Taxonomy of Late Jurassic – Early Cretaceous aptchi from Bulgaria

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With 11 figures

Abstract: This paper presents the taxonomic revision of Late Jurassic and Early Cretaceous aptchi housed at the National Museum of Natural History, Sofia (Bulgaria). The aptchi came from the pelagic, flysch-like and flysch deposits of Central and North Bulgaria, and most of them have been initially described by Stefanov (1961). The taxonomic revision has led to the determination of 23 species and subspecies of six genera. A new species named Mortilletilamellaptychus stefanovi is described. The collection contains also the holotype of Didayilamellaptychus filicostatus (Stefanov), which was previously elevated from a variety to species level by Mečhova et al. (2010). A valve of Didayilamellaptychus cf. didayi preserved in the body chamber of a Neolissoceras supports the hypothesis that lamellaptychi and perhaps punctaptychi belong to the natural system of ammonites of family Haploceratidae Zittel, 1884. It became evident that the state of preservation may strongly affect the taxonomic determination of the aptchi. Only in exceptional cases (occurrence of both valves in a pair with different state of preservation) this preservation phenomenon can be revealed and erroneous determination of any of the valves could be possibly avoided.

Key words: Late Jurassic, Early Cretaceous, Bulgaria, aptchi, ammonites, parataxonomy, preservation, new species.

1. Introduction

This paper presents a taxonomic revision of collection of Late Jurassic and Early Cretaceous aptchi housed at the National Museum of Natural History, Sofia. Most of this collection, 54 specimens of Early Cretaceous aptchi from Bulgaria, were initially described by July Stefanov in 1961. Stefanov was one of the talented and most promising Bulgarian palaeontologists of the 20th century. Unfortunately, he died tragically in 1966 at the age of 34. At the time of the publication (Stefanov 1961), one part of the aptchi collection was housed at the Geological Institute of the Bulgarian Academy of Sciences (GI-BAS) and another, smaller part – in the Palaeontological Museum of Sofia University. The National Museum of Natural History, Sofia (NMNS) was later (1974) restored as an autonomous institution within the Bulgarian Academy of Sciences. On that occasion, only part of the geological collections from GI-BAS was moved to NMNHS in the years following 1974. The reason of this selective moving is unknown. To our knowledge, the aptchi collection of July Stefanov was one of the few important palaeontological collections that were
moved to the NMNHS. The specimens of this collection, described earlier by Stefanov, have successive museum registration numbers NMNHS F-30809 through to 30876.

Nineteen Late Jurassic and Early Cretaceous specimens of aptychi not described earlier are also included in this taxonomic account. They have older museum numbers previously assigned (random numbers between NMNHS F-335 and NMNHS F-9928) and are marked with an asterisk in the text. As a result of the taxonomical reappraisal of the Bulgarian material (completed by Z.V.), one new species is erected, named in honour of July Stefanov. Unfortunately, some twelve specimens from the collection remain undetermined because of poor or fragmentary preservation.

This study aims to facilitate further investigation of the collection. Future research could focus on the shell microstructure and/or on the systematic position of certain problematic specimens for which open nomenclature is used here.

One of the reasons to revise the Bulgarian collection were also the new results reported in the Ph.D. thesis of L. Kratochvílová (2004), where she proposed a serious rearrangement of the taxonomy of Early Cretaceous aptychi. The results of her thesis served as a basis for the suggested new classification (Měchová et al. 2008, 2010).

At the time of publication (1961), Stefanov’s specimens were one of the few significant collections of Early Cretaceous aptychi alongside the collections of Trauth (1927-1938) and Gąsiorowski (1959, 1962). The paper of Stefanov (1961) and the present contribution, where new material is added, extend considerably the knowledge about the distribution of aptychi from Western and Central to Eastern Europe. Stefanov (1961) had described the collection accurately and in
accordance with the aptychi classification at that time. Since then, however, the knowledge on Early Cretaceous ribbed aptychi has evolved significantly to warrant a review.

As part of the present taxonomic reappraisal, when possible, the stratigraphic level of the aptychi occurrences was critically reviewed using information from the museum labels and the paper by Stefanov (1961). The official lithostratigraphic units, which in most cases were introduced after 1961 (Tenchov 1993) are provided here as well. We consider the revised age determinations confident enough since we have not observed evidence of redeposition and also because the revised ages conform to the range of occurrences of the respective taxa as described in the literature with just one exception (specimen NMNHS F-30841, see Appendix 1).

The data about the localities and horizons as well as Stefanov's original determinations are summarized in Appendix 1. The original determinations of Stefanov are given for each specimen in order to facilitate future research and correlation with his personal archive and, most importantly, with later Bulgarian publications in which these taxa are cited.

2. Geological setting

The bulk of the aptychi described in this paper were collected from Lower Cretaceous rocks, by number of specimens in ascending order, from the Berriasian to the Hauterivian. Little portion of our material, only 7 specimens, came from Upper Jurassic outcrops (Kimmeridgian and Tithonian). A few of the aptychi studied have poorly known stratigraphic positions, but fall into the stratigraphic framework outlined. Commonly, the aptychi have scattered occurrences of randomly dispersed examples and data about other associated macrofossils preserved are missing. They occur within the pelagic, flysch-like and flysch deposits, of great thicknesses that are widely exposed in Central and Northern Bulgaria and crop out on a minor scale in Western Bulgaria.

The sedimentary successions of Late Jurassic to Early Cretaceous age that yielded the studied here aptychi are subdivided into several formal lithostratigraphic units, which alternate gradually one after the other. The lithostratigraphic background taken into consideration for this study includes: Gintsi Formation (nodular limestones, ammonitico rosso-type, Kimmeridgian – Tithonian), Glozhene Formation (regularly-beded, mainly micritic limestones, Tithonian – Berriasian), Ticha Formation (marl-limestone alternation with turbidity sandstones, Tithonian), Cherniosam Formation (limestones-shales-siltstones-graywackes in a repeated rhythmic alternation, Tithonian – Valanginian), Kamchya Formation (irregular alternation of silty marls, siltstones and sandstones, Berriasian – Hauterivian), Hanevtsi Formation (silty marls with interbeds of siltstones, Berriasian – Hauterivian), Salash Formation (irregular marl-limestone alternation, Valanginian – Hauterivian), and Gorna Oryahovitsa Formation (marls with rare interbeds of sandstones and siltstones, Hauterivian) [for details see Zagorchhev et al. (2009), and references cited therein]. There is a general agreement that these sequences were deposited in wide pelagic environments during the Late Jurassic times which were replaced from the end of the Tithonian onwards by long-living foredeep depositional setting.

Regionally, the rocks which yielded the aptychi associate largely with the most prominent and most elevated element of the Balkan orogenic system (the Balkan Zone) and less with its foreland (the Moesian Platform) in Bulgaria (Zagorchhev et al. 2009). Just one locality is in the inner parts of the orogen (the Srednogorie Zone). In terms of its geographic distribution, the localities of the studied aptychi display an unequal density of occurrence. The main share of the account that follows refers to the localities from a region of the Central Bulgaria, between the towns of Teteven and Elena (Lovech and Gabrovo districts). Outside this area, a smaller number of localities in North-eastern Bulgaria (Targovishte, Shumen, and Varna districts), and Western Bulgaria (Sofia, Montana and Vratsa districts) exist. The localities, ages and stratigraphic positions of the aptychi are listed for each sample in Appendix 1. A map showing the approximate geographical and geological position of the main localities of aptychi and the distribution of the Upper Jurassic and Lower Cretaceous rocks in Bulgaria is given in Fig. 1.

3. Aptychi and their taxonomy

The pairs of calcareous and ribbed valves of aptychi have already been reported in the literature for almost 200 years. The relationship between aptychi and ammonites was suggested already before the mid-19th century. Opinions about their systematic position, classification, function, and position in the soft body and in the living chamber of ammonites have changed, however, several times. The valves of aptychi are considered to be either opercula of ammonite shells (e.g., Trauth 1927-1938; Schindewolf 1958) or the man-
dible of a jaw apparatus (e. g. LEHMANN 1972). Some researchers suggest that aptychi had both functions (LEHMANN & KULICKI 1990). ENGESER & KEUPP (2002) summarized the biological function and phylogensis of Jurassic and Cretaceous aptychi and ammonites. Those of the Neoammonoidea, in which calcareous aptychi have been reported; they referred to a new informal taxonomic unit, Aptychophora.

The calcitic ribbed aptychi occur in the palaeontological record most frequently as isolated valves. Rarely, both valves are found together, and only exceptionally, within the living chamber of an ammonite. Consequently, aptychi classification is entirely artificial. For more details see MÉCHOVA et al. (2010: 225-239). Therefore, the aptychi belong to the category of artificial groups, similarly to other fossils such as holothurian ossicles, conodonts, coleoid hooklets, and others.

The first artificial classification of aptychi was worked out by TRAUT (1927-1938). For the Mesozoic aptychi, he created 14 genera. The genera were divided into species, which were often subdivided into varieties (var.). TRAUT also used the designation ‘forma typica’ (f. typ.) after the species name when introducing subspecies.

