

Obliquorhynchia (gen. nov.): An asymmetric brachiopod from the middle Danian Faxø Formation, Denmark

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The diverse brachiopod fauna from the middle Danian cool-water coral mounds of the Faxø Formation, Denmark, includes the new genus *Obliquorhynchia* that exhibits an asymmetric folding of the frontal commissure, a rare feature in brachiopods. Two of the most abundant brachiopod species found in the Faxø Formation, '*Rhynchonella*' *flustracea* and '*Rhynchonella*' *faxensis*, are considered conspecific and are both referred to *Obliquorhynchia*. In the literature, the species name *flustracea* has been ascribed to von Schlotheim. However, the original species name proposed by von Schlotheim in his catalogue (1832, 65, no 62) was *lustraceus*. This remained a *nomen nudum* until von Buch (1834) published a description based on the material of von Schlotheim and changed the name to *flustracea*. The species is thus ascribed to von Buch. A lectotype for *Obliquorhynchia flustracea* (von Buch 1834) is designated and illustrated here.

Keywords: *Obliquorhynchia* (gen. nov.), '*Rhynchonella*' *flustracea*, '*Rhynchonella*' *faxensis*, asymmetric brachiopods, middle Danian, Faxø Formation, Denmark.

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Brachiopods are very common in most of the coral and bryozoan mound facies of the middle Danian Faxø Formation in eastern Denmark. The most common brachiopod species '*Rhynchonella*' *flustracea* and '*Rhynchonella*' *faxensis* are present in all the coral mound facies, with the exception of mudstone and floatstone facies. They are here considered as conspecific and are referred to as *Obliquorhynchia flustracea* (as revised herein). The specimens exhibit commissural asymmetry, which is a relatively rare feature in articulated brachiopods (Fürsich & Palmer 1984). The success of this species was probably due to an adaptation to a life between the branches of the scleractinian coral *Dendrophyllia candelabrum* (Asgaard 1968). The species is very commonly found sitting in this position.

Modern asymmetric brachiopods are known from tropical reef systems and cool-water coral mounds at relatively deep, cool settings, notably from the Atlantic Ocean (Elliott 1948, 1958; Atkins 1959, 1960, 1961; Freiwald *et al.* 2002; Freiwald *et al.* 2004; Henry & Roberts 2007). In the fossil record asymmetric brachiopods are commonly found in association with tropical coral

reef and cool-water coral mound facies (Rózycki 1948; Ager 1965, 1967; Asgaard 1968). Asymmetry in Mesozoic brachiopods from tropical reefs is particularly prevalent in the order Rhynchonellida (Afanasjeva 2014). The form of asymmetry in this order is mainly confined to the frontal commissure and is described as commissural asymmetry. The asymmetry is most conspicuous at the commissure, but will in general affect the overall shape of the brachiopod.

The two former species *Terebratula flustracea* von Buch 1834 and *Rhynchonella faxensis* Posselt 1894 from the Faxø Formation, exposed in the Faxø limestone quarry in eastern Denmark, both exhibit commissural asymmetries to varying degrees. Starting with the work of Asgaard (1968) *Terebratula flustracea* von Buch and *Rhynchonella faxensis* Posselt have been referred to with the genus name *Rhynchonella* in inverted commas. For the sake of simplicity, this form is used throughout in the present paper when referring to older works.

'*R.*' *flustracea* was described by von Buch (1834, 1835) based on the material collected by von Schlotheim in

coral limestone in the Faxø quarry. *R. faxensis* was described by Posselt (1894) as a new species based on 20 specimens collected in the quarry. He noted that the specimens of *R. faxensis* were rather similar to *R. flustracea* and relatively rare, but erected the new species on the basis of minor details in external morphology such as number of ribs and occasional uniplication of the commissure. In the original material collected by von Schlotheim, which comprised nine syntypes (now one lectotype and eight paralectotypes, as revised herein) of *R. flustracea* (Museum Für Naturkunde Leibniz-Institut Berlin, number MB.B.9116.1–9), one paralectotype actually possesses the characteristics that Posselt (1894) used in his description of *R. faxensis* as a new species, such as fewer ribs and a uniplicate commissure.

The aim of this study is to erect a new rhynchonellid brachiopod genus, *Obliquorhynchia* gen. nov. based on material from the middle Danian Faxø Formation, and to describe the variation within the two types of asymmetric brachiopods here classified as one species, *Obliquorhynchia flustracea*.

Geological setting

The Faxø Formation represents a middle Danian cool-water complex of interfingering coral and bryozoan mounds (Lauridsen *et al.* 2012). The coral mounds were established by the azooxanthellate scleractinian coral species *Dendrophyllia candelabrum* (Hennig 1899), *Oculina becki* (Nielsen 1922) and *Faksephyllia faxøensis* (Lyell 1837), shortly after the mass extinction at the Cretaceous–Palaeogene (K/Pg) boundary. Two million years after the K/Pg boundary the coral mounds started to grow on top of bryozoan mounds in relatively deep water below the photic zone over the easternmost part of the Ringkøbing–Fyn High, limiting the Danish Basin to the south (Floris 1980; Bernecker & Weidlich 1990, 2005; Lauridsen *et al.* 2012; Lauridsen & Bjerager 2014). The formation consists of a number of different bryozoan and coral limestone facies (Lauridsen *et al.* 2012). The formation is exposed in the Faxø limestone quarry, Denmark, in the Limhamn quarry, Malmö, Southern Sweden, and has been encountered in several boreholes south of Faxø. The Baunekule facies

