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RESEARCH PAPER

The systematic position of the Lower Cretaceous heteromorphic ammonite *Pictetia* Uhlig, 1883

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Abstract The heteromorphic ammonite genus *Pictetia* has previously been included in the Lytoceratidae. A re-assessment of literature data and a detailed analysis of the suture shows that *Pictetia* lacks a septal lobe as well as a bifid internal lobe and lateral lobe, all features indicative of the Lytoceratidae. This and the quadrilobate suture line, combined with the loose coiling of the shell, indicate that it should be included in the polyphyletic suborder "Ancyloceratina". Any further systematic assessment is impossible at the moment.

Keywords Lower Cretaceous · Aptian · Albian · Ammonoidea · Ancyloceratina · Systematic · Suture

Kurzfassung Bisher wurde die heteromorphe Ammonitengattung *Pictetia* zu den Lytoceratidae gestellt. Die Auswertung von Literaturdaten sowie genaue Untersuchungen der Suturlinie zeigen, dass die charakteristischen Merkmale der Lytoceratidae, wie der Septallobus, ein bifider Intern- und Lateralobus, bei *Pictetia* nicht ausgebildet sind. Dies und die quadrilobate Suturlinie sowie das lose aufgewundene Gehäuse erfordern eine systematische Zuordnung zur polyphyletischen Gruppe der „Ancyloceratina". Eine nähere taxonomische Einordnung ist zur Zeit nicht möglich.

Schlüsselwörter Unterkreide · Aptium · Albium · Ammonoidea · Ancyloceratina · Systematik · Sutur

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Abbreviations

MAo	Keupp Collection, housed at Freie Universität Berlin
PIMUZ	Paläontologisches Institut und Museum der Universität Zürich
BMNH	The Natural History Museum, London
wh	Whorl height
wb	Whorl breadth

Introduction

The Lower Cretaceous (Aptian, Albian) ammonite genus *Pictetia* combines characters that have repeatedly stimulated discussion about its systematic position. Its whorl expansion rate, ornamentation and its strongly incised suture line show accordance with the Lytoceratidae Neumayr 1875, where it is included in the subfamily Lytoceratinae (Arkell et al. 1957; Wright et al. 1996; Fischer and Gauthier 2006). On the other hand, its loose criocone coiling, the quadrilobate suture line and its lobe development are rather suggestive of an ancyloceratid ammonite (Schindewolf 1961). Although Wiedmann (1966) stated that suture characteristics instead of ornamentation should be used to reconstruct phylogenetic relations among the Ammonoidea, the systematic assessment of *Pictetia* is based mainly on external characters of the conch, which are actually lytoceratid. Additionally, its complexly incised suture has also repeatedly been interpreted as being lytoceratid by, for example, Quenstedt (1846–1849), Haug (1900), Jacob (1908) and Howarth (1974), who included the genus—based also on its typically lytoceratid ornamentation—in the Lytoceratidae and regarded it as an uncoiled representative. This lytoceratid assignment of

Pictetia was followed by most subsequent workers (e.g. Casey 1960; Schindewolf 1961; Kennedy and Klinger 1978; Rodda and Murphy 1992; Wright et al. 1996; Kennedy in Fischer and Gauthier 2006).

In the context of a detailed reinvestigation of the Lytoceratoidea by one of us (RH), based on our own material, public and private collections, and a literature review (ca. 2,500 citations), it was shown that *Pictetia* has some individual characteristics that enable a more detailed understanding of its systematic position. The scope of this paper is to review and discuss the previous systematic diagnosis of the genus. Species currently included in *Pictetia* are discussed together with comments on their stratigraphic position.

Systematic palaeontology

In this text, we apply the suture line terminology of Wedekind (1916) with E (external lobe), L (lateral lobe), U (umbilical lobe) and I (internal lobe) (see also Kullmann and Wiedmann 1970).

Suborder "Ancyloceratina" Wiedmann, 1966

Comments: The "Ancyloceratina" is a "wastebasket" for almost all Cretaceous heteromorphic ammonites. It incorporates taxa with quadrilobate primary sutures or quinquelobate primary sutures and quadrilobate sutures in later ontogenetic stages (Wright et al. 1996). Furthermore, it contains groups with anaptychi and aptychi. Engeser and Keupp (2002) therefore concluded that the "Ancyloceratina" sensu Wiedmann (1966) represent a polyphyletic group, a view that is followed here. Thus, "Ancyloceratina" is used throughout the text in quotation.

Superfamily unknown

Family unknown

Subfamily unknown

Genus *Pictetia* Uhlig, 1883

Type species: Crioceras astierianus d'Orbigny 1840–1842, by subsequent designation of Spath (1923: 21).

Diagnosis: The diagnosis given in the first edition of the "Treatise" (Arkell et al. 1957: L196) is very short and insufficient: "Loosely coiled with whorls not touching, section circular to depressed; body chamber may straighten; surface with feeble, irregular, weakly crinkled ribs". A more comprehensive diagnosis was given by Casey (1960: 3): "Feebly ornamented lytoceratids with the whorls disconnected though apparently forming a regular spiral, as in Crioceratites. The whorls vary from subcircular with no impressed zone to depressed, kidney-shaped, with shallow embayment of the dorsum. Fine, irregular striae, indistinctly striae, indistinctly fimbriate ornament on the test, but are reproduced poorly, if at all, on the internal mould. Suture line with simple lobe-formula I, U, L, E, but highly complex; saddles bifid and mostly slender-stemmed, lobes bifid, widely spaced and deeply ramified. Body chamber unknown". Kennedy and Klinger (1978: 324) state: "Loosely coiled with whorls separated throughout; body chamber may straighten. Whorl section rounded, compressed to depressed; ornamented by weak, irregular, feebly crinkled ribs".

