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Taxonomy and palaeoecology of terebratulid brachiopods (*Sellithyris subsella*-group) from the Late Jurassic of northwestern Switzerland

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Key words: Terebratulid brachiopods, *Sellithyris subsella*-group, taxonomy, palaeoecology, Late Jurassic, Kimmeridgian, northwestern Switzerland

ABSTRACT

Brachiopods from the Kimmeridgian of the northwestern Swiss Jura range, sampled at three localities, were separated in four intraspecific variations (A, B, C and D) of the terebratulid species *"Terebratula" subsella* Leymerie. Var. A, regarded to be the least specialized form, occurs, together with intermediate forms, abundantly in each locality. Var. B, C and D, respectively, seem to be restricted to Solothurn and Porrentruy. The variations and their distribution characterize the different palaeocommunities. Var. C was found to be identical with *"Terebratula" suprajurensis* Thurmann.

Shell size and shape of these brachiopods are discussed in the light of the overall faunal composition in each setting. Taphonomic studies imply soft bottom sediments and, in the Solothurn Turtle Limestone, *in situ* preservation and the presence of predators. The morphological differences of the terebratulids are interpreted as facies dependent phaenotypes, whereas conclusions on stratigraphic correlations can not be drawn.

With the attribution of *"Terebratula" subsella* to *Sellithyris* Middlemiss, hitherto used almost exclusively for Cretaceous species, this genus ranges back to the Late Jurassic. Possible phylogenetic links of Cretaceous and Jurassic representatives are briefly discussed.

ZUSAMMENFASSUNG

Brachiopoden aus dem Kimmeridgian von drei Lokalitäten des nordwestlichen Schweizer Jura wurden vier Variationen (A, B, C und D) der terebratuliden Spezies «*Terebratula*» *subsella* Leymerie zugeteilt. Als die wahrscheinlich am wenigsten spezialisierte Form ist var. A, zusammen mit intermediären Formen, an jeder Lokalität häufig. Var. B, bzw. C und D scheinen auf die Lokalität Solothurn bzw. Pruntrut beschränkt zu sein. Die Variationen und ihre Verteilung charakterisieren die einzelnen Paläogemeinschaften. Var. C entspricht «*Terebratula*» *suprajurensis* Thurmann.

Schalengrösse und -gestalt dieser Brachiopoden werden im Zusammenhang mit der an jeder Lokalität vorkommenden Fauna diskutiert. Taphonomische Untersuchungen weisen auf Weichboden-Sedimente und, im Falle der Solothurner Schildkrötenkalke, auf *in situ* Erhaltung und die Anwesenheit von räuberischen Tieren hin. Die morphologischen Unterschiede der Terebratuliden werden als faziesabhängige Phänotypen gedeutet, wogegen in Bezug auf stratigraphische Korrelationen keine Schlüsse gezogen werden können.

Mit der Zuordnung von «*Terebratula*» *subsella* zu *Sellithyris* Middlemiss reicht diese bisher vor allem für Kreide-Brachiopoden verwendete Gattung in den Oberjura zurück. Mögliche stammesgeschichtliche Beziehungen zwischen kretazischen und jurassischen Gattungsvertretern werden kurz diskutiert.

1. Introduction

Late Jurassic terebratulid brachiopods have long been known to occur abundantly in shallow marine limestones of the Reuchenette Formation in northwestern Switzerland (Greppin 1870). In recent years, the Solothurn Turtle Limestone, a famous Late Jurassic lagerstätte of marine turtles and other vertebrates has been the focus of palaeoecological studies (Meyer 1994). The main vertebrate bearing horizon, the so-called "Rätschenbank", has yielded a diverse invertebrate fauna. Certain levels contain brachiopods that sometimes build up whole clusters extending for more than $^1/_4$ m^2. They evidently belong to a palaeocommunity of yet undescribed terebratulid brachiopods. A preliminary examination revealed that these terebratulids have to be placed in the *Sellithyris subsella*-group. This lead to an extended study of other representatives of this group and to an investigation of the taxonomic status of the name-giving *"Terebratula" subsella.*

2. Material and methods

2.1. Geological setting of sampled localities (Fig. 1)

Saignelégier (Franches montagnes)
Some 100 specimens were collected randomly at the border of a road near Pré Petitjean (571.900/236.000, 6 km ENE Saignelégier JU, Switzerland). They come from a marly unit, the so-called Pterocera-marls (Gygi & Persoz 1986) in the Reuchenette Formation (Early Kimmeridgian). In some specimens the test shows a pattern of very faint brownish stripes (traces of original coloration?).

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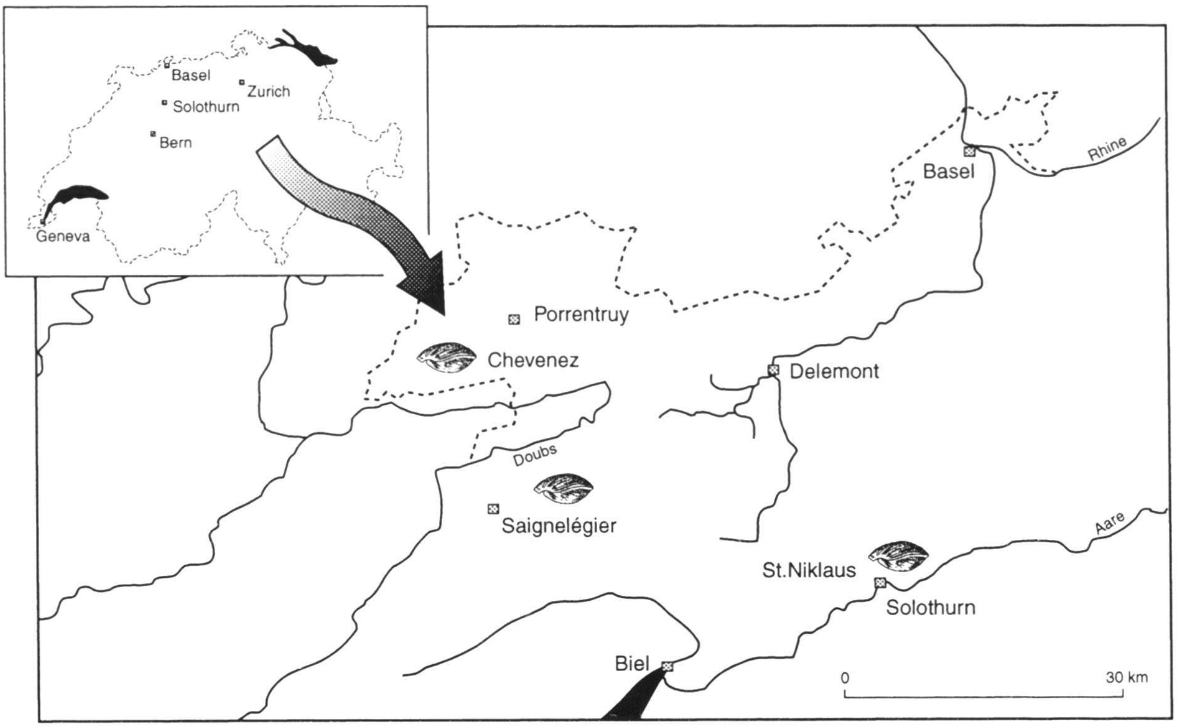

Fig. 1. Map of Switzerland with brachiopod localities sampled from Late Jurassic sediments.

