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# The genus *Fortunella* (Brachiopoda, Rhynchonellida) and its related species in the Upper Jurassic and Lower Cretaceous

By Heinz Sulser[1]) and Sebastián Calzada[2])

ABSTRACT

The following brachiopod species were assigned to the rhynchonellid genus *Fortunella* Calzada 1985 (type species *Fortunella fortunae* from the Hauterivian of South-East-Spain): *F. monsalvensis* (Gilliéron), *F. fastigata* (Gilliéron), both from the Oxfordian of the Swiss Prealps of Fribourg; *F. makridini* (Tchoumatchenco) from the Oxfordian of the Russian Platform and from Algeria; *F. praemoutoniana* sp. n. from the Lower Cretaceous of the Swiss Prealps of Vaud; *F. moutoniana* (D'Orbigny) from the Barremian of South-East-France; *F. acutifrons* (Sulser & Föllmi) from the Aptian of Vorarlberg (Austria). The species of *Fortunella*, similar to the genus *Lacunosella* in their internal structure, differ from the latter by their much reduced costate or complete smooth shells. The habitat of *Fortunella* seems to be confined to fine-grained sediments in a deeper water environment. According to the present knowledge the stratigraphical range of the genus is from the Lower Oxfordian to the Upper Aptian. It covers a geographical area, comprehending South-East-Spain, the Alps, the Russian Platform and Algeria. Ten further nominal species with unknown internal morphology are included in *Fortunella* tentatively.

ZUSAMMENFASSUNG

Die folgenden Brachiopodenarten wurden der Rhynchonelliden-Gattung *Fortunella* Calzada 1985 (Typusart *Fortunella fortunae* aus dem Hauterivian von Südost-Spanien) zugewiesen: *F. monsalvensis* (Gilliéron), *F. fastigata* (Gilliéron), beide aus dem Oxfordian der freiburgischen Voralpen der Schweiz; *F. makridini* (Tchoumatchenco) aus dem Oxfordian der russischen Plattform und von Algerien; *F. praemoutoniana* sp. n. aus der unteren Kreide der waadtländischen Voralpen der Schweiz; *F. moutoniana* (D'Orbigny) aus dem Barremian von Südost-Frankreich; *F. acutifrons* (Sulser & Föllmi) aus dem Aptian von Vorarlberg (Österreich). Die Arten von *Fortunella*, ähnlich der Gattung *Lacunosella* in ihrer inneren Struktur, unterscheiden sich von der letzteren durch spärlich berippte oder völlig glatte Schalen. Der Lebensraum von *Fortunella* scheint auf feinsandige Sedimente des tieferen Wassers beschränkt zu sein. Nach dem gegenwärtigen Kenntnisstand erstreckt sich die Gattung stratigraphisch vom unteren Oxfordian bis ins obere Aptian. Sie deckt einen geographischen Raum ab, der von Südost-Spanien, über die Alpen bis zur russischen Plattform und Algerien reicht. Von zehn weiteren nominellen Spezies mit unbekannter Innenmorphologie wird ihre Zugehörigkeit zu *Fortunella* vermutet.

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RESUMEN

Se asignan al género *Fortunella* CALZADA, 1985 (especie-tipo *Fortunella fortunae* del Hauteriviense del SE de España) las siguientes especies: *F. monsalvensis* (GILLIÉRON), *F. fastigata* (GILLIÉRON), ambas del Oxfordiense de los Prealpes suizos de Friburgo; *F. makridini* (TCHOUMATCHENCO) del Oxfordiense de la Plataforma rusa y de Argelia; *F. praemoutoniana* sp. n. del Cretácico inferior de los Prealpes suizos de Vaud; *F. moutoniana* (D'ORBIGNY) del Barremiense del SE de Francia y *F. acutifrons* (SULSER & FÖLLMI) del Aptiense de Vorarlberg (Austria). Las especies de *Fortunella* son muy semejantes a las de *Lacunosella* en su morfologia interna, pero difieren por su costulación nula o muy reducida. El género *Fortunella* está asociado generalmente a sedimentos de grano fino, propios de aguas relativamente profundas. La distribución estratigráfica de *Fortunella*, por el momento, abarca del Oxfordiense inferior al Aptiense superior. Cubre la siguiente área geográfica: SE de España, los Alpes, la Plataforma rusa y Argelia. Diez especies, cuyo interior se desconoce, se asignan tentativamente al género *Fortunella*.

## 1. Introduction

When the brachiopod species *"Rhynchonella" monsalvensis* and *"Rhynchonella" fastigata* from the Oxfordian of the Swiss alps, established by GILLIÉRON (1873), were treated by HAAS (1887) in his work of revision, he recognized the relationship between these smooth forms and a group of ribbed rhynchonellids based on QUENSTEDT's *"Rhynchonella lacunosa"*. WIŚNIEWSKA (1932) investigated the internal structures of these brachiopods and found that the crura are of the falcifer type. She erected the genus *Lacunosella,* in which she included besides the ordinary ribbed rhynchonellids also scarcely ribbed and entirely smooth forms. CHILDS (1969) confirmed and completed the diagnosis of WIŚNIEWSKA's genus. Additional features are the missing or much reduced dorsal septum, the lack of a septalium and non-persistent dental lamellae. With the increasing knowledge of these brachiopods it became evident, that the costate lacunosellids were usually associated with sponges and lived on more or less coarse substrates, whereas the smooth forms had their habitat in fine-grained sediments. The latter ones were separated from *Lacunosella* and united to the genus *Fortunella* by CALZADA (1985). Several jurassic and cretaceous species originally described as *Rhynchonella* or *Lacunosella* are considered to belong to it. In this paper some species are assigned definitely, some others tentatively, to *Fortunella.*

## 2. Systematic descriptions

Order **Rhynchonellida** KUHN 1949
Superfamily **Rhynchonellacea** GRAY 1848
? Family **Basiliolidae** COOPER 1959

Genus *Fortunella* CALZADA 1985

*Type species. Fortunella fortunae* CALZADA 1985.

*Diagnosis* (as given by CALZADA 1985). Shell non costate, capillate in early stages, uniplicate. Pedicle collar. Crura falcifer.

The shape of the shell of the following species which are included in this genus was described by prior authors (see GILLIÉRON 1873; HAAS 1887; KILIAN 1888; JACOB & FALLOT 1913; SULSER & FÖLLMI 1984; CALZADA 1985). The internal structures, unknown hitherto, were studied by serial sections. Both external and internal morphology are summarized in the tables 1 and 2.

## *Fortunella fortunae* CALZADA 1985

1985 *Fortunella fortunae* CALZADA: p. 78; Pl. 1, Figs. 2–4, Text-Fig. 2A.

*Holotype* in CALZADA (1985, Pl. 1, Fig. 4a–d) from the Lower Hauterivian (deep facies) of the Sierra del Lugar near Fortuna, prov. Murcia, South-East-Spain. Geological Museum, Seminario of Barcelona (32.491-13).

*Diagnosis* (translated from CALZADA 1985). *Fortunella* with an apical sulcus on the ventral valve, without any ribs on either valve or lateral commissure.

*Remarks.* Nothing new can be said about this species which was adequately described and figured in CALZADA (1985). At present it is known only from the type locality.

## *Fortunella monsalvensis* (GILLIÉRON 1873)

Plate 1, Figs. 1–3, Text-Fig. 1

1873 *Rhynchonella monsalvensis* GILLIÉRON: p. 244; Pl. 10, Figs. 11, 12.
1876 *Rhynchonella monsalvensis* GILL.; FAVRE: p. 67; Pl. 7, Figs. 6, 7.
1887 *Rhynchonella monsalvensis* GILL.; HAAS: p. 99; Pl. 8, Figs. 1–14.
?1908 *Rhynchonella monsalvensis* GILL.; LEWINSKI: p. 436; Pl. 22, Figs. 12–14.
1913 *Rhynchonella monsalvensis* GILL.; JACOB & FALLOT: p. 23; Pl. 1, Figs. 24, 25.
1917 *Rhynchonella monsalvensis* GILL.; ROLLIER: p. 141.
?1932 *Lacunosella monsalvensis* (GILL.); WIŚNIEWSKA: p. 53; Pl. 5, Figs. 12, 13, Text-Fig. 15.
1957 *Rhynchonella monsalvensis* GILL.; GUILLAUME: p. 16; Text-Fig. 3.
1984 *Lacunosella monsalvensis* (GILL.); SULSER & FÖLLMI: p. 626.

