



Pseudoteloceras, a new stephanoceratid genus (Ammonitida) of the lower Humphriesianum Zone (lower Bajocian, Middle Jurassic) from western Tethys



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ABSTRACT

The new dimorphic genus *Pseudoteloceras* (type-species: *P. crosillense* gen. et sp. nov.) is defined within the subfamily Stephanoceratinae. It constitutes the terminal step of an early Bajocian phyletic trend that produces *Teloceras*-like morphologies throughout the lower Humphriesianum Zone of the western Mediterranean-Caucasian Subrealm, at an older chronological interval and with morpho-structural features that stand apart from those of the best known genus *Teloceras* of the uppermost Humphriesianum and lower Niortense zones at the early/late Bajocian transition. Three new species are described: *P. crosillense*, *P. maerteni* and *P. boursicoti*. Their biochronostratigraphical ranges are confirmed by the distribution in expanded sections of the Subalpine Basin in Submediterranean Province (Digne area) and the taphonomic analysis of fossil assemblages from the condensed sections of the "Oolithe ferrugineuse de Bayeux" Formation in Calvados, North West European Province. The biochronostratigraphical range of *Pseudoteloceras* gen. nov. is limited to the Romani Subzone, lower Humphriesianum Zone. *P. crosillense* gen. et sp. nov. marks a well-defined biohorizon of the upper Romani Subzone in the Digne stratigraphical successions. The extreme degree of the cadiconic morphology in the inner whorls of *P. boursicoti* gen. et sp. nov., and the biostratigraphical gap separating the first appearance of the genus *Teloceras* in the upper Humphriesianum Zone, support its erection as a new taxon *Pseudoteloceras* gen. nov. A fourth species, *Pseudoteloceras geometricum* (Maubeuge), is interpreted as the earliest species of this phyletic lineage, derived from *Stemmatoceras* and widely distributed through western Tethys in the lower Humphriesianum Zone.

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1. Introduction

The pandemic family Stephanoceratidae Neumayr, 1875, one of the five families of the Middle to Late Jurassic superfamily Stephanoceratoidea Neumayr, 1875, evolves from the Otoitidae Mascke, 1907, at the Aalenian/Bajocian transition (Fernandez-Lopez, 2014; Fernandez-Lopez and Pavia, 2015) and ranges throughout the Bajocian and Bathonian. It consists of three classical subfamilies Stephanoceratinae Neumayr, 1875, Garantianinae Wetzel, 1937, and Cadomitinae Westermann, 1956, and in addition two new early Bajocian subfamilies were recently defined: Mollistephaninae Fernandez-Lopez and Pavia, 2015, and Frebolditinae Fernandez-Lopez and Pavia, 2015 (for diagnostic

features see Fernandez-Lopez and Pavia, 2015, p. 2, and references therein).

The subfamily Stephanoceratinae is characterized by serpenticonic, planorbiconic, platyconic and cadiconic shells and primary ribs with tubercles at the furcation points on the outer flank, and secondary ribs uninterrupted on the venter. Two dimorphs are differentiated: (1) microconchs [m] with lateral lappets and short body-chambers that are ribbed to the termination, and (2) macroconchs [M] with a simple aperture and relatively long body-chamber (in excess of 360°) that is smooth or distantly ribbed. The septal suture is usually complex with 1st lateral saddle E/L asymmetric and higher than the second lateral saddle L/U, dominant 1st lateral lobe, supplementary lobe (U₂) on L/U, and well-developed, retracted umbilical lobe (U) (Arkell et al., 1957; Callomon, 1981, 1985; Page, 1993, 1996, 2008; Moyne and Neige, 2004; Howarth, 2013; Fernandez-Lopez, 2014).

On the basis of these morpho-structural features, Stephanoceratinae display diverse evolutionary trends interpreted as a

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monophyletic group. This subfamily clade brings together a morphologically complex group of lineages and supraspecific taxa throughout early to early-late Bajocian, such as:

- *Albarracinites* Fernandez-Lopez, 1985, planorbicones distributed in the Discites and Laeviuscula zones (type species *A. albarraciniensis* Fernandez-Lopez, 1985, p. 301, pl. 36, fig. 1, holotype from the Laeviuscula Zone, Albarracin, Spain).
- *Skirroceras* Mascke, 1907 (and synonyms proposed by Arkell et al., 1957), planorbicones or platycones to serpenticones distributed from the Laeviuscula to the lowermost Humphriesianum zones (type-species *Ammonites Humphriesianum macer* Quenstedt 1886, in 1883–1888, p. 528, pl. 65, fig. 11, lectotype designed by Buckman, 1921 in 1909–1930, pl. 248, from the “Humphriesianum-Oolith”, Swabia, Germany).
- *Stephanoceras* Waagen, 1869 (and synonyms proposed by Arkell et al., 1957), platycones to planorbicones distributed from the upper Laeviuscula to the lowermost Niortense zones (type species *Ammonites Humphriesianus* J. de C. Sowerby, 1825 in Sowerby and Sowerby, 1812–1846, pl. 500, holotype from the lower Bajocian, Osborne, Dorset, England).
- *Teloceras* Mascke, 1907, cadicones distributed from the uppermost Humphriesianum to the lower Niortense zones (type species *Ammonites blagdeni* J. Sowerby, 1818 in Sowerby and Sowerby, 1812–1846, p. 231, pl. 201, holotype from the uppermost Humphriesianum Zone, Osborne, Dorset).

With respect to this group of selected taxa, it is worth mentioning that the transition from *Stephanoceras* to *Teloceras* is represented by the subcadiconic to planorbiconic forms historically referred to as a branch of the genus *Stemmatoceras*, Mascke, 1907, but recently assembled into the subgenus *Teloceras* (*Pavicer*) Gauthier, Rioult and Trévisan, 1996, from the upper part of the Humphriesianum Zone (type-species *Stemmatoceras hoffmanni* Schmidtil and Krumbeck, 1938, p. 348, pl. 13, fig. 6, lectotype designed by Pavia, 1983, p. 115, pl. 21, fig. 4, from the “Obere Humphriesi-Schichten”, North Bavaria, Germany).

Besides *Teloceras* (*Pavicer*), a second lineage involving subcadiconic to planorbiconic stephanoceratins evolves into the subfamily Cadomitinae whose dimorphic partner is [M] *Cadomites* Munier-Chalmas, 1892 (type-species *Ammonites Deslongchampsii* Defrance in d'Orbigny, 1846 in 1842–1851, p. 405, pl. 138, figs. 1–2, holotype by original designation from the upper Bajocian of Calvados, France) and [m] *Polyplectites* Mascke, 1907 (type-species *Ammonites linguiferus* d'Orbigny, 1846 in 1842–1851, p. 402, pl. 136, figs. 4–5, neotype designed by Westermann, 1954, p. 338, on de Grossouvre, 1930, pl. 40, fig. 10, from the upper Bajocian of Calvados, France) span from the uppermost lower Bajocian Humphriesianum Zone to the upper Bathonian/lower Callovian transition (Sandoval, 1983; Fernandez-Lopez, 1985; Dietl and Herold, 1986; Fernandez-Lopez and Pavia, 2015). The genus *Lokuticeras* Galácz, 1994 (type-species *Lokuticeras rossbrunnense* Galácz, 1994, p. 165, pl. 1, fig. 1, holotype from the uppermost Humphriesianum Zone, Lókút, Bakony Mountains, Hungary) and its microconch counterpart *Masckeites* Buckman, 1920 in 1909–1930 (type-species *Masckeites densus* Buckman, 1920 in 1909–1930, pl. 152, holotype from the Humphriesianum Zone of Sherborne, Dorset) may be regarded as the ancestor of Cadomitinae in the uppermost Humphriesianum Zone (Galácz, 1994; Pavia and Zunino, 2012).

A third group of Stephanoceratinae includes two mid-lower Bajocian subcadiconic to planorbiconic genera whose phyletic position is still debated in relation to the taxa discussed above: (1) *Kumatostephanus* Buckman, 1922 (type-species *Kumatostephanus kumaterus* Buckman, 1922 in 1909–1930, pls. 345 a–b, holotype from the Propinquans Zone of Sherborne, Dorset) and (2)

Stemmatoceras Mascke, 1907 (type species *Ammonites Humphriesianum coronatus* Quenstedt, 1886 in 1883–1888, p. 539, pl. 66, fig. 11 = *Stemmatoceras frechi* Renz, 1904, holotype from the Humphriesianum-Oolith of Eningen, Swabia, Germany, refigured by Weisert, 1932, p. 23, pl. 18, fig. 4, as *Stemmatoceras coronatum*, Schlegelmilch, 1985, p. 77, pl. 27, fig. 6, and Ohmert, 1990, pl. 1, fig. 1), referred to as the passage between the Propinquans and the Humphriesianum zones, whose strong, club-like ribbing and less deeply incised suture lines do not support any clear connection to the most typical stephanoceratins, as indicated by many authors (e.g., Ohmert, 1994; Ohmert et al., 1995; Chandler et al., 2013; Dietze et al., 2015).

A further stock of subcadiconic to planorbiconic Stephanoceratinae consists of *Teloceras*-like forms in the inner whorls, with strong ribbing, large and depressed whorl-section, and crater-like umbilicus. Frequently referred to as *Stemmatoceras*, they are limited to the uppermost Propinquans and the basal Humphriesianum zones (Maubeuge, 1951; Mouterde, 1953; Morton, 1971; Parsons, 1976; Pavia, 1983; Fernandez-Lopez, 1985; Callomon and Chandler, 1990; Ohmert, 1988, 1990, 1994; Ohmert et al., 1995; Gauthier et al., 1996; Pavia and Martire, 2010; Pavia et al., 2013; Chandler & Whicher, 2015). Most of these records may be referred to the “*Ammonites Blagdeni* non Sowerby, 1818” described by d'Orbigny (1847 in 1842–1851) from the lower Bajocian of Les-Moutiers-en-Cinglais in Calvados. We focus our attention here on these particular *Teloceras*-like ammonites with supplementary field researches on the lower Bajocian of the Digne successions (Pavia, 1983) and of the area south of Caen (Pavia et al., 2013, 2015) where the presently unnamed species are fairly common and constitute a homogeneous morphological trend that is different from that of *Teloceras* s.s.