Discussion: The type species of *Pictetia—P. astieriana*—has been figured by d'Orbigny (1840–1842) in a somewhat idealized manner, but the original has been refigured elsewhere repeatedly (Basse 1952; there misspelled as *Pictetia astieri* Puzos; Arkell et al. 1957; Kennedy and Klinger 1978: 325, fig. 49; Fischer and Gauthier 2006: 252, pl. 40), so it is well documented in the literature. Kennedy, in Fischer and Gauthier (2006), gives a detailed and sufficient description of the lectotype of the type species based on the only specimen figured by d'Orbigny (1840–1842). He specifically mentioned a dorsal flattening, and—judging from our material—the dorsal zone in the type species *P. astieriana* can vary between subrounded via a flattening to the presence of a weak dorsal impression (see below). Rodda and Murphy (1992), however, excluded forms with such a dorsal impression from *Pictetia* (*P. depressa*), an approach that cannot be followed here. Due to its general shell morphology and suture, *P. depressa* is retained as typical member of the genus by the authors. The dorsal zone may be a result of the earliest whorls coming into contact with the succeeding whorls (Föllmi 1989a, b), which can unequivocally be seen in *P. depressa* (Fig. 1F, G) and is expected from the preservation of the type as well as specimens MAo-519 and MAo-1045 (Fig. 1A, B).

Spath (1923) mentioned two completely septate, large, straight portions (BMNH C.5439 and C5440) labelled as "*Ancyloceras astierianum* (*Crioceras*), d'Orbigny, Escragnolles, Var." from the Astier collection, figured by Kennedy and Klinger (1978: 326, fig. 50, 327, fig. 51), and considered by them to be doubtful paralectotypes. As discussed in Rodda and Murphy (1992), it is highly doubtful that these fragments belong to *Pictetia*. Föllmi (1989a, b: 116, pl. 2, fig. 7a, b) figured a fragment of *P. astieriana* (here refigured as Fig. 2K, L), which was inferred to have parts of the body chamber preserved. A reinvestigation, however, shows that it is fully septate, and thus no body chamber of *Pictetia* has been recorded so far.

The systematic position of *Pictetia* has been discussed controversially in the past. Based on its typical lytoceratid ornamentation, Quenstedt (1846–1849), Haug (1900), Jacob (1908) and Howarth (1974) included the genus in the Lytoceratidae and regarded it as an uncoiled representative.

Fig. 1 *Pictetia astieriana* (d'Orbigny 1840–1842). **A** MAo-519 from Ambatolafia, Madagascar, Albian, lateral view; **B** MAo-1045 from Ambatolafia, Madagascar, Albian, lateral and **C** ventral view; **D**, **E** PIMUZ 002843 from the Strahlkopf, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian (original of Föllmi 1986, pl. 13, fig. 4); **F** *Pictetia depressa* Pictet and Campiche (1861) MAo-100 from Mangyshlak (Kazakhstan), ventral and **G** lateral view

This view was followed by Arkell et al. (1957), Casey (1960) and other, later, authors (e.g. Kennedy and Klinger 1978; Rodda and Murphy 1992; Wright et al. 1996; Kennedy in Fischer and Gauthier 2006). Schindewolf (1961: 679), on the other hand, examined the d'Orbigny original and highlighted the quadrilobate nature of the suture, which is in accordance with Spath (1923) and Casey (1960) in his generic diagnosis of *Pictetia*. A quadrilobate suture line, however, is exclusively known from the "Ancyloceratina", which are characterized by either quadrilobate or quinquelobate primary sutures followed by a quadrilobate suture from the early growth stages on (Wiedmann and Kakabadze 1993). This then demands the attribution of *Pictetia* to this suborder, which has already been done by Hyatt (1900) and Matsumoto (1980). Schindewolf (1961) stated that "*Pictetia* selbst mit seinem ausgerollten Gehäuse, nur einem Umbilikallobus und dem dreispitzigen Innenlobus fällt dagegen weit aus dem Rahmen der Lytoceratidae heraus und scheint mir trotz seiner schwachen Skulptur eher zu den (…) Formen mit anormaler Gehäusegestalt (Ancyloceratacea) zu gehören, für die derartige Charaktere der Lobenlinie bezeichnend sind." ["…*Pictetia* itself with its uncoiled phragmocone, only one umbilical lobe and a trifid internal lobe is far beyond the frame of the Lytoceratidae, and it appears to me, in spite of its weak sculpture, that it rather belongs to (…) the forms with aberrant shell morphology (Ancyloceratacea), for which those characters of the suture line are indicative"].

