

APTYCHI FROM THE BERRIASIAN/VALANGINIAN (FRANCE AND SPAIN): NEW STRATIGRAPHICAL AND MORPHOLOGICAL DETAILS

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Abstract: Late Berriasian–earliest Valanginian lamellaptychi (Cephalopoda) are described in detail for the first time. With one exception, all species belong to early representatives of *Mortilletilamellaptychus*. The majority of the well dated aptychi come from the cephalopod-rich sediments of the Vocontian Basin in south-eastern France; others are from south-eastern Spain. *Thorolamellaptychus anglesensis* sp. nov. is introduced.

Key words: Lamellaptychi, Berriasian/Valanginian, Vocontian Basin, Betic Cordillera.

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INTRODUCTION

In addition to ammonites and belemnites, Early Cretaceous sediments often yield other cephalopod fossils, although these remain largely unfamiliar or not described. In the cephalopod-rich sediments of south-eastern France (Vocontian Basin) and Spain (Betic Cordillera), aptychi occur quite frequently. In the present account, a small, but significant collection of aptychi is described. The material comes from sediments close to the Berriasian-Valanginian boundary at Angles, Vergol, Barret-le-Bas, Pusteau and Rémuzat (France). Among these new species is *Thorolamellaptychus anglesensis* sp. nov. from the Late Berriasian of Angles. In addition, one specimen from the latest Berriasian of south-eastern Spain (Cañada Lengua) is considered. The locations of the study areas are shown in Fig. 1.

GEOLOGICAL SETTING

In general, the Late Berriasian to earliest Valanginian sediments of the Vocontian Basin are dominated by marly-calcareous strata with marly interbeds. Most of the specimens studied come from well known sections at Angles, Vergol and Barret-le-Bas; a few of them are from Pusteau and Rémuzat. These Berriasian/Valanginian deposits have not been studied in detail, but there is a considerable amount of information on the distribution of the cephalopods and other fossil groups in unpublished reports. The ammonite

zonation for the latest Berriasian to earliest Valanginian follows that of Reboulet *et al.* (2014). The stratigraphic data on the distribution of the aptychi studied were collected mainly by one of the authors (JK).

Angles (Alpes de Haute-Provence): Berriasian to Aptian sediments are well exposed along the road to the village of Angles (Busnardo *et al.*, 1979; Giraud, 1995). It is one of the sections (also including sections near Barret-le-Bas) that were previously chosen as alternative para- or hypostratotypes for the Valanginian (Busnardo *et al.*, 1979), since the Valanginian stratotype in Switzerland was recognized as being condensed and to some degree containing sedimentary gaps (Remane, 1973). However, at Angles, the (uppermost) Berriasian - lowermost Valanginian has not yet been well studied with regard to macro-fossils, compared to the better exposed lowermost Valanginian to lowermost Hauterivian (Atrops and Reboulet, 1993). The Berriasian–Valanginian boundary or basal Valanginian was placed, with a certain amount of error, on the basis of calpionellids, around a slumped interval (beds ANG-V201-207; Le Hégarat and Ferry, 1990, p. 371).

Vergol (Drôme): At Vergol, to the north of Montbrun-les-Bains, Berriasian-Valanginian sediments are well exposed (Blanc *et al.*, 1994; Reboulet, 1996; McArthur *et al.*, 2007, p. 395–398; Kenjo *et al.*, 2014). One of the very few papers that dealt with aptychi of the Vocontian Basin described taphonomical aspects (Reboulet and Rard, 2008).

Barret-le-Bas (Haut Alpes): Sections in the vicinity of Barret-le-Bas were chosen as potential Valanginian