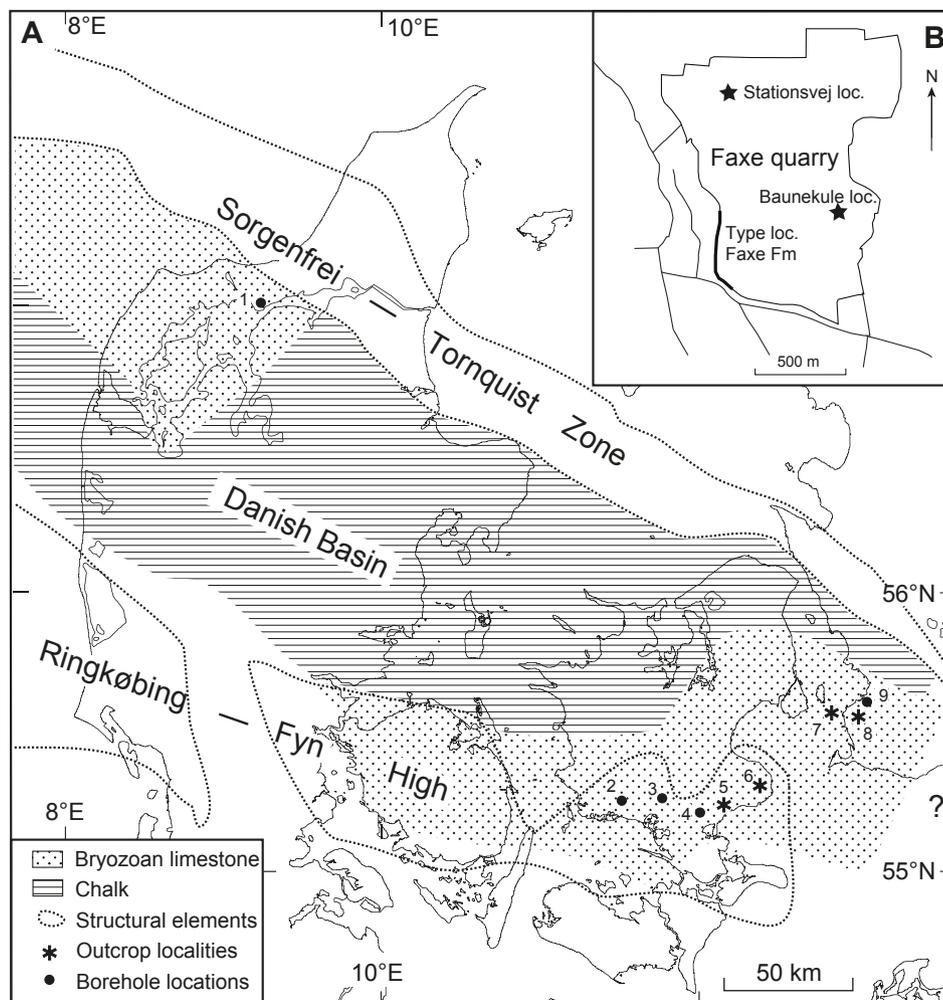


Fig. 1. A: Map of the Danish Basin with the main structural elements and distribution of middle Danian bryozoan limestone, including isolated coral mound complexes and chalk (coccolith Zone 5 of Thomsen 1995). Locations of selected outcrops and boreholes where middle Danian coral limestone have been encountered: 1, Aggersborggaard; 2, Spjellerup; 3, Herlufsholm; 4, Everdrup; 5, Faxø quarry; 6, Stevns Klint; 7, Flinterenden-Trindelenden, Øresund (both submarine outcrop and borings); 8, Limhamn quarry; 9, Malmö. B: Map of Faxø limestone quarry with the Baunekule facies localities and type section of the Faxø Formation indicated. Modified from Lauridsen & Bjerager (2014).

of Lauridsen *et al.* (2012) occurs in the upper part of the formation. It consists of non-consolidated coral rudstone to floatstone forming isolated, lensoidal bodies in the coral mound flanks. The facies contains a well-preserved high-diversity fauna of calcitic and originally aragonitic-shelled invertebrates. More than 300 species have been described from the facies, comprising more than 80% of the species from the Faxe Formation (Lauridsen & Bjerager 2014; Lauridsen & Schnetler 2014). The Baunekule facies is known from the east-central and north-western parts of the quarry (Fig. 1). Ravn (1903) described the facies for the first time; however, the section with this occurrence located in the centre of the quarry has been removed by quarrying. In the 1970s the facies was recorded from a locality in the east-central part below the road Stationsvej by Sten Lennart Jakobsen and Søren Bo Andersen, but this has now also been quarried away. In the 1990s a new occurrence of the Baunekule facies was exposed nearby (Lauridsen *et al.* 2012). Currently, the facies is not exposed in the quarry.

Material and methods

The material studied in the present paper was collected by the late Alice Rasmussen in the beginning of the 1990s at the Stationsvej locality in the Faxe limestone

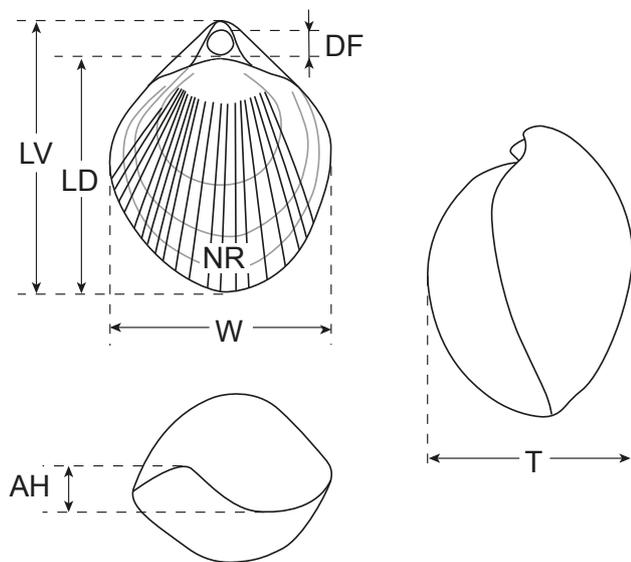


Fig. 2. Measured dimensions referred to in the text. LV: length of the ventral valve. LD: length of the dorsal valve. W: width. DF: diameter of the foramen. NR: number of ribs. T: thickness. AH: height of asymmetry. It is measured from the lowest to the highest point on the frontal commissure line on the anterior part of the specimen. AH is here shown on a sinistroasymmetric specimen.

quarry. More material was collected by the authors in the type section of the Faxe Formation in the western part of the quarry (Lauridsen *et al.* 2012). The samples are housed at Østsjællands Museum, Denmark. The material from the Baunekule facies comprises 2986 specimens with both dorsal and ventral valves intact, 12 ventral valves and 9 dorsal valves. The material from the type section alone comprises 940 specimens.

Bivariate regressions, Hotelling's T^2 test and a principal component analysis (PCA) were undertaken in order to investigate if '*R.* *flustracea*' and '*R.* *faxensis*' represent two species or if they are conspecific. The statistical tests and PCA analysis are based on standard measurements commonly used in the descriptions of new brachiopod species (e.g. Steinich 1965; Surlyk 1970; Johansen 1987; see Fig. 2). Both inner and external morphologies have been assessed.

A total of 10 specimens from the Baunekule facies were attached by the ventral valve to a glass slide with UV hardening glue and opened manually using dissection needles to expose the inner morphology. The dimensions of the morphological features here are however, difficult to quantify due to poor preservation of the crura and overgrowth of calcite crystals, and no statistical tests were carried out on the inner morphology.