Wiedmann and Kakabadze (1993)—based on suture line investigations of numerous Cretaceous heteromorphs—showed that the development of L (trifid vs. bifid) can by no means be used for higher order taxonomic separation, as found in numerous papers (genera: Spath 1939; Breistroffer 1952; families: Egoân 1969, 1974; superfamilies: Wright et al. 1996; suborders: Beznosov and Mihajlova 1983; Monks 1999), because a trifid or bifid L can occur within the same genus or even species, as exemplified by *Ptychoceras*. In conclusion, L is instable within the quadrilobate heteromorphs (see also Kakabadze 2004). At first sight, this may also apply to *Pictetia*: the suture line of the type species is inferred to have a bifid L, while it is trifid in *P. depressa* (Pictet and Campiche 1861). However, upon comparing the suture of Casey's specimen of *P. depressa* (Casey 1960: pl. 1, fig. 1a) with that of the types of *P. astieriana* (Fig. 3A), the suture of *P. depressa* (Fig. 3B) seems to share more similarities with the suture of *P. astieriana.* This shows the morphological variability of L and its uselessness for specifically separating the two species. Thus, to include *Pictetia* in the Lytoceratidae exclusively based on a bifid L and to exclude *P. depressa* from *Pictetia* due to its trifid L, as done by Rodda and Murphy (1992), is an approach that cannot be followed. Furthermore, it is disputable whether or not a trifid L occurs in *Pictetia* at all. As can be seen from the various suture lines of *Pictetia* (Fig. 3A–C, E; see also Spath 1923: pl. 1, fig. 8), there is no typically and symmetrically developed L that permits a clear recognition of either a bifid or trifid geometry. Instead, L appears to represent an asymmetrically developed bifid lobe with the ventral branch being more strongly developed.

The internal lobe in *Pictetia* is trifid. While all early Liassic Lytoceratidae share this feature, all younger Lytoceratidae show a bifid I (generating a septal lobe; see below), which provides a further sutural argument against the lytoceratid nature of *Pictetia* (Salfeld 1924; Schindewolf 1961, 1968; Mihajlova 1983; see also Wiedmann 1966: 50, fig. 36). Föllmi (1986) suggested that a well-developed and incised internal saddle in E (siphonal saddle) of *Pictetia* (Fig. 3A–C, E) also differs from the development of external lobes of typical *Lytoceras*. In fact, most Lytoceratidae only show a weakly developed internal saddle in E, which is often simple or weakly subdivided and highly triangular in shape (e.g. *L. adeloides* in Pugin 1964; Roman 1938; Schindewolf 1961; Mihajlova 1983; Stevens 1985; Meister 1986; Fig. 3D). Finally, all Cretaceous Lytoceratidae have a septal lobe (I_s of Wiedmann

1966) which has not been recorded to occur in *Pictetia* and cannot be observed in our material. For these reasons—the loose coiling, a quadrilobate suture, a trifid I, the lack of a septal lobe and, potentially, the internally subdivided E—we exclude *Pictetia* from the Lytoceratidae and place it within the polyphyletic "Ancyloceratina". All ornamental similarities with the Lytoceratidae (ornamentation, constrictions, etc.) are merely regarded as plesiomorphic characters, which, in the case of *Pictetia*, cannot be used for higher order systematic assignment. Consequently, the derivations of *Pictetia* from *Biasaloceras* (=*Lytoceras*; Wiedmann and Dieni 1968), as suggested by Drušic (1956), or from the Hemilytoceratinae sensu Müller (1955), are considered highly unlikely.

Based on the material currently available, it is difficult to place it in any superfamily with confidence, as we do not know its primary suture, its adult body chamber or the type of jaw apparatus, which may provide arguments for further systematic assessments.

Species included: P. astieriana and *P. depressa* are well-founded species. The status of *P. ovalis* is problematic (see discussion below).

Occurrence: Pictetia is a rare genus. What we understand to belong to *Pictetia* is recorded and figured from the Lower to Middle Albian of France, England, Switzerland, Kazakhstan, Madagascar, South Africa and USA (California), and possibly Bulgaria. However, *Pictetia* is mentioned from several regions, but not figured (e.g. Gümbel 1861: Germany; Heim and Seitz 1934: Austria; Price 1874: England; Hitzel 1905: southern France; Spath 1930: India; Medina and Riccardi 2005: Argentina). These identifications need to be regarded as unreliable records, especially because—as Casey (1980) stated—fragments of "Ancyloceratina" can simulate *Pictetia* (e.g. *Crioceras pictetiaeforme* Karakasch 1907: 138, pl. 36, fig. 5). The possible occurrence of *Pictetia* in Japan (Matsumoto 1980) is a poorly preserved and pathologic ammonite fragment (Katto and Obata 1975, fig. 2) that could be anything, but does not look like any of the *Pictetia* specimens figured or seen by us, so we doubt this identification.

Pictetia astieriana (d'Orbigny 1840–1842)

Figs. 1A–E, 2A–P, 3A, C, E

Type: Lectotype is *Crioceras astierianus* d'Orbigny, 1840–1842: 468–470, pl. 115, figs. 3–5, specimen BMNH 46953 from the Astier collection, designated by Spath (1923).

1842 *Crioceras astierianus*, d'Orb.: 468–470, pl. 115bis, figs. 3–5.

1849 *Crioceras Astierianus* d'Orbigny. Quenstedt: 280, pl. 20, fig. 9.

1861 *Crioceras Astierianus* d'Orb. Pictet and Campiche: 27, pl. 45, figs. 1 and 2.

