

ONTOGENY AND VARIABILITY IN RIBBING OF LATE VALANGINIAN LAMELLAPTYCHI (AMMONITINA)

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Abstract: Late Valanginian (Early Cretaceous) lamellaptychi of the genus *Mortilletilamellaptychus* were collected from seven ammonite-controlled sections in south-eastern France demonstrate distinct changes in ribbing during growth. Simpler juvenile ribbing, which is essentially uniform for all of the specimens studied, differs distinctly from the complicated arrangement of the adult ribs. Changes in ribbing morphology were observed in the five species studied, two of which were identified as new (i.e. *Mortilletilamellaptychus heterocostatus* sp. nov. and *M. bicostatus* sp. nov.).

Key words: Lamellaptychi, *Mortilletilamellaptychus*, ontogeny, Late Valanginian, south-eastern France.

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INTRODUCTION

Aptychi are a specific group of fossils that usually represent the isolated solid parts of extinct ammonites. It is supposed that the function of aptychi most commonly combine feeding (jaw) and protection (operculum). Within the framework of the commonly used term aptychi specialists distinguish also a number of lower categories or groups of aptychi. These groups are called according to their generic names as punctaptychi, lamellaptychi, etc.

Calcite valves of ribbed aptychi from the lower part of the Upper Valanginian represent, both quantitatively and qualitatively, the richest part of a large collection of Early Cretaceous aptychi, gathered in recent years by the co-authors of this work. The aptychi come from outcrops with ammonite-calibrated deposits in south-eastern France, stratigraphically belonging to the *Saynoceras verrucosum* and *Neocomites peregrinus* zones. These outcrops are in the vicinity of Vergol (i.e. Vergol s.s. and Vergol Ferme Chilet) and north of Vergol (Col d'Aulan; this section is also known as Morénas). Sections near Angles (the Angles Valanginian hypostratotype and Source de l'Asse de Moriez), near Buis-les Baronnies (Vallon de Péchières), and a section near La Charce yielded additional aptychi.

Valves of the genus *Mortilletilamellaptychus* were selected for the study of the ontogeny and variability in ribbing. These valves belong to five species, two of which are recognized as new. The collection consists of a large num-

ber of valves of various sizes, ranging from near-juvenile to adult ones. For the first time, it was possible to study the distribution and morphological variability of these aptychi in detail, owing to the firm ammonite-controlled age of these sediments and the bed-by-bed collection of the valves.

GEOLOGICAL SETTING

Typically, the more distal parts of the Vocontian Basin are characterized by the alternation of calcareous and clayey sediments (Cotillon *et al.*, 1980; Giraud *et al.*, 1995; Reboulet and Atrops, 1997). Reboulet *et al.* (2003) concluded that for the latest Lower Valanginian and early Upper Valanginian, the bulk of the carbonate muds were transported from shallow platform environments to the basin and were not solely the result of the production of calcareous nannoplankton.

The distal sediments of the Upper Valanginian are characterized by rather uniform and well-correlative sets of calcareous beds alternating with sets of marl-dominated sediments (Cotillon *et al.*, 1980). The uppermost part of the Lower Valanginian and the lowermost part of the Upper Valanginian generally consist of four thicker calcareous to marly-calcareous beds (“tetraeder” or “T-beds” of Bulot *et al.*, 1993), yielding in the upper part the ubiquitous and abundant *Saynoceras verrucosum*. These beds are succeeded by a marl-dominated interval, the lowermost part of

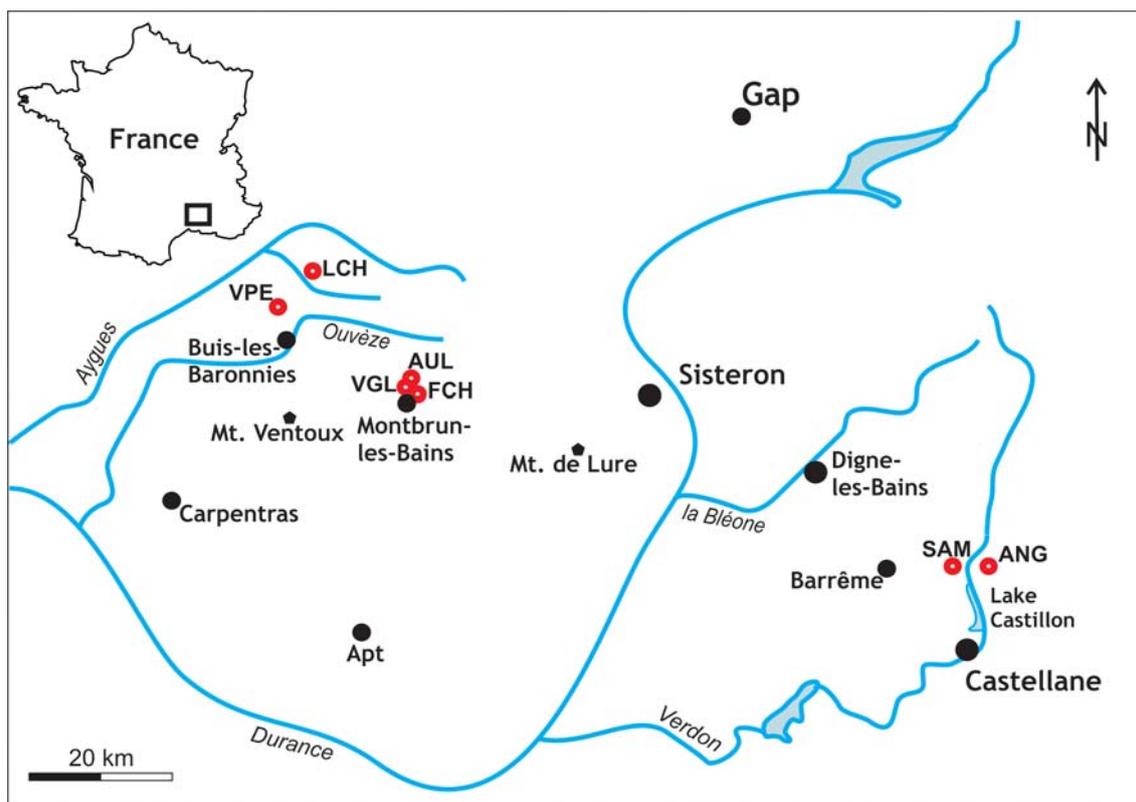


Fig. 1. Geographical location of the studied sections. The following acronyms are used: ANG – Angles, AUL – Col d’Aulan, FCH – Vergol Ferme Chilet, LCH – La Charce, SAM – Source de l’Asse de Moriez, VGL – Vergol, and VPE – Vallon de Péchières. Open red circle indicate location of sections studied.

which still yields rare *S. verrucosum* not present in the upper part. The latter is the Neocomites neocomiensis Horizon, modified after Atrops and Reboulet (1993; Tab. 1). Thus, in addition to the standard two-fold division of the Verrucosum Zone (Reboulet *et al.*, 2014), it was thought useful to informally adopt a three-fold division of that zone, although this never was formally accepted as a chronostratigraphic unit (Bulot *et al.*, 1996; Klein and Hoedemaker, 1999). The present authors use the three-fold subdivision only for convenience in assigning the interval that lack ammonites of any of the index species. This interval is characterized by a low-diversity cephalopod fauna, the disappearance of several belemnite taxa (Janssen and Clément, 2002), the occurrence of sandy-calcareous intercalations (tempestites and/or turbidites), and the most positive δC^{13} values of the Weissert event (McArthur *et al.*, 2007). The succeeding calcareous beds represent the Karakaschiceras pronecostatum Subzone, separated from the younger calcareous beds of the Peregrinus Subzone by another marl-dominated interval. In some cases, these marl-dominated units in part are slumped.