All individuals from the Baunekule facies were examined in terms of external symmetry/asymmetry expressed by the frontal commissure. Asymmetry on the commissure is either 'left-handed' or 'right-handed' and is expressed as a bend on the frontal commissure in anterior view, and is comparable to the period of a sine wave where one side is sloping upwards with respect to the other side. If the left side of the commissure, in anterior view with the ventral valve oriented downwards, slopes upwards with respect to the right side, it is referred to as 'sinistroasymmetry' (Fig. 2), and if the right side slopes upwards with respect to the left side, it is referred to as 'dextroasymmetry'.

A total of 48 complete specimens from the Baunekule facies were selected in order to quantify and compare the morphological variation. The morphological dimensions measured are defined in Fig. 2. AH is a morphological dimension that measures the degree of asymmetry. It is measured from the lowest to the highest point on the frontal commissure line on the anterior part of the specimen. Symmetrical individuals have an AH value of 0 mm. An asymmetrical individual has an AH value higher than 0 mm. A higher AH value thus equals a higher degree of asymmetry expressed by the frontal commissure.

Principal component analysis (PCA), Hotelling's T^2 test and regressions were conducted using the PAST software package (Hammer *et al.* 2001; Hammer & Harper 2006; Hammer 2012).

Photographed specimens, with the exception of the designated lectotype, have been coated with ammonium chloride.

Abbreviations used: OESM – Østsjællands Museum; MB – Museum Für Naturkunde Leibniz-Institut Berlin.

Results

Six of the opened specimens have their crura covered in calcitic crystals and it was not possible to determine the type of crura or hinge. However, four specimens have intact and well-preserved hinges and crura,

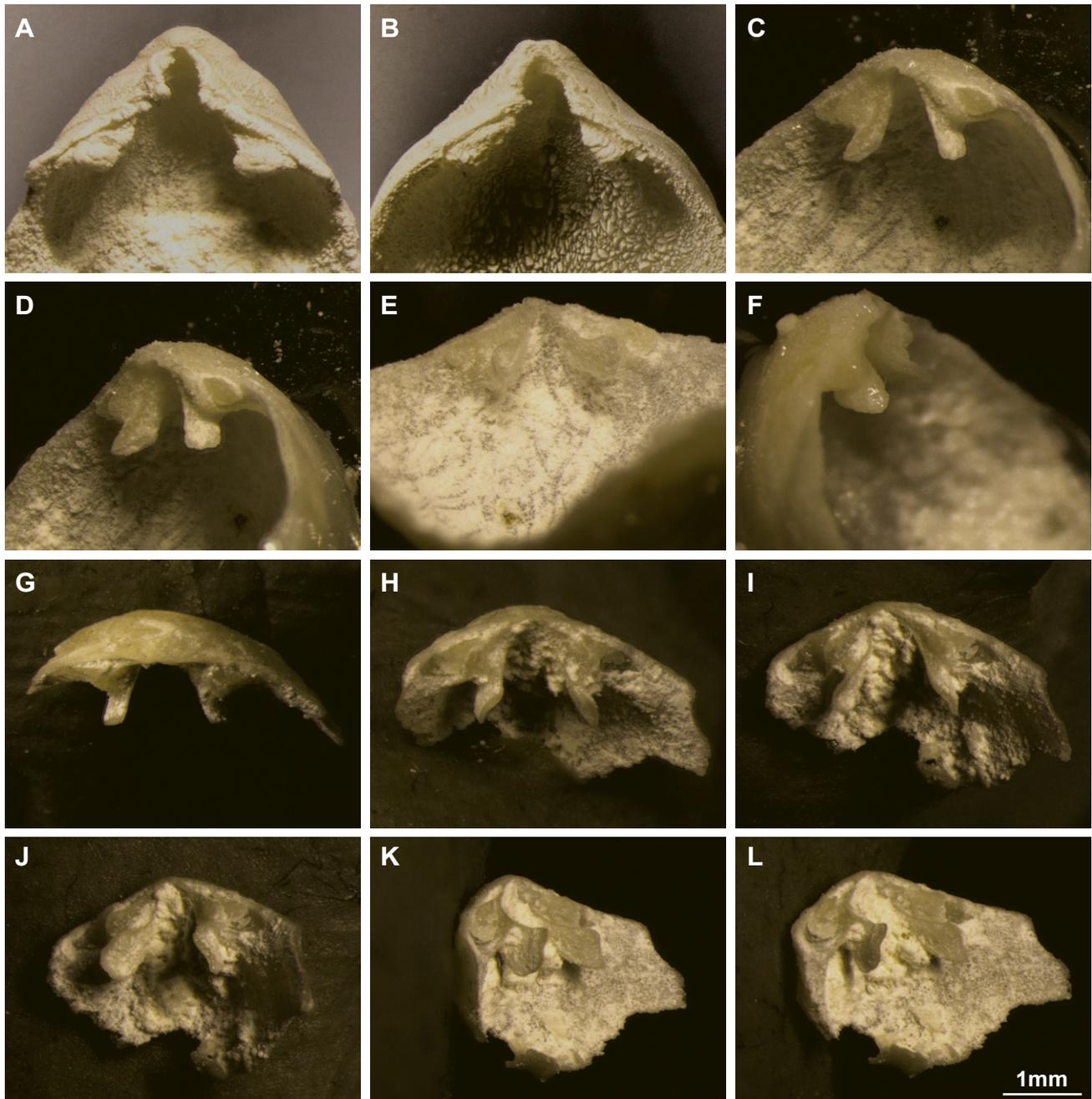


Fig. 3. Internal structures of *Obliquorhynchia flustracea* (von Buch 1834). The new genus *Obliquorhynchia* is erected in this paper. **A:** Hingeline with thick, robust, triangular hinge teeth, OESM-10064-0116. **B:** Hingeline with thick, robust, triangular hinge teeth, OESM-10064-0117. **C–F:** Ventral, dorso-ventral, posterior and lateral view of crura, OESM-10064-0118. **G–L:** Ventral, posterior-ventral, tilted posterior-ventral, ventro-lateral and tilted ventral and ventro-lateral view, OESM-10064-0119. The external morphology of specimens reflects the characteristics formerly used to describe and distinguish '*R.*' *flustracea* (von Buch 1834) (A and C–F) and '*R.*' *faxensis* (Posselt 1894) (B and G–L). Scale bar = 1 mm for all pictures.

allowing them to be referred to subfamily level. The specimens reflect the morphology used as characteristic of *'R.'* *flustracea* and *'R.'* *faxensis* respectively. The type of hinge and crura is the same in both types (Fig. 3).

