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Lower Cretaceous Terebratulidae of the Jura region

1. REVISION OF SOME SPECIES DESCRIBED BY PICTET AND DE LORIO (1872)

By FRANK A. MIDDLEMISS¹⁾

ZUSAMMENFASSUNG

Es werden 17 Arten von PICTET & DE LORIO revidiert. Ihre innere Struktur wurde mit Hilfe von Serieschnitten untersucht und für diejenigen Arten abgebildet, deren innere Struktur nicht bereits früher beschrieben worden ist. Die Arten werden den Gattungen *Sellithyris*, *Loriolithyris*, *Musculina*, *Costithyris* und *Collinithyris* zugeordnet, deren zwei letzte neu sind. Die geographische und stratigraphische Verbreitung aller Arten wurde genau studiert. Alle Arten sind Teil einer Fauna, die zwischen tethyschem und borealem Bereich liegt.

ABSTRACT

Seventeen of PICTET & DE LORIO's species are revised. Their internal structure has been examined by means of serial sections, which are figured for those species whose internal structures have not previously been described. The species are referred to the genera *Sellithyris*, *Loriolithyris*, *Musculina*, *Costithyris* and *Collinithyris*, of which the last two are new. The geographical and stratigraphical distributions of all the species have been restudied in detail. They are shown to form part of a fauna situated intermediately between the Tethyan and Boreal realms.

Introduction

During the third quarter of the nineteenth century a model of objective and accurate description and of judicious classification of Cretaceous brachiopods was provided by Swiss workers in the series of publication grouped together as "Matériaux pour la Paléontologie Suisse". The crown of this work was PICTET's "Description des fossiles du terrain crétacé des environs de Sainte-Croix", in which the authoritative study of the Jura brachiopods was written last and finished by DE LORIO (1872).

Revision of this work has long been needed and I was pleased to be afforded the opportunity of revising the terebratulid part of the fauna when invited in 1977 to take part in the Swiss Hauterivian project. As few of the species are confined to the Hauterivian it seemed the most reasonable policy to undertake a review of the whole Lower Cretaceous fauna of the Jura region and the present contribution embodies the first part of the results.

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The descriptions published by PICTET & DE LORIO are so perceptive that in most cases nothing needs to be added or altered as regards the external characters of the species. In these cases all that was needed was an investigation of the internal skeletal structures leading to assignment of the species to modern genera, and a reassessment of the geographical and stratigraphical distribution. The present contribution therefore is confined to those species which required such minimum revision; description of new species, and also detailed consideration of the Aptian fauna, are deferred until later.

Systematic palaeontology

Note. – Numbers of specimens given under the heading “material” refer only to those from the Jura region which I have examined.

Phylum **Brachiopoda** DUMERIL 1806

Class **Articulata** HUXLEY 1869

Order **Terebratulida** WAAGEN 1883

Suborder **Terebratulidina** WAAGEN 1883

Superfamily **Terebratulacea** GRAY 1840

Family **Terebratulidae** GRAY 1840

Of the species dealt with in this article, PICTET included the following in his “subgenus *Terebratula*”: *carteroniana*, *campichei*, *essertensis*, *valdensis*, *latifrons*, *russillensis*, *germaini*, *acuta* (= *sanctaecrucis*), *sella*, *sueuri*. DE LORIO suggested that the last might prove to belong in *Waldheimia*.

The species *montmollini* and *collinaria* were included, although doubtfully, in the section *Waldheimia* s.s. of the “subgenus *Waldheimia*”, implying that they were considered “long-looped” species, or in modern terminology, members of the Terebratellidina. The species *semistriata*, *marcousana*, *ebrodunensis*, *cruciana* and *etalloni* were included in the section *Eudesia* of the “subgenus *Waldheimia*”, because of confusion with the external appearance of the true *Eudesia*. All these seven species are here shown to be terebratulids.

On the contrary, “*Terebratula*” *villersensis* DE LORIO and “*Terebratula*” *aubersonensis* PICTET have been investigated in the course of this revision and proved to be terebratellidines.

Subfamily **Sellithyridinae** MUIR-WOOD 1965

Genus *Costithyris* nov. gen.

Type species: Terebratula semistriata DEFRANCE 1828.

Name. – Latin “costa” – a rib.

Diagnosis. – Sellithyridinae with ribbed shells. Shell subcircular to oval in ventral profile, with 8–30 or more radiating ribs, either simple or increasing by bifurcation. Umbo suberect; beak ridges rounded; foramen mesothyrid, may be attrite. Anterior commissure rectimarginate to episulcate, superimposed upon multiplication. Hinge plates concave, becoming cuneate, not sharply differentiated from inner socket ridges. Crural processes slightly inclined towards midline, not flanged. Loop lamellae narrow and thin. Transverse band high-arched and slightly trapezoidal. Euseptoidum present but small; dorsal adductor scars may be flanked by faint euseptoidum-like ridges.

Remarks. – As in *Loriolithyris* the transverse band is delicate and rarely preserved; I have seen it only in *C. semistriata*.

The close relationship of the four species here included is implicitly recognized in PICTET's descriptions but he and DE LORIOI regarded them as long-looped, including them in their “Groupe *Eudesia*”, a subdivision of *Waldheimia*, itself treated as a subgenus of *Terebratula*. Most authors during the last hundred years have followed PICTET in referring to these species, and particularly *semistriata*, as *Eudesia* (e.g. BAUMBERGER 1903–10, FREI 1925, SCHARDT 1900, SCHARDT & DUBOIS 1903) and the Marnes d'Uttins at Chamblon have been called by SCHARDT and subsequent authors the “Marnes a *Eudesia semistriata*”. *Costithyris* and the Jurassic genus *Eudesia* are indeed remarkably similar in external appearance and present an excellent example of external homoeomorphy, except that *Costithyris* lacks the sharp beak ridges of *Eudesia*. A glance at the internal structures shows immediately, however, that *Eudesia* is a member of the Terebratellidina, *Costithyris* of the Terebratulidina. BOGDANOVA & LOBACHEVA (1966) figured as *Eudesia semistriata* (DEFRANCE) a form from the Neocomian of the Kopet Daga which is clearly a terebratellidine. The same species was later assigned to a new genus *Glosseudesia* by LOBACHEVA (1974). This is certainly not *semistriata* DEFRANCE but an unnamed species which perhaps demonstrates the survival of the *Eudesia* group in the Cretaceous. SMIRNOVA (1972) figured a specimen from the Albion of Turkmenistan as *Eudesia tekedgikensis* which has the external appearance of a true *Eudesia* and may provide evidence of the survival of the genus into the Middle Cretaceous.

Costithyris is referred to the Sellithyridinae because of the close similarity of the internal structures to those of *Sellithyris*. This is especially seen in the initially concave hinge plates, becoming less concave and becoming cuneate at an early stage: the characteristically pear-shaped anterior extensions of the hinge plates supporting the free crural bases (Fig. 1, 5.2; Fig. 3, 6.4): the thin delicate descending lamellae of the loop: the euseptoidum-like ridges laterally bounding the dorsal adductor scars. On the evidence of internal structures alone the species would be assigned to *Sellithyris*, the only important difference being the relative lack of differentiation between their hinge plates and their inner socket ridges. Even in external appearance some of the acutely episulcate forms of *C. semistriata* from the Paris Basin, in which ribbing is confined to the anterior part of the shell, almost grade into *S. sella*. However, the constant presence of longitudinal ribbing makes generic separation necessary.

Detailed structure of the hinge plates and attached crural bases suggests the presence of two groups of species, *C. ebrodunensis* being more closely related to *C. semistriata* and *C. cruciana* to *C. marcoussana*.

Species included. – *T. semistriata* DEFRANCE, *T. marcoussana* D'ORBIGNY, *T. ebrodunensis* DE LORIOL, *T. cruciana* PICTET.

Range of the genus. – Valanginian to Barremian.

Costithyris semistriata (DEFRANCE 1828)

Fig. 1

- + 1828 *Terebratula semistriata* DEFRANCE, p. 156.
- 1839 *Terebratula suborbicularis* D'ARCHIAC, p. 311.
- 1842 *Terebratula suborbicularis* D'ARCHIAC; LEYMERIE, p. 11, Pl. 14, Fig. 2a–c.
- 1842 *Terebratula suborbicularis* D'ARCH. var. *longirostris* LEYMERIE, p. 18, Pl. 14, Fig. 3.
- 1842 *Terebratula biangularis* DESHAYES; LEYMERIE, p. 11, Pl. 14, Fig. 4a–c.
- V 1849 *Terebratula semistriata* DEFRANCE; D'ORBIGNY, p. 83, Pl. 508, Fig. 1–10.
- 1861 *Terebratula semistriata* DEFRANCE; DE LORIOL, p. 122, Pl. 15, Fig. 18.
- 1871 *Terebratula suborbicularis* D'ARCHIAC; QUENSTEDT, p. 298, Pl. 45, Fig. 78–80.
- V 1872 *Terebratula* (*Waldheimia*, Section *Eudesia*) *semistriata* DEFRANCE; PICTET & DE LORIOL, p. 110, Pl. 206, Fig. 1–5.
- NON 1966 “*Eudesia*” *semistriata* (DEFRANCE): BOGDANOVA & LOBACHEVA, p. 68, Pl. 6, Fig. 4–7.
- NON 1974 *Glosseudesia semistriata* (DEFRANCE); LOBACHEVA, p. 147.

Neotype. – Specimen 1942-1/1627/1 in the Muséum National d'Histoire Naturelle, Paris (Coll. M. Lallier, 1840), from the Neocomian of Auxerre.

DEFRANCE's establishment of this species (1828) was not accompanied by a figure or designation of type series of specimens. D'ORBIGNY (1849) makes no reference to DEFRANCE's type specimens and no specimens have been preserved in Paris as those which DEFRANCE used. According to Miss Y. Gayrard (in litt., December 1980) the type material was formerly kept at Caen and was destroyed in 1944 during the war. The specimen chosen as Neotype is from one of the localities named by DEFRANCE and agrees well with his brief description. It agrees well with D'ORBIGNY's Plate 508, Figure 4, as regards the character of the ribbing, the smooth area around both beaks, the slight biplication and the characters of the umbo and foramen. It possesses also the characters regarded by PICTET & DE LORIOL (p. 111) as normal for the species.

Dimensions of Neotype. – L. 25, W. 24, T. 14.

Material. – About 70 specimens from the Upper Hauterivian of Chamblon (Vaud), Le Landeron (Neuchâtel) and Longeville (Doubs).

External morphology. – The external morphology of this species was adequately described and diagnosed by PICTET & DE LORIOL.

Internal structures. – The hinge plates become flatter anteriorly; the attached crural bases are well-developed.

Remarks. – Episulcation can be well-developed, especially among specimens from the Paris Basin. This led DESHAYES (in LEYMERIE 1842) to recognize a “var. *biangularis*” for the acutely episulcate forms at Auxerre. LEYMERIE (1842) also

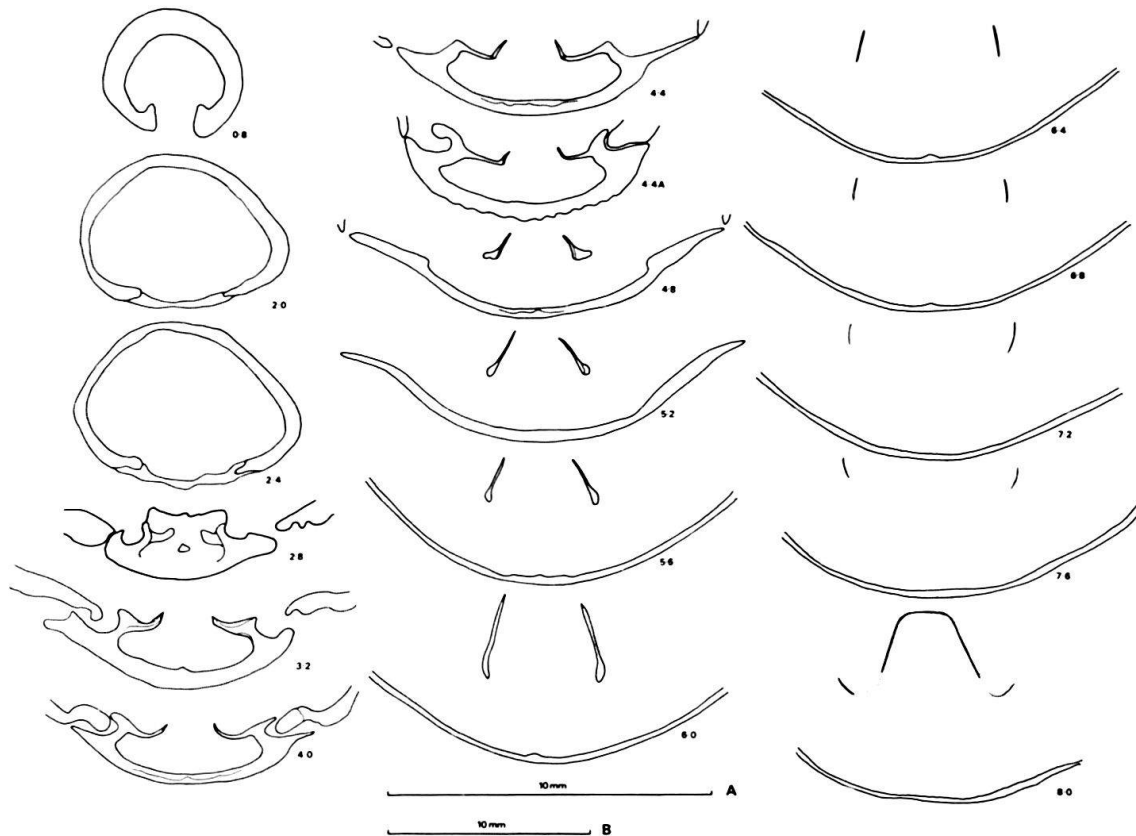


Fig. 1. Serial sections through *Costithyris semistriata* (DEFRANCE). The wide symphytium is seen at 2.0 and 2.4. 2.8 shows the initially concave hinge plates enclosed in the cardinal process. Crural bases first appear at 3.2. Maximum height of the crural processes is at 6.0. The thin, wide descending lamellae of the loop are seen at 7.2 and 7.6, the high arched transverse band at 8.0. Sections 2.8 and 3.2 are enlarged with respect to the other sections. 604/2/1, Neuchâtel Coll., Upper Hauterivian, Chamblon, Vaud, except 4.4A which is from BN 1, Besançon Coll., Hauterivian, Longeville, Doubs. Dimensions of specimens: 604/2/1: L. 21, W. 20, T. 11; BN 1: L. 20.25, W. 17.25, T. 12.5. A = scale for sections 2.8 and 3.2. B = scale for the remaining sections.

recognized a “var. *longirostris*” at Auxerre – an elongate form characterized specially by elongate umbo and symphytium.