This study aims to (1) define the systematic status of these *Teloceras*-like stephanoceratins by erecting a new genus with new or renamed specific taxa, (2) characterize these taxa by morphostructural criteria by comparison with other Stephanoceratinae of the passage between the Propinquans and the Humphriesianum zones, (3) delineate possible phyletic relationships and palaeobiogeographical constraints.

2. Material and methods

This study is based on the ammonites collected from two different stratigraphical contexts pertaining to the Mediterranean and the north-western European Jurassic areas of the Mediterranean-Caucasian Subrealm (Fernandez-Lopez and Pavia, 2015):

- (1) The thick Bajocian successions of the Digne area (Subalpine Basin, SE France) where the sections of the “Marno-calcaires à *Cancellophycus*” Formation (Graciansky et al., 1982) are expanded and the fossils are preserved following resedimentation processes. Specimens come from the sections of the Ravin du Feston and the Ravin de la Coueste at Chaudon (Digne area, Alpes de Haute Provence: Pavia, 1983; Pavia and Zunino, 2012) (Fig. 1).
- (2) The thin Bajocian successions of the sector south of Caen (Calvados, NW France) where the condensed sections of the “Oolithe ferrugineuse de Bayeux” Formation (Rioult et al., 1991, and references therein) are reduced by recurrent discontinuities and the fossils are commonly preserved as reelaborated elements (i.e. exhumed and displaced before their final burial: Fernandez-Lopez, 1991, 1995, 2007, 2011; Fernandez-Lopez & Pavia, 2015). The specimens come from outcrops of Feuguerolles-sur-Orne, Bretteville-sur-Odon, Evrecy, Maizet and Les Fours à Chaux at Croisilles (Fig. 2) (Gauthier et al., 1996; Pavia and Martire, 2010; Pavia et al., 2013, 2015).



Fig. 1. The lower part of the Humphriesianum Zone in the section of Chaudon, cropping out just beside the Napoleonic Road from Norante-Chaudon to Digne, Subalpine Basin. Numbers of beds are the same as used by Pavia (1983): odd numbers refer to marly limestone beds, even numbers to marly interbeds.

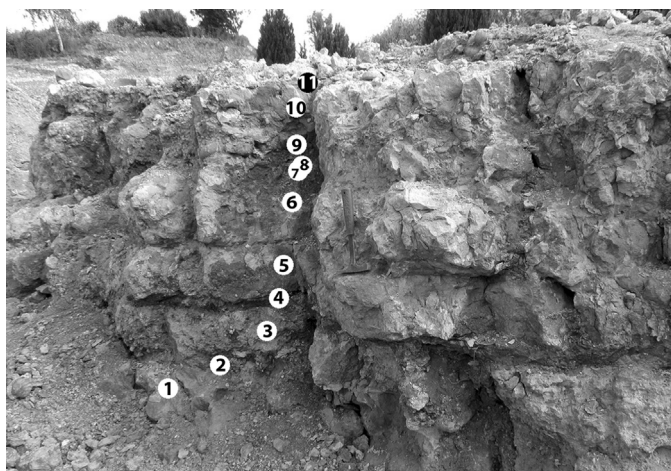


Fig. 2. The section of Les Fours à Chaux at Croisilles. Numbers of beds are the same as used by Pavia et al. (2015). Beds 1–9 refer to the lower Bajocian (Laevisculata to Humphriesianum zones), beds 10–11 to lowermost upper Bajocian (Niortense Zone). Bed 6 is the source of the *Pseudoteloceras* gen. nov. specimens discussed herein.

Ammonites from the Bajocian of Digne are essential for biostratigraphical purposes as they allow defining the stratigraphical succession of taxa in chronological order, whereas the well preserved fossils of Calvados aid in the description of structural and morphological features. The integration of data from two such different geological settings is possible as the cited authors demonstrated that a detailed taphonomic analysis could provide biochronological information even from fossils obtained from condensed sections (see also Fernandez-Lopez and Pavia, 2015). In particular, Pavia et al. (2013, 2015), respectively for the sections of Maizet and Croisilles in Calvados, distinguished between resedimented specimens (i.e. taphonomic elements displaced after accumulation on the sea floor and prior to the burial; therefore, coeval to the encasing sediment) and re-elaborated ones (i.e. taphonomic elements exhumed and displaced before the final burial in expanded deposits; therefore, older than the sedimentary matrix). Such analyses, based on diverse mechanisms of taphonomic alteration (Fernandez-Lopez, 1991, 1995, 2007, 2011), allow the temporal order of the preserved

specimens to be ascertained within the biochronological succession and the diverse depositional patterns represented by the stratigraphical intervals of the study.

The biostratigraphical and biostratigraphical classifications and units proposed by Rioult et al. (1997) are referred to herein as they are accepted almost unanimously (see Sandoval et al., 2001, 2002; Callomon, 2003; Fernandez-Lopez and Pavia, 2015, and references therein). The ammonite Standard Zonation, dividing the Bajocian Stage of the Mediterranean-Caucasian Subrealm, is as follows from bottom up: lower Bajocian: Discites Zone, Laeviuscula Zone, Propinquans Zone (Patella, Hebridica subzones), Humphriesianum Zone (Romani, Umbilicum, Blagdeni subzones); upper Bajocian: Niortense Zone, Garantiana Zone, Parkinsoni Zone.

The morphological terminology used in the following descriptions follow the Glossary of the *Treatise on Invertebrate Paleontology* (Arkell et al., 1957) and other terms presented by Westermann (1996, 2005) and by Fernandez-Lopez (2014). Ammonite abbreviations and measurements (in mm) are as follows: M, macroconch; m, microconch; D, maximum shell diameter; H, whorl height; h, % of whorl height to diameter; W, whorl width; w, % of whorl width to diameter; U, umbilical diameter; u, % of umbilicus to diameter; W/H, ratio of whorl width to whorl height; Ni/2, internal ribs per half whorl; Ne/2, external ribs per half whorl; Ne/Ni, ratio of external to internal ribs.

All the studied specimens are stored in the paleontological collections of the Museo di Geologia e Paleontologia of the Torino University, with code MGPT-PU and have successive catalogue numbers, except for one ammonite provisionally housed in the Lionel Maerten collection (code LM, Ver-sur-Mer, France).

3. Systematic palaeontology

Class Cephalopoda Cuvier, 1795

Subclass Ammonoidea von Zittel, 1884

Order Ammonitida Fischer, 1882

Superfamily Stephanoceratoidea Neumayr, 1875

Family Stephanoceratidae Neumayr, 1875

Subfamily Stephanoceratinae Neumayr, 1875

3.1. Genus *Pseudoteloceras* nov.

Type-species. *Pseudoteloceras croisillense* gen. et sp. nov. (Fig. 3).

Other species. Two nominal species are assigned to the new genus: *Pseudoteloceras maerteni* gen. et sp. nov. and *Pseudoteloceras boursicoti* gen. et sp. nov., both from the lower Bajocian, lower Humphriesianum Zone, Romani Subzone. A further taxon is represented by *Teloceras geometricum* Maubeuge, 1951 (p. 76, pl. 4, fig. 4) from an undefined layer of the Humphriesianum Zone at Halanzy, on the Franco-Belgian boundary, the morphology of which modifies from subcadiconic to planorbiconic with depressed trapezoidal whorl section; for Maubeuge's taxon we propose the new combination *Pseudoteloceras geometricum* (Maubeuge). Its holotype, the only known type-specimen, was doubtfully referred to the "zone à *T. blagdeni*?" by Maubeuge (1951, p. 76); it is a re-elaborated internal mould that, if the original biostratigraphical reference is correct, was derived from the underlying fossil assemblage that mixes ammonites indicative of layers from the topmost Propinquans to the middle Humphriesianum zones. Therefore it can be interpreted as pre-Blagdeni Subzone and probably belonging to the Romani Subzone.

Etymology. Genus name *Teloceras* combined with the prefix "pseudo" with the meaning "resembling or imitating".

Diagnosis. Shells of small to medium size (micro- and macroconchs generally between 50 and 360 mm in diameter, respectively), evolute subcadicones, cadicones in the inner whorls,

becoming planorbicones in the outer whorls, with depressed trapezoidal to subelliptical whorl section in the phragmocone and whorl-width proportionally reduced towards the adult body-chamber; coarse, strong, spaced and slightly sinuous primary ribs; prominent tubercles in the trifurcation points on the ventrolateral shoulder and straight or convex to forward projected secondaries. Microconchs with rounded-depressed whorl section egressed on the body-chamber; pointed to obsolete tubercles on the ventrolateral shoulder.

Description. Macroconchs are subcadicones of medium size with depressed, subtrapezoidal to elliptical section. The umbilicus is open, but relatively deep with steep flanks up to the acute ventrolateral shoulder in the inner whorls. The venter is slightly arched to flatten. Primary ribs are distant, sinuous, enlarged in the distal part and sometimes sharp. Trifurcation points lie in the outer flank at the ventrolateral shoulder and correspond to high tubercles, stout on the phragmocone and spiniform on the shells (or composite moulds). Secondary ribs cross the venter without interruption and describe a feeble to pronounced forward bend. Microconchs are small (50–60 mm) with rounded whorl-section, angular at the furcation point, just outside the mid-flank, with pointed to smoothed tubercles. Single ribs occur between bifurcate pairs. Peristome bears medium-long and narrow lappets. Suture line (Fig. 4) shows narrow and deeply incised E/L, large, slightly oblique lateral lobe, L/U saddle larger than E/L and symmetrically bipartite by a wide U_2 , U_3 retracted and deep as U_2 .

Regarding the microconchs, the dimorphic pairing is established only for *P. croisillense* gen. et sp. nov. and is evidenced by the co-occurrence of macro- and micro-counterparts in the same beds of the Chaudon section (see Pavia, 1983). Any other microconch counterpart of *Pseudoteloceras* gen. nov. is so far unknown. Our view is that it would be very difficult to corroborate from literature. The dimorphic coupling of *Pseudoteloceras* gen. nov. should be recognised only by co-occurrence of forms in the same fossil assemblage.