The investigated sections (Fig. 1) can be viewed as clustered in two closely related areas. One area comprises outcrops to the north of Castellane (Alpes de Haute-Provence) while the other exposures are situated to the north of Montbrun-les-Bains and Buis-les-Baronnies (Drôme).

Angles to Moriez area (Alpes de Haute-Provence): Along the road to the hamlet of Angles, sediments that are Berriasian to Aptian in age are well exposed (Busnardo *et*

al., 1979; Giraud, 1995). One of the sections was chosen as a hypostratotype for the Valanginian succession (Busnardo *et al.*, 1979). Here, the latest Lower Valanginian to earliest Hauterivian is well-exposed and ammonites occur abundantly (Atrops and Reboulet, 1993; Bulot *et al.*, 1993; Reboulet and Atrops, 1999). The Neocomiensis Horizon exhibits only very rarely sandy-calcareous intercalations, and if present at all, they appear only as very thin (mm) intercalations. The Source de l’Asse de Moriez section (comparable to the profile depicted in Bulot *et al.*, 1993, p. 24) is exposed to the west of Lake Castillon, west of the Angles profile. It is well comparable to the latter, but especially in the younger parts, partially concealed, owing to abundant vegetation.

Montbrun-les-Bains to Buis-les-Baronnies area (Drôme). Vergol s.s., Vergol Ferme Chilet, Col d’Aulan (N of Montbrun-les-Bains): In all these localities, Upper Valanginian sediments are well-exposed, yielding abundant cephalopod remains (Reboulet, 1996; Reboulet and Atrops, 1999; Janssen and Clément, 2002; Reboulet *et al.*, 2003; Reboulet and Rard, 2008). Typically, the sediments between the Verrucosum Horizon and the Pronecostatum Subzone contain abundant sandy-calcareous intercalations, mm to a few cm in thickness, in places with cephalopod remains (belemnites, rhyncholites, aptychi).

La Charce (NNE of Buis-les-Baronnies): Here, the oldest part of the Verrucosum Zone is missing. Below the first bed of the Valanginian–Hauterivian section (bed 204 in Bulot *et al.*, 1993; bed 100 in Reboulet, 1996) a few slumped calcareous beds occur and belong to the upper part of

Table 1

Ammonite zonation as used herein, modified after Reboulet *et al.* (2009, 2014)

| Sub-stage | Zone | Subzone | Horizon | |
|-----------------------------|-------------|---------------|---------------|--|
| Late Valanginian (p.p.) | Peregrinus | Nicklei | | |
| | | Peregrinus | | |
| | Verrucosum | Pronecostatum | | |
| | | Verrucosum | Neocomiensis | |
| | | | Verrucosum | |
| Early Valanginian (p.p.) | Biassalense | | Platycostatus | |
| | Biassalense | | | |

the Neocomiensis Horizon, as they yield typical “post-Verrucosum event” kinds of belemnites (Janssen and Clément, 2002). This slump is preceded by more than 15 m of marly sediments with sandstone intercalations (up to 20 cm with hummocky cross-bedding) and a few marly-calcareous beds, most probably separated from the lower part of the section by an erosional or non-depositional hiatus. At least the Verrucosum Horizon and the upper part of the Early Valanginian seem to be absent here. Probably these sediments are missing as a result of the development of a submarine canyon.

Vallon des Péchières (NW of Buis-les-Baronnies):

The section is closely comparable to sections in the area of Vergol. It differs from the latter in having more frequent sandy intercalations and in the occurrence of two distinct levels approximately 1 cm thick that consists solely of millions of aptychi.

BASIC MORPHOLOGY AND PRESERVATION OF MATERIALS

Basic features of calcitic-ribbed lamellaptychi originally consisted of two valves, arranged in pairs; their function, history of studies, preservation and morphology have been discussed in many works (see Měchová *et al.*, 2010; Parent *et al.*, 2014 and references therein).

The basic morphology of the aforementioned aptychi and size parameters are illustrated in Figures 2 and 3. Most of these valves show incomplete preservation and in terms of the parameters presented in the figure, the real length of valves L frequently was not measurable. Therefore, only the incomplete, preserved length L' was measured.

The greater part of the valves originated in the intercalated marls. They are often separated, isolated, lying weathered on the surface of these relatively soft layers. With certain exceptions, they are preserved as fragments only. These valves usually lack a larger or smaller part of the apical area and lateral margin, these being the most vulnerable to erosion. Consequently, as the preserved terminal point and outer margins of the valves are decisive for the correct determination of the species, many of the specimens proved to be indeterminable beyond their generic affiliation.

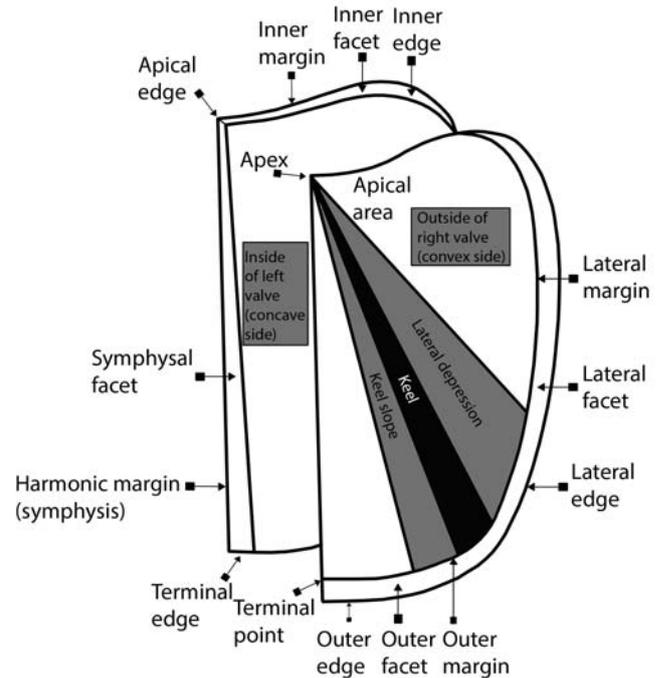


Fig. 2. Descriptive terminology of aptychi (according to Měchová *et al.*, 2010)

