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Little-known brachiopods from the Cretaceous of the Helvetic realm of NE Switzerland (Alpstein) and W Austria (Vorarlberg)

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Abstract Three species from different stratigraphical levels of the Cretaceous of the Helvetic Alps are described. (1) Rhynchonellid specimens from the upper Öhrli-Kalk (Öhrli Formation, Late Berriasian) of NE Switzerland (Alpstein) identified as *Lamellaerhynchia heimi* (Sulser 2008) [Rhynchonellida, Hemithiridoidea]. Its range appears to be limited to a small area of the carbonate platform of the northern Alpstein chain. Based on internal and external morphological criteria *L. heimi* differs from other species of *Lamellaerhynchia,* as well as from *Burrirhynchia* cf. *sayni* (Jacob & Fallot 1913), occurring in the younger carbonate platform of the Schrattenkalk Formation (Early Aptian). (2) Recently collected material in various localities of the Altmann Member (Tierwis Formation, Late Hauterivian to Early Barremian) in the Alpstein area identified as *Oblongarcula* cf. *alemannica* Owen 1977 [Terebratellidina, Laqueoidea]. This species is closely related or identical to *O. alemannica* of the North European Boreal province and gives a reference to the occurrence of the genus *Oblongarcula* in the Tethyan domain of the Alps. Partially silicified specimens enable in rare cases a direct access to internal structures after that they were exposed by an acid treatment. (3) *Tulipina koutaisensis* (Loriol 1896) [Terebratellidina, Kingenoidea], known from Aptian deposits in the central Caucasus of Georgia, has been recorded as a rare species in the Plattenwald-Bed (Selun Member of the Garschella Formation, Albian) of W Austria (Vorarlberg). The localised occurrence and the temporal gap between the Caucasian and the Helvetic *T. koutaisensis* suggest an east–west directed migration along the northern margin of the Tethys Ocean during the Early Cretaceous.

Keywords Brachiopoda · Systematics · Early/Middle Cretaceous · Swiss and Austrian Helvetic

Abbreviations

NMSG Naturmuseum St. Gallen, Switzerland
MHNG Muséum d'histoire naturelle de la ville de Genève, Switzerland

1 Introduction

Recent studies on the Early and Middle Cretaceous brachiopods of the Helvetic Alps are sparse despite the fact that their occurrence has been documented since long by Moesch (1878), Vacek (1879) and by the geological works of Albert Heim (1905), Arnold Heim (1910–1916), Heim and Baumberger (1933) and Heim and Seitz (1934). More recently, two studies about brachiopods of the Cretaceous of Vorarlberg in W Austria were published and included new species (Sulser and Föllmi 1984; Sulser and Friebe 2002), and Sulser (2008) has provided an overview on the present knowledge of the Cretaceous brachiopods in NE Switzerland (Alpstein, Churfirsten) and Vorarlberg (Sulser 2008). This is in contrast to numerous recent publications,

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which deal with the brachiopods of the same period in non-alpine domains throughout Europe. In the present paper, some little-known species are described which is an important complement to the brachiopod fauna of the alpine Cretaceous.

2 Geographical and geological setting

The brachiopods described in this study were collected from six localities in the Alpstein, Switzerland and from one locality in Vorarlberg, Austria (Fig. 1). These are covered by the topographical maps *Landeskarte der Schweiz 1:25,000*, *Säntis* (*Blatt 1115*), and *Diepoldsau* (*Blatt 1096*), and by the geological maps *Geologischer Atlas der Schweiz 1:25,000*, *Säntis* (*Blatt 1115*), *Diepoldsau* (*1096*), *St. Margrethen* (*Blatt 1076*), and *Feldkirch* (*Blatt 1116*).

Details regarding the chronostratigraphic stages, formations and other lithostratigraphic units of the above six localities are provided in the descriptions of the individual brachiopod species. For locality Öhrlisattel refer to *Lamellaerhynchia heimi*, for the localities Altmannsattel, Löchlibetter, Tierwis, Chreialp-Litten, Wildhuser Schafboden-Tristen refer to *Oblongarcula* cf. *alemannica*, and for the locality Plattenwald near Klaus refer to *Tulipina koutaisensis*.

3 Materials and methods

The specimens were generally articulated, but frequently crushed or deformed. Even when qualitatively satisfactory, beak, foramen and interarea were often deformed, so that specimens that permitted the examination of both internal and external morphology are rather rare.

The shells are figured in dorsal-, ventral-, lateral- and anterior view. In the anterior view the dorsal valve is at the top.

To study the internal morphology we used methods depending on the nature of preservation. These sections were made each 0.1–0.2 mm, and they were briefly etched

