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First record of the brachiopod *Erymnaria* in the Chruteren Member (Euthal Formation) from a new Palaeogene site in the Brülisau Schuppenzone of northeastern Switzerland (Canton St. Gallen) with remarks on shell asymmetry

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Abstract

A small, smooth-shelled rhynchonellid brachiopod, *Erymnaria* Cooper, 1959 was discovered in a previously unknown locality in the so-called Brülisau Schuppenzone (imbricate zone) of the South Helvetic region of northeastern Switzerland. It is the first record of this genus in this region and in Switzerland in general. It is comparable to the type species of *Erymnaria*, *E. polymorpha* (Massalongo, 1850). Its specific identity is currently undetermined, and the species is referred to *Erymnaria* sp. 1. The main characteristic of *Erymnaria* sp.1 is its asymmetric shell. This prompted a comparison of *E.* sp. 1 with other known asymmetric brachiopods. Questions of asymmetry and variability within the same genus and with brachiopods in general are discussed. Another, larger brachiopod species found at the new site is tentatively named *Erymnaria*? sp. 2. The site can be assigned to the Chruteren Member (Euthal Formation) of Early Ypresian age, dated by large Foraminifera. Thus, the previous distribution area of the Chruteren Member can be extended.

Keywords: Brachiopoda, Early Ypresian, South Helvetic, Large Foraminifera

Zusammenfassung

Ein kleiner glattschaliger rhynchonellider Brachiopode, *Erymnaria* Cooper, 1959 wurde in einer bislang unbekannten Lokalität der sogenannten Brülisau-Schuppenzone in der südhelvetischen Region der Nordostschweiz entdeckt. Es ist der Erstfund in dieser Region und in der Schweiz überhaupt. Die Form ist vergleichbar mit der Typusart von *Erymnaria*, *E. polymorpha* (Massalongo, 1850). Deren Identität ist zurzeit nicht bestätigt und die Spezies wird als *Erymnaria* sp.1 bezeichnet. Ein Hauptmerkmal von *Erymnaria* sp.1 ist die asymmetrische Schale. Dies war Anlass zu einer Gegenüberstellung von *E.* sp.1 mit anderen bekannten asymmetrischen Brachiopoden. Fragen zu Asymmetrie und Variabilität innerhalb des gleichen Genus und bei Brachiopoden im Allgemeinen werden diskutiert. Eine andere, grössere Brachiopoden-Art aus der neuen Fundstelle wird vorläufig *Erymnaria*? sp. 2 genannt. Die Fundschicht kann dem Chruteren-Member (Euthal-Formation) des frühen Yprésien zugeordnet und mit Grossforaminiferen datiert werden. Damit kann das bisherige Verbreitungsgebiet des Chruteren-Members erweitert werden.

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1 Introduction to the brachiopods of Switzerland

Brachiopods are known from the Mesozoic in many regions in Switzerland. They are found in the Triassic of the Eastern Alpine strata of eastern Canton Graubünden and in the Jura region of northern Switzerland. Jurassic brachiopods are diverse in the central Swiss Jura, the southern Alps of Ticino, and regionally from the Helvetic Alps, where Cretaceous brachiopods are well represented. Cretaceous brachiopods are known also from the westernmost Jura mountains. Less well known is the brachiopod fauna from the entire Mesozoic in the Roman Préalpes and the klippen of central Switzerland, where they form a distinctive faunal community (Sulser, 2016a). A complete overview of the current knowledge of fossil brachiopods in Switzerland is given by Sulser (2016b).

Several publications concerning the Cretaceous brachiopods of the Helvetic Alps in northeastern Switzerland and Vorarlberg (westernmost Austria) have greatly increased our knowledge of the distribution of species (Kürsteiner & Sulser, 2015; Sulser, 2008; Sulser & Friebe, 2002; Sulser & Kürsteiner, 2018; Sulser et al., 2013).

In Cenozoic sediments, brachiopods are comparatively rare. Some species in the South Helvetic region of the Brülisau Schuppenzone (imbricate zone) were described by Sulser et al. (2010). They occur in the Einsiedeln Member (Euthal Formation) and in the Scharti Member (Bürgen Formation), Early Lutetian in age.

Recently, we found brachiopods from a new site in the same region. They are assigned to *Erymnaria*, a genus, which was previously unknown in Switzerland and described here in detail. In the first part the palaeogeographic position of the new locality in the Helvetic sedimentation area is discussed. Furthermore, details about the fossil content, lithology, facies, and ecology are discussed.

2 Material and methods

The brachiopods were collected from very hard sedimentary rocks by hammering and chiseling, with subsequent preparation using an air tool. Many of the brachiopods, which were extracted are deformed, broken and incomplete. However, a minority have a shell shape more-or-less intact and could be used for descriptive purposes.

We investigated the internal structure of specimens selected by the use of a standard method, i.e., by cutting a series of transverse sections taken at 0.2 mm intervals. The serial sections were photographed and used for drawing by the use of a binocular microscope. The poor conditions of preservation, however, limited this process. Notwithstanding this, we could describe the type of crura characteristic for the genus *Erymnaria* using some typical sections.

In addition, we used a simple method, proposed by Cooper (1959), to make visible the septiform type of crura. This was done by placing a specimen with well-preserved umbo under water to trace the crura and their supporting plates diverging from the beak.

All figured material is deposited in the Naturmuseum St. Gallen.

3 Geological setting

Populations of brachiopods representing *Erymnaria* were discovered at a locality named «Schörgisknorren West» (Coordinates: 2′758′235/1′243′920/515 m. a. s.l.) in the eastern part of the Fähneren towards the Rhine valley in the Brülisau Schuppenzone, approximatively 2.5 km west of the community Oberriet (Canton St. Gallen) (Fig. 1). This is so far the only known locality for this genus in Switzerland. All specimens were collected from blocks derived from the erosional edge of a compact sedimentary succession which may extend 4–6 m in total thickness. This stratum has layering almost parallel to the dip of slope (Fig. 2). The lowermost parts are slightly laminated and significantly finer grained than the more massive middle and upper parts.