Population	**Saignelégier**		**Solothurn**		**Porrentruy**	
Number of specimens	36		50		60	
Length (L) mm	range: 12.2 - 29.5	average: 21.8	range: 13.3 - 34.2	average: 26.6	range: 9.6 - 42.4	average: 25.9
Breadth (B) mm	range: 11.0 - 26.5	average: 19.1	range: 10.4 - 30.0	average: 22.3	range: 7.3 - 32.6	average: 21.5
Thickness (T) mm	range: 6.1 - 18.7	average: 11.9	range: 5.8 - 19.3	average: 13.6	range: 4.8 - 21.8	average: 14.1
Relative breadth (B/L)	range: 0.76 - 0.98	average: 0.88	range: 0.68 - 1.02	average: 0.84	range: 0.60 - 1.06	average: 0.84
Relative thickness (T/L)	range: 0.47 - 0.65	average: 0.55	range: 0.38 - 0.69	average: 0.51	range: 0.46 - 0.65	average: 0.54

Tab. 1. Shell dimensions.

Porrentruy (Ajoie)

About 300 specimens were collected randomly near Chevenez (567.150/249.850, 6.5 km WSW Porrentruy JU, Switzerland). The specimens come from the Banné-Marl member. The brachiopods are partially silicified, but not coherent enough for preparation by acid treatment.

Solothurn

All brachiopods (about 150 specimens) come from a palaeontological excavation project near St. Niklaus (about 3 km NE Solothurn, Switzerland) that focused mainly on the taphonomy and palaeoecology of the Solothurn Turtle Limestone (Meyer 1989, 1994). The brachiopods were collected from a single limestone bed, the so-called "Rätschenbank". As most specimens were distorted or partially broken by sedimentary compaction or tectonic movement, only well preserved material was used for further examination.

The Solothurn Turtle Limestone Member forms part of the uppermost unit of the Reuchenette Formation in the Solothurn area and is of Late Kimmeridgian (*sensu* gallico) age (Gygi 1995).

The specimens are deposited at the Palaeontological Institute and Museum, University of Zürich (PIMUZ). The one of Fig. 17 is deposited at the Natural Museum Solothurn.

2.2. *Measurement of the specimens and description*

Shell length, breadth, thickness and calculated relative values of well preserved specimens from all three localities are given in Table 1 and Figures 2 & 3. Shells smaller than 15–20 mm

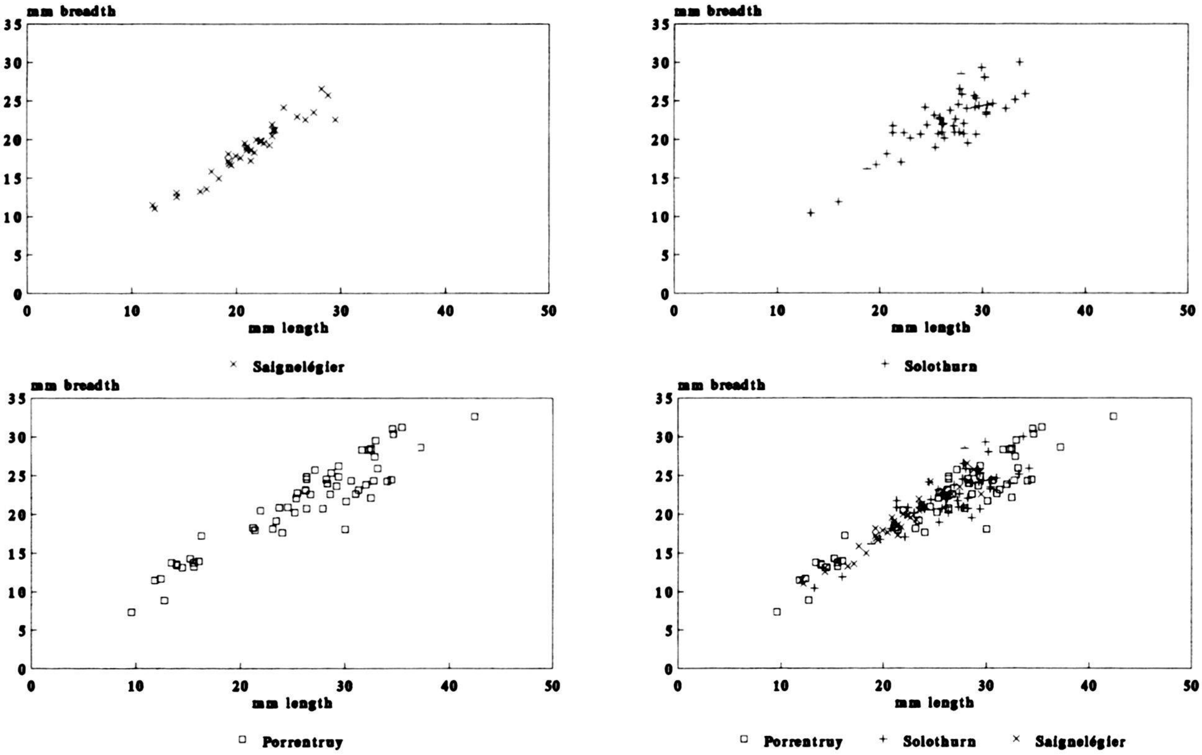

Fig. 2. Breadth/length ratios of specimens from the localities Saignelégier, Solothurn and Porrentruy.

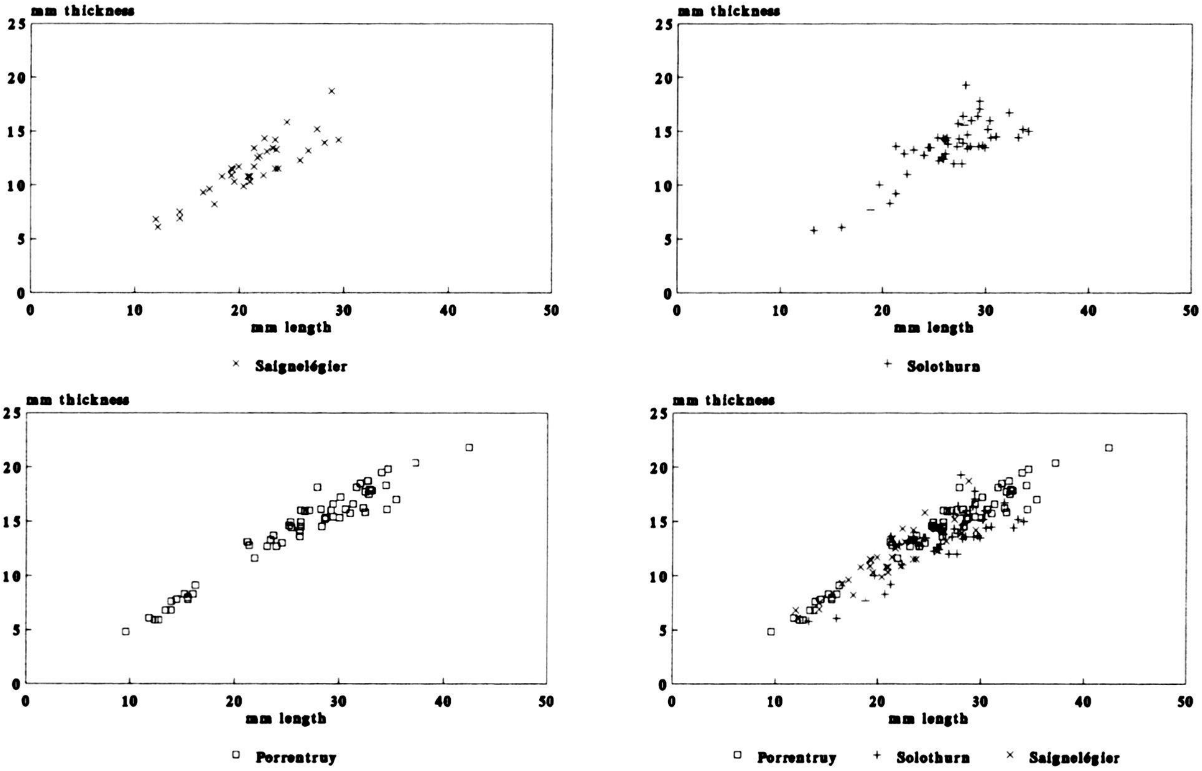

Fig. 3. Thickness/length ratios of specimens from the localities Saignelégier, Solothurn and Porrentruy.