Thus, for the ribbed aptychi of Late Jurassic and Earliest Cretaceous age (genera Punctaptychus and Lamellaptychus) the classification based on the nomenclature of TRAUT (1927-1938) was widely used in the last century. A huge amount of new, not yet known findings of latest Jurassic/Early Cretaceous aptychi of both genera, collected in the framework of Deep Sea Drilling Project (RENZ 1972-1983) or in Romania (TURCULET 1994-2000) led to certain turnover in the elaboration of the classification of ribbed aptychi based on the nomenclature of TRAUT. An almost deadlock in the description and conception of other new species (and largely subspecies) following the rules of TRAUT, heading towards quadrinominal nomenclature (for details see MÉCHOVA et al. 2010), urged TURCULET (1994) to the definition of subgenera. For the general designation of taxa he explicitly used the term parataxa. He proposed the original para-genus Lamellaptychus TRAUT, 1927 to be divided into four para-subgenera: Beyrichilamellaptychus, Lamellosuslamellaptychus, Thorolamellaptychus and Didayilamellaptychus. These para-genera were subdivided in para-species and para-subspecies.

However, none of the previous and subsequent authors used the prefix “para-“ as a classification category (e.g. para-species). They understood the term parataxa exclusively as a common designation.

On the basis of further abundant findings of latest Jurassic/Early Cretaceous aptychi in the Western Carpathians and Eastern Alps and data from the literature, MÉCHOVA et al. (2010) concluded that TURCULET’s subgeneric division fails to cover the range of variability in ribbed aptychi, so it would be perhaps suitable to determine some other new subgenera. However, this would cause an expansion of the old genus Lamellaptychus into a disproportionate number of subgenera. Therefore, MÉCHOVA et al. (2008, 2010) suggested elevating TURCULET’s subgenera to the level of independent genera. These authors proposed to group them into two new families: Punctaptychidae and Lamellaptychidae. Thus, the category of subgenus remains potentially open for the future.

In this paper, the classification of ribbed aptychi as proposed by MÉCHOVA et al. (2008, 2010) is followed. This classification uses taxa on the levels of families, genera, species and subspecies taken from natural taxonomy, but which are in fact artificial taxa (parataxa). Such parataxa could also be possibly designated by terms, such as ‘form family’, ‘form genus’ and ‘form species’, but we avoid them in the text that follows in order to simplify it.

ENGESER & KEUPP (2002) collected arguments, known earlier, that perfectly calcified thin to thick-walled valves with well developed ribs (lamellaptychi and punctaptychi) belonged to ammonites of the family Haploceratidae ZITTEL, 1884. This is well confirmed by the same stratigraphic range of both fossil groups (Kimmeridgian – Hauterivian; see e.g., WRIGHT et al. 1996). The classification of the lamellaptychi and punctaptychi to a single family of ammonites is also supported by the fact that they are characterised by shape uniformity of valves, which is marked also by the ratio of valve width (Lat) to valve length (L). The value Lat/L moves in a narrow range from 0.43 to 0.56. However, some representatives of Thorolamellaptychus (Lat/L = 0.57-0.60) and Didayilamellaptychus didayi (Lat/L about 0.65) are an exception.

4. Systematic palaeontology

Most of the taxa treated in the present paper were described recently in detail and their critical synonymy was given by MÉCHOVA et al. (2010). When these authors compiled their manuscript, they did not have at their disposal the extensive monograph by TURCULET (2000) on Romanian calcareous aptychi. In his monograph TURCULET (2000) summarises his lifelong re-
search on Late Jurassic (mostly) and Early Cretaceous aptychi. The classification he uses is based on his division of the genera *Lamellaptychus* and *Punctaptychus* into subgenera (Turculet 1994). However, some of the subgenera determined by him do not comply with nomenclatorial rules for the category of typical subgenera. Not all illustrations of Turculet (2000) are of satisfactory quality to assess the justification of some of his specific determinations. For this reason, our concept of species in the taxonomic part is supplemented only with the synonymy of those Early Cretaceous species which are described and illustrated clearly enough by Turculet (2000), but which were not included in the paper of Měchová et al. (2010).

For all the taxa recently described by Měchová et al. (2010) which we recognised in the Bulgarian material without any doubts, we provide an abridged synonymy only, i.e. the primary reference of papers, where the type material was described and illustrated. In Měchová et al. (2010) full synonymy and other relevant information can be found. Thus, for the taxa discussed already in detail by Měchová et al. (2010), only a brief description supplemented in some cases by remarks and measurements of the Bulgarian material is presented.

Three species of aptychi, including one new taxon (*Mortillitilamellaptychus* stefanovi n. sp., *Thorolamellaptychus* cf. *aplanatus*, and *Laevaptychus longus*) that were not discussed in the monograph of Měchová et al. (2010) are here presented with full synonymy and described in more details.

Part of Stefanov’s published material was re-photographed and is here illustrated with improved quality. All figured specimens with the exception of one (Fig. 8.10) were coated with ammonium chloride before photographing.

The details of geographical and geological setting in Bulgaria, as well as reference data on particular specimens, are to be found in the Appendix 1. Thus, under the sections “Distribution” only the occurrences outside Bulgaria are mentioned.

**Measurements and abbreviations:** The basic morphology of valves of aptychi and measured values is presented on Fig. 2. All the well preserved specimens are measured. The values taken from fragmental specimens are denoted by apostrophe (‘L’, ‘Lat’) to indicate an uncertainty of the measurement. L = total length of the valve; S = distance between the apex and the terminal point; Lat = maximum valve width; pW = width projection (distance between the terminal point and the projection of point of maximum width); Fm = formation, referring to the official lithostratigraphic unit; t. = in the old museum numbers of specimens refers to a mapping site, [= точка in Bulgarian]; NMNHS F- – prefix of the numeration in the collections in the National Museum of Natural History, Sofia.

**Family Punctaptychidae Měchová, Houša & Vašíček, 2008**

**Diagnosis:** Ribbed aptychi with valves composed of four calcareous layers. Outer lamellar layer overlain by porous (punctate) layer in apical area.

**Genus Punctaptychus Trauth, 1927**

**Type species:** *Aptychus punctatus Zittel*, 1868, p. 52.

**Diagnosis:** Thick-walled valves with simple ribbing. Ribs subparallel to the symphysal margin. Most of ribs end at outer margin, a few at symphysal margin.

**Punctaptychus punctatus (Zittel, 1868)**

1868 *Aptychus punctatus* Voltz. – Zittel, p. 52, pl. 1, fig. 15a, b.

2000 *Punctaptychus (Beyrichipunctaptychus) punctatus punctatus* Voltz. – Turculet, p. 129, pl. 10, figs. 2-3, 6, ? 1, 4-5, 7-9; pl. 11, figs. 1, 3, ? 2, 4-9.

2010 *Punctaptychus punctatus* (Zittel). – Měchová et al., p. 231, fig. 8A (cum syn.).

**Material:** Three poorly preserved specimens, NMNHS F-30839, 30841, and 337* (see Appendix 1 for details).

**Measurements:** Specimen NMNHS F-30841: L = 27.6 mm, Lat = 15.0 mm, S = 25.8 mm, Lat/L = 0.54.

**Description:** Small to large-sized valves. The outer margin is wide and rounded. Ribs are simple and slightly bent. Near the symphysal margin in the terminal area, ribs are thin and run close to each other. The punctate layer is preserved only partly.

**Distribution:** Upper Jurassic to Upper Berriasian of the Mediterranean area (Měchová et al. 2010).

**Punctaptychus divergens** Trauth, 1935

Fig. 3.1

1935 *Punctaptychus punctatus* (Voltz) var. n. divergens. – Trauth, p. 321, text-fig. 1.

2000 *Punctaptychus (Beyrichipunctaptychus) punctatus divergens* Trauth. – Turculet, p. 132, pl. 12, fig. 2, ? 3-5, pl. 13, figs. 1-3, non fig. 4 (=Punctaptychus rectecostatus Cuzzi, 1962).

2010 *Punctaptychus divergens* Trauth. – Měchová et al., p. 234, fig. 8C (cum syn.).
Material: One specimen, NMNHS F-336* (see Appendix 1 for details).

Description: Valve large in size. The ribs in the terminal area are arranged in a fan-like pattern.

Distribution: Newer data place the earliest occurrence of the species in the Middle Tithonian of Eastern Alps (Boorová et al. 2000). *P. divergens* was also proven in the lowermost Berriasian of Spain (Vašíček & Hoedemaeker 1997).

*Punctaptychus* sp.

Fig. 3.2

Material: Four specimens, NMNHS F-335*, 338*, 1890*, 1891* (see Appendix 1 for details).

Remarks: Due to poor preservation the determination of these specimens was possible to a genus level only.


Diagnosis: Ribbed aptychi, with valves formed by three calcareous layers. Valve surface with conspicuous ribs.

Genus *Beyrichilamellaptychus* Turculet, 1994

Type species: *Aptychus beyrichi* Oppel, 1865, p. 547.

Diagnosis: Majority of curved ribs converge along significant section of symphysal margin, where ribs become thinner and sub-parallel striped pattern condenses. In late evolutionary forms ribbing pattern may be characterized by some of end ribs being discordant to previous ribs.