The calcareous coarse sandstone with glauconite and larger litho- and bioclasts (shell fragments, foraminifera) is very hard and compact and can be divided into thick massive banks. The colour of the weathered surface is beige-brown, whereas fresh material shows a greenish to nearly black colour.

The composition and structure of the sediment can be seen especially well in weathered surfaces and in polished cuts (Fig. 3). Besides well-rounded quartz grains, some of which may reach 5 mm in diameter, there are many coarse and angular sediment particles measuring several mm in diameter that are probably intraformationally reworked. Phosphatic components are also present. Rounded particles of dark green glauconite are ubiquitous, some reaching up to 2 mm in diameter, but most are much smaller.

These coarse bio-detritic calcareous sandstones, rich in glauconite and fine sand (glauconitic sandstone = "Greensand"), contain silty rock and micritic clasts. In particular, debris from bivalves and echinoderms are present but usually partly dissolved. Due to the characteristic fauna, these deposits are assigned to the Euthal Formation (Menkveld-Gfeller in Funk et al., 2013).

Menkveld-Gfeller et al. (2016) and Herb (1988) noted that the Lower Palaeogene deposits are only preserved as relics, partly in the form of reworked boulders with locally very different lithologies. Rapid lateral facies changes are typical, ranging from sandy debris to red algal limestones, higher energy bio-detritic limestones to glauconitic deposits, the latter indicating intervals with

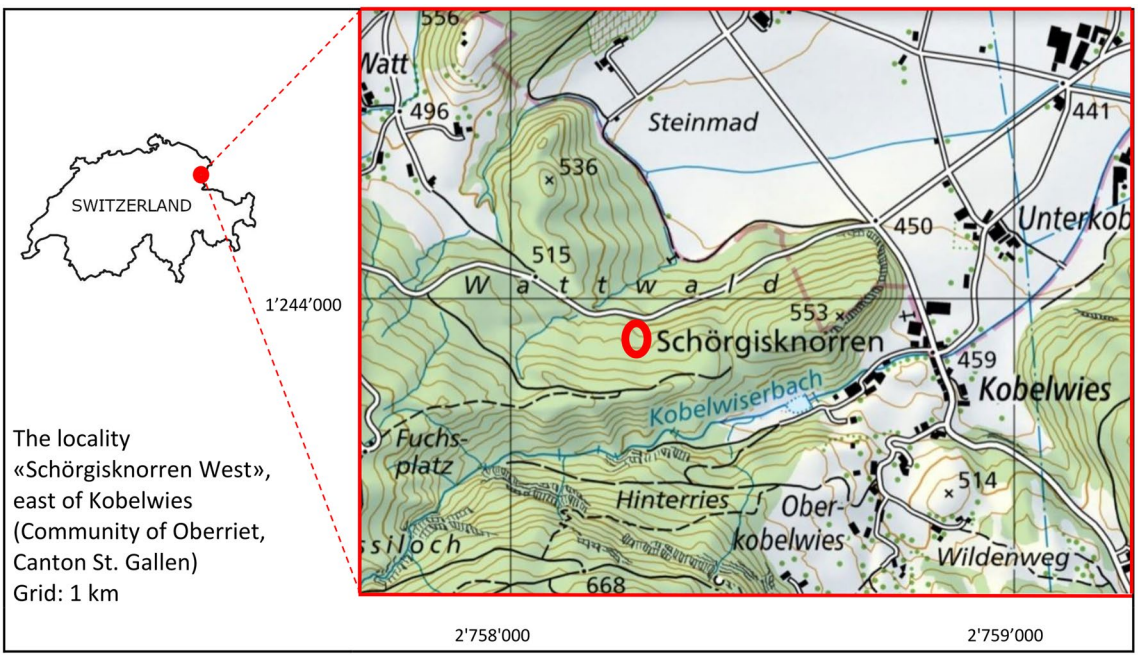

Fig. 1 Geographic location of the studied site (© swisstopo, geo.admin.ch)

Fig. 2 Outcrop of a part of the Chruteren Member at the locality Schörgisknorren West, Subhelvetic of the Säntis Massif (Brülisau Schuppenzone), Canton St. Gallen (Switzerland)

Fig. 3 A polished section shows the calcareous coarse sandstone with glauconite and larger litho- and bioclasts (shell fragments, foraminifera). Width of picture approximatively 8 cm. NMSG-F-14506

low sedimentation rates. All the lithologies mentioned occur below the so-called "Middle Greensand" (base of the Einsiedeln Member) of the Euthal Formation. The mostly sandy sediments—formed in the south-easternmost depositional area—are attributed to the Batöni Member, while the more calcareous to clayey sediments in the adjoining northwest area belong to the Chruteren Member (Menkveld-Gfeller et al., 2016), (Fig. 4).

Based on the facies development, we assign all these brachiopod-bearing strata to the Chruteren Member. This agrees with the descriptions by Friedl and Zurbrügg (1988) at the type locality Chruterenalp: below the "Middle Greensand" there is a horizon with glauconite-bearing biomicrite, which merges upwards into the Middle Greensand through an increase in fine-grained detrital quartz. The depositional environment of these beds is attributed by Friedl and Zurbrügg (1988) to the more distal area of the shelf, which is clearly influenced by bio-detritic sediment derived from a more proximal area. The deposition of the Chruteren Member took place in more shallow water than the Fliegenspitz Member (Menkveld-Gfeller et al., 2016).