Distribution. – Valanginian of the Belley region (Ain) (Geneva Museum, Richard Coll.). Hauterivian and Barremian of Vaud, Neuchâtel, Doubs and Jura. Hauterivian of Salève. Hauterivian of Aube, Yonne, Haute Marne and Meuse.

The species is entirely confined to the Jura region and the southeast Paris Basin.

Costithyris ebrodunensis (DE LORIO 1864)

Fig. 2

- Terebratula ebrodunensis* Agassiz, M.S. name, Neuchâtel Museum.
 PARS 1849 *Terebratula semistriata* DEFRANCE; D'ORBIGNY, p. 83.
 1859 *Rhynchonella ebrodunensis* AGASSIZ; DESOR & GRESSLY, p. 31 (*nomen nudum*).
 + 1864 *Terebratula ebrodunensis* AGASSIZ; DE LORIO, p. 444, Fig. 1-6 of plate.
 1872 *Terebratula* (*Waldheimia*, section *Eudesia*) *ebrodunensis* AGASSIZ; PICTET & DE LORIO, p. 115, Pl. 206, Fig. 11-16.

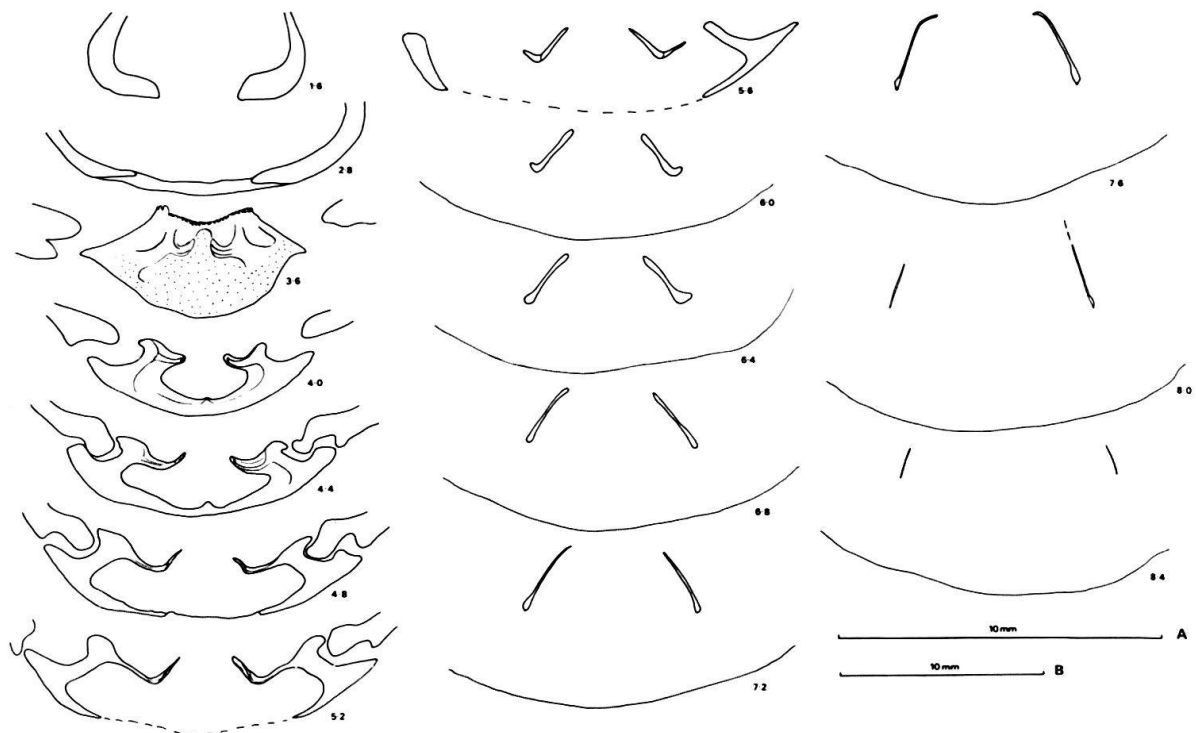


Fig. 2. Serial sections through *Costithyris ebrodunensis* (DE LORIO). The wide symphytium is seen at 2.8, the initially concave hinge plates enclosed in the cardinal process at 3.6. Crural bases first appear at 4.0. Maximum height of the crural processes is at 7.6. The transverse band was not preserved in this specimen. Section 3.6 is enlarged with respect to the other sections; stipple in the section represents punctate skeletal tissue. 27/2D/3. Neuchâtel Coll., Barremian, La Russille. Dimensions of specimen: L. 27, W. 26.5, T. 14. A = scale for section 3.6. B = scale for the remaining sections.

Lectotype (here chosen). – The specimen figured by PICTET & DE LORIO 1872, as Plate 206, Figure 11. The specimen is in the Muséum d'Histoire Naturelle at Geneva.

The ideal lectotype would have been the specimen bearing Agassiz's M.S. label. The existence of this specimen in the Neuchâtel Museum was known to D'ORBIGNY (1849, p. 83) and to DESOR & GRESSLY (1859, p. 31), as well as to DE LORIO (1864) and PICTET & DE LORIO, but it now seems to be lost (Remane, in litt., 1980). DE LORIO gives no localities for his figured specimens of 1864 and Favre, in his manuscript card index at Geneva, does not mention them; neither have they been found at Lausanne. PICTET & LORIO's figured specimens of 1872 are therefore the earliest well-documented examples of the species.

Material. – 23 specimens from the "Lower Urgonian" of La Russille.

Internal structures. – As in *C. semistriata*, the hinge plates become flatter anteriorly and even slightly resupinate, and the attached crural bases are high and well-developed.

Distribution. – Confined to the Barremian of Vaud and Doubs.

Costithyris marcoussana (D'ORBIGNY 1849)

Fig. 3

V + 1849 *Terebratula Marcousana* D'ORBIGNY, p. 82, Pl. 507, Fig. 11–14.

1861 *Terebratula marcousana* D'ORBIGNY; GÜMBEL, p. 563.

V 1872 *Terebratula* (*Waldheimia*, section *Eudesia*) *marcousana* D'ORBIGNY; PICTET & DE LORIO, p. 113, Pl. 206, Fig. 6–10.

Lectotype. – Here chosen. Specimen 5163a/1, Muséum National d'Histoire Naturelle, Paris; from the Neocomian of Nozeroy. This appears to be the specimen figured by D'ORBIGNY as Plate 507, Figures 11–13, although the figure is somewhat idealized.

Dimensions of lectotype. – L. 21.25, W. 17.5, T. 14.5

Paralectotype. – Specimen 5163/1, Muséum National d'Histoire Naturelle, Paris, from the Neocomian of Morteau, which appears to be the specimen figured by D'ORBIGNY as Plate 507, Figure 14.

Material. – 20 specimens from the Hauterivian and “urgonian” of Ste-Croix, Les Verrières and Morteau.

Internal structures. – The hinge plates are more uniformly concave and the attached crural bases are smaller than in *C. semistriata*.

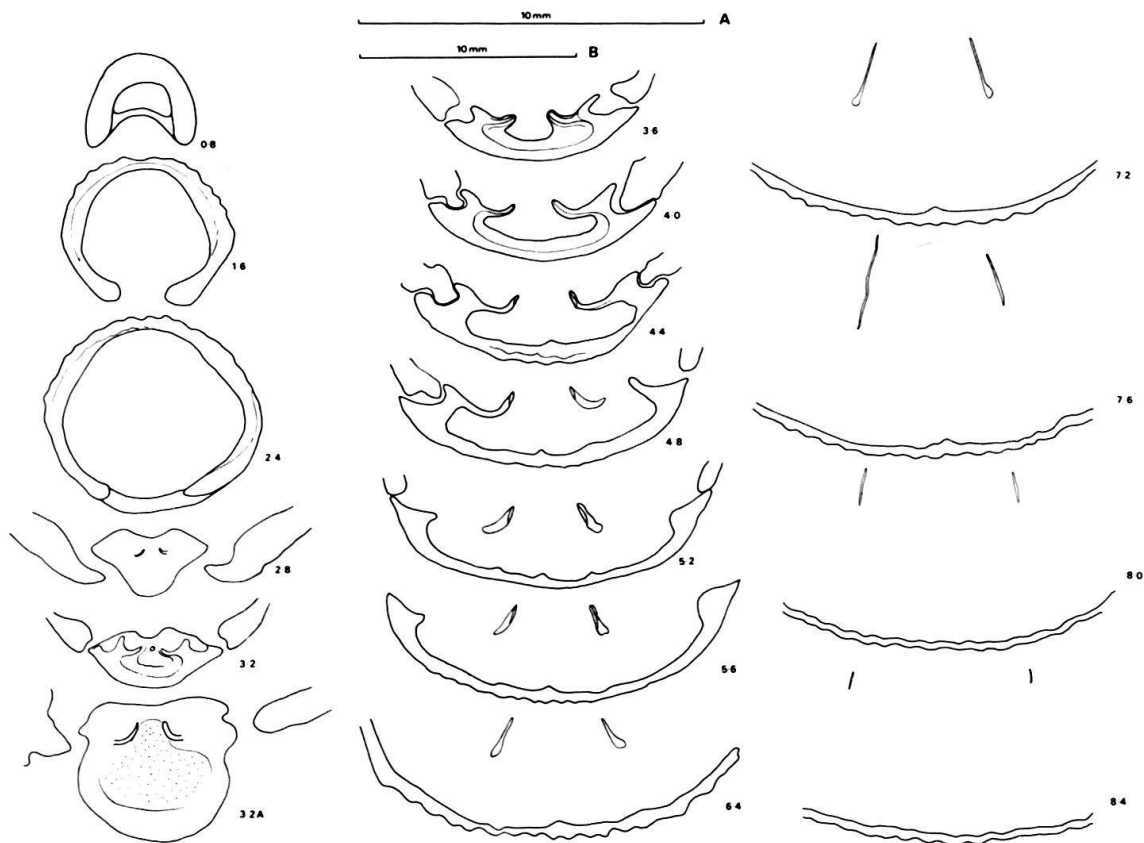


Fig. 3. Serial sections through *Costithyris marcousana* (D'ORBIGNY). Pedicle collar is seen at 0.8 and symphytium at 2.4. The initially concave hinge plates are seen at 2.8, 3.2 and 3.2A. Stipple in 3.2A represents punctate skeletal tissue. Plicate ribbing is first seen at 7.6. The transverse band was not preserved in this specimen. Sections 2.8 and 3.2A are enlarged with respect to the other sections. 49/7G/1, Neuchâtel Coll., Hauterivian, Les Verrières, Neuchâtel, except for 3.2A, which is from 49/9G/2, Hauterivian, Morteau, Doubs. Dimensions of specimens: 49/7G/1: L. 23, W. 18.5, T. 13.5; 49/9G/2: L. 24.75, W. 23, T. 16.25. A = scale for sections 2.8 and 3.2A. B = scale for the remaining sections.

Distribution. – Hauterivian (mainly) and Barremian (rarely) of Vaud, Neuchâtel, Doubs and Jura. D'ORBIGNY (1849) records it from the "lower Neocomian" of Basses Alpes, GÜMBEL (1861) from the "Lower Neocomian" of Betzau (Bavarian Alps).

Costithyris cruciana (Pictet 1872)

Fig. 4

V + 1872 *Terebratula* (*Waldheimia*, section *Eudesia*) *cruciana* PICTET & DE LORIO, p. 117, Pl. 206, Fig. 17–22.

Lectotype (here chosen). – The specimen figured by PICTET & DE LORIO (1872) as Plate 206, Figure 17. The specimen is preserved in the Lausanne Museum on card 16676.

Paralectotypes. – The original of Figure 18 is on the same card as the lectotype. The original of Figure 22 (a very good specimen) is also in the Lausanne Museum (card 21498). The original of Figure 19 is in the Geneva Museum, as is also another specimen claimed to be the original of Figure 22 (neither is numbered).

Material. – 12 specimens from the Hauterivian of Morteau (Doubs).

Internal structures. – The shape of the hinge plates and attached crural bases resemble that of *C. marcoussana* rather than *C. semistriata*.