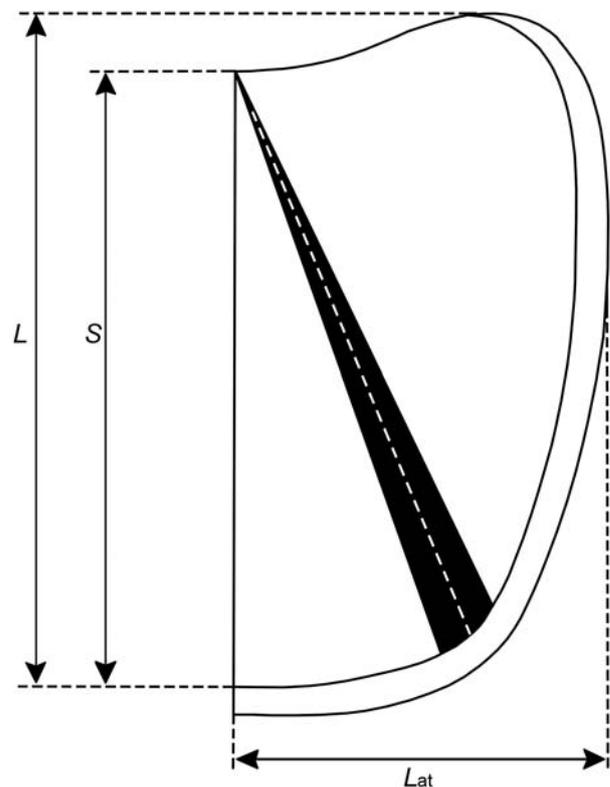


Fig. 3. Length dimensions measured on the aptychi.

Table 2

Correlation and stratigraphical position of the marly beds studied

| VII. d. Péchières | La Charce area | Vergol area | Angles area | Ammonite subzones/horizons |
|-------------------|---------------------------|------------------|------------------|----------------------------|
| VPE | LCH | VGL, FCH, AUL | ANG-V, SAM | |
| 325b–326 | <i>209a(nn)–209b(115)</i> | <i>125b–126</i> | <i>325b–326</i> | Peregrinus |
| 324a–325 | <i>209(114)–a(nn)</i> | <i>124a–125a</i> | <i>324a–325</i> | Peregrinus |
| 324–a | <i>209(114)</i> | 124–a | <i>324–a</i> | Peregrinus |
| | <i>208(111)–a(112)</i> | <i>121–122</i> | 321–a/322 | Pronecostatum |
| | <i>207b(110)–208(111)</i> | 120–121 | 320–321 | Pronecostatum |
| | <i>207a(109)–b(110)</i> | 119–120 | 319–320 | Pronecostatum |
| | <i>nn(108)–207a(109)</i> | 118–119 | <i>318–319</i> | Pronecostatum |
| | <i>nn–(nn)108</i> | 117–118 | <i>317–318</i> | Pronecostatum |
| | <i>206(105)–207(107)</i> | 115–116 | <i>315–316</i> | Pronecostatum |
| | 205c(nn) | <i>114d</i> | <i>nn</i> | Pronecostatum |
| | | <i>111a–112</i> | 312b–d | "Neocomiensis" |
| 308–309 | | 108–109 | <i>309–310</i> | "Neocomiensis" |
| | | 107c–108 | <i>308–309</i> | "Neocomiensis" |
| | | 107b–c | <i>307–308</i> | "Neocomiensis" |
| | | 107a–b | <i>306b2–307</i> | "Neocomiensis" |

Bold numbers refer to the studied beds, and bed numbers in italics are correlated to the bold bed numbers but have yielded none of the aptychi mentioned in this paper. Note that in the La Charce section several beds were already featured in other papers. Bed numbers, e.g. 205 are *sensu* e.g. Bulot (1993), bed numbers e.g. 104b are *sensu* Reboulet (1996 etc.); *nn* indicates beds that are not numbered.

Only a relatively small number of valves came from the calcareous beds. These valves are often preserved (near) complete, providing the possibility of measuring all of the necessary size parameters. However, their ribbing is preserved in less perfect state than the ribbing of the valves found in the marly beds. Only occasionally, both valves were preserved.

In the paragraphs under "Material" the best preserved specimens are marked with double designation. The first designation with the acronym RGM indicates the number of selected specimens figured in this paper or specimens significant for a more precise documentation of species. The second designation refers to the field numbering in the field diary. A unique acronym given first, designates the locality. It is followed by the bed-number of the section, where the discovery occurred (see Tab. 2). These marks serve to provide better orientation in the documentation of sections. Whenever more than one specimen was collected in the same section, the number of the bed is followed by a slash and a number for the order of sampling.

SYSTEMATIC PALAEOLOGY

The taxonomy of ribbed aptychi in the present account is based on the parataxonomic classification, proposed by Měchová *et al.* (2010). In the synonymy of species, the present authors mention the paper in which the species was assigned and illustrated for the first time, followed by a few of the most recently published papers on the species, where more detailed synonymy usually is presented. The sections studied were designated using following abbreviations: VGL = Vergol *s.s.*, FCH = Vergol Ferme Chilet, AUL = Col

d' Aulan, ANG–V = Angles (Valanginian hypostratotype), VPE = Vallon de Péchières, SAM = Source de l'Asse de Moriez, and LCH = La Charce. All specimens (RGM 780014–780034 and also the group under acronyms of the sections) are deposited in the Natural History Museum in Leiden (the Netherlands).

In terms of species description, the following terms are used for general sizes of the valves: small or juvenile (valves up to the size of L = 12 mm), medium (size from 13 to 20 mm) and large (> 20 mm).

Family Lamellaptychidae Měchová, Houša et Vašíček, 2008

The family is characterized by three calcite layers distinguishable in cross-section. The external surface of the valves is strongly ribbed.

Genus *Mortilletilamellaptychus* Měchová, Vašíček et Houša, 2010

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

Remarks: The genus with thin to medium-thick valves. The juvenile ribs are thin. In the area of the symphyasal margin, the ribs sharply converge towards the terminal point and end at the symphyasal margin. In stratigraphically younger specimens, the arrangement of adult ribs is complicated, by comparison with the juvenile ones. Adult ribs end at the outer margin.

Mortilletilamellaptychus mendrisiensis (Renz et Habicht, 1985)

Remarks: The valves are characterized by convergence of the ribs along the symphyasal margin over a long distance. Adult ribs are slightly bent, nearly straight, and they end at the outer margin.