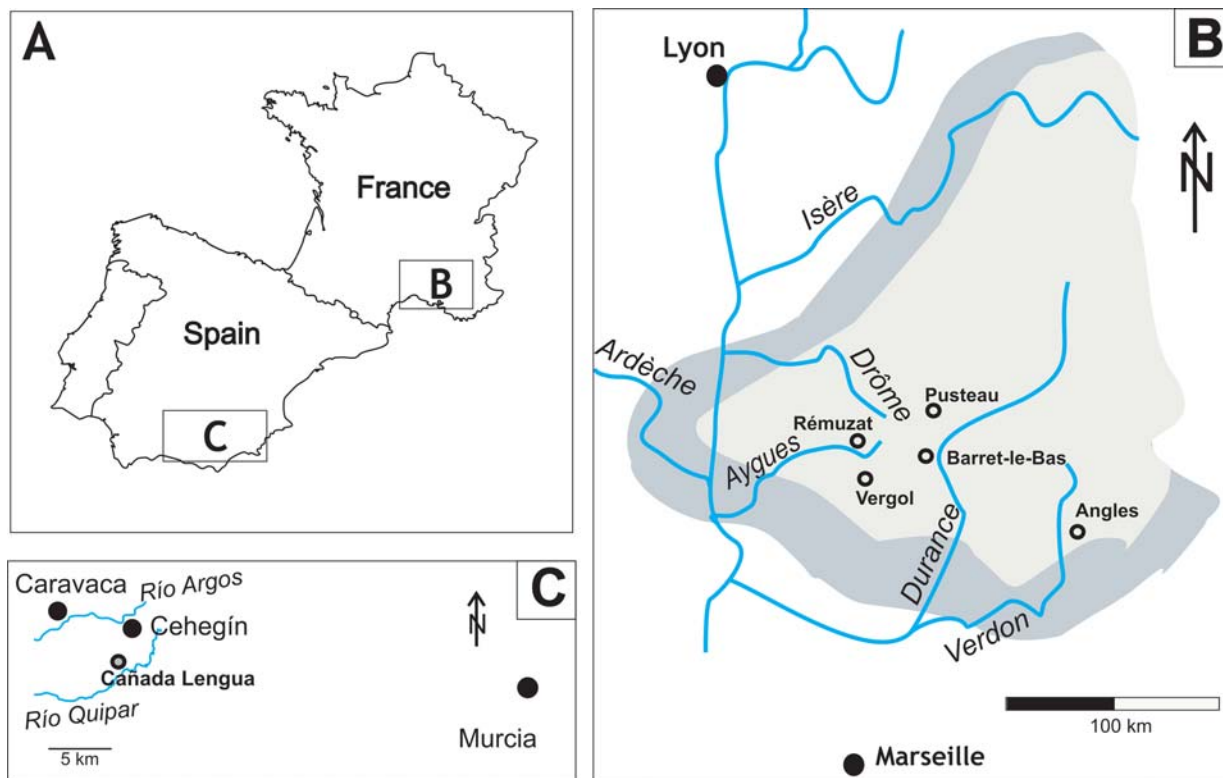


Fig. 1. General locations of the study areas. The outline of the Vocontian Basin is shown in grey in Fig. 1B.

hypostratotype sections (Busnardo *et al.*, 1979). The latest Berriasian (from the Otopeta Subzone upwards) to earliest Late Valanginian sediments are especially well exposed and contain quite abundant cephalopods. Remane and Thieuloy (1973a, p. 91, 93) provide details about the geographical location and the section.

Pusteau (Hautes Alpes): The section of Pusteau (section M, cf. Remane and Thieuloy, 1973b, p. 101) is nowadays not visible, because of the spread of vegetation and human activity (construction and agriculture). It was more or less comparable to the top part of the nearby exposure at La Faurie (section LF, cf. Remane and Thieuloy, 1973b, p. 101), rich in ammonites from the Otopeta Subzone and the base of the Pertransiens Zone.

Rémuzat (Drôme): This section is about 2 km to the south of the village along the D94 road, at the bank of the Aygues River. Here, patchy exposures of latest Berriasian to lowermost Valanginian age occur.

Cañada Lengua: This section, situated to the south of Cehegín (Province of Murcia, Spain) displays ammonitico rosso-like facies (red coloured sediments) for part of the Upper Berriasian (lower Alpillensis Subzone), while the uppermost Berriasian (from the top of the Alpillensis Subzone to the Otopeta Subzone) is represented by nodular, calcareous sediments, intercalated with marly-calcareous deposits. These sediments contain abundant bioclastic material. The lowermost Valanginian (Pertransiens Zone) consists of well bedded, calcareous sediments with minor, marly intercalations. Cephalopods are quite common (Company and Tavera, 1982, 2015; Ogg *et al.*, 1988; Aguado *et al.*, 2000; Janssen, 2003).

BASIC MORPHOLOGY AND MATERIAL PRESERVATION

Aptychi are calcite valves, typically subtrigonal, arranged in pairs. In recent years, they were usually considered to be the mandibles or jaw apparatus of ammonites (cf. Parent *et al.*, 2014 with references). Aptychi were not parts of the aragonitic ammonite shells. They occur especially as isolated valves (see, e.g., Měchová *et al.*, 2010; Vašíček *et al.*, 2012).