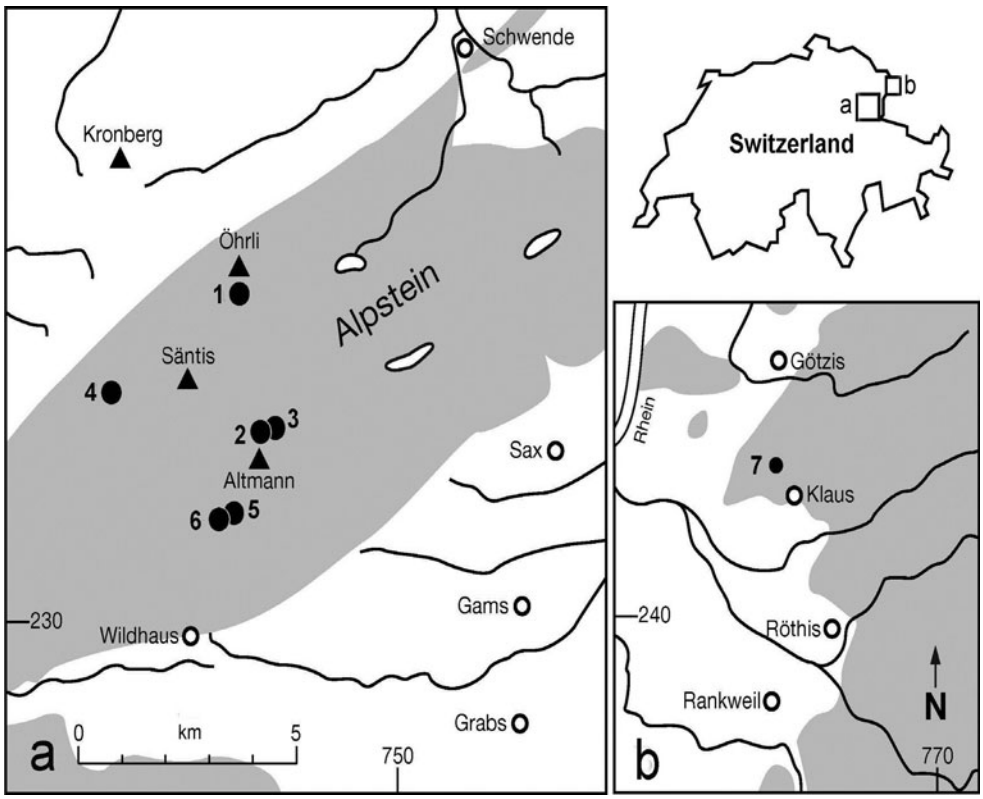

Fig. 1 Map showing *grey*-coloured areas of the Säntis nappe of the Alpstein, northeastern Switzerland (**a**) and in Vorarlberg, Western Austria (**b**). Locations where brachiopods were collected are marked by *black circles*. **a** *Locality 1* is Öhrlisattel (1.5 km northeast of the Säntis), *locality 2* is Altmannsattel (type locality of the Altmann Member, Point 2368, 120 m northwest of the Altmann), *locality 3* is Löchlibetter (south of Point 2162, 400 m northeast of the Altmann), *locality 4* is Tierwis (Paratype locality of the Altmann Member, on the path to the Grenzchopf, 1.2 km west of the Säntis), *locality 5* is Chreialp-Litten (1.5 km south of Altmann), *locality 6* is Wildhuser Schafboden-Tristen (1 km southeast of the Wildhuser Schafberg), and locality. **b** *Locality 7* is Plattenwald (near Klaus, 10 km northeast of Feldkirch, Vorarlberg). *Black triangles* represent mountain peaks

in 5 % hydrochloric acid, rinsed, dried, soaked with acetone and pressed on to acetate-foil. The foils were magnified, and with transmitted light the projections were hand-drawn. The distance from the posterior end of the ventral valve is indicated in millimetres.

For brachiopods in a phosphorite matrix, acetate peels proved mostly unsuitable for the recognition of fine structures. In such cases the sections were photographed. In the case of silicified brachiopods, in addition to the section method, the internal structures could be carefully exposed and directly observed through stepwise application of 2–3 % hydrochloric acid. The mostly incomplete silicification of internal structures was a handicap for achieving satisfactory results, which therefore are rather an exception.

The brachiopods in this study were largely collected by one of us (P. Kürsteiner), mostly together with Karl Tschanz (Zürich). The newly collected material was integrated into the collection of the Naturmuseum St. Gallen (NMSG) and the Muséum d'histoire naturelle de la ville de Genève (MHNG). Additionally, we have also studied specimens in the collections of the Naturmuseum St. Gallen (NMSG), Paläontologisches Institut und Museum der Universität Zürich (PIMUZ), inatura Erlebnis Naturschau Dornbirn (VNS), Muséum d'histoire naturelle de la ville de Genève (MHNG), and the Geological Institute of the Swiss Federal Institute of Technology in Zürich (ETHZH, Churfirsten-collection, Arnold Heim).

4 Systematic palaeontology

Phylum	Brachiopoda Duméril 1806
Subphylum	Rhynchonelliformea Williams et al. 1996
Class	Rhynchonellata Williams et al. 1996
Order	Rhynchonellida Kuhn 1949
Superfamily	Hemithiridoidea Rzhonsnitskaia 1956
Family	Cyclothyrididae Makridin 1955
Subfamily	Cyclothyridinae Makridin 1955
Genus	*Lamellaerhynchia* Burri 1953

Type species *Terebratula rostriformis* Roemer 1836

Lamellaerhynchia heimi (Sulser 2008)

?1916 *Rhynchonella irregularis* (non Pictet); Arn. Heim: p. 459
1999 *Burrirhynchia* sp. Sulser: p. 88 (with Fig.)
2008 *Burrirhynchia heimi* Sulser: p. 103, Fig. 5a–c

Species name. In honour of Arnold Heim, who in 1907 defined the Öhrlikopf as the type locality of the Öhrli Formation.

Holotype. The specimen described as the holotype (NMSG P. 5189) is 13.8 mm long, 15.3 mm in width and 7.4 mm thick (Fig. 2a) and was recovered from the upper Öhrli-Kalk (Öhrli Formation) of the north face of the Muschelenberg (=type locality of the species). It is depicted in dorsal-, ventral-, lateral-, and frontal view.

Type locality. North face of the Muschelenberg, towards Hinter-Öhrligrueb, Kanton Appenzell I.R., Northeastern Switzerland (Fig. 1a).

Occurrence. Muschelenberg, Hüenerberg, Hängeten, Altenalptürm (all from Alpstein).

Age. Late Berriasian: Upper Öhrli-Kalk of the Öhrli Formation (Revision by Grasmück-Pfluger 1962).

Material. Ten well-preserved specimens (from a total of about 100) from the locality Öhrlisattel (Fig. 1a).

Diagnosis. Shell moderately biconvex, shallow-uniplicate, in outline subtrigonal, multicostate, beak straight to suberect, pedicle foramen rimmed, septalium and low dorsal septum present, crura raduliform.

Description. External morphology (Fig. 2a, b). Shell moderately equibiconvex, on average 14 (8–17) mm long, 16 (8–21) mm wide and 8.5 (4–12) mm thick, when more

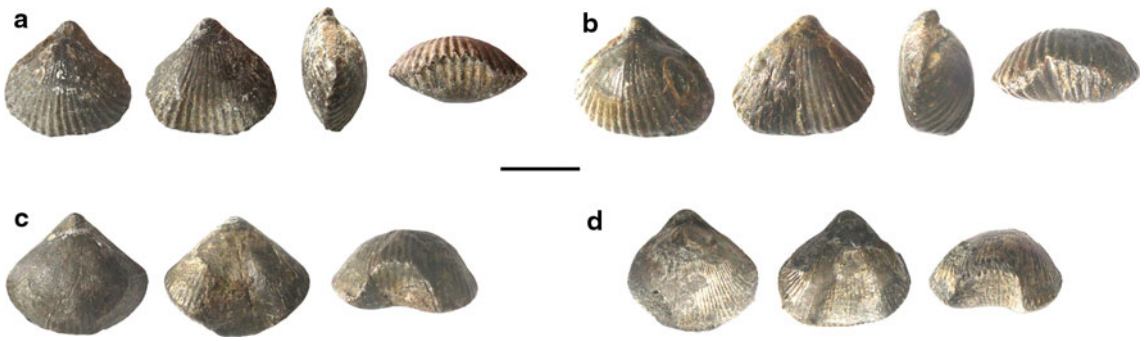

Fig. 2 **a–b** *Lamellaerhynchia heimi* (Sulser), Upper Öhrli-Kalk (Öhrli Formation), both specimens from Öhrlisattel. **a** Holotype (NMSG P. 5189); **b** paratype (NMSG P. 5190), dorsal, ventral, lateral and anterior view. **c–d** *Burrirhynchia* cf. *sayni* (Jacob & Fallot), Rawil Member (Schrattenkalk Formation), both specimens from Mattstock (Bärenfall) near Amden (Canton St. Gallen, Switzerland), dorsal, ventral and anterior view (NMSG P. 5191). *Scale bar* 1 cm

than 10 mm long, width always slightly wider than long. Bluntly trigonal outline, anterior commissure uniplicate, rarely almost rectimarginate. Dorsal valve without fold, ventral valve with weakly developed sulcus anteriorly. About 20 (14–24) radial costae, covering the whole shell, rounded in profile, rarely bifurcating. Beak prominent, straight to suberect, pedicle foramen rimmed, round to oval, hypothyride. Deltidial plates fused. Beak ridges with blunted edges, apical angle 90°–105°.