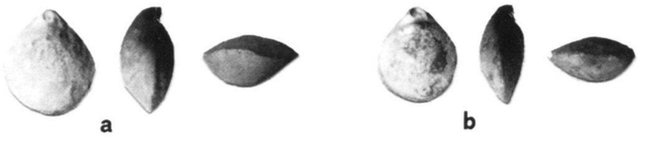

Fig. 4. Juveniles of *Sellithyris subsella* from Saignelégier (specimen a) and Porrentruy (specimen b). Dorsal, lateral and frontal views. 0.9 × natural size. PIMUZ Nr. 019661/662.

Fig. 5. *Sellithyris subsella* var. A from Saignelégier (specimen a and b), Solothurn (specimen c) and Porrentruy (specimen d). Dorsal, ventral, lateral and frontal views. 0.9 × natural size. PIMUZ Nr. 019663/666.

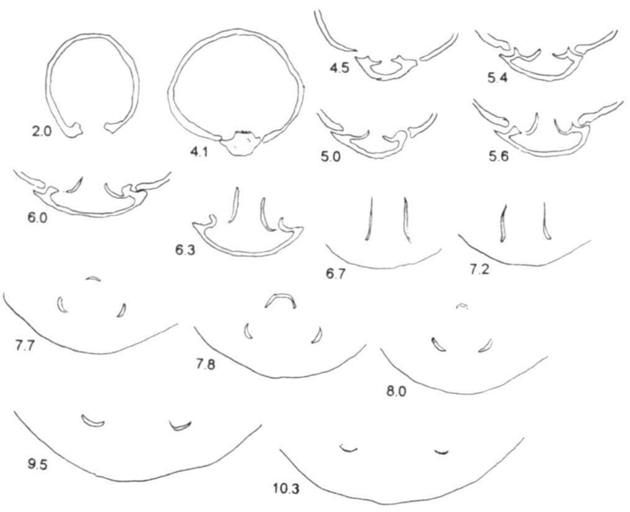

Fig. 6. Transversal sections of *Sellithyris subsella* var. A from Saignelégier. Numerals represent distances in millimetres from pedicle umbo. Measurements of the specimen: length = 23.2, breadth = 22.0, width = 15.1 mm. 2.5 × nat. size.

in length are circular, rectimarginate, and with a flat profile (Fig. 4). In larger specimens the morphological differences become evident and are described as variations A, B, C and D of *Sellithyris subsella.* As will be demonstrated in section 3.4, this species is maintained for all investigated terebratulids. The generic assignment is discussed in section 3.3.

2.2.1. Var. A

Exterior (Fig. 5)

Shell length 20–30 mm; breadth 0.75–0.95, thickness 0.55–0.60% of the length, respectively. Shell surface smooth, biconvex in lateral view, more inflated ventrally than dorsally, dorsal valve flattened anteriorly. Maximal thickness between midvalve and posterior third of shell. Outline subcircular to longitudinally oval, broadest at about midvalve. Plication begins on anterior third, becoming distinct near the anterior commissure. Type of plication varies from undulated to gently sulciplicate. Folds smooth, subparallel, in 4–7.5 mm distance, depression almost flat. Fine growth lines are distributed over the shell surface without anterior crowding. Lateral commissure straight or slightly bowed in ventral direction, turning dorsally in a flat angle at begin of plication. Beak neat, erect to suberect, mesothyrid, beak ridges very faint, rounded. Apical angle 70–90°. Pedicle opening circular, 1.5–3 mm in diameter, surrounded by a fine rim, slightly labiate above the hinge line. Deltidial plates fused (sometimes imperfectly) to symphytium.

Interior (Fig. 6)

Ventral valve: pedicle collar present, pointed. Hinge teeth prolongated, thin, tapering, club-like, forming a kind of open mouth together with denticulum, the latter becoming diffuse in the plane of articulation.

Dorsal valve: cardinal process flat, myophore slightly bilobate, 0.4 mm long. Hinge plates thin, concave or nearly flat. Dental sockets sphaerical, internal ridges well separated from hinge plates. Crural lamellae subparallel to convergent, crural process 3.5–5 mm high. Transverse band rounded-triangular, situated in about 3/4 length of brachidium. Loop reaches midvalve, the anterior ends (wings) having a distance of 6.5–7 mm. Euseptoid not observed.

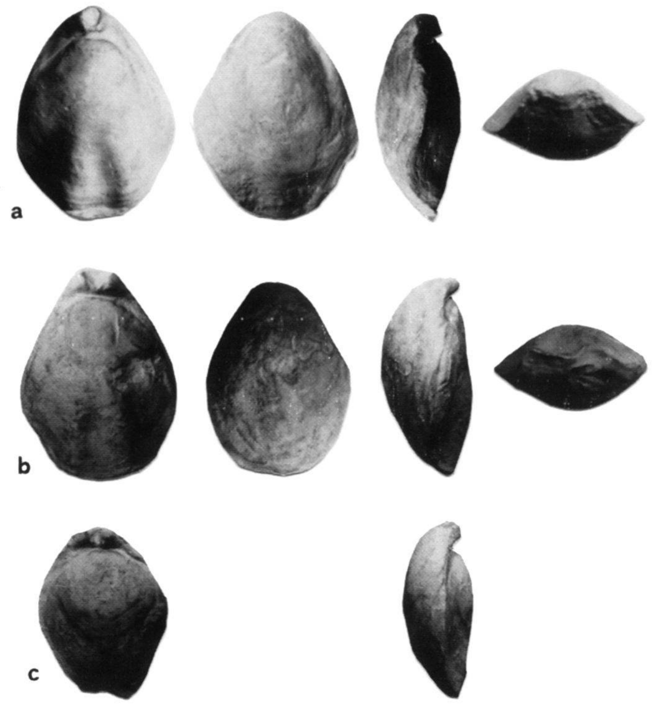

Fig. 7. *Sellithyris subsella* var. B from Solothurn (specimen a and b: dorsal, ventral, lateral and frontal views; specimen c: dorsal and lateral view). 0.9 × natural size. PIMUZ Nr. 019667/669.

2.2.2. Var. B

Exterior (Fig. 7)
Shell length 32–36 mm; breadth <0.75, thickness <0.50% of length, respectively. Shell surface smooth, inequally biconvex and compressed in lateral view. Ventral valve regularly curved, but of varying convexity, dorsal valve less inflated, almost flat anteriorly. Maximal thickness at midvalve or slightly posterior. Outline subpentagonal to longitudinally oval or subrhomboidal, often somewhat asymmetric with regard to the lateral edges. Maximal breadth at midvalve or slightly anterior. Plication on anterior third of shell. Plication undulated or low-sulciplicate, folds rounded to smooth-angular, divergent, with a shallow depression up to 3 mm depth and 6–11 mm breadth at the anterior commissure. The corresponding median fold on the ventral valve is weak and scarcely visible. Growth lamellae present, more frequent on anterior half of the shell. Lateral commissure straight posteriorly, turning to the front in an obtuse angle. Beak rather massive, suberect to erect, occasionally incurved, beak ridges inconspicuous, rounded. Apical angle 50–80°. Foramen circular or longitudinally oval in about equal portions of all examined specimens, rimmed, 1.5–3 mm in diameter. Deltidial plates fused more or less completely to symphytium, with small earlike projections on each side towards the hinge line.