Mortilletilamellaptychus mendrisiensis mendrisiensis
(Renz et Habicht, 1985)

Fig. 4A–E

- *1985 *Lamellaptychus mendrisiensis* new form – Renz et Habicht, p. 411, pl. 4, fig. 9.
- v 2010 *Mortilletilamellaptychus mendrisiensis mendrisiensis* (Renz et Habicht) – Měchová *et al.*, p. 249, fig. 9N [cum. syn.].
- v 2012 *Mortilletilamellaptychus mendrisiensis mendrisiensis* (Renz et Habicht) – Vašíček *et al.*, p. 256, figs 5.1 a, b, 5.2 [cum syn.].

Material: Some tens of valves, most of them preserved as fragments: VGL107b-c/1 = RGM 780014, VGL107b-c/2 = RGM 780015, VGL107b-c/4; ANG-V319-320 = RGM 780016, ANG-V319-320* (the differently preserved specimen in this bed), ANG-V320-321/1 = RGM 780017, ANG-V320-321/4 = RGM 780018; FCH115-116, FCH118-119/2; LCH205c = RGM 708035 being the best-preserved or morphologically most important specimens.

Description: Small- to medium-sized valves. The juvenile valves are vaulted and they lack the keel and lateral depression. The lateral depression accompanied by the inflection of ribs can be present on valves of larger size.

The ribs are thin and closely spaced. There is a long convergence of the ribs along the symphyseal margin. In the flank area, they are more or less straight and obliquely oriented. The last ribs end at the outer margin. They are straight to slightly bend, but not parallel to the outline of the outer margin of the valve. In the terminal area of the larger valves, there is a bundle of numerous closely spaced ribs that are thinner than the ribs on the flanks. This bundle of ribs ends at the outer margin. The number of ribs in the bundle increases with increasing size of the valve.

Measurements: The fragments of the smallest valves reach the estimated length L of about 10 mm. The valves with dimensions of over 15 mm usually display a lateral depression and a bundle of thin and closely spaced ribs in the terminal area. One of the most complete valves is specimen LCH 57026. Its parameters are: L' (close to L) = 16.5 mm, S = 15.5 mm, Lat = 8.6 mm. The largest valves probably do not exceed 20 mm.

Remarks: The juvenile valves lack a lateral depression. Their ribs converge over a long distance along the symphysis and end at its margin. More adult valves develop a negligible lateral depression with inflected ribs. In the terminal area, rather thin ribs develop a bundle which closely follows the ribs on the edge of the symphysis. The bundle ends at the outer margin.

M. morbiensis (Renz et Habicht, 1985) shows a certain similarity to *M. m. mendrisiensis*. However, *M. morbiensis* differ by the presence of a distinct keel and a lateral depression. Its ribs converge over a short distance in the symphyseal area at a rather more acute angle, compared to *M. m. mendrisiensis*. In the terminal zone, thin and closely spaced ribs do not develop as a bundle and the shape of the last ribs approaches the shape of the outer margin. The two species also differ in their stratigraphical occurrence. *M. mendrisiensis undulocostatus* (Boorová *et al.*, 2000) differs in having an undulation of the ribs in the vicinity of the symphyseal margin.

Distribution: The subspecies was recorded from the Upper Valanginian of Switzerland, Bulgaria and the Outer and Central Western Carpathians in the Slovak Republic. The possible occurrence of the species in the Lower Hauterivian of the Slovak Republic, mentioned in Vašíček *et al.* (1994), has not been confirmed so far.

Occurrence: *M. m. mendrisiensis* was found at the Vergol *s.s.* locality in the Neocomiensis Horizon and at the localities in Vergol Ferme Chilet, Vallon de Péchières, Angles and La Charce in the Pronecostatum Subzone (Verrucosum Zone).

Mortilletilamellaptychus beyrichodidayi (Trauth, 1938)

Fig. 4F–J

- *1938 *Lamellaptychus beyricho-didayi* n. f. – Trauth, p. 200, pl. 14, fig. 5.
- ?1978 *Lamellaptychus stellariformis* n. sp. – Renz, p. 904, pl. 1, fig. 9.
- ?1996 *Lamellaptychus stellariformis* Renz – Eliáš *et al.*, pl. 5, fig. 4.
- v ?2010 *Mortilletilamellaptychus stellariformis* Renz – Měchová *et al.*, p. 250, fig. 10B.
- v 2010 *Mortilletilamellaptychus beyrichodidayi* (Trauth) – Měchová *et al.*, p. 251, fig. 10D [cum syn.].

Material: Some tens of valves mostly preserved as fragments. The best preserved valves are specimens AUL118-119/1, 2, 3 = RGM 780019; ANG-V312b-d/1 = RGM 780020; VPE324-a/1 = RGM 780021; FCH120-121 = RGM 780022; VGL107b-c/5 = RGM 780023 and LCH205c = RGM 780036.

