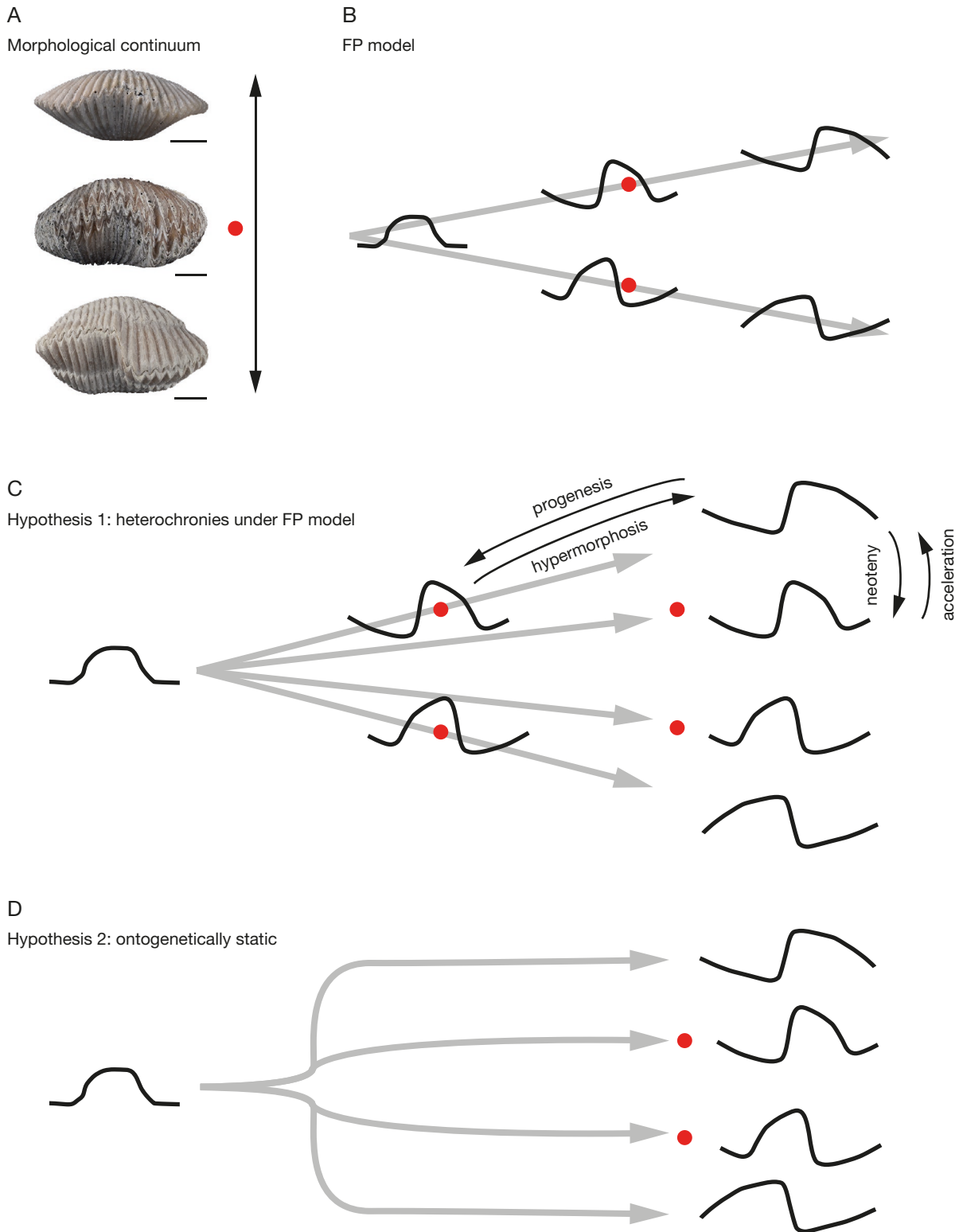
FIG. 5. — Hypotheses about evolution of the anterior margin: **A**, three specimens exhibiting the morphological continuum between monoplicate margin to asymmetrical and atypical morphologies (varying degree of asymmetry, **red dots**); **B**, hypothesis derived from Fürsich & Palmer (1984) (FP) model; **C**, hypothesis 1: given the FP model, the two kinds of heterochronies that can relate atypical forms to asymmetric ones; **D**, hypothesis 2: the degree of asymmetry is ontogenetically static, meaning that this character does not change through ontogeny. Scale bars: 5 mm.