Discussion. *Teloceras* s.s., to which many authors referred these forms of the Romani Subzone (e.g., Callomon and Chandler, 1990; Chandler and Whicher, 2015; Ohmert et al., 1995), shows cadicones with regularly increasing whorl-width through the ontogeny, umbilical egression in the last whorl, shorter adult body-chamber (brevidomic or mesodomic; i.e., body-chamber with length whorl less than 360 degrees), denser primary ribs and tubercles, except in *T. banksi* of the lowermost upper Bajocian, more complex suture lines with deeply incised primary and secondary elements. Moreover, it is observed that *Teloceras* s.s. is recorded as beginning from the topmost Umbilicum Subzone with *T. acuticostatum*.

Chandler et al. (2013, p. 296) suggested a possible phyletic connection between the “*Teloceras*” of the Romani Subzone (recte *Pseudoteloceras croisillense* gen. et sp. nov.) and the *Kumatostephanus* present in Dorset up to the Humphriesianum Zone. Apart from this biochronologic anomaly (*Kumatostephanus* is recorded from the Laeviuscula and the lower Propinquans zones everywhere in the West-Tethys areas), *Kumatostephanus* shows coronate inner whorls becoming serpenticonic in the adult stage. A further stephanoceratin of the mid-lower Bajocian is *Stemmatoceras*, from which *Pseudoteloceras* gen. nov. differs for distinctive features such as more depressed trapezoidal whorl section, prominent ventrolateral shoulder, more spaced primary ribs, and blunt to spiniform tubercles.

Species of *Stemmatoceras* show a wide dispersion throughout the West-Tethys areas: from the central-European sector where they are most frequently listed in the upper Propinquans Zone (Hebridica Subzone, equivalent to the German Pinguis Subzone) and in the basal Humphriesianum Zone (Gassmann and Ohmert, 1990; Ohmert, 1990, 1994; Ohmert et al., 1995), to the Submediterranean (central France: Fernandez-Lopez and

Mouterde, 1994, p. 122) and Mediterranean (Della Bruna and Martire, 1985; Sandoval, 1990; Galacz, 1991) provinces. The records from the East-Pacific Realm enlarge the possible range of the species, but most records are not clearly and confidently congeneric within Mascke's taxon, or pertain to different species (Hall and Westermann, 1980; Westermann, 1992).

The type-species *Stemmatoceras frechi* was carefully described by Ohmert et al. (1995, p. 81, pl. 5, figs. 1–4, pl. 6, figs. 1–2) who highlighted its morphological features in relation to both *Stephanoceras* and *Teloceras*. Its morphology can be summarized as follow: medium-sized to large subcadiconic shell with depressed trapezoidal inner whorls becoming elliptical during ontogenesis; moderately open and deep umbilicus with rounded walls; spaced, slightly projected and concave primary ribs (24 on the last whorl at 87 mm diameter of the holotype); stout tubercles at the trifurcation point with regular intercalary ribs; suture line characterized by well-incised accessory elements of the lateral saddles and a deeply retracted umbilical lobe (Ohmert et al., 1995, fig. 17: very different to that one produced by Schlegelmilch, 1985, p. 77!). Besides the type-species, Ohmert et al. (1995) described two species, *S. rauricum* Ohmert, 1995 and *S. triplex* (Weisert, 1932). Moreover, Mascke (1907, p. 30) listed many taxa from the same layer of *S. frechi* that need formal definition as *nomina nuda* such as “*S. crassispina*”, “*S. ellipticum*” (see Pavia, 1983, fig. 28), and “*S. robustum*” (personal observation of the coauthor G. P. in the geo-palaeontological Museum of Göttingen). Ohmert et al. (1995) referred to Mascke's genus a further coeval species, *Teloceras geometricum* Maubeuge, whose teloceriform features are out of the morphological spectrum of *Stemmatoceras* and it is referred more appropriately to *Pseudoteloceras* gen. nov.

As to the microconch equivalent of *Stemmatoceras*, the best candidate is the genus *Platystomites* Westermann, 1954 (Ohmert et al., 1995). The holotype of the type-species (“*Gerzenites* (*Platystomites*) *platystomus*” Westermann, 1954, p. 220, pl. 17, fig. 6, by original designation) comes from the “*Pinguis-Schichten*” of Goslar (N Germany), i.e. it is referred to the Hebridica Subzone as the type of *Stemmatoceras frechi*. In details, Ohmert et al. (1995, p. 82) specified that the microconch counterpart of *Stemmatoceras frechi* is *Platystomites postrugosus* (Westermann, 1954).

It is just worth noting the strict analogies among the microconchs of *Stemmatoceras* and *Pseudoteloceras* gen. nov. This evidence supports the evolutionary lineage connecting the latter genus to the former one, possibly through the large, fragmentary and unnamed specimen of *Stemmatoceras* with a trapezoidal whorl-section and depressed venter figured by Ohmert (1988, p. 339, pl. 8, fig. 9; 1990, p. 123, pl. 1, fig. 2). Based on the *Stemmatoceras* group of the central-European lower Bajocian, Hebridica Subzone, the appearance of the *Teloceras*-like morphology is first documented by *Pseudoteloceras geometricum* (Maubeuge) largely documented within the lower Humphriesianum Zone, from the Mediterranean Province (Alpi Feltrine, north-eastern Italy: Della Bruna and Martire, 1985 as “*Kumatostephanus* (*Stemmatoceras*) *geometricum*”) to the NW European Province (Halanzy at the Franco-Belgian boundary, Maubeuge, 1951; Dorset, southern England: Parsons, 2006, unpublished manuscript, pls. 11–12, as “*Teloceras blagdeniforme*” from the Sherborne area).

The so-called *Stemmatoceras dubium* Schmidtil and Krumbeck, 1938, *Stemmatoceras hoffmanni* Schmidtil and Krumbeck, 1938, *Ammonites subcoronatum* Oppel, 1856 in 1856–1858, and *Skirroceras? triptoleum* Buckman, 1912, are biostratigraphically located in the upper part of the Humphriesianum Zone (topmost Umbilicum and Blagdeni subzones), and disconnected from the stephanoceratids of the basal Humphriesianum Zone as demonstrated by Pavia (1983) from the sections of the Digne area. Their morphology strongly recalls that of *Stemmatoceras*, and for this reason most authors have assigned them to Mascke's genus (e.g.,

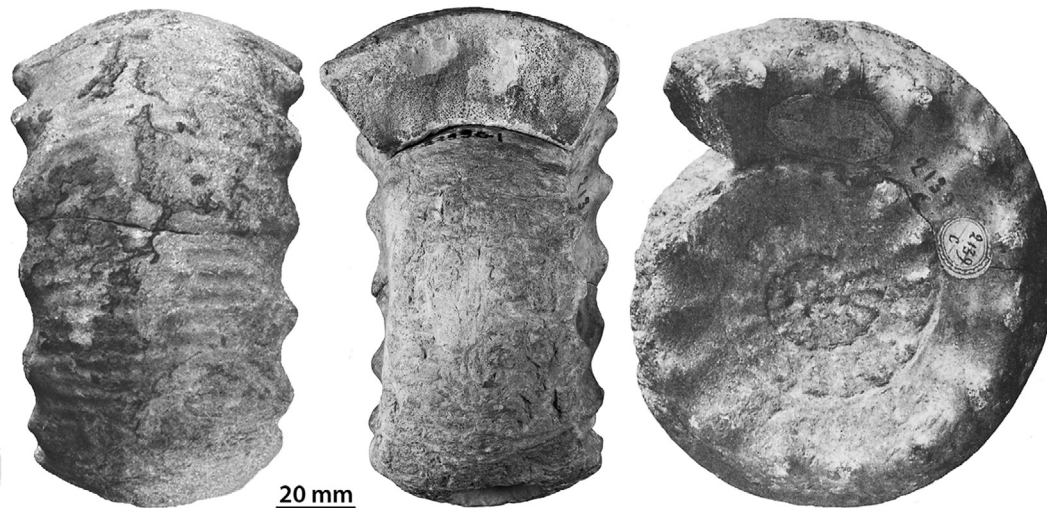


Fig. 3. The holotype of *Pseudoteloceras croisillense* gen. et sp. nov., housed in the Museum d'Histoire Naturelle de Paris (Collection d'Orbigny: MNHN.F.R04116, formerly MHNP-2139c). Modified from Pavia, 1983, text-fig. 29. Asterisk marks the beginning of the body-chamber.

Fernandez-Lopez, 1985). However, Pavia (1983, p. 107) highlighted the absence of equivalent morphologies between the typical *Stemmatoceras frechi* of the transition from Propinquans to Humphriesianum zones and these *Stemmatoceras*-like forms of the topmost Umbilicum and Blagdeni subzones. For this set of species, intermediate between *Stephanoceras* and *Teloceras*, Gauthier et al. (1996) proposed the new nomenclatural combination *Teloceras* (*Paviceras*), whose type-species is *Teloceras* (*Paviceras*) *hoffmanni* (Schmidtill and Krumbeck, 1938). Further taxa of the upper Humphriesianum Zone, referable to *Paviceras*, are *Teloceras* (*Paviceras*) *blagdeniforme* (Roché, 1939) from the upper Humphriesianum Zone ("couches à Cad. *Blagdeni* du Mont d'Or Lyonnais" in Roché, 1939, p. 236; see also Gauthier et al., 1996, p. 35 from Feuguerolles-sur-Orne, and Pavia et al., 2015, from Croisilles), *Stemmatoceras* sp. nov. 2 from the Iberian Range (Fernandez-Lopez, 1985, p. 292), *Stemmatoceras* cf. *frechi* (Renz) form the Subbetic Domain (Sandoval, 1983, p. 252).

Occurrence. *Pseudoteloceras* gen. nov. is known from different bioprovinces of the early Bajocian West-Tethys. Its biochronostratigraphical range is so-far limited to the lower Humphriesianum Zone, Romani Subzone:

- NW European Province: Calvados (d'Orbigny, 1847 in 1842–1851; Gauthier et al., 1996; Pavia and Martire, 2010; Pavia et al.,

2013, 2015), Dorset (Parsons, 1976; Callomon and Chandler, 1990; Chandler & Whicher, 2015).