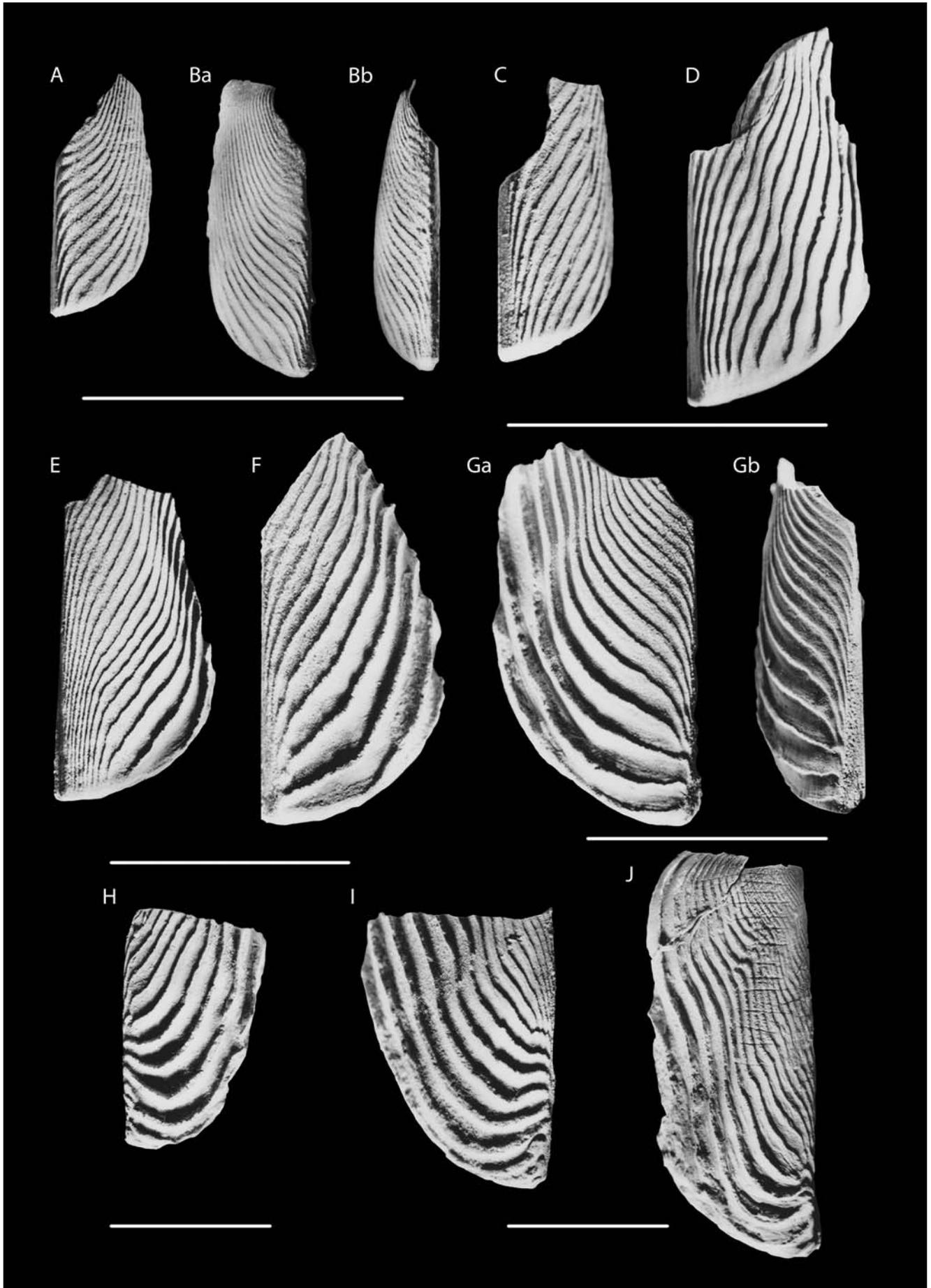
Description: Valves of medium to large size. A negligible keel, bearing a shallow, lateral depression can be present on the flanks of the valves. There are two types of ribbing. The juvenile ribs are thin and closely spaced. They run towards the symphyseal margin at an angle of 45° on the flanks. Close to the symphyseal margin, they are sharply inflected and converge obliquely along the margin over a long distance at an acute angle towards the terminal point. Radial lines that cause a slight undulation of the ribs towards their end can occur at the symphyseal area. The adult ribs are rather thick and the inter-rib spaces are wider. The first adult ribs approximately follow the outline in the marginal area. The ribs gradually run into the symphyseal margin at an angle of about 90° until they start to incline back to the apex. Broad lobe-like bending is gradually formed on the aforementioned ribs. The juvenile ribs converge with the adult ribs with an only indicated to distinct discordance. A few of the first adult ribs can display a short S-shaped bending, sometimes with undulation of the ribs, in the contact zone in the vicinity of the symphysis. The last rib on the adult valves is often incomplete.

Measurements: Juvenile valves are not sufficiently known, because of the fragmented preservation. However, it is estimated, on the basis of the density of ribbing, that some of the smallest valves probably reached a length of about 20 mm. The largest, nearly complete valve (spec. RGM 780023) is 27 mm long.

Remarks: It is difficult to assess, whether some of the juvenile valves determined as *M. m. mendrisiensis* are not the juvenile valves of *M. beyrichodidayi*, because only the more adult valves can be distinguished with certainty. Rather large-sized valves of *M. beyrichodidayi* differ in the prominent distinction between juvenile and thicker adult ribs (see Fig. 4G). In the contact zone, one to two, exceptionally five juvenile ribs are negligibly to distinctly discordant in relation to the adult ribs (see Fig. 4I). The adult ribs develop a simple, broad, arched lobe in the marginal area. The last ribs incline towards the apex (see Fig. 4J). *M. beyrichodidayi* differ from the related species *M. bicurvatus* by a simpler arrangement of the adult ribs.

Distribution: Trauth (1938) recorded the species from the Neocomian of Barrême and Měchová *et al.* (2010) from the upper part of the Lower Valanginian (the Busnardoites campylotoxus Zone *sensu* Reboulet *et al.*, 2009) to the Upper Valanginian (including the Peregrinus Subzone in the Outer and Central Western Carpathians in the Slovak Republic and from the Upper Valanginian in the Northern Calcareous Alps in Austria).

Occurrence: *M. beyrichodidayi* occurred in Vergol *s.s.*, Vergol Ferme Chilet, Col d'Aulan, Angles and La Charce in the Upper Valanginian in the Neocomiensis Horizon and Pronecostatum Subzone (Verrucosum Zone). It also occurred in the Peregrinus Subzone of Vallon de Péchières.



Mortilletilamellaptychus bicurvatus (Renz et Habicht, 1985)

Fig. 5A–C

- partim 1867 *Aptychus seranonis* Coquand – Pictet, pl. 28, fig. 9a,b.
 1938 *Lamellaptychus sub-mortilleti* n. n. var. n. *retroflexa* – Trauth, p. 201, pl. 14, fig. 6.
 1985 *Lamellaptychus bicurvatus* new name – Renz et Habicht, p. 409, pl. 3, figs 25–28.
 v 2010 *Mortilamellaptychus bicurvatus* (Renz et Habicht). – Měchová *et al.*, p. 250, fig. 10C [cum syn.]
 v 2012 *Mortilamellaptychus bicurvatus* (Renz et Habicht) – Vašíček *et al.*, p. 258, fig. 5.3.

Material: Over twenty valves. The best-preserved valves are specimens VGL107b-c/2 = RGM 780024; FCH108-109/1, FCH108-109/3 = RGM 780025; VPE325b-326; SAM 320-321 = RGM 780026, and ANG-V312b-d/2.

Description: Medium-sized valves. On the larger valves, a slight keel and a shallow depression can be developed. Two types of ribbing occur. The juvenile ribs are thin and closely spaced. In the vicinity of the symphyasal margin, they converge over a relatively long distance along the margin at an acute angle. The adult ribs are thick and more widely spaced. The convergence of the adult ribs with the juvenile ribs does not display any discordance. In the symphyasal area, they start to bend rather consistently in an S-shape form. In the beginning, the slightly S-shaped ribs run rather S-shaped and obliquely oriented towards the terminal point. The S-shaped bending gradually increases and a subangular lobe is developed in the lower part of the ribs. Towards the end, the ribs run to the terminal margin. The last ribs on the large-sized valves are incomplete. Some valves display radial lines that cause a slight undulation of the ribs.

Measurements: Based on fragments of the valves, their size can be estimated to be about 14–20 mm.

