

THE AMMONITES OF THE BIFRONS ZONE (TOARCIAN,
LOWER JURASSIC) FROM MIHAILOVIĆI (NORTHERN
MONTENEGRO)

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Abstract

The base of the red pelagic nodular limestones exposed near the Mihailovići Pass (Northern Montenegro) yielded condensed Toarcian fossil assemblage consisting uniquely of ammonites. The ammonites were collected from marker horizon associated with prominent hardground surface. This assemblage is composed both of species of worldwide distribution and proper Tethyan dispersal. It includes frequent *Lytoceras* and common *Phylloceras* and *Ammonitina*. The latter allowed the biostratigraphic definition of the fossiliferous horizon as mid-Bifrons Subzone of the Lower Toarcian Bifrons Zone. Thirteen ammonite taxa were studied: *Phylloceras heterophyllum* (Sowerby), *P. prinzi* Géczy, *Calliphylloceras nilssoni* (Hebert), *Lytoceras toarcense* Rulleau, *Nodicoeloceras angelonii* (Ramaccioni), *Hildoceras lusitanicum* Meister, *H. bifrons* (Bruguière), *Cingolites* aff. *picenus* Sassaroli & Venturi, *Osperleioceras subexaratum* (Bonarelli), *Harpoceras mediterraneum* Pinna, *Phymatoceras anomalum* Merla, *Ph. gr. narbonense* Buckman and *Ph. cf. formosum* Rulleau & Elmi. One specimen was defined as *Harpoceras* sp. n. since it did not match any species from the literature, but might be erected as a new specific name if further materials appear.

Key words: Lower Jurassic, Toarcian, Bifrons Zone ammonites, Montenegro

Introduction. The Mihailovići section crops out at 6 km ENE of the town of Pljevlja (Northern Montenegro), near the Montenegro–Serbian border (Fig. 1A). This section has been treated several times earlier (e.g. RAMPNOUX) [1], since it has won the recognition of a key-Lower–Middle Jurassic sequence in Montenegro and the adjacent areas. Each of the previous works yielded contributions, but

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despite these profusions, we have recently proposed new data on the facies and stratigraphic distribution of the fossils (foraminifers and ammonites) from Mihailovići [2]. The section consists of highly-condensed and discontinuous pelagic and platform slope carbonates spanning from the Sinemurian to the Bajocian (Fig. 1B). The Toarcian part of the sequence is a typical example of the facies *ammonitico rosso*. It is composed of 3-m-thick red nodular limestones lying by prominent hardground surface upon 15-m-thick grey crinoidal-bioclastic limestones of Sinemurian age. Another hardground sets off the Toarcian, from 3-m-thick pale-red and fawn-grey micritic limestones that were referred to the Bajocian [2]. The top of the section is reduced by fault on which it comes into contact with serpentinites of the Diabase-radiolarite Formation.

In this framework, the Mihailovići sequence includes two major sedimentary brakes (missing the Pliensbachian-basal Toarcian, and the Aalenian) and two minor gaps (within the Sinemurian and probably around the Lower–Upper Toarcian transition) [2]. The ammonites considered herein came from a marker horizon related to the hardground surface at the base of the Toarcian. It is associated with a flooding event that has been revealed to be of more than local scale [2]. The ammonite assemblage contains species of worldwide distribution, as well as examples characteristic of the Tethyan localities, including common Phylloceratina, frequent Lytoceratina and a high proportion of Ammonitina. The latter enabled the ammonite-bearing level to be referred to a narrow biostratigraphic interval matching the mid-Bifrons Subzone of the Lower Toarcian Bifrons Zone [3].