- Sub-Mediterranean Province: Central Massif of France (Mouterde, 1953; Fernandez-Lopez and Mouterde, 1994), Iberian Range (Fernandez-Lopez, 1985), Subalpine Basin (Pavia, 1983).
- Mediterranean Province: Southern Alps (Clari and Pavia, 1980; Della Bruna and Martire, 1985).

3.2. *Pseudoteloceras croisillense* gen. et sp. nov.

Figs. 3–6 7/A–H and 8/A–F–H and 8/A–F
Macroconchs [M]

v 1847 *Ammonites Blagdeni*, Sowerby – d'Orbigny, 1842–1851, p. 396, pl. 132.

1850 *Ammonites Blagdeni*, Sow. – Morris and Lycett, p. 110, pl. 14, fig. 3.

? 1907 *Stepheoceras Blagdeni* – Haug, p. 1008.

1933 *Teloceras* sp. – Arkell, p. 221.

1976 *Teloceras* (T.) *blagdeniformis* (Roché) – Parsons, p. 131 (CP2965, figured by Parsons, 2006, pls. 3–4, unpublished manuscript).

1976 *Teloceras* (T.) *blagdeniformis* (Roché) – Parsons, p. 134 (CP2555, figured by Parsons, 2006, pl. 10, fig. 1 as *Teloceras labrum*, unpublished manuscript).

v 1983 *Kumatostephanus* (*Stemmatoceras*) sp. – Pavia, p. 108, pl. 17, figs. 1–3.

v 1990 *Teloceras labrum* Buckman – Callomon and Chandler, p. 99, pl. 4, fig. 1.

v 1993 *Teloceras*? sp. – Pavia in Fischer, 1993, p. 120, pl. 43, fig. 1, pl. 44, fig. 1.

? 1996 *Kumatostephanus* (*Stemmatoceras*) sp. – Gauthier et al., p. 33.

v 2010 "*Stemmatoceras*" *blagdeni* – Pavia and Martire, p. 77.

v 2013 "*Teloceras Blagdeni* (sensu d'Orbigny)" – Pavia et al., p. 141.

v 2015 ?*Stemmatoceras* nov. sp. 1 – Pavia et al., p. 10, fig. 12.

v 2015 *Teloceras* cf. *labrum* (S. Buckman) – Chandler and Whicher, pl. 35, fig. 1.

non 2006 *Teloceras blagdeniforme* (Roché) – Parsons, pls. 11–12 (unpublished manuscript) = *Pseudoteloceras geometricum* (Maubeuge).

Microconch [m]

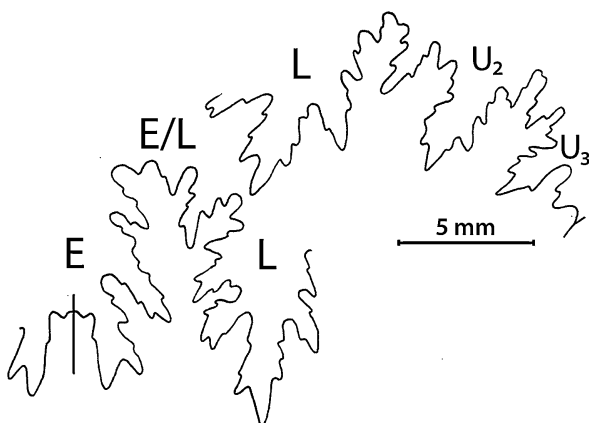


Fig. 4. Suture lines of *Pseudoteloceras croisillense* gen. et sp. nov. A. Paratype MGPT-PU112505 [m]. Chaudon section Bed 395.

? 1954 *Normannites* (*Gerzenites*) *crassicosatus*, Westermann, p. 227, pl. 19, figs. 1–2, non pl. 18, fig. 6 = holotype of *Platystomites crassicosatus* (Westermann).

v 1983 *Gerzenites* (*Platystomites*) *postrugosus* (Westermann) – Pavia, p. 139, pl. 26, figs. 1–3, 4–6.

Diagnosis. Macroconchs (adult diameter over 360 mm): evolute subcadicones with trapezoidal whorl-section, feebly arched venter, spiniform to large tubercles at the trifurcation point and straight secondary ribs. Microconchs (diameter up to 60 mm): subcadicones with rounded whorl-section and pointed to reduced tubercles at the bifurcation point with intercalary ribs.

Etymology. The species is named basing on the section of Croisilles, some four kilometres south of Les-Moutiers-en-Cinglais in Calvados (NW France).

Nomenclatural status. This species has been recorded with the name *Teloceras* (*T.*) *blagdeniforme* (Roché) by Mouterde (1953) from the Humphriesianum Zone of the French Central Massif and by Parsons (1976) from the Romani Subzone of Sherborne in Dorset, based on the references in the text of Roché (1939) to d'Orbigny's figure and description (see Parsons, 2006, unpublished manuscript). However, Pavia (1983, p. 109) stated that d'Orbigny's specimen cannot be regarded as the type of the species *blagdeniforme* because Roché (1939, p. 236) based its discussion on a particular ammonite “J'en figure un de très grande taille qui provient de la Ste Baume, dans mon étude sur les « couches à Cad. Blagdeni du Mont d'Or Lyonnais »”; this ammonite was described in detail and figured in a paper already listed “sous presse” in 1939 but printed four years later (Roché, 1943) because of the war. Such a delay does not prevent acceptance of Roché's original description made on a fossil in the hands of the author that is different from d'Orbigny's specimen, as discussed below. In conclusion, we confirm the proposition of Pavia (1983, p. 109) that the lectotype of *Teloceras* (*Paviceras*) *blagdeniforme* (Roché) is the specimen figured by Roché (1943, pl. 2, fig. 1), whereas d'Orbigny's specimen is free of any nomenclatural charge and may be used as holotype of the new taxon *Pseudoteloceras croisillense* gen. et sp. nov.

Holotype. Specimen MNHN.F.R04116 (formerly MHNP-2139c in d'Orbigny's Collection) housed in the Museum d'Histoire Naturelle de Paris, the single specimen cited by d'Orbigny (1847 in 1842–1851: cf. Pavia in Fischer, 1993) coming from the area of Les-Moutiers-en-Cinglais (Fig. 3).

Locus typicus. D'Orbigny (1847 in 1842–1851, p. 396) did not give any indication useful to identify the type-locality of the holotype, except a general reference to the area of Les-Moutiers-en-Cinglais in Calvados. However, by lithofacies and preservational features, the fossil may be referred to bed 6 of the section described by Pavia et al. (2015) at “Les Fours à Chaux” (49°00'28.59"N and 0°26'02.91"E) in the municipality of Croisilles, just south of Moutiers. The large pre-adult paratype collected from bed 6 of the Croisilles section (Fig. 5) adds further information in defining the formal statement of the species: it exactly fits with the holotype's morphological features and the lithofacies of their internal moulds are the same. The site of Les Fours à Chaux at Croisilles is thus here indicated as the most probable type-locality of *Pseudoteloceras croisillense* gen. et sp. nov.

Stratum typicum. The resedimented ammonites (*Chondroceras evolvenscens*, *C. gervillii* and *Poecilomorphus cycloides* in Pavia et al., 2015) allow reference of Bed 6 of the section Les Fours à Chaux to the upper part of the Romani Subzone, Humphriesianum Zone, lower Bajocian.

Paratypes. Specimens MGPT-PU112498 [M] from Maizet and MGPT-PU112523 [M] from Croisilles. Twenty specimens from the section of Chaudon are considered as paratypes too: [M] MGPT-PU112501–112504, MGPT-PU112506–112507, MGPT-PU112515, MGPT-PU112517–112519, MGPT-PU112525; [m] MGPT-PU112505, MGPT-PU112508–112514, MGPT-PU112516.



Fig. 5. A large, pre-adult specimen of *Pseudoteloceras croisillense* gen. et sp. nov. in the lower part of Bed 6 in the section of Les Fours à Chaux (cf. Pavia et al., 2015). Unfortunately, vertical faulting broke the fossil: it was possible to recover only the external whorl that is presently stored with code MGPT-PU112523. Asterisk marks the beginning of the body-chamber.

Material. Three specimens of the lower Humphriesianum Zone, Romani Subzone from the “Oolithe ferrugineuse de Bayeux” Formation: the holotype MHNP-2139c and the paratypes MGPT-PU112523 and MGPT-PU112498 respectively from Croisilles and Maizet. Further specimens come from an interval of the “Marno-calcaires à *Cancellophycus*” Formation of the Digne area aged to early Humphriesianum Chron, latest Romani Subchron (Pavia, 1983): 1 [M] and 1 [m] at the section of Feston; 37 [M] and 41 [m] at the section of Chaudon. The largest specimens in collection measure 265 mm diameter (MGPT-PU112506, Fig. 6) and 290 mm in diameter (MGPT-PU112519) both from bed 395 of the Chaudon section (Pavia, 1983). We also took account of the fossil CP2965 from Dorset cited by Parson (1976, p. 131) and figured on Plates 3–4 of his unpublished manuscript (Parsons, 2006) that provides information useful for a more complete and documented description of the new species.

Measurements. See Table 1.

Description. The material from the Subalpine Basin comprises macro- and microconchs that allow description of both dimorphs of the new species.