Fig. 2 *Pictetia astieriana* (d'Orbigny 1840–1842). **A**, **B** PIMUZ 002851 from the Strahlkopf, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian; **C** MAo-733 from Ambatolafia, Madagascar, Albian; **D** MAo-736 from Ambatolafia, Madagascar, Albian; **E–G** PIMUZ DP/20 from the Emmabach section, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian holotype of *Pictetia oberhauseri* Föllmi, 1986, pl. 14, fig. 1a–c; **H** PIMUZ DP/10 002845 from the Strahlkopf, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian; **I**, **J** PIMUZ 002845 from the Müselbach 2 section, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian (original of Föllmi 1986, pl. 13, fig. 6); **K**, **L** PIMUZ DP/10 from the Emmabach section, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian (original of Föllmi 1986, pl. 13, fig. 7a, b); **M**, **N** PIMUZ 002843 from the Strahlkopf, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian, the same as Fig. 1D, E, for size comparison; **O**, **P** PIMUZ Br 1/20 from the Strahlkopf, Vorarlberg, Austria, "Plattenwald Schicht" from the Garschella Formation, Albian/Cenomanian ▶

1923 *Pictetia astieriana* (d'Orbigny). Spath: 27, pl. 1, fig. 7, text-fig. 7.

1949 *Pictetia Astieri* d'Orb. Collignon: pl. 8, fig. 2a, b.

1952 *Pictetia astieri* Puzos. Basse: 603, pl. 3, fig. 4a, 606, fig. 5.

1958 *Pictetia astieriana* (d'Orbigny). Drushchits in Orlov: pl. 21, fig. 1.

?1958 *Pictetia depressa* (Pictet). Drushchits in Orlov: pl. 21, fig. 2.

1963 *Pictetia astieri* d'Orb. Collignon: 7, pl. 243, fig. 1044.

1978 *Pictetia astieriana* (d'Orbigny, 1840–1842). Kennedy and Klinger: 325, fig. 49.

?1978 *Pictetia* aff. *depressa* (Pictet and Campiche, 1861). Kennedy and Klinger: 328, fig. 52a–c.

non 1978 *Pictetia astieriana* (d'Orbigny, 1840–1842). Kennedy and Klinger: 326, fig. 50, 327, fig. 51.

1986 *Pictetia astieriana* (d'Orbigny, 1841). Föllmi: 185–186, pl. 13, figs. 4–8.

1986 *Pictetia oberhauseri* Föllmi: pl. 14, fig. 1.

1986 *Pictetia* sp. nov. Föllmi: pl. 14, fig. 2.

1986 *Pictetia* sp. Föllmi: pl. 14, fig. 3.

1989a *Pictetia astieriana* (d'Orbigny, 1841). Föllmi: 116, pl. 2, figs. 4–8.

1989a *Pictetia oberhauseri* Föllmi: 116–117, pl. 2, fig. 9, pl. 3, fig. 1.

1989a *Pictetia* sp. nov. Föllmi: pl. 3, fig. 2.

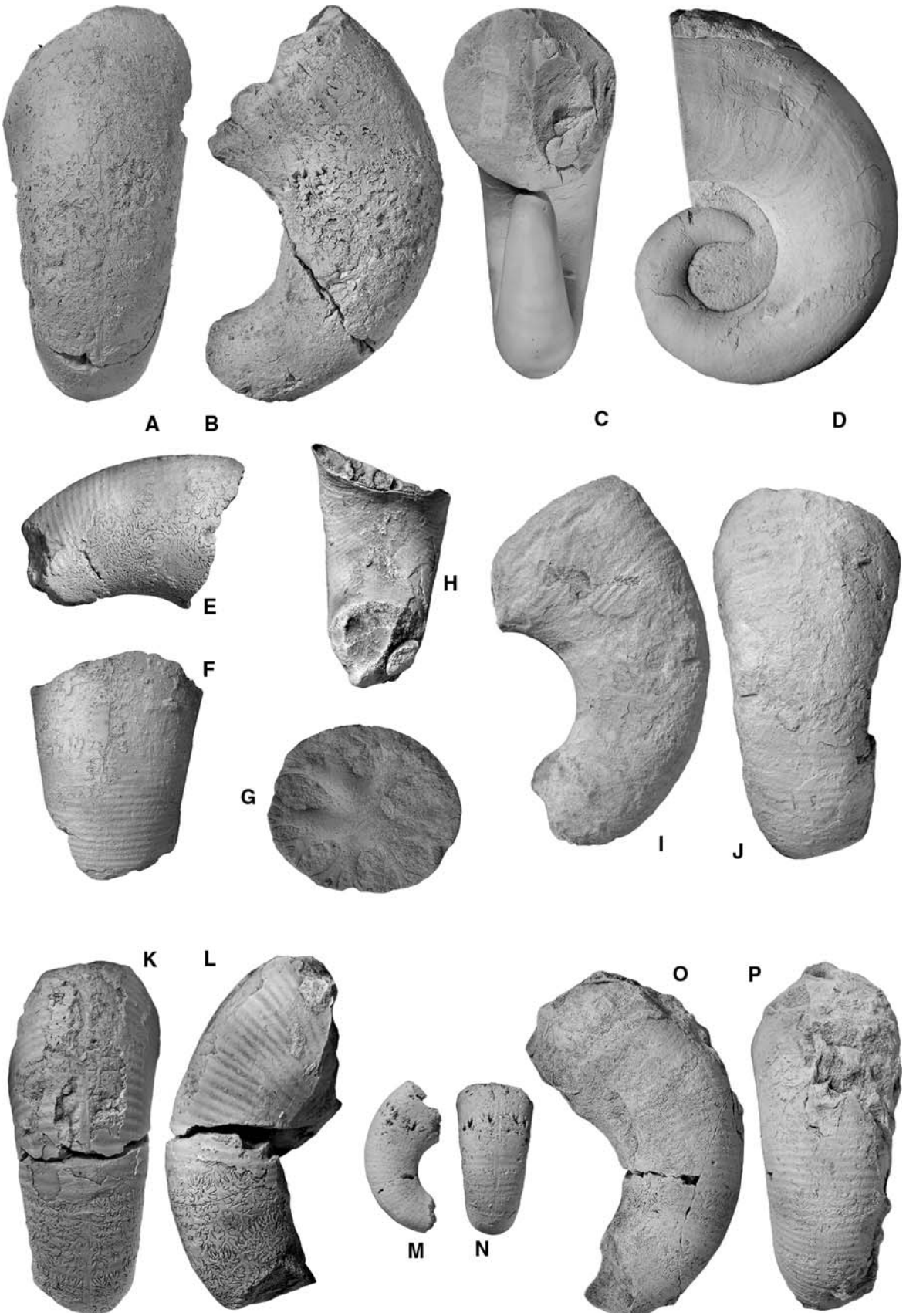
1989a *Pictetia* sp. Föllmi: pl. 3, fig. 3.