Remarks: The juvenile ribs show the character of ribbing of *M. m. mendrisiensis*. The ribbing runs into a slightly S-shaped bending of obliquely running ribs that pass into a remarkable S-shaped bending in the terminal region. *M. bicurvatus* differs from *M. beyrichodidayi* in the S-shaped arrangement of a higher number of the adult ribs. *M. beyrichodidayi* do lack the S-shaped bending, or the bending is negligible only on the first adult ribs.

Distribution: *M. bicurvatus* occurs in the Upper Valanginian of Switzerland, France, Bulgaria, and in the Northern Calcareous Alps in Austria, and the Outer and Central Western Carpathians in the Slovak Republic (Verrucosum Zone).

Occurrence: *M. bicurvatus* was found at Vergol *s.s.*, Vergol Ferme Chilet, Angles and Source de l'Asse de Moriez in the Neocomiensis Horizon and Pronocostatum Subzone (Verrucosum

Zone). However, at Vallon de Péchières, it occurs in the lowermost part of the Peregrinus Subzone.

Mortilletilamellaptychus heterocostatus new species

Fig. 5D–H

Holotype: Specimen RGM 780029 = SAM320-321/2, illustrated here in the Fig. 5F.

Etymology: heterocostate – after different arrangement of the juvenile and adult ribs.

Material: Some tens of valves are preserved as fragments only, but the specimens AUL120-121 = RGM 780027; VPE324a-325 = RGM 780028; SAM320-321/2 = RGM 780029; FCH107a-b/2, FCH117-118 = RGM 780030, FCH118-119/1, FCH119-120/1, 2; VPE324a-325 = RGM 780031; ANG-V321-a/322, ANG-V320-321/3, are well preserved.

Measurement: Holotype is a partially preserved valve with $L' = 17.0$ mm.

Type locality: Section of Source de l'Asse de Moriez, horizon SAM320-321.

Type level: Late Valanginian, Verrucosum Zone, Pronocostatum Subzone.

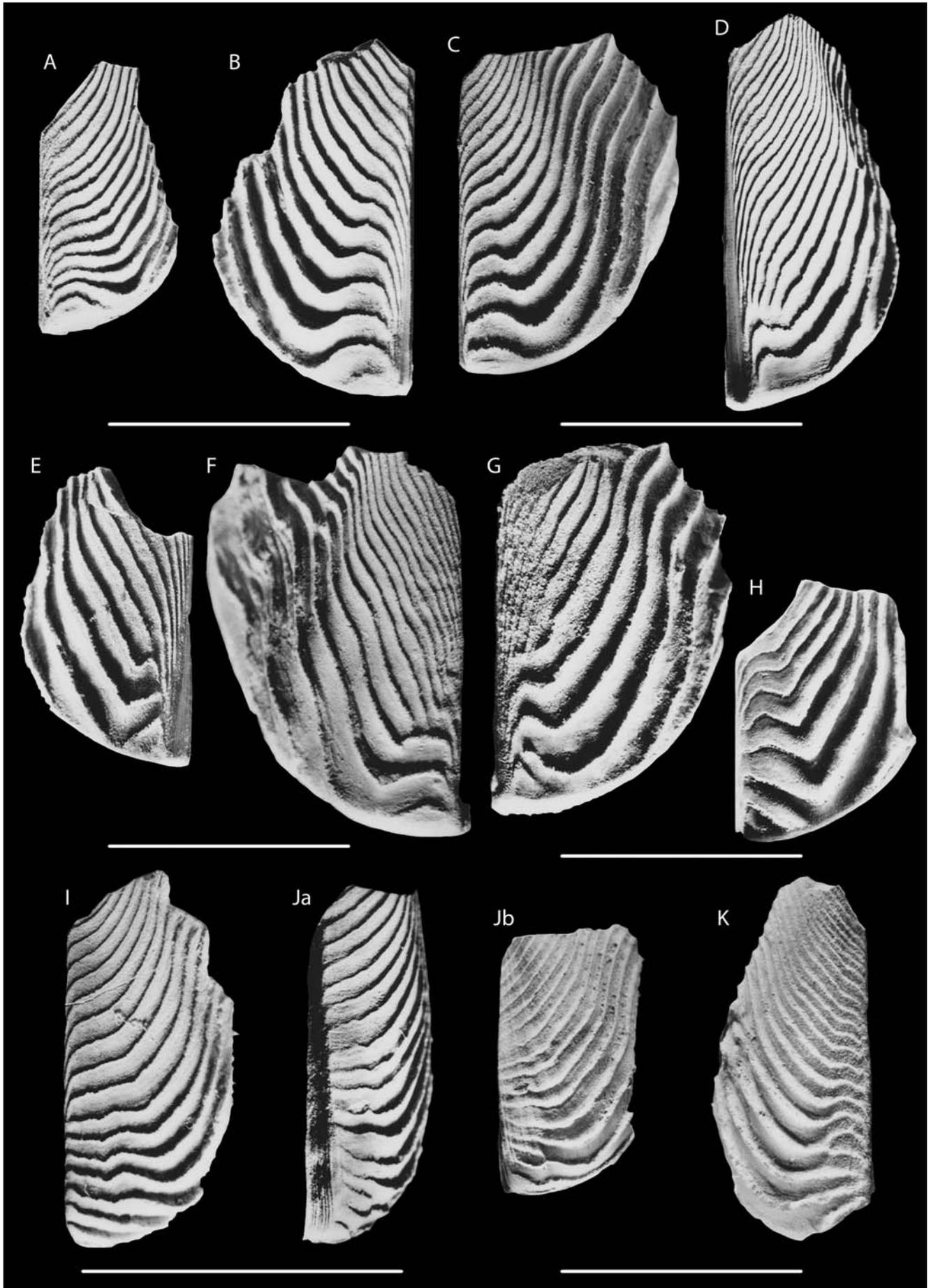
Diagnosis: The juvenile ribs converge towards the symphyasal margin over a long distance. The adult ribs converge with the juvenile ribs with a remarkable discordance.

Description: Valves of medium to large size, with a slight keel and minor lateral depression. The latter is usually accentuated by the inflection of the ribbing. On the flanks, the oblique, juvenile ribs are bent in the vicinity of the symphyasal margin towards the terminal point and they converge along it over a long distance at an acute angle. The juvenile ribs can be slightly undulated, owing to the possible presence of radial lines and they are bent in an S-shaped manner. Consequently, a distinct discordance occurs, followed by a connection of the adult ribs. The adult ribs are S-shaped, round or subangular to angular manner. The end parts of the S-shaped ribs run towards the terminal point. Three to four juvenile ribs end in the contact zone between the juvenile and adult ribs. Near the symphysis, one or two juvenile ribs can continue to run over the first adult ribs. The number of S-shaped ribs increases with the increasing size of valves. The last of them is usually incomplete. On large-sized valves, the S-shaped bending of the ribs disappears. The last incomplete ribs incline towards the apex.