DISCUSSION

In contrast to disymmetry, which can appear in all orders of brachiopods and impacts all parts of the shell, a truly asymmetrical shape (antisymmetry here) impacts only the anterior shell margin via a vertical or oblique shift. It is only known from extinct rhynchonellid species (Jurassic, Cretaceous and early Cenozoic) with no known examples of antisymmetry among extant species. This raises the question: what favours symmetry breaking?

Sediment type (e.g. marly, finely detrital) might impact the positioning of the shells and lead to asymmetry, if one or the other side of the shell was buried in soft sediments (Berrocal-Casero *et al.* 2017; Berrocal-Casero & Garcia-Joral 2023). This would correspond to an adaptation during growth to soft/unstable bottom conditions. However, their argument seems weak. Such a position of the specimens on one side or the other as a half-buried position in the sediment would render a part of the lophophore non-operational. Dissymmetrical brachiopod specimens can present dissymmetrical length of half a lophophore as reported by Elliott (1958) for *Macandrevia cranium* (Müller, 1776) (Holocene), Hoverd (1985, 1986) for *Notosaria nigricans* (Sowerby, 1846) illustrated after damage, or Schrøder *et al.* (2017) for *Obliquorhynchia flustracea* (Buch, 1834) (Danian). However, these cases are likely one-off events due to very localised conditions and do not represent entire populations like true antisymmetry. Even a semi-infaunal life position (e.g. Richardson 1997) could not lead to such antisymmetry. A small part of the posterior shell anchored in the sediment is unlikely to give rise to asymmetry, although it does match with some developing strategies to stay above the muddy seafloor (Ager 1967). Asymmetry is neither observed in cases of strongly curved or thickened ventral umbo nor when the pedicle system is atrophied resulting in a free lying position. In many cases, brachiopods developed strategies to stay at the water-substrate interface (Richardson 1997). Even in adult strophomenides (concavo-convex brachiopods in more-or-less infaunal position during the Palaeozoic), their margins (laterals and anterior) always stayed above the sediment preventing any sediment from entering the shell and with long anchoring spines to stabilise them (Grant 1966; Rudwick 1970). We therefore think it unlikely that asymmetry could be due to relationships with or adaptation to soft substrates.

We do note, however, that some inarticulate brachiopods like lingulides are adapted for an infaunal way of life in vertical burrows in a soft substrate (homogeneous fine sand or clayey fine sand). The shells move in a single plane attached by a relatively long pedicle, and the burrow walls are lined and strengthened by a mucous film secreted by the mantle and pedicle mantle. This mucous lubricates the movement of the specimens in burrows in substrates that are neither too coarse nor too muddy (cf. Emig 1982). Furthermore, the shell is positioned near the top of the burrow, which allows the continuous function of filtering. In water, fine particles are retained by the mucus on the marginal setae (cf. Emig *in* Kaesler 1997: figs 407, 408). As a consequence, no cases of asymmetry are known in lingulides.

Obviously, if asymmetry persist over many generations there must be a hereditary transmission of this character. As asymmetrical brachiopods are only known among fossils discussion of genetic determination is highly speculative. However, the distribution of the morphologies may provide some insights about it. First, the varying degree of asymmetry we observed among specimens points towards a complex genetic determinism, because two clearly separated morphologies are not as observed in other species (Fürsich & Palmer 1984; Gaspard 1991; Gaspard & Charbonnier 2020). On the other hand, the frequent appearance of asymmetry in rhynchonellids suggests that asymmetry might arise due to a simple genetic switch. The causes of such switches remain unknown and their relationship to fitness is hard to evaluate. However, Palmer (2005) proposed that the asymmetry may enhance the seawater flow through the mantle cavity leading to better feeding abilities. This hypothesis, while understandable, has never been properly tested. The frequency of asymmetry appearances in rhynchonellids also raises the possibility of reversion (i.e., asymmetry loss with return to symmetrical shell). However, for a group diagnosed by asymmetric shells, it is hard to distinguish between reversion to classical shell shapes versus extinction of the original species.