*Beyrichilamellaptychus beyrichi* (Oppel, 1865)

1865 *Aptychus Beyrichi* Opp. – Oppel, p. 547.
1868 *Aptychus Beyrichi* Opp. – Zittel, p. 54, pl. 1, figs. 16, 17 (type), 18, ?19.
2000 *Lamellaptychus (Beyrichilamellaptychus) beyrichi beyrichi* (Oppel) em. Trauth, f. typ. Trauth. – Turculet, p. 85, pl. 1, figs. 2-3, ?figs 4-15, pl. 2, fig. 2, ?figs. 1, 3-4, pl. 24, fig. 9.
2010 *Beyrichilamellaptychus beyrichi* (Oppel) – Měchová et al., p. 239, fig. 9B (cum syn.).
Fig. 3. Representatives of the genus Punctaptychus. 1 – Punctaptychus divergens TRAUTH, NMNHS F-336; Shipkovski Mineral Baths, Lovech District, Tithonian, Cherniosam Fm. 2 – Punctaptychus sp., NMNHS F-335; Erden Village, Montana District, Tithonian, Ginci Fm – Glozhene Fm. Valve with not preserved punctate layer.

Material: Two fragmental specimens, NMNHS F-9738*, 9740* (see Appendix 1 for details). Two other specimens, one poorly preserved specimen NMNHS F-30825 and one negative imprint NMNHS F-9737*) are referred to as Beyrichilamellaptychus cf. beyrichi in Appendix 1.

Description: Small to medium-sized valves, slightly vaulted, without a keel or a lateral depression. Along the symphysal margin in the terminal part of valves the ribs are straight, thin and densely spaced. They converge to the symphysal margin at a relatively acute angle.

Distribution: The stratigraphic interval and area of distribution of B. beyrichi is very wide. TURCULET (2000) reported it from the Oxfordian to the Berriasian.

Beyrichilamellaptychus studeri (OOSTER, 1857)

Fig. 4

1857 Trigonellites Studeri OOSTER. – OOSTER, p. 26, pl. 7, fig. 4 (type), non figs. 1-3,6 (= Mortilletilamellaptychus breggiensis RENZ & HABICHT, 1985), non fig. 7 (= M. ex gr. mortilleti PICTET & DE LORIOL, 1858), non fig. 5 (= Thorolamellaptychus sp.).

1961 Lamellaptychus mortilleti (PICTET & LORIOL) var. radiata STEFANOV. – STEFANOV, p. 219, 225-6, 227-228, pl. 3, fig. 3.

2010 Beyrichilamellaptychus studeri (OOSTER). – MÉCHOVÁ et al., p. 242, fig. 9D (cum syn.).

Material: One pair of valves, NMNHS F-30843 (see Appendix 1 for details).

Description: Small to medium-sized valves. Juvenile ribs are closely spaced. They converge almost subparallel along the symphysal margin. Adult (peripheral) ribs follow the shape of valves and are discordant to the juvenile ribs.
Fig. 4. Beyrichilamellaptychus studeri (Ooster), NMNHS F-30843; east of Todorchetata Village, Gabrovo District, Upper Valanginian, Kamchia Fm.

Remarks: Stefanov (1961) referred the specimen to as Lamellaptychus mortilleti var. radiata. The thin, dense ribs along its symphysal margin, which were regarded by Stefanov as radial lines, represent in fact the terminal parts of fine juvenile ribs of the “beyrichi” type.

Distribution: According to Měchová et al. (2010) the stratigraphic range of this species is from the Late Tithonian to the lower part of the Early Valanginian.

Fig. 5. Some representatives of the genus Mortilletilamellaptychus. 1 – Mortilletilamellaptychus mendrisiensis mendrisiensis (Renz & Habicht), NMNHS F-30834; Mecha polyana Village (not existing any more), Svože municipality, Sofia District, Upper Valanginian, Salash Fm; a – note the left valve favourably illuminated; b – note the right valve favourably illuminated. The left valve belongs undoubtedly to M. m. mendrisiensis while the right valve, deformed into the plane of bedding with poorly visible symphysal area could be erroneously identified as M. mortilleti (Pictet & de Loriol). 2 – Mortilletilamellaptychus mendrisiensis mendrisiensis (Renz & Habicht), NMNHS F-30824, Kapinets Village, Antonovo municipality, Targovishte District, Lower Hauterivian, Hanevtsi Fm. 3 – Mortilletilamellaptychus bicurvatus (Renz & Habicht), NMNHS F-30812; south of the hamlet Hristova mahala, Troyan municipality, Lovech District, Upper Valanginian, Cherniosam Fm.
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Fig. 6. Mortilletilamellaptychus stefanovi n. sp., NMNHS F-30833, holotype with copy of the original label of Stefanov; Makotsevo Village, southeast of the peak Ademitsa, Gorna Malina municipality, Sofia District, Berriasian, Cherniosam Fm (Tithonian - Berriasian flysch).

in the symphysal area; its left valve, however, bears characteristic ribbing near the symphysal margin of terminal area, what supports its reference to M. m. mendrisiensis (see further notes in the chapter 'Preservation, palaeoecologic and taphonomic notes').

Distribution: Upper Valanginian of Switzerland (Renz & Habicht 1985) and Upper Valanginian to ?Lower Hauterivian of Central Western Carpathians (Vašíček et al. 1994).

Mortilletilamellaptychus bicurvatus (Renz & Habicht, 1985)
Fig. 5.3

1938 Lamellaptychus sub-mortilleti n. var. n. retroflexa. – Trauth, p. 201, pl. 14, fig. 6 (type).

pars 1961 Lamellaptychus mortilleti (Pictet & Lortioli). – Stefanov, p. 217, pl. 3, fig. 1, non fig. 4 (= undeterminable).


2010 Mortilletilamellaptychus bicurvatus (Renz & Habicht). – Měchová et al., p. 250, fig. 10C (cum syn.).

Material: One specimen, NMNHS F-30812 (see Appendix 1 for details).

Description: The juvenile ribs converge along the symphysal margin. Adult ribs at first broadly bend back to the apex, and then are short, S-shaped in the vicinity of the symphysal margin.

Remarks: The specimen NMNHS F-30827 previously determined as Lamellaptychus mortilleti (Stefanov 1961, pl. 3, fig. 4) is undeterminable because the valve is broken along the symphysal margin.

Distribution: Upper Valanginian of the Western Carpathian, Northern Calcareous Alps and Switzerland (Měchová et al. 2010).

Mortilletilamellaptychus stefanovi n. sp.
Fig. 6

non 1938 Lamellaptychus sub-mortilleti n. var. n. retroflexa. – Trauth, p. 201, pl. 14, fig. 6 (= Mortilletilamellaptychus bicurvatus Renz & Habicht, 1985).

1961 Lamellaptychus submortilleti Trauth var. retroflexa Trauth. – Stefanov, p. 220, pl. 3, fig. 7.

?par 1985 Lamellaptychus bicurvatus new name. – Renz & Habicht, p. 3, fig. 27 only (non figs. 25-26, 28 = Mortilletilamellaptychus bicurvatus).

Etymology: In honour of July Stefanov.

Holotype: Valve NMNHS F-30833 (35, t. 237 (M. Hr.) described and illustrated by Stefanov (1961, p. 220, pl. 3, fig. 7; and re-illustrated herein in Fig. 6), and referred to Lamellaptychus submortilleti var. retroflexa Trauth.

Type horizon and locality: Berriasian (as part of the Tithonian-Berriasian flysch) near Makotsevo Village, south-
east of the peak Ademitsa, Gorna Malina municipality, Sofia District.

**Material:** The holotype only.

**Measurements:** \( L = 14.2 \text{ mm}, S = 13.0 \text{ mm}, \text{Lat} = 9.5 \text{ mm}, \text{Lat/L} = 0.67 \). The high value of the index is influenced by the considerable deformation of the valve.

**Diagnosis:** Dense and thin ribs are simple on the flanks. Double undulation of ribs in immediate vicinity of symphysal margin.

**Description:** The valve is small in size, secondarily flat, apparently wide. Ribs are thin and dense. The juvenile part of the valve is poorly preserved. Juvenile ribs are probably of the “mortilleti” type. Adult ribs are complicated in the close vicinity of the symphysal margin, where they are S-shaped (“zig-zag bends” according to Stefanov). Along the symphysal margin, the ribs run to the terminal apex. The convexity of the valve is strongly affected by deformation onto the bedding plane.

**Remarks:** Stefanov (1961) identified this valve with the Trauth’s subspecies Lamellaptychus submortilleti var. retroflexa. Later Renz & Habicht (1985) selected Trauth’s specimen as holotype of new species Lamellaptychus bicurvatus. However, the specimen of Stefanov differs from the valve of Trauth (1938), as well as from the prevailing majority of valves of Renz & Habicht (1985) by having a very short portion with S-shaped ribs and by not having the first bend of ribs widely convex. Only a single, incomplete valve, illustrated by them (Renz & Habicht 1985, pl. 3, fig. 27) seems to be close to the Bulgarian species. Because of its markedly higher stratigraphic position, it is referred here to the new species with a question mark.