Distribution. – Hauterivian (mainly) and Barremian (rarely) of Vaud and Doubs. PICTET (1872) records it also from the Upper Valanginian of Ste-Croix. It is entirely confined to the most central part of the Jura.

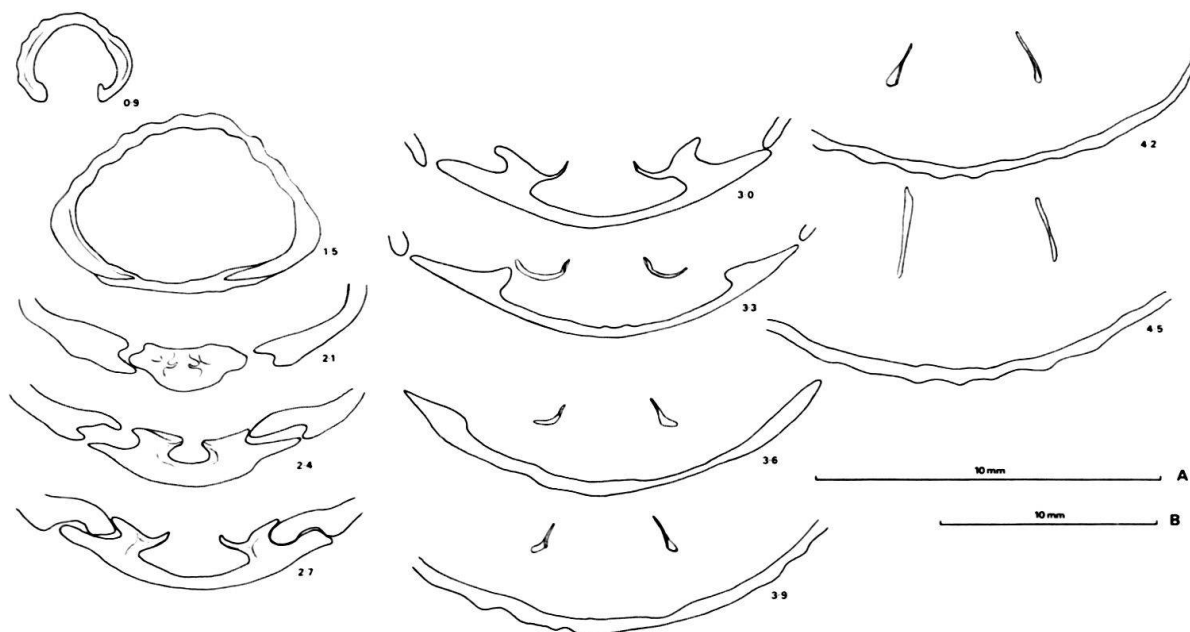


Fig. 4. Serial sections through *Costithyris cruciana* (Pictet). The wide symphytium is seen at 1.5. In the same section the plicate ribbing is first clearly seen; note how irregular it is. The initially concave hinge plates, enclosed in the cardinal process, are seen at 2.1. At 2.7 is the first faint appearance of crural bases. Descending lamellae and transverse band were not preserved in this specimen. Sections 1.5–3.0 are enlarged with respect to the other sections. 27/2D/1, Neuchâtel Coll., Hauterivian, Morteau, Doubs. Dimensions of specimen: L. 16, W. 13.25, T. 8. A = scale for sections 1.5–3.0. B = scale for the remaining sections.

Terebratula etalloni PICTET 1872

V + 1872 *Terebratula* (*Waldheimia*, section *Eudesia*) *Etalloni* PICTET & DE LORIO, p. 118, Pl. 205, Fig. 22.

Holotype. – The specimen figured by PICTET & DE LORIO (1872) as Plate 205, Figure 22; in the Muséum d'Histoire Naturelle at Geneva (unnumbered) (Lower Neocomian of Cinquétral, Jura).

Remarks. – The type specimen is small and apparently juvenile and it is difficult to understand why PICTET regarded it as a separate species.

Genus *Sellithyris* MIDDLEMISS 1959

Type species: *Terebratula sella* J. DE C. SOWERBY 1823.

The most recent diagnosis of this genus was given by MIDDLEMISS (1976).

Sellithyris sella (J. DE C. SOWERBY 1823)

- V + 1823 *Terebratula sella* J. DE C. SOWERBY, p. 53, Pl. 437, Fig. 1.
- 1849 *Terebratula sella* SOW.; D'ORBIGNY, p. 91, Pl. 510, Fig. 6–12.
- V 1855 *Terebratula sella* J. DE C. SOW.; DAVIDSON, p. 59, Pl. 7, Fig. 4–10.
- V 1872 *Terebratula sella* SOW.; PICTET & DE LORIO, p. 78, Pl. 202, Fig. 19.
- V 1959 *Sellithyris sella* (J. DE C. SOWERBY); MIDDLEMISS, p. 113, Pl. 16, Fig. 1–4.
- V 1965 *Sellithyris sella* (J. DE C. SOWERBY); MUIR-WOOD, Fig. 658–2.
- 1966 *Sellithyris sella* (SOWERBY); BOGDANOVA & LOBACHEVA, p. 49, Pl. 4, Fig. 1–4.
- V 1968a *Sellithyris sella* (J. DE C. SOWERBY); MIDDLEMISS, p. 185, Pl. A, Fig. 6 and 7.
- V 1968b *Sellithyris sella* (J. DE C. SOWERBY); MIDDLEMISS, Pl. 1, Fig. 1–11.
- 1968 *Sellithyris sella* (J. DE C. SOW.); DETRE, Pl. 1, Fig. 1–5; Pl. 2, Fig. 1–4; Pl. 3, Fig. 1–3.
- 1972 *Sellithyris sella sella* (SOWERBY); SMIRNOVA, p. 76, Pl. 7, Fig. 1.
- 1975 *Sellithyris sella* (J. DE C. SOWERBY); CALZADA, p. 33, Pl. 6, Fig. 1–5.

Holotype. – BM B61547, Sowerby Coll., Hythe, Kent, England.

This species was diagnosed and described by MIDDLEMISS (1959). Serial sections were figured by MIDDLEMISS (1959, 1968a, 1968b), BOGDANOVA & LOBACHEVA (1966), SMIRNOVA (1972) and CALZADA (1975).

Material. – 46 specimens from the Upper Valanginian and Lower Hauterivian of the Ste-Croix district and Censeau.

Distribution. – This species is first known in the uppermost Valanginian (Astieria Marl horizon) in the Ste-Croix district (Vaud) and at Villers-le-Lac (Doubs), and also in the uppermost Valanginian Oolitenkalk of Vorarlberg. According to SMIRNOVA (1972) it occurs in the Valanginian of the northern Caucasus and Mangyshlak. *S. sella lindensis*, which I described (MIDDLEMISS 1976) as a subspecies, is common in the Claxby Ironstone of Lincolnshire (England), which is of uppermost Valanginian–Lower Hauterivian age, and in the coeval shallow water sediments of the Salzgitter–Goslar–Brunswick area of Germany. I now regard this as a separate species, *S. lindensis*. *S. sella* became widespread in the Hauterivian and is known from that stage in southwest Morocco, Var, Salève (Haute-Savoie), the central Jura region (where it is particularly abundant in the Hauterivian marls of

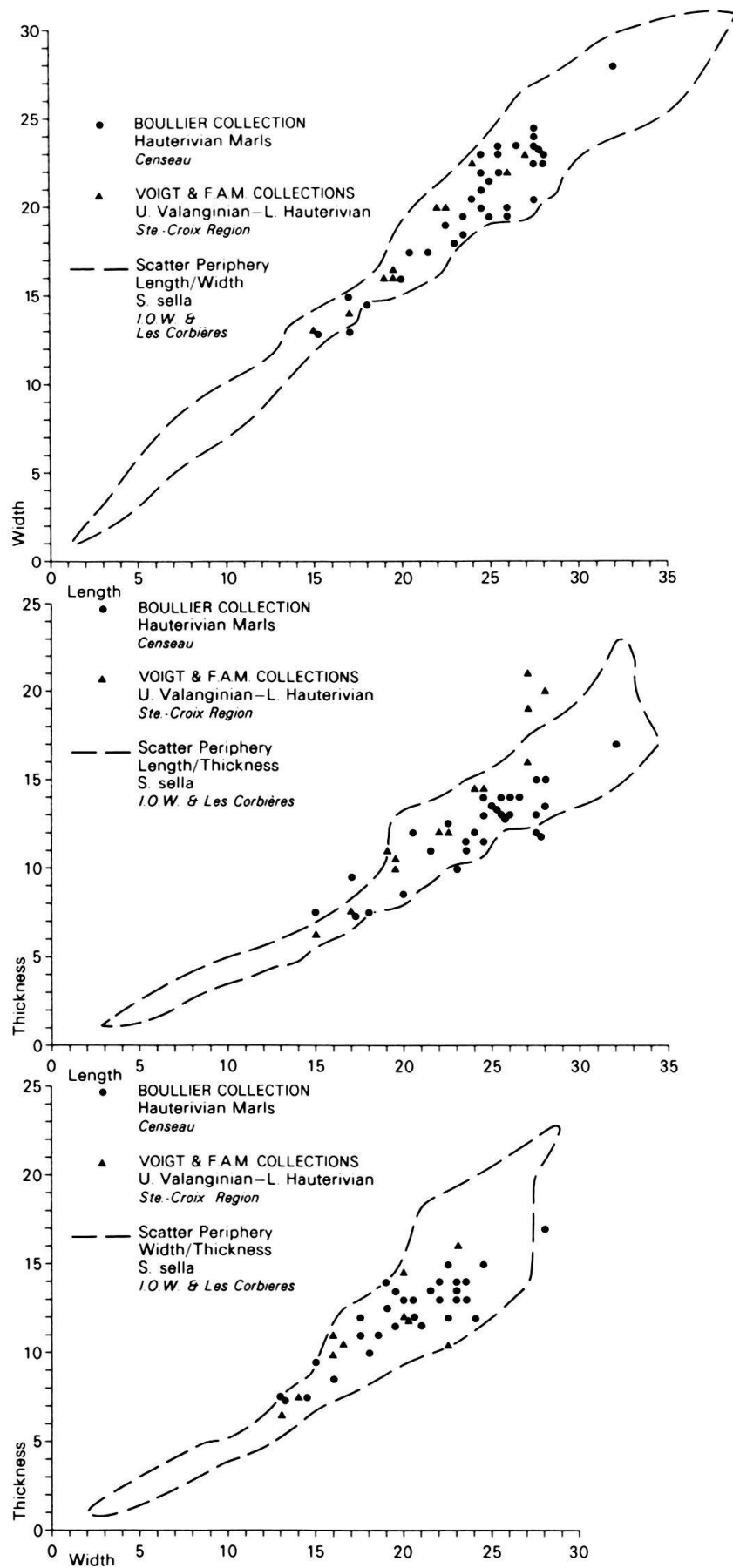


Fig. 5A, B and C. Scatter diagrams of length, width and thickness in *Sellithyrus sella*.

Censeau, Jura), the southeast Paris Basin (Marnes à Spatangues), Vorarlberg, northeast Bulgaria and the Kopet Daga (BOGDANOVA & LOBACHEVA 1966).

It is much less abundant in the Barremian, when neither the urgonian facies of southern Europe nor the generally argillaceous conditions of northern Europe were congenial to it. It occurs rather rarely in the Barremian of southwest Morocco, Ardèche, Bouches-du-Rhône, the Vercors (Isère), Haute-Savoie, Vaud and Doubs, Haute-Marne (according to CORROY 1925), Vorarlberg and (according to SMIRNOVA 1972) Turkmenistan.

The species reached its maximum abundance in the Lower Aptian. ROCH (1930) says that it occurs in the Bedoulian of southwest Morocco. It is certainly a characteristic Lower Aptian species in eastern Spain, the Santander district, Les Corbières and La Clape (Aude), Gard and Ardèche, the Apt district (Vaucluse), the Vercors, at La Perte du Rhône (Ain), La Presta and Boveresse (Neuchâtel), in Aube, Yonne and Haute-Marne and, especially, in southern England (Isle of Wight and the Weald) where it is by far the most abundant Lower Aptian brachiopod. It is known in central Switzerland (Schwyz), where its occurrence is probably Aptian, and is common in the Aptian of the Bakony Forest.

I am not aware of any definite evidence that *S. sella* s.s. continued into the Upper Aptian, although the subspecies *S. sella shanklinensis* is characteristic of the Upper Aptian of southern England. At that time also some species evolved which are distinctive, although still closely related to *S. sella* (*S. upwarensis* [WALKER], *S. coxwellensis* MIDDLEMISS, *S. viae* CALZADA). ROCH (1930) and AMBROGGI (1963) both claim *S. sella* from the Gargasian of southwest Morocco (without figures).

S. sella s.s. originated in the Jura faunal province and spread northwards to southern England only in the Lower Aptian. It can be distinguished from *S. lindensis* of northern England and northern Germany by the allometric development of thickness relative to length and width, a development which is isometric in *S. lindensis* (MIDDLEMISS 1976). Figure 5 demonstrates the close agreement of forty typical Upper Valanginian–Hauterivian Jura specimens with the development pattern of the much more numerous representatives of the species in the Lower Aptian of the Isle of Wight and Les Corbières (from MIDDLEMISS 1968a, Fig. 7a–c). Figure 5 should be compared with the corresponding graphs for *S. sella lindensis* given by MIDDLEMISS (1976, Fig. 5), and for *S. sella shanklinensis* by MIDDLEMISS (1968b, Fig. 6–8). Still more exaggerated allometry in the development of relative thickness is shown by forms of *Sellithyris* which occur in the Lower Cretaceous of the High Plateaux region of Algeria (not yet described) and which are possibly to be referred to a separate subspecies.