Terminology used for description and size parameters are represented in Figures 2 and 3 (according to Měchová *et al.*, 2010). The abbreviations used for the measurements are: L – length or size of the valve; S – distance between the terminal point and the apex (an objective parameter, if L is not measurable); and Lat – maximal width of the valve. Where the valve was incomplete, only the preserved length L' was measured. The ratio Lat/L indicates whether the valve is “slender” or “wide”. To acquire simple basic information about the size of the valves of lamellaptychi, the authors propose the recognition of small (L < 12 mm), medium (size from 12.5 to 20 mm) and large (L > 20.5 mm).

With regard to evident changes in ribbing during the growth of specimens, valves pass from the juvenile stage (i.e. valves small in size, with simple, initial ribbing) into the adult stage (i.e. in dimensions larger valves with different, more complicated ribbing). Valves with ribbing transitional between these variants can be designated subadult.

The majority of the aptychi studied were collected from the surfaces of beds of marly limestones. In general, the specimens are complete or almost complete and only a few are

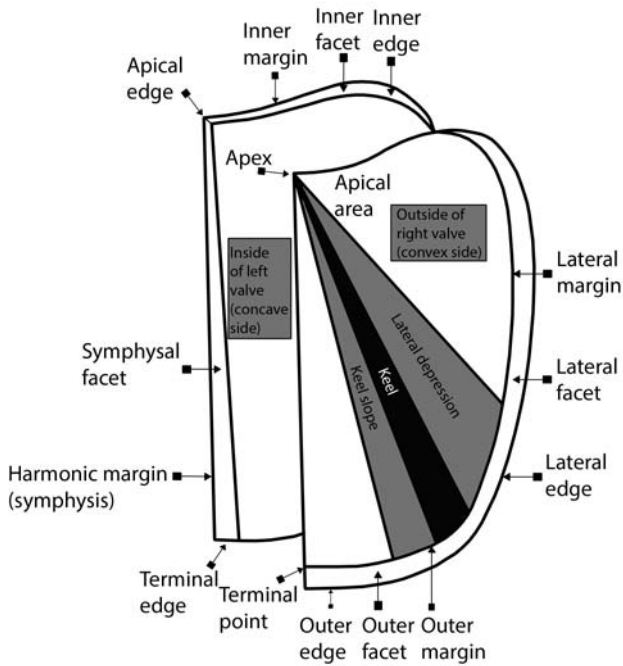


Fig. 2. Morphological terminology of aptychi valves (according to Měchová *et al.*, 2010).

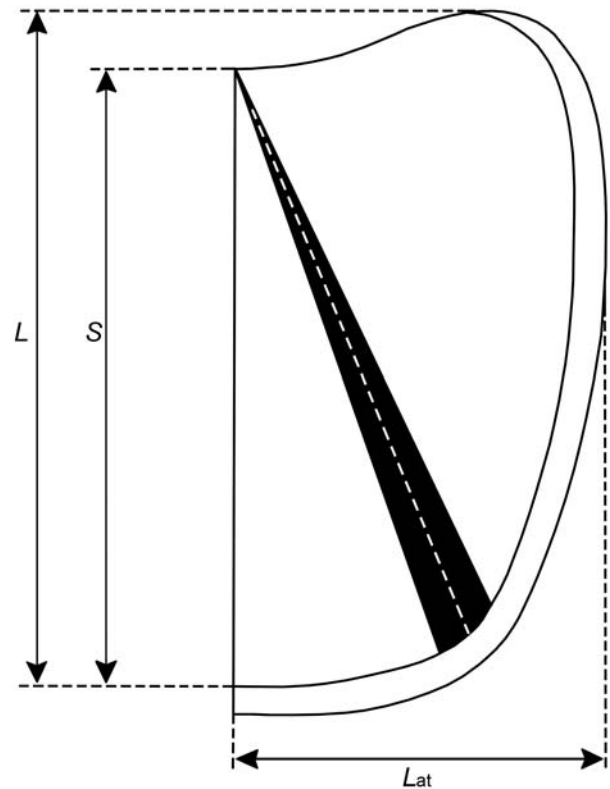


Fig. 3. Length parameters measured on the aptychi valves.

fragmentary. The aptychi from the Vergol locality were collected exclusively as weathered, isolated valves in the marly interbeds, and most of them are only fragments.