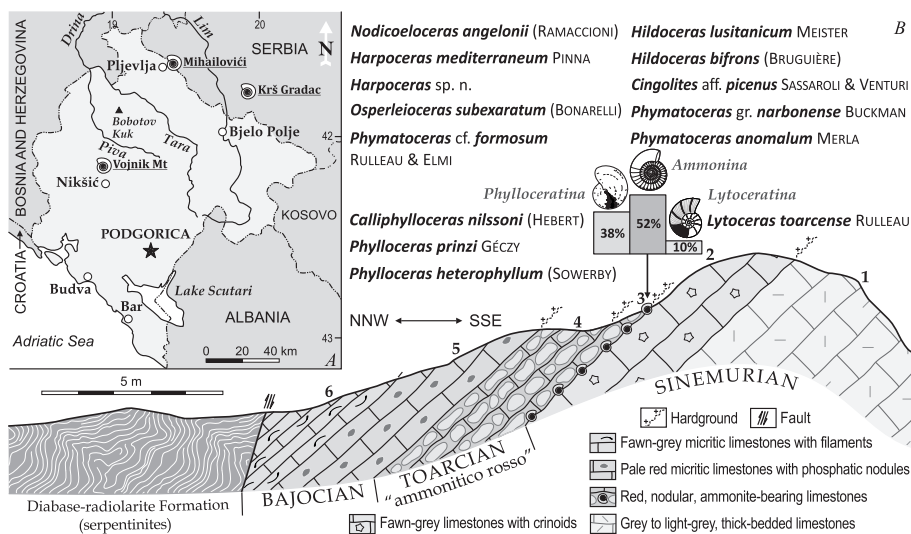


Fig. 1. A) Location map of Mihailovići section (Montenegro). B) The Mihailovići sequence represented with ammonite species described in this study (2-D bar-diagram gives the percentage of Phylloceratina, Lytoceratina and Ammonitina in association). Lithology and labelling of the section retain these given by RABRENOVIĆ et al. [2]

Material. This study stands on newly-obtained ammonites that are part of the Geological Institute collections (Coll. No F.SR.2012.2). The ammonites (vary-sized phragmocones and few fragments) are preserved as internal moulds. Usually, the flanks originally oriented upwards are bioeroded or diagenetically diluted. Apart from a few members of the families of Lytoceratidae, Dactylioceratidae and Phymatoceratidae, the two families of ammonites that dominate Mihailovići fossiliferous bed are the Phylloceratidae and the Hildoceratidae. The latter two yielded almost equal numbers of specimens. The Dactylioceratidae, the Hildoceratidae and the Phymatoceratidae are more variable, while the Phylloceratidae and the Lytoceratidae are relatively closely defined and present less difficult problems of determination. Therefore, descriptions of different species include more or less details.

Family PHYLLOCERATIDAE Zittel, 1884 (Fig. 2a–f; Fig. 3a–e).

The bulk of the phylloceratids in Mihailovići section includes the genus *Calliphyloceras*, and it contains one species – *C. nilssoni* (Hebert). The next genus in phylloceratid occurrence is *Phylloceras*, represented by two species: *P. heterophyllum* (Sowerby), and *P. prinzi* Géczy. Both genera consist of probably smooth, involute and compressed ammonites with highly ornate suture-lines. *Phylloceras* differs from *Calliphyloceras* in having higher and less compressed whorls, and suture-line with five or more diphylic lateral saddles. Typically, *Calliphyloceras* have several shallow periodic sigmoid constrictions and suture-line with triphyllic 1st and 2nd lateral saddles. *P. heterophyllum* and *C. nilssoni* are species showing wide stratigraphic dispersal in the Toarcian, but they have a prominent maximum abundance in the Lower Toarcian Bifrons Zone [3]. This agrees with the position of our material. *Phylloceras prinzi* Géczy is less-common and probably coeval Tethyan species, reported before from Bakonycsérnye (Hungary) and Lombardy (Italy) [4].

Phylloceras heterophyllum (Sowerby) is one of the best-known phylloceratids and reveals wide geographic distribution. Since the fate of Sowerby's original from Whitby (UK) (SOWERBY, 1820, pl. 266, lectotype [5]) is unknown, the main sources for comparisons are the interpretations based on well-dated examples from Whitby and Lyon Area (France), given by RULLEAU [6–8], RULLEAU et al. [9], and the revised d'Orbigny collection (JOLY in FISCHER) [10]. The ammonites of Mihailovići (Fig. 2a–d) do not appear to differ in any respect from British and French specimens, even being just wholly septates and without tests preserved. They have the same involute and slightly compressed elliptical whorls and narrowly-varying ratios of whorl and umbilical width against diameter (0.58–0.59 and 0.08–0.09 respectively), and stratigraphic position, which is similar to that recorded in France and UK.