Internal morphology (Fig. 3). Ventral valve proximally with slightly converging, distally with subparallel dental plates, toward the plane of articulation detached of the inner wall of the valve. Dorsal valve without cardinal process, septalium present (section 3.0), but reduced. Hinge plates proximally connected by a thin, roof-shaped lamella (sections 3.2 and 3.6), then separated and aligning horizontally (section 4.3). Dental sockets deeply rounded, semi-circular in cross section, in which hinge teeth equipped with a dentalium are inserted obliquely (section 4.3). Crural bases reinforced, crura raduliform, dorsally slightly concave, with jagged ends (section 6.2). Median septum low, thick (section 3.2), persisting up to one third of the valve length.

Discussion. This species, introduced by Sulser (2008) and only briefly commented, can be assigned to the Cyclothyridae on account of the rimmed foramen, the prominent beak, and the shape of the crura. The determining skeletal features for the reassignment from the originally ascribed genus *Burrirhynchia* to *Lamellaerhynchia* are the shell covered with radial costae, the wedge-shaped dorsal septum, and the reduced septalium. In comparison to *L. heimi*, *L. rostriformis* (Roemer 1836) is larger, the outline is more wide-rounded, the rib-pattern coarser, the individual ribs more angular in profile and the septalium is missing. The areal region of *L. rostriformis* is more distinctive, the interarea flatter, more extensive (cf. Burri 1956, Owen and Thurrell 1968). *L. renauxiana* (d'Orbigny 1850) grows into a significantly larger and comparatively thicker form. Additionally it shows a pronounced uniplication, which is partially asymmetrically distorted. Otherwise, *L. heimi* keeps rather constant in its shape. It exhibits discrete characteristics, which distinguish it as a separate species.

The establishment of *L. heimi* as a separate species, however, requires further clarification. The species from the Öhrli-Kalk has been mixed up with the small rhynchonellid *Burrirhynchia gibbsiana* var. *sayni* (Jacob & Fallot 1913) from the Early Aptian Schrattenkalk Formation (Rawil Member, previously lower Orbitolinen-Bed). The confusion of the two species was partially due to the fact that early alpine geologists were not able to strictly distinguish the lithologically similar Öhrli- and Schrattenkalk. *B. gibbsiana* var. *sayni* occurs throughout the Helvetic realm (it has often been referred to *Rhynchonella gibbsiana* or *R. gibbsi*, from which the obsolete name "Gibbsi-beds" was derived). Owen (1956) had shown that the *Burrirhynchia gibbsiana* (J. de C. Sowerby 1826) occurs in the Early Albian of southern England as an endemic species. The form from the Helvetic Alps, provisionally named here *Burrirhynchia cf. sayni*, was originally described from the Barremian of the French Alps. Its internal structure is unknown.

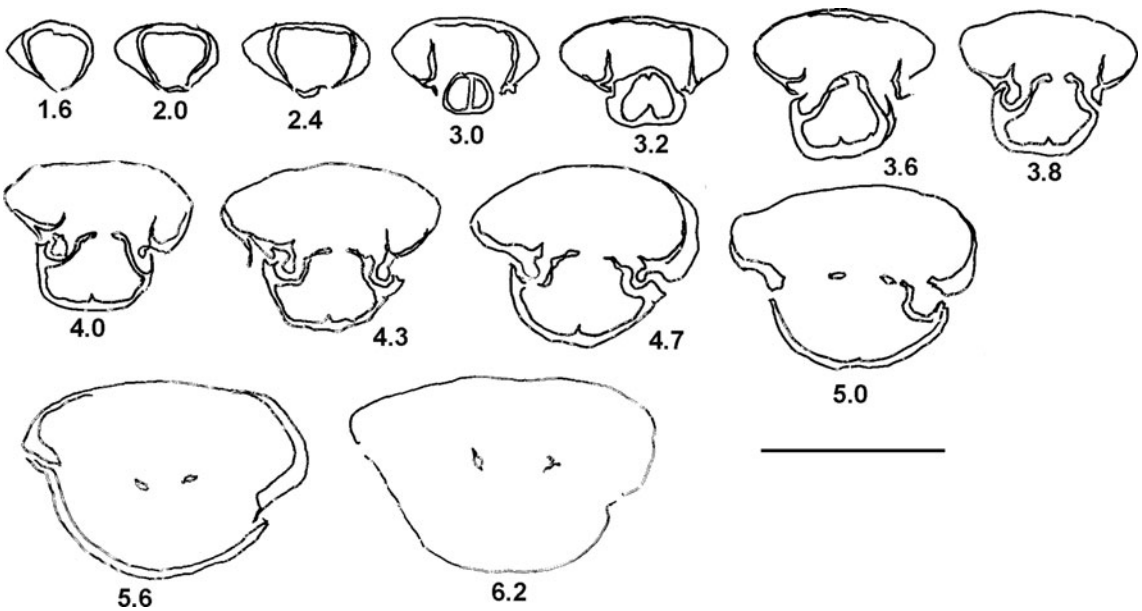

Fig. 3 *Lamellaerhynchia heimi*, Upper Öhrli-Kalk (Öhrli Formation), from Öhrlisattel,. Transverse serial sections, specimen 16.4 mm long, 17.4 mm wide and 10.2 mm thick. The *numbers* of the sections indicate the distance in mm from the posterior end of the shell. *Scale bar* 1 cm

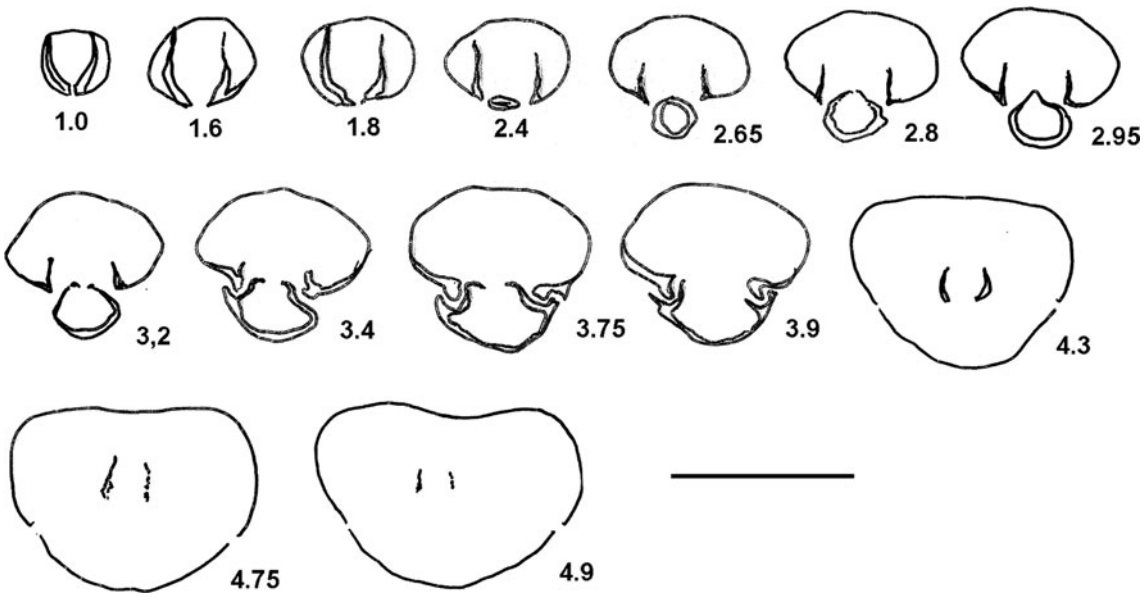

Fig. 4 *Burrirhynchia* cf. *sayni*, Rawil Member (Schrattenkalk Formation), from Mattstock (Bärenfall) near Amden (Canton St.Gallen, Switzerland). Transverse serial sections, specimen 13.0 mm long, 15.2 mm wide and 11.3 mm thick. *Scale bar* is 1 cm