*Lectotype* (selected here), figured in HAAS (1887, Pl. 8, Figs. 3a–e) from the "Calcaire à ciment" (Oxfordian; cordatum zone according to GUILLAUME 1957) of Sous-Planière near Châtel-St. Denis, Prealps of Fribourg, Switzerland. Museum of Geology, Lausanne, Inventary-No. 40826.

*Diagnosis. Fortunella* with oval to subtriangular outline and subequally biconvex, depressed profile. Ribs (if any) only in traces at the front. Very week anterior fold.

*Remarks.* This species seems to be confined mainly to the Alps of Fribourg, but was detected also in the Oxfordian of the region of Les Diablerets, canton of Vaud (RENEVIER 1890: p. 225). According to JACOB & FALLOT it is not known from the South-East of France. The reference for the occurrence in Poland (WIŚNIEWSKA 1932) is doubtful; the probably related Polish form bears a distinct costation. The relation to the similar but younger (upper Portlandian) *Fortunella*? *monsalvensiformis* (JACOB & FALLOT 1913) from the northern part of Provence, France, remains also to be cleared.

Apart from the occasional development of rudimentary ribs and the depth and length of the ventral sulcus *F. monsalvensis* generally shows a rather limited variability (compare figures in HAAS 1887).

ROLLIER (1917) considered the possibility that *F. monsalvensis* might represent juvenile specimens of *F. fastigata*. Such an extreme case of ontogenetical dimorphism does not fit the conception of shell growth in brachiopods and cannot be accepted.

## *Fortunella fastigata* (GILLIÉRON 1873)

Plate 1, Figs. 4, 5, Text-Figs. 2, 3

1863 *Rhynchonella acutiloba* EUD.-DESL.; OOSTER: p. 49; Pl. 16, Figs. 3–8.
1873 *Rhynchonella fastigata* GILLIÉRON: p. 245; Pl. 10, Figs. 13, 14.
1876 *Rhynchonella fastigata* GILL.; FAVRE: p. 68; Pl. 7, Fig. 8.

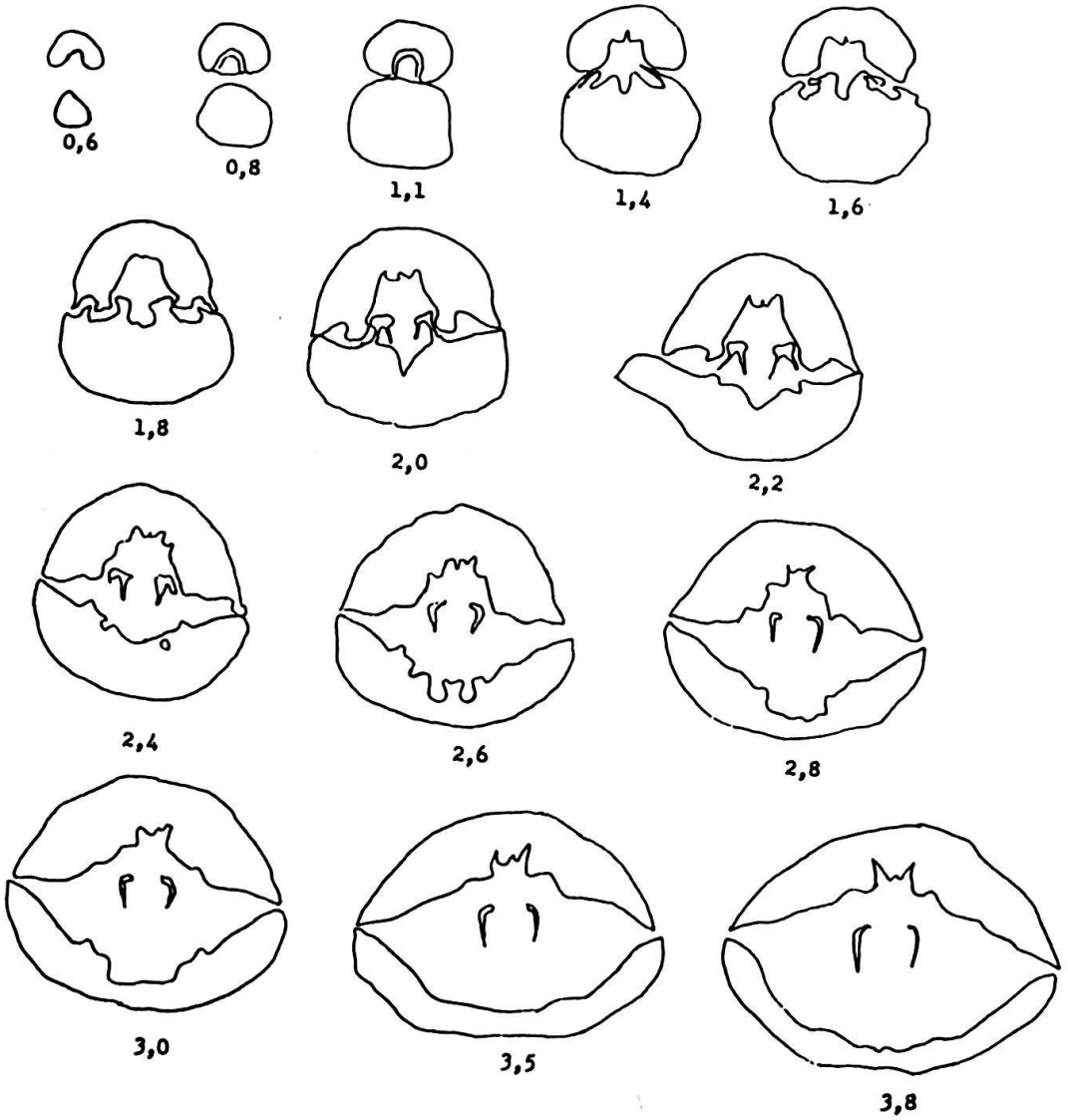


Fig. 1. Transverse serial sections of *Fortunella monsalvensis* (Gilliéron). Oxfordian. Sous-Planière near Châtel-St. Denis, Switzerland. Numerals represent distance in millimetres from pedicle umbo (× 3).

1887 *Rhynchonella fastigata* Gill.; Haas: p. 103; Pl. 8, Figs. 20–22, Pl. 10, Fig. 11.
1887 *Rhynchonella monsalvensis* Gill. var. *heimi* Haas: p. 100; Pl. 8, Figs. 15–19.
1913 *Rhynchonella fastigata* Gill.; Jacob & Fallot: p. 23; Pl. 1, Fig. 23 (20–22?).
1917 *Rhynchonella fastigata* Gill.; Rollier: p. 141.
1984 *Lacunosella? fastigata* (Gill.); Sulser & Föllmi: p. 626.

*Lectotype* (selected here) in Haas (1887, Pl. 8, Figs. 22a–e; reproduced in Jacob & Fallot 1913, Pl. 1, Figs. 23a–c) from the "Calcaire à ciment" (Oxfordian; cordatum Zone) of Sous-Planière near Châtel-St. Denis, Prealps of Fribourg, Switzerland. Museum of Geology, Lausanne, Inventary-No. 4055.

*Diagnosis. Fortunella* with cynocephalous profile. Ventral valve geniculate at mid-length. Pronounced lingual extension.