Phylloceras prinzi Géczy was determined on single ammonite (Fig. 2e, f). This is a phragmocone with the very beginning of the body-chamber (79.5 mm diameter), having ratios of whorl height and umbilical width against diameter,

which are 0.59 and 0.06. Geographically, the closest example is the holotype from Hungary (GÉCZY, p. 17, pl. 3, Fig. 5) [4]. *P. prinzi* is distinguished from *P. heterophyllum* by its much wider whorls, smaller umbilicus and prominent undercut umbilical walls.

Calliphyloceras nilssoni (Hebert) is the dominant phylloceratid in Mihailovići ammonite assemblage. We figure two examples (Fig. 3a–e) that are septated throughout. The range in diameters of our ammonites varies from 49 to 110.5 mm. Ratios of whorl height and umbilical width against diameter show minor variability (from 0.52 to 0.59 and from 0.11 to 0.13 respectively). The smaller ammonites usually carry 5 to 7 sigmoid constrictions, whereas the bigger ammonites can take up to 8 constrictions. It is difficult to compare these examples with the lectotype of species from Millau (France) (Joly in Fischer, p. 97, pl. 32, Figs 3a–c) [10], since the lectotype is too small (22.3 mm diameter), but they appear to be very similar. Interestingly, the bulk of *C. nilssoni* from NW Europe consists of small ammonites [6–10]. This species is rather exceptional in Tethyan assemblages, where the phylloceratids often attain diameters more than 110 mm. Tethyan *Calliphyloceras* displays sufficiently different morphology from the NW European examples of the genus to warrant another set of species [4]. The ammonites of Mihailovići seem to be an unusual case of size distribution of *C. nilssoni* in having much bigger sizes. However, there is no doubt that they belong to this species, as its coeval Tethyan fellows are generally more involute and bearing much more constrictions.

Family LYTOCERATIDAE Neumayr, 1875 (Fig. 3f–i). The ammonite-bearing bed of Mihailovići section yielded a few ammonites of the genus *Lytoceras*, identified as *L. toarcense* Rulleau. This is a newly-proposed specific name for the lytoceratids of the Bifrons Zone [8]. It was based on specimen of Dumortier’s collection, from La Verpillière (France), originally assigned to another species (*Ammonites trautscholdi* Opper), which has Upper Toarcian occurrence and in fact belongs to the genus *Alocolytoceras* [8]. Except for the holotype, there are five more paratypes from the Lyon Region (Rulleau, Fig. 4 – the holotype, Fig. 5 – paratype) [8]. *Lytoceras toarcense* includes small and smooth, very evolute ammonites, with semi-circular whorls, which are usually bearing two shallow, straight to weakly curved radial constrictions per each whorl. Our specimens (Fig. 3f–i) are too leached, more evolute and bigger than the type specimens, having just feebly compressed whorls, but they display shape and positions of constrictions that exactly coincide with those at the French specimens.

Family DACTYLIOCERATIDAE Hyatt, 1807 (Fig. 3j, k). The Dactylioceratidae is the usual basis for the ammonite biozonation of the Lower Toarcian strata in Europe [3]. According to PINNA, LEVI-SETTI [11], no substantial differences in occurrence of this family exist between the NW European and Tethyan localities until the top of the Tenuicostatum Zone. We agree that later a prominent palaeogeographic differentiation involved the dactylioceratid

distribution. It is clear that the genus *Nodicoeloceras* made the first associations of primitive cadicones and became common at the base of the next ammonite zone, the Falciferum Zone, but this radiation closed soon and single survivors continued upwards into the Bifrons Zone [3]. However, this genus seems to persist throughout the top of the Bifrons Zone in Tethyan areas, leaving too many specimens, with new morphology, dominated by planulate coiling that requires new systematics [11].

Surprisingly, the Mihailovići fossiliferous bed provided one single dactyloceratid of the genus *Nodicoeloceras* (Fig. 3j, k). According to the previous data [1], the genus *Peronoceras* also occur though no figured specimens exist and this occurrence is problematical. We identified *Nodicoeloceras angelonii* (Ramaccioni), a species from the Bifrons Zone in Italy [11]. The holotype comes from the Lower Toarcian at Monte Cucco