Sellithyris carteroniana (D'ORBIGNY 1849)

- 1839 *Terebratula biplicata* SOWERBY; ROEMER, p. 22, Pl. 18, Fig. 10.
- V + 1849 *Terebratula carteroniana* D'ORBIGNY, p. 80, Pl. 507, Fig. 1–5.
- 1864 *Terebratula Carteroniana* D'ORB.; CREDNER, p. 560, Pl. 20, Fig. 8–10.
- V 1872 *Terebratula Carteroniana* D'ORBIGNY; PICTET & DE LORIOL, p. 60, Pl. 201, Fig. 1–4.
- 1968a *Sellithyris carteroniana* (D'ORBIGNY); MIDDLEMISS, p. 187, Pl. B, Fig. 1–2.
- 1972 *Sellithyris carteroniana* (ORBIGNY); SMIRNOVA, p. 78, Pl. 7, Fig. 4 (NON Fig. 3).
- V 1976 *Sellithyris carteroniana* (D'ORBIGNY); MIDDLEMISS, p. 43, Pl. 2, Fig. 4–6. Pl. 3, Fig. 1–3.

Holotype. – MN 5160, Morteau, France.

The most recent diagnosis and detailed study of this species was by MIDDLEMISS (1976). Serial sections were figured by MIDDLEMISS (1968a, 1976) and SMIRNOVA (1972).

Material. – 26 specimens from the Valanginian of various localities in the Swiss and French Jura; 5 from the Hauterivian Pierre Jaune of Le Landeron.

Distribution. – The species was at its greatest numerical abundance in the Valanginian of the central Jura, where it is particularly characteristic of the Calcaire Roux. It is also known from this stage at Le Fontanil and Mallevall (Isère), Arbigneu (Ain) and Molard de Vions (Savoie). CORROY (1925) records it in the littoral facies of the southeast Paris Basin. During this stage it also entered north Germany and is locally common in the condensed late Valanginian–Hauterivian deposits at Grenzlerberg (near Salzgitter) and the transgressive Hauterivian of the Schöppenstedt area.

In the Hauterivian it was less numerous but reached its maximum geographical spread, extending from Aude through Var, the southern and central Jura region, Yonne and Aube (according to CORROY 1925) to the Lower Saxon Basin. GÜMBEL (1866) records it from the “Lower Neocomian” of Betzau in the Bavarian Alps and SMIRNOVA (1972) from the Lower Hauterivian of the northern Caucasus.

Occurrence of this species above the Hauterivian is doubtful. PICTET & DE LORIOLO (1872) record some poor specimens possibly of this species from the urgonian facies at Mauremont (Vaud). In the Vorarlberger Naturschau at Dornbirn there are several specimens labelled “*T. russillensis*” but having commissural and beak characters more resembling *S. carteroniana*; these came from the Barremian Schrattenkalk and the urgonian of Klien, Vorarlberg. At Grenoble (Madame Arnaud Coll.) are two specimens, believed to be from the Aptian of the Vercors, which closely resemble *S. carteroniana*.

Sellithyris campichei (PICTET 1872)

Fig. 6

V + 1872 *Terebratula Campichei* PICTET, p. 63, Pl. 201, Fig. 5–6.

Lectotype (here chosen). – The specimen figured by PICTET & DE LORIOLO 1872 as Plate 201, Figure 5. The specimen is in the Muséum d'Histoire Naturelle at Geneva, stated in the text (p. 64) to be from the Valanginian of Ste-Croix, on the label to be from that of Villers-le-Lac.

Paralectotype. – The specimen figured by PICTET & DE LORIOLO 1872 as Plate 201, Figure 6.

Material. – 7 specimens from the Valanginian of Villers-le-Lac. This species has not been redescribed since 1872.

Internal structures. – These closely resemble those of *S. sella*.

Distribution. – Valanginian of the central Jura region only. A rare species.



Fig. 6. Serial sections through *Sellithyris campichei* (Pictet). Pedicle collar is seen at 1.6 and symphytium at 3.6. The initially concave hinge plates, enclosed in the cardinal process, are seen at 4.0. Crural bases first appear at 4.4. Descending lamellae and transverse band were not preserved in this specimen. Sections 4.0–4.8 are enlarged with respect to the other sections. 609/2/1, Neuchâtel Coll., Upper Valanginian, Villers-le-Lac, Doubs. Dimensions of specimen: L. 20, W. 17.5, T. 12.75. A = scale for sections 4.0–4.8. B = scale for the remaining sections.

Sellithyris essertensis (Pictet 1872)

Fig. 7

1866 *Terebratula acuta*, var. *urgonensis* DE LORIOL, p. 86.

V + 1872 *Terebratula essertensis* PICTET, p. 64, Pl. 201, Fig. 7–10.

Lectotype (here chosen). – The specimen figured by PICTET & DE LORIOL (1872) as Plate 201, Figure 7, from the “urgonian” of Essert. The specimen is in the Muséum d’Histoire Naturelle at Geneva.

Paralectotypes. – The remaining specimens figured by PICTET & DE LORIOL on Plate 201. All are at Geneva.

Material. – 66 specimens from the urgonian rocks of various localities in the Swiss and French Jura. This species has not been redescribed since 1872.

Internal structures. – These do not differ essentially from those of *S. sella*.

Distribution. – This is a characteristic species of the urgonian facies in both south and central parts of the Jura region; particularly at Essert (Haute-Savoie), where its abundance gives a marked local character to the fauna. PICTET & DE LORIOL state that it occurs in the upper urgonian at Orgon (Bouches-du-Rhône). It is known, although rarely, in the Barremian of Oliva (Valencia region, eastern Spain) (Champtier Coll.) and in Ibiza (Barremian?). It occurs rarely in the Aptian of La Presta (Neuchâtel) and of Salève (Haute-Savoie) (Geneva Museum) and is recorded by PICTET & DE LORIOL also from the Lower Aptian of Boveresse (Neuchâtel) and La Perte du Rhône (Ain).

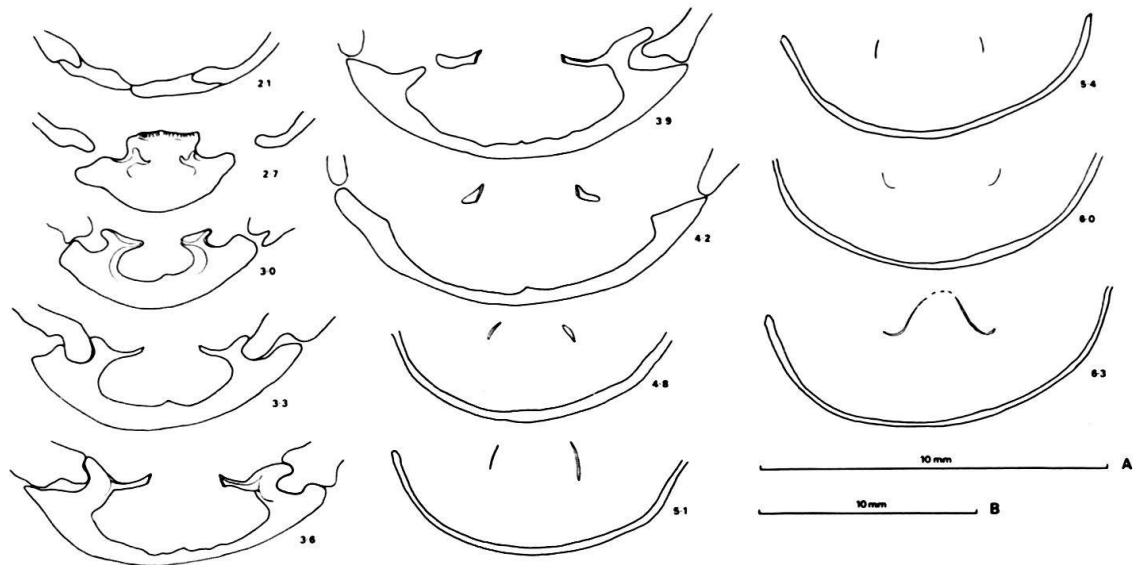


Fig. 7. Serial sections through *Sellithyris essertensis* (Pictet). The wide symphytium is seen at 2.1 and the initially concave hinge plates, enclosed in the cardinal process, at 2.7. Crural bases first appear at 3.3. Maximum height of the crural processes is at 5.1 and the high-arched transverse band at 6.3. Sections 2.1–4.2 are enlarged with respect to the other sections. 27/2D/2, Neuchâtel Coll., Barremian. La Goulette. Dimensions of specimen: L. 14.25, W. 11.5, T. 8.5. A = scale for sections 2.1–4.2. B = scale for the remaining sections.

Sellithyris montmollini (Pictet 1872)

Fig. 8, 9

+ 1872 *Terebratula* (*Waldheimia*) *Montmollini* Pictet, p. 91, Pl. 203, Fig. 4–5.

Lectotype (here chosen). – The specimen figured by Pictet & de Loriol (1872) as Plate 203, Figure 4, from the Neocomian of Censeau. The specimen is in the Muséum d'Histoire Naturelle at Geneva (Coll. Pictet).

Paralectotype. – The specimen figured by Pictet & de Loriol as Plate 203, Figure 3.

Material. – 40 specimens from the Upper Valanginian of Villers-le-Lac. This species has not been redescribed since 1872.

Remarks. – This species is assigned to the genus *Sellithyris* because of its oval, sulcinate to gently episulcate external form together with its concave hinge plates, well-differentiated from the inner socket ridges; the thin descending lamellae; the broad and moderately high-arched transverse band; the presence of euseptoidum-like ridges flanking the euseptoidum in the posterior part of the brachial valve. It differs from *S. sella* in possessing high, well-developed attached crural bases and in the characteristically curved shape of the free crural bases immediately anterior of the hinge plates.

Distribution. – Valanginian, and possibly Hauterivian, of the central Jura region. It also occurs rarely in the transgressive Hauterivian of the Schöppenstedt area of Germany (Roemer Museum, Hildesheim; Göttingen Museum); thus it was one of the Jura species which migrated northwards at that time.

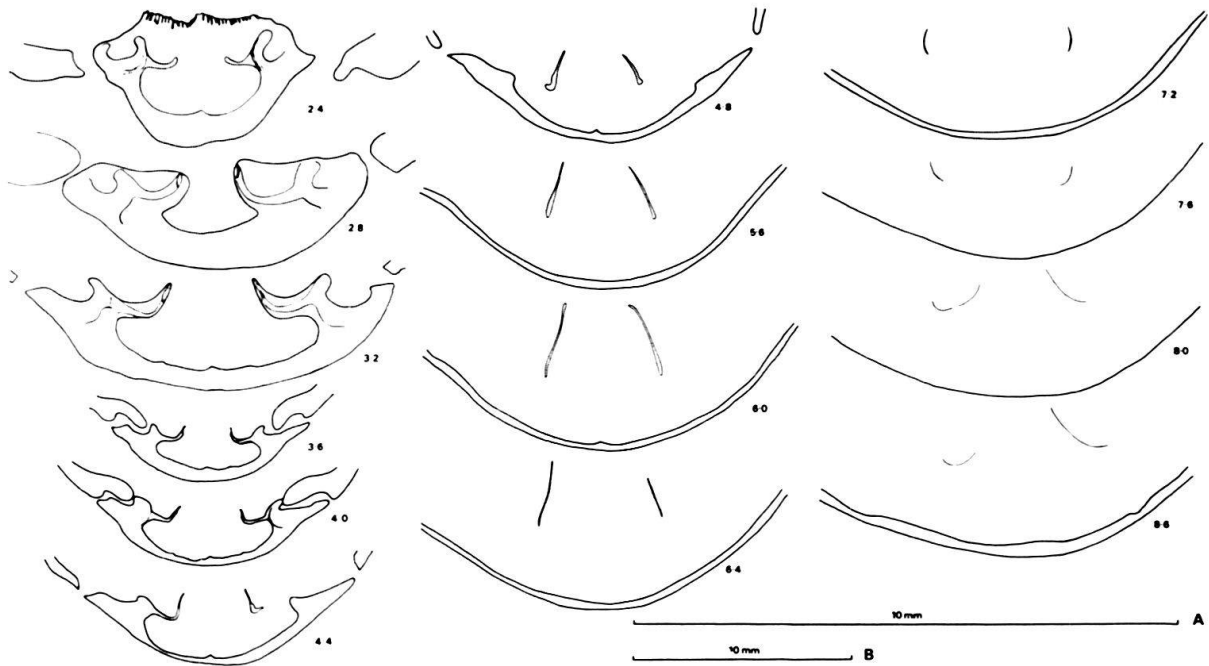


Fig.8. Serial sections through *Sellithyris montmollini* (Pictet). The initially concave hinge plates, enclosed in the cardinal process, are seen at 2.4. Crural bases first appear at 2.8 and become medially concave at 4.0 and 4.4. Maximum height of the crural processes is seen at 6.0, the thin descending lamellae at 7.6 and the moderately high-arched transverse band (upper part damaged) at 8.0 and 8.6. Sections 2.4-3.2 are enlarged with respect to the other sections. 609/4/1, Neuchâtel Coll., Upper Valanginian, Villers-le-Lac, Doubs. Dimensions of specimen: L. 22, W. 18.25, T. 10. A = scale for sections 2.4-3.2. B = scale for the remaining sections.