1989b *Pictetia oberhauseri* sp. nov. Föllmi: 78, fig. 43.6

1992 *Pictetia astieriana* (Orbigny). Rodda and Murphy: 437, figs 1–3, 6.

1992 *Pictetia* sp. Rodda and Murphy: 437, figs 4 and 5.

2006 *Pictetia astieriana* (d'Orbigny, 1840–1842). Kennedy in Fischer and Gauthier: 139, pl. 40, fig. 5a–c.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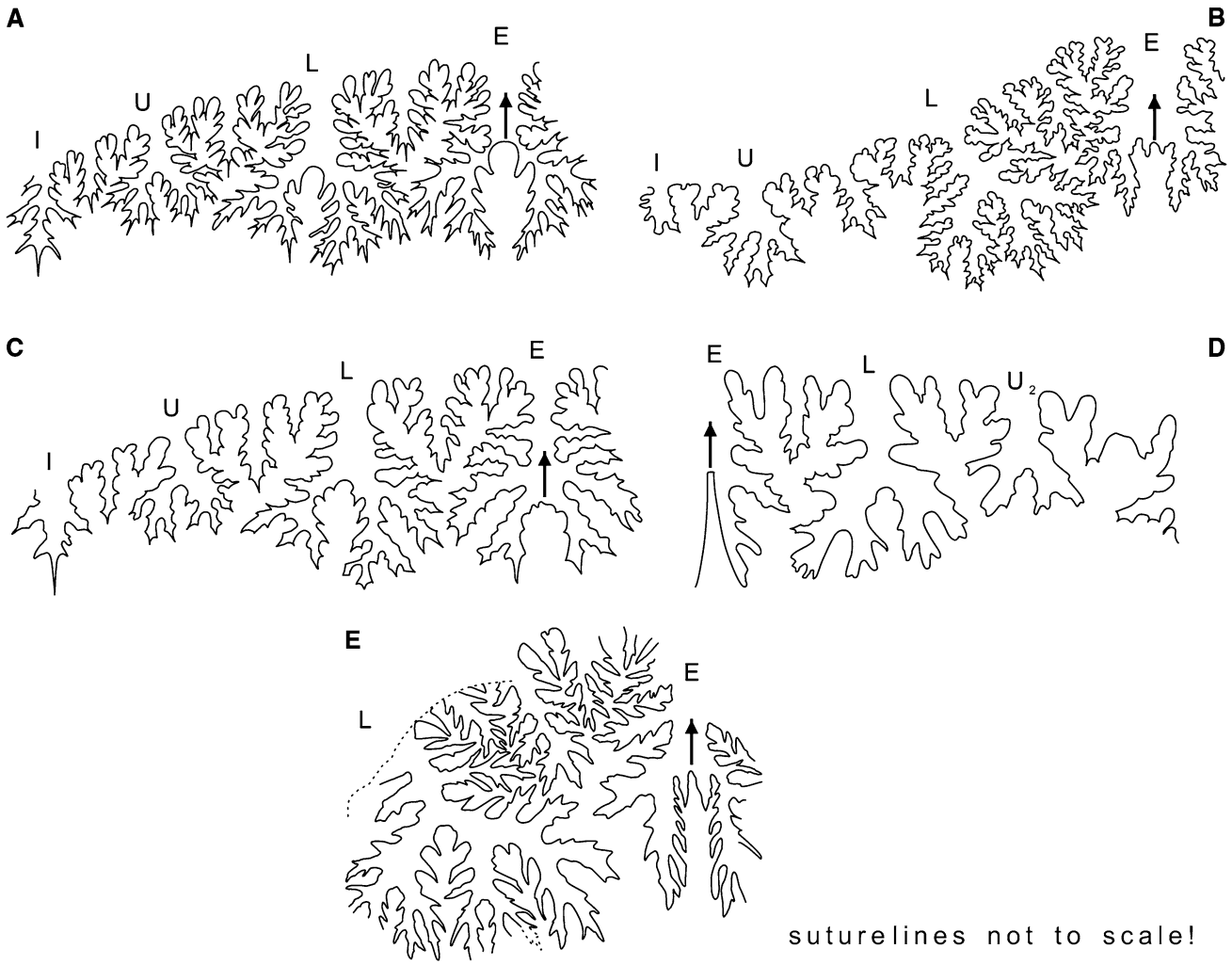