*Remarks.* This species may occur in regions outside the Alps of Fribourg, where its stratigraphical level is the "Calcaire à ciment" and the slightly younger "Calcaire con-

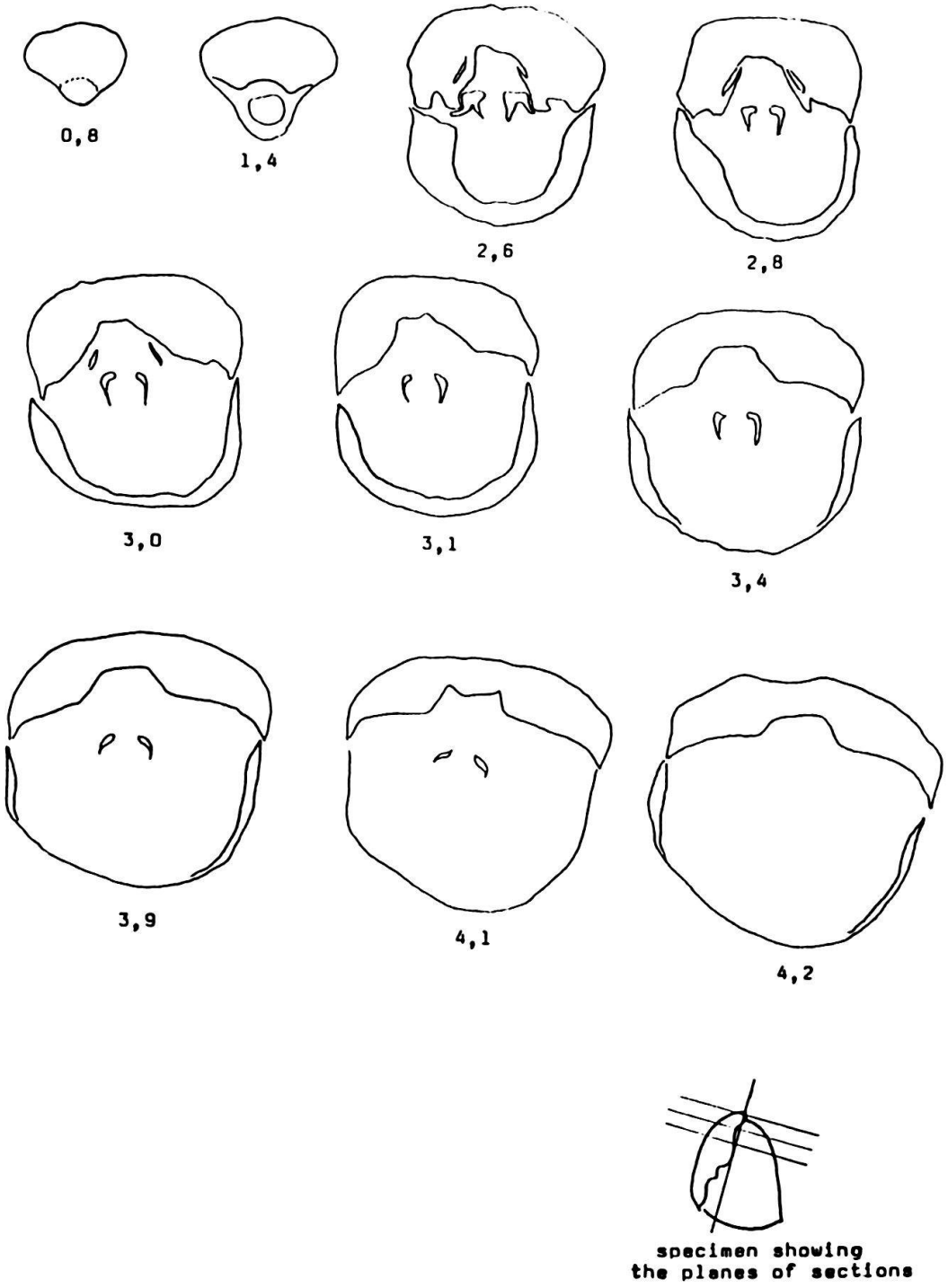


Fig. 2. Transverse serial sections of *Fortunella fastigata* (Gilliéron). Oxfordian. Sous-Planière near Châtel-St. Denis, Switzerland. Numerals represent distance in millimetres from pedicle umbo (× 3).

crétionné" (see Guillaume 1957: p. 7). According to Jacob & Fallot (1913) it occurs in still younger strata of the Kimmeridgian and Portlandian (?) in South-East-France.

Unfortunately most of the specimens of this species are broken. In view of their distinctive shape the degree of variability is low and seldom affects the characteristic

cynocephalous profile. We consider that *F. monsalvensis* var. *heimi* Haas falls within the variability of the normal type. Transitional forms of questionable assignment (possible confusion with *F. monsalvensis)* are rare if existing at all. In adult individuals the articulation of the shell seems to be weakened as the ventral umbo is frequently shifted over the dorsal one.

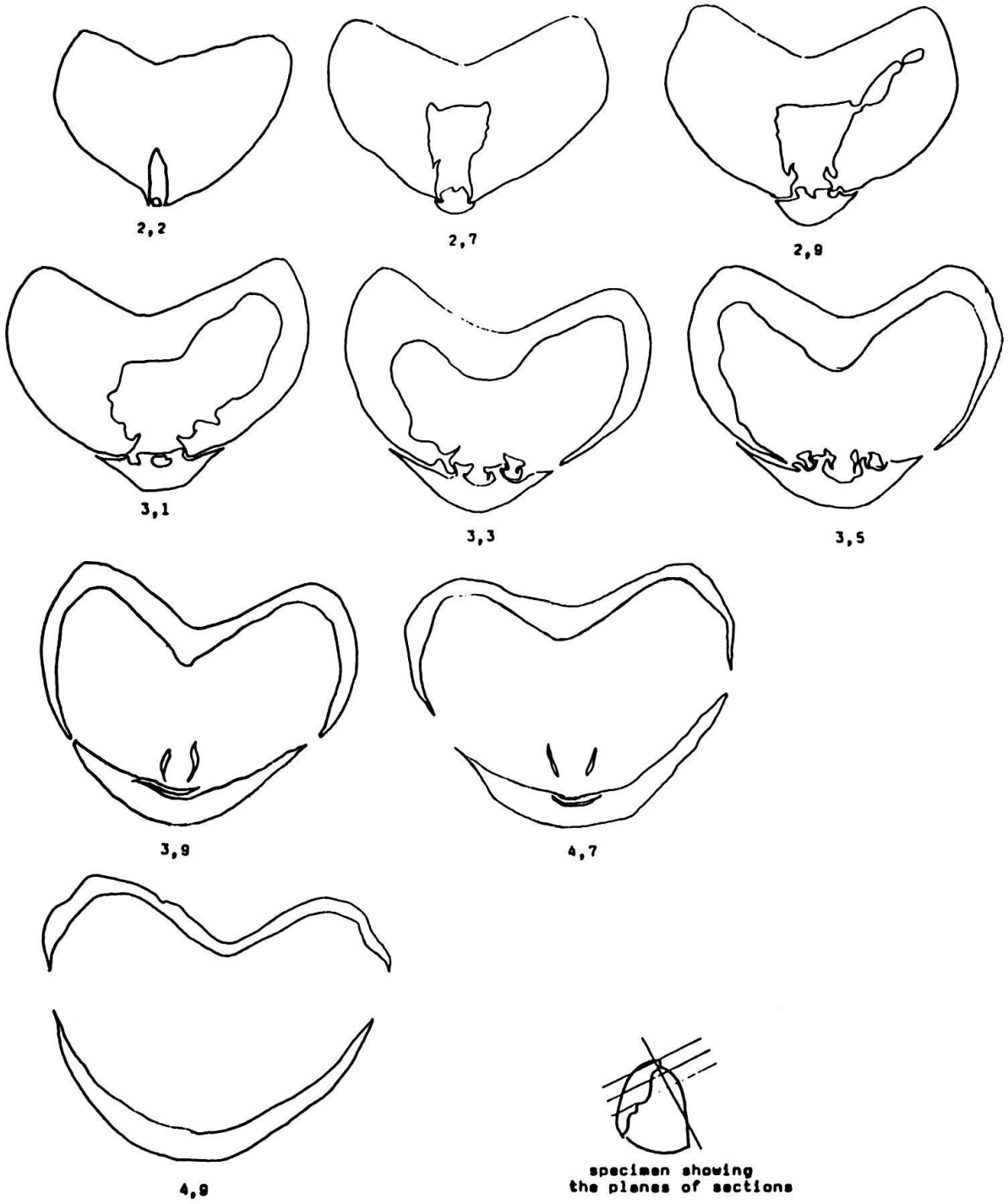


Fig. 3. Transverse serial sections of *Fortunella fastigata* (Gilliéron). Oxfordian. Sous-Planière near Châtel-St. Denis, Switzerland. Due to the particular shape of the shell oblique sections (see sketch) were chosen to show insertion of the teeth (section 3,3). Numerals represent distance in millimetres from pedicle umbo (× 2,5).

### *Fortunella makridini* (Tchoumatchenco 1987)

1964 *Lacunosella* aff. *fastigata* (Gill.); Makridin: p. 199; Pl. 11, Fig. 15.
1987 *Lacunosella (Lacunosella) makridini* Tchoumatchenco: p. 50; Pl. 3, Figs. 1, 2, Text-Fig. 4.

*Holotype,* selected by Tchoumatchenco (1987), in Makridin (1964, Pl. 11, Fig. 15), from the Upper Oxfordian of the syneclise of Moscow, USSR. University of Kharkov (196/35034).