The morphological variations between *'R.'* *flustracea* and *'R.'* *faxensis* were quantified and compared based on 48 specimens. Of these specimens, 38 were picked at random among both adults and juveniles in the different symmetry groupings: adults were subdivided into sinistroasymmetric, dextroasymmetric, uniplicate, rectimarginate and 'peculiar' asymmetric, whereas juvenile specimens were subdivided into sinistroasymmetric, dextroasymmetric and rectimarginate. The remaining 10 specimens were picked at random from 89 specimens. These specimens exhibit traits characteristic of *'R.'* *faxensis* and are all asymmetric.

The frontal commissure is rectimarginate, uniplicate, sinistroasymmetric or dextroasymmetric. There is a higher frequency of commissural asymmetry in adult individuals (58.7%) compared to juveniles (8.8%) and there is a lower frequency of adults exhibiting a

rectimarginate commissure (8.5%) compared to juveniles (16.5%) (Fig. 4A). Only 4.5% of the specimens exhibit uniplication of the frontal commissure. A few of the adult specimens (2%) display a different form of asymmetry which cannot be ascribed to any of the aforementioned forms. Asymmetry is still present, but in contrast to sinistro- and dextroasymmetry, this asymmetry is most conspicuous in brachial and ventral views, with only little asymmetry expressed by the frontal commissure. This form is regarded as 'peculiar' asymmetry, only observed in adult specimens (Fig. 4A, Fig. 5A–C).

Bivariate linear regressions, RMA algorithm, on LV/LD, LV/W and LV/AH were applied in order to test whether there is a correlation between the morphological measurements of *'R.'* *flustracea* and *'R.'* *faxensis*. The fitted line in the scatter plot of LV/LD is $y = 0.8679x - 0.0249$ ($Tn-2 = 76.00$, $t = 2.00$, $P < 0.05$) (Fig. 4B). The fitted line in the scatter plot of LV/W is $y = 0.9253x - 0.4434$ ($Tn-2 = 28.87$, $t = 2.00$, $P < 0.05$) (Fig. 4C). In the scatter plot of LV/AH the data are fitted to an exponential function by log transformation: $y = 0.0222e^{0.4712x}$ ($Tn-2 = 14.71$, $t = 2.045$, $P < 0.05$) (Fig.

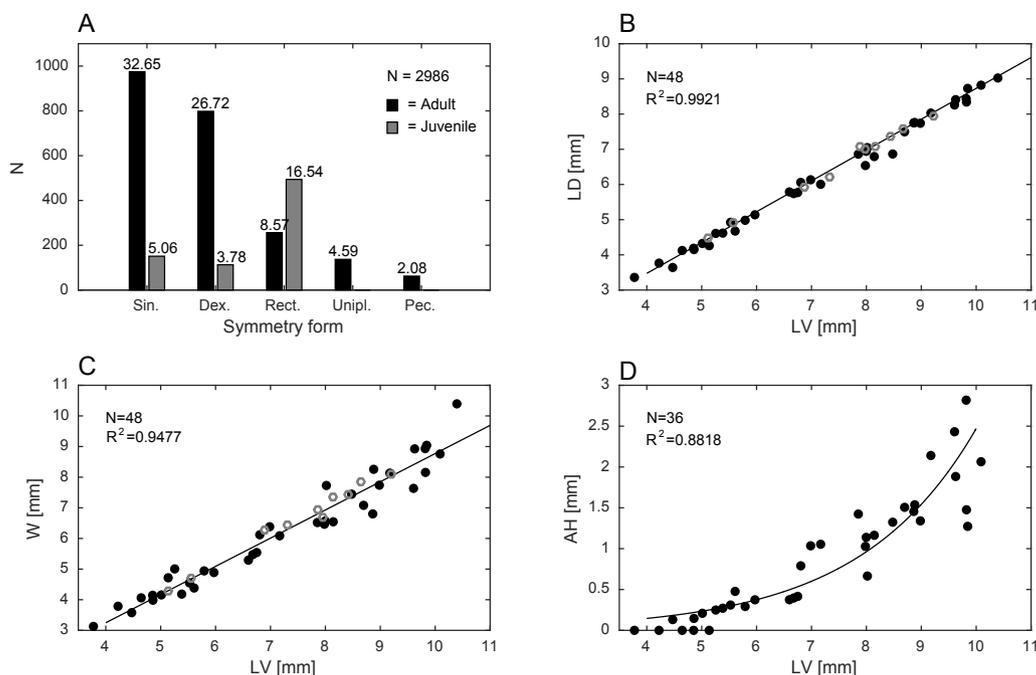


Fig. 4. A: Histogram showing the distribution of specimens according to symmetry/asymmetry expressed by the frontal commissure. Adult: black, juvenile: grey, N: number of specimens, Sin.: sinistroasymmetry, Dex.: dextroasymmetry, Rect.: rectimarginate, Unipl.: uniplicate, Pec.: peculiar. Values above each column show the distribution of specimens in percentage of the total sample size of 2986 specimens. **B–D:** Scatter diagrams plotting with regression lines, showing intraspecific variability of *Obliquorhynchia flustracea* (von Buch 1834), r: correlation coefficient, N: number of specimens, black filled dots are specimens exhibiting traits of both *'R.'* *flustracea* (von Buch 1834) and *'R.'* *faxensis* (Posselt 1894), grey open circles exhibit traits with closer resemblance to *'R.'* *faxensis* (Posselt 1894). Both types of specimen are used in calculation of regression lines and level of significance. **B:** LV/LD: length of ventral valve plotted against length of dorsal valve. **C:** LV/W: length of ventral valve plotted against width. **D:** LV/AH: length of ventral valve plotted against height of asymmetry. The onset of asymmetry is established when the specimen has reached a length (LV) between 4 and 6 mm.

4D). Only the data where AH > 0 mm are included in the exponential model (N = 31). All three plots show significant correlation between the morphological dimensions, indicating that '*R.*' *flustracea* and '*R.*' *faxensis* belong to the same species.