Here we showed, using population analyses of morphologies: 1) that all the asymmetrical shapes in *Cyclothyris difformis* constitute a single morphogroup found in both investigated locations; and 2) that the degree of lateral shift of the fold was stable throughout ontogeny while the degree of marginal fold amplitude increased. Most of the currently known examples of true antisymmetry in brachiopods seem to have comparable characteristics, which suggests a similar developmental-genetic basis. But detailed morphometric studies of other antisymmetric species might shed light on its determinism and evolution.

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APPENDICES

APPENDIX 1. — Information about specimens: names of pictures, id of photographic session, id of replicates for the test of the protocol variance and localities.
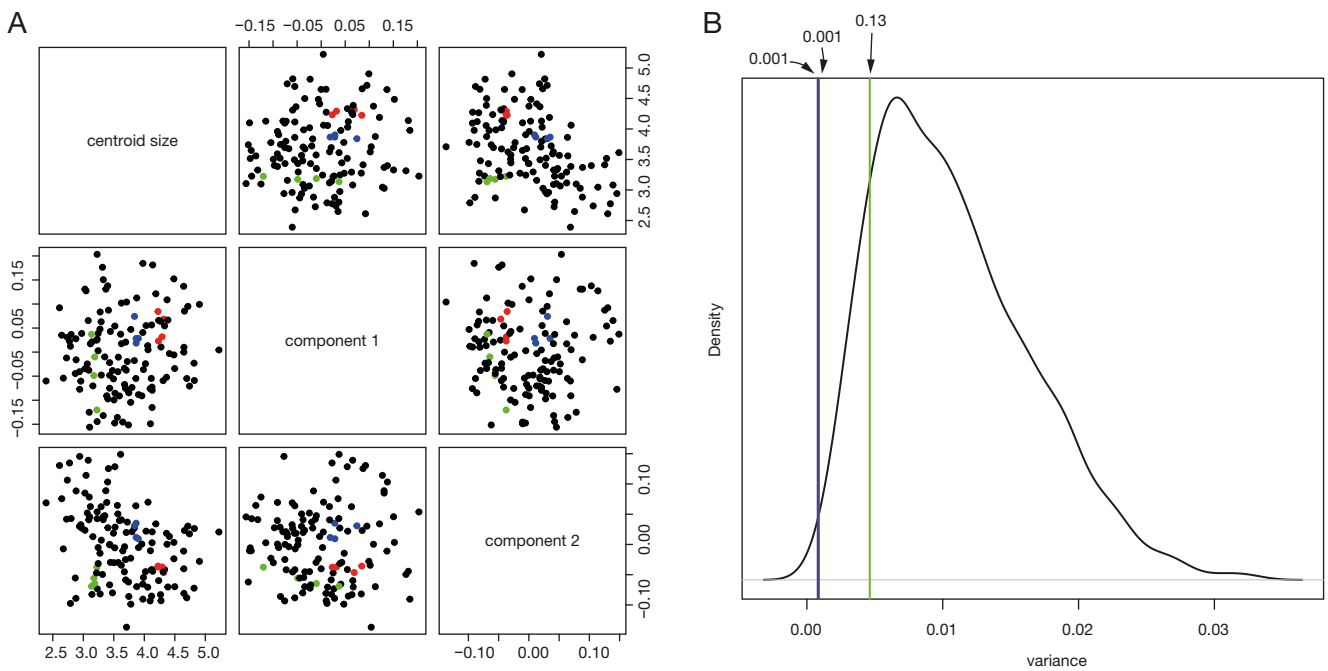
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_DSC0396.ps	s1	r2	Cher	_DSC0468.ps	s2	–	Cher
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_DSC0401.ps	s1	–	Cher	_DSC0473.ps	s3	r3	Cher
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APPENDIX 2. — Coordinates of semilandmarks (n = 23) of all specimens' margins: https://doi.org/10.5852/cr-palevol2024v23a13_s1
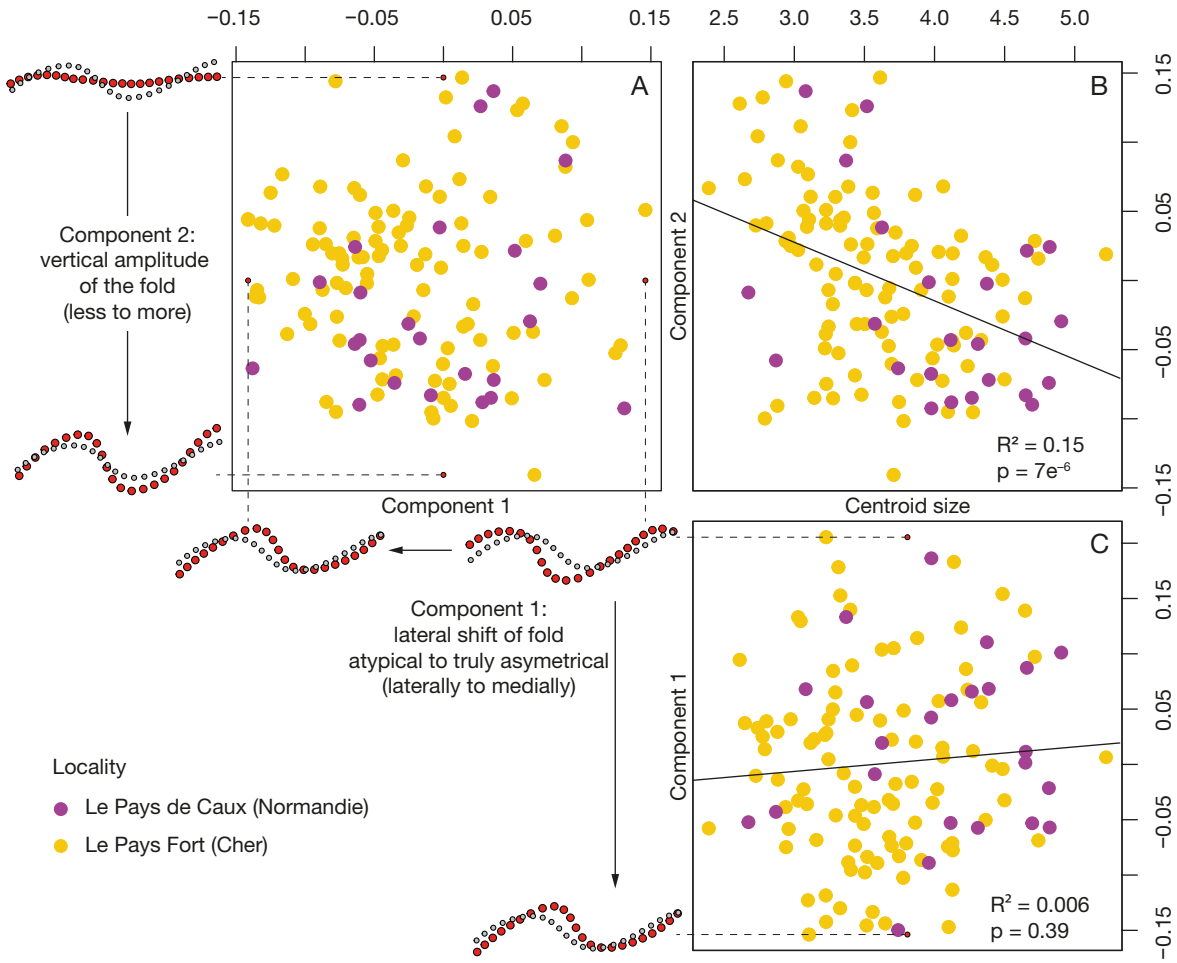
APPENDIX 3. — PCA on raw margin shapes. Colours correspond to sides.