The collection will be stored at the Naturalis Biodiversity Center, Leiden, the Netherlands (= Rijksmuseum voor Geologie en Mineralogie; hence the acronym RGM in the Taxonomy section); the collection numbers are RGM 780001–780013.

TAXONOMY

The classification adopted follows Měchová *et al.* (2010).

Family LAMELLAPTYCHIDAE Měchová, Houša et Vašíček, 2008

Genus *Mortilletilamellaptychus* Měchová, Vašíček et Houša, 2010

Type species: *Aptychus Mortilleti* Pictet et de Loriol, 1858.

Mortilletilamellaptychus morbiensis (Renz et Habicht, 1985)
Fig. 4A–F

1968 *Lamellaptychus mortilleti* (Pict. et Loriol) – Jaksch, fig. 30.

1978 *Lamellaptychus mortilleti* (Pictet et Loriol) – Renz, pl. 1, figs 3a, b.

*1985 *Lamellaptychus morbiensis* new form – Renz et Habicht, p. 410, pl. 4, figs 4, 10.

partim 1985 *Lamellaptychus mortilleti* (Pictet et Loriol) – Renz

et Habicht, p. 397, pl. 1, fig. 23, ?figs 24, 25, non fig. 26 (*L. mortilletinoricus* Trauth), non pl. 2, figs 1–5 (= *M. ex gr. mortilleti*).

1994 *Lamellaptychus mortilleti mortilleti* (Pictet et Loriol) – Vašíček *et al.*, p. 72, pl. 23, fig. 9.

1996 *Lamellaptychus mortilleti mortilleti* (Pictet et Loriol) – Vašíček, pl. 3, figs 3, 4.

2000 *Lamellaptychus mortilleti mortilleti* (Pictet et Loriol) – Boorová *et al.*, pl. 14, fig. 10.

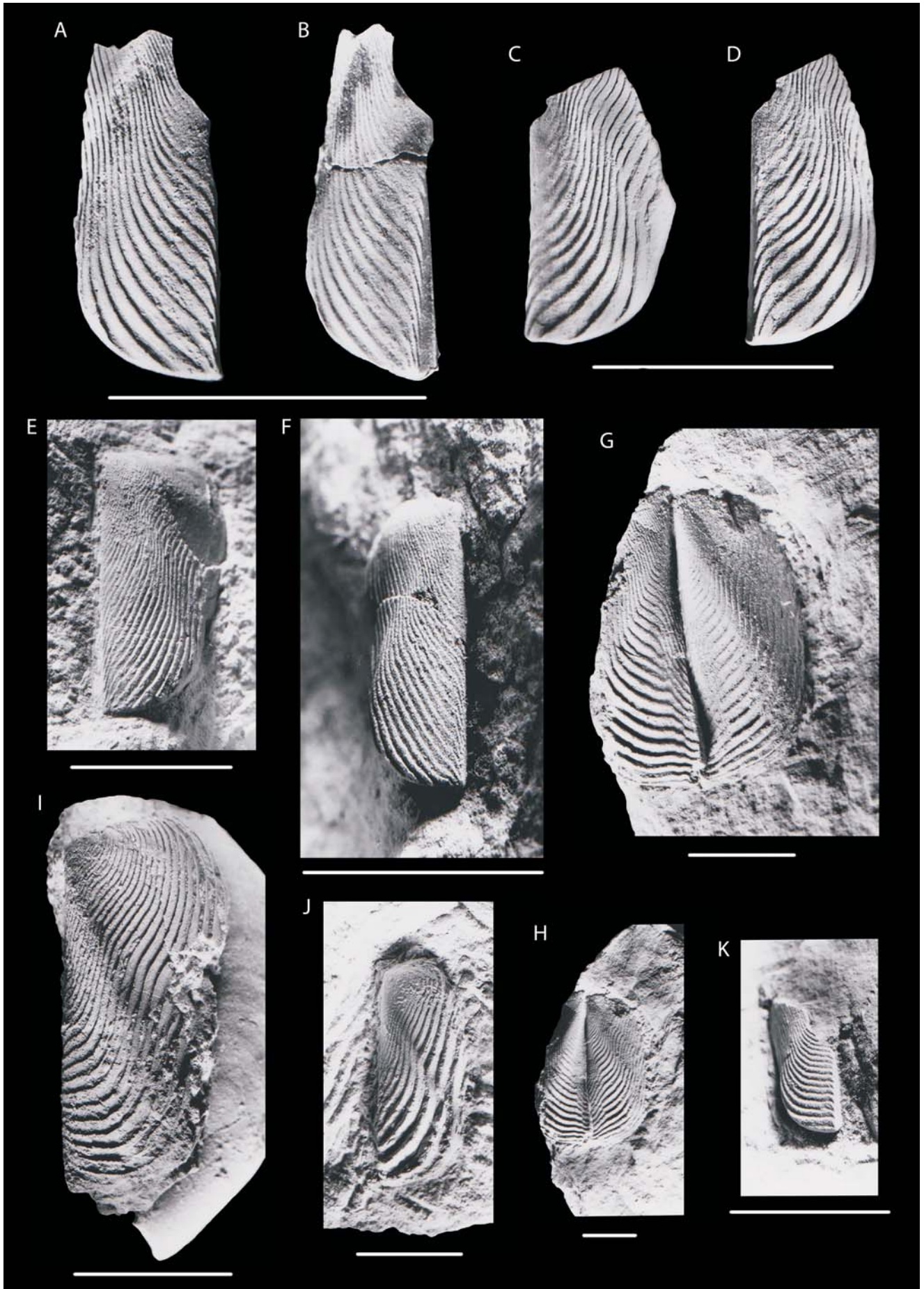
2000 *Lamellaptychus (Lamellosuslamellaptychus) mortilleti mortilleti* (Pictet et Loriol) – Turculet, p. 110, pl. 8, figs 3, ?4.