Juvenile shells appear smooth, but ribs are visible when the specimens are coated in ammonium chloride, normally in the form of weakly developed striate or finely capillate costae. Some adults and juvenile specimens with apparently smooth shell surfaces are recognised even when coated. This is due to diagenetic dissolution of the outer layer of the calcitic shell, thus causing the shell surface to appear smooth (Fig. 5B). The number of ribs (NR) varies from 7 to 49 measured on the ventral valve. NR has not been included in the statistical analyses due to this variability and differences in preservation of the external layer of the calcitic shell. The measurements of thickness (T) are not normally distributed and are excluded from the analyses.

Principal component analysis (PCA) and Hotelling's T^2 test were conducted on 10 specimens exhibiting traits characteristic of '*R.*' *flustracea* (5 sinistro- and 5 dextroasymmetric), and 10 specimens exhibiting traits characteristic of '*R.*' *faxensis* (5 sinistro- and 5 dextroasymmetric) (Fig. 6). The characteristics are very subtle and only confined to the external shell morphology. In most instances, it is impossible to distinguish specimens based on the description of Posselt (1894), since there is a gradual transition between '*R.*' *faxensis* and '*R.*' *flustracea* (Fig. 5D). The specimens used are those showing the largest differences in external morphology. The PCA analysis (multivariate normality $E_p = 10.48$ and $p = 0.39 > 0.05$) of '*R.*' *flustracea*, illustrates that all of the *faxensis* population falls within the 95% confidence ellipse describing the '*R.*' *flustracea* population, indicating they belong to the same species. The PC1 component or axis is interpreted as a size axis: All five variables, AH, DF, LV, LD, W tilt more or less towards the right, illustrating that they increase in value

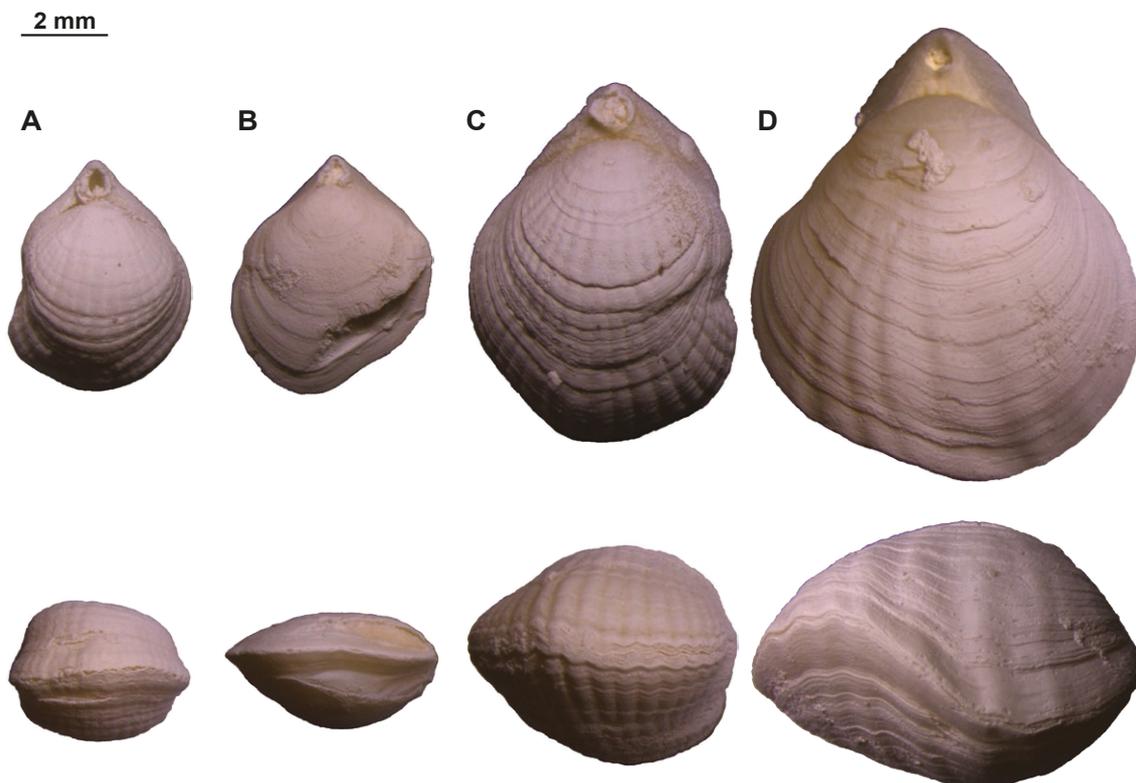


Fig. 5. *Obliquorhynchia flustracea* (von Buch 1834). All specimens are from the Baunekule facies, Faxe Formation. Each specimen is shown in dorsal and frontal view. **A–C** are examples of peculiar asymmetry. **A:** An asymmetric specimen where the asymmetry affects especially the left side of both valves, OESM-10064-0112. **B:** A specimen with no visible ribs, caused by diagenetic dissolution of the outer layer of the calcitic shell, with asymmetry affecting the right and anterior part of both valves, OESM-10064-0113. **C:** A specimen with asymmetry affecting the right side of both valves and the frontal commissure, OESM-10064-0114. **D:** A strongly sinistroasymmetric specimen, but with few and flattened costae and an extremely small foramen with no significant pedicle collar development compared to the size of specimen, transitional between '*R.*' *faxensis* and '*R.*' *flustracea* OESM-10064-0115. Scale bar = 2 mm.

with higher scores on PC1. PC2 is interpreted as an asymmetry/width difference axis as indicated by the upward-directed AH vector (Fig. 6). Thus, specimens with high scores on this axis are more asymmetric, longer and narrower, whereas specimens with lower scores are wider, shorter and less asymmetric. PC1 represents 95.7 % of the total variance and PC2 3.1 %. Variance-covariance matrix was used for the PCA plot. The Hotelling's T^2 test, which is a multivariate analogue to the t test, calculates the probability $p = 0.12$ (Box' $M = 27.9$ and $p = 0.18$ $p > 0.05$), indicating that the two species show no significant difference based on the five selected variables.

Systematic palaeontology

Phylum Brachiopoda Duméril 1806

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer & Popov 1996

Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov 1996

Order Rhynchonellida Kuhn 1949

Superfamily Pugnacoidea Rzhonsnitskaia 1956

Family Basiliolidae Cooper 1959

Subfamily Basiliolinae Cooper 1959

Obliquorhynchia gen. nov.

Lectotype. *Terebratula flustracea* MB.B.9116.1, original from the collection of von Schlotheim (1832, cat. 65 no 62), described by von Buch (1834, p. 63); here designated as lectotype and illustrated in Fig. 7A–D.