Lamellaerhynchia heimi and *Burrirhynchia* cf. *sayni* differ both in external shape and in internal structure. *L. heimi* is slimmer and less globular. *B.* cf. *sayni* has finer costae, their number is higher (25–35), the anterior commissure wide uniplicate, the shell generally less wide (Fig. 2c, d). In *B.* cf. *sayni* septalium and dorsal septum are missing, the strong dental plates progress horizontally, the crura are shorter, extending to about one third valve length (Fig. 4).

At the type locality, the occurrence of *L. heimi* seems to be restricted to a discrete horizon in the lower part of the upper Öhrli-Kalk where it is abundant and associated with fragments of the oyster *Alectryonia* (*Lopha*). The horizon in question was referred to by Grasmück-Pfluger (1962) as a gnarly-schistous, oncolithic, soft band of marlstone containing echinoderm remains and sponge spicules. *L. heimi* seems to show a certain degree of frequency variability in its lateral persistence, which could indicate a facies dependency. In shallow-water carbonates, characterised by reef forming corals, *L. heimi* is associated with the brachiopods *Psilothyris tamarindus* (J. de. Sowerby) and *Loriolithyris valdensis* (Loriol). While the occurrence of *L. heimi* is limited to the type area of the Helvetic region, *L. valdensis* has a wider geographic and stratigraphic distribution.

Lamellaerhynchia heimi can readily be distinguished from other cyclothyrid rhynchonellids and can be regarded as the ancestral form of the genus. It is the characteristic fossil of the upper Öhrli-Kalk, and it remains unclear whether it occurs in other, facially and temporally comparable deposits of the Cretaceous Helvetic or elsewhere. With regard to relevant log descriptions, which document the fossil assemblages this seems unlikely (Burger 1985). The equivalent of the eastern continuation of the Öhrli Formation in Vorarlberg is the shallow-water facies of the Örfla Formation. This contains a different brachiopod assemblage, not examined in detail as yet, but where *L. heimi* seems to be absent. Föllmi et al. (2007) regard these two stratigraphic units as synonymous and the younger name (Örfla) as obsolete.

Lamellaerhynchia heimi of Barremian and *Burrirhynchia* cf. *sayni* of Aptian age occur in slightly marly beds of two carbonate platforms with a large temporal gap of some tens of millions of years. The external resemblance might result from an analogous mode of life in similar palaeoenvironments. A similar case can be observed in the terebratulids *Loriolithyris valdensis* of the Öhrlikalk and *Sellithyris sella* (J. de C. Sowerby) of the Schrattenkalk. Whether the morphological resemblance is due to adaptations in two coral dominated platforms needs to be substantiated by examining more examples. A point which has to be paid attention to also is the polymorphism and polytypism of both species.

Order	Terebratulida Waagen 1883
Suborder	Terebratellidina Muir-Wood 1955
Superfamily	Laqueoidea Thomson 1927
Family	Terebrataliidae Richardson 1975
Subfamily	Gemmarculinae Elliott 1947
Genus	*Oblongarcula* Elliott 1959

Type species *Terebratula oblonga* J. de C. Sowerby 1829

Oblongarcula cf. *alemannica* Owen 1977

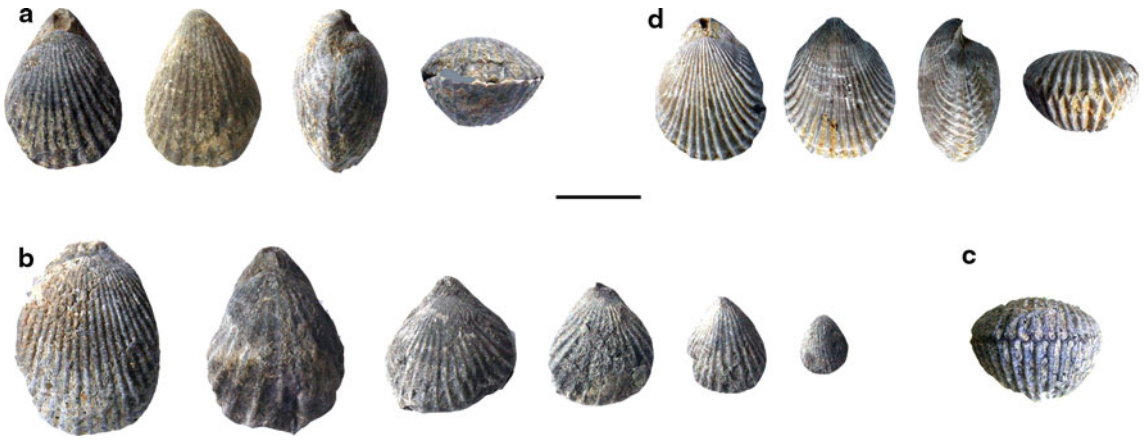

Fig. 5 **a–c** *Oblongarcula* cf. *alemannica* Owen, Altmann Member (Tierwis Formation). **a** From Löchlibetter (NMSG coll. Kürsteiner 5A.09.05), dorsal, ventral, lateral and anterior view. **b** From Altmannsattel, size series showing variation of outline and costation (NMSG coll. Kürsteiner 5A.06.18). **c** From Altmannsattel (NMSG coll. Kürsteiner 5A.06.18), anterior view showing zigzag pattern of costae (= same specimen as the left one of Fig. 5b). **d** *Oblongarcula alemannica* Owen, Hauterivian/Barremian, from Mönchewahlberg near Wolfenbüttel, about 10 km south of Braunschweig, Lower Saxony, Germany, dorsal, ventral, lateral and anterior view (NMSG P. 5192). *Scale bar* is 1 cm