Fig. 3 Suture lines of *Pictetia* and *Lytoceras*. **A** Copy of the suture line of the lectotype of *Pictetia astieriana* (d'Orbigny) as figured in d'Orbigny (1840–1842). **B** Suture line of the lectotype of *Pictetia depressa* (Pictet and Campiche) as figured in Pictet and Campiche (1861–1864, pl. 14, fig. 3d). **C** Reproduction of the suture line of *Pictetia astieriana*, figured by Pictet and Campiche (1861–1864, pl. 14, fig. 1c). **D** Suture line of *Pictetia vogdti* (Karakasch, 1907), as figured in Druŝic (1956) (=*Lytoceras vogdti*). **E** Parts of the suture line of *Pictetia astieriana* (d'Orbigny 1840–1842) with E and L well visible (No. MAo-733)

Material: In total 45 specimens. Keupp Collection MAo-519, MAo-1045, MAo-733 and MAo-736 with shell preservation (loose from the area around Ambatolafia, Mahajunga Basin, Lower or Middle Albian, Madagascar); the original suite of Föllmi (1986, 1989a, b) from the Garschella Formation of Vorarlberg (Austria): PIMUZ 002843–002848, PIMUZ 002850–002852, AF 1/7-13, AN 11/2-3, BR 1/10-20, BN 16/1, BR 1/23, BR 1/25-26, BS 2/1, DP 11–12 and 14–18, DP 13, housed in the Palaeontological Museum, Zurich.

Description: None of the specimens have their initial whorls preserved, but judging from the comparatively dense coiling in MAo-519 and 1045 (Fig. 1A, B), the earliest whorls may have been in contact with another up to a diameter of less than 1 cm. After this stage, coiling is criocone with a high whorl expansion rate. The whorl section is rounded or sub-rounded to slightly oval (Fig. 2C) with or without a more or less well visible dorsal zone, characterised by a very shallow depression or a flattening (Fig. 2H). Larger fragments can become somewhat depressed (Fig. 2G). In internal moulds, concave to projected ribs that are somewhat blunt and subrectangular in cross-section cross the venter more or less rectangularly (Fig. 2K–P) or slightly prorsiradiate (Fig. 2E, F). Where the aragonitic shell is preserved, very dense and fine lirae that can split about mid-flank are superimposed on the ribbing (Fig. 2D). In the dorsal area, a projected sinus of weakly developed ribs occurs (Fig. 2H). At the dorsal shoulder, the ribbing strengthens, and from about 40 mm in diameter, the ribbing first bends strongly straight backwards at the dorsal shoulder to become prorsiradiate to weakly sinuous and sometimes slightly fimbriate in the

lowermost part of the whorl (Fig. 2D). The ribbing then becomes more irregular, consisting of bundles of a few ribs, and developing weak bulges. The crowding of these bulges may indicate a growth stage close to adulthood. However, no body chamber is preserved. PIMUZ 002849 is the largest fragment we have seen (wh: 54 mm, wb: 62 mm). It is depressed in whorl section and is still fully septate.

In specimen MAo-733, the shell has been polished off, and remnants of the shell material are preserved in very faint depressions, indicating the presence of regularly spaced but weakly developed varices (5–6 per half whorl). This is also visible in MAo-519, with about six to seven constrictions per half whorl. This is not observed in the internal moulds of the Föllmi collection.

The quadrilobate suture line of the type (Fig. 3A) shows strongly incised and slender elements with an asymmetrical bifid (pseudo-trifid) L. This can also be seen in early growth stages (PIMUZ 002843: wh: ca. 8 mm, wb: ca. 7.5 mm). A small but well-developed and distinct saddle internally subdivides E, which is very characteristic of all fragments where E is preserved (e.g. Fig. 3E).

Discussion: Kennedy in Fischer and Gauthier (2006) gives a description of the lectotype of *P. astieriana*, and there is no doubt that our material can be included in the species due to its overall fit with respect to whorl section, whorl expansion rate, and ornamentation. Although badly preserved in most of our material, the character of the ribbing is in accordance with that known from other figured specimens (e.g. Quenstedt 1846–1849; Rodda and Murphy 1992). It is interesting to note the occurrence of dorsal impression/flattening in our material, which is sometimes well developed. *P. astieriana* figured by Pictet and Campiche (1861–1864, pl. 45, fig. 1b) also show this dorsal impression. In the original of d'Orbigny (1840–1842), mentioned by Kennedy in Fischer and Gauthier (2006), weak dorsal flattening occurs. Other specimens seem to lack this dorsal longitudinal furrow, and its occurrence or absence may be an expression of some intraspecific variation. The specimen figured by Spath (1923, pl. 1, fig. 7) shows good accordance in ornament with our material and that of Rodda and Murphy (1992). In most respects, the holotype of *Pictetia oberhauseri* Föllmi, 1986 (here refigured in Fig. 2E–H) fits with *P. astieriana*, except for its more depressed whorl section. We regard this as variation within one species, and consequently regard *P. oberhauseri* as a junior synonym of the nominal species. A comparable more depressed whorl section occurs in *P. depressa* from Mangyshlak (Drushchits in Luppov 1958, pl. 21, fig. 2) and in *Pictetia* aff. *depressa* (Pictet and Campiche) of Kennedy and Klinger (1978: 328, fig. 52a–c), which is also tentatively included in *P. astieriana* here. This also refers to *Pictetia* sp. nov. and *Pictetia* sp. of Föllmi (1986), which deviate only slightly by means of the whorl section and minor details of the suture from *P. astieriana*. The fragment referred to as *Pictetia* sp. by Rodda and Murphy (1992) was excluded by them from *P. astieriana* due to its weaker mode of coiling, but, given the variation in our material, we do not hesitate to include it in *P. astieriana*.