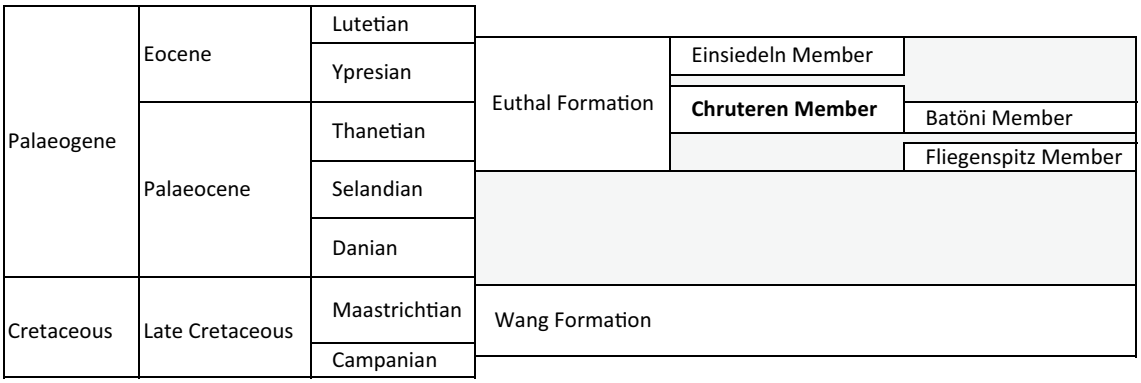

Fig. 4 Litho- and chronostratigraphic classification of the studied Palaeogene sediments

4 Palaeogeography

The Palaeogene of Schörgisknorren West is tectonically part of the Brülisau Schuppenzone. On the geological map of Switzerland 1:25′000, sheet nr. 23, the outcropping sedimentary rocks of that area were not assigned to a particular stratigraphic stage, but merely called the "Schuppenzone," Eocene and Upper Cretaceous.

The Chruteren Member has so far only been reported from the Einsiedeln Schuppenzone and the Säntis Nappe (Menkveld-Gfeller et al., 2016). Eugster et al. (1960) stated that the southernmost transgressive type of the "Einsiedlen facies" (Nummulitic limestones overlying the Wang Beds) should belong to the very southern part of the Helvetic sedimentation area.

Their findings are based on the interpretations of Meesmann (1926) and Leupold (1942, and in Decrouez & Menkveld-Gfeller, 2003). Meesmann (1926) recorded "thrust fragments of Wang Beds with overlying transgressive Nummulitic limestone (Zone III of Arnold Heim) occurring in the Fähnern syncline" and explained the striking diversity within the Nummulitic limestones by the assumption that the "individual packages originated from sites some of which are more southern and others more northern." This fits very well with our observations in the area where we found that local tectonics are complex and that the outcrops are derived from discrete rock units having different palaeogeographical origins.

In the "Flysch Nappe with Wang relicts" at the Fähnerenspitz and on the eastern slope of the Fähneren, Leupold (in Decrouez & Menkveld-Gfeller, 2003) described the "facies zone with Einsiedeln nummulitic limestones reefs" and thereby the nummulite reefs of Schörgis—"nummulitic formations on Wang Beds"—limestones with very small nummulites, which are overlain by the "middle greensand of the Einsiedeln facies and basal parts of Einsiedeln nummulite limestones." He adds that the "middle greensand 3" contains very thick nummulite reefs on the east side of the Fähnerenspitz, where they overlie the Wang Beds.

Leupold (1942, 1964) indicated an origin from the southern Helvetic depositional area and a rapid disappearance of the "Lower Eocene nummulite limestones overlying the Wang Beds" towards the northwest.

These descriptions of the depositional area of the "nummulitic formations overlying the Wang Beds" confirm our interpretation of the investigated strata as belonging to the Chruteren Member. The distribution area of this member defined in Menkveld-Gfeller et al. (2016) can now be extended to the Brülisau Schuppenzone.

5 Fauna

Beside the rhynchonellid brachiopod species described later in this article, there are terebratulids present, but due to very poor preservation these are not reliably determinable (Fig. 5). There are tiny oysters and fragments of other bivalves and abundant echinoderm debris. Tiny nummulitids, often found in clusters, are macroscopically visible. Small, cylindrical, or longer, worm-shaped phosphatized parts may represent coprolites and/or may be phosphatized infill of burrows (bioturbation). Often the chambers of foraminiferans are filled with glauconite (Fig. 6).

Among other vertebrate remains that are occasionally found, lamniform shark teeth dominate, mostly crowns or parts of crowns without roots from a few mm to slightly more than a cm in size. One fragment of a small shark tooth is referred to *Hexanchus* cf. *agassizi* (determination R. Kindlimann, Aathal). A small questionable tooth-fragment might be from a bony fish with durophagous dentition. Several tiny hemispheric bryozoan colonies (Cheilostomata: Lunulitidae?) measuring 2–4 mm were extracted from small, lighter-coloured micritic breccia components.

Fig. 5 Brachiopods *Erymnaria* sp. 1 (left) with a terebratulid (right), embedded in the sediment. NMSG-F-14505

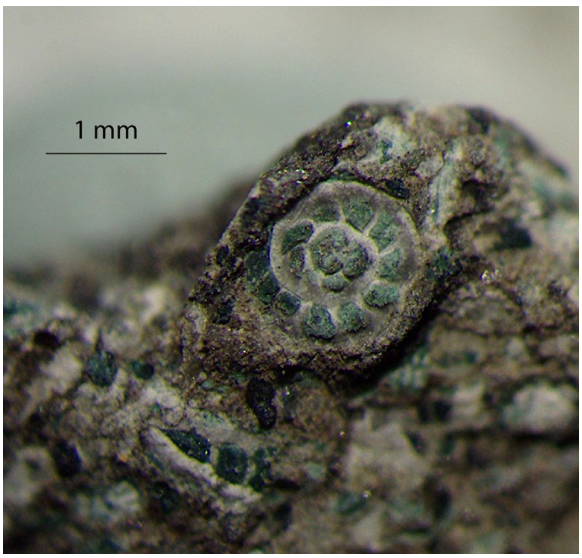

Fig. 6 Broken (nearly equatorial section) nummulite of the group *Nummulites deserti*: chambers infilled with glauconite (NMSG-F-14531)

Thin sections exhibit the following components: large foraminiferans such as nummulites and discocyclines as well as other rotaliid and textulariid foraminiferans, glauconite, and quartz in silt to sand fraction. Corallinaceae, oyster-shell debris, serpulid fragments, and bryozoans are common. Echinoid debris (mostly etched) as well as fine-sandy rock or micritic clasts, probably reworked intraformationally or from the underlying strata (Wang Formation and lowest Palaeogene), are also present.