**Distribution:** The holotype is from the Chernosiam Formation, Berriasian of Bulgaria. The specimen of Renz & Habicht (1985, pl. 3, fig. 27) comes from the Upper Valanginian of the Breggia section (Maiolica Formation), Switzerland.

**Genus Thorolamellaptychus** Turculet, 1994

**Type species:** Aptychus thoro Oppel, 1863, p. 250.

**Diagnosis:** Thin and dense ribs in the juvenile and the adult stage follow the shape of the valves. All or almost all ribs end on the symphysal margin. More complicated ribbing at final developmental stages.

Thorolamellaptychus cf. aplanatus (Gilliéron, 1873)  
Fig. 7.1

*cf. 1994 Lamellaptychus aplanatus aplanatus (Gilliéron). – Vašiček et al., p. 76, pl. 23, fig. 6.*

**Material:** A single, relatively well preserved valve, NMNHS F-30865 (see Appendix 1 for details).

**Measurements:** NMNHS F-30865: \( L = 19.3 \text{ mm}, \text{Lat} = 9.4 \text{ mm}, \text{Lat/L} = 0.49 \).

**Description:** The valve is strongly convex, without a keel and without a depression. Simple, thin, dense ribs follow the shape of the valve. Juvenile, imperfectly preserved ribs in the symphysal area are reminiscent somewhat of ribbing of the “beyrichi” type. Simple ribbing can also be seen in specimens that are illustrated under the name Lamellaptychus aff. aplanatus by Renz & Habicht (1985, pl. 3, figs. 4, 7). Such juvenile ribbing differs somewhat from typical representatives of T. aplanatus, and consequently, the specimen is left here in open nomenclature.

**Remarks:** This is most probably the specimen mentioned by Stefanov (1961: 223), assigned tentatively to Lamellaptychus herthae var. laevadsymphysalis, but which he did not describe.

**Distribution:** According to Renz & Habicht (1985) typical specimens of Th. aplanatus come from Valanginian of Mediterranean area in Europe and of Atlantic area (Deep Sea Drilling Project).

Thorolamellaptychus trauthi (Renz & Habicht, 1985)  
Fig. 7.2

2010 Thorolamellaptychus trauthi (Renz & Habicht). – Méchová et al., p. 256, fig. 10K (cum syn.).

**Material:** One specimen, NMNHS F-30853 (see Appendix 1 for details).

**Description:** In the juvenile part the simple ribs are directed towards the symphysal margin at an angle of about 45°. Above the keel, the adult ribs bend in a broad arch-like manner back towards the apex. Near the symphysal facet, they bend sigmoidally. The end branch of the ribs points towards the terminal edge.

**Distribution:** The species is reported from Upper Berrian to Upper Valanginian of Switzerland, Western Carpathians and in the Alps (for details see Méchová et al. 2010).

**Genus Didayilamellaptychus** Turculet, 1994

**Type species:** Aptychus didayi Coquand, 1841, p. 389.

**Diagnosis:** Usually thick-walled, medium- to large-sized
Fig. 7. Representatives of the genus Thorolamellaptychus. 1 - Thorolamellaptychus cf. aplanatus (Gilliéron), NMNHS F-30865; east of Makotsevo Village, Gorna Malina municipality, Sofia District, Berriasian, Cherniosam Fm. 2 - Thorolamellaptychus trauthi (Renzi & Habicht), NMNHS F-30853; north of Beli Osam Village, Troyan municipality, Lovech District, Upper Valanginian, Cherniosam Fm.

Fig. 8. Some representatives of the genus Didayilamellaptychus. 1 - Didayilamellaptychus didayi (Coquand), NMNHS F-30844; inner surface of valve with growth lines, close to the outer margin with serpulid encrustations, southwest of Chernevo Village, Varna District, Lower Hauterivian, Gorna Oryahovitsa Fm. 2 - Didayilamellaptychus didayi (Coquand) with sessile serpulids and bryozoa, NMNHS F-9925; countryside Teke dere near Shumen, Hauterivian, Gorna Oryahovitsa Fm. 3 - Didayilamellaptychus seranonis (Coquand), NMNHS F-30861, Zlatitsa river, Gaganitsa Village, Montana District, Upper Valanginian, Salash Fm. 4 - Didayilamellaptychus cf. seranonis (Coquand, 1841), NMNHS F-30818; corroded surface of valve, strong corroded ribs with pervading growth lines, Chernevo Village, Varna District, Lower Hauterivian, Gorna Oryahovitsa Fm. 5 - Didayilamellaptychus angulodidayi (Trauth), NMNHS F-30850; west of Balgarski izvor Village, Lovech District, Lower Hauterivian, Gorna Oryahovitsa Fm. 6 - Didayilamellaptychus angulocostatus (Peters), NMNHS F-30831 with radial lines; southwest of Chernevo Village, Varna District, Lower Hauterivian, Gorna Oryahovitsa Fm. 7 - Didayilamellaptychus cf. angulocostatus (Peters), juvenile specimen NMNHS F-30840; Balgarski izvor Village, Lovech District, Upper Valanginian, Gorna Oryahovitsa Fm. 8 - Didayilamellaptychus angulicostatus (Pictet & de Loriol), NMNHS F-30816; Gaganitsa Village, Montana District, ?Hauterivian, Salash Fm. 9 - Didayilamellaptychus cristobalensis (O’Connell), NMNHS F-30817; southwest of Chernevo Village, Varna District, Lower Hauterivian, Gorna Oryahovitsa Fm. 10 - Didayilamellaptychus renzi Mëchovâ, Vašièek & HouSa, NMNHS F-30856 with radial lines; Krapchene Village, Montana District, Lower Hauterivian, Salash Fm. Specimen not coated with ammonium chloride before photographing.
valves with strong ribs, only infrequently with thin ones. Adult ribs bend back in a curved to angular manner. In some specimens curved and angular ribbing occurs simultaneously. The last few ribs can be incomplete.

**Didayilamellaptychus didayi** (Coquand, 1841)

Figs. 8.1, 8.2

1841 *Aptychus Didayi* (nobis). – Coquand, p. 389, pl. 9, fig. 10.

pars 1961 *Lamellaptychus didayi* (Coquand). – Stefanov, p. 216, pl. 2, figs. 1-3, 5-7, non fig. 4 (=Didayilamellaptychus cf. didayi).

1961 *Lamellaptychus subdidayi* Trauth. – Stefanov, p. 217, pl. 2, figs. 8-10.


2010 *Didayilamellaptychus didayi* (Coquand). – Mečová et al., p. 257, fig. 11A (cum syn.).

**Material:** Fourteen specimens, NMNHS F-30810, 30811, 30813, 30828, 30837, 30844, 30852, 30852*, 30864, 30835, 30822, 30820 (see Appendix 1 for details).

**Measurements:** Specimen NMNHS F-30852 is the largest among the ribbed aptychi: L = about 31.5 mm.

**Description:** The valves are wide, with a prominent keel and a shallow lateral depression. The strong and widely spaced ribs begin to bend in a broad arch back towards the apex, approximately, at the area of lateral depression. The width of the valves is notable. In the lateral depression area, the ribs are bent in a sigmoidal pattern.

**Distribution:** Lower Valanginian to uppermost Lower Hauterivian in the Mediterranean area (for details see Mečová et al. 2010).

**Didayilamellaptychus seranonis** (Coquand, 1841)

Fig. 9

1841 *Aptychus Seranonis* (nobis). – Coquand, p. 390, pl. 9, fig. 13.

pars 1961 *Lamellaptychus angulocostatus* (Peters) var. atlantica (Hennig), transition to *Lamellaptychus seranonis* (Coquand). – Stefanov, p. 215, pl. 1, fig. 12, non fig. 8 (=Didayilamellaptychus cf. angulocostatus (Peters, 1854).

1972 *Lamellaptychus I.* – Thomson, p. 35, fig. 2a, c, ?b.

2010 *Didayilamellaptychus seranonis* (Coquand). – Mečová et al., p. 258, fig. 11B (cum syn.).

**Material:** One specimen, NMNHS F-30861 (see Appendix 1 for details).

**Description:** Slender valves, with a keel and a lateral depression. In maturity, the ribs are strong and spread apart. The ribs between the keel and the symphysal margin bend poorly preserved. Because of the considerable imperfection of preservation of the symphysal area, the width of the valve, rough ribbing and marked (fractal) bend of ribs on the flank of the valve, the determination of this specimen is uncertain. We tentatively assign it into group of *Didayilamellaptychus didayi* (Coquand).

**Remarks:** Stefanov (1961, pl. 3, fig. 9, see also here Fig. 9) illustrated the aptychus NMNHS F-30847 occurring in the body chamber of an ammonite determined correctly as *Neolissoceras grasiannum* (d'Orbigny), NMNHS F-30848, from north of the hamlet Enochovtsi, Troyan municipality, Lovech District, Lower Hauterivian, Kamchia Fm.
back in a curved to subangular manner towards the apex. In the lateral depression, the ribs may be slightly to sigmo­idally bent.

**Distribution:** From the uppermost Lower Valanginian to the Lower Hauterivian of the Mediterranean area (for more details see MÉCHOVÁ et al. 2010).