The record of *P. astieriana* from Bulgaria and its description (Ivanov 1993) are considered uncertain, as the figured ammonite fragment could be anything.

Breistroffer (1947) introduced *Pictetia* n. sp. (without figures) from the Albian of France and separated it from *P. astieriana* due to its more subrounded whorl section, but this variation rather points at *P. astieriana*.

Referring to the reproduction of the type in Spath (1923: 23, fig. 7), Föllmi (1989a) stated that the initial whorls of *P. astieriana* may have been in contact with the preceding up to a diameter of 13 mm, which cannot be seen in the original illustration in d'Orbigny (1840–1842). However, judging from the repeated photographic reproduction of the type (Kennedy and Klinger 1978: 325, fig. 49; Fischer and Gauthier 2006: pl. 40, fig. 5a), this seems to be the case, as it may be in MAo-1045.

The suture lines of our specimens (Fig. 3E) are identical to that of the type (Fig. 3A) and that of Pictet and Campiche (1861) (Fig. 3c). However, the weak significance of the suture line for specific separation within *Pictetia* finds its expression in the specimen of *P. depressa* figured by Casey (1960: pl. 1, fig. 1a, b), which shows identical slender sutural elements of an asymmetrical bifid L like in *P. astieriana*.

Occurrence: Well-documented and figured records come from England, France, Austria and Switzerland from the Middle Albian *dentatus* zone (see also Casey 1960; Kennedy and Hancock 1976; Owen 1971). *P. astieriana* is listed but not figured from Bavaria (Gümbel 1861) and the *dentatus* zone of Austria (Heim and Seitz 1934). Two records from California come from the *hulenense* and *packardi* zones, respectively, suggesting that they come from the Early to Earliest Middle Albian (Amédro and Robaszynski 2005). Our Madagascan material comes from condensed deposits, and the associated ammonite fauna suggests a *besairie/inaequinodum* zonal age (Early Albian). A record from Japan (Toshimitsu and Hirano 2000) refers to the fragment of Katto and Katto and Obata (1975, fig. 2), which is not a *Pictetia*.

Pictetia depressa (Pictet and Campiche, 1861)

Fig. 1F, G, 3B

Type: Lectotype is the original Pictet and Campiche 1861, pl. 45, fig. 3a–d, by subsequent designation of Casey (1960).

1861 *Crioceras depressum* Pictet and Campiche: 28, pl. 45, fig. 3–4.

1923 *Pictetia astieriana* (d′Orbigny). Spath: pl. 1, fig. 7, text-fig. 8.

1960 *Pictetia depressa* (Pictet and Campiche). Casey: 5, pl. 1, fig. 1a–c, text-fig. 1a–d (with synonymy).

non 1962 *Pictetia depressa* (Pictet et Campiche). Collignon: 13, pl. 221, fig. 957.

1978 *Pictetia* aff. *depressa* (Pictet and Campiche, 1861). Kennedy and Klinger: 328, fig. 52d–f.

1980 *Pictetia depressa* (Pictet and Campiche). Casey: pl. 101, fig. 2.

?1993 *Pictetia depressa* (Pictet and Campiche) Ivanov: pl. 3, fig. 6.

2000 *Pictetia depressa* (Pictet). Keupp: 60.

Material: One specimen only (MAo-100) from the Mangyshlak area, Kazakhstan; no further locality details are available.

Description: Specimen MAo-100 (Fig. 1F, G) has a whorl breadth of 23 mm at a diameter of about 35.5 mm. Whorls are normally coiled until about 12 mm, then criocone coiling occurs with a rapid whorl expansion rate and rapid increase of the wh/wb ratio, thus giving an inflated appearance even in early growth stages. The whorl section is depressed and slightly kidney-shaped. A weak dorsal impression can be detected. The ornament consists of very weak, fine and close ribbing, as in *P. astieriana*. A suture line is not preserved.

Discussion: Based on its very depressed whorl section and its rapid whorl expansion rate, we refer this specimen to *P. depressa*, although the dorsal zone is not so strongly developed as in the lectotype. However, the specimen beautifully illustrates that the initial whorls are in contact, and the dorsal impression may indeed be the result of this early ontogenetic characteristic, which also appears to be valid for *P. astieriana*. Rodda and Murphy (1992) excluded *P. depressa* from *Pictetia* due to its impressed dorsum, but this feature—although more weakly developed—also occurs in *P. astieriana*. Together with the characteristic whorl expansion rate and the nature of the suture line with a trifid I and the lack of a septal lobe, there is little doubt that this taxon is a true *Pictetia*. From *P. astieriana*, it differs by its kidney-like whorl section and the well-developed impressed dorsal zone. As in *P. astieriana*, a siphonal saddle internally subdivides the external lobe (Fig. 3B). This is lacking in *P. depressa* of Collignon (1962: 13, fig. 957), which is why Föllmi (1989a) stated that this specimen instead represents a fragment of a lytoceratid, a view followed here. The specimen figured by Casey (1980, pl. 101, fig. 2) is not very informative, as the whorl section has not been figured, but judging from its stratigraphic position (see below), it may be *P. depressa* rather than *P. astieriana*.