Measurements: None of the valves collected is complete. The smallest valve reaches an estimated length of $L = 13$ mm; the largest valve over 20 mm.

Remarks: The ribbing differs according to the size of valves. On the smallest valve, the adult ribs are not developed yet. The first adult ribs are angularly S-shaped in the terminal zone. One or two complete S-shaped ribs are present (see Fig. 5D). The juvenile ribs

Fig. 4. Late Valanginian lamellaptychi of the Vocontian Basin. Scale bar is 10 mm. **A–E.** *Mortilletilamellaptychus mendrisiensis* (Renz et Habicht). A – Juvenile valve of the specimen RGM 780014 ($L' = 7.2$ mm). Vergol *s.s.* section, Neocomiensis Horizon; Ba – side view, Bb – view of the symphyasal area of the juvenile specimen RGM 780016 ($L' = 9.0$ mm). Angles section, Pronocostatum Subzone; C – Specimen RGM 780015 of the medium-sized valve ($L' = 14.5$ mm). Same location as the specimen in Fig. A; D – Specimen RGM 780017 with bundle of ribs indicated in the terminal zone ($L' = 10.5$ mm). Angles section, Pronocostatum Subzone; E – Medium-sized specimen RGM 780018 ($L' = 14.0$ mm) with a well-developed bundle of thin ribs in the terminal area and with a lateral depression. Same location as the specimen in Fig. D. **F–J.** *Mortilletilamellaptychus beyrichodidayi* (Trauth, 1938). F – Specimen RGM 780019 ($L' = 17.0$ mm). Col d'Aulan section, Pronocostatum Subzone; Ga – side view, Gb – view of the symphyasal area of the specimen 780020 ($L' = 16.0$ mm). Angles section, Neocomiensis Horizon; H – Specimen RGM 780021 ($L' = 16.0$ mm). Vallon de Péchières section, Peregrinus Subzone; I – Specimen RGM 780022 with discordance between the juvenile and adult ribs ($L' = 18.5$ mm). Vergol Ferme Chilet section, Pronocostatum Subzone; J – The largest and most complete specimen RGM 780023 ($L' = 27.0$ mm). Vergol *s.s.* section, Neocomiensis Horizon.



end on the S-shaped ribs with a distinct discordance. Consequently, the number of the angular S-shaped ribs (see Fig. 5G) increases. The last adult ribs are incomplete and they incline towards the apex. *M. heterocostatus* sp. nov. differs significantly from all related species of *Mortilletilamellaptychus* in a discordant position of the juvenile ribs in relation to the adult ribs and by angular S-shaped ribs.

Occurrence: The oldest representatives of *M. heterocostatus* sp. nov. were found in the Neocomiensis Horizon (Verrucosum Zone) at the Vergol Ferme Chilet locality. They mainly occur in the Pronocostatum Subzone in Vergol Ferme Chilet as well as in the localities Col d'Aulan, Angles and Source de l'Asse de Moriez. At present, the last occurrence appears to be in the lowermost part of the Peregrinus Zone in Vallon de Péchières.

Mortilletilamellaptychus bicostatus new species

Fig. 5I–K

Holotype: Specimen RGM 780033 = FCH107a-b-sst, illustrated here in the Fig. 5J.

Etymology: *bicostatus* – after two types of the ribbing.

Material: Tens of incomplete valves. The best-preserved specimens are VPE308-309 = RGM 780032; FCH107a-b/3 = RGM 780033, FCH107c-108, FCH107c-108, FCH108-109/2 = RGM 780034; VGL134-a/2.

Measurement: Partially preserved valve with $L' = 12.7$ mm.

Type locality: Section of Vergol – Fme. Chilet, marly bed FCH107a-b-sst.

Type level: Late Valanginian, Verrucosum Zone, Neocomiensis Horizon.

Diagnosis: The juvenile ribs converge just in a short distance along the symphyasal margin. In the outer marginal area, the adult ribs bent in an arch-shape manner. In the area of the symphysis, they incline very slightly towards the apex.

Description: Thick-walled, markedly vaulted valves. Medium in size, without a distinct keel, with a shallow lateral depression. The juvenile ribs, running on the flanks at an angle of about 45°, are thin and closely spaced. Close to the symphyasal margin, they bend towards the terminal point and they converge along it in just a short distance. The adult ribs, that are only slightly thicker than the juvenile ribs, display a slight lobe-like bending on the flanks and consequently, they run in a long and relatively straight section towards the symphyasal margin. They connect with the symphyasal margin at an angle of almost 90°. The ribs incline first towards the terminal point, then towards the apex. The last ribs are incomplete. On some specimens, a short rib may appear, inserted between the last complete ribs in the area of the symphysis. Most of the valves have a radial line, which causes a slight undulation of the ribs.

Measurements: Incomplete valves reach an estimated size of about 15 to 18 mm.

Remarks: *M. bicostatus* sp. nov. differs significantly from the aforementioned species by the arrangement of the juvenile ribs. Close to each other, they are bent towards the terminal point. After a short distance, they end at the terminal margin. The arrangement of the adult ribs is relatively simple. After the arch-like bending on the flank of the valve, they simply end at the symphyasal margin at an angle of about 90°. The ribs incline first slightly towards the terminal point, then backwards to the apex.

Fragments of valves without preserved juvenile ribs, assigned in Vašíček (1996, pl. 4, fig 6) to *Lamellaptychus* sp. 2, probably also belong to *M. bicostatus* sp. nov. They occur in the Upper Valanginian of the Outer Western Carpathians of the Czech Republic.

Occurrence: *M. bicostatus* sp. nov. occurs most frequently in the Late Valanginian in the Verrucosum Zone (in the Neocomiensis Horizon) of Vergol Ferme Chilet and Vallon de Péchières. Only one fragment came from the upper part of the Peregrinus Subzone of Vergol s.s.

DISCUSSION

In the contribution of Měchová *et al.* (2010), the importance of the arrangement of the juvenile ribs for the proposal of a new classification of lamellaptychi is stressed. In terms of the juvenile ribs, four further genera were newly distinguished within the original genus *Lamellaptychus* Trauth, 1927. Most of them were proposed by Turculet (1994) as subgenera, differing in the basic arrangement of the adult ribs. The recent systematics is based on consideration of the significant role of the juvenile ribbing to the original system for purposes of classification. This has turned out to be especially important within the genus *Mortilletilamellaptychus*.

A typical feature of all five species consisting of thick-walled valves, described above, is that their ribbing changes with increasing size of valves. The juvenile ribbing differs distinctly from the arrangement of adult ribs. *Mortilletilamellaptychus bicostatus* sp. nov. differs from the others described herein in the arrangement of the juvenile ribs. Its juvenile ribs converge along the vicinity of the symphyasal margin towards the terminal point only over a very short distance. The short convergence of the ribs near the symphyasal margin is developed by the early representatives of *Mortilletilamellaptychus*. In the case of the other four species, the ribs converge over a comparatively long distance.