2010 *Mortilletilamellaptychus mortilletioides* sp. nov. – Měchová *et al.*, p. 245, fig. 9G.

2015 *Mortilletilamellaptychus cf. morbiensis* (Renz et Habicht) – Vašíček *et al.*, p. 340, fig. 3I.

Material: Vergol: five specimens (V121 = RGM780001, V121b = RGM780002, V123 = RGM780003, V123* = RGM780004, V125 = RGM780005) from the marly beds between W043 to W051 (cf. McArthur *et al.*, 2007, p. 395 for corresponding beds); 1 specimen from Barret-le-Bas (spec. BLB44153 = RGM780006), and 3 specimens from bed 7 (cf. Remane and Thieuloy, 1973b, p. 103) of Pusteau (spec. no. P45226, 45228A, and 455258 = RGM780007–780009).

Description: Thin-walled valves with a prominent, rounded keel and with a lateral depression. The area between the keel and the symphysal margin of adult valves is slightly curved concavely. The ribs are thin and are both closely and widely spaced. The juvenile parts of valves are not preserved. The first preserved ribs run to the symphysal margin at an angle of approximately 45°. Close to the symphysis, the ribs are inclined more sharply to the terminal point, at an angle of about 30°. Consequently, they converge along



the symphyseal margin over a rather long distance. The lengths of converging ribs decrease towards the end of the symphyseal margin. In some specimens, the ribs in the lateral depression are slightly inflected. However, in general they show a significant, sigmoidal bending. The last 4 to 5 ribs end at the outer margin. These ribs usually are negligibly inflected parallel to the outer margin of the valves.

Measurements: One juvenile valve (RGM780008) is only 7.7 mm long, while the other specimens are of medium size. The biggest and most complete valve (RGM780009) has the following dimensions: L = 18.0 mm, S = 16.4 mm, Lat = 9.2 mm, Lat/L = 0.53 mm.

Remarks: Significant elements of *M. morbiensis* are the distinct keel, the depression below the keel, and the rather long convergence of the ribs, which are closely aligned alongside of the symphyseal margin. The latter is only evident, where the valves are appropriately inclined to be photographed, which in turn reduces the visibility of the keel. On the basis of the material of the present authors, it was noted that the ribs in the lateral depression do not necessarily show sigmoidal bending. The sigmoid bending in the lateral depression appears to be absent, especially in small valves. However, it occurs in specimens of medium (subadult) valves, but becomes less visible or can even disappear completely in larger valves. Because of the poor quality of the photographic documentation of the Rumanian material in Turculet and Avram (1995) and Turculet (2000), it is impossible to say whether some valves indicated as *L. (L.) mortilleti* may actually belong to *L. morbiensis*. Related species, such as *M. mortileti*, differ in their rib morphology. Their ribs converge along the symphysis over only a short distance. The figured specimens lack a distinct keel and the depression situated below it. *M. mendrisiensis* (Renz et Habicht, 1985) displays ribs that converge to an area along the symphysis and differs with respect to part of the converging ribs, which end at the outer margin of the valves. However, this feature is unknown in *M. morbiensis*. Měchová *et al.* (2010) proposed *M. mortilletioides* on the basis of its long convergence of the ribs along the symphysis. In addition, typical features are the distinct keel and the depression below the keel. However, as this morphological feature appears typical for *M. morbiensis*, *M. mortilletioides* becomes a synonym of the former species.