Many of the benthic foraminiferans present could not be identified. However, representatives of the genera *Bigerina*, *Gaudryina*, ?*Halkyardia* and *Fabiania* were collected. Planktonic foraminiferans are very rare, if present they are probably reworked. The genus *Assilina*, another large foraminifera, was not reported.

According to Herb (1988), these southern Helvetic rocks contain primitive nummulites from the Thanetian-Ypresian transition. The nummulite fauna reported here is not very diverse, the A-forms (megalospheric generation) dominate.

The nummulites are very small, always showing very few whorls (2 to 3), i.e., the environment was probably not favourable for further development. The nummulites are therefore very difficult to determine, as the juvenile stage is not really typical for the species. Probably, the nummulites belong to the group of *Nummulites deserti* and can be determined with some reservations as *N.* aff. *globulus* or *N.* aff. *atacius*, which both represent Early Ypresian forms. Papazzoni et al. (2014) described other, temporally corresponding, nummulite species from Spilecco (Northern Italy).

Discocyclines are quite common and were identified as *Discocyclina tenuis* (Douvillé, 1922). This species occurs in the Late Thanetian and Ypresian. It is also described from the *Erymnaria*-bearing Spilecco limestones (Papazzoni et al., 2014).

6 Systematic palaeontology

Phylum	Brachiopoda Duméril, 1806
Subphylum	Rhynchonelliformea Williams, Carlson, Holmer & Popov, 1996
Class	Rhynchonellata Williams, Carlson, Holmer & Popov, 1996
Order	Rhynchonellida Kuhn, 1949
Superfamily	Pugnacoidea Rzhonitskaia, 1956
Family	Erymnariidae Cooper, 1959
Subfamily	Erymnariinae Cooper, 1959
Genus	*Erymnaria* Cooper, 1959
Type species	*Terebratula polymorpha* Massalongo, 1850
Type locality	Spilecco west of Bolca (Verona, northern Italy)
Type horizon	Eocene (Early Ypresian), NP 10, "Spilecciano" (Papazzoni et al., 2014).

6.1 *Erymnaria* sp. 1

About a dozen fairly well-preserved specimens were available for study.

6.1.1 Description

External morphology (Fig. 7):

Shell size: length 9–12 mm, width 8–12 mm, thickness 4–10 mm, maximum width in the middle or in the anterior half of the shell. Surface smooth with calcitic fibres. Outline irregular-triangular or rounded-pentagonal. Lateral profile inequivalve, gently convex, lateral commissure variable. Uniplication (commonly in median position) shifted to left or right in variable degree, anterior commissure therefore twisted, giving the shell an