*Diagnosis.* An original diagnosis was not given. The present authors' diagnosis is as follows: *Fortunella* with planoconvex shell, the brachial valve being 3 times more convex than the ventral one. Smooth, with the exception of one smooth costa on each wing.

*Remarks.* The serial sections figured by Tchoumatchenco seem to have been made along an oblique plane, resulting in an abnormal position of the pedicle collar (more ventral), of the deltidial plates (more convergent ventrally) and of other characters. The same can be seen in the figures showing an anterior sinus (outline ligate). With a change of the orientation this sinus would disappear. The peculiar shape of the shell implies a close relationship to *F. fastigata.*

*F. makridini* seems to occupy the widest geographic range of the known members of the genus *Fortunella.* Published records according to Tchoumatchenco (1987) are from the russian Platform (Upper Oxfordian) as well as from Algeria (Upper Oxfordian–Lower Kimmeridgian).

### *Fortunella praemoutoniana* sp. n.

Plate 2, Figs. 1, 2, Text-Figs. 4, 5.

*Derivation of name: praemoutoniana* – the species appears in a stratigraphically earlier level than the similarly shaped *F. moutoniana.*

1913 *Rhynchonella* cf. *cherennensis* var. *moutoniformis* Jacob & Fallot: p. 38; Pl. 4, Figs. 17–21, Pl. 11.
1918 *Rhynchonella* cf. *cherennensis* var. *moutoniformis* Jacob & Fallot; Jeannet: p. 574, 575, 580, 581.
1984 *"Rhynchonella* cf. *cherennensis* var. *moutoniformis"* Jacob & Fallot; Sulser & Föllmi: p. 626.

*Lectotype* (selected here) in Jacob & Fallot (1913, Pl. 4, Figs. 17a–c and Pl. 11, Fig. 1), from the "Couches à Brachiopodes" (Berriasian or Valanginian ?, see remarks) of Leysin, Prealps of Vaud, Switzerland. Collection Lugeon 1906, Museum of Geology, Lausanne, Inventary-No. 40825.

*Diagnosis. Fortunella* with inequally curved valves. No ribs. Lingual extension acute or rounded, often shifted laterally (resulting in an asymmetrical shape of the shell).

*Remarks.* This species is known only from the area of Leysin at the southern slope of Tour d'Aï in the alps of Vaud. Its age is still a point of some discussion. As these brachiopods rest on a corroded surface of Upper Portlandian (with *Calpionella alpina),* they are considered by most authors to be of lower cretaceous age. Investigations by Berliat (1943), Weiss (1949) and Klaus (1960) revealed that these fossils were embedded in a transgressive sediment of Cenomanian age (with *Globotruncana appenninica).* The inside of the shell is filled by a glauconitic limestone in which the presence of foraminifera of the *Rotalipora ?cushmani*-group could be demonstrated, pointing to an age of Upper Cenomanian (by courtesy of Prof. H. Rieber and Prof. H. Bolli). The thin-layered brachiopod beds give reasons to believe that the macrofauna was worked up and the primary sediment completely eliminated. Thus a Berriasian age of *Fortunella praemoutoniana* is probable.

A smooth brachiopod was named *Rhynchonella cherennensis* var. *moutoniformis* by Jacob & Fallot, in contrast to the costate species. Both forms occur in the same stratigraphical level and at the same locality (Hauterivian of Saint-Pierre-de-Chérennes, Dép. Isère, France). *Rhynchonella* cf. *cherennensis* var. *moutoniformis*, the name used by the same authors for the brachiopods from Leysin, is very similar in

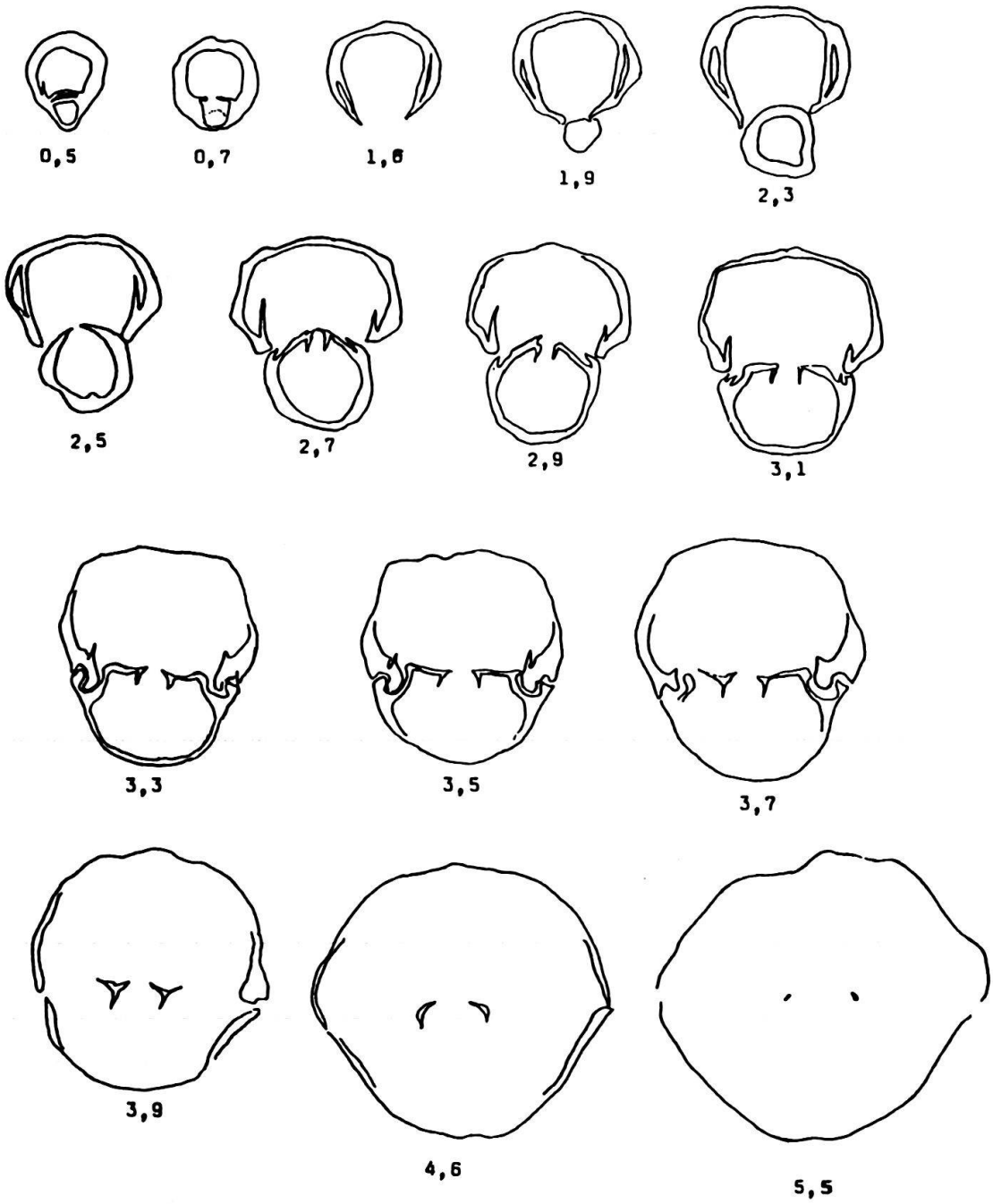


Fig. 4. Transverse serial sections of *Fortunella praemoutoniana* sp. n. "Couches à Brachiopodes". Leysin, Switzerland. Hinge plates convex at posterior part, then becoming horizontal. Numerals represent distance in millimetres from pedicle umbo (× 3).