1836 *Terebratula oblonga* Sow.; Roemer: 46, Pl. 2, Fig. 23
1838 *Terebratula oblonga* Sow.; von Buch: 159, Pl. 16, Fig. 2
1839 *Terebratula pectiniformis* Roemer (non Schlotheim): 20, Pl. 18, Fig. 9
1848 *Terebratula oblonga* d'Orbigny (sic!): 113, Pl. 515, Fig. 7–19
1850 *Terebratula oblonga* Sow.; Strombeck: 76, Pl. 4, Fig. 1–19
1864 *Terebratula oblonga* Sow.; Meyer: 254, Pl. 11, Fig. 12–14
1871 *Terebratula puscheana* Roemer; Quenstedt: 275, Pl. 44, Fig. 139
1874 *Terebratula oblonga* Sow.; Davidson: 26, Pl. 2, Fig. 29–31
1878 *Waldheimia oblonga* Sow.; Moesch: 34
1916 *Rhynchonella lata* (non d'Orb.); Heim: 398
1933 *Terebratella oblonga* d'Orb. (!); Heim & Baumberger: 175, 180
? 1933 *Terebratella neocomiensis* (non d'Orb.); Heim & Baumberger: 176
1959 *Oblongarcula oblonga* (J. de C. Sowerby); Elliott: 147
1977 *Oblongarcula alemannica* Owen: 227-230, Textfig. 14, Pl. 3, Fig. 5
1999 *Burrirhynchia*? sp. Sulser: p. 88–89 (with Fig.)
2008 *Oblongarcula* cf. *alemannica* Owen; Sulser: 106, Abb. 5, Fig. Q-U

Occurrence. Northwestern Germany; northeastern France; northeastern Switzerland: Alpstein (Altmannsattel, Chreialp, Löchlibetter, Tierwis, Wildhuser Schafboden), Churfirsten (Glatthalde [doubtful locality description by Arnold Heim]); Austria: Vorarlberg (Hohenems, Unterklien, Breiterberg).

Age. Late Hauterivian/Early Barremian; Altmann-Member of the Tierwis Formation.

Material. 25 well preserved specimens from different localities of the Altmann region (Fig. 1a).

Description. External morphology (Fig. 5a–c). Shell acutely biconvex, rectimarginate, subpentagonal to elongate-oval or bluntly trigonal in outline (Fig. 5b), on average 17.5 (6.5–26) mm long, 12 (5.5–20) mm wide and 9.5 (3.0–20) mm thick. 10–25 strong, deeply incised, occasionally bifurcating and intercalating costae, which draw a zigzag-line at the anterior commissure (Fig. 5c). Beak straight to suberect, beak-ridges sharp. Interarea flat, hinge line curved. Pedicle foramen large, round, mesothyrid, deltidial plates fused. Apical angle about 60°.

Internal morphology (Figs. 6, 7). Ventral valve: dental lamellae lightly concave, hinge teeth blunt (Fig. 7b, section 1.4; Fig. 7c, section 1.6). Dorsal valve: cardinal process poorly developed if at all (see black point in Fig. 7b, section 2.4 and Fig. 7c, section 1.6). Dental sockets with well-marked inner and outer ridges. Septalium present (Fig. 7a, sections 2.8 and 3.0), hinge plates fused, becoming weekly inclined and triangular in connection with median septum (Fig. 7c, sections 2.2–3.0). Septum persists through mid-valve. Crural bases in juvenile specimen with pointed ends of descending branches (Fig. 6b). Loop not observed.

Discussion. The shell is distinguished by marked ribs and might be misidentified as a rhynchonellid brachiopod when the calcitic shell structure is silicified and cannot be

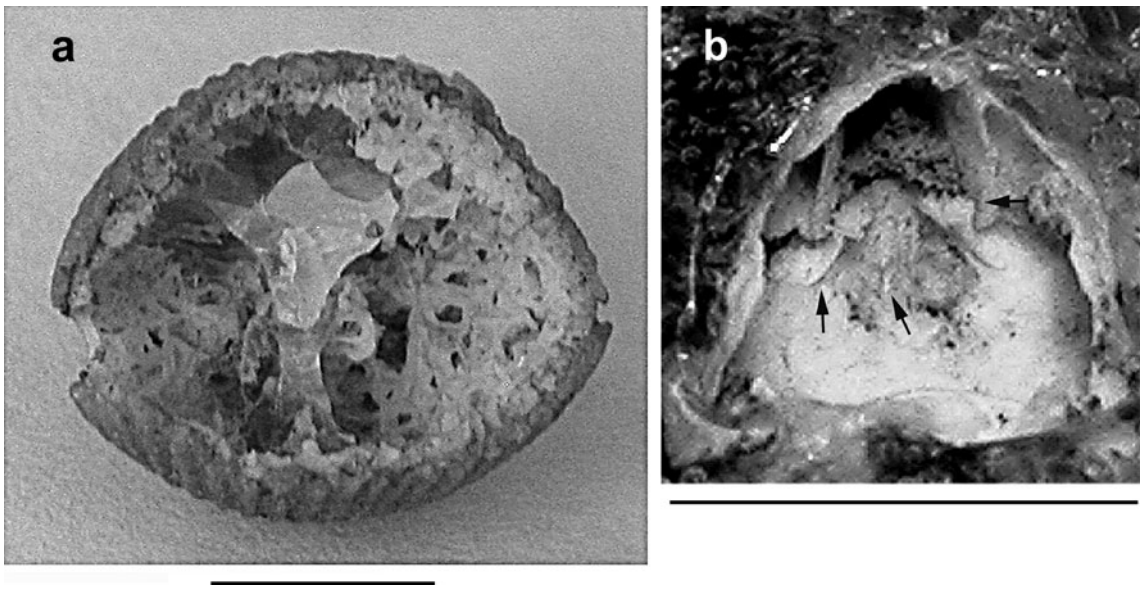

Fig. 6 **a**, **b** *Oblongarcula* cf. *alemannica* Owen, Altmann Member (Tierwis Formation). Silicified internal structures prepared by exposure to acid. **a** Dorsal valve interior from Tierwis near Grenzchopf, showing with compact hinge plate (NMSG P. 5193). **b** Juvenile specimen from Löchlibetter, showing a pair of dental lamellae with lateral umbonal cavities, in between initial stages of articulated hinge plates (*horizontal arrow*), crural bases with pointed ends of descending branches (*vertical arrow*), in the center a knob, probably the initial stage of median septum (*oblique arrow*) (NMSG P. 5194). *Scale bars* 5 mm