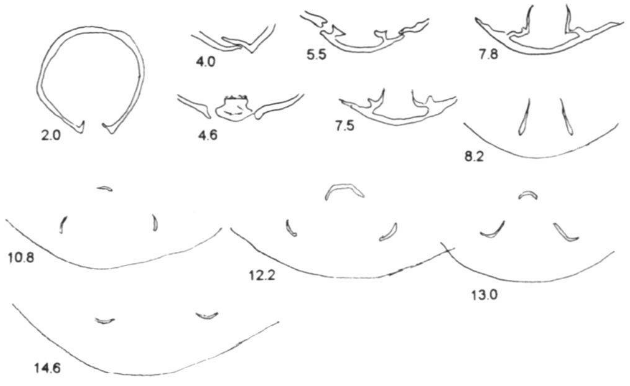

Fig. 8. Transversal sections of *Sellithyris subsella* var. B from Solothurn. Numerals represent distances in millimetres from pedicle umbo. Measurements of the specimen: length = 32.9, breadth = 28.0, width = 14.5 mm. 2.5 × nat. size.

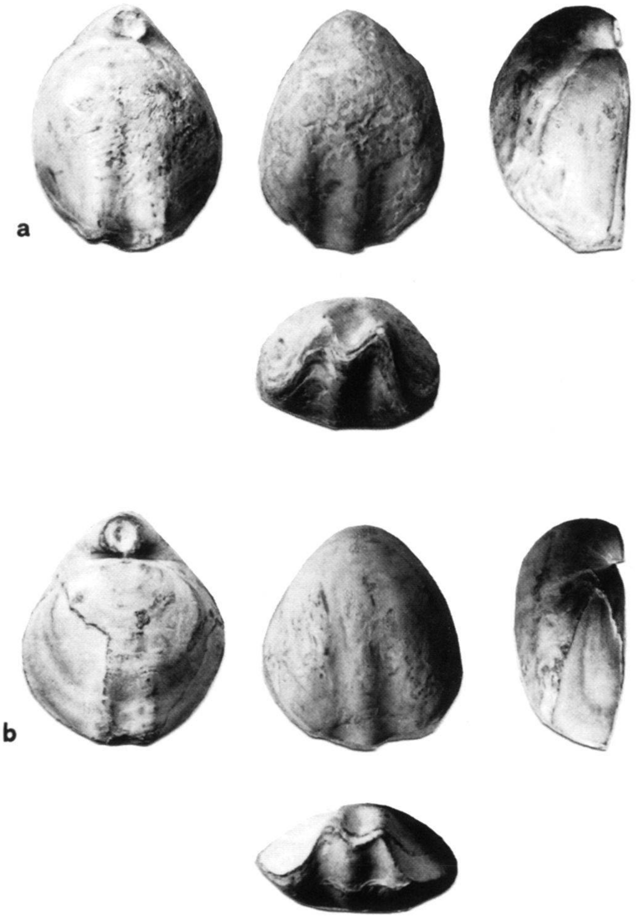

Fig. 9. *Sellithyris subsella* var. C (= *suprajurensis*) from Porrentruy (specimen a and b). Dorsal, ventral, lateral and frontal views. 0.9 × natural size. PIMUZ Nr. 019670/671.

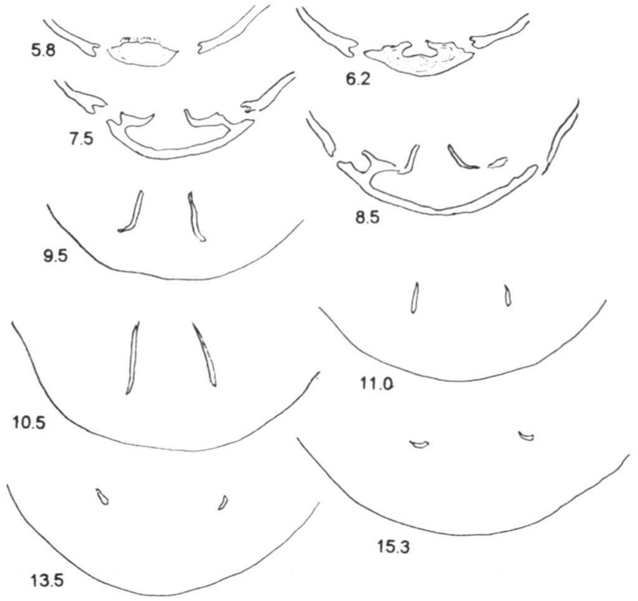

Fig. 10. Transversal sections of *Sellithyris subsella* var. C from Porrentruy. Numerals represent distances in millimetres from pedicle umbo. Measurements of the specimen: length = 31.8, breadth = 25.3, width = 17.8 mm. 2.5 × nat. size.

Fig. 11. *Sellithyris subsella* var. D from Porrentruy (specimen a and b: dorsal and frontal views; specimen c: dorsal, ventral and frontal views). Intermediate form of var. A and var. B from Solothurn (specimen d: dorsal, lateral and frontal view). Intermediate form of var. A and var. C from Saignelégier (specimen e: dorsal, ventral and frontal view). 0.9 × natural size. PIMUZ Nr. 019672/676.

Interior (Fig. 8)
As described above.

2.2.3. Var. C (= *suprajurensis* Thurmann)

Exterior (Fig. 9)
Shell length 30–45 mm; breadth 0.80–0.90, thickness 0.52–0.60% of the length, respectively. (In the description by Thurmann the following shell dimensions were given: length 32, width 28, thickness 16–19 mm. It is not clear whether these are average or maximum values). Shell surface smooth, plane-convex in lateral view. The median line of the ventral valve describes a very regular curve in prolongation of the beak down to the front. The dorsal valve becomes flat after a small initial curvature of some millimeters. Maximal thickness at midvalve or slightly posterior. Outline prevailingly subpentagonal, rarely oval or subcircular. Maximal breadth at midvalve or slightly posterior. Plication in anterior third of shell, distinctly sulciplicate, folds angular, subparallel with deep (up to 5 mm) depression, 3–10 mm broad at the anterior commissure. Corresponding median fold on ventral valve easily discernible. Growth lamellae occasionally near the anterior commissure. Lateral commissure straight posteriorly, then ventrally directed, turning dorsally in a 90° angle at the begin of plication. Beak very thick, mostly erect, in very large specimens sometimes deeply incurved dorsally, in smaller specimens suberect to erect. Pedicle opening large, markedly rimmed, 2.5–4 mm in diameter, in majority circular, in 10% of all specimens oval, both longitudinally or transversally. No beak ridges. Apical angle 60–90°. Deltidial plates fused to symphytium, forming protruded lips towards hinge line.

Interior (Fig. 10)
As described above. A minute difference may be seen in the dental sockets: their internal ridges are not so well separated from the hinge plates. In the serial sections of Figure 10 the transverse band is not visible.

2.2.4. Var. D (Fig. 11)

This variation is of very similar appearance in all characters as described for var. C, except the reduced relative breadth which is always below 0.80 (range: 0.60–0.78) and the relative thickness which may exceed 0.60 (range: 0.52–0.65). The length is not more than 35 mm.