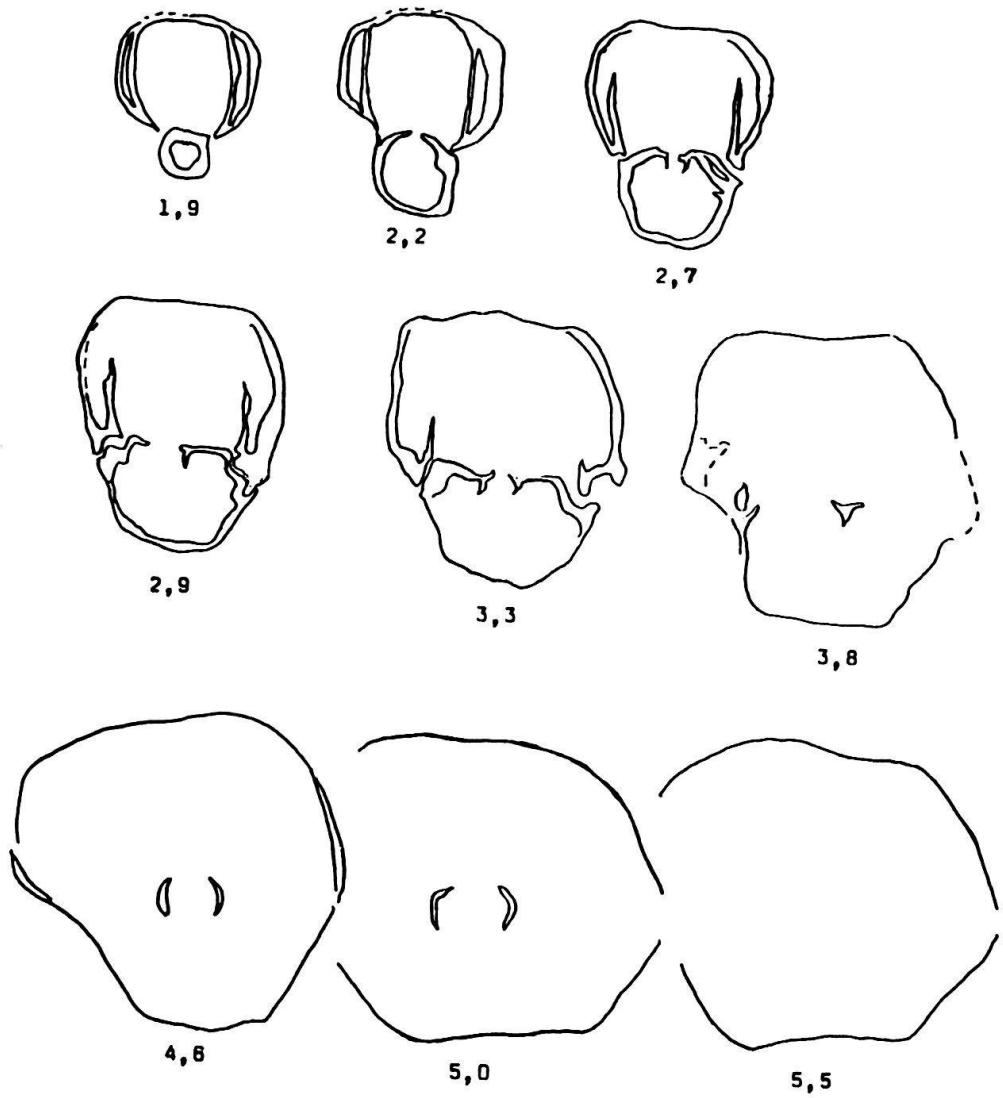


Fig. 5. Transverse serial sections of *Fortunella praemoutoniana* sp. n. "Couches à Brachiopodes". Leysin, Switzerland. Numerals represent distance in millimetres from pedicle umbo (× 3).

shape, but larger on average. As commented above it is very probable that it appears earlier, near the transition of the jurassic to the cretaceous area. This form is therefore regarded as species of its own and is given a new name.

## *Fortunella moutoniana* (D'Orbigny 1847)

Plate 2, Figs. 3–5, Text-Fig. 6

1847 *Rhynchonella moutoniana* D'Orbigny: p. 15 (text only).
1851 *Rhynchonella moutoniana* D'Orbigny: Pl. 494, Figs. 17–20 (16–19 in the text).
1888 *Rhynchonella moutoni* var. Kilian: p. 689; Pl. 17, Fig. 5.
1889 *Rhynchonella moutoni* var. Kilian: p. 437, Fig. 59.
1896 *Rhynchonella moutoniana* D'Orbigny; Loriol: p. 161; Pl. 6, Fig. 25.
?1907 *Rhynchonella moutoni* D'Orbigny; Karakasch: p. 204; Pl. 21, Figs. 7, 10.
?1907 *Rhynchonella tschernyschewi* Karakasch: p. 208; Pl. 21, Fig. 3.

1910 *Rhynchonella moutoniana* D'Orb. mut. *major* Kilian: Pl. 7, Fig. 4.
1913 *Rhynchonella moutoniana* D'Orb.; Jacob & Fallot: p. 39; Pl. 4, Figs. 22–24.
non 1960 *Lacunosella montaniana* (sic) (D'Orb.); Makridin (russian treatise): Pl. 50, Fig. 14.
1972 *Lacunosella? moutoniana* (D'Orb.); Ager et al.: p. 188.
1972 *Lacunosella moutoniana* (D'Orb.); Smirnova: p. 29; Pl. 1, Figs. 7–9; Text-Figs. 5, 6.
?1973 *Lacunosella moutoniana* (D'Orb.); Smirnova: p. 180; Text-Figs. 1, 2.
?1986 *Lacunosella moutoniana* (D'Orb.); Lobacheva: p. 129.
?1990 *Lacunosella moutoniana* (D'Orb.); Smirnova: p. 7, Pl. 1, Fig. 6.

*Diagnosis. Fortunella* with subpentagonal outline, inequivalve. 1–3 flattened lateral ribs near the commissure. Lingual extension usually rounded, as high as broad.

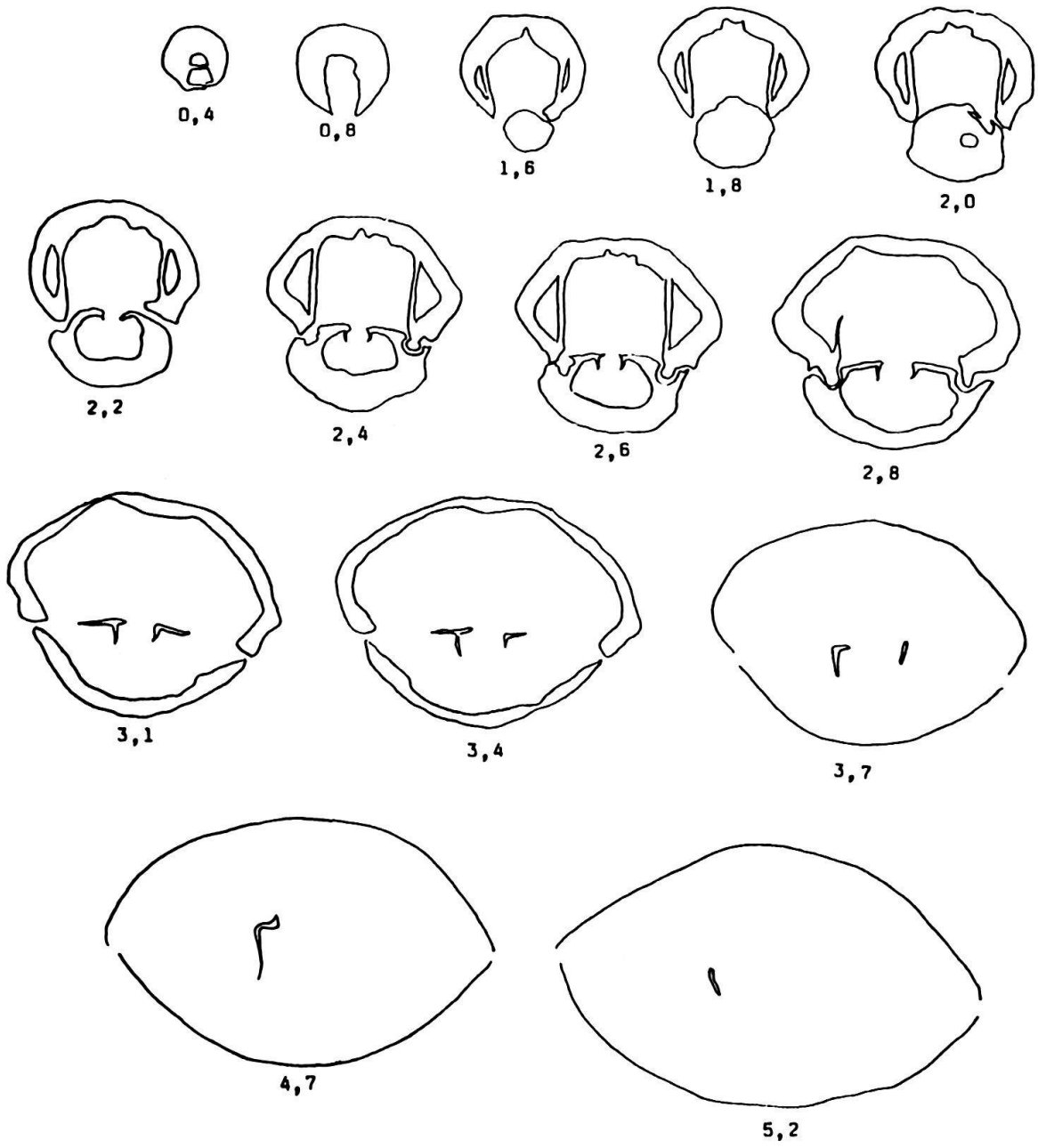


Fig. 6. Transverse serial sections of *Fortunella moutoniana* (D'Orbigny). Barremian. Combe-petite, Montagne de Lure, South-East-France. Numerals represent distance in millimetres from pedicle umbo (× 3).