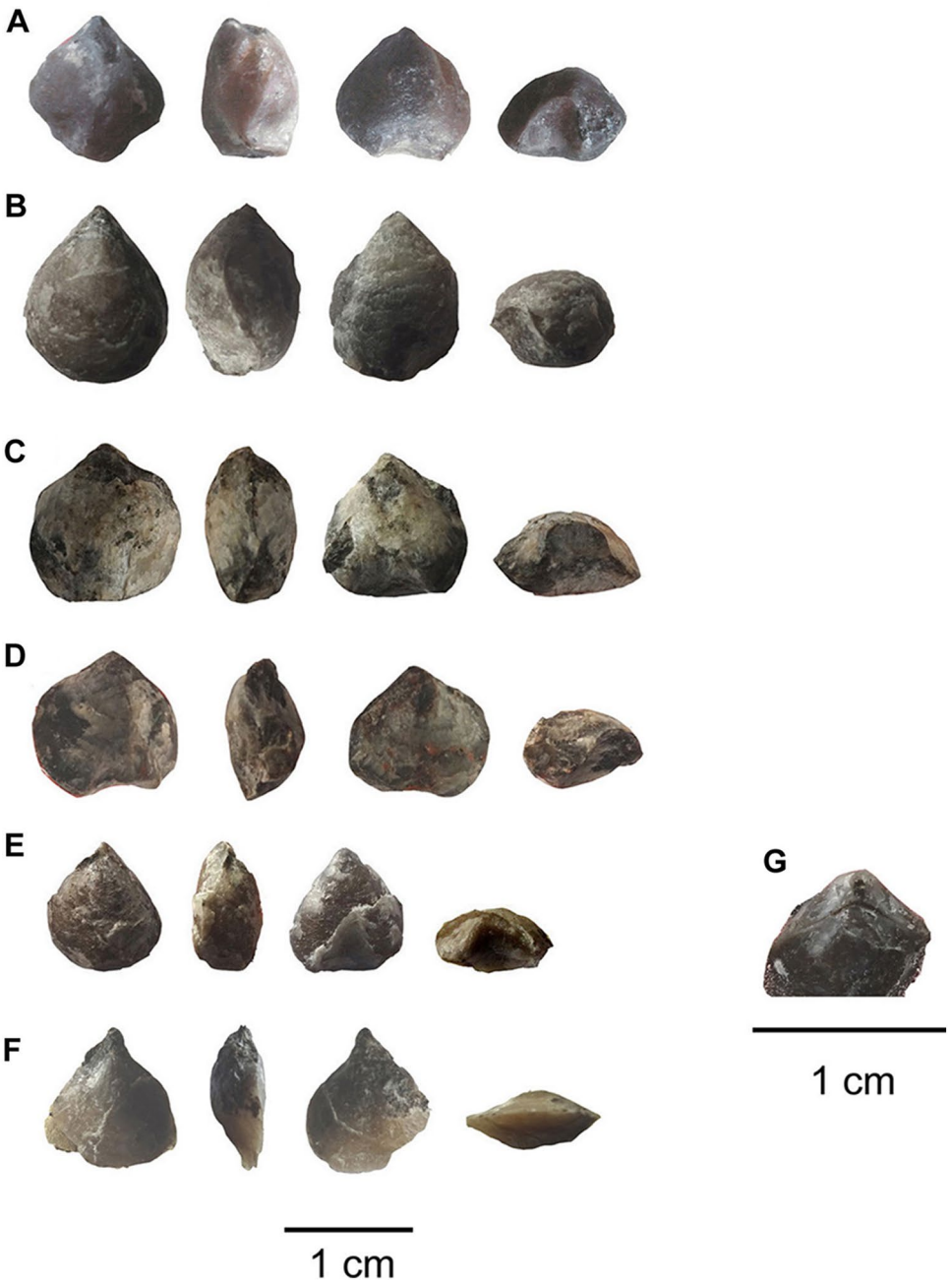

Fig. 7 *Erymnaria* sp. 1, several specimens in dorsal, lateral, ventral, and anterior view (dorsal valve up), showing the variability of the outline, the apical angle, the convexity, and the degree of frontal asymmetry. A (NMSG-F-14532, cast): uniplication shifted gently left, B (NMSG-F-14500): shifted markedly left, C (NMSG-F-14497): shifted gently right, D (NMSG-F-14498): shifted markedly right. E (NMSG-F-14499): almost median positioned, F (NMSG-F-14501): flat juvenile specimen with elongated beak region und rectimarginate anterior commissure, G (NMSG-F-14502): dorsal view of well-preserved posterior region with round, slightly rimmed foramen, and rounded area

asymmetric shape. Beak erect and short (Fig. 7A–F). Foramen hypothyrid, rounded (diameter 0.5 mm) with small rims. Umbo with rounded area (Fig. 7G).
Internal morphology (Fig. 8):

Ventral valve: Dental lamellae parallel or subparallel, persistent (Fig. 8A, sections 2.05 mm and 2.2 mm; Fig. 8D, sections 2.1 mm–2.35 mm)—Dorsal valve: Strong hinge plates, fused in the plane of shell articulation (Fig. 8B), more anterior separated and becoming supports of the crura, thus forming the septiform type (Fig. 8C). Crura forming a pair of curved septa adhering to the wall of dorsal valve up to half-shell length (Fig. 8A, section 2.65 mm; Fig. 8D, sections 2.5 mm and 2.65 mm). Septiform crura made visible by placing the beak region under water (Fig. 9).

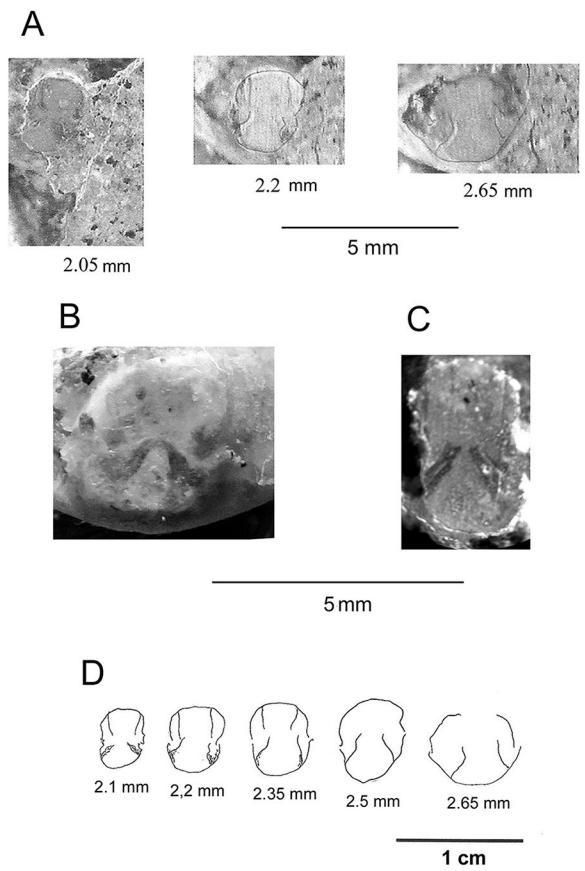

Fig. 8 *Erymnaria* sp. 1. **A** Transverse sections (ventral valve up): section 2.05 mm at the plane of articulation shows the rounded teeth with their dental lamellae in the ventral valve, and the large dental sockets marked by the hinge plates in the dorsal valve. Sections 2.2 mm and 2.65 show the sigmoid-like septiform crura in the dorsal valve, in section 2.2 mm the persistent dental lamellae in the ventral valve. **B** Transverse section (ventral valve up) at the plane of articulation with fused hinge plates, on the right a prominent tooth with dental lamella, loosely inserted in the socket. **C** (like B): transverse section anterior to the plane of articulation shows separated hinge plates forming the supporting plates, characteristic for the septiform crura type. **D** Transverse sections, 2.1–2.65 mm of an almost complete series (ventral valve up), showing the persistent parallel dental lamellae in the ventral valve, and the developing crura. The stage of crural development, when becoming detached from the valve floor, could not be observed

6.1.2 Remarks

The impunctate shell with calcitic fibres is characteristic of rhynchonellid brachiopods. The asymmetric shape, together with septiform crura in the internal structures characterizes the genus *Erymnaria* Cooper (1959). It is named *Erymnaria* sp. 1

6.2 *Erymnaria*? sp. 2

The description of shell morphology was based on 4 specimens: 2 double-valved shells, and 2 ventral valves attached to the sediment. Study of the internal morphology not possible due to the lack of material.

6.2.1 Description

External morphology (Fig. 10):

Shell size: length 16–19 mm, width 17–19 mm, thickness of isolated shells 12–13 mm, maximum width in the middle or in the anterior half of the shell. The surface is rather smooth showing rhynchonellid calcitic fibres. Flat concentric stripes and traces of costae at the anterior edge of the valve (to observe in Fig. 10C and D). The outline is subtriangular (Fig. 10B and C), subcircular (Fig. 10A), or intermediate (Fig. 10D). Lateral profile inequivalve, gently convex, lateral commissure variable. Uniplication not located medianly, anterior commissure therefore twisted, giving the shell an asymmetric form. Beak and foramen not well preserved. Umbo truncated.