Derivation of name. From latin 'obliquus' meaning 'sloping' and 'rhynchia' as the genus belongs to the order Rhynchonellida.

Diagnosis. Small subtriangular to rounded-subpentagonal in outline; greatest width about mid valve; globose subequibiconvex to dorsibiconvex; shell surface finely capillate to costellate; frontal commissure varies from rectimarginate, strongly asymmetric to occasionally broadly uniplicate; beak short, erect or suberect; foramen small, circular, submesothyrid; pedicle collar well-developed; deltidial plates small, conjunct, auriculate; ventral valve with thick, triangular hinge teeth; widely spaced crura, widening anteriorly with inner surface concave and outer surface strongly convex, hamiform; outer hinge plate narrow, no inner hinge plate; dorsal valve without median septum or median ridge.

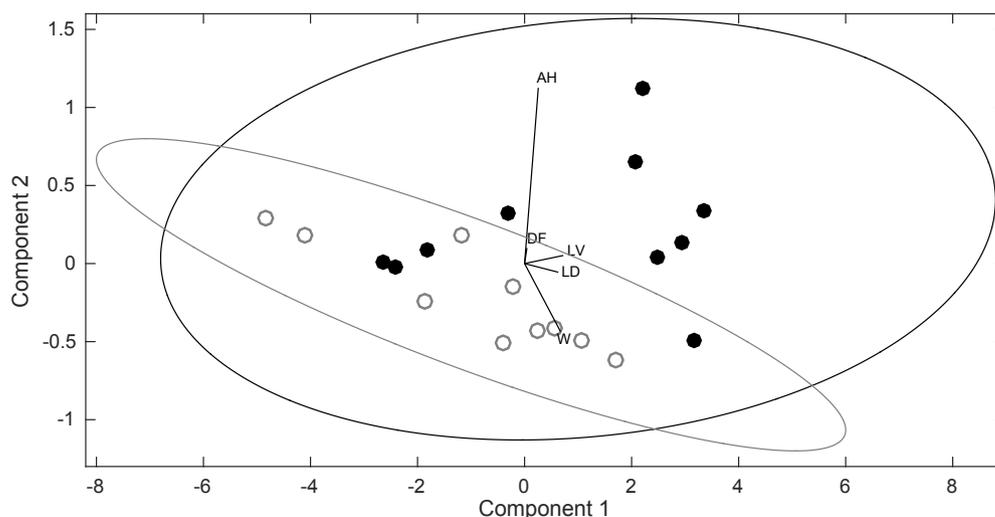


Fig. 6. Principal component analysis (PCA) of measured dimensions LV, LD, W, DF and AH of *Obliquorhynchia flustracea* (von Buch 1834). Ten specimens exhibiting traits characteristic of '*R.* *flustracea*' (von Buch 1834) (5 sinistro- and 5 dextroasymmetric), and 10 specimens exhibiting traits characteristic of '*R.* *faxensis*' (Posselt 1894) (5 sinistro- and 5 dextroasymmetric). A plot of scores and loadings on PC1 and PC2 of the species is shown together with the 95% confidence ellipses. Black filled dots: '*R.* *flustracea*' (von Buch 1834). Grey open dots: '*R.* *faxensis*' (Posselt 1894). Axis PC1 is interpreted as being controlled mainly by size, while PC2 is affected primarily by asymmetry (AH) and width (W).

Remarks on the diagnosis. The type of crura is one of the most important characters when defining the affinity to superfamilies in the revised classification of the order Rhynchonellida used in the Treatise on Invertebrate Paleontology, part H, volume 4 (Savage *et al.* 2002a). The type of crura of this taxon was previously misidentified as raduliform (Asgaard 1968) which would group it as a genus under the superfamily Rhynchonelloidea (Owen & Manceñido 2002). The crura are in fact hamiform and not raduliform. The absence of a median septum and a cardinal process places the taxon in the superfamily Pugnacoidea, family Basiliolidae (Savage *et al.* 2002b). These features and the occurrence of asymmetry place the taxon in the subfamily Basiliolinae. The material differs from the existing basiliolid genera in this subfamily in having hamiform crura together with a larger number of and finer ribs and predominantly strong asymmetry, justifying the erection of the new genus *Obliquorhynchia*.

***Obliquorhynchia flustracea* (von Buch 1834)**

Fig. 3, Fig. 5, Fig. 7, Fig. 8

1832 *Terebratula lustraceus*, von Schlotheim, catalogue 65, no 62 (*nomen nudum*)