*Remarks.* Among the *Fortunella* species this form is the most conspicuous in size and shows the most constant development of width, relative to the length. For this study specimens were available from the region of Grenoble and from the Montagne de Lure near Sisteron, South-East-France, but no topotype material was at our disposal. These forms were described by KILIAN as an unnamed variety, which, by comparison with the type of D'ORBIGNY from the Barremian of Escragnolles (France), shows some differences: it is somewhat smaller, its lingual extension more tapering, its costation reduced to traces and it bears a more massive beak. In our opinion these forms fall within the variability of the species and there is no necessity to separate them. *F. moutoniana* was reported by LORIOL (1896) and also by SMIRNOVA (1972 and 1973, with further references) and LOBACHEVA (1986) to occur in the Crimea, but the published figures (with the exception of those by LORIOL) show a distinct and evidently more constant costation. The figure of *Lacunosella moutoniana* sensu SMIRNOVA, given in her latest publication (1990), fits well into the features of the genus *Fortunella,* but the description is so short that no valid conclusion can be drawn.

### *Fortunella acutifrons* (SULSER & FÖLLMI 1984)

1984 *Lacunosella acutifrons* SULSER & FÖLLMI: p. 619; Text-Figs. 1–5.

*Holotype* in SULSER & FÖLLMI (1984, Text-Figs. 1 and 3), from the Upper Aptian of "Untere Wäldlealp" near Ebnit, Vorarlberg, Austria. Paleontological Institute and Museum of the University of Zurich, Invent.-Nr. H/3.

*Diagnosis. Fortunella* with subquadratic to subrhomboidal outline. Rudimentary ribs at lateral commissure, with sharp anterior fold and acute uniplication.

*Remarks.* This species is presently known only from a single outcrop at the type locality (fide FÖLLMI, personal communication). An attempt to obtain further specimens from this place, did not yield any more rhynchonellids suited for new studies. Thus no information in addition to the original description is available.

The following nominal species are included in *Fortunella* tentatively, according to external characters only:

*Rhynchonella decipiens* D'ORBIGNY 1847; Barremian, South-East-France.

*Rhynchonella spoliata* SUESS 1859; Portlandian, Czechoslovakia (North-Moravia).

*Rhynchonella decipiens* sensu OOSTER 1863; Aptian (?), Bernese Alps, Switzerland.

*Rhynchonella boissieri* PICTET 1867; Berriasian, South-East-France (Berrias).

*Rhynchonella capillata* ZITTEL 1870; Portlandian, South-Poland (West-Galicia).

*Rhynchonella tchkmeriensis* LORIOL 1896; Aptian (?), Caucasus.

*Rhynchonella monsalvensiformis* JACOB & FALLOT 1913; Portlandian, South-East-France.

*Rhynchonella cherennensis* var. *moutoniformis* JACOB & FALLOT 1913; Hauterivian, South-East-France.

*Rhynchonella cherennensis* var. *undulata* JACOB & FALLOT 1913; Hauterivian, South-East-France.

*Rhynchonella decipiens* sensu MUIR-WOOD 1953; Infravalanginian (?), East-Greenland.

| Fortunella species | Shell dimensions: Average length, width, thickness | Outline | Profile | Dorsal valve | Ventral valve | Lateral commissure | Anterior commissure | Costation |
|---|---|---|---|---|---|---|---|---|
| F. fortunae | L = 16, W = 18, T = 13 mm. | Subpentagonal to subrhomboidal, often asymmetrical. | Inequally biconvex, cynocephalous. | Strongly convex, carinate in anterior half of the valve. | Slightly sulcate near the apex. | Inflected ventrally, turning toward the front in a rounded curve. | Sharply uniplicate (V-shaped), often asymmetrical. | None. |
| F. monselvensis | L = 17, W = 19, T = 9 mm. | Transverse-oval to subtriangular. | More or less equally biconvex, depressed. | Slightly curved. No fold. | Slightly curved. Shallow sulcus in anterior part. | Straight. | Broadly uniplicate, sometimes with slight undulations. | Usually none, rarely traces of diffuse ribs on anterior half of valve. |
| F. fastigata | W = 20 mm, L and T not defined, much dependent on orientation of the shell. | Subpentagonal, maximum width at midvalve or posteriorly. | Cynocephalous. | Curved posteriorly, then almost flat, often somewhat concave near the front. Fold narrow, rounded. | Slightly curved, geniculate at midvalve. Sulcus becoming broader anteriorly. | Straight posteriorly, undulated anterolaterally. | Lingual extension acute, sometimes rounded at its very end. | 2-3 smooth costae laterally developed at about midvalve |
| F. praemoutoniana | L = 18, W = 20, T = 13 mm. | Oval to subpentagonal, moderately trilobate. | Inequivalve, angle between dorsal valve and anterolateral commissure up to 90° and more. | Moderately curved posteriorly, slightly curved or almost flat anteriorly. No fold, but often carinate near the front. | Slightly curved. Sulcus broad or narrow, becoming deeper anteriorly. | Slightly inflected ventrally, turning toward the front in a rounded curve. | Marked lingual extension, at its end either rounded or acute, often shifted laterally (asymmetrical). | None. |
| F. makridini | L = 12, W = 14, T = 12 mm (for Algerian specimens). | Subpentagonal, maximum width posteriorly. (See also remarks on F. fastigata) | Cynocephalous. | Strongly convex with prominent umbo and with middle carina beginning near the umbo. | Slightly curved, almost plane, geniculate. | Almost straight, slightly inflected ventrally. | V-shaped, symmetrical, strongly uniplicate. Lingual extension triangular, sharply acute at its end. | Only a smooth costa on each wing. |
| F. moutoniana | L = 26, W = 29, T = 17 mm. | Subpentagonal. | Inequivalve, angle between dorsal valve and anterolateral commissure mostly 70-80°. | Slightly and regularly curved. Fold on anterior part small and rounded. | Slightly curved. Sulcus becoming broader and deeper anterior of midvalve. | Slightly inflected ventrally, turning toward the front in a rounded undulated curve. | Lingual extension rounded, as high as broad, rarely acute at its end. | Usually 1-3 flattened lateral ribs near the commissure, rarely without any trace of costation. |
| F. acutifrons | L = 23, W = 25 T = 19 mm. | Subquadratic to subrhomboidal. | Valves inequal, joining in obtuse angle at the front. | Strongly curved posteriorly, almost flat at the front. Fold developed near the front, sharp. | Slightly curved, geniculate at beginning anterior third. | Straight posteriorly, then suddenly inflected ventrally, undulated, zigzag-shaped anterolaterally. | Lingual extension narrow, V-shaped, higher than broad, with small (3-4 mm high), acute secondary extensions on each side. | Lateral costae at anterior part, near the commissure becoming angular. |

Table 1: *External criteria for specific distinction.*
All species show an erect to suberect, usually small beak, a small pedicle opening (where observable), an apical angle between 90–110° and the lack of beak ridges.