The record of *P. depressa* from Bulgaria (Ivanov 1993) is considered uncertain, as the figured ammonite fragment could be anything. A narrow sulcus described by Ivanov (1993) points to *Pictetia*; however, the preservation of the specimen may not be sufficient for specific determination.

Occurrence: P. depressa is recorded from the *Leymeriella tardefurcata* to *Douvilleiceras mammillatum* zones of Europe, Lower Albian (Pictet and Campiche 1861; Casey 1980). It also occurs in Kazakhstan.

Other species previously included in *Pictetia*

There are a number of species referred to as *Pictetia* in the literature that have, however, undergone revision in the past and are no longer included in the genus. We will list these taxa with their current generic assessments and the relevant literature below.

Pictetia arcuata Collignon (1962: 13, pl. 221, fig. 958) has been included by Rodda and Murphy (1992) in *Pictetia*, but it was Collignon (1963) himself who included it in *Ephamulina*, a view followed by, for example, Kennedy et al. (2000), Szives and Monks (2002) and herein.

Pictetia belliseptata (Anthula, 1899) sensu Dimitrova (1967: 28, pl. 10, fig. 6) is based on *Lytoceras belliseptatum*. The holotype has been refigured by Kennedy and Klinger (1978: 304, fig. 40–43), who show it to be an *Argonauticeras*.

Pictetia crassecostata Collignon (1963: 8, pl. 243, fig. 1046) has been excluded from the genus due to its trifid L by Rodda and Murphy (1992). As discussed above, this is not regarded as an indicative character. However, they also considered its coarse and nonfimbriate ornament to be atypical. Furthermore, it shows strong constrictions crossing the dorsal side. Together with its much slower whorl expansion rate, it appears that it instead may represent a fragment of *Ephamulina*.

Pictetia ovalis Collignon (1963: 8, pl. 243, fig. 1045) is based on one specimen only, the original of which we have not seen. Judging from Collignon's illustration, the ornament—consisting of slightly flexuous ribs that bend backwards at the ventral shoulder—deviates from that of *Pictetia,* and we prefer to exclude it from *Pictetia* at the moment. Apart from Madagascar, *P. ovalis* from southern America is mentioned but never figured (e.g. Riccardi and Medina 2002; Medina and Riccardi 2005).

Pictetia vogdti (Karakasch, 1907) of Druŝic (1956) and Druŝic (1960) and Kudrâvcev (1960) is based on *Lytoceras vogdti* Karakasch, 1907, which needs to be kept within *Lytoceras* due to its normal coiling, bifid I, two umbilical lobes and a septal lobe (e.g. Schindewolf 1961; Förster 1975). Furthermore, it shows a weakly subdivided E with a

characteristic lytoceratid development (Druŝic 1956: 84, fig. 36; see Fig 3D for reproduction).

Hamites "*Pictetia*" *longispinus* Uhlig, 1883 and *Pictetia inermis* Haug, 1889 are included in *Acantholytoceras* Spath, 1923, which was included in the Lytoceratidae by Kilian (1910: 253), Gignoux (1920: 121), Roman (1938: 37) and Luppov (1952: 181). Today, however, it is kept in the "Ancyloceratina" (Wright et al. 1996).

Conclusions

The literature data, in line with our material, shows that the generic diagnosis needs to be amended. In particular, an elongated shaft cannot be confirmed and a body chamber has never been recorded for the genus. The earliest whorls are in contact to a diameter of about 10 mm, (sometimes) leaving a dorsal impression in later growth stages. Due to the quadrilobate suture, it is excluded from the Lytoceratidae Neumayr 1875 and is included into the "Ancyloceratina" Wiedmann 1966. Further sutural arguments are the trifid internal lobe, the lack of a septal lobe, and an internal subdivision of the external lobe by a well-developed narrow siphonal saddle, which is only poorly developed in the Lytoceratidae. As its primary suture is unknown, further positioning within the "Ancyloceratina" appears impossible at the moment.

The two species *P. depressa* (Lower Albian) and *P. astieriana* (Middle to Lower Upper Albian) appear to be well founded, considering only the types. As progressively more material emerges, it becomes more difficult to draw a clear line of distinction between the species, as the shift from rounded to subrounded and oval whorl section with or without dorsal impression/dorsal zone appears to be gradual. It may well be that we are looking at variations of a monospecific genus with chronostratigraphic significance. Therefore, variations in the whorl section from rounded to slightly depressed that can be observed in *P. astieriana* are not considered to be a reliable diagnostic feature for specific separation (e.g. *P. oberhauseri*). The use of the development of L (trifid vs. bifid) to specifically separate within the genus is not feasible, as it appears to be asymmetrically bifid/trifid irrespective of the species. Due to the few records and the mostly fragmentary preservation, there are only limited data on intraspecific size variations. The scarce material does not permit the recognition of sexual dimorphism, which is well-developed amongst some heteromorphic ammonites (Kennedy and Cobban 1976; Davis et al. 1996).

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