**Didayilamellaptychus cf. seranonis (COQUAND, 1841)**

Fig. 8.4

1961 Lamellaptychus seranonis (COQUAND) var. radiata

*Remarks:* Specimen NMNHS F-30818 is a corroded fragmental valve, which STEFANOVA (1961: 221) described as a new variety of the species *seranonis*. We think, however, that the differences, pointed out by the author, are caused by corrosion and do not justify defining a new variety.

**Didayilamellaptychus angulodidayi (TRAUTH, 1938)**

Fig. 8.5

1849 *Aptychus Didayi* COQUAND. – QUENSTEDT, p. 314, pl. 22, fig. 21a, b.

1938 Lamellaptychus angulo-didayi n. f. typ. – TRAUTH, p. 212, pl. 14, figs. 28-29.

2010 Didayilamellaptychus angulodidayi (TRAUTH). – MÉCHOVA et al., p. 260, fig. 11E (cum syn.).

*Material:* One specimen, NMNHS F-30850 (see Appendix 1 for details).

*Description:* Valve with a prominent keel and lateral depression. In the juvenile part of valve, the ribs are angular; whereas subangular arch-shaped ribs are observed in the adult part of the valve, which end on the symphysal facet.

*Distribution:* The author of this species placed the type material in the Neocomian. MÉCHOVÁ et al. (2010) reported a distribution from the Upper Valanginian to the Lower Hauterivian in the Western Carpathians.

**Didayilamellaptychus angulocostatus (PETERS, 1854)**

Fig. 8.6

1854 Aptychus angulocostatus PETERS. – PETERS, p. 441.

pars 1961 Lamellaptychus angulocostatus (PETERS). – STEFANOVA, p. 212, pl. 1, figs. 1-3, ? 4, non fig. 6 (Didayilamellaptychus angulocostatus (PICTET & DE LORIOU, 1858).


2000 Lamellaptychus (Didayilamellaptychus) angulocostatus (PETERS) f. typ. TRAUTH. – TURCULET, p. 126, pl. 23, figs. 7, 9-10, 17, ? figs. 11, 13, 15-16, non fig. 12 (= *D. renzi* MÉCHOVA et al.), non fig. 14 (= *D. angulicostatus* PICTET & DE LORIOU), pl. 24, figs. 2, 4-5, non figs. 3, 6 (= D. renzi MÉCHOVA et al.).

2000 Lamellaptychus (Didayilamellaptychus) angulocostatus longus TRAUTH. – TURCULET, p. 126, pl. 24, fig. 1.

2010 Didayilamellaptychus angulocostatus (PETERS). – MÉCHOVA et al., p. 260, fig. 11F (cum syn.).

*Material:* Seven specimens, NMNHS F-30809; 30814, 30819, 30830, 30831, 9905*, 9906*. (see Appendix 1 for details).

*Description:* Valves with a keel but without a lateral depression. Ribs on the flank of valves run subparallel to the symphysal margin. In the area of the keel, the ribs are angular.

*Remarks:* In specimen NMNHS F-30819 the right valve is deformed by lateral pressure, so it would belong to var. “longa”; while the left valve is with a broken arch, pressed into the bedding plane, so it would belong to var. “lata”. These observations suggest that the varieties *longa* and *lata* are not supported in taxonomy and are result of deformation. The specimen NMNHS F-30831 shows radial lines (Fig. 8.6).

**Didayilamellaptychus cf. angulocostatus (PETERS, 1854)**

Fig. 8.7


pars 1961 Lamellaptychus angulocostatus (PETERS) var. atlantica (HENNING). – STEFANOVA, p. 215, pl. 1, fig. 8, non fig. 12 (= Didayilamellaptychus seranonis (COQUAND, 1841)).

*Material:* Three specimens, NMNHS F-30832, 30840, 30845 (see Appendix 1 for details).

*Remarks:* Specimen NMNHS F-30840 is a juvenile valve, with a well preserved terminal area. Specimen NMNHS F-30845 is also a juvenile valve, very poorly preserved. Specimen NMNHS F-30832 is a poorly preserved fragment.
1858 *Aptychus angulicostatus*. – *Pictet & de Loriol*, p. 46, pl. 10, fig. 3 (type), 26-12, non figs. 4-5 (= Didayilamellaptychus cf. renzi Měchová, Vašíček & Houša, 2010).

1910 *Aptychus angulicostatus* Pict. and de Loriol. – Kilian, pl. 5, fig. 2b, non fig. 2a (= D. cf. renzi).

* pars 1961 *Lamellaptychus angulocostatus* (Peters). – Stefanov, pl. 1, fig. 6, non figs. 1-3 (= Didayilamellaptychus angulocostatus (Peters, 1854), non fig. 4 (= Didayilamellaptychus cf. angulocostatus).

1961 *Lamellaptychus angulocostatus* (Peters) var. fractocosta Trauth. – Stefanov, pl. 1, fig. 5.


2010 *Didayilamellaptychus angulicostatus* (Pictet and Loriol). – Měchová et al., p. 262, fig. 11G. H (cum syn.).

**Material:** Four specimens, MNHS F-30815, 30816, 30826, 30846 (see Appendix 1 for details).

**Measurements:** Among all specimens, MNHS F-30846 is a typical one: L = 26.6 mm, Lat = 12.0 mm, Lat/L = 0.45.

**Description:** Valves with a prominent keel and lateral depression. In the region between the keel and the symphysal margin, the ribs are angularly bent and run back towards the apex. In the depression area, the ribs are gently inflected to sigmoidally bent.

**Distribution:** Upper part of Upper Hauterivian of whole Mediterranean area (Měchová et al. 2010).

*Didayilamellaptychus cristobalensis* (O’Connell, 1921)  

**Fig. 8.9**

1921 *Aptychus cristobalensis*, new species. – O’Connell, p. 7, figs. 7 (type)-8.

1961 *Lamellaptychus angulocostatus* (Peters) var. cristobalensis (O’Connell). – Stefanov, p. 213, pl. 1, fig. 11.

2010 *Didayilamellaptychus cristobalensis* (O’Connell). – Měchová et al., p. 263, fig. 11J (cum syn.).

**Material:** Two specimens, MNHS F-30817, 9904* (see Appendix 1 for details).

**Description:** The valves are with keel and a faint lateral depression. The juvenile ribs are bent angularly in the area of keel. The adult ribs become arch-shaped to rounded. Their arrangement between the keel and the symphysal margin is complicated by less distinct to evident crenulation.

**Distribution:** The type material comes from Caribbean area and its stratigraphical position is not clear. In the Slovakian Carpathians the species is known from the Upper Hauterivian (Měchová et al. 2010).

*Didayilamellaptychus filicostatus* (Stefanov), MNHS F-30836, holotype with copy of the original label of Stefanov; Ropot Village (west of Komshitsa Village), Godech municipality, Sofia District, Lower Hauterivian, Salash Fm.  

**Fig. 10.** *Didayilamellaptychus filicostatus* (Stefanov, 1961)  

**Fig. 10**

1961 *Lamellaptychus angulocostatus* (Peters) var. filicosta n. var. – Stefanov, p. 214, 225, 227, pl. 1, fig. 9.

2010 *Didayilamellaptychus filicostatus* (Stefanov). – Měchová et al., p. 266, fig. 11L (cum syn.).

**Material:** One incomplete specimen, the holotype MNHS F-30836, from Ropot Village, Godech municipality, Sofia district (see Appendix 1 for more details).
Measurements: \( L = 13.5 \) mm.

Description: The valve is of medium size with an indistinct keel and without a lateral depression. Closely spaced and relatively thin ribs on the flank run subparallel to the symphysal margin. In the area of the keel, the juvenile ribs are angularly fractured at an acute angle. The angle between the branches of angular fractured ribs is almost symmetric. The adult ribs become gradually less symmetric. The last few ribs in the terminal area are rounded.

Distribution: The holotype is from the Lower Hauterivian (Stefanov 1961). The species is also reported from the Upper Hauterivian of Spain and the Carpathians (Měchová et al. 2010).

*Didayilamellaptychus renzi* Měchová, Vašíček & Houša 2010

Fig. 8.10

1961 *Lamellaptychus angulocostatus* (Peters) var. radiata Träuth. – Stefanov, p. 213, pl. 1, figs. 7, 10; text-figs. 1-2.

1972 *Lamellaptychus angulocostatus atlanticus* (Henning). – Renz, p. 617, pl. 4, figs. 2a, b, 3 (type), ?4.

2000 *Lamellaptychus (Didayilamellaptychus) angulocostatus angulocostatus* (Peters) f. typ. Träuth. – Turculet, p. 23, fig. 12, pl. 24 figs. 3, 6.

2010 *Didayilamellaptychus renzi* Měchová, Vašíček & Houša. – Měchová et al., p. 266, fig. 11M, N (cum syn.).

Material: Four specimens, NMNHS F-30856, 30857, 30858, 30859 (see Appendix 1 for details).

Measurements: NMNHS F-30856: \( L = 23.4 \) mm, \( Lat = 12.5 \) mm, \( S = 22.0 \) mm, \( Lat/L = 0.53 \).