Adult peristomes of macroconchs are unknown but growth lines of largest shells are concave (cf. Callomon and Chandler, 1990); the length of the body-chamber exceeds one whorl. The coiling is evolute with umbilicus a bit more than 50%. Shells are subcadiconic with subtrapezoidal whorl section ($W/H = 2.3$ to 1.9 on the holotype), depressed venter gently arched in the middle and plan at the ventrolateral shoulder, flanks regularly sloped to

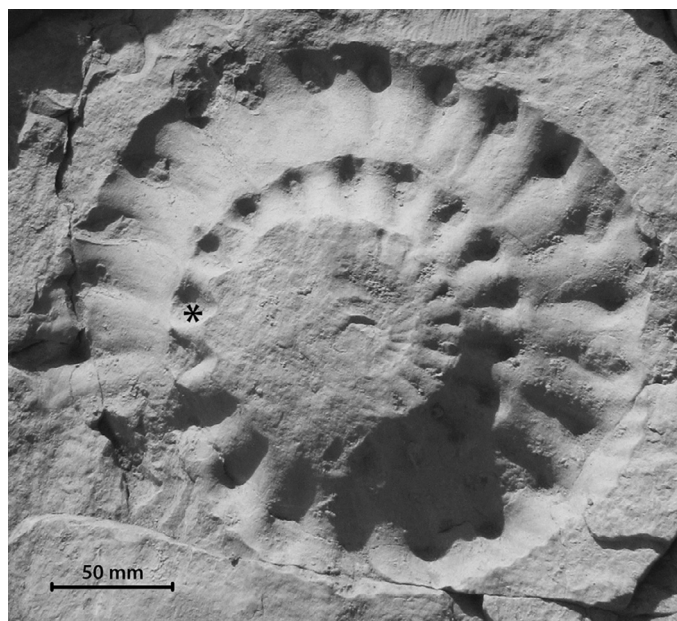


Fig. 6. A large external mould of *Pseudoteloceras croisillense* gen. et sp. nov. from Bed 395 of the section of Chaudon, Digne area. The equivalent internal mould is stored with code MGPT-PU112506 [M]. Asterisk marks the beginning of the body-chamber.

the spiral centre without any umbilical wall; there is no evidence of uncoiling of the whorl (egression) in any studied specimens (Fig. 6) even at 290 mm diameter. Ornament consists of coarse, acute and sinuous primary ribs, trifurcate with additional intercalary ribs. Secondary ribs are blunt, feebly convex to straight on the venter (Fig. 7/A and 7/D); they fade on the adult body-chamber. Tubercles of macroconchs are spiniform in the inner to medium whorls, whereas they enlarge and modify the lateral outline of the shell on the outer whorls (Figs. 3 and 7/C).

On microconchs, the body-chamber is 210–220° and bears long, not distally enlarged lateral lappets (Fig. 8/E). Whorl section is subcircular with regularly arched venter and maximum width on the mid-flanks; the body-chamber becomes more and more egressed. Ribbing is sharp with sinuous primaries and gently projected secondaries; the latter become prominent on the outer body-chamber. Tubercles are pointed, but may be reduced to a

bulge on the bifurcation point. The septal suture is visible on pyritized internal mould of microconchs from Chaudon (Figs. 4 and 8/B). It shows narrow and deeply incised E/L saddle, large and slightly oblique lateral lobe lying on the ventrolateral shoulder and on the umbilical seam in the inner whorls, L/U saddle larger than E/L and symmetrically bipartite by a wide U_2 , U_3 clearly retracted and deep as U_2 ; near the umbilical seam a short U_n is clearly visible.

Discussion. *Pseudoteloceras croisillense* gen. et sp. nov. shows a certain degree of ornament variability on macroconchs: the specimens from Chaudon show a higher density of primary ribs, whereas in Dorset specimens the secondary ribs are less accentuated becoming obsolete on the venter (Callomon and Chandler, 1990; Chandler & Whicher, 2015). Consistent in all specimens is the absence of umbilical walls, the proportional reduction of the whorl-width in the outer whorls that does not increase in the last ontogenetic growth phase, and the furcation rate (Ne/Ni) with average value 3.4.

Regarding the microconchs, the dimorphic status of *P. croisillense* gen. et sp. nov. is indicated by the co-occurrence of the macro- and micro-counterparts in the same beds of the Chaudon section (see Pavia, 1983, table IIIb; confirmation by 2015 studies on the same section). Pavia (1983, p. 139) identified these microconchs as *Gerzenites* (*Platystomites*) *postrugosus* (Westermann, 1954), but Ohmert et al. (1995, p. 82) assumed that Westermann's taxon fits more appropriately *Stemmatoceras frechi* (Renz, 1904) on the basis of well-preserved specimens coming from the Hebridica Subzone of Lörrach, SW Germany.

Regarding the references in the synonymy list, the holotype of *Teloceras labrum* Buckman, 1922 (in 1909–1930) comes from the so-called *Epalxites* hemera that refers to the upper part of the Humphriesian Zone according to Buckman's Type Ammonites (1925 in 1909–30, V, p. 74). It shows a more arched ventral side and the suture line is typical of the genus *Teloceras*: L narrow, 2nd lateral saddle asymmetrically divided, little retraction of the umbilical lobe. Thus, the specimen cited by Callomon and Chandler (1990, p. 99; see also Chandler & Whicher, 2015) as *Teloceras labrum* cannot be attributed to Buckman's taxon on both morphological and stratigraphical grounds; it fits *Pseudoteloceras croisillense* gen. et sp. nov. The lectotype of *Teloceras* (*Paviceras*) *blagdeniforme* (Roché, 1939: see above) comes from the “couches à Cad. Blagdeni du Mont d'Or Lyonnais” (Roché, 1939, p. 206), i.e. the uppermost Humphriesianum Zone; its whorl-section is subrectangular on the phragmocone and becomes elliptical in the last whorl; the venter is

Table 1

Measurements for *Pseudoteloceras croisillense* gen. et sp. nov. Some parameters on Chaudon specimens cannot be taken because of deformation by compaction of the composite moulds, except occasionally as for MGPT-PU112510 and MGPT-PU112511. Paratype MGPT-PU112517 refers to Pavia' paper (1983, pl. 26/2). Status of specimens: h = holotype, p = paratype. M = Macroconchs, m = microconchs. Figures in [] refer to maximum D. Measurements of whorl-width are taken on the interspace between tubercles or (in brackets) on the tubercles.

Specimens	Figures		D mm	H mm	h	W mm	w	U mm	u	W/H	Ni/2	Ne/2	Ne/Ni
h – MNHN.F.R04116	Fig. 3	[M]	134.0	36.0	.27	67.0 (74.0)	.55 (.50)	67.0	.50	1.9 (2.1)	8	28	3.5
			106.0	27.0	.25	61.0 (65.0)	.61 (.56)	52.0	.50	2.3 (2.4)	7	24	3.4
– CP2965	–	[M]	140.0	44.0	.31	– (81.0)	– (.58)	72.0	.52	– (1.8)	8	26	3.3
			121.0	42.0	.34	– (70.0)	– (.58)	65.0	.54	– (1.7)	7	42	3.2
p – PU112501	Fig. 6G	[M]	116.6 [126]	33.6	.30	–	–	ca .63	ca .54	–	10	36	3.6
p – PU112502	Fig. 6H	[M]	85.0	25.4	.30	–	–	38.3	.48	–	10	35	3.5
p – PU112506	Fig. 5	[M]	ca 150 [165]	ca 42	ca .28	–	–	ca 81	ca .54	–	11	37	3.4
p – PU112507	Fig. 6F	[M]	ca 50	ca 17	ca .34	–	–	ca 25	ca .50	–	10	35	3.5
p – PU112525	Fig. 6E	[M]	39.7	12.8	.32	–	–	18.1	.46	–	10	32	3.2
P – PU112505	Fig. 3	[m]	30.5 [45]	9.4	.32	ca 14.0	47	13.2	.43	ca 1.3	11	27	2.5
p – PU112508	Fig. 6D	[m]	ca 46.5 [50]	ca 14	ca .30	–	–	ca 19	ca .40	–	11	23	2.1
p – PU112509	Fig. 7A	[m]	ca 56 [70]	ca 20	ca .38	–	–	ca 23.5	ca .42	–	10	26	2.6
p – PU112510	Fig. 7C	[m]	44.3	14.7	.33	19.8 (21.0)	.47 (.45)	17.4	.39	1.3 (.1.4)	11	27	2.5
p – PU112511	Fig. 7B	[m]	27.5 [40.7]	8.5	.31	13.3	.48	11.4	.41	1.6	11	24	2.2
p – PU112513	Fig. 7E	[m]	48.1 [51]	ca 15.8	.33	–	–	ca 20.3	ca .42	–	11	23	2.1
p – PU112516	Fig. 7F	[m]	ca 46.5 [48.4]	ca 14.3	ca .31	–	–	ca 19.5	ca .42	–	11	23	2.1
p – PU112517	Pavia' 83	[m]	ca 43 [51]	ca 13.6	.32	–	–	ca 18.1	ca .42	–	13	26	2.0