| Fortunella species | Ventral valve | Dorsal valve | General remarks |
|---|---|---|---|
| F. fortunae | Deltidial plates fused (?).<br>Low pedicle collar present.<br>Dental lamellae and lateral cavities not visible.<br>Hinge teeth rather thick, well inserted (somewhat oblique) in dental sockets.<br>Denticula present. | Hinge plates horizontal, somewhat convex.<br>Falcifer crura subparallel, well developed, showing irregularly Y-shaped sections.<br>Sockets broad, with well defined inner and outer ridges. | Posterior parts of both valves infilled with secondary material. |
| F. monsalvensis | Deltidial plates, dental lamellae and lateral cavities not visible.<br>Hinge teeth truncated, inserted somewhat loosely in dental sockets. | Hinge plates short.<br>Falcifer crura developed early, forming characteristic "knobs" first, then parallel blades, slightly bent dorsally.<br>Sockets with inner and outer ridges, crenulated at the bottom. | Posterior parts of both valves infilled with secondary material. |
| F. fastigata | Deltidial plates not visible.<br>Lateral cavities very narrow, situated on inside.<br>Hinge teeth more or less hidden . | Hinge plates, crura and sockets similar as in F. monsalvensis, but crura at distal end slightly shorter, twisted laterally . | Posterior parts of both valves mostly infilled with secondary material.<br>Inner structures very similar to F. monsalvensis. |
| F. makridini | Deltidial plates non fused (?).<br>Pedicle collar strong.<br>Delthyrial cavity squared.<br>Dental lamellae subparallel, persistent.<br>Hinge teeth rather broad, well inserted in dental sockets. | Hinge plates large and persistent, well developed horizontally.<br>Falcifer crura developed early, blades becoming S-shaped anteriorly, but at their end being straight and parallel, expanding ventrally. | Posterior parts of both valves infilled slightly with secondary material.<br>The plane of the sections is somewhat oblique. |
| F. praemoutoniana | Deltidial plates fused (?).<br>Pedicle collar present.<br>Dental lamellae converging ventrally, reduced.<br>Lateral cavities narrow.<br>Hinge teeth comparatively thick, rounded, well inserted (somewhat oblique) in dental sockets. | Hinge plates horizontal, thin, sometimes convex proximally.<br>Falcifer crura visible early, remaining rather short, showing sections of a star-like triangle first, then becoming "saussage"-shaped in constant size.<br>Sockets broad, with defined inner and outer ridges. | |
| F. moutoniana | Deltidial plates fused (?).<br>Pedicle collar present.<br>Dental lamellae parallel, persistent.<br>Lateral cavities triangular.<br>Hinge teeth rather small, globulous, well inserted in dental sockets. | Hinge plates horizontal, separated early.<br>Falcifer crura proximally with dominating horizontal structures, then growing longer and becoming persistent.<br>Sockets with marked outer ridge, inner ridge weak. | Dorsal valve infilled with callose material. |
| F. acutifrons | Deltidial plates fused (?), distally curved at outside.<br>Pedicle collar not observed.<br>Dental lamellae parallel, reduced.<br>Lateral cavities triangular, narrow.<br>Hinge teeth broadened at the bottom, crenulated, well inserted in dental sockets. | Hinge plates horizontal, convex proximally.<br>Falcifer crura short, thin, with broad horizontal structures on ventral side.<br>Sockets with clear outer and inner ridges. | |

Table 2: *Internal criteria for specific distinction.*
All species show the presence of denticula (weak in *F. acutifrons)* and the lack of a dorsal septum.

## 3. Conclusions

Based on internal characters seven species are assigned here to the genus *Fortunella.* As a consequence its distribution is enlarged both geographically and chronostratigraphically. According to the present knowledge *Fortunella* ranges from the Lower Oxfordian to the Upper Aptian. It is reported from South-East-Spain, South-East-France, from the alpine chains of Switzerland and Austria, and from the Soviet Union and Algeria. Several other species, not yet assigned with certainty to the genus, are described from the Carpathians and Greenland.

Russian authors erected the genus *Rionirhynchia* (type species: *R. tsessiensis)* for small smooth rhynchonellids of the Early Cretaceous of western Georgia, USSR (KAMYSCHAN & KVAKHADZE 1980). In their description they mention occasional ribs near the anterior margin, dental lamellae converging dorsally (without reaching the bottom of the valve) and narrow crura of the prefalcifer type. The external and internal features of the two species assigned to *Rionirhynchia* are close to *Fortunella.* Some features of *Rionirhynchia* may be the presence of strong growth lines, the strong tendency to subequally convex valves and the more thickened crura. Whether both genera, assigned to the family Basiliolidae COOPER, should be considered synonymous (with *Fortunella* as junior synonym) remains a matter of thorough analysis and is not discussed here.

With regard to the external shell characters it is difficult to point out gradual changes when species from the Lower Jurassic, the Jurassic/Cretaceous border and the Lower Cretaceous are compared. Neither the outline of the profile nor the anterior commissure nor the costation show any clear trends in this sense (Table 1). In the internal structure the most evident difference between the jurassic and cretaceous species is observed in the crura. In the early development of the crura, i.e. soon after giving off the crural bases from the hinge plates, long thin blades appear in *Fortunella monsalvensis* and *F. fastigata,* as it is seen in *Lacunosella.* In the cretaceous species the proximal parts of the crura show transitional triangular structures, evidently due to an extended stage of the crural base with adhearing elements of the hinge plates. At the distal end the crura are present in their usual form. Other trends in the internal morphology are less marked. In the cretaceous species some variation can be seen in the persistence and geometry of the dental lamellae. Unfortunately, in the jurassic species these structures are hidden by the filling of secondary material. It should be mentioned that some characters are remarkably constant in all investigated *Fortunella* species, such as the presence of denticula and the lack of the dorsal septum, as it is known from *Lacunosella* (Table 2).

As already mentioned *Fortunella* is thought to have lived in a deeper water environment. For the Oxfordian *F. monsalvensis* and *F. fastigata* of the alpine belt this is confirmed by the arguments given by GUILLAUME (1957, p. 56) on the sedimentary conditions of the Prealps of Fribourg during the upper jurassic time. In this area the Oxfordian is characterized by a change of the litoral facies to deeper sedimentation. The pertinent strata present a prevailing fauna of nectic organisms and only subordinate benthic forms such as brachiopods and urchins. The same is true for the phosphatized bed in which the aptian *F. acutifrons* is found and which also corresponds to a deep water facies (FÖLLMI 1986).

Fig. 7. *Fortunella monsalvensis* (Gilliéron), showing the narrow pedicle opening (× 2).

From its appearance at the begin of the Upper Jurassic the *Lacunosella/Fortunella*-stock has produced forms with a tendency to reduce costation. The main development of smooth "alpine" species seems to have taken place in late jurassic and early cretaceous time though. A weak tendency to an asymmetry of the anterior commissure is known in several *Lacunosella* species. It may be that the loss of costation (as a stabilizing element) gave rise to a more pronounced asymmetry in *Fortunella* species as seen e.g. in *F. praemoutoniana* (Jacob & Fallot 1913, Pl. 11).

All *Fortunella* species seem to exhibit a very narrow pedicle opening (Text-Fig. 7), leaving doubts about the attachment of the shell by a functional pedicle. This mode of fixation, considered as the normal one for brachiopods, was probably difficult and a pedicle more or less "superfluous" in a supposed habitat of muddy bottom. It is presumed that the conspicuous internal thickening at the posterior end of the shell and the resulting increased weight in the apical part served as a means of favourable positioning of these brachiopods in their special environment.

It is not clear whether these smooth forms should be considered monophyletic, as descendants of *Lacunosella,* or polyphyletic, with repeatedly occurring unability to develop costation during ontogenese. As far as can be judged now clear evolutionary trends within the genus *Fortunella,* i.e. a gradual reduction of costation or a progressive change in crural development[3]), are hardly recognizable. For that reason we think that the environment-induced speciation seems to be the more likely.

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[3]) Smirnova (1973) who studied ontogenetical changes in crural development observed a change from the prefalcifer to the falcifer type in *Lacunosella*. As this seems to be true also for other brachiopods with falcifer crura such as *Orbirhynchia* this feature may be just a general rule of development for this type of crura without an indication of evolutionary trends.

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# Plate 1

All figured specimens in natural size.
a: dorsal valve; b: ventral valve; c: profile; d: anterior commissure; e: hinge from posterior.

*Fortunella monsalvensis* (Gilliéron). Oxfordian, Prealps of Fribourg, Switzerland.

Figs. 1a–e: Specimen with typically undulated anterior commissure. Sous-Planière near Châtel-St. Denis. Lectotype, Museum of Geology, Lausanne, Inventary-No. 40826.