6.2.2 Remarks

Larger than *Erymnaria* sp. 1, but similar in general shape, with a less pronounced asymmetry. The internal characters remain unknown. We tentatively named these brachiopods *Erymnaria*? sp. 2. It cannot be excluded with certainty that these rare specimens might represent excessively large shells of *Erymnaria* sp.1.

7 History of the genus *Erymnaria*

Erymnaria was established by Cooper (1959) with the type species *Terebratula polymorpha* Massalongo, 1850. This genus is hitherto known with certainty only from the Eocene near Bolca (Northern Italy). However, there are indications that *E. polymorpha* might occur also in the Late Cretaceous (Scaglia rossa) in the region of

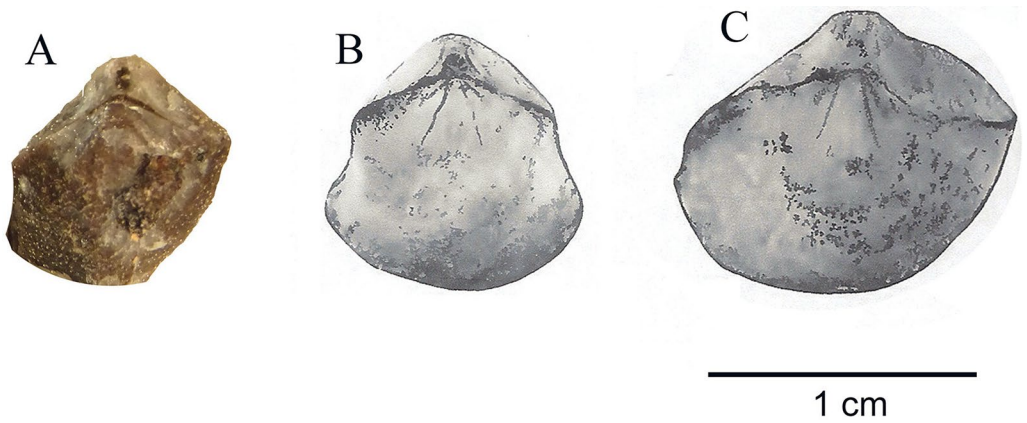

Fig. 9 **A** Dorsal view of a specimen of *Erymnaria* sp. 1 under water, shows the diverging inner lines beyond the hinge line, which trace the septiform crura and (indistinctly) the outer lines which trace the crural supporting plates (NMSG-F-14502). For comparison see the analogous markers (**B** and **C**) in two specimens of *Erymnaria polymorpha* in Cooper (1959, tabl. 18B, figs. 34 and 25)

Verona, Italy (Castellarin, 1960, p. 5; Malaroda, 1962, p. 132; Premoli & Luterbacher, 1966, p. 1242, all cited following Hagn et al., 1968). Cooper did not designate a lectotype, but he selected several hypotypes (1959, pl. 18B, figs. 26–30, 35, 36), and he sectioned one specimen (pl. 22B, figs. 4–9) to show the cardinalia, and especially the septiform crura, which define the genus. With its asymmetric appearance *Erymnaria* can easily be differentiated from *Streptaria* Cooper (1959), which has a very similar asymmetric shape but stands in clear contrast to *Erymnaria* by its falciform crura.

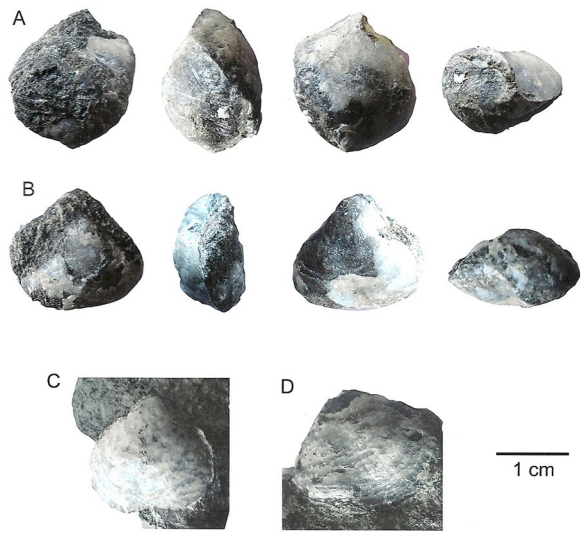

Fig. 10 *Erymnaria*? sp. 2. **A** (NMSG-F-14546, cast), **B** (NMSG-F-14547): two specimens in dorsal, lateral, ventral, and anterior view (dorsal valve up), showing the changing outline, the lateral commissure, and the asymmetric anterior commissure. In both specimens the uniplication is shifted to the left. **C**, **D** Ventral valves in matrix. (NMSG-F-14503, NMSG-F-14504)

Cooper (1959) also assigned *Terebratula bolcensis* Massalongo, 1850, which is of the same age and locality as *E. polymorpha*, to *Erymnaria*, despite poor information about the internal structures. *Erymnaria bolcensis* is symmetric and has a smooth shell. It is interesting to note that asymmetry is not a generic character. *E. polymorpha*, *E.* sp. 1 and *Erymnaria*? sp. 2 in our study display changing degrees of asymmetry and only a few specimens are almost exactly symmetric. *E. bolcensis* might fall into the variability of *E. polymorpha*, which rarely has smooth shells and thus be a junior synonym of that species. This question is still open.

In his publication about the Cenozoic brachiopods of Italy, Davidson (1870) described and figured *Terebratula polymorpha* and *T. bolcensis* (pl. 20, figs. 14, 19 and fig. 4). Other forms with affinities to *Erymnaria* in Davidson's work are from different places and should not be used for comparison. Both species were also mentioned by subsequent authors (Hagn et al., 1968: pl. 9, figs. 4, 5). Motchurova-Dekova and Taddei Ruggiero (2000: text fig. 4) sectioned the type species *E. polymorpha* and figured a series of transverse sections.

The designation *Erymnaria cubensis* Cooper (1959) was based on a single specimen. It occurs in the Eocene near Matanzas, northwestern Cuba. Its symmetric shape resembles *E. bolcensis*.