3. Palaeontology

Order	Terebratulida Waagen 1883
Superfamily	Terebratulacea Gray 1840
Family	Terebratulidae Gray 1840
Subfamily	Sellithyridinae Muir-Wood 1965
Genus	*Sellithyris* Middlemiss 1959
Species	*Sellithyris subsella* (Leymerie 1846)

3.1. Previous research

1846 *Terebratula subsella* Leymerie: 249; pl. 10, fig. 5
1862 *Terebratula suprajurensis* Thurmann; Thurmann & Etallon: 283, pl. 41, figs. 1d–f (1a–c?)
pars 1867 *Terebratula suprajurensis* Et.; Moesch: 189, 200
1868/71 *Terebratula* cfr. *bisuffarcinata* Schlotheim; Quenstedt: 397, pl. 49, fig. 37
1869 *Terebratula suprajurensis* Th. (syn. *T. subsella* Sow.); Jaccard: 193, 199
1870 *Terebratula suprajurensis* Th.; Greppin: 99
1871 *Terebratula subsella* Leymerie; Struckmann: 217, 219, 221, 229
1872 *Terebratula subsella* Leymerie; De Loriol et al.: 412; pl. 25, figs. 2–20
1874 *Terebratula subsella* Leymerie; De Loriol & Pellat: 236, pl. 25, figs. 17–18
1874 *Terebratula subsella* Leym.; Brauns: 371–372
1875 *Terebratula subsella* Leymerie; Douvillé: 124
1875 *Terebratula subsella* Leym.; Douvillé: 124
non? 1878 *Terebratula subsella* Leymerie; De Loriol: 170–171; pl. 23, figs. 13–15
1878 *Terebratula subsella* Leymerie; Davidson: 148–149, pl. 19, figs. 10–12
1881 *Terebratula subsella* Leymerie; De Loriol: 105–106; pl. 14, figs. 21–22
1886 *Terebratula suprajurensis* (Thurmann) Etallon; Douvillé: 87
1886 *Terebratula subsella* Leymerie; Douvillé: 86–87
1893 *Terebratula subsella* Leymerie; Haas: 137–138, pl. 21, figs. 1–5, 9–17
1893 *Terebratula subsella* var. *suprajurensis* Thurmann; Haas: 138, pl. 21, figs. 6–8
1893 *Terebratula subsella* Leymerie; Siemiradzki: 138
1905 *Terebratula subsella* Leym.; Schmidt: 143–144, pl. 2, figs. 5–10
1918 *Terebratula subsella* Leymerie; Rollier: 237
1918 *Terebratula suprajurensis* (Thurm.) Etallon; Rollier: 238
1964 *Loboidothyris subsella* (Leymerie); Makridin: 221–223; pl. 13, figs. 5–6
1965 *Epithyris subsella* (Leymerie); Barczyk: 276; pl. 33, figs. 1, 4
1969 *Sellithyris subsella* (Leymerie); Barczyk: 51–52; pl. 10, figs. 4–7, textfigs. 53–54
1970 "*Terebratula*" *subsella* Leymerie; Westphal: 58
1983 *Habrobrochus subsella* (Leymerie); Cooper: 87–88; pl. 31, figs. 26–32, pl. 70, figs. 19–20
non 1983 "*Terebratula*" *suprajurensis* Thurmann; Cooper: 161; pl. 41, figs. 8–10, pl. 57, figs. 13–18
1989 "*Terebratula*" *suprajurensis* Thurmann; Meyer: 190
1990 "*Terebratula*" *subsella* Leym.; Alméras et al.: 23
1990 "*Terebratula*" *suprajurensis* Et.; Alméras et al. 23

For completion of the synonymy list see Brauns (1874), Davidson (1878) and Barczyk (1969).

Terebratula subsella Leymerie was erected in 1846 and originally reported from the Paris basin in the French "Département Aube". It is common in many places of central and north-east France and seems to occur since the mid-Oxfordian and throughout the Kimmeridgian.

De Loriol (1878, 1881) devoted several publications to this species and attributed rare and in most cases badly preserved specimens from the *tenuilobatus* Zone ("Badener-Schichten") of Baden and Oberbuchsiten in the Swiss Jura to it. But he expressed also doubts and considered at least some of his specific attributions as tentative. This led him to synonymize *Terebratula suprajurensis* Thurmann (in Thurmann & Etallon 1862) of the northwestern Swiss Jura with *T. subsella.*

T. suprajurensis has been erected for a conspicuous form supplied by a massive beak and a very large pedicle foramen, occurring in the "Zone ptérocérienne" (Kimmeridgian) in the area of Porrentruy/Courgenay. Douvillé (1886) quoted it from the French Jura in the region of La Baume. Figures 1d–f of plate 41 in Thurmann & Etallon (1862) depict the characteristics of this form rather well. Haas (1893) agreed that *T. suprajurensis,* in spite of its characteristics, is related to the "normal" *T. subsella* by numerous transition forms. He pointed to the most obvious aspects of the shell, i.e. the robust, incurved beak of variable thickness and the dominant deep plication at the frontal region, and saved the taxon as a variety of *subsella.* Douvillé (loc. cit.) retained both taxa as species, but clearly based his conclusion on a comparison of the type figures. Rollier (1918) too gave both *T. suprajurensis* and *T. subsella* the status of species. Occurrences of the typical *suprajurensis* are probably restricted to the region around Porrentruy. Occasionally the name was used for the terebratulids of the Solothurn Turtle Limestone. From the present study it becomes evident that the separation of *T. subsella* and *T. suprajurensis* on a species level is not justified. A conception similar to the one of Haas (loc. cit.) is accepted here (see section 3.4).

It seems unlikely that *T. subsella* occurs in the "Argovian" facies of northern Switzerland. The alleged terebratulids from this region may belong to the closely related *Loboidothyris subselloides* Westphal (1970), a species from the Late Jurassic (Weisser Jura γ) in southern Germany. The only confirmed reference of *T. subsella* in the "Rauracian" facies of the northwestern Swiss Jura is Haas (1893), and it is mentioned by several other authors from the Kimmeridgian, e.g. of the "Gorges de l'Areuse" (Schardt & Dubois 1902), the "Vallée de la Brévine" (Rickenbach 1926), the region of "Les Verrières" (Mühlethaler 1932).

Barczyk (1965, 1969) was the first to give a thorough analysis of what he thought to be Leymerie's species. He noted the striking variability of the anterior commissure which ranges from rectimarginate to undulate, biplicate and sulciplicate. Cooper (1983) advocated for the frequent misinterpretation of *T. subsella.* He studied the internal structures by excavation from the matrix and undertook a taxonomical revision of *T. subsella* s.l. He erected two new species which he assigned to new genera: *Terebratula subsella* Leymerie = *Habrobrochus* n.g. *subsella* for the Kimmeridgian of northern Germany and *Terebratula subsella* auct. pars = *Xestosina* n.g. *arguta* n.sp. for the Kimmeridgian of France. For these examinations no topo-