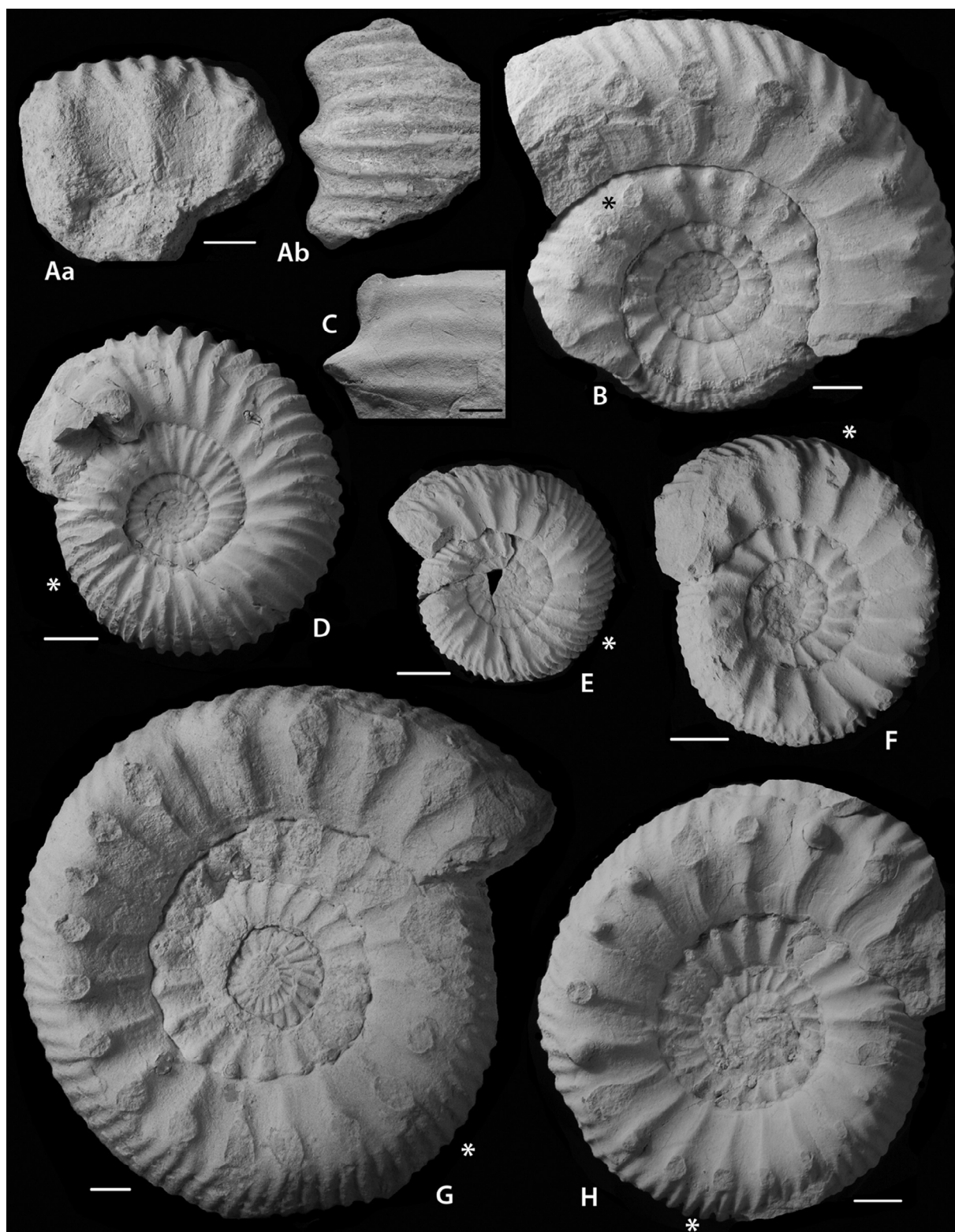


Fig. 7. A–G: *Pseudoteloceras croisillense* gen. et sp. nov. [M] et [m].

A: paratype MGPT-PU112498 [M], Maizet section, Bed 4. B: paratype MGPT-PU112503 [M], Chaudon section, Bed 391. C: paratype MGPT-PU112504 [M], Chaudon section, Bed 391. D: paratype MGPT-PU112508 [m], Chaudon section, Bed 395 (cf. Pavia, 1983, pl. 26, fig. 1). E: paratype MGPT-PU112525 [M], Chaudon section, Bed 395. F: paratype MGPT-PU112507 [M], Chaudon section, Bed 395. G: paratype MGPT-PU112501 [M], Chaudon section, Bed 395 (cf. Pavia, 1983, pl. 17, fig. 1). H: paratype MGPT-PU112502 [M], Chaudon section, Bed 395 (cf. Pavia, 1983, pl. 17, fig. 2).

Scale bars = 10 mm. Asterisk marks the beginning of the body-chamber.

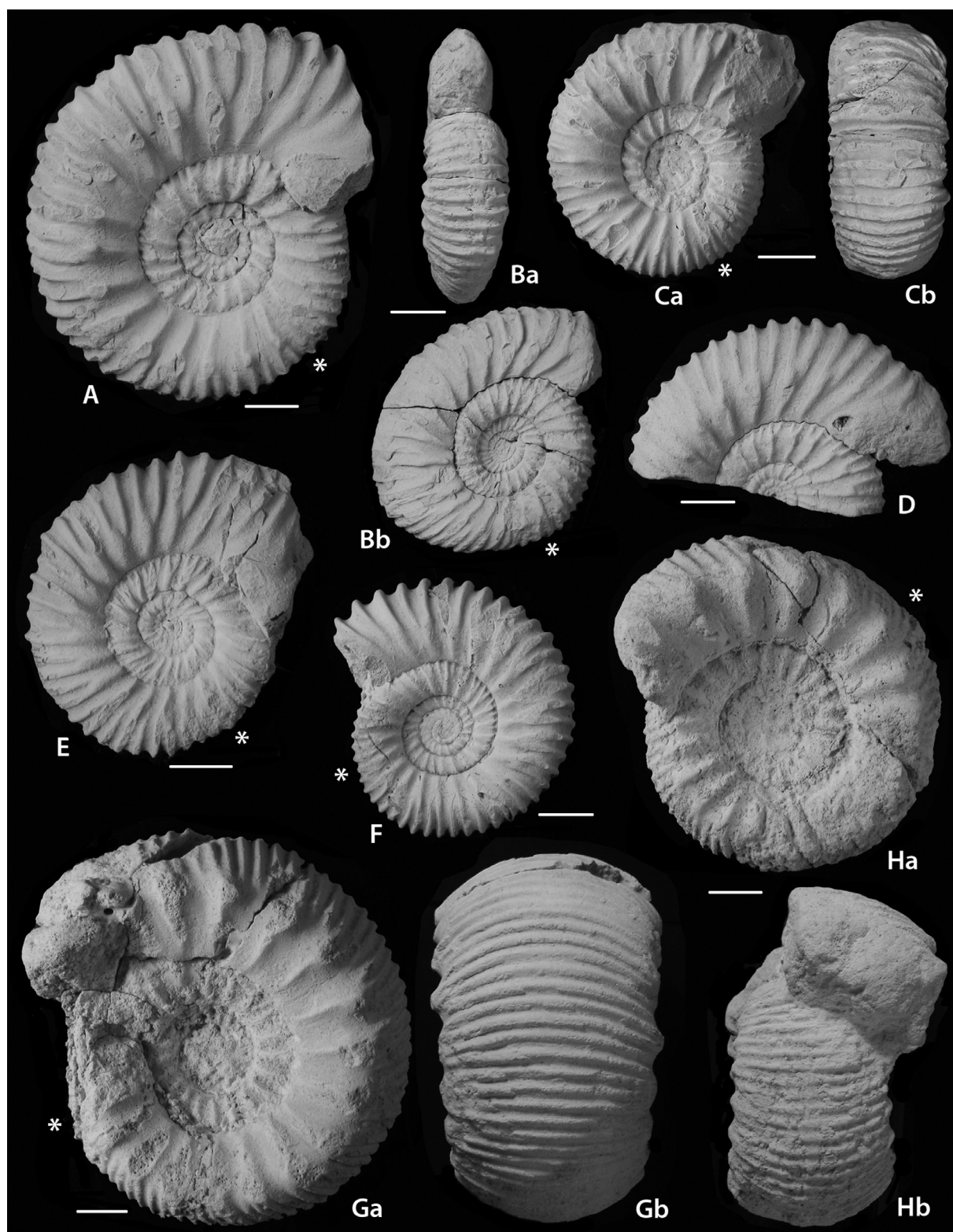


Fig. 8. A–F: *Pseudoteloceras croisillense* gen. et sp. nov. [m].

A: paratype MGPT-PU112509, Chaudon section, Bed 395 (Pavia, 1983, pl. 26, fig. 5). B: paratype MGPT-PU112511, Chaudon section, Bed 395. C: paratype MGPT-PU112510, Chaudon section, Bed 395. D: paratype MGPT-PU112514, Chaudon section, Bed 395. E: paratype MGPT-PU112513, Chaudon section, Bed 395. F: paratype MGPT-PU112516, Chaudon section, Bed 395.

G–H: *Pseudoteloceras maerteni* gen. et sp. nov. [M]

G: holotype MGPT-PU112499, Les Fours à Chaux section, Bed 6. H: paratype MGPT-PU112500, Les Fours à Chaux section, Bed 6. Both specimens collected by L. Maerten. Scale bars = 10 mm. Asterisk marks the beginning of the body-chamber.

Table 2

Measurements for *Pseudoteloceras maerteni* gen. et sp. nov. Status of specimens: h = holotype, p = paratype. M = Macroconchs, m = microconchs. Figures in [] refer to maximum D. Measurements of whorl-width are taken on the interspace between tubercles or (in brackets) on the tubercles.

Specimens	Figures		D mm	H mm	h	W mm	w	U mm	u	W/H	Ni/2	Ne/2	Ne/Ni
h – PU112499	Fig. 7G	M	69.5 [74.4]	23.5	.34	40.9 (44.1)	.63 (.59)	27.2	.39	1.7 (1.9)	10	41	4.1
p – PU112500	Fig. 7H	M	59.4	17.8	.30	35.4 (39.1)	.66 (.60)	23.7	.40	2.0 (2.2)	12	37	3.7

arched; the umbilical egression of the external half of the body-chamber is marked; flanks show well definite umbilical walls; primary ribs are dense and straight with rectiradiate secondaries.

Distribution. *Pseudoteloceras croisillense* gen. et sp. nov. occurs in the upper Romani Subzone, lower Humphriesianum Zone. Its distribution is mainly documented in the North West European Province: Calvados (d'Orbigny, 1847 in 1842–1851; Haug, 1907; Pavia and Martire, 2010; Pavia et al., 2013) and Dorset (Morris and Lycett, 1850; Arkell, 1933; Parsons, 1976; Callomon and Chandler, 1990; Chandler and Whicher, 2015). However, the taxon is common also in the Subalpine Basin (Pavia, 1983) where a *Pseudoteloceras croisillense* Biohorizon may be defined at the upper part of the Romani Subzone (see Conclusions).

3.3. *Pseudoteloceras maerteni* gen. et sp. nov.

Figs. 8/G–H

Macroconch [M]

? 1953 *Teloceras blagdeniforme* Roché – Mouterde, p. 91.

v 1980 *Stemmatoceras “blagdeni”* – Clari and Pavia, p. 88.

? 1985 *Stemmatoceras* sp. nov. 1 – Fernandez-Lopez, p. 290, pl. 31, fig. 1.

? 1994 *Teloceras? blagdeni* (Sowerby) sensu d'Orbigny – Fernandez-Lopez and Mouterde, p. 122.

1996 *Teloceras (Teloceras?) labrum* Buckman – Gauthier et al., p. 34, pl. 1, fig. 2 (non fig. 6).

2006 *Teloceras blagdeniforme* – Parsons, pl. 10, fig. 2 (unpublished manuscript)

v 2015 ?*Stemmatoceras* nov. sp. 2 – Pavia et al., p. 10.

Diagnosis. Moderately evolute subcadicones; depressed, subelliptical whorl-section with short umbilical walls, slightly rounded flanks and arched venter; strong primary ribs, convex secondaries and strong tubercles at the trifurcation point.

Etymology. The species is dedicated to Lionel Maerten (Ver-sur-Mer, Calvados, France) who amicably collaborated in sampling the section Les-Fours-à-Chaux at Croisilles and collected both specimens that compose the type-series of this new taxon.