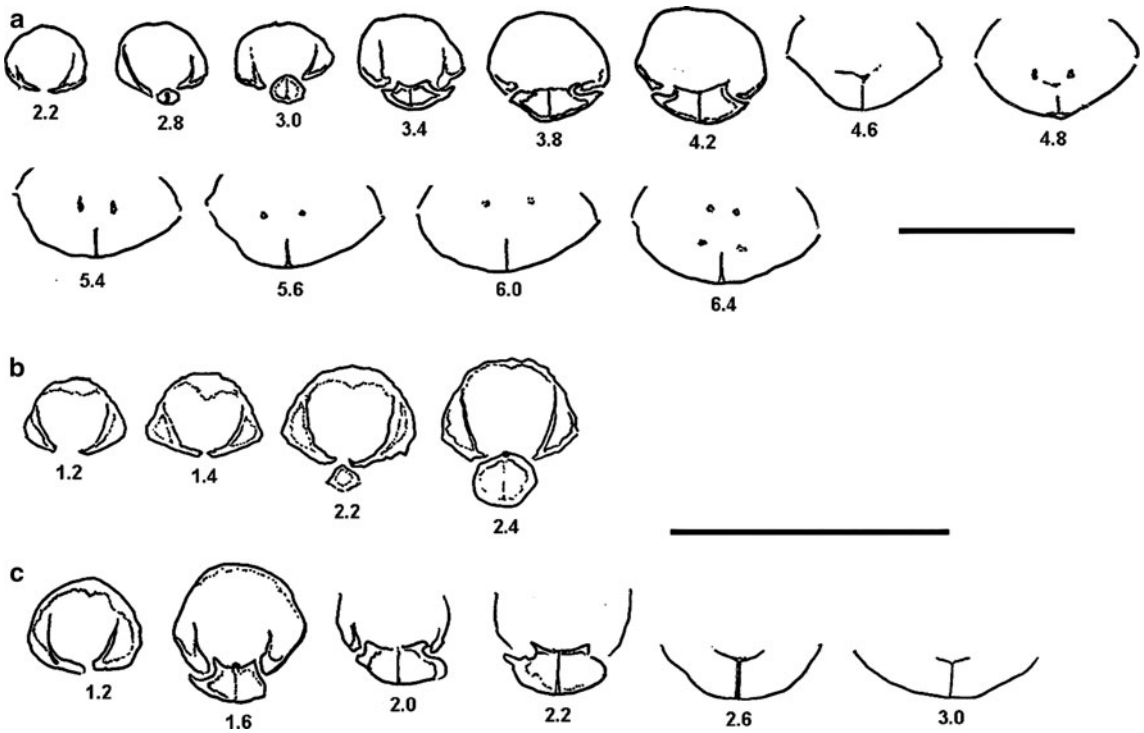

Fig. 7 **a**–**c** *Oblongarcula* cf. *alemannica* Owen, Altmann Member (Tierwis Formation), Transverse serial sections. **a** Specimen 17.6 mm long, 12.4 mm wide and 9.0 mm thick, from Löchlibetter. **b** Specimen 18.1 mm long, 13.7 mm wide and 11.1 mm thick, from Löchlibetter; **c** Specimen 12.7 mm long, 10.2 mm wide and 8.3 mm thick, from Altmannsattel. The numbers of the sections indicate the distance in mm from the posterior end of the shell. *Scale bars* are 1 cm

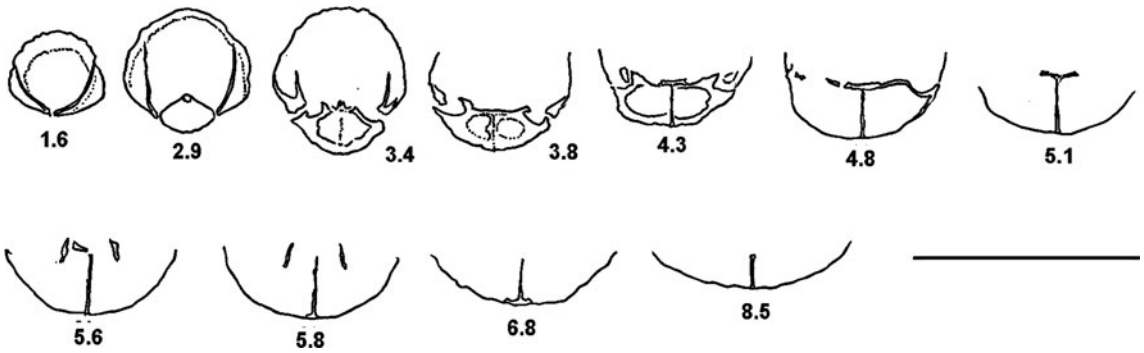

Fig. 8 *Oblongarcula alemannica* Owen, Hauterivian/Barremian, from Mönchewahlberg near Wolfenbüttel, about 10 km south of Braunschweig, Lower Saxony, Germany. Transverse serial sections, specimen 18.7 mm long, 12.5 mm wide and 12.8 mm thick. The *numbers* of the sections indicate the distance in mm from the posterior end of the shell. *Scale bar* is 1 cm

assessed. Kempf (1966, p. 12) who logged the section at the Altmannsattel referred to these brachiopods in question as "Rhynchonellen". Sulser (1999) also referred to them as a questionable *Burrirhynchia*? sp., before more favourably preserved specimens were found.

The serial sections show these brachiopods in an entirely different light. An important diagnostic feature of the brachidium is a plane-undivided, slightly trough-shaped valve plate, which is supported by a high, drawn-out dorsal septum. Partially silicified specimens, after acid preparation permitted direct observation of this characteristic element of the interior organisation (Fig. 6a). This strongly supports their assignment to the terebratellid genus *Oblongarcula*. The genera *Psilothyris* Cooper and *Belothyris* Smirnova show a similar internal organisation, but their smooth shells exclude a possible confusion. The affirmation for the assignment finally resulted from the comparison with the serial sections of *Oblongarcula alemannica* published by Owen (1977).

Oblongarcula has long been known from the Hilskonglomerat (Hauterivian) in northwestern Germany (Schöppenstedt and Berklingen near Braunschweig) and northeastern France. Roemer (1836) referred to it as *Terebratula oblonga*, which J. de C. Sowerby (1829) had established for correspondent forms in South England and which has become the type species of *Oblongarcula* (Elliott 1959). Owen (1977) compared the German and English specimens and established the new species *O. alemannica* for the former. We figure a German specimen from Mönchewahlberg near Braunschweig (Fig. 5d) and have sectioned another one (Fig. 8). The separation into two species is hardly visible in the exterior morphology and relies essentially on a minimal divergence of the internal structure. This is a blunt, short protuberance located in the centre of the proximal hinge plate (Owen 1977, text-fig. 14, sections 6–9), which cannot be recognized in *O. oblonga* (Owen 1977, text-fig. 16). Owen himself qualified his approach by regarding *O. alemannica* as a possible regional variation of *O. oblonga.* The short temporal interval between *O. alemannica* (Hauterivian) and *O. oblonga* (Aptian) can also not justify a separation of both taxa. Therefore, the status of two independent species is still questionable. Nevertheless, we adhere to *O. alemannica* and take it as reference species by naming the relevant specimens from the Helvetic Altmann Member *Oblongarcula* cf. *alemannica*.

Our collected material occurs in a glauconitic, schistous limestone, near the base of the Altmann Member, partially enriched in a shellbed and associated with echinoid spines. Besides elongate shells, especially among the smaller examples, wide and flat forms can be distinguished, which possess length/width-ratios near 1:1. In contrast, the variability of the rib density- and refinement seems to be independent of individual size (Fig. 5b, showing individuals in the size series).

Superfamily	Kingenoidea Elliott 1948
Family	Kingenidae Elliott 1948
Subfamily	Kingeninae Elliott 1948
Genus	*Tulipina* Smirnova 1962

Type species *Zeilleria koutaisensis* de Loriol 1896

Tulipina koutaisensis (de Loriol 1896)

1896 *Zeilleria Koutaisensis* Loriol: 145–147; Pl. 5, Fig. 19–24
1962 *Tulipina koutaisensis* (Loriol); Smirnova: 103–105; Textfig. 5, 6
1972 *Tulipina koutaisensis* (Loriol); Smirnova: 104–105; Pl. 9, Fig. 7
1990 *Tulipina koutaisensis* (Loriol); Smirnova: 136–137, Textfig. 85, Pl. 35, Fig. 2, 3
2002 *Kingena*-like, unidentified brachiopods: Sulser & Friebe: 423, Fig. 13A, B

Type locality. Kutaissi (Georgia) at the south foot of the Central Caucasus Mountains, about 60 km east of the Black Sea.