In his pioneering work, Rothpletz (1886) tried to establish a brachiopod classification based on internal structures. In his "Trigona-Sippe", based on *Terebratula* (= *Caucasella*) *trigona* Quenstedt, 1852, he assembled rhynchonellids with—in new terms—septiform crura. Both *Caucasella* Moiseev, 1934 and *Septocrurella*

Wišniewska, 1932, are Jurassic rhynchonellids with septiform crura and, together with *Erymnaria,* comprise the family Erymnariidae.

Up to this time, *Erymnaria* had been known only from the Palaeogene. Cooper (1959) argued that this genus might range back into the Mesozoic. About a decade later, the proof of this conjecture was provided by Hagn et al. (1968). These authors described *E. rauschi* from the Cretaceous (Middle Gosau, Late Santonian) in the foreland of Untersberg mountain (Salzburg, Austria). *E. rauschi* is 15 to over 20 mm long and has smooth shells with an asymmetric form.

Other Erymnariidae from the Cretaceous of southern Italy were described by Motchurova-Dekova & Taddei Ruggiero (2000): *Erymnaria matensis* (Capasso, 1977) from the Late Cenomanian. These authors introduced the new genus *Costerymnaria* for a previously unknown species where the whole shell is distinctly costate: *C. italica*, *C. apula*, *C.* sp., all from the Late Campanian.

In connection with the costate genus *Costerymnaria,* the homeomorph *Obliquorhynchia* Schrøder et al. (2016) from the Faxe Formation (lowest Palaeogene, Middle Danian, Denmark) requires consideration. Synonymy with *Costerymnaria* can be excluded since its species show falci- or hamiform crura. These species, the asymmetric *Obliquorhynchia flustracea* and the symmetric *O. faxensis,* bear similiarities with *Erymnaria polymorpha* and *E. bolcensis*. The asymmetry of *Obliquorhynchia flustracea*, as the study by Schrøder et al. (2016) demonstrates, advances ontogenetic development. *O. faxensis* and *O. flustracea* are considered conspecific (Schrøder et al., 2016). The relations between *Erymnaria polymorpha* and *E. bolcensis* are not yet clear. However, a small specimen of *E.* sp. 1 in the present study (Fig. 7F) exhibiting a rectimarginate anterior commissure that we consider to be a juvenile shell, supports an identical ontogenetic development.

8 Discussion

8.1 *Erymnaria* from the new site

Erymnaria sp. 1 from the new locality described here is very similar to the type species of the genus, *Erymnaria polymorpha* (Massalongo, 1850). The variable shape of shells available from the new locality is difficult to describe accurately. *E.* sp. 1 is literally a polymorph as the name of the type species suggests, but a confident determination to species-level is not possible. *E.* sp. 1 is smooth, whereas in the population of *E. polymorpha* a part of the specimens displays rudimentary ribs at the anterior edge. In the studied material of *E.* sp. 1 there are rare, very small and probably juvenile, specimens with a usually rectimarginate anterior commissure. They are similar to the symmetric *Erymnaria bolcensis* from the type locality Spilecco. As mentioned before we assume that *E. bolcensis* is not a separate species but young individuals of *E. polymorpha.*

Erymnaria? sp. 2 from the same locality resembles in size and shape the Cretaceous *Erymnaria rauschi* Hagn et al., 1968, which was described from the Late Santonian (Salzburg, Austria). It is not yet clear whether *E. rauschi* is restricted to the Cretaceous. Hagn (1956) pointed out that this species, or related forms, may also occur in equivalent forms in the Spilecco strata near Lake Garda, which that author designated as Early Eocene. Similar forms are also reported from the Spilecciano of the Vicentin from the Late Palaeocene.

Prior to the present publication, *Erymnaria* has not been reported from the Palaeogene in the South Helvetic Brülisau Schuppenzone of the Säntis-Fähneren region (Sulser et al., 2010).

8.2 Depositional environment

Brachiopod shells preserved with both valves indicate that their habitat was rather close to the place where they were buried. But many brachiopods and most of the tiny oysters show damaged single valves. Together with the commonly incompletely preserved microfossils they indicate a high-energy environment of deposition.

Benthic foraminiferans, and therefore also large foraminiferans such as nummulites, are facies dependent. All large foraminiferans from the investigated site show only a few whorls. It seems that the environment was not favourable, hindering further growth. Perhaps the conditions were simply not stable enough for the large foraminiferans to grow to maximum size. For example, sporadic influxes of sand deposits might have occurred and influenced the depositional environment.

We note that A-forms of the nummulites markedly predominate. This could indicate a relatively undisturbed community since the initial natural ratio of A-/B forms is about 10/1 according to Aigner (1985) or even much higher (Papazzoni & Seddighi, 2018). However, here we interpret this ratio differently: since A-forms are easier to transport than B-forms, the diversity of the fauna is very low, and many other biogenic particles are present in the rock in various orientations or as fragments. This is probably an allochthonous association, considered by Aigner (1985) as residual sediment: the energy was sufficient to flush out a large part of the matrix, but not strong enough to transport the A-forms out of this depositional area.

8.3 Aspects of asymmetry concerning *Erymnaria*

The asymmetric shape of the specimens from the new locality is the most characteristic feature of *Erymnaria*. It is known that this deviation from normally symmetric valves can be linked to its living habitat. It has been

described from brachiopods living in the neighbourhood of corals (e.g., Ager, 1965) and in mass accumulations where they are attached in dense clusters in high-energy environments (Schrøder et al., 2017). There may be further reasons for this growth variation, e.g., lack of nutrients. By contrast, no clear indications exist that asymmetry can be a purely genetically fixed feature. It occurs in different genera, mainly in rhynchonellids which may dispose of a genetic flexibility which allows asymmetry as an ecophenotypic adaptation (Gaspard & Charbonnier, 2020).

Asymmetric forms are a minority with the phylum, but within that small group they show considerable variation. In the case of *Erymnaria* populations, better preservation and a broader spectrum of growth stages would enable to gain a better understanding of how and under which conditions asymmetry with its different aspects result.