Distribution: Renz and Habicht (1985) indicated that their specimens occur in Valanginian-Hauterivian boundary deposits. However, recent discoveries (Měchová *et al.*, 2010; Vašíček *et al.*, 2015) in the Outer Western Carpathians (Czech Republic), Eastern Alps (Austria), Spain and Rumania show evidence of occurrence in the Late Berriasian–Early Valanginian.

Occurrence: The present material comes from the Late Berriasian of Vergol and Barret-le-Bas (Alpillensis Subzone), and from the Otopeta Subzone (Boissieri Zone) of Pusteau.

Mortilletilamellaptychus ticinensis (Renz et Habicht, 1985)
Fig. 4G, H

- 1867 *Aptychus Seranonis*, Coquand – Pictet, p. 123, pl. 28, figs 9 a,b, 10 a,b, ?8 a,b.
1938 *Lamellaptychus mortilleti* (Pictet et Loriol) – Trauth, p. 145, pl. 10, figs 27, 28.
*1985 *Lamellaptychus ticinensis* new name – Renz et Habicht, p. 409, pl. 3, figs 29, 31, ?30, pl. 4, figs 1, 2, ?3.
1985 *Lamellaptychus?*, new form – Renz et Habicht, p. 401, pl. 2, fig. 14.

Material: One rather well preserved specimen from Rémuzat consisting of two incomplete valves (spec. R53659 = RGM780010). The right valve is better preserved.

Description: Adult valves with quite a wide, though not high keel, bearing a shallow lateral depression. The area between the keel and the symphyseal margin is slightly concave. Initially, the ribs are thin and closely spaced. Juvenile ribs between the keel and the symphyseal margin converge towards the symphyseal margin at an angle of 45°. Near the symphysis, the ribs are slightly S-shaped and they converge along the symphysis over a rather long distance, at an angle of approximately 10°. On the left valve, this kind of ribbing ends with slightly discordant ribs. However, this discordance is missing on the right valve. Here, complete ribs originate from two incomplete ribs. Instead of the gradual bending of ribs in the vicinity of the symphysis, a slight sigmoidal bend occurs. Thereafter, these ribs run towards the symphyseal margin at an angle of about 30°. The aforementioned sigmoidal bend is missing in the last ribs. They run towards the symphyseal margin at a gradually increasing angle. In the terminal area, they converge with the margin at an angle which reaches nearly 90°. The last 2 or 3 ribs bend backwards towards the apex near the symphysis. On the flanks, the last ribs follow the outline of the outer margin of the valve.

Measurements: S = 28 mm, Lat = 13 mm at minimum.

Remarks: Renz and Habicht (1985) designated the specimen figured by Pictet (1867, pl. 28, fig. 10) as the holotype. However, the valve in pl. 28, fig. 9 is more complete. The French specimens are especially similar to Pictet's specimen (1867, pl. 28, fig. 9) and to the valves illustrated by Renz and Habicht (1985, pl. 4, figs 1, 2), while the valve figured in their plate 4, figure 3 most probably does not belong to this species.

Distribution: The topotypical specimens (cf. Renz and Habicht, 1985) apparently came from the Late Valanginian of southern Switzerland. However, the ambiguously determined specimen (*loc. cit.* pl. 2, fig. 14) comes from the Early Valanginian.

Occurrence: The present specimen comes from the Pertransiens Zone (Early Valanginian) of Rémuzat.