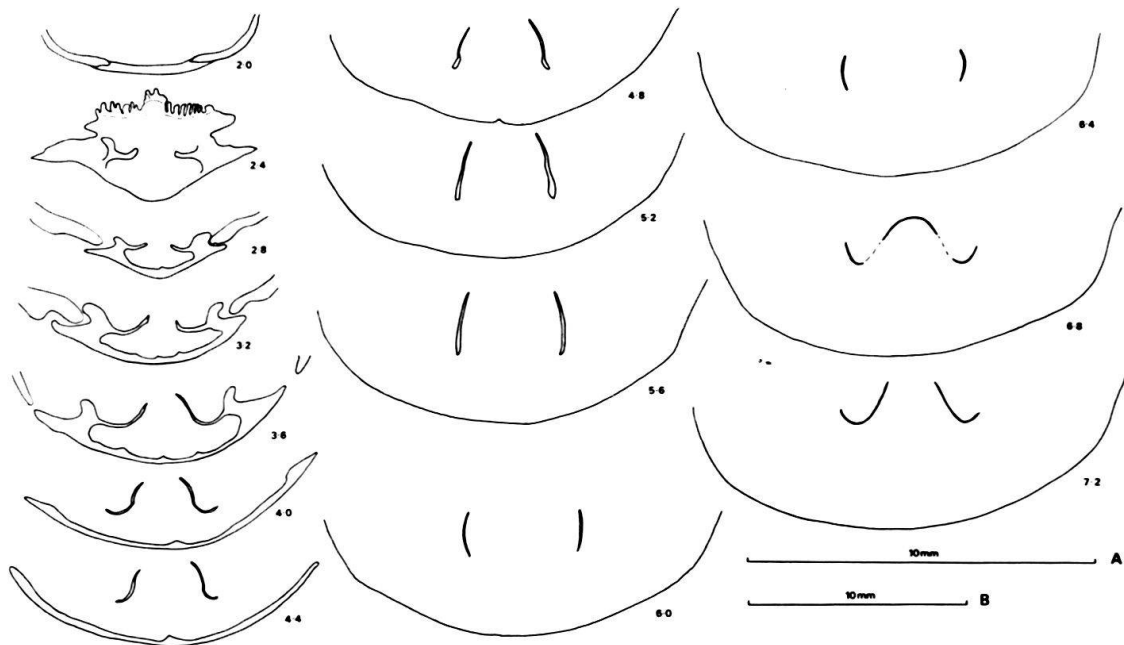


Fig.9. Serial sections through *Sellithyris montmollini* (Pictet). The wide symphytium is seen at 2.0 and the initially concave hinge plates, enclosed in the cardinal process, at 2.4. Crural bases first appear at 3.2. The medially concave shape of the free crural bases is well-shown at 4.0 and 4.4. Maximum height of the crural processes is at 5.2 and the moderately high-arched transverse band at 6.8. Section 2.4 is enlarged with respect to the other sections. Cv35, Göttingen Coll., Upper Valanginian or Lower Hauterivian, Gross Vahlberg, Brunswick. Dimensions of specimen: L. 21, W. 15, T. 10. A = scale for section 2.4. B = scale for the remaining sections.

Genus *Musculina* SCHUCHERT & LE VENE 1929

Type species: *Terebratula biplicata acuta* VON BUCH 1834 (= *Terebratula sanctaegrucis* CATZIGRAS 1948)

The most recent diagnosis of this genus was given by MIDDLEMISS (1976).

Musculina sanctaegrucis (CATZIGRAS 1948)

- 1834 *Terebratula biplicata acuta* VON BUCH, p. 108 (non *Terebratula acuta* J. SOWERBY 1816).
 1835 *Terebratula biplicata acuta* VON BUCH, p. 128 (non *Terebratula acuta* J. SOWERBY 1816).
 1849 *Terebratula praelonga* SOW.; D'ORBIGNY, p. 75, Pl. 505, Fig. 1-7 (non *Terebratula praelonga* J. DE C. SOWERBY 1836).
 V 1851 *Terebratula biplicata acuta* VON BUCH; QUENSTEDT, p. 473, Pl. 38, Fig. 2 (as *T. acuta*).
 V 1861 *Terebratula acuta* QUENST.; DE LORIOL, p. 115, Pl. 15, Fig. 1-10.
 1867 *Terebratula biplicata acuta* VON BUCH; QUENSTEDT, p. 565, Pl. 48, Fig. 2.
 1871 *Terebratula biplicata acuta* VON BUCH; QUENSTEDT, p. 384, Pl. 48, Fig. 70-74 (as *T. acuta*).
 V 1872 *Terebratula acuta* QUENST.; PICTET & DE LORIOL, p. 14, Pl. 202, Fig. 14-18.
 1885 *Terebratula biplicata acuta* VON BUCH; QUENSTEDT, p. 720, Pl. 55, Fig. 41.
 1907 *Musculus acutus* QUENST.; BUCKMAN, p. 530.
 1929 *Musculina acuta* QUENST.; SCHUCHERT & LE VENE, p. 120.
 + 1948 *Terebratula sanctae crucis* CATZIGRAS, p. 391, Fig. 1 (1-4, 8, 10, 12, 15-17, 19).
 1960 "*Terebratula*" *acuta acuta* QUENST.; SMIRNOVA, p. 374, Pl. 1, Fig. 2.
 1962 *Terebratula sanctae crucis* CATZ.; LEFAVRAIS-RAYMOND, Pl. 6, Fig. 2.
 V 1965 *Musculina biennensis* MUIR-WOOD in MOORE, p. H793, Fig. 658 (1), 659 (2).
 1966 *Sellithyris acuta* (QUENST.); BOGDANOVA & LOBACHEVA, p. 56, Fig. 20, Pl. 5, Fig. 1-2.
 V 1968a *Musculina sanctaegrucis* (CATZIGRAS); MIDDLEMISS, p. 19, Fig. 9, Pl. B, Fig. 3-4.
 1972 *Sellithyris acuta* (QUENST.); SMIRNOVA, p. 80, Fig. 39, Pl. 7, Fig. 3 (non Fig. 4).
 V 1975 *Musculina sanctaegrucis* (CATZIGRAS); DIENI & MIDDLEMISS, p. 179, Pl. 32, Fig. 12-15.
 V 1976 *Musculina santaegrucis* (CATZIGRAS); MIDDLEMISS, p. 53, Pl. 5, Fig. 7-8, Pl. 6, Fig. 1-3.

Holotype. – The specimen figured by QUENSTEDT (1851, 1867, 1871, 1885) from the Neocomian of Neuchâtel. The specimen is in the Geologisch-Paläontologisches Institut und Museum, Tübingen (labelled 48/70). Diagnosis and full discussion of this species were given by DIENI & MIDDLEMISS (in DIENI, MIDDLEMISS & OWEN 1975) and by MIDDLEMISS (1976). Serial sections were figured by BOGDANOVA & LOBACHEVA (1966); MIDDLEMISS (1968a, 1976); SMIRNOVA (1972); DIENI, MIDDLEMISS & OWEN (1975) and CALZADA (1975).

Material. – About 200 specimens from the Hauterivian of various localities in the Swiss and French Jura.

Distribution. – This is the most abundant species of the Hauterivian throughout the southern and central Jura region and the southeast Paris Basin. It is particularly characteristic of the Hauterivian Marl lithofacies but also occurs in other lithofacies. It is first known in the Lower Valanginian of Provence, where it is quite common in the Petite Lumachelle horizon to the south of Castellane (Basses-Alpes). It also occurs in the Valanginian of Oliva (Valencia, eastern Spain; Champetier Coll.), in strata possibly of Valanginian age in Les Corbières (Aude) and, very rarely, in the Valanginian Oolitenkalk of Vorarlberg.

In the Hauterivian, besides the Jura region, it occurs in Tarragona Province, eastern Spain (CALZADA 1976); Ibiza (age uncertain; Rangheard Coll.): Roussillon and the central Pyrenees: Aude: Bouches-du-Rhône, Var and Basses-Alpes: eastern

Sardinia: at Salève (Haute-Savoie) and in the Belley area (Ain): Meuse, Haute-Marne, Aube, Yonne and Nièvre: the Lower Saxon Basin. SMIRNOVA (1960, 1972) figured it from the Hauterivian of the Crimea and northern Caucasus, BOGDANOVA & LOBACHEVA (1966) from that of the Kopet Daga.

In the Barremian it was much more restricted, being known only in the central Jura region (Jura, Vaud) and, according to CORROY (1925) in the Lower Barremian neritic facies of Berry (Paris Basin). It continued very locally into the Lower Aptian, occurring certainly in that stage in Les Corbières (Aude) (Charrière Coll.) and claimed by MALLADA (1887) to occur in the "urgo-aptian" of Morella (eastern Spain). It may possibly occur also in the Aptian of Val de Travers (Neuchâtel) (Göttingen Coll.).

Genus *Loriolithyris* MIDDLEMISS 1968

Type species: Terebratula russillensis DE LORIOL 1866

Loriolithyris russillensis (DE LORIOL 1866)

- + 1866 *Terebratula russillensis* DE LORIOL, p. 88, Pl. E, Fig. 12–15.
- 1867 *Terebratula russillensis* DE LORIOL, p. 393, Pl. C, Fig. 28–31.
- 1869 *Terebratula russillensis* DE LORIOL, p. 28, Pl. 4, Fig. 1.
- V 1872 *Terebratula russillensis* DE LORIOL; PICTET & DE LORIOL, p. 68, Pl. 202, Fig. 1–8.
- ? 1964 *Sellithyris* (?) *russillensis* (DE LORIOL); AGER, p. 340.
- NON 1966 *Sellithyris russillensis* (DE LORIOL); BOGDANOVA & LOBACHEVA, p. 53, Pl. 5, Fig. 5–6.
- V 1968a *Loriolithyris russillensis* (DE LORIOL); MIDDLEMISS, p. 176, Pl. A, Fig. 1–4.
- V 1980 *Loriolithyris russillensis* (DE LORIOL); MIDDLEMISS, p. 522, Pl. 55, Fig. 1–4.

Lectotype (designated *Middlemiss* 1968). – The specimen figured by PICTET & DE LORIOL (1872) as Plate 202, Figure 4, from the "urgonian" of La Russille. The specimen is in the Muséum d'Histoire Naturelle at Geneva, No. CB1520.

Serial sections and further discussion of this species were provided by MIDDLEMISS (1968 and 1980).

Material. – 6 specimens from the urgonian rocks of La Russille, 53 from the Upper Hauterivian of Chamblon, 2 from the Lower Hauterivian of Auberson, 8 from the ?Hauterivian of Villers-le-Lac.

Distribution. – This species is even more characteristic of the Barremian than *S. essertensis* since it occurs abundantly over a wider area than the latter species. Nevertheless the overall range is long – from Valanginian to Aptian.

In the Valanginian the species is certainly known from Oliva (Valencia, Spain) (Champetier Coll.), from strata in Les Corbières (Aude) of possibly Valanginian age, and from Auberson, Villers-le-Lac and other places in the central Jura region. In the Hauterivian it is known from southwest Morocco, Oliva (Champetier Coll.), Les Corbières and La Clape (Aude), the southern and central Jura and the southeast Paris Basin, and also in the southern Dobrogea (Romania) (BĂRBULESCU et al. 1975).

In the Barremian the species abounds throughout the central and southern Jura region, the southeast Paris Basin (basal Barremian only according to CORROY 1925), the Chartreuse and other parts of Isère, and at Orgon and the Etang de Berre (Bouches-du-Rhône). It also occurs fairly commonly at Brouzet and Allègre (Gard), Les

Corbières (Aude), the Barcelona–Tarragona region (Calzada Coll.), Oliva (Valencia) (Champetier Coll.) and southwest Morocco. Eastwards it is a rare form in the urgonian facies of Klien (Vorarlberg).

The species continued into the Aptian in southwest Morocco, eastern Spain (“urgo-aptian” according to MALLADA 1887), Les Corbières and La Clape, Alpes-Maritimes, the Vercors (especially near Rencurel) (Grenoble Coll.), La Presta and Boveresse (Neuchâtel).

Loriolithyris russillensis latifrons (Pictet 1872)

Fig. 10

V + 1872 *Terebratula latifrons* Pictet, p. 67, Pl. 201, Fig. 16, 17.

Lectotype (here chosen). – The specimen figured by Pictet & de Loriol 1872 as Plate 201, Figure 16, from the Valanginian of Villers-le-Lac. The specimen is in the Muséum d'Histoire Naturelle at Geneva. The specimen figured as Figure 17 is an untypical depressed form.

Material. – 8 specimens from the Upper Valanginian of Villers-le-Lac.

Internal structures. – Cardinal process slightly bifid. Small dorsal umbonal cavity present. Hinge plates deeply concave, faintly piped, clearly differentiated from the inner socket ridges by sigmoid curves; becoming less differentiated anteriorly.



Fig. 10. Serial sections through *Loriolithyris russillensis latifrons* (Pictet). The initial concave shape of the hinge plates is shown at 2.8 and 3.2, the first clear indication of attached crural bases occurring at 4.4. Transverse band not preserved. Section 3.2 is enlarged in order to show detail of the juvenile hinge plates. 608/3/1, Neuchâtel Coll., Upper Valanginian, Villers-le-Lac, Doubs. Dimensions of specimen: L. 21.25, W. 20.25, T. 13.25. A = scale for section 3.2. B = scale for the remaining sections.

Euseptoidum distinct and flanked in the region of the hinge plates and crura by two widely-spaced euseptoidum-like ridges.