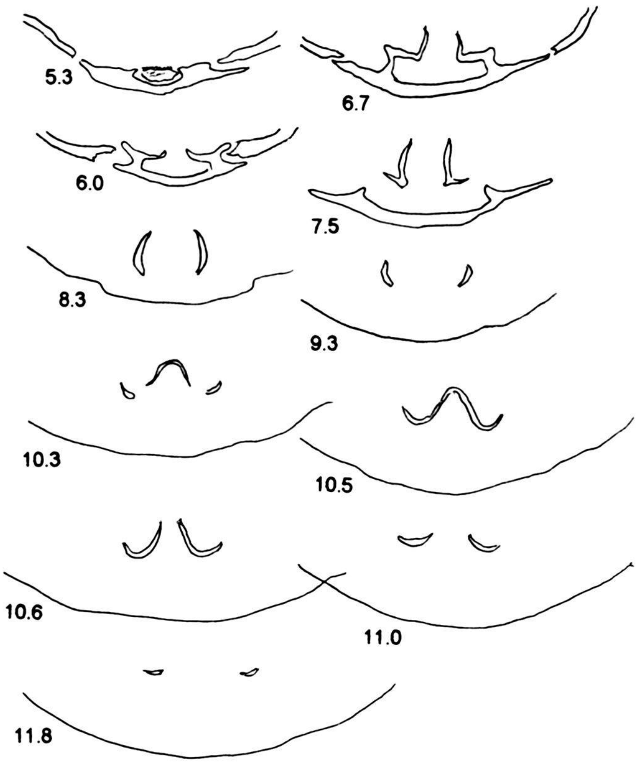

Fig. 12. Transversal sections of *Loboidothyris zieteni* from the Lower Kimmeridgian ("Badener-Schichten"). Numerals represent distances in millimetres from pedicle umbo. Measurements of the specimen: length = 34.9, breadth = 26.0, width = 18.0 mm. 2.5 × nat. size.

type material of Leymerie's species was used. Furthermore, no attempt was made to refer to regional distribution. Alméras et al. (1990), in a proposal for a biostratigraphical scale of the French Jurassic, based on brachiopods, list the following species: *"Terebratula" subsella* Leym./Early Kimmeridgian, *cymodoce* Zone p.p – *"Terebratula" suprajurensis* Et./Early Kimmeridgian, upper *cymodoce* Zone and basal *mutabilis* Zone – *"Terebratula"* gr. *subselloides* (Westphal)/Late Kimmeridgian, *mutabilis* Zone p.p. – *Xestosina arguta* Cooper/ Late Kimmeridgian, *eudoxus* Zone.

3.2. Terebratulids related to *"Terebratula" subsella*

The brachiopods which may be placed in the *subsella*-group are part of a larger group which was named earlier the "biplicates". This in allusion to the shape of the shell which shows near the front region two more or less pronounced folds on the dorsal valve. *"Terebratula bisuffarcinata"* and *"Terebratula bicanaliculata"*, both established by Schlotheim 1820 for Kimmeridgian biplicates, were used in a broad sense for different species and these taxa are now regarded as obsolete. The Jurassic biplicates are generally regarded to be the ancestors of *Sellithyris*, *Loriolithyris* and other genera of the Early Cretaceous.

Subsella-like terebratulids are reported from Middle Oxfordian sediments, but the main characteristics are not developed before the Kimmeridgian stage. *Loboidothyris subselloides* Westphal from the Swabian Jura, already mentioned above, has the same rounded, weakly biconvex shell like *T. subsella*, the beak, however, is less massive and the anterior sulciplication wider. The length of the internal loop extends only to one third of the dorsal valve, whereas in *subsella* it reaches midvalve, as shown in the present study. The loop length is probably the best character to differentiate between both species.

Terebratula gagnebini Etallon 1862 occurs in the upper part of Late Kimmeridgian ("Marnes virguliennes") in the region of Porrentruy. Little is known about this rare form which is small, rather thick, pentagonal in outline, biplicate and supplied by a robust beak. It may represent a late offshoot of *T. subsella*.

Loboidothyris zieteni (De Loriol 1878) [*Terebratula ulmensis* Rollier 1918 is a synonym] appears at the Early Kimmeridgian ("Badener-Schichten"). It is known from the "Argovian" facies and is especially frequent in northern Switzerland. Its occurrence in the western Swiss and French Jura is not confirmed. It is clearly distinguishable from *T. subsella* by the interior structures. In L. *zieteni* the transverse band is rounded and the distal ends of the brachidium do not reach midvalve (Fig. 12).

A very similar form, named *Terebratula engeli* by Rollier (1918), from the French Late Oxfordian is either regarded a synonym of *L. zieteni* or a stratigraphically somewhat earlier form (Westphal 1970, Boullier 1976).

Sellithyris pseudosella Barczyk 1969 from the Late Oxfordian and Early Kimmeridgian of the Holy Cross Mountains in Poland shows a considerable similarity to *T. subsella*. It differs from the former by the position of the maximal breadth which is nearer to the anterior commissure and by having a substraight lateral commissure.

3.3. Generic assignment of *"Terebratula" subsella*

Epithyris, *Postepithyris*, *Loboidothyris*, *Sellithyris* and *Loriolithyris* are some of the more traditional genera which are possible candidates for the placement of *Terebratula subsella*. They have in common that their diagnoses are limited to some general features which enables a reasonable grouping and assignment of species without narrowing other characters which determine the specific level.

Epithyris Phillips (1841) was used for *T. subsella* by Barczyk in his publication 1965. This genus was based on *Terebratula maxillata* J. de C. Sowerby of Bathonian age. Its anterior commissure is variable, changing from plane to bi- and quadriplicate. Internally, the convex hinge plates are distinctly different from *T. subsella*.

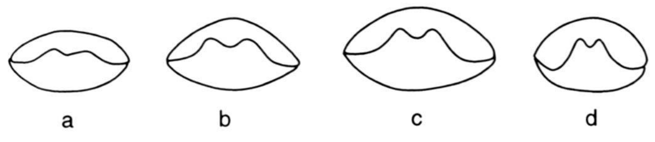

Fig. 13. Variable shapes of biplicate anterior commissure in the genus *Sellithyris*. a–c: *Sellithyris subsella*. a: smooth sulciplication in var. A; b: moderate sulciplication in var. B; c: marked sulciplication tending to episulcation in var. C. d: *Sellithyris sella*. Episulcation in specimen from the Barremian ("Drusberg-Schichten") of Chöpfenberg, Kanton Schwyz, Switzerland.

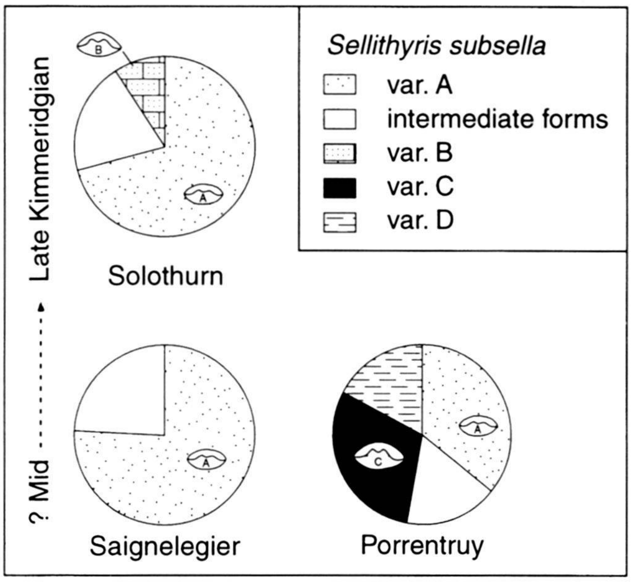

Fig. 14. Pie-diagrams of the sampled localities showing the percentage of the different variations of *Sellithyris subsella*.

Postepithyris Makridin (1960), based on the Oxfordian *Terebratula cincta* Cotteau from the Paris basin, but defined on a Russian specimen of questionable identity, was thoroughly revised by Boullier (1981). It resembles much *Epithyris* in outline, beak and type of plication. With respect to internal morphology both genera have in common a conspicuous cardinal process (which is flat and short in *T. subsella*), the convex hinge plates and pronounced convergent crura towards the center of the shell.