1834 *Terebratula flustracea*, von Buch, p. 63

1834 *Terebratula flustracea*, Leonhard & Bronn, p. 619, 623

1835 *Terebratula flustracea*, von Buch, p. 83

1848 *Rhynchonella danica*, d'Orbigny, p. 295

1866 *Terebratula flustracea*, Fischer-Benzon, p. 17

1885 *Rhynchonella flustracea*, Lundgren, p. 39, pl. 1 fig. 35–37

1894 *Rhynchonella flustracea*, Posselt, p. 31–32 pl. 2 fig. 1–3

1894 *Rhynchonella faxensis*, Posselt, p. 30–31 pl. 2 fig. 4–9

1909 *Rhynchonella flustracea*, Nielsen, p. 158

1968 '*Rhynchonella*' *flustracea*, Asgaard, p. 110 fig. 4

1968 '*Rhynchonella*' *faxensis*, Asgaard, p. 112 fig. 5

1970 '*Rhynchonella*' *flustracea*, Asgaard, p. 363

1987 '*Rhynchonella*' *faxensis*, Meyer, pl. 8 fig. 6–10

2008 '*Rhynchonella*' *flustracea*, Dulai *et al.*, p. 199–200

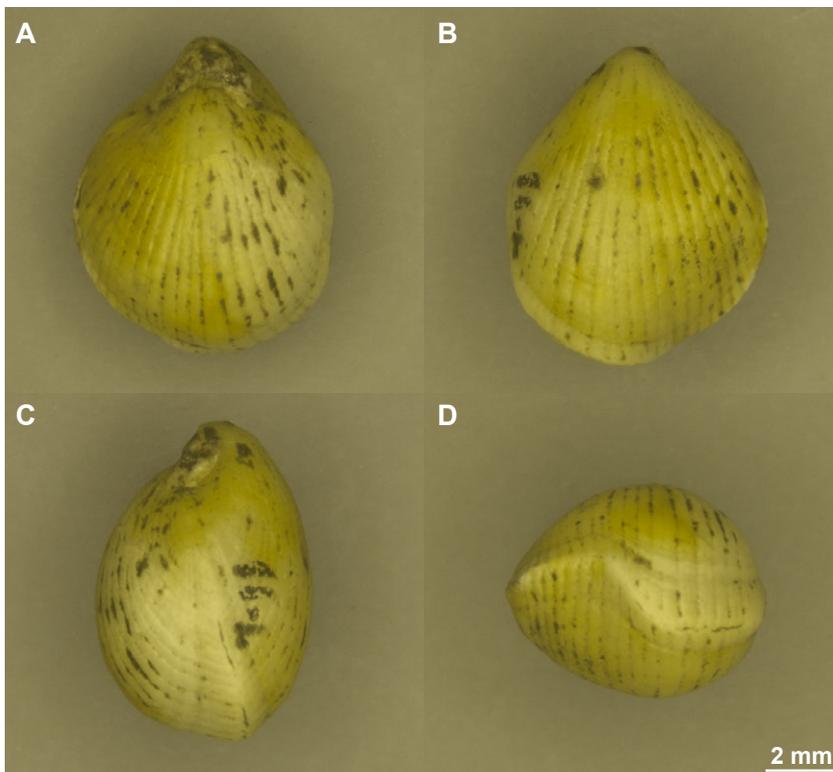


Fig. 7. A–D: Dorsal, ventral, lateral and anterior view of the lectotype of *Obliquorhynchia flustracea* (von Buch 1834), MB.B.9116.1. Scale bar = 2 mm.

2008 '*Rhynchonella*' *faxensis*, Dulai *et al.*, p. 200

2010 '*Rhynchonella*' *flustracea*, Motchurova-Dekova & Harper, p. 109–117, fig. 3–4

2012 '*Rhynchonella*' *flustracea*, Lauridsen *et al.*, fig. 10A

2012 '*Rhynchonella*' *faxensis*, Lauridsen *et al.*, fig. 10J

Lectotype. *Terebratula flustracea* MB.B.9116.1, original from the collection of von Schlotheim (1832, cat. 65 no 62) described by von Buch (1834, p. 63); here designated as lectotype and illustrated in Fig. 7A–D.

Material. The material was collected by Alice Rasmussen at the Stationsvej locality where the Baunekule facies was exposed in the 1990s. It is housed at Østsjællands Museum, Denmark. The material of von Schlotheim was collected from coral limestones in the Faxe limestone quarry. The samples are housed at the Museum Für Naturkunde, Berlin, Germany.

Stratigraphical age. Middle Danian.

Occurrence. *Obliquorhynchia flustracea* (von Buch 1834) is known from the middle Danian Faxe Formation, Faxe limestone quarry in Denmark (von Buch 1834, 1835; Posselt 1894; Nielsen 1909; Asgaard 1968, 1970; Lauridsen *et al.* 2012), Annetorp in south-west Sweden (Lundgren 1885), and the Vigny Formation, France (Meyer 1987). It is only found in association with the scleractinian coral *Dendrophyllia candelabrum*.

Diagnosis. As for the genus.

Description, external characters. Shell relatively small, the adult shell reaches a length of 5–11 mm, measured at the ventral valve. Subpentagonal in outline and rounded anteriorly. Shell varies from globose sub-equibiconvex to dorsibiconvex. Juvenile specimens mainly symmetrical subtriangular to subpentagonal in outline in both dorsal and ventral view. Most adults exhibit strong commissural asymmetry which affects the overall shape of the individual in dorsal, ventral and frontal views. Frontal commissure either rectimarginate, strongly sinistral or dextroasymmetric, occasionally broadly uniplicate. In some specimens that exhibit uniplication the sulcus is shifted towards either right or left in frontal view. Such specimens are considered dextro- or sinistral asymmetric or transitional between uniplicate and asymmetric. Maximum width anterior to the midline of the shell. Presence and form of ribs varies greatly between both individuals and growth stages. In juveniles, ribs are striate or finely capillate. In adults, ribs are normally

present in the form of stronger costae. Uniplicate specimens generally have fewer ribs, taking the form as broader and rounded costae, in some cases only recognisable in the sulcus. Number of ribs varies from 7 to 49 measured on the ventral valve. Ribs begin in the umbonal region but are more pronounced at the anterior margin. The number of ribs is greatest along the margin, due to intercalation. Faint growth lines are present in older growth stages. Specimens exhibiting sinistral- or dextroasymmetry show positive, exponential correlation between size of individuals (LV) and degree of asymmetry (AH) (Fig. 4D, Fig. 8). Beak suberect to erect in adults. Deltidial plates small and separated, auriculate in juveniles and conjunct in adults. During ontogenesis the foramen changes from triangular hypothyrid to circular submesothyrid with a well-developed pedicle collar.

Description, internal characters. Ventral valve has thick, robust, triangular hinge teeth. Outer hinge plates narrow and without inner hinge plates. Dorsal valve has widely spaced hamiform crura, with inner surface concave and outer surface strongly convex, widening to anteriorly almost spatulate in dorsoventral view (Fig. 3). Dorsal valve has no median septum or median ridge.

Remarks. The name of the species was proposed by von Schlotheim in *Systematisches Verzeichniss der Petrefacten-Sammlung des verstorbenen wirklichen Geheimen Raths* under the species name *lustraceus* (1832, catalogue 65, no 62). This is a catalogue of von Schlotheim's manuscript names and collections. It includes no illustrations or species descriptions. The species name and a description were published by von Buch (1834, 1835), but the species name was changed to *flustracea*, with reference to the nine specimens in the collection of von Schlotheim. Von Buch did not include an illustration of the species in this or any later works (1834, 1835, 1840). Neither von Schlotheim nor von Buch designated a holotype and there are no illustrations found in any of the earlier works of von Schlotheim, such as *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinertes und fossiler Überreste des Thier- und Pflanzenreichs* (1820) or *Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht* (1813, 1822). Von Schlotheim has been cited as author of the species name *flustracea*, even though it is von Buch (1834, 1835) who actually published the description under the name *flustracea* and not *lustraceus* which was the manuscript name originally proposed by von Schlotheim. The species name *lustraceus* is thus considered a *nomen nudum*. The lack of illustration in von Buch's (1834) description could pose a problem of the validity of the name. However, he cited the col-

lection of von Schlotheim of nine syntype specimens instead. This collection (MB.B.9116.1–9) still exists and is accessible at the Museum für Naturkunde in Berlin. The species is thus ascribed to von Buch (1834) (see Art. 50 and 51 of ICZN 1999). After the designation of a lectotype herein, the collection no longer consists of nine syntypes, but of one lectotype and eight paralectotypes. Of the now eight paralectotypes of

Obliquorhynchia flustracea (MB.B.9116.2–9) one specimen actually possesses the characteristics e.g. fewer number of ribs and uniplication that Posselt (1894) used in his description of '*R.* *faxensis*'. He included an illustration but did not designate a holotype and never referred to a specific collection or a set of syntypes. '*R.* *faxensis*' is thus considered a junior synonym of *Obliquorhynchia flustracea* (see. Art 11 of ICZN 1999).