Remarks. – I discussed this species of PICTET & DE LORIOI in the context of the occurrence of similar forms in Les Corbières (MIDDLEMISS 1968a) and southwest Morocco (MIDDLEMISS 1980). In 1968 I argued that, because of gradation of and overlap between the characters of the species, *T. latifrons* and *T. russillensis* were conspecific and I regarded *latifrons* as a variety of *L. russillensis* of infrasubspecific rank. In 1980 I pointed out that in both southwest France and southwest Morocco forms apparently referable to *L. russillensis* show continuous variation, in the same assemblages, into other forms with the same characters except for the proportions of shell shape, which are those of *T. latifrons*. The internal skeletal arrangements revealed by serial sectioning are closely comparable in all these forms. Specimens from the Jura region which PICTET recognized as *T. latifrons* are distinct from *L. russillensis* on account of their small umbones and foramina rather than of their

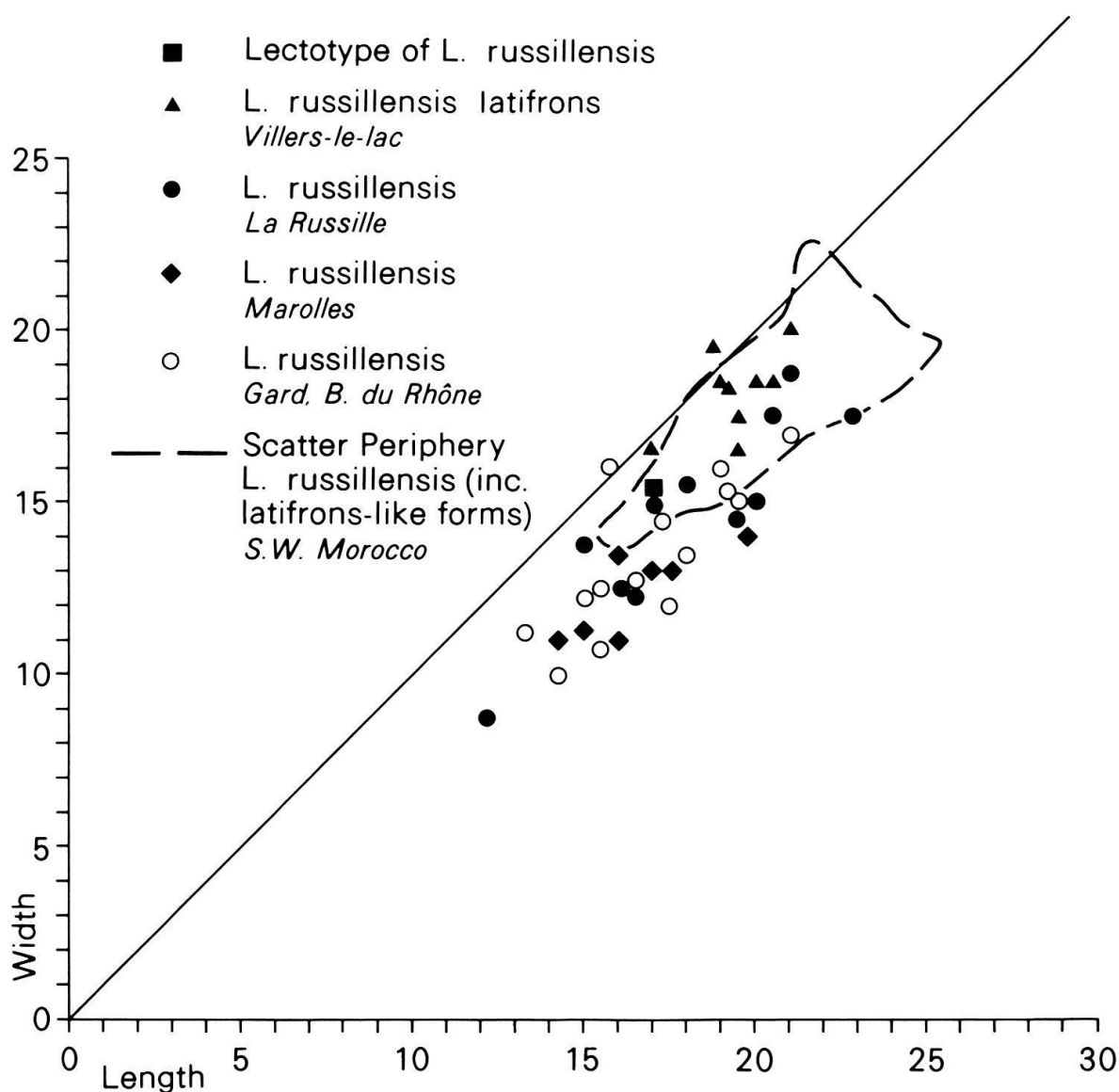


Fig. 11. Scatter diagram of length and width in *Loriolithyris russillensis* and *L. russillensis latifrons*.

wide depressed shape. They usually display *russillensis*-like folding of the shell and as regards shape there seems to be complete gradation between the two species. PICTET stressed in his description that in *T. latifrons* the shell was wider than long, but in fact that is very rarely the case; in the lectotype length and width are about equal and Figure 11 demonstrates little difference in the length/width ratio between *russillensis* and *latifrons*.

The typical *T. latifrons* forms, with small umbo and foramen in addition to the wide depressed shape, are, both according to PICTET and on the evidence of the Geneva and Neuchâtel collections, confined to the Upper Valanginian of Villers-le-Lac and Vesençy (Ain) (although the latter specimen, PICTET's Figure 17, does not agree with his description and is dubious). I therefore hold to my 1980 conclusion that *L. russillensis* was a species group very variable in proportions of length, width and thickness, some members of which, in part of the Jura region and for a short time in the Upper Valanginian, became locally sufficiently differentiated to deserve recognition as a geographical subspecies.

PICTET himself considered that *T. latifrons* was most nearly related to *L. germaini*. This is rejected here because of a) the characteristic presence of *latifrons*-like forms among the populations of *L. russillensis* in southwest France and southwest Morocco and the absence of *L. germaini* from those regions, b) the internal structures of *L. russillensis latifrons*.

Distribution. – Upper Valanginian of the central Jura region only.

Loriolithyris valdensis (DE LORIO 1868)

- V + 1868 *Terebratula valdensis* DE LORIO, p. 52, Pl. 4, Fig. 9–12.
- V 1872 *Terebratula valdensis* DE LORIO; PICTET & DE LORIO, p. 66, Pl. 201, Fig. 11–15.
- NON 1939 *Terebratula valdensis* var. *kentugajensis* MOISSIEV, p. 200, Pl. 2, Fig. 6.
- 1960 “*Terebratula*” *valdensis* DE LORIO; SMIRNOVA, p. 374, Pl. 1, Fig. 1.
- PARS 1966 *Selliithyris valdensis* (DE LORIO); BOGDANOVA & LOBACHEVA, p. 55, Pl. 5, Fig. 7 (non Pl. 7, Fig. 11).
- V 1968a *Loriolithyris valdensis* (DE LORIO); MIDDLEMISS, p. 182, Pl. A, Fig. 5.
- 1972 *Selliithyris valdensis* (DE LORIO); SMIRNOVA, p. 81, Pl. 7, Fig. 5.
- V 1975 *Loriolithyris valdensis* (DE LORIO); DIENI & MIDDLEMISS, p. 182, Pl. 36, Fig. 9–10.
- V 1980 *Loriolithyris valdensis* (DE LORIO); MIDDLEMISS, p. 524, Pl. 55, Fig. 5–9.

Lectotype. – Muséum d'Histoire Naturelle, Geneva (Arzier Coll.) No. CB 1505. Designated by MIDDLEMISS (1968). Figured by DE LORIO (1868), Plate 4, Figure 9a–d, from Bed B of the Valanginian, Arzier quarries, Vaud.

The most recent diagnosis of this species was given by DIENI & MIDDLEMISS (in DIENI, MIDDLEMISS & OWEN 1975). Serial sections were figured by BOGDANOVA & LOBACHEVA (1966); MIDDLEMISS (1968a); CALZADA (1975); DIENI, MIDDLEMISS & OWEN (1975).

Material. – 7 specimens from the Berriasian of Monnetier. About 250 specimens from the Valanginian of Arzier and other localities in the Swiss Jura.

Distribution. – This species is noteworthy for its early appearance in the Cretaceous of the Jura region, since it occurs commonly in the Berriasian at Monnetier and Grande Varappe (Salève, Haute-Savoie).

However, the species is particularly characteristic of the Valanginian, in which stage it is abundant throughout the central and southern Jura region and occurs at Mallevall and Le Fontanil (Isère), in Basses-Alpes, Var, Bouches-du-Rhône and in eastern Sardinia. It has not yet been recorded from southwest France but is known in the Castellon Province (eastern Spain) and at Oliva (Valencia Province) (Cham-petier Coll.), in southeast Spain at La Querola (Durand Delga Coll.) and other localities near Alicante (Fourcade Coll.), and in southwest Morocco. Northwestwards, CORROY (1925) records its occurrence in the Valanginian of the southeast Paris Basin. Eastwards it probably occurs, although rarely, in the Oolitenkalk facies of the Valanginian in Vorarlberg, and SMIRNOVA (1972) records it in the Valanginian of Georgia.

The species continued in reduced numbers into the Hauterivian of several areas, notably Doubs and Jura: the southeast Paris Basin: Basses-Alpes, Bouches-du-Rhône and Var: east central Sardinia: the Castellon Province of Spain (Calzada Coll.): southwest Morocco: the Lower Hauterivian of northeast Bulgaria (Jaffrezo Coll.) and, according to SMIRNOVA (1972), the Lower Hauterivian of the northern Caucasus. It continued still more rarely into the Barremian of Vaud and of southwest Morocco and into the Aptian of southwest Morocco and of La Presta (Neuchâtel).

Loriolithyris germaini (PICTET 1872)

Fig. 12

V + 1872 *Terebratula germaini* PICTET, p. 71, Pl. 202, Fig. 12, 13.

Lectotype (here chosen). – Specimen CB 1694 in the Muséum d'Histoire Naturelle at Geneva, from the Valanginian of Métabief, Doubs; figured by PICTET & DE LORIOLE (1872) as Plate 202, Figure 12.

Paralectotype. – Specimen CB 1693 in the Muséum d'Histoire Naturelle at Geneva; same horizon and locality as the lectotype; figured by PICTET & DE LORIOLE (1872) as Plate 202, Figure 13.

Material. – 32 specimens from the Valanginian of Villers-le-Lac; 2 from the Upper Valanginian of Ste-Croix. This species has not been redescribed since 1872.

Internal structures. – Cardinal process gently bifid. Hinge plates thin, concave, sharply differentiated from the inner socket ridges, piped, with small crural bases. Euseptoidum massive but short, flanked by faint euseptoidum-like ridges in posteriormost part of brachial valve.

Remarks. – The descending lamellae and transverse band of the loop are probably thin and delicate, as in all species of *Loriolithyris*, as they have not yet been found preserved in this species.

PICTET recognized the relationship of this species to *T. russillensis*, *T. latifrons* and *T. valdensis* and was particularly careful to differentiate it from them. *T. germaini* is here referred to *Loriolithyris* mainly because the shape of the hinge plates in cross section is so characteristic of that genus.

PICTET commented that the folding of the shell was very similar to that in *T. salevensis*. This is interesting in view of the fact that *L. germaini* has a close

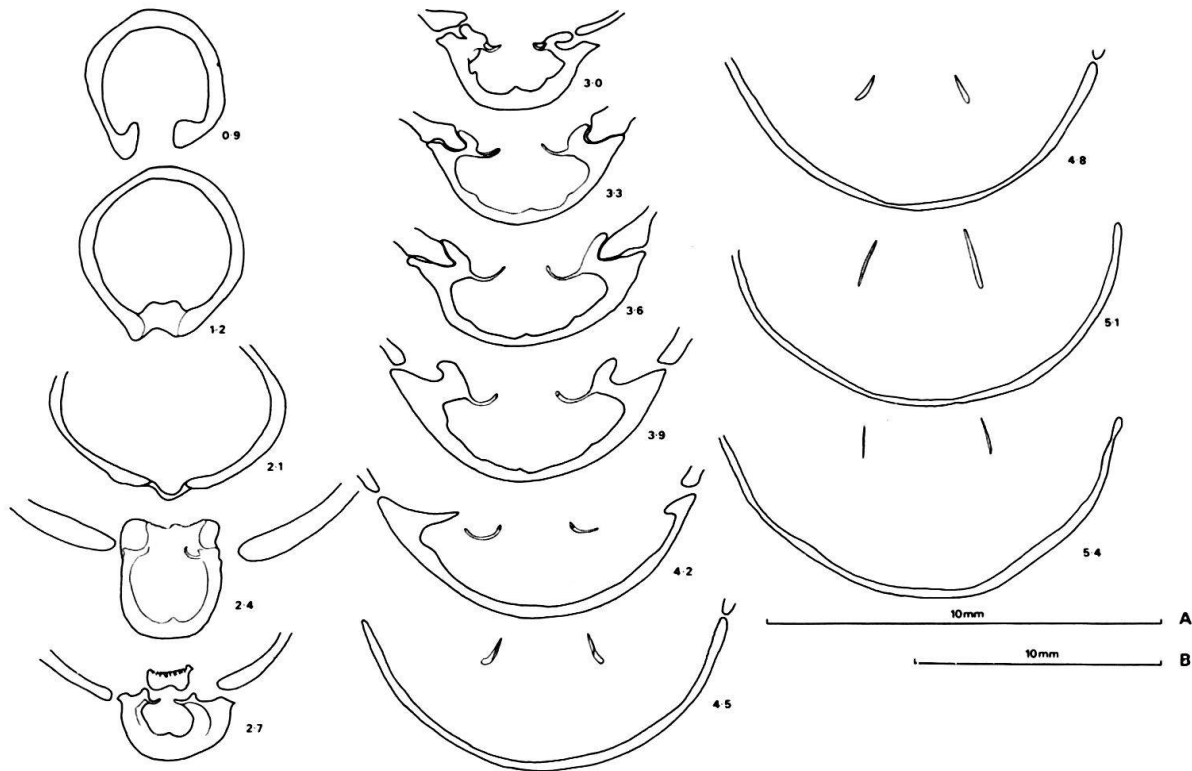


Fig. 12. Serial sections through *Lariolithyrus germani* (Pictet). The initially concave hinge plates are seen within the cardinal process at 2.4. The small attached crural bases, first clearly seen at 3.6, give rise to piped hinge plates. Maximum height of the crural processes is seen at 5.1. Transverse band not preserved. Section 2.4 is enlarged in order to show detail of the juvenile hinge plates. 22G/6/2, Neuchâtel Coll., Upper Valanginian, Villers-le-Lac, Doubs. Dimensions of specimen: L. 15.5, W. 13.25, T. 10.25. A = scale for section 2.4. B = scale for the remaining sections.

external homeomorph in an undescribed species locally abundant in the Aptian of the Oviedo district (northern Spain). The latter is related to, and probably congeneric with, *T. salevensis*.