The internal characters of *Loboidothyris* Buckman (1918) were redefined by Westphal (1970) when he placed different Late Jurassic species in this genus. The massive and short umbo, the large and labiate pedicle opening, the flattened beak ridges, the hidden symphytium match well with *T. subsella*. On the other hand, the loop length reaches typically 30% of the dorsal valve length (in *T. subsella* it is 50%). A tendency of plication at the anterior commissure may be present but never becomes dominant as in *T. subsella*.

Sellithyris Middlemiss (1959), used by Barczyk for *T. subsella* in his publication 1969, is normally used for Cretaceous terebratulids. The biplication is one of the constant characters of this genus. But the development of the median sulcus, the changing characteristics of biplication, the apical angle, the globosity of the shell, the aspect of the lateral "wings" may change with regard to the species which Middlemiss placed in this genus. The most important internal structures, such as the concave hinge plates, the small bilobate cardinal processes, the narrow lamellae of the loop, the position of the rounded transverse band are quite consistent with the corresponding features, seen in *T. subsella*.

Loriolithyris Middlemiss (1968) is very similar to *Sellithyris* and might be taken as a subgenus of the latter. Main discriminating character are the thin, concave and very regularly bowed hinge plates in form of small dishes.

Moeschia Boullier (1976) is similar in external morphology to *Loboidothyris*. Taking into account the strictly defined characters of the internal structures, it is difficult to see which degree of flexibility is left for a possible attribution of further species to this genus. A similar situation exists for *Habrobrochus* and *Xestosina*, both created by Cooper (1983), when he separated the species which he thought were hidden in *T. subsella* auctt. The numerical loop data, measured at a single or a few specimens only, are difficult to interpret for a possible extension of that genus.

We decide to place *T. subsella* in *Sellithyris* which in our opinion offers an appropriate home for this species. The internal structures of *Sellithyris sella* (J. de C. Sow.), the type species of *Sellithyris*, allow readily the addition of *subsella* to that genus. Both species are distinctly different in the M-shaped anterior commissure, i.e. in the development of the two anterior folds. The narrowing of the folds, the depth of the median depression and the sulci on both sides of the folds are distinctive. In other words, *S. sella* has a pronounced episulcate anterior commissure, whereas in the sulciplicate *S. subsella* lateral depressions are hardly recognizable (Fig. 13). With the assignment of the Late Jurassic *T. subsella* to *Sellithyris*, at least one of the presumed link between the Jurassic and Cretaceous biplicate terebratulids may be indicated.

3.4 Comparison of var. A, B, C and D of *Sellithyris subsella*

At the beginning of the Kimmeridgian stage brachiopods, especially the terebratulids, were generally becoming less diversified, but remained abundant and showed much variability in discrete areas. This is probably due to environmental factors. Valuable diagnostic features for establishing well-defined species are rare. The development of the brachiopod fauna during this time seems to be influenced to a great part by an increasing provincialism (Alméras et al. 1990).

The sampled brachiopods from the localities Saignelégier, Porrentruy and Solothurn were analyzed and compared. There is no doubt that they all belong to a group of closely related

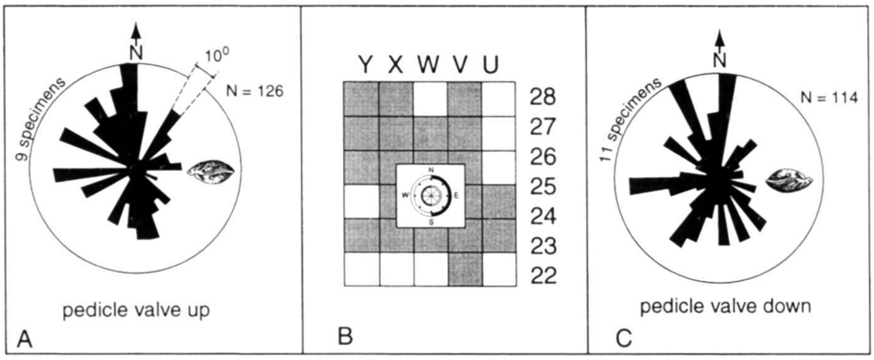

Fig. 15. Rose diagrams of *Sellithyris subsella* from St. Niklaus (Solothurn). A displays terebratulids with the pedicle valve up. B shows the measured surface (1 m grid) and C displays the orientation of terebratulids with the pedicle valve down.

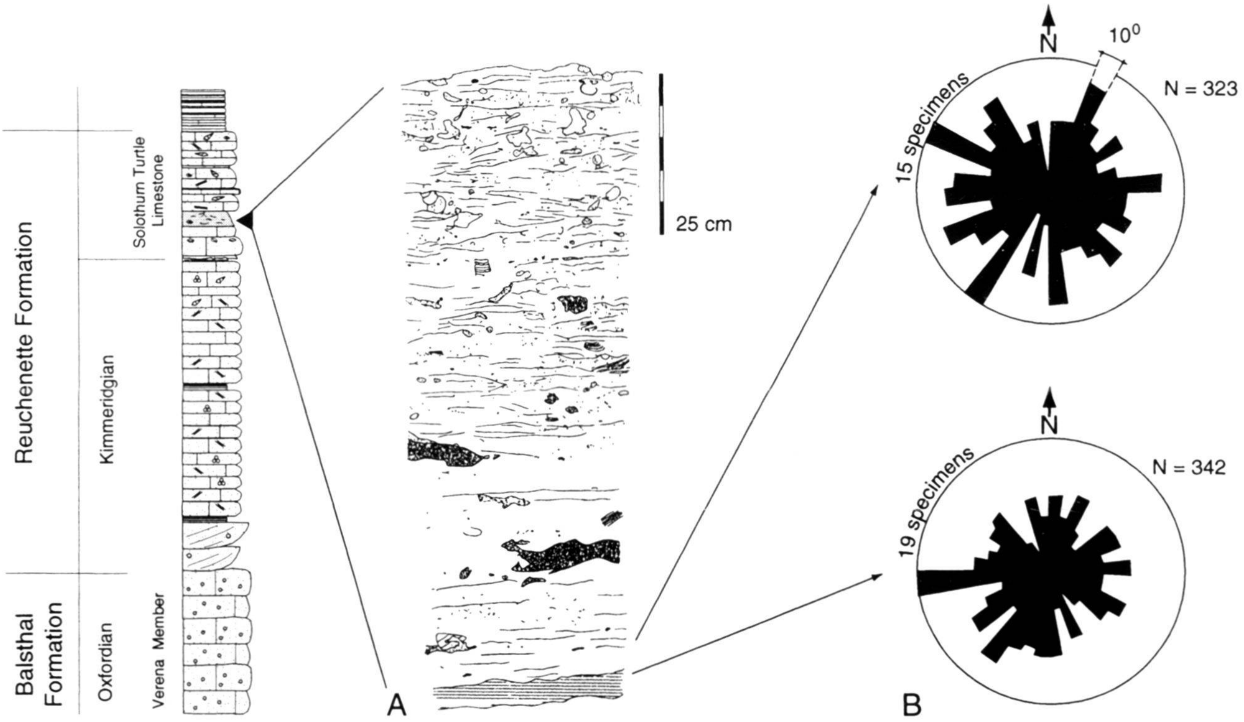

Fig. 16. Overall section of the Late Jurassic Reuchenette Formation near St. Niklaus (Solothurn). A shows polished section of the sampled horizon. B display rose-diagrams of measured specimens of *Sellithyris subsella*.

terebratulids for which *Sellithyris subsella* (Leymerie) claims priority. Several authors had tried to redefine *S. subsella* s.s. and to separate it from the bulk of similar Kimmeridgian terebratulids that were erroneously summarized under this name (e.g. Douvillé 1886, Haas 1893, Cooper 1983). Apart from this pretentious task which certainly has not been accomplished yet, *S. subsella* is a widespread brachiopod in many parts of Europe. Outside of France it has been reported from Switzerland, southern England, northern Germany, Poland and Russia.