Holotype. Specimen MGPT-PU112499 housed in the paleontological collections of the Museo di Geologia e Paleontologia of the Torino University. The holotype comes from the base of Bed 6 of the section of Croisilles (Fig. 8/G).

Locus typicus. The type locality of the holotype is the site Les Fours à Chaux (49°00'28.59"N and 0°26'02.91"E) in the municipality of Croisilles, South of Caen in Calvados (Pavia et al., 2015).

Stratum typicum. The resedimented ammonites (*Chondroceras evolvens*, *C. gervillii* and *Poecilomorphus cycloides* in Pavia et al., 2015) allow referring Bed 6 of the section at Les Fours à Chaux to the upper part of the Romani Subzone, Humphriesianum Zone, Lower Bajocian.

Paratypes. Specimen MGPT-PU112500 [M] from Bed 6 of the section of Croisilles, the same place as the holotype.

Material. The holotype MGPT-PU112499 and the paratype MGPT-PU112500, from the Oolithe ferrugineuse de Bayeux Formation, are reelaborated fossils at the base of Bed 6 of the Croisilles section (see Pavia et al., 2015). The lithofacies of their internal moulds is a bioclastic packstone with fine and scattered Fe-ooids that is similar to that of the encasing bed 6 but totally

different from those of the underlying Bed 5; thus the two fossils have to derive from a layer between beds 5 and 6 not recorded in the succession. Bed 5 has been referred to as the lower part of the Romani Subzone (Pavia et al., 2015), so that the holotype and the paratype of *Pseudoteloceras maerteni* gen. et sp. nov. have to be dated at the middle or late Romani Chron.

Measurements. See Table 2.

Description. Both holotype and paratype from Croisilles are immature macroconchs with a short tract of the body-chamber. Suture lines, though not easily detectable, do not show any approximation.

The coiling of macroconchs is moderately evolute with umbilicus at 39–40%. Shells are subcadiconic; the subelliptical whorl section (W/H = 1.7–2.0) shows slightly rounded flanks with inclined umbilical walls, and arched venter. Ornament consists of coarse, sinuous primary trifurcate ribs with additional free secondaries regularly intercalated each triple bundle. Secondary ribs are blunt, gently projected forward. Tubercles lie on the ventrolateral shoulder, are pointed in the inner whorls on the umbilical seam and enlarge on the last whorls. The septal suture of these macroconchs cannot be drawn due to unfavourable preservation of the internal moulds. No microconch counterpart has been identified in the field or in the literature.

Discussion. The morphological features confirm that the definition of *Pseudoteloceras maerteni* gen. et sp. nov. as a new species is clear, though the sample is small. The diagnostic features of the species consist of a narrow umbilicus compared with conspecific taxa (39–40 vs 48–40), the degree of forward projection of the secondary ribs and the subelliptical whorl section with arched venter and short umbilical walls. On the other hand, the subcadiconic architecture with just slightly rounded flanks and the tubercles on the umbilical seam allow this species to be placed in *Pseudoteloceras* gen. nov., rather than in *Stemmatoceras* that is distinguished by its elliptical whorl-section with regularly rounded flank and venter and by blunt tubercles often reduced to a bulge at the furcation point. However, these morphological features assign *P. maerteni* gen. et sp. nov. to an intermediate position in the phyletic trend from *Stemmatoceras* to *Pseudoteloceras* gen. nov.

Distribution. *Pseudoteloceras maerteni* gen. et sp. nov. is present in different sites of the West-Tethys domain, from NW European Province (Gauthier et al., 1996; Parsons, 2006) to the Submediterranean (Mouterde, 1953; Fernandez-Lopez, 1985; Fernandez-Lopez and Mouterde, 1994) and the Mediterranean provinces (Clari and Pavia, 1980). These references confirm our view that this species occurs in the lower Humphriesianum Zone.

3.4. *Pseudoteloceras boursicoti* gen. et sp. nov.

Figs. 8/A–Dv 2013 *Teloceras labrum* – Pavia et al., p. 141.

v 2015 *Teloceras* cf. *labrum* (S. Buckman) – Chandler and Whicher, pl. 34, fig. 5.

Diagnosis. Evolute cadicones in the inner whorls; trapezoidal whorl-section with rounded umbilical walls, slightly rounded flanks and feebly arched venter; strong and sharp primary ribs, convex secondaries projected forward; spiniform, directed backwards tubercles at the trifurcation point.

Etymology. The species is dedicated to Pierre-Ives Boursicot (Villedieu-la-Blouère, Maine-et-Loire, France) who collected the holotype in the temporary outcrop of Evrecy, South of Caen, whose succession is similar to that of Maizet (Pavia et al., 2013).

Holotype. Specimen MGPT-PU112524 housed in the paleontological collections of the Museo di Geologia e Paleontologia of the Torino University (Fig. 9/A). The holotype is a resedimented fossil coming from a packstone with randomly dispersed fine Fe-ooids of

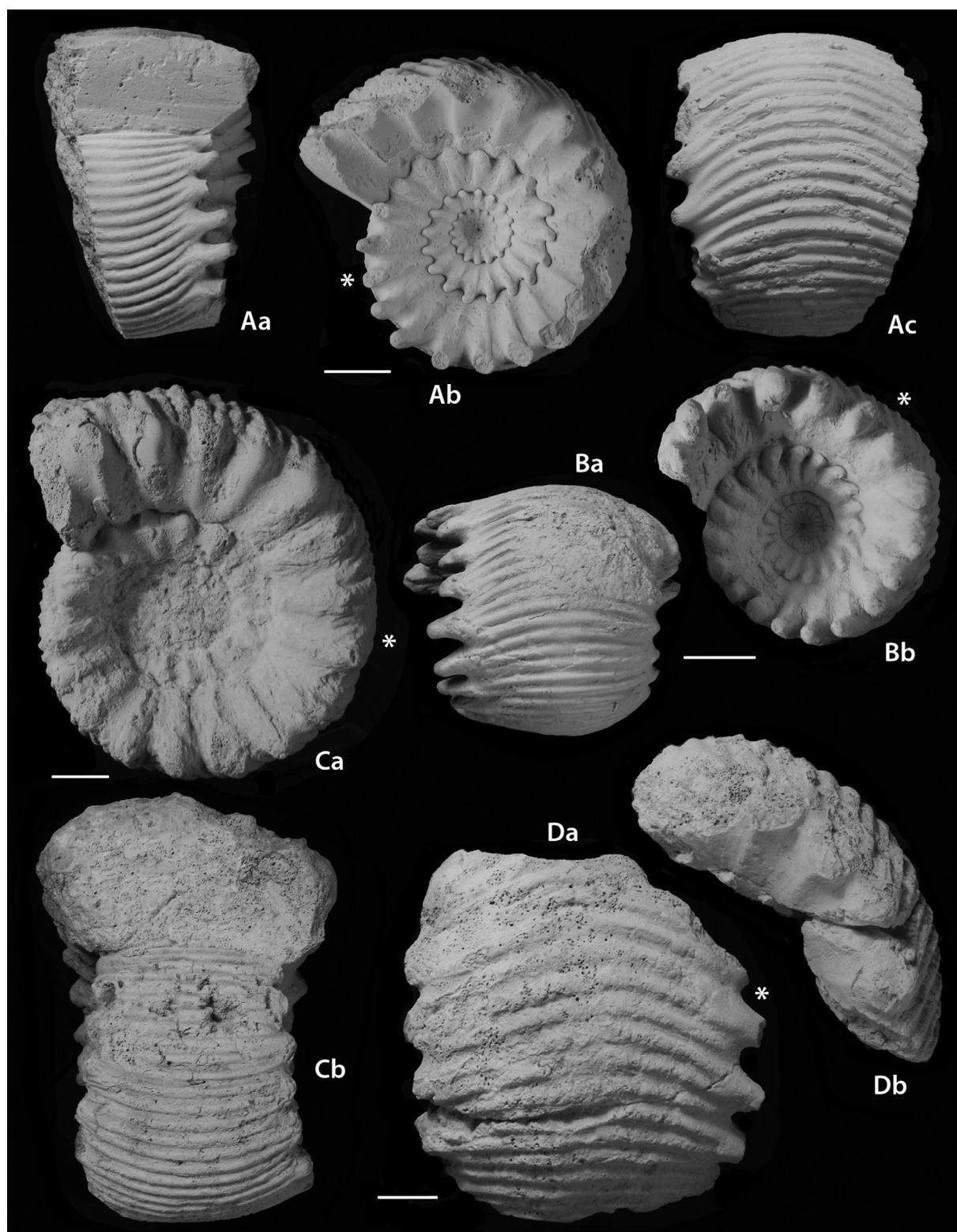


Fig. 9. A–D: *Pseudoteloceras boursicoti* gen. et sp. nov. [M].

A: holotype MGPT-PU112524, Evrecy section, specimen collected by Pierre-Ives Boursicot. B: paratype LM-541, Maizet section, Bed 4, specimen collected by Lionel Maerten.

C: paratype MGPT-PU112520, Bretteville section, Bed 7. D: paratype MGPT-PU112521, Maizet section, Bed 4.

Scale bars = 10 mm. Asterisk marks the beginning of the body-chamber.

Table 3

Measurements for *Pseudoteloceras boursicoti* gen. et sp. nov. Status of specimens: h = holotype, p = paratype. M = Macroconchs, m = microconchs. Figures in [] refer to maximum D. Measurements of whorl-width are taken on the interspace between tubercles or (in brackets) on the tubercles.

Specimens	Figures		D mm	H mm	h	W mm	w	U mm	u	W/H	Ni/2	Ne/2	Ne/Ni
h – PU112524	Fig. 8A	[M]	46.6 [52.1]	14.3	.31	34.4 (39.8)	.85 (.66)	25.5	.55	2.4 (2.8)	9	25	2.8
p – PU112520	Fig. 8C	[M]	68.0	21.1	.31	44.1 (51.4)	.76 (.65)	31.0	.46	2.1 (2.4)	10	35	3.5
			54.0	16.3	.30	38.0 (43.4)	.80 (.70)	21.5	.40	2.3 (2.7)	9	35	3.8
p – LM-541	Fig. 8B	[M]	36.3	10.7	.29	28.8 (34.2)	.94 (.71)	17.1	.47	2.4 (3.2)	9	28	3.1
p – PU112521	Fig. 8D	[M]	–	21.3	–	55.0 (62.0)	–	–	–	2.6 (2.9)	–	–	3.0

the section of Evrecy, whose lithofacies is equivalent to that described in Bed 4 of the section of Maizet (Pavia et al., 2013, p. 141).