Distribution. – Confined to the Valanginian of Doubs and Vaud.

Subfamily *Rectithyridinae* MUIR-WOOD 1965

Genus *Collinithyrus* nov. gen.

Type species: *Terebratula collinaria* D'ORBIGNY 1849

Diagnosis. – Rectithyridinae with smooth shells, subcircular or pentagonal to elongate in ventral profile. Umbo suberect; symphytium well-exposed and bordered; beak ridges rounded. Anterior commissure uniplicate to gently sulcinate. Hinge plates initially horizontal, becoming very gently concave, cuneate, not clearly differentiated from inner socket ridges. Free crura flanged. Loop lamellae thin. Transverse band low-arched. Euseptoidum present but small.

Remarks. – Both external appearance and internal structures suggest that this genus is most closely related to *Moutonithyrus* (MIDDLEMISS 1976, p.63). The relationship of *T. sueuri* to *T. moutoniana* was specifically recognized by PICTET. The

resemblance is shown particularly by the form of the hinge plates and of the transverse band.

Species included. – *T. collinaria* D'ORBIGNY 1849, *T. sueuri* PICTET 1872.

Range of the genus. – Valanginian to Aptian.

Collinithyris collinaria (D'ORBIGNY 1849)

Fig. 13

- + 1849 *Terebratula collinaria* D'ORBIGNY, p. 81, Pl. 507, Fig. 6–10.
 1863 *Terebratula collinaria* D'ORBIGNY; OOSTER, p. 18, Pl. 4, Fig. 15, 22 (?Fig. 16–18).
 V 1872 *Terebratula (Waldheimia) collinaria* D'ORBIGNY; PICTET & DE LORIO, p. 107, Pl. 205, Fig. 15, 16.

Holotype. – The specimen figured by D'ORBIGNY (1849), Plate 507, Figures 6–10, from the Neocomian of Marolles. The present whereabouts of this specimen is not known; it is not in the collections of the Muséum National d'Histoire Naturelle, Paris (Y. Gayrard, in litt., December 1980). Specimen 5164/B14397, in the d'Orbigny Collection at that Museum, is labelled *Magellania (Aulacothyris) Collinaria*, Marolles, but is, in fact, a specimen of *Rugitela hippopus* (ROEMER).

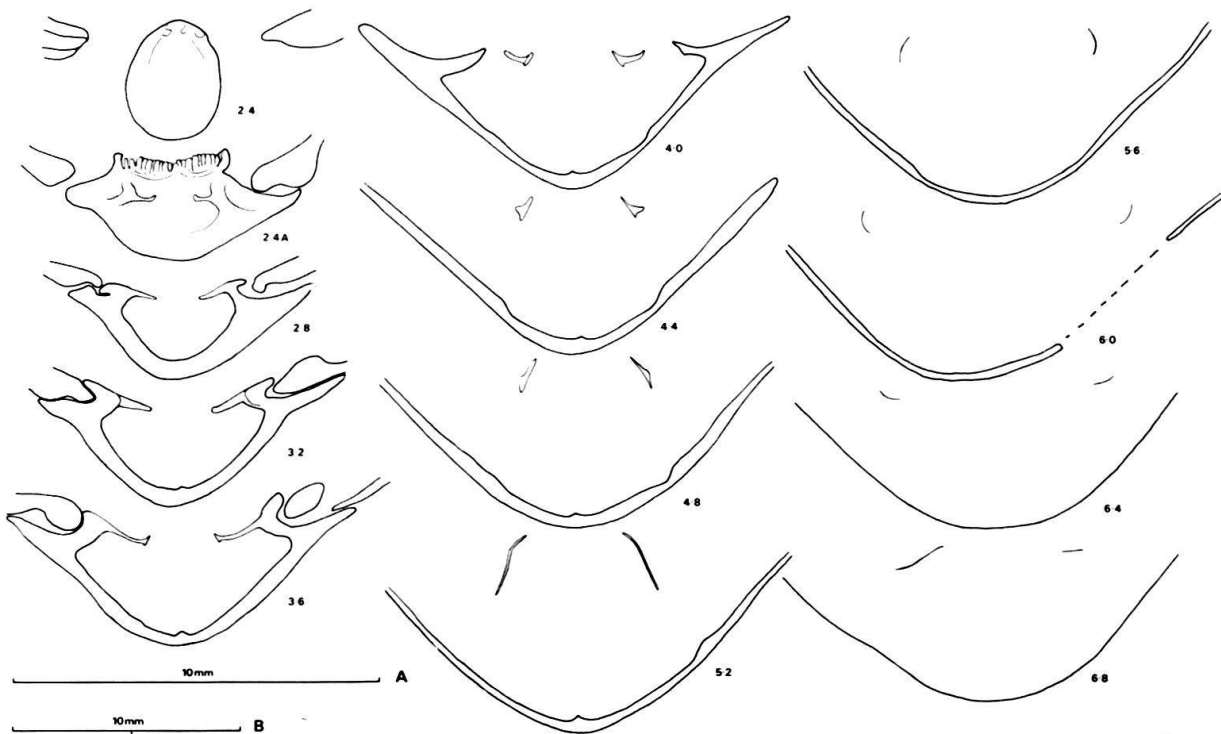


Fig. 13. Serial sections through *Collinithyris collinaria* (D'ORBIGNY). The initially horizontal hinge plates are seen within the cardinal process at 2.4 and 2.4A; they become gently concave and cuneate by 3.6. The keeled and flanged free crural bases are seen at 4.4 and 4.8, maximum height of the crural processes at 5.2 and the very wide loop at 6.0. Sections 2.4 and 2.4A are enlarged with respect to the other sections in order to show detail of the juvenile hinge plates and of the cardinal process. 22G/7/3, except for section 2.4, which is from 22G/7/1. Both specimens Neuchâtel Coll., Valanginian, Villers-le-Lac, Doubs. Dimensions of specimens: 22G/7/3: L. 21.5, W. 21.25, T. 11.75; 22G/7/1: L. 20.5, W. 19.0, T. 10.75.

A = scale for sections 2.4 and 2.4A. B = scale for the remaining sections.

Material. – 29 specimens from the Valanginian of Villers-le-Lac; 2 from the Upper Valanginian of Ste-Croix; 3 from the Upper Valanginian of Les Verrières.

Internal structures. – This species differs from *C. sueuri* in having keeled hinge plates and crura and a very wide loop (0.54 of width of shell, cf. 0.38 in *C. sueuri*).

Remarks. – This species has several homeomorphs in the Lower Cretaceous which share its deep and dramatic uniplication. At least two of these are rhynchonellids – *Lacunosella moutoniana* D'ORBIGNY and *Orbirhynchia malagaensis* OWEN. At least two homeomorphs have been incorrectly identified with *C. collinaria*: *Paraboubeithyris plicae* in the Lower Cretaceous of southwest Morocco (MIDDLEMISS 1980) and a so-far undescribed terebratulid in the Aptian of the Vercors.

Distribution. – Valanginian of the central Jura region and of Le Fontanil and Mallevall (Isère). According to GOČANIN (1938) it is present in the Valanginian “beds with *Terebratula moutoniana*” of the Belgrade area (Yugoslavia).

It occurs more rarely in the Hauterivian of Auberson (Vaud) and, according to PICTET & DE LORIO, Censeau (Jura). CORROY (1925) names it as one of the species which invaded the neritic facies of Aube in the Hauterivian.

PICTET & DE LORIO say that it occurs in the lower urgonian at Annecy; CORROY (1925) claims it in the basal Aptian of Haute-Marne.

OOSTER (1863) lists it in the Cretaceous of the Bernese and Vaudoises Alps, without detailed horizon.

Collinithyris sueuri (PICTET 1872)

Fig. 14, 15

V + 1872 *Terebratula Sueuri* PICTET, p. 89, Pl. 203, Fig. 6–8

Lectotype (here chosen). – Specimen CB1686 in the Muséum d'Histoire Naturelle at Geneva, from the Valanginian of Ste-Croix; figured by PICTET & DE LORIO (1872) as Plate 203, Figure 6.

Paralectotype. – Specimen CB1687 in the Muséum d'Histoire Naturelle at Geneva, from the “Hils” of Schöppenstedt; figured by PICTET & DE LORIO (1872) as Plate 203, Figure 8.

Material. – 6 specimens from the Upper Valanginian of Villers-le-Lac.

Internal structures. – As for genus.

Remarks. – There is an undescribed species occurring in the Upper Valanginian at Villers-le-Lac which strongly resembles *C. sueuri* externally but is a terebratellid. This, or a very similar species, occurs also in the Lower Cretaceous of southwest Morocco, where it seems to have been wrongly identified as “*T. sueuri*” by ROCH (1930), GIGOUT (1951) and AMBROGGI (1963). The occurrence of these two externally similar but quite unrelated species together in the Jura region is a good example of homochronous homeomorphy.

Distribution. – Valanginian of the central Jura region; also of Oliva (Valencia, Spain) and possibly La Querola (Alicante, Spain); it also occurs in Ibiza (age

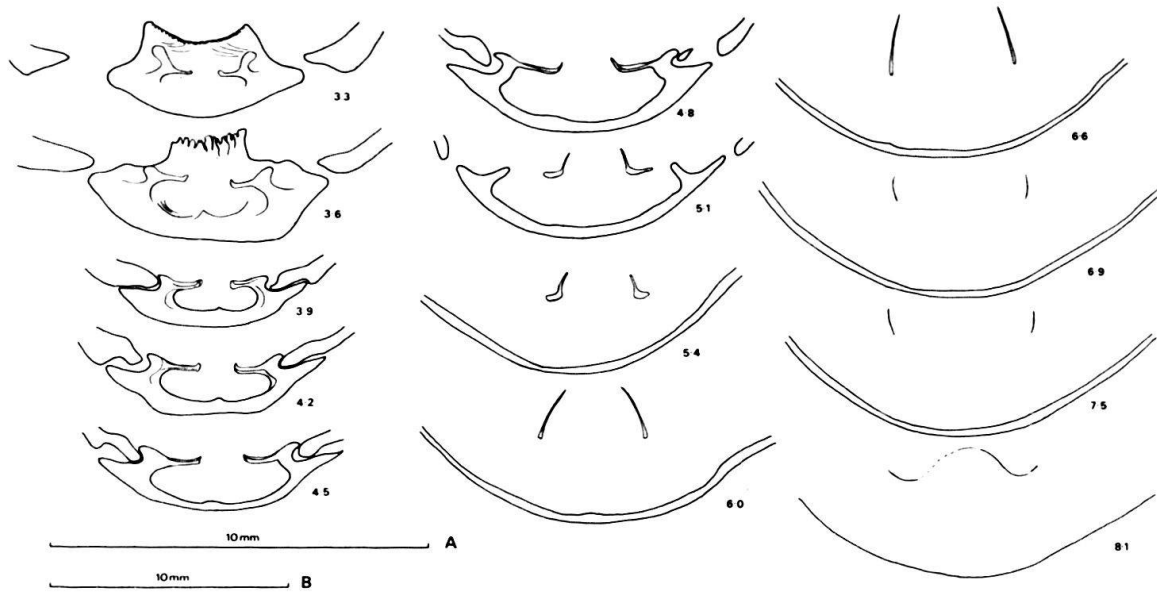


Fig. 14. Serial sections through *Collinithyris sueuri* (Pictet). The initially horizontal hinge plates, already provided with attached crural bases, are seen within the cardinal process at 3.3 and 3.6 and the cuneate hinge plates at 3.9–4.8. The free crural bases at 5.1 and 5.4 are flanged but not keeled. Maximum height of the crural processes is seen at 6.6 and the low-arched transverse band at 8.1. Sections 3.3 and 3.6 are enlarged with respect to the other sections. 22G/6/2, Neuchâtel Coll., Upper Valanginian, Villers-le-Lac, Doubs. Dimensions of specimen: L. 20.5, W. 16, T. 9.25. A = scale for sections 3.3 and 3.6. B = scale for the remaining sections.