Brachiopods are commonly divided by a plane of symmetry into two halves. The plane of symmetry lies vertical to both valves along a median line. Usually, brachiopods possess a bilateral symmetry. The comparably small number of asymmetric brachiopods have lost this bilateral symmetry (Fig. 11).

However, asymmetry takes different forms. Two groups can be distinguished. In Fig. 11A and B asymmetry seems to be restricted to the anterior part of the shell (commissural asymmetry) and becomes more evident as growth advances. Costation appears to stabilize the valves and protects them from early deformation (similar to the effect of corrugated iron). Examples of this effect can be observed in high energy shallow-water environments, where ribbed brachiopods dominate (Ager, 1965). In our case both left and right halves remain intact until later they seem to shift against each other as the plane of symmetry functions as a supposed hinge. As the symmetry develops in the course of growth, asymmetry becomes visible at the anterior commissure. This is sketched in Fig. 11A, indicated by arrows. *Septaliphoria felberi* Sulser, 2016a, is an example of this. This type of asymmetry is also represented by species of *Torquirhynchia* Childs, 1969, *Lacunosella* Wisniewska, 1932, and others. This form of asymmetry retains a partial symmetry when the shell is rotated over 180 degrees along the median axis. The anterior commissure of *Septaliphoria felberi* shows an angled edge. In detrital sediments, the rotation of the embedded shell may have an ecological significance in that it enables half of the shell to remain open for feeding (Fürsich & Palmer, 1984). Smooth shells are less resistant to deformation, the commissural asymmetry showing arches (e.g. *Erymnaria rauschi* Hagn in Fig. 11B). A species with this type of asymmetry is illustrated also by *Obliquorhynchia flustracea* (von Buch), which is—as mentioned above—the result of ecological conditions. A

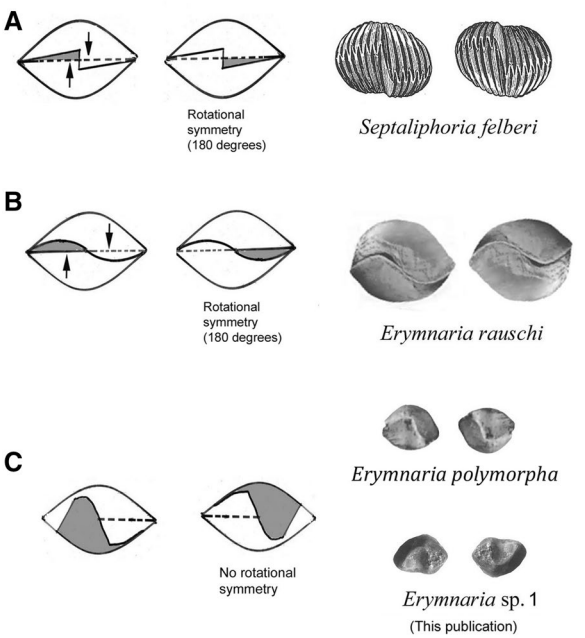

Fig. 11 **A** Asymmetric rhynchonellid costate brachiopod (*Septaliphoria felberi*) retaining rotational symmetry. The convergent shifted growth trajectory is visible at the anterior commissure as sharp edge. **B** Asymmetric rhynchonellid smooth brachiopod (*Erymnaria rauschi*) retaining rotational symmetry. The shifted growth trajectory (convergent) is visible at the anterior commissure in large arches, possibly caused by the reduced resistance of the smooth shell. **C** Asymmetric rhynchonellid brachiopods (*Erymnaria polymorpha* and *Erymnaria* sp. 1) with rotational symmetry lost

rotational symmetry (or commissural asymmetry) is also maintained in this case.

Erymnaria polymorpha and *E.* sp. 1 developed a more complex asymmetry. Anterior uniplication arises early in growing shells and is shifted to the left or to the right. Finally, the whole body of the shell becomes more-or-less distorted (Fig. 11C). A rotational (i.e., partial) symmetry as sketched in Fig. 11A and B disappears. It is the more distinct, the more the uniplication is developed. This more rigid type of asymmetry is also known from species of *Streptaria.*

9 Conclusions

(1) Brachiopods sampled from a new site in the Palaeogene zone of the South Helvetic of northwestern Switzerland were assigned to the rhynchonellid *Erymnaria*, a genus hitherto not known in this region.
(2) The brachiopods were named *Erymnaria* sp.1 and tentatively *Erymnaria*? sp. 2. Due to the scarce and

insufficiently preserved material of the latter, the study of internal characters was not possible.

(3) *Erymnaria* sp. 1 and *Erymnaria*? sp. 2, respectively, can be compared with the type species *Erymnaria polymorpha* (Massalongo) and *Erymnaria rauschi* Hagn et al., respectively. However, their precise identity remains uncertain.

(4) Studies of large foraminiferans from the new locality allowed us to date these *Erymnaria*-bearing sediments as Early Ypresian and to assign them lithostratigraphically to the Chruteren Member of the Euthal Formation. This may explain the occurrence of a previously unknown brachiopod at this locality in a here previously unknown lithostratigraphic unit.

(5) The rather bad preservation of brachiopod shells and the often incompletely preserved microfossils indicate a high-energy environment of deposition and hence some probably short transport. Also, the very low diversity of the whole fauna and the occurrence of biogenic particles in unrolled condition or as fragments indicate transportation before embedding. The ratio of A-/B-forms of the nummulites is interpreted as residual sediment.

(6) Both *Erymnaria* sp. 1 and *Erymnaria*? sp. 2 display an asymmetry. Their deviation from the normal bilateral symmetry of the brachiopod shell is different. This prompted a study of the phenomenon of brachiopod, in general.

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Authors' contributions
PK, KT, UM and TB visited the outcrop. PK, KT and TB collected samples, and processed and photographed them. HS prepared, described and determined the brachiopods. TB made the descriptions of outcrop and rocks and, together with UM, interpreted the depositional conditions. UM determined the Foraminifera, and took care of the bio- and lithostratigraphic and palaeogeographic interpretation. All authors read and approved the final manuscript.

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Declarations

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Competing interests
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