PC 2: 19.4%

PC 1: 73.84%
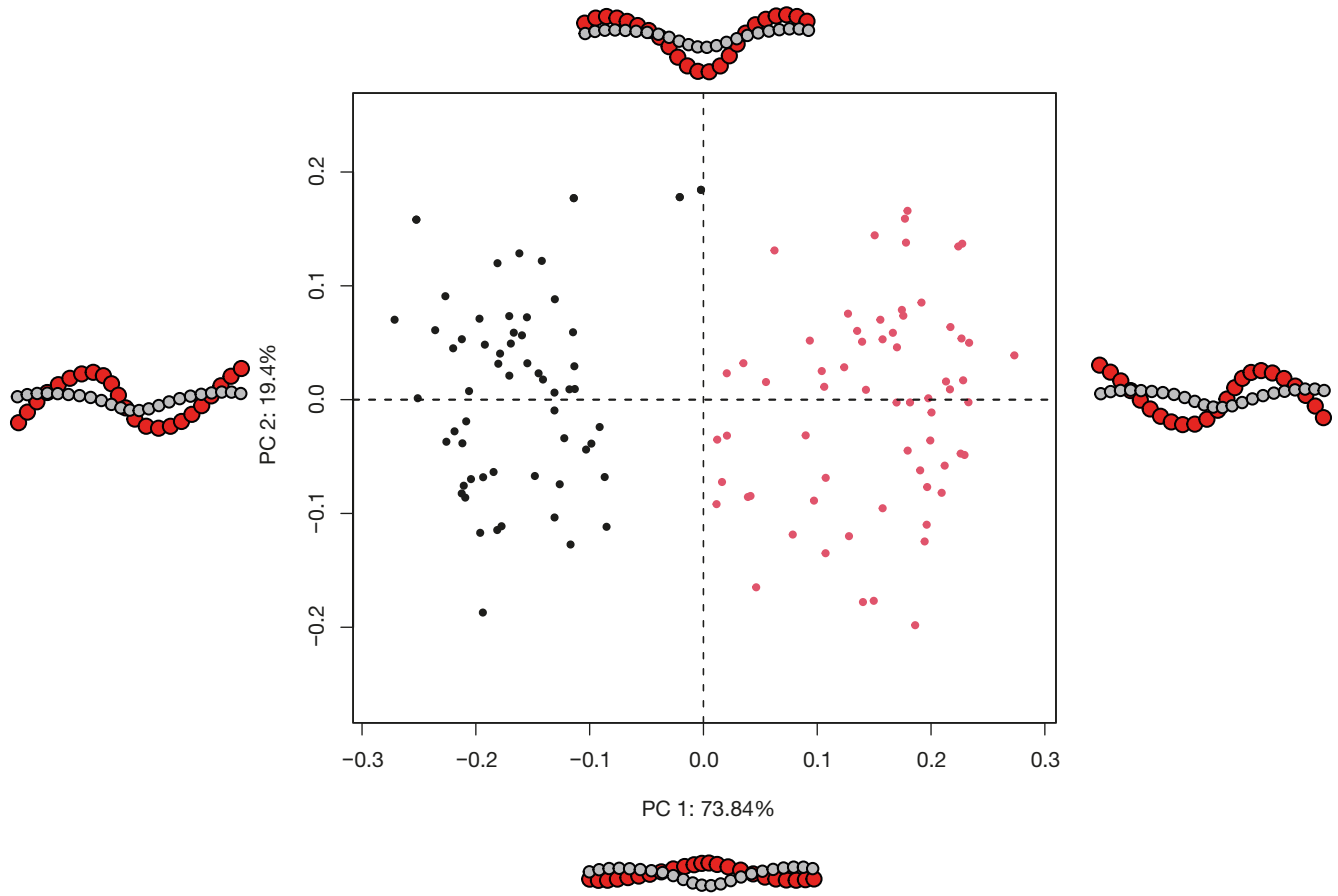
APPENDIX 4. — Plots of all specimens including replicates in colours (**red**, r1; **blue**, r2; **green**, r3; see ids in Appendix 1) and variance induced by protocol.

A

B

Density

variance

APPENDIX 5. — PCA on flipped specimens. Colours represent the two different localities.

Component 2:
vertical amplitude
of the fold
(less to more)

Component 1

Component 1:
lateral shift of fold
atypical to truly asymetrical
(laterally to medially)

Locality
● Le Pays de Caux (Normandie)
● Le Pays Fort (Cher)

Component 2

Centroid size

R² = 0.15
p = 7e⁻⁶

Component 1

R² = 0.006
p = 0.39

APPENDIX 6. — Density plots of: **A**, PC1; **B**, PC2; and **C**, centroid sizes for the two localities: Le Pays de Caux (**purple**) and Le Pays Fort (**yellow**).

APPENDIX 7. — Video of 3D-surface of a shell: https://doi.org/10.5852/cr-palevol2024v23a13_s2