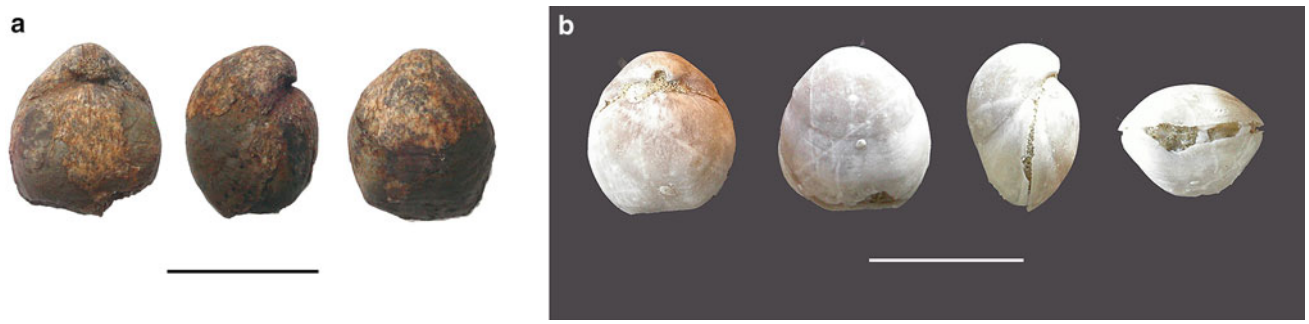

Fig. 9 **a**, **b** *Tulipina koutaisensis* (Loriol). **a** Plattenwald Member (Garschella Formation, Albian), from Plattenwald, Vorarlberg, Austria (NMSG P. 5195), dorsal, lateral and ventral view. **b** Late Hauterivian to Early Barremian, from Kutaissi, Central Caucasus, Georgia (MHNG GEPI 81032), dorsal, ventral, lateral and anterior view. *Scale bars* 1 cm

Occurrence. Kutaissi (Georgia), Plattenwald near Klaus (Vorarlberg), Austria (Fig. 1b).

Age. Late Barremian to Early Aptian of Georgia; Albian of Vorarlberg (Garschella Formation: Plattenwald-Bed of the Selun Member).

Material. 2 specimens from the locality Plattenwald in Vorarlberg (Fig. 1g)

Description. External morphology (Fig. 9a). Shell small (11 mm long, 10 mm wide and 9 mm thick, only 2 specimens inspected), smooth, strongly biconvex, globose with subcircular outline, anterior commissure flat to slightly sulcate, lateral commissure straight. Beak thick, much incurved, pressed towards the posterior part of dorsal valve. Pedicle foramen small, apical region rounded.

Internal morphology (Fig. 10). Ventral valve: dental lamellae short, not persistent (sections 1.7–2.8). Dorsal valve: dental sockets and articulation of hinge teeth diffuse (sections 4.0 and 4.3). Cardinal process not observed. Septalium deep, cup-like (sections 3.6–4.0). Crural bases reinforced (section 4.5). Median septum proximately high, distally becoming low and truncated (sections 5.3 and 7.6), persisting through at least mid-valve. Long V-shaped, reflected loop with a pair of broad, obliquely connected ascending bands, descending bands united with median septum (section 5.7).

Discussion. The brachiopod fauna from the Plattenwald-Bed of Vorarlberg is dominated by the terebratulid *Moutonithyris dutempleana* (d'Orbigny), whereas the rhynchonellid *Burrirhynchia tripartita* (Pictet) and *Orbirhynchia parkinsoni* (Owen) are not frequent. *Tulipina koutaisensis* is so far only represented by a few specimens. Because of its hood-shaped shell it was provisionally referred to as "kingenoid" in Sulser and Friebe (2002, p. 425, Fig. 13). More extensive studies have now permitted its determination and assignment to *Zeilleria koutaisensis* Loriol, on which Smirnova (1962) based her genus *Tulipina*. The exterior appearance already suggests that it is identic with the form of the Plattenwald locality (Fig. 9a, b), and the comparison of serial sections with those on a specimen from Favre's (1875) Caucasian collection confirms this (Figs. 10, 11). The latter sections are practically identical with the ones in Smirnova (1962, text-fig. 6). In the reconstruction of the internal structures by Smirnova (1962, text-fig. 5) *T. koutaisensis* shows a *Kingena*-like, long, vertically lying loop, in which the median septum is connected with the descending lamellae.

It is interesting to note that Favre (1875) conducted in 1871 a scientific expedition to the Central Caucasus. The brachiopod-population of more than 20 specimens, collected in Kutaissi—in what today is Georgia—was named *Zeilleria koutaisensis* by de Loriol (1896), and is stored in the Muséum d'histoire naturelle de Genève.

An unusual structural element at the base of the dorsal septum in the sections of the Caucasian specimens (Smirnova 1962, text-fig. 6; Fig. 11, marked by arrow in section 5.2) is missing in the specimens from Plattenwald. These are preserved as moulds and slightly weathered along the septum, on account of which the mentioned structure was probably destroyed. Its function is not known. Maybe it served as an expanded attachment place for the adductor muscle on the dorsal side. With regard to the rather weak seeming anchoring of the valves (Fig. 10, sections 3.6–4.3 and Fig. 11, sections 2.2–2.7), a strengthened adductor muscle could have supported the articulation of these small shells.

Previously *T. koutaisensis* had only been recognised in the type area of the central Caucasus, for which Smirnova (1962) specified a Late Barremian to Early Aptian age. Favre (1875) had already suggested a pre-Albian age based on the co-incidence of ammonites from the group "*Crioceras*" (=*Crioceratites*). Additional verification of the stratigraphical situation is complicated because recent publications from Georgia are unavailable for political reasons. However for the sediments in question, an Albian age can be excluded on the basis of co-occurring ammonites (D. Ruban, Rostow, Ukraine, personal communication).