Description: The valves are with prominent keel and, usually, with a shallow lateral depression. The ribs are thin, closely spaced, and bend at an acute angle. They reach symphysal margin at an angle of about 10°. The last few ribs usually lose the angular character.

Distribution: According to Měchová et al. (2010) *D. renzi* occurs in the Hauterivian across a relatively vast area (from the Caribbean and the Atlantic to Europe (Bulgaria, the Western Carpathians, Switzerland and Spain).

Family uncertain

Genus *Laevaptychus* Träuth, 1927

Type species: *Aptychus meneghinii* de Zigno, 1870, p. 11.

Diagnosis: Thick-walled calcareous aptychi. Cellular structure observed on otherwise smooth surface.

Remarks: On the basis of the shape of valves Gasirowski (1960: 91) subdivided the Jurassic representatives of the genus *Laevaptychus* into 7 subgenera. He followed the original idea of Träuth (1931). The most suitable parameters measured on the valves seem to be: \( L, S, W (= Lat \) in Lamellaptychidae), \( pW \), and ratios of these values (\( S/L, pW/L, W/L \)), as illustrated e.g. in text-fig. 2 in Turculet & Grigore 2006. The patterns are similar to the parameters illustrated on Fig. 2 herein. However, Gasirowski (1960) did not give proper descriptions of his subgenera. Gasirowski’s classification, however, without closer analyse, was used, subsequently, by Turculet & Grigore (2006). The genus *Laevaptychus* has not been revised for the last 50 years, thus its family affiliation remains unclear.

*Laevaptychus longus* (v. Meyer, 1831)

Fig. 11

1831 *Aptychus laevis longus*. – V. Meyer, p. 128, pl. 59, figs. 6-7.

2006 *Laevaptychus (Latuslaevaptychus) longus longus* (Meyer). – Turculet & Grigore, p. 30, pl. 1, figs. 4-6 (cum syn.).
Material: A single, complete left valve, NMNHS F-339* (For details see Appendix 1).

Measurements: NMNHS F-339 is the largest in the collection. The measured parameters and calculated indexes, which are designated partly differently from those of lamellaptychi, are based on the schematic illustration of Turculet & G Gregore (2006, text-fig. 2). The length L = 52.2 mm, the distance between the apex and the terminal point S = 44.1 mm, the maximum valve width W = 35.3 mm, the distance between the terminal point and the projection of point of maximum width pW = 33.0 mm; W/L = 0.67, pW/L = 0.63, S/L = 0.84.

Description: The valve is of large size, thick-walled, with elongated outline. The venter is apparently smooth; however, its cellular structure is perceptible on the surface and is easily seen under stereomicroscope.

Remarks: Valve morphology and calculated indexes correspond to L. longus. According to Gasiorowski's classification L. longus belongs to subgenus Latuslaevaptchus.

Distribution: L. longus is known from many European countries. Trauth (1931) reported it from the Oxfordian to Tithonian in autochthonous deposits of England, France, Switzerland, Germany, and in nappes of the Western and Eastern Alps and the Carpathians. Turculet & Gregore (2006) reported it from Oxfordian to Lower Tithonian occurrences in the area of Svinita in Romania.

5. Preservation, palaeoecologic and taphonomic notes

The preservation of the studied aptychi varies considerably. Both valves of the pair are preserved together very rarely (only in three cases). In the two of the paired specimens both valves are similarly preserved. In one case, however, because of preservational deformation, the valves of the pair differ (NMNHS F-30834, see Fig. 5.1a, b, and Stefanov 1961, pl. 1, fig. 3 and pl. 3, fig. 6); one of the valves of the pair has a broken arch and is pressed into the bedding plane; whereas the other valve has a keel that is more distinct as a result of the deformation. The compressed valve is secondarily widened. If they have been found separately, these two valves of one species, according to e.g. Trauth's (1938) classification, would be referred to two different taxa; the wider form - to the variety lata, whereas the narrower one - to the variety longa.

The pair of valves illustrated on Fig. 5.1a, b differs also in the preservation of symphal margin in the terminal area. The contact zone between both valves in the flat valve is slightly submerged below the other valve and is corroded. Consequently, only the bend of ribs in close vicinity of symphal margin towards the terminal apex is visible. Using this feature only, the valve could be determined as Mortilamellaptychus mortilleti (Picter & de Loriol). The opposite valve, however, has preserved ribs in the terminal area that run along the symphal margin in a section longer than in the case of Mortilamellaptychus mortilleti (Fig. 5.1a). Because of this feature, the valve is here referred to Mortilletilamellaptychus mendrisiensis mendrisiensis (Renz & Habicht). In summary, both valves belong to M. m. mendrisiensis. This example emphasizes the importance of preservation of the terminal and symphal area of the valves for correct determination.

Another problem connected with the preservation of valves can be the partial dissolution of the valve calcareous surface layer. This is well demonstrated, for instance, in the otherwise well preserved specimen NMNHS F-30841, on which the punctate layer is well preserved only in a small area. Such partial dissolution is even more obvious on the incomplete, large valve of specimen NMNHS F-335, which lacks almost entirely the punctate layer (Fig. 3.2). In the latter specimen, when only the ribbing of the symphal area (with non-preserved punctate layer!) is considered, the valve would be assigned to Lamellaptychus rectecostatus (Peters, 1854). However, with regard to the strength of ribs and the size of the valve, it is rather close to Punctaptychus rectecostatus Cuzzi, 1962. Finally, because of the dissolution phenomenon and the incompleteness of the valve, specimen NMNHS F-335 is here tentatively determined as Punctaptychus sp.

In lamellaptychi the corrosion of valves causes sometimes the growth lines between the ribs to be more conspicuous. However, deeper corrosion may affect also the ribbing so that the shape of ribs becomes apparently variable (see Fig. 8.4). Thus, a higher degree of dissolution may cause the ribbing to appear ostensibly simpler than they actually were, similarly to the simplification of suture lines in strongly corroded ammonite shells.

The inner surface of calcareous aptychi, if exposed, exhibits dense growth lines. If this side is well preserved, as in NMNHS F-30844 (Fig. 8.1), non-uniform growth lines are observed. The same specimen, NMNHS F-30844, was photographed from the opposite side by Stefanov (1961, pl. 2, fig. 2). Multiple thin lines alternate with single thicker lines at regular intervals, which is interpreted as periodicity in animal growth.

Some of the specimens possess on the outer surface of valves radial lines, having a form of very thin ribs
that can be photographed only under suitable illumination (e.g., Fig. 8.6). (The same valve was illustrated by Stefanov (1961, pl. 1, fig. 2), but without obvious radial lines.) In some specific cases, these fine radial lines do not take any clear morphological effect, thus whitening with ammonium chloride makes them invisible in photographs. Because of their black colour (probably due to the remains of original, now carbonized organic matter), such lines can be seen on the photographs only if the specimen is not whitened (Fig. 8.10).

If, after the death of the living organism (the host ammonite), the isolated valves lay on the muddy bottom for a sufficiently long period before burial, they could be colonized by sessile organisms as documented on a valve in Fig. 8.2. In this case serpulids and a bryozoan are attached to the valve. A similar, but less clear example is a side of the valve with growth lines illustrated in Fig. 8.1.

6. Conclusions

As a result of the present taxonomic reappraisal of the Late Jurassic and Early Cretaceous aptychi from Bulgaria, 23 taxa from the species group, which are assigned to six genera within the families Punctaptychidae, Lamellaptychidae and one uncertain family, were recognised. One new species Mortilletilamellaptychus stefanovi was erected. Apart from the holotype of M. stefanovi sp. nov., the Bulgarian collection contains also the holotype of Didayilamellaptychus filicostatus (Stefanov), which was previously elevated from a variety to a species level by Stefanov (1961, pi. 3, fig. 9, and Fig. 9 herein) is of special interest. Neolissoceras belongs to the family Haploceratidae. This finding is a further confirmation of the hypothesis that both lamellaptychi and ?punctaptychi belong to the family Haploceratidae Zittel, 1884 in the natural system of ammonites.

The state of preservation may strongly affect the correct determination of aptychi. Only in exceptional cases like the illustrated occurrence of both valves in a pair with different state of preservation (Fig. 5.1a, b) this preservation phenomenon can be revealed and wrong determination of any of the valves could be possibly avoided.

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References


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Appendix

Appendix 1. Annotated list of all studied material of aptychi.