Fig. 4. Lamellaptychi from the Berriasian/Valanginian boundary deposits. Scale bar is 10 mm. All specimens were treated with ammonium chloride prior to photography. **A–F.** *Mortilletilamellaptychus morbiensis* (Renz et Habicht, 1985); **A, B.** Juvenile spec. RGM780004 (L = 11 mm); **A** – view of the lateral depression, **B** – view of the symphyseal area (photographed after fracturing of valve); Vergol section, Late Berriasian, Alpillensis Subzone, bed W046-047; **C, D.** Spec. RGM780001 with close ribbing (L' = 12 mm); **C** – view of the lateral depression, **D** – view of the symphyseal area; Vergol section, Late Berriasian, Alpillensis Subzone, bed W043-044; **E.** Spec. RGM780006 with dense ribbing (L = 18.2 mm); Pusteau section, Late Berriasian, Otopeta Subzone, bed 7; **F.** Spec. RGM780007 (S = 14.0 mm); Barret-le-Bas, Late Berriasian, Alpillensis Subzone. **G, H.** *Mortilletilamellaptychus ticinensis* (Renz and Habicht, 1985), spec. RGM 780010; **G** – better view of the left valve (S = 28 mm), **H** – better view of the right valve (S = 28 mm); Rémuzat, Early Valanginian, Pertransiens Zone. **I.** *Mortilletilamellaptychus helveticus* (Renz and Habicht), spec. RGM780011 (L = 24.8 mm); Cañada Lengua, Late Berriasian, Alpillensis Subzone, bed CLG103. **J.** *Mortilletilamellaptychus ambiguus* (Renz, 1979), spec. RGM780012 (S = 19.5 mm); Angles, Late Berriasian, Otopeta Subzone, bed ANG-V186. **K.** *Thorolamellaptychus anglesensis* sp. nov., spec. RGM780013, holotype (L' = 8 mm); Angles, Late Berriasian, Otopeta Subzone, top bed ANG-V179.

Mortilletilamellaptychus helveticus (Renz et Habicht, 1985)
Fig. 4I

- partim 1985 *Lamellaptychus helveticus* new form – Renz et Habicht, p. 398, pl. 2, fig. 7, non fig. 8 (= *M. mortilletinoricus* Trauth), ?fig. 9.
*2010 *Mortilletilamellaptychus helveticus* (Renz et Habicht) – Měchová *et al.*, p. 247, fig. 9K [cum syn.].

Material: One partially preserved valve [RGM780011] with an incomplete lateral area beneath the apex; southern Spain, Cañada Lengua, bed CL103.

Description: Adult valve with distinct keel and only a shallow, lateral depression. The area between the keel and the symphyasal margin is rather narrow. The ribbing is thin and closely spaced. In the incompletely preserved juvenile area, the ribs between the keel and the symphyasal margin run obliquely towards the symphysis at an angle of 35°. In the vicinity of the symphysis, the ribs recline from the original direction and converge along the short section of the margin at an angle of 15°. The convergence of the ribs along the symphysis disappears in the middle part of the valve. The ribs between the keel and the symphyasal margin gradually become rounded and they simply end at the symphysis. Adult ribs are increasingly rounded and towards the end, they bend more distinctly back to the apex. The ribs in the lateral depression show only a slight inflection.

Measurements: L = 24.8 mm, S = 22.9 mm, Lat = 12 mm at minimum.

Distribution: The holotype of Renz and Habicht (1985, pl. 2, fig. 7) comes from sediments of the Berriasian-Valanginian boundary in south Switzerland.

Occurrence: The specimens comes from the Late Berriasian Alpi-lensis Zone of Cañada Lengua.

Mortilletilamellaptychus ambiguus (Renz, 1979)
Fig. 4J

- * 1979 *Lamellaptychus ambiguus* n. sp. – Renz, p. 593, pl. 1, figs 13 a,b, 14.
1985 *Lamellaptychus ambiguus* Renz – Renz et Habicht, p. 406, pl. 3, figs 21, 22.
1985 *Lamellaptychus* aff. *ambiguus* Renz – Renz et Habicht, p. 406, pl. 5, figs 19, 20.

Material: Subadult valve (RGM780012), well-preserved in the symphyasal area from bed ANG-V186 (AV17).

Description: Valve with a distinct carinate keel and a lateral depression. The area between the keel and the symphyasal margin is slightly curved concavely. The ribbing is thin and closely spaced at the beginning and it is solid and widely spaced in the terminal zone. The ribs in the juvenile area incline to the symphysis at an angle of about 30°. Near the symphysis, the ribs recline slightly and they converge along the symphyasal margin. In the terminal area, the ribs become more solid and they follow the original direction, even though they are slightly inflected and follow the external outline of the valve. The convergence of ribs at the symphyasal margin disappears completely. The last two ribs run parallel to the periphery of the valve and close to the symphyasal margin, they bend towards the apex. Below the keel, the ribs are sigmoidally bent.