When the specimens of Saignelégier, Porrentruy and Solothurn are compared it becomes evident that it is not possible to discriminate the respective forms in a way that would allow a specific or subspecific splitting. The articulation apparatus, the hinge teeth and hinge plates, the features of the crura and the brachidium show only few and, as we think, negligible differences in the sectioned specimens. Otherwise the shell morphology presents a pronounced polymorphism, as described in section 2.2.

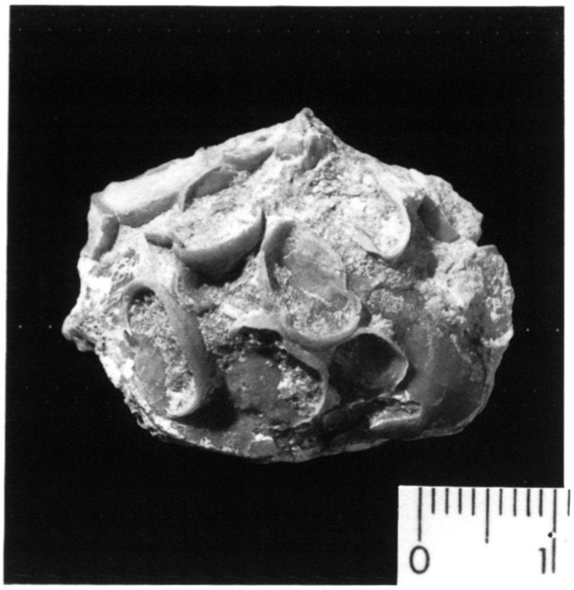

Fig. 17. Oysters (*Nanogyra* sp.) encrusting *Sellithyris* in the Solothurn Turtle Limestone (Photo by A. Werthemann, Bern).

No topotype material of this species was studied. But comparing descriptions and figures from many publications, we assume that the stock of Saignelégier represents well *S. subsella* as originally intended. The designation of a lectotype is open, but would have to go back to Leymerie. This is of little palaeontological value in view of the extreme morphological variability of this species, unless it is supplemented by a series of paratypes.

The shell outline shows transitions from subpentagonal to oval and subcircular, the shape of lateral profile and the type of plication are used to discriminate the four variations in each of the sampled locality, as proposed in this study. Forms with "mixed" characters are retained as intermediates (Fig. 11).

Sellithyris subsella var. A, with a shell length of 20–30 mm, is homogenous with regard to the neat beak, the circular, gently rimmed foramen, the weak sulciplication, the narrow low folds and the very shallow (if at all) median depression. It represents the bulk of the specimens sampled in Saignelégier and Solothurn, and it is abundant in Porrentruy.

Var. B, with a shell length exceeding 30 mm, shows long and thin individuals, whose valves are flat-biconvex. The beak is moderately massive, with a rimmed foramen, circular or oval, up to 3 mm in diameter. This variations is known from Solothurn only.

Var. C (= *suprajurensis*) are large individuals of 30–45 mm shell length, found only in Porrentruy. They are distinctly subpentagonal and present a regularly curved ventral valve, whereas the dorsal valve is essentially flat. A sharp subparallel plication, producing a pronounced sulciplication at the anterior commissure, the massive beak and the large, conspicuously rimmed and labiate, mostly circular foramen are further criteria for the identification of this variation.

Fig. 18. Signs of bite marks in specimens of *Sellithyris subsella* var. B from Solothurn. Natural size. PIMUZ Nr. 019677.

Var. D is thick with a reduced pentagonal, rounded outline, and transversal section. The other characteristics of both var. C and var. D are the same. Like var. C its occurrence is restricted to Porrentruy.

The relative abundance of the four variations at the sampled localities can be seen from Figure 14.

4. Taphonomy

The examined brachiopods all belong to *Sellithyris subsella* (Leymerie), and there are no obvious differences that would justify the creation of a new species. Nevertheless, intraspecific variations can be observed, based on the overall shell morphology. *Sellithyris subsella* var. C (= *suprajurensis*) grew to a conspicuous, stout form of considerable dimensions. The Banné-Marls near Porrentruy have yielded the largest individuals, among those might even be gerontic specimens. These soft bottoms contain infaunal bivalves (*Gresslya* sp.), epibenthic pectinids (*Camptonectes* sp., *Velata* sp.), small bioherms of oysters, strombid gastropods (*Harpagodes* sp.), sea urchins, remains of pycnodontid fishes, marine turtles and crocodiles.

A very similar fauna has been found in the Solothurn Turtle Limestone. Within that limestone succession, we find the less developed *Sellithyris subsella* var. B. It is a thin, somewhat wretched form. This terebratulid occurs in dense clusters of up to 100 specimens near the base of the observed horizon (see Fig. 15). On the same surface, several hemicidarid sea urchins with their spines still attached and completely preserved astropectinid starfishes have been found. This indicates rapid burial (Meyer 1988). For 905 specimens of *Sellithyris* directional data are available, measured at different intervals within the main fossil bearing unit. The rose-diagrams show no orientation maxima, regardless of their respective position within the sediment (Fig. 16). This and the above observation clearly indicate an *in situ* preservation of the brachiopods. Few specimens show encrusting oysters (*Nanogyra* sp.) which indicate a prolonged exposure at the sediment-water interface (Fig. 17). Furthermore, some of the specimens of var. B show signs of predation. The presence of bite scars and marks around the anterior flat part suggests a preferred attack site (Fig. 18). Possible predators include pycnodontid fishes (*Proscinetes* etc., for more details see Müller 1995), hybodontid sharks or occasional hazards by the mesosuchian crocodile *Machimosaurus hugii* whose preferred diet included marine turtles (Meyer 1989, 1994).

Deformed or cracked parts on both sides of the ventral beak of the terebratulids may document the pressure on the less firm dorsal valve which transmitted these forces by an intact articulation of the shell to the hinge area. Finally, the changing form of the pedicle opening (round and oval) may be a consequence of such violations.

Most of the brachiopods are confined to the lower third of the bed. In this context it is interesting to mention that the upper two thirds show an increasing proportion of sea urchins whereas the density of semi-infaunal strombid gastropods and also terebratulids decrease. Meyer (1994) concluded that this is in fact due to an increase in algal growth resulting from the input of nutrient rich waters.

5. Conclusions

Sellithyris subsella var. A seems to be the smallest and least specialized form and is the stock for further developments as seen in var. B or var. C. More generally speaking, shell size and shape of the observed terebratulids indicate different ecophaenotypes.

The pie diagrams (Fig. 14) of all three localities show that only two of the observed forms are restricted to a specific part of the Late Jurassic (var. C & D). All others have a much wider range. This suggests that those terebratulid brachiopods are clearly facies-dependent and should not be used for stratigraphic correlation, although some attempts have been made in the Jurassic of adjacent France (Debrand-Passard 1984). Apparently *Sellithyris subsella* was also vital enough to reproduce its stock into Cretaceous time. The chosen genus name implies the relation of *S. subsella* with morphologically similar, stratigraphically younger terebratulids which extend into the Cretaceous. *Sellithyris sella* has a pronounced episulcate anterior commissure, in contrast to *S. subsella* with a variable sulciplicate type (Fig. 13). It is just speculative arguing whether the transition from sulciplication to episulcation on this generic level may have a phylogenetic significance.

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