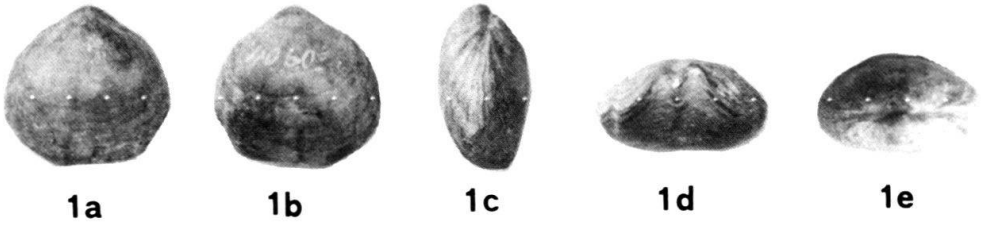
Figs. 2a–d: Specimen with broad anterior uniplication. Same locality. Reproduced in Haas 1887 (Pl. 8, Figs. 4a–d). Museum of Geology, Lausanne, Inventary-No. 40827.

Fig. 3d: Specimen with multiple undulations anteriorly. Same locality. Reproduced in Haas 1887 (Pl. 8, Figs. 12a–c). Museum of Geology, Lausanne, Inventary-No. 40828.

*Fortunella fastigata* (Gilliéron). Oxfordian, Prealps of Fribourg, Switzerland.

Figs. 4a–e: Specimen with typical acute lingual extension and moderately cynocephalous profile. Sous-Planière near Châtel-St. Denis. Lectotype, Museum of Geology, Lausanne, Inventary-No. 4055.

Figs. 5a–e: Same specimen as in Figures 4a–e. Surface of shell uniformly coloured for photography.



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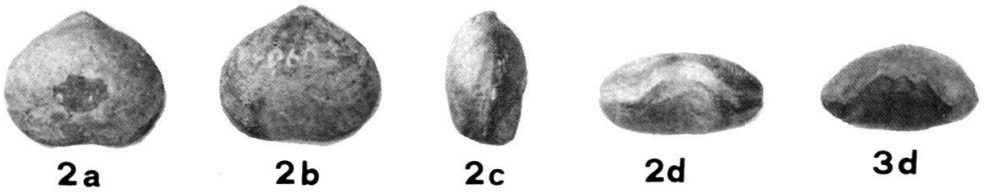

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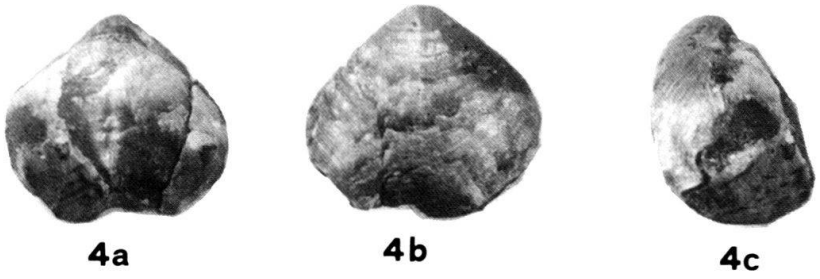

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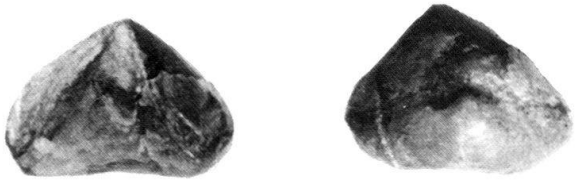


4d 4e

5a 5b 5c

5d 5e

## Plate 2

All figured specimens in natural size.
a: dorsal valve; b: ventral valve; c: profile; d: anterior commissure; e: hinge from posterior.

*Fortunella praemoutoniana* sp. n. Lower Cretaceous ("Couches à Brachiopodes"), Prealps of Vaud, Switzerland.

Figs. 1a–e: Strongly inequivalve specimen with V-shaped anterior commissure. Leysin ("English Sanatorium"). Lectotype, Museum of Geology, Lausanne, Inventary-No. 40825.

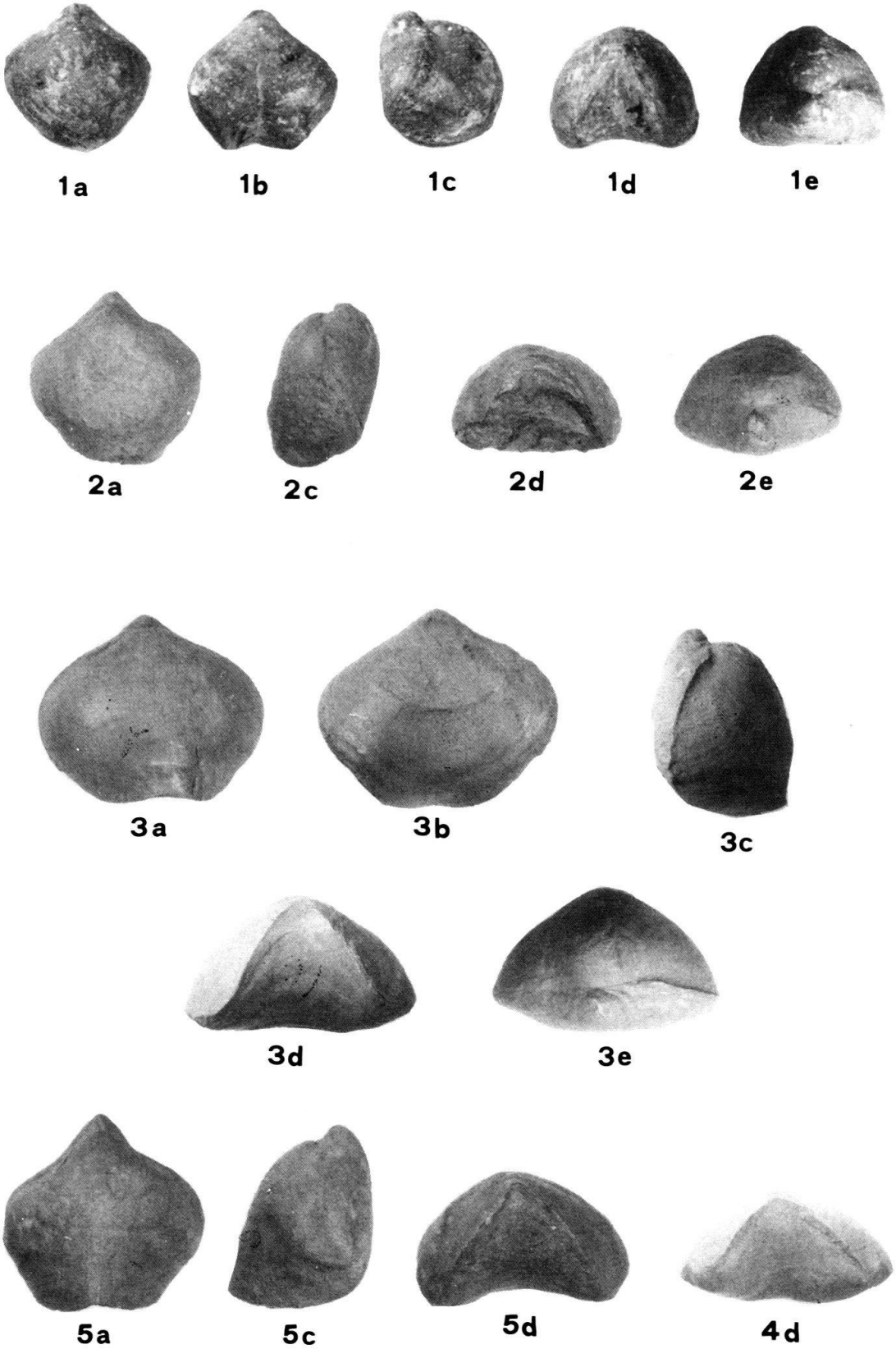
Figs. 2a, c–e: Less thick specimen with rounded anterior uniplication. Same locality. Shell coloured for photography. Collection H. Sulser.

*Fortunella moutoniana* (D'Orbigny). Barremian of South-East-France.
All specimens coloured for photography.

Figs. 3a–e: Specimen with rounded, high anterior uniplication. La Balme de Recurel near Villard-de-Lans (about 20 km southwest of Grenoble), Dép. Isère, France. Collection H. Sulser.

Fig. 4d: Specimen with similar, but somewhat flattened uniplication. Same locality. Collection H. Sulser.

Figs. 5a, c, d: Specimen with acute anterior commissure. Combe-petite, Montagne de Lure, Dép. Basses-Alpes, France. Collection H. Sulser.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