Measurement: S = 19.5 mm.

Remarks: The valves illustrated by Renz (1979) and by Renz and Habicht (1985) are considerably incomplete. The valve described in the present account probably is the best preserved specimen of *M. ambiguus* currently known. Two types of ribbing, i.e. different ribbing in the juvenile and adult part of the valve, are clearly distinguishable. The arrangement of the ribbing is continuously oblique, even in the terminal zone, and the ribs end in their short inclination towards the apex in the symphyasal area.

Distribution: *M. ambiguus* was obtained from a core drill, apparently from the Berriasian sediments of the Western Bermuda Rise (Renz, 1979). In addition, other specimens (Renz and Habicht, 1985) come from the Valanginian sediments of south Switzerland.

Occurrence: The material of the authors comes from the Otopeta Subzone (Late Berriasian) of Angles (SE France).

Genus *Thorolamellaptychus* Turculet, 1994

Type species: *Aptychus Thoro* Oppel, 1863.

Thorolamellaptychus anglesensis sp. nov.
Fig. 4K

Holotype: The valve figured in Fig. 4K (RGM780013).

Etymology: Named after its occurrence near the village of Angles.

Material: One fragment of an otherwise well preserved small valve.

Measurements: The incomplete valve reaches a length of 10 mm. However, in the incomplete symphyasal area, it reaches only 6.5 mm.

Type locality: Angles (Valanginian hypostratotype).

Type horizon: Bed ANG-V179, uppermost Berriasian.

Diagnosis: Thin and closely spaced ribbing, with remarkable keel and lateral depression. Ribs run towards the symphyasal margin in right angle. Near the symphyasal margin, the last ribs are short and bend towards the terminal point.

Description: Valve with a distinct keel and a preserved part of the lateral depression, situated below it. All ribs are similarly thin and occur evenly spaced. After the rounded bend near the keel, the ribs run nearly straight towards the symphyasal margin. They converge with it at an angle of about 80°. Close to the symphyasal margin, approximately half of the terminal ribs incline over a very short distance towards the terminal point. In the area of the lateral depression, the ribs are straight and very closely spaced.

Remarks: The basic morphology of the ribbing is similar to that of *T. aplanatus* (Gillieron, 1873). However, *T. anglesensis* differs from the latter and other related species in the terminal bend of the ribs towards the terminal point and not to the apex.

Occurrence: Angles, Late Berriasian (Otopeta Subzone, bed ANG-V179, AV10 top).

DISCUSSION

In the collection of aptychi described here from the Upper Berriasian of the Vocontian Basin, valves of *M. morbiensis* predominate in numbers. The rather large number of valves of various sizes permitted a detailed revision of this poorly known species. This revision has shown that *M. morbiensis* is morphologically very close to *M. mortilleti* and identical with *M. mortilletiodes* of Měchová *et al.* (2010). All other members of the genus described here are represented only by single occurrences. However, they are well to exceptionally well preserved valves of rather large size, which document the changes in ribbing from the initial juvenile ribs to their final growth stages and thus contribute to improved knowledge of *M. helveticus*, *M. ambiguus* and *M. ticinensis*.

A single representative of *Thorolamellaptychus* is a small, but well preserved fragment. It is referable to *T. anglesensis* sp. nov. and differs from other representatives of the genus by having the final ribs bent from near the symphyasal margin to the terminal point.

CONCLUSIONS

In contrast to the general abundant occurrence of lamellaptychi with guide ammonites in the Valanginian of the Vocontian Basin (France) and of in south-eastern Spain, they occur only rarely in the sediments close to the Berriasian/Valanginian boundary. The sediments yielded four species of the genus *Mortilletilamellaptychus* that are poorly known in terms of stratigraphy and only one representative of the genus *Thorolamellaptychus*. *Mortilletilamellaptychus* is represented by abundant occurrences of *M. morbiensis*, while *M. ambiguous*, *M. helveticus* and *M. ticinensis* are generally rare. The valves of the last mentioned species are well preserved and belong to the largest specimens described so far. This permits the recognition of significant changes in the ribbing of juvenile and adult valves not previously noted.

Th. anglesensis sp. nov. is remarkable for having an arrangement of ribs not previously observed.

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