<table>
<thead>
<tr>
<th>Museum number</th>
<th>Names appearing on the old museum labels and/or in STEFANOV (1961)</th>
<th>Locality</th>
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<td>1891*</td>
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<td>335*</td>
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**Punctaptychus punctatus** (ZITTEL, 1868)
- Borushitsa River, Gabrovo District
- Berriasian, Kamchia Fm

**Punctaptychus divergens** TRAUCH, 1935
- Shipkovski Mineral Baths, Lovech District
- Tithonian, Cherniosam Fm

**Punctaptychus sp.**
- Barlya Village, Sofia District
- Tithonian, Ginci Fm – Glozhene Fm

**Beyrichilamellaptychus beyrichi** (OPPEL, 1865)
- Veselina River, south of Todyuvtsi Village, V. Tarnovo District
- Berriasian, Hanevtsi Fm

**Beyrichilamellaptychus cf. beyrichi** (OPPEL, 1865)
- South of the hamlet Lipov kat, Varna District
- Valanginian or Tithonian, ?Ticha Fm

**Mortilletilamellaptychus studeri** (OSTER, 1857)
- North of Shipkovo Village, Lovech District
- Berriasian, Cherniosam Fm

**Mortilletilamellaptychus mendrisiensis mendrisiensis** (RENZ & HABICH, 1985)
- east of Todorchetata Village, Gabrovo District
- Upper Valanginian, Kamchia Fm

**Mortilletilamellaptychus bicuscurus** (RENZ ET HABICH, 1985)
- south of the hamlet Hristova Mahala, Troyan municipality, Lovech District
- Upper Valanginian, Cherniosam Fm
<table>
<thead>
<tr>
<th>Museum number NMNHS F- (original old number)</th>
<th>Names appearing on the old museum labels and/or in STEFANOV (1961)</th>
<th>Locality</th>
<th>Horizon</th>
<th>Illustrated in</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>30833 (35, t. 237 (M. Hr.))</td>
<td>Lamellaptychus mortilleti Trauth var. retroflexa Trauth</td>
<td>Makotsevo Village, southeast of the peak Ademitsa, Sofia District</td>
<td>Berriasian, Cherniosam Fm (Tithonian – Berriasian flysch)</td>
<td>STEFANOV (1961, pl. 3, fig. 7); this paper, Fig. 6.</td>
<td><strong>HOLOTYPE</strong></td>
</tr>
<tr>
<td>30865 (37, t. 237)</td>
<td>Lamellaptychus herthaes (Winkler) var. laevadsymphysalis Trauth</td>
<td>east of Makotsevo Village, Sofia District</td>
<td>Berriasian, Cherniosam Fm</td>
<td>This paper, Fig. 7.1.</td>
<td>this is perhaps the specimen mentioned by STEFANOV (1961, p. 223)</td>
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<tr>
<td>30853 (10194, t. 10194)</td>
<td>Lamellaptychus mortilleti (Picte &amp; Loriol) var. longa Trauth</td>
<td>north of Beli Osam Village, Lovech District</td>
<td>Upper Valanginian, Cherniosam Fm</td>
<td>This paper, Fig. 7.2.</td>
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<tr>
<td>30810</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>Balgarski izvor Village, Lovech District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>STEFANOV (1961, pl. 2, fig. 5)</td>
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<tr>
<td>30811</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>Balgarski izvor Village, Lovech District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>STEFANOV (1961, pl. 2, fig. 6)</td>
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<tr>
<td>30813</td>
<td>Lamellaptychus didayi (Coquand), (transmission to subdidayi)</td>
<td>Chernevo Village, Varna District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>STEFANOV (1961, pl. 2, fig. 7)</td>
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<tr>
<td>30828 (67, t. 231)</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>north of Stolat Village, Gabrovo District</td>
<td>Lower Hauterivian, Hanevtsi Fm</td>
<td>STEFANOV (1961, pl. 2, fig. 5)</td>
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<tr>
<td>30837 (62, t. 241)</td>
<td>Lamellaptychus subdidayi Trauth [transmission to Lamellaptychus didayi (Coquand)]</td>
<td>south of Gradnitsa Village, Gabrovo District</td>
<td>Lower Hauterivian</td>
<td>STEFANOV (1961, pl. 2, fig. 8)</td>
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<td>30844</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>southwest of Chernevo Village, Varna District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>STEFANOV (1961, pl. 2, fig. 2); this paper, Fig. 8.1.</td>
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<tr>
<td>30852</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>west of Balgarski izvor Village, Lovech District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>STEFANOV (1961, pl. 2, fig. 1)</td>
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<tr>
<td>388*</td>
<td>Aptychus sp.</td>
<td>Omurtag, Targovishte District</td>
<td>Hauterivian, Kamchia Fm</td>
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</tr>
<tr>
<td>30864</td>
<td>Lamellaptychus subdidayi Trauth</td>
<td>southwest of Chernevo Village, Varna District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm (the upper part of the section)</td>
<td>STEFANOV (1961, pl. 2, fig. 9)</td>
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<tr>
<td>30835 (2185)</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>Debe Neuro Village (Lozarski dol), Lovech District</td>
<td>Valanginian, Kamchia Fm</td>
<td></td>
<td>juvenile specimen</td>
</tr>
<tr>
<td>9925* (332)</td>
<td>Lamellaptychus sp.</td>
<td>Teke dere, near Shumen</td>
<td>Hauterivian, Gorna Oryahovitsa Fm</td>
<td>This paper, Fig. 8.2.</td>
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</tr>
<tr>
<td>9926* (333)</td>
<td>Lamellaptychus sp.</td>
<td>Teke dere, near Shumen</td>
<td>Hauterivian, Gorna Oryahovitsa Fm</td>
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<tr>
<td>Museum number</td>
<td>Names appearing on the old museum labels and/or in Stefanov (1961)</td>
<td>Locality</td>
<td>Horizon</td>
<td>Illustrated in</td>
<td>Remarks</td>
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<tr>
<td>NMNHS F-</td>
<td>Lamellaptychus subdidayi Trauth [transition to Lamellaptychus didayi (Coquand)]</td>
<td>Palilula Village, Vratsa District</td>
<td>Upper Valanginian, Salash Fm</td>
<td>Stefanov 1961, pl. 2, fig. 10</td>
<td>Fragment</td>
</tr>
<tr>
<td>30820</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>D. Vlahovska hamlet, Troyan municipality (to the north of Troyan), Lovech District</td>
<td>Hauterivian, Kamchia Fm</td>
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</table>

Didayilamellaptychus cf. didayi (Coquand, 1841)

<table>
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<tr>
<th>Museum number</th>
<th>Names appearing on the old museum labels and/or in Stefanov (1961)</th>
<th>Locality</th>
<th>Horizon</th>
<th>Illustrated in</th>
<th>Remarks</th>
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<tbody>
<tr>
<td>30851</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>west of Balgarski izvor Village, Lovech District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td></td>
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<tr>
<td>30829 (425)</td>
<td>Lamellaptychus didayi (Coquand)</td>
<td>Shipkovo Village, Lovech District</td>
<td>Berriasian, Cherniosam Fm</td>
<td>Stefanov (1961, pl. 2, fig. 4)</td>
<td></td>
</tr>
<tr>
<td>30847 (1016, 1492)</td>
<td>Lamellaptychus beyrichi (Oppel) var. fractocosta Trauth</td>
<td>north of the hamlet Enchovtsi, Troyan municipality, Lovech District</td>
<td>Lower Hauterivian, Kamchia Fm</td>
<td>Stefanov (1961, pl. 3, figs 8 and 9); this paper Fig. 9.</td>
<td>Aptychus occurring in the body chamber of Neolissoceras grassianum (d’Orbigny)</td>
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Didayilamellaptychus seranonis (Coquand, 1841)

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<th>Museum number</th>
<th>Names appearing on the old museum labels and/or in Stefanov (1961)</th>
<th>Locality</th>
<th>Horizon</th>
<th>Illustrated in</th>
<th>Remarks</th>
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<tbody>
<tr>
<td>30861</td>
<td>Lamellaptychus angulocostatus (Peters) var. atlantica (Hennig), transition to Lamellaptychus seranonis (Coquand)</td>
<td>Zlatitsa River, Gaganitsa Village, Montana District</td>
<td>Upper Valanginian, Salash Fm</td>
<td>Stefanov (1961, pl. 1, fig. 12); this paper, Fig. 8.3.</td>
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Didayilamellaptychus cf. seranonis (Coquand, 1841)

<table>
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<th>Museum number</th>
<th>Names appearing on the old museum labels and/or in Stefanov (1961)</th>
<th>Locality</th>
<th>Horizon</th>
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<tbody>
<tr>
<td>30818</td>
<td>Lamellaptychus seranonis (Coquand) var. radiata n. var.</td>
<td>Chernevo Village, Varna District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>Stefanov (1961, pl. 3, fig. 5); this paper, Fig. 8.4.</td>
<td>Holotype of L. seranonis radiata Stefanov</td>
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<tr>
<td>30842 (1269)</td>
<td>Lamellaptychus seranonis (Coquand) var. radiata n. var.</td>
<td>northwest of Stubel Village, Montana District</td>
<td>unknown, Salash Fm</td>
<td></td>
<td>Only fragment of valve</td>
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Didayilamellaptychus angulodidayi (Trauth, 1938)

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<th>Museum number</th>
<th>Names appearing on the old museum labels and/or in Stefanov (1961)</th>
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<tr>
<td>30850</td>
<td>Lamellaptychus angulocostatus pet. n. var. Steph.</td>
<td>west of Balgarski izvor Village, Lovech District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>This paper, Fig. 8.5.</td>
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Didayilamellaptychus angulocostatus (Peters, 1854)