Fig. 5. Late Valanginian lamellaptychi of the Vocontian Basin. Scale bar is 10 mm. All specimens covered by ammonium chloride before photographing. **A–C.** *Mortilletilamellaptychus bicurvatus* (Renz and Habicht, 1985). **A** – Juvenile specimen RGM 780024 ($L' = 11.3$ mm). Vergol s.s. section, Neocomiensis Horizon; **B** – Specimen RGM 780025 ($L' = 15.0$ mm). Vergol Ferme Chilet section, Neocomiensis Horizon; **C** – Specimen RGM 780026 ($L' = 14.3$ mm). Source de l'Asse de Moriez section, Pronocostatum Subzone. **D–H:** *Mortilletilamellaptychus heterocostatus* sp. nov. **D** – Juvenile specimen RGM 780027 with the first adult ribs ($L' = 16.0$ mm). Col d'Aulan section, Pronocostatum Subzone; **E** – Specimen RGM 780028 with the angular adult ribs ($L' = 11.5$ mm). Vallon de Péchières section, Peregrinus Subzone; **F** – Specimen RGM 780029, holotype ($L' = 17.0$ mm). Source de l'Asse de Moriez, Pronocostatum Subzone; **G** – More adult specimen RGM 780030 ($L' = 17.0$ mm). Vergol Ferme Chilet section, Pronocostatum Subzone; **H** – Fragment of an anomalous specimen RGM 780031 ($L' = 11.0$ mm). Vallon de Péchières section, Peregrinus Subzone. **I–K.** *Mortilletilamellaptychus bicostatus* sp. nov. **I** – Specimen RGM 780032 ($L' = 12.0$ mm). Vallon de Péchières section, Neocomiensis Horizon; **Ja** – view of the symphyasal area, **Jb** – side view of the specimen RGM 780033, holotype ($L' = 12.7$ mm). Vergol Ferme Chilet section, Neocomiensis Horizon; **K** – Specimen RGM 780034 with a bifurcated rib in the terminal area ($L' = 15.0$ mm). The same location as the previous specimen.

The second group of valves studied is more interesting in the view of the diversity of the ribbing. With increasing size of the valves, the juvenile ribs gradually change into thicker ribs that differ in their arrangement. The simplest ribbing is found in *M. mendrisiensis mendrisiensis*. The typical subspecies that are the focus of the present contribution, differs from *M. mendrisiensis undulocostatus* (Boorová et al., 2000) in the simple arrangement of the ribs in the symphysal zone. The simplicity of their arrangement is also typical for all species that belong to the aforementioned group.

The specimens of *M. m. mendrisiensis* collected are small- to medium-sized valves. Their adult ribs are straight to slightly bend in the marginal area and they end on the marginal outline. The small valves are simply vaulted. A slight lateral depression is developed on the larger valves. The ribs on the largest valves do not end at the symphysal margin. In this area, several non-adult near-symphysal ribs end in accordance with the adult ribs, i.e. on the marginal outline. These ribs form a bundle of remarkable thinner ribs than the ones that follow.

M. beyrichodidayi displays relatively simpler arrangement of the adult ribs, compared to the following four species. The designation of *M. beyrichodidayi* by Trauth (1938) is not fully concise. The juvenile ribs do not run in the same manner as the ribbing of *Beyricholamellaptychus beyrichi* (Oppel), but they are developed similarly to the ribs of *M. m. mendrisiensis*. However, the adult ribbing resembles *Didayilamellaptychus didayi* (Coquand). When viewed in detail, the ribbing ontogeny has been well-preserved in the transition area between the juvenile and adult ribbing of the material studied. First, a slight discordance between the juvenile and adult ribs can be seen in the terminal area. The adult ribs, few in number, follow the shape of the marginal outline. Later, they bend slightly backwards to the apex in an arched-like manner. Very close to the symphysal margin, simple to double, serrated undulation occurs. The last adult ribs show a distinct sigmoidal bending and remarkable inclination towards the apex in the marginal zone.

The typical feature is that the convergence of the juvenile ribs with the adult ribs shows only an indistinct discordance. The adult ribs of *M. bicurvatus* start to differentiate from the juvenile ribs in a slight S-shaped bending of obliquely oriented ribs, which appears in the marginal-terminal area. Then, the S-shaped bending becomes stronger. In the lower part of the S-shape bend, which is larger, the lower bend is formed in a lobe-like shape. The ribs are S-shaped over the whole size of the valves. A small tooth-like projection is sometimes developed in the area of transition of the lower bend to the upper bend.

The most complicated arrangement of the juvenile and adult ribbing can be seen on the valves of *M. heterocostatus* sp. nov. The convergence of the juvenile ribs in relation to the adult ribs is distinctly discordant; a bundle of the juvenile ribs ends on the first adult rib. Already the first juvenile rib is remarkably S-shaped in terminal area. The S-shaped bending is subangular to angular. The first S-shaped rib can be serrated. The end parts of the adult ribs incline towards the terminal point. Only the last adult ribs, which lack the complete S-shaped bending, incline towards the apex.

The last three of the aforementioned species are determinable after they reach the medium size of the valves. They have similar juvenile ribbing which corresponds to that of *M. m. mendrisiensis*. The description presented above leads to some possible doubt, as to whether *M. m. mendrisiensis* can be established as an independent species or should be considered only as the juvenile stage of *M. beyrichodidayi*, *M. bicurvatus* and *M. heterocostatus* sp. nov. The comparable stratigraphical occurrence of all species described here supports the first option only partially. *M. m. mendrisiensis* was found only in the Verrucosum Zone and not in the Peregrinus Zone. However, it should be remembered that the material studied does not come from the entire Peregrinus Zone, but only from the lower part of it. In the upper beds of the *Olcostephanus nicklesi* Subzone, the species mentioned above were not recorded.

CONCLUSIONS

On the basis of part of a collection of Early Cretaceous aptychi, originating in French sections of the Verrucosum and Peregrinus zones (lower part of the Upper Valanginian), and consisting of five species, the authors were able to detect distinct changes in the ribbing ontogeny on valves of the aptychi of *Mortilletilamellaptychus*.

The species studied can be divided into two groups. The first is represented by *M. bicostatus* sp. nov., which belongs to an older group of species of *Mortilletilamellaptychus*. This group is characterized by the short convergence of the juvenile ribs towards the terminal point in the symphysal area. The second group, accounting for the majority of the specimens is represented by a more diverse composition of species. Their common feature is the arrangement of the juvenile ribs which converge in a longer distance along the symphysal margin. The differences between the species studied become evident in the development of the adult ribs.

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