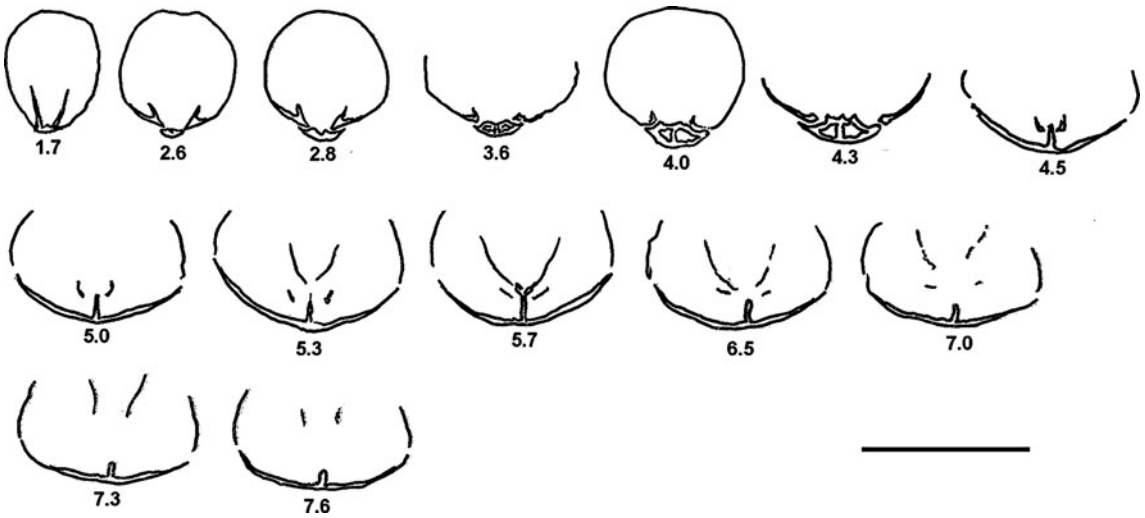

Fig. 10 *Tulipina koutaisensis* (Loriol). Plattenwald Member (Garschella Formation, Albian), from Plattenwald near Klaus, Vorarlberg, Austria. Transverse serial sections, specimen 11 mm long, 10.0 mm wide and 9.1 mm thick. The *numbers* of the sections indicate the distance in mm from the posterior end of the shell. *Scale bar* is 1 cm

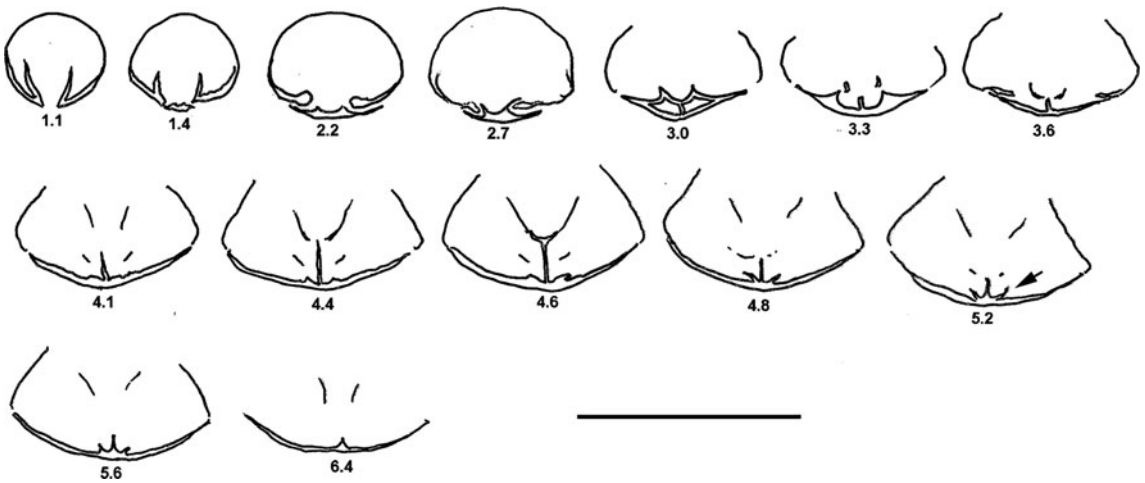

Fig. 11 *Tulipina koutaisensis* (Loriol). Late Hauterivian to Early Barremian, from Kutaissi, Central Caucasus, Georgia. Transverse serial sections, specimen 10.0 mm long 9.3 mm wide and 7.6 mm thick. *Scale bar* is 1 cm

5 Conclusions and prospects

5.1 *Lamellaerhynchia heimi*

Within the Berriasian brachiopod assemblage of Europe, the rhynchonellids represent a relatively small group with only a few genera. In her review, Gaspard (1999) mentioned *Lacunosella*, *Monticlarella* und *Peregrinella* as the main genera. At present, the Berriasian *Lamellaerhynchia heimi* is the oldest alpine representative of the genus. From the Valanginian onwards it is widespread among Early Cretaceous neritic brachiopods of Europe, northern Africa, Mexico and western Russia with about 20 described species. *Lamellaerhynchia* is well represented by distinct species in the Jura Mountains of northwestern Switzerland and probably occurs with further species in the Cretaceous of the Helvetic realm.

5.2 *Oblongarcula*

Its occurrence in the alpine Cretaceous confirms the occasional occurrence of *Terebratella oblonga* in fossil lists of geological works (Moesch 1878; Heim and Baumberger 1933). This genus has so far been described from the Boreal province of northern Europe and southern England. Some questionable species, probably belonging to *Oblongarcula* have been described, such as *Terebratella neocomiensis* d'Orbigny and *T. exquisita* Loriol, see Pictet

(1872). It seems that *Oblongarcula* advanced as far as the Helvetic realm in the border zone to the Tethys. Assuming that a transgression occurred in the latest Hauterivian (Haq et al. 1987), faunal exchanges between the individual zones have become possible.

5.3 *Oblongarcula* cf. *alemannica*

Silicified specimens can be prepared by treatment with acid and directly reveal details of the internal structure, but complete silicification of all calcitic parts is rare. However, as shells of small and medium-sized specimens are common in the collected material, there is a potential to document early stages (see Fig. 6b and its comment) and reconstruct ontogenetical development, usually only known from recent brachiopods. This is a difficult work, but should be carried out in the future, because it offers the chance to elucidate internal structures being built in the course of individual growth in extinct genera such as *Oblongarcula* (see e.g. Gaspard 2003).

5.4 *Tulipina koutaisensis*

In a comparative study of Early Cretaceous brachiopods, Lobacheva (1986) stated that many "European" species are known from an earlier age in western and central Asia. This also holds true for *Tulipina koutaisensis*. This species had previously been recorded from the Late Barremian to Early Aptian of the central Caucasus in Georgia. The time gap until it appeared in the strongly condensed Early to Late Albian (?Early Cenomanian) Plattenwald-Bed would comprise about 10 million years. Covering—what is today—an about 2,500 km long distance corresponds to a migration rate of 25 m per 100 years. Sessile brachiopods can only actively move during a short phase of the larval stage. The rate of dispersal is influenced by several factors, which makes it difficult to estimate. One of the factors is the prevailing westerly ocean-current along the northern margin of the Tethys, which transported *T. koutaisensis* from Georgia to Vorarlberg, the only two places from where the species is presently known. Föllmi (1986, 1989) reported the unusual occurrence of a dropstone in the Albian of Vorarlberg, which was probably derived from gneiss in the Bohemian Massif, and he ascribed its eastern provenance to the prevailing ocean current at that time. *T. koutaisensis* in the Helvetic of Vorarlberg would at least support this assumption.

5.5 *General conclusions*

The Early Cretaceous brachiopods of Europe to a certain extent show both widely-distributed and strictly endemic species. Palaeogeographical and palaeoecological factors influence this pattern, but also the autecology of the brachiopods and, therefore, their resistance or adaptability towards such factors. Taxonomical uncertainties are still a handicap in answering the question to what extent an "alpine group" of various stratigraphical levels can be distinguished from groups of other provenances. In the light of these questions an improved taxonomical record of the involved brachiopod species in realms such as the Helvetic Alps remains an actual task.

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