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<th>Names appearing on the old museum labels and/or in Stefanov (1961)</th>
<th>Locality</th>
<th>Horizon</th>
<th>Illustrated in</th>
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<tbody>
<tr>
<td>30814 (194/t. 1257)</td>
<td>Lamellaptychus angulocostatus (Peters)</td>
<td>Gaganitsa Village, Montana District</td>
<td>?Hauterivian, Salash Fm</td>
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<td>Note from the original label: “Association Phyllopachyceras eichwaldi (Karakasch), Hauterivian - Barremian”.</td>
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<tr>
<td>30819 (239, t. 982)</td>
<td>Lamellaptychus angulocostatus (Peters)</td>
<td>southeast of Komshtitsa Village, Sofia District</td>
<td>Lower Hauterivian, Salash Fm</td>
<td>Stefanov (1961, pl. 1, fig. 3)</td>
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<td>30830</td>
<td>Lamellaptychus angulocostatus (Peters)</td>
<td>southwest of Chernevo Village, Varna District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>Stefanov (1961, pl. 1, fig. 1)</td>
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<td>Museum number</td>
<td>Names appearing on the old museum labels and/or in Stefanov (1961)</td>
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<td>30831</td>
<td>Lamellaptychus angulocostatus (Peters)</td>
<td>southwest of Chernevo Village, Varna District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>Stefanov (1961, pl. 1, fig. 2); this paper, Fig. 8.6.</td>
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<td>9905*, 9906*</td>
<td>Lamellaptychus sp.</td>
<td>Railway station Kaspichan, Shumen District</td>
<td>Hauterivian, Gorna Oryahovitsa Fm</td>
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<tr>
<td>30840 (14, t. 162)</td>
<td>Lamellaptychus angulocostatus (Peters) var. atlantica (Peters)</td>
<td>Balgarski izvor Village, Lovech District</td>
<td>Upper Valanginian, Gorna Oryahovitsa Fm</td>
<td>Stefanov (1961, pl. 1, fig. 8); this paper, Fig. 8.7.</td>
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<td>30832</td>
<td>Lamellaptychus angulocostatus (Peters) var. fractocosta Peters</td>
<td>Gaganitsa Village, Montana District</td>
<td>Berriasian, Salash Fm</td>
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<td>30845 (5361, t. 5361)</td>
<td>Lamellaptychus angulocostatus (Peters)</td>
<td>Borima Village, Lovech District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>Stefanov (1961, pl. 1, fig. 4)</td>
<td>juvenile specimen, note from the original label: &quot;Association of Phyllopachyceras infundibulum and Lytoceras sp.&quot;</td>
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<tr>
<td>30815, 30816 (194, t. 1257)</td>
<td>Lamellaptychus angulocostatus (Peters) var. longa Trauth</td>
<td>Gaganitsa Village, Montana District</td>
<td>?Hauterivian, Salash Fm</td>
<td>This paper, Fig. 8.8.</td>
<td>note from the original label: &quot;Association Phyllopachyceras eichwaldi (Karakasch), Hauterivian - Barremian&quot;</td>
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<td>30826</td>
<td>Lamellaptychus angulocostatus (Peters)</td>
<td>Zlatitsa River, Gaganitsa Village, Montana District</td>
<td>Berriasian, Salash Fm</td>
<td>Stefanov (1961, pl. 1, fig. 6)</td>
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<td>30846</td>
<td>Lamellaptychus angulocostatus (Peters) var. fractocosta Trauth</td>
<td>Gaganitsa Village, Montana District</td>
<td>Berriasian, Salash Fm</td>
<td>Stefanov (1961, pl. 1, fig. 5)</td>
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<td>30817</td>
<td>Lamellaptychus angulocostatus (Peters) var. cristobalensis (O'Connell)</td>
<td>southwest of Chernevo Village, Varna District</td>
<td>Lower Hauterivian, Gorna Oryahovitsa Fm</td>
<td>Stefanov (1961, pl. 1, fig. 11); this paper, Fig. 8.9.</td>
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<td>9904*</td>
<td>Lamellaptychus sp.</td>
<td>Railway station Kaspichan, Shumen District</td>
<td>Hauterivian, Gorna Oryahovitsa Fm</td>
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<tr>
<td>30836 (155, t. 882)</td>
<td>Lamellaptychus angulocostatus (Peters) var. filicosta n. var.</td>
<td>Ropot Village (west of Komshitsa), Sofia District</td>
<td>Lower Hauterivian, Salash Fm</td>
<td>Stefanov (1961, pl. 1, fig. 9); this paper, Fig. 10.</td>
<td>HOLOTYPE</td>
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<td>30856</td>
<td>Lamellaptychus angulocostatus (Peters) var. radiata Trauth</td>
<td>east of Krachene Village, Montana District</td>
<td>Lower Hauterivian, Salash Fm</td>
<td>Stefanov (1961, pl. 1, fig. 7); this paper, Fig. 8.10.</td>
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<td>Horizon</td>
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<tr>
<td>30857</td>
<td>Lamellaptychus angulocostatus (Peters) var. radiata Trauth</td>
<td>east of Krapchene Village, Montana District</td>
<td>Lower Hauterivian, Salash Fm</td>
<td>Stefanov (1961, pl. 1, fig. 10)</td>
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<tr>
<td>30858</td>
<td>Lamellaptychus angulocostatus (Peters) var. radiata Trauth</td>
<td>east of Krapchene Village, Montana District</td>
<td>Lower Hauterivian, Salash Fm</td>
<td>Stefanov (1961, text fig. 2)</td>
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<tr>
<td>30859</td>
<td>Lamellaptychus angulocostatus (Peters) var. radiata Trauth</td>
<td>east of Krapchene Village, Montana District</td>
<td>Lower Hauterivian, Salash Fm</td>
<td>Stefanov (1961, text fig. 1)</td>
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### Laevaptychus longus (v. Meyer, 1831)

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<th>Horizon</th>
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<tr>
<td>339*</td>
<td>Punctaptychus sp.</td>
<td>Cherni Osam Village, Lovech District</td>
<td>Tithonian, Cherniosam Fm</td>
<td>This paper, Fig. 11.</td>
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### Undeterminable specimens

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<tr>
<td>30862, 30863</td>
<td>Lamellaptychus mortilleti (Pictet &amp; Loriol) 1858</td>
<td>south of the hamlet Hristova mahala, Lovech District</td>
<td>Upper Valanginian, Cherniosam Fm</td>
<td>on same piece of rock as # 30812 (Mortilletilamellaptychus bicurva-tus), illustrated in Stefanov 1961, pl. 3, fig. 1 and herein, Fig. 5.3.</td>
<td></td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Number (212)</th>
<th>Name</th>
<th>Locality</th>
<th>Horizon</th>
<th>Illustrated in</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>2426* (1303 (212))</td>
<td>Lamellaptychus beyrichi var. longa Trauth</td>
<td>Veselina River, south of Todyuvtsi Village, V. Tarnovo District</td>
<td>Berriasian, Hanevtsi Fm</td>
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<table>
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<tr>
<th>Number (10324)</th>
<th>Name</th>
<th>Locality</th>
<th>Horizon</th>
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<th>Remarks</th>
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<tbody>
<tr>
<td>30823 (10324)</td>
<td>Lamellaptychus subdidayi Trauth</td>
<td>west of Ribno Village, Troyan municipality, Lovech District</td>
<td>Berriasian – Neocomian</td>
<td></td>
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<table>
<thead>
<tr>
<th>Number (11240)</th>
<th>Name</th>
<th>Locality</th>
<th>Horizon</th>
<th>Illustrated in</th>
<th>Remarks</th>
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</thead>
<tbody>
<tr>
<td>30838 (11240)</td>
<td>Lamellaptychus mortilleti (Pictet &amp; Loriol), transition to Lamellaptychus aplanatus (Gilliéron).</td>
<td>northeast of Krapchene Village, Montana District</td>
<td>Valanginian, Salash Fm</td>
<td>juvenile fragment</td>
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<tr>
<th>Number (2419)</th>
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<th>Horizon</th>
<th>Illustrated in</th>
<th>Remarks</th>
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</thead>
<tbody>
<tr>
<td>30827 (2419)</td>
<td>Lamellaptychus mortilleti (Pictet &amp; Loriol), transition to Lamellaptychus aplanatus (Gilliéron).</td>
<td>Vidima River, south of the hamlet Skandaloto, Troyan municipality, Lovech District</td>
<td>Upper Valanginian, Kamchia Fm</td>
<td>Stefanov (1961, pl. 3, fig. 4).</td>
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<thead>
<tr>
<th>Number (10194)</th>
<th>Name</th>
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<th>Horizon</th>
<th>Illustrated in</th>
<th>Remarks</th>
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</thead>
<tbody>
<tr>
<td>30855 (10194)</td>
<td>Lamellaptychus n. sp.</td>
<td>south of Balgarski izvor Village, Lovech District</td>
<td>Upper Valanginian, Gorna Oryahovitsa Fm</td>
<td>note of J. Stefanov: “Association of N. neocomiensis and Thurman-nia. Beautiful specimen, possibly new species?”</td>
<td></td>
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<table>
<thead>
<tr>
<th>Number (9927, 9928)</th>
<th>Name</th>
<th>Locality</th>
<th>Horizon</th>
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<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>9927*, 9928*</td>
<td>Lamellaptychus sp.</td>
<td>Teke dere, near Shumen</td>
<td>Hauterivian, Gorna Oryahovitsa Fm</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>