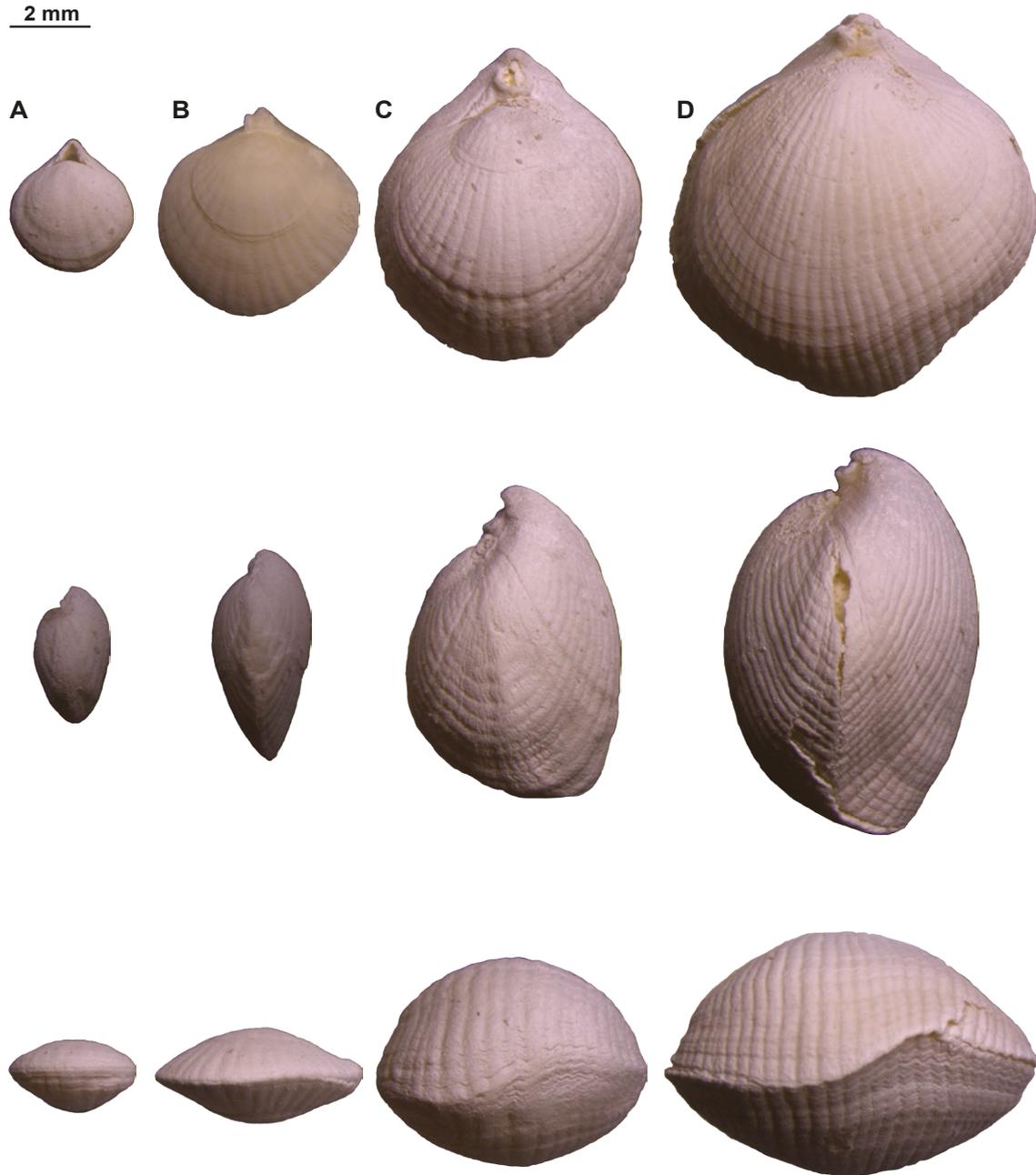


Fig. 8. *Obliquorhynchia flustracea* (von Buch 1834). All specimens are from the Baunekule facies, Faxse Formation, Faxse limestone quarry. Each specimen is shown in dorsal, lateral and frontal view. **A:** Symmetrical specimen with a rectimarginate commissure line and with few and capillate ribs, OESM-10064-0111. **B:** Specimen with incipient dextrosymmetry noticeable in brachial and frontal view, OESM-10064-0078. **C:** Specimen with developed dextrosymmetry that is evident in all views, OESM-10064-0073. **D:** Strongly dextrosymmetrical specimen, OESM-10064-0110. Scale bar = 2 mm.

Conclusions

The external morphology of *Obliquorhynchia flustracea* (von Buch 1834) is extremely variable. The original characteristics used to distinguish 'R.' *flustracea* (von Buch 1834) and 'R.' *faxensis* (Posselt 1894) are exclusively confined to minor details in the external morphology. In the literature, there has been a tendency to refer to 'R.' *flustracea* as the 'asymmetric' species and 'R.' *faxensis* as the 'symmetric, uniplicate' species. However, both von Buch (1834, 1835) and Posselt (1894) stated that 'R.' *flustracea* had an extremely variable morphology and may commonly be asymmetric, but also symmetric specimens have been encountered.

Frequency distributions of specimens from the Baunekule facies show a prevalence of commissural asymmetry in adults. Together with the correlation between LV and AH and the onset of asymmetry there seems to be a correlation between ontogenetic development and degree of asymmetry.

The bivariate regressions show that there is a significant positive correlation between the morphometric dimensions when both types are included. The principal component analysis (PCA) and Hotelling's T^2 test show that there might be differences between specimens, but these are not significant, indicating, together with the regressions, that 'R.' *flustracea* and 'R.' *faxensis* are conspecific. The descriptions and illustrations of Posselt (1894) and Asgaard (1968) rather seem to reflect end members and differences in ontogenetic development of *Obliquorhynchia flustracea* (von Buch 1834) than two separate species.

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