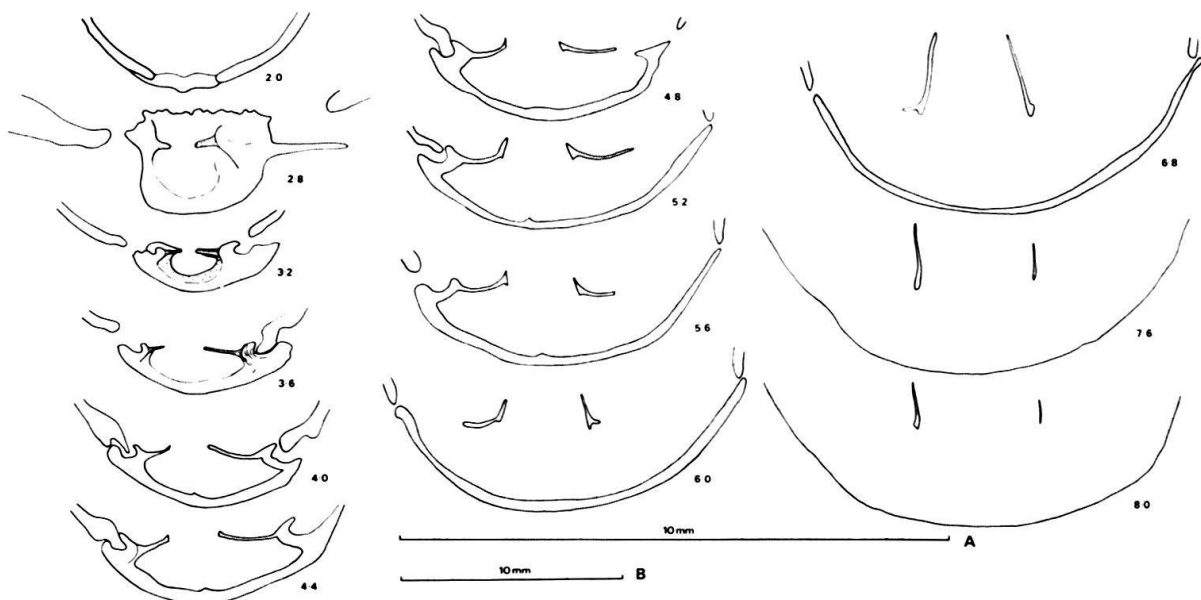


Fig. 15. Serial sections through *Collinithyris sueuri* (Pictet). The initially horizontal hinge plates are seen, enclosed in the cardinal process, at 2.8. Crural bases in this specimen are not developed until 4.0. The cuneate hinge plates are very gently concave at 4.0–5.6. The transverse band was not preserved in this specimen. Section 2.8 is enlarged with respect to the other sections. BM BB 81108, Lower Hauterivian, Schöppenstedt, Brunswick. Dimensions of specimen: L. 28.5, W. 18.5, T. 12. A = scale for section 2.8. B = scale for the remaining sections.

Table 1: Collections in which the species revised have been examined by the author.

	Southwest Morocco	East Spain	North Spain	Southwest France	Provence	Subalpine Chains	South Jura	Central Jura	Southeast Paris Basin	England	Lower Saxon Basin	Helvetikum	Northeast Bulgaria
<i>Costithyrus semistriata</i>							GEN	BM BES NEU	MN BM PM GEN GOT LAU				
<i>Costithyrus ebrodunensis</i>								BM SM NEU GEN LAU					
<i>Costithyrus marcoussana</i>								BM SM LAU NEU					
<i>Costithyrus cruciana</i>								GEN LAU NEU					
<i>"Terebratula" etalloni</i>								GEN LAU					
<i>Sellithyrus sella</i>	PM	GEN BM CAL	BM WIE	BM MN EM PM GEN	MN PM BM GEN FAM	PM ARN	SM GEN	SM NEU GEN LAU BM	MN PM BM GEN LAU	BM SM IGS IOW	BM SM HAN HIL GOT KRE BIE EM	VOR	JAF
				JAF FAM GRE DD				BES BOU VOI					

<i>Sellithyris carteroniana</i>	FAM JAF DD	BM GEN	GRE GEN	GEN FAM	MN PM NEU BM GEN BES FAM VOI	BM HAN HIL GOT	VOR
<i>Sellithyris campichei</i>					GEN NEU		
<i>Sellithyris essertensis</i>	CH RAN			GEN SM BM NEU PM GEN			
<i>Sellithyris montmolini</i>					NEU GEN	HIL GOT	
<i>Musculina sanctaerucis</i>	CH RAN	PM FAM JAF CHA BM DD	PAD PM FAM EST	NEU GEN BM	FAM VOI SM EM BM MN NEU BES LAU PM GOT	BM SM HIL BIE MUN	VOR
<i>Loriolithyris russillensis</i>	BM PM	CH CAL	PM SM MN EM GRE BM	PM GRE ARN	SM NEU PM GEN BES BM LAU FAM		VOR

<i>L. russillensis latifrons</i>	Southwest Morocco	East Spain	North Spain	Southwest France	Provence	Subalpine Chains	South Jura	Central Jura	South-east Paris Basin	England	Lower Saxon Basin	Helvetikum	Northeast Bulgaria
							GEN	GEN NEU					
<i>Loriolithyris valdensis</i>	BM	DD		PAD	GRE	GRE	FAM	NEU	MN			VOR	JAF
	PM	FOU		GEN	PM		GEN	BM	PM				
	AG	CH		BM				GEN	BM				
		CAL		FAM				MN					
								BES					
								SM					
<i>Loriolithyris germaini</i>								GEN					
								NEU					
								BM					
<i>Collinithyrus collinaria</i>						GRE		BM					
								MN					
								GEN					
								NEU					
								LAU					
<i>Collinithyrus sueuri</i>		DD					GEN	GEN			BM	VOR	
		RAN						BM					
								LAU					

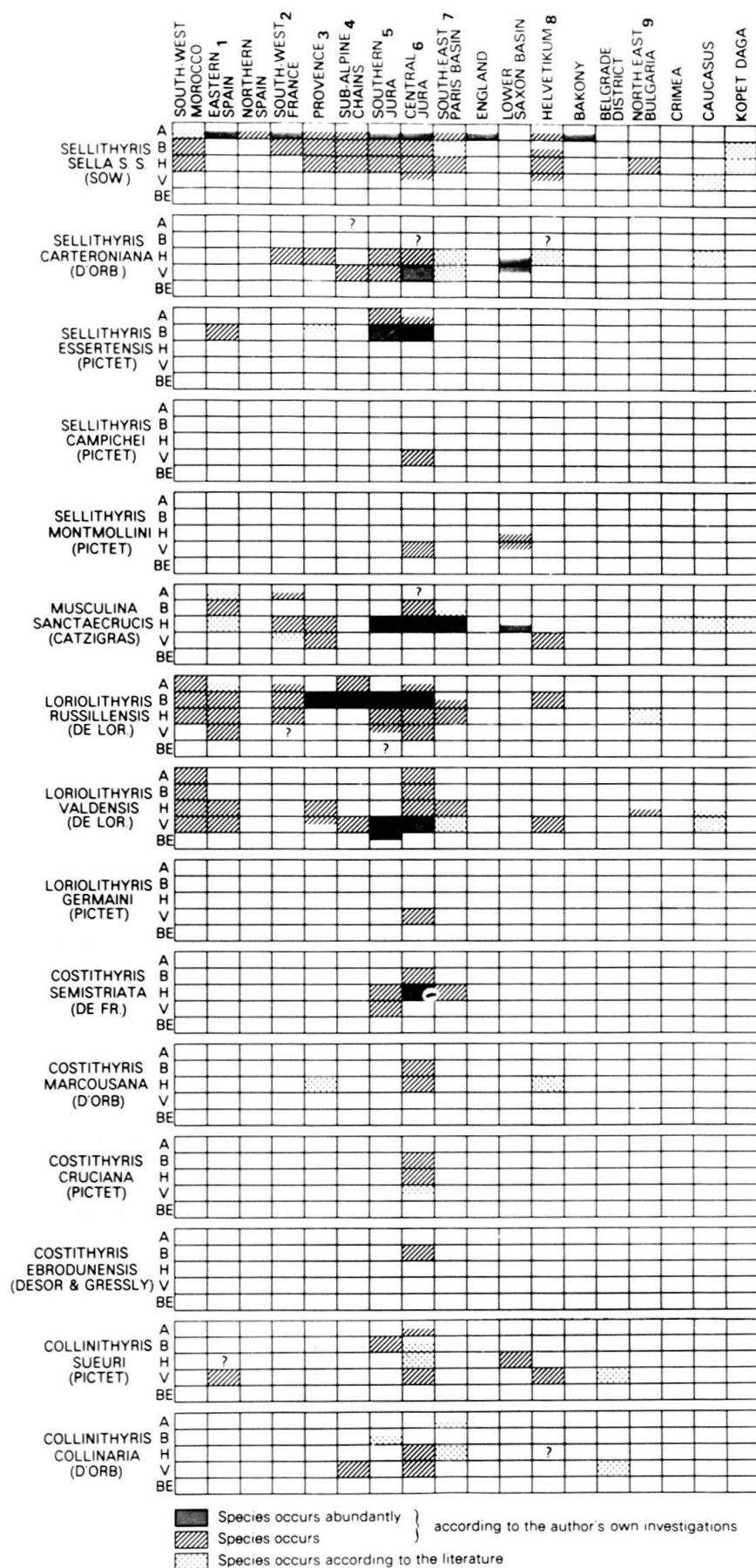
uncertain). Valanginian Oolitenkalk of Vorarlberg. Valanginian “beds with *Terebratula moutoniana*” of the Belgrade area (Yugoslavia) according to GOČANIN 1938.

The species continued into the Hauterivian of the central Jura region, according to PICTET & DE LORIO, and migrated at that time into the Lower Saxon Basin, where it is found rarely at Schöppenstedt. It occurs in the Barremian of Essert (Haute-Savoie) and, according to PICTET & DE LORIO, in the lower urgonian of Morteau (Doubs). Its final appearance seems to be in the Aptian of La Presta (Neuchâtel).

The Jura terebratulid fauna

It can be seen from Figure 16 that the species revised in this article are all concentrated in the central Jura region as a metropolis. From there they can be traced both west and east along a narrow geographical zone which is marginal between the Tethyan (or Mesogean) and Boreal realms. This zone extends westwards through the southern Jura, Isère, Provence, Languedoc and eastern Spain to southwest Morocco; eastwards through the Helvetic regions of central Switzerland, Vorarlberg and the Bavarian Alps, with eastern outliers appearing in northeast

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- AG: Ager Coll. (with the author)
 ARN: M^{re} Arnaud Coll., Grenoble
 BES: Laboratoire de Géologie Structurale et Appliquée, Besançon
 BIE: Stadtmuseum Bielefeld
 BM: British Museum (Natural History), London
 BOU: Boullier Coll. (with the author)
 CAL: Calzada Coll., Barcelona (and with the author)
 CH: Champetier Coll. (with the author)
 CHA: Charrière Coll., Paris (and with the author)
 DD: Durand Delga Coll. (with the author)
 EM: Ecole des Mines, Paris
 EST: Esterle Coll. (with the author)
 FAM: Author's Coll.
 FOU: Fourcade Coll. (with the author)
 GEN: Muséum d'Histoire Naturelle, Geneva
 GOT: Geologisch-Paläontologisches Institut, Göttingen
 GRE: Institut Dolomieu, Grenoble
 HAN: Niedersächsisches Landesamt für Bodenforschung, Hannover
 HIL: Roemer-Museum, Hildesheim
 IGS: Institute of Geological Sciences, London
 IOW: Museum of Isle of Wight Geology, Sandown
 KRE: Geologisches Landesamt Nordrhein-Westfalen, Krefeld
 LAU: University Museum, Lausanne
 MN: Muséum Nationale d'Histoire Naturelle, Paris
 MUN: Westfälische Willhelms-Universität, Münster
 NEU: Institut de Géologie, Neuchâtel
 PAD: Istituto di Geologia, Paleontologia e Geologia Applicata, Padova
 PM: Université Pierre et Marie Curie, Paris
 RAN: Rangheard Coll. (with the author)
 SM: Sedgwick Museum, Cambridge
 VOI: Voigt Coll. (with the author)
 VOR: Vorarlberger Naturschau, Dornbirn
 WIE: Wienands Coll. (with the author)



Bulgaria, the Crimea, Caucasus and Kopet Daga. The southeast Paris Basin acted as northwestern suburb of the central Jura metropolis (see MIDDLEMISS 1979, especially Fig. 1).

The only notable exceptions to this ribbon-like geographical distribution of the species are a) *Sellithyris sella*, which in the Aptian spread northwards to northern Spain and southern England and southwards to the Bakony Forest, and b) four species, *Sellithyris carteroniana*, *S. montmollini*, *Musculina sanctaecrucis* and *Collinitthyris sueuri*, which took advantage of the Upper Valanginian–Hauterivian transgression to invade the Lower Saxon Basin to the north.

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Fig. 16. Stratigraphical and geographical distribution of some Lower Cretaceous terebratulid species of the Jura region.

A = Aptian; B = Barremian; H = Hauterivian; V = Valanginian; BE = Berriasian. 1 = including the Balearic Islands; 2 = Pyrénées Orientales, Aude, Hérault, Gard, Ardèche; 3 = including Sardinia; 4 = Isère; 5 = Savoie, Haute-Savoie, Ain; 6 = Vaud, Neuchâtel, Biel region, Jura, Doubs; 7 = Yonne, Aube, Haute Marne, Meuse; 8 = central Switzerland, Vorarlberg, Bavarian Alps; 9 = southern Dobrogea.

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