Locus typicus. The type locality of the holotype is the northern sector of the Evrecy municipality (49°06'04.45"N and 0°29'52.59"E) where a temporary trench was opened in 2008 on a building site; thus at present no section is visible.

Stratum typicum. The resedimented ammonites associated to the holotype (*Chondroceras evolvenscens*, *C. gervillii* and *Poecilomorphus cycloides*: Boursicot, pers. comm.) allow referring the source bed to the Lower Bajocian, Humphriesianum Zone, upper Romani Subzone by comparison with the Maizet section.

Paratypes. Specimen MGPT-PU112520 from Bretteville, specimens LM-541 and MGPT-PU112521 from Maizet.

Material. This new taxon is represented only by macroconchs; microconchs are hitherto unknown. The type-series totals five specimens of the lower Humphriesianum Zone, Romani Subzone from the Oolithe ferrugineuse de Bayeux" Formation: the holotype from Evrecy (MGPT-PU112524), a reelaborated fossil from Bed 7 at Bretteville (MGPT-PU112520), a resedimented specimen and a reelaborated one from Bed 4 at Maizet, respectively LM-541 (plaster mould MGPT-PU112522) and MGPT-PU112521, a resedimented specimen from Bed 6 at Croisilles (MGPT-PU112525). The resedimented specimens come from a bed in which the ammonite assemblage is characterized by *Chondroceras evolvenscens*, *C. gervillii* and *Poecilomorphus cycloides*, and refers to the Romani Subzone. The two reelaborated specimens (MGPT-PU112520 and MGPT-PU112521) do not conflict with this biostratigraphical location because (1) the lithofacies of their internal moulds are equivalent to that of Bed 7 at Bretteville, Bed 4 at Maizet and Bed 6 at Croisilles, (2) MGPT-PU112520 from Bed 7 of Bretteville is regarded as a fossil reelaborated from the underlying Bed 6, and MGPT-PU112521 from Bed 4 at Maizet (erroneously stated to be from Bed 3 by Pavia et al., 2013, p. 141) is interpreted as derived from a directly underlying bed not recorded in the stratigraphical succession, but referred to the Romani Subzone.

Measurements. See Table 3.

Description. The coiling is evolute with umbilicus that varies from 46 to 55% during growth. Shells are cadiconic; the trapezoidal whorl-section (W/H = 2.1 to 2.8) shows slightly rounded flanks with short umbilical walls; the venter is flattened, just a little arched in the middle and pagodiform on the ventrolateral shoulders due to the long tubercles; no evidence of umbilical egression at the last preserved whorl. Ornament consists of spaced, slightly sinuous, trifurcate primary ribs with additional free secondaries intercalated each triple bundle; primaries are feeble on the umbilical wall and increase in relief towards the tubercles. Secondary ribs are blunt and bundle on tubercles; they regularly project forward. Tubercles lie on the ventrolateral shoulder, are pointed in the inner whorls on the umbilical seam and enlarge on the pre-adult stage; on specimens with the neomorphic shells, the tubercles develop spines turned backward (Fig. 9A and 9B). The septal suture is hardly visible because of shell cover and bad preservation of internal moulds; nevertheless, it is composed of a narrow and deeply incised E/L saddle, large, slightly oblique lateral lobe located on the marginal part of the flattened venter,

shallow L/U saddle symmetrically bipartite by a wide U₂, U₃ deeply retracted.

Discussion. The convexity of the secondary ribs on the venter is particularly accentuated in the holotype of *Pseudoteloceras boursicoti* gen. et sp. nov. This feature marks a clear difference in comparison with the congeneric species. Another distinctive characteristic is represented by the spiniform tubercles directed backwards that produce a pagodiform outline of the venter. The variability of the species is further expressed by the ratio of whorl width to whorl height (W/H 2.1–2.8 with the holotype in a middle position) and the furcation degree of the primary ribs (Ni/Ne 2.8–3.7).

Distribution. The type-series of *Pseudoteloceras boursicoti* gen. et sp. nov. comes from the lower Bajocian, Humphriesianum Zone, Romani Subzone of the southern area of Caen, Calvados, NW France. The coeval record from Dorset (Chandler & Whicher, 2015) certifies a larger distribution of the species within the north-western European lower Humphriesianum Zone.

4. Conclusions

Pseudoteloceras gen. nov. represents a distinct phyletic lineage within the subfamily Stephanoceratinae. Its morphological features displayed in the inner whorls of the macroconchs are similar to those of the best known genus *Teloceras*. The differences from *Teloceras* are mainly morpho-structural and biochronological. *Pseudoteloceras* gen. nov. displays (1) subcadicones with planorbic outer whorls, regularly decreasing whorl-width towards the adult body-chamber without umbilical egression up to 300 mm diameter, (2) wider spaced primary ribbing, (3) convex secondary ribbing sometimes highly projected forward in the mid-venter, (4) simpler suture line. Moreover, *Pseudoteloceras* gen. nov. is older than *Teloceras*: the biochronologic range of *Pseudoteloceras* gen. nov. is limited to the early Humphriesianum Chron in the Western Tethys as supported by the literature and the new species, whereas the oldest *Teloceras* s.l. are recorded from the topmost Umbilicum Subzone.

The phyletic origin of *Pseudoteloceras* gen. nov. is likely to occur in the *Stemmatoceras* group of the Hebridica Subzone, upper Propinquans Zone, of the central-European lower Bajocian. In particular, we refer to the specimen *Stemmatoceras* sp. described by Ohmert (1988, p. 339, pl. 8, fig. 9; 1990, p. 123, pl. 1, fig. 2; original by Scholz, 1966) from the "Pinguis Subzone" of Glems bei Reutlingen, Germany, that shows an "unusual" subtrapezoidal whorl-section, depressed venter and pointed tubercles at the ventrolateral shoulder. The following step, with subcadiconic appearance and *Teloceras*-like morphology, is represented by *Pseudoteloceras geometricum* (Maubeuge). *P. boursicoti* gen. et sp. nov. may be regarded as the end term of a phyletic trend developed during the late Romani Subzone that finishes with the most accentuated *Teloceras*-like architecture in the inner whorls.

Pseudoteloceras geometricum is interpreted here as the earliest species of the new lineage. The three new species described in detail may be sequentially arranged in the upper Romani Subzone. The subcadicones with subelliptical whorl-section of *Pseudoteloceras maerteni* gen. et sp. nov., possibly located to the middle Romani

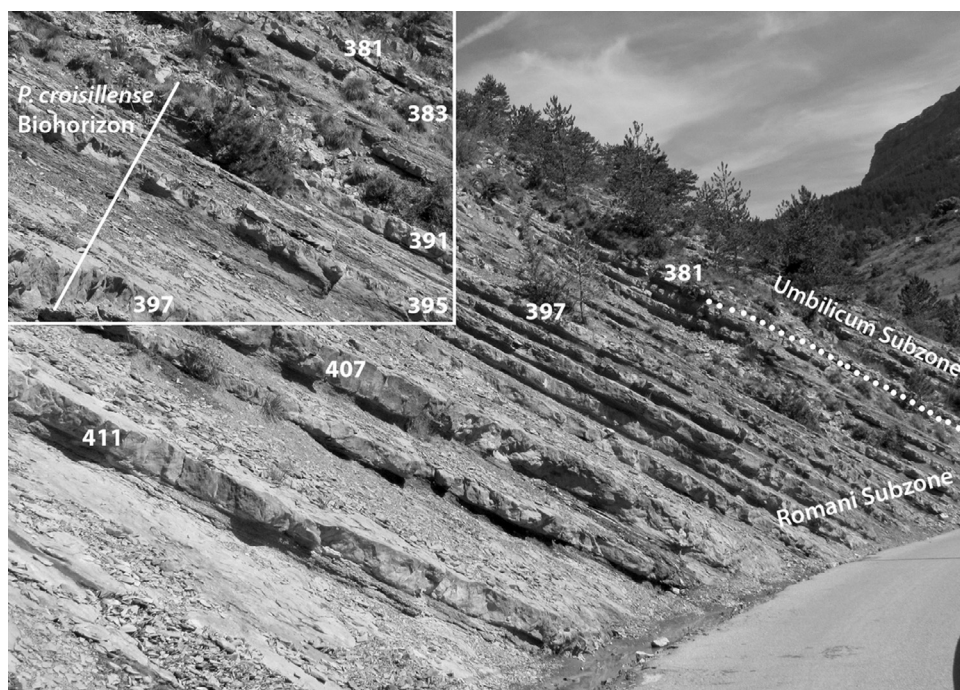


Fig. 10. The *Pseudoteloceras croisillense* Biohorizon (1.5 m thick) in the upper part of the Romani Subzone of the section of Chaudon, Digne area: beds 397 to 387. Bed 381 marks the beginning of the Umbilicium Subzone. 2015 research on the section did not confirm the presence of *P. croisillense* gen. et sp. nov. in the stratigraphical interval from beds 386 to 382, at the top of the Romani Subzone, as indicated by Pavia (1983, Tab IIIb).

Subzone, anticipated the definitive trapezoidal and cadiconic architecture of the inner whorls shown by *Pseudoteloceras croisillense* gen. et sp. nov. and *Pseudoteloceras boursicoti* gen. et sp. nov. In general, the latter three species refer to the upper Romani Subzone, the *Gervillii* Horizon (Fernandez-Lopez and Mouterde, 1994; Rioult et al., 1997, p. 49). The results from the section of Chaudon in the Subalpine Basin (Pavia, 1983, tab. IIIb) are more precise and reduce the distribution of *P. croisillense* gen. et sp. nov. to a relatively thin set of beds in the upper part of the Romani Subzone, so that it is possible to define a local *Pseudoteloceras croisillense* Biohorizon (Fig. 10) whose correlation potential needs to be confirmed in other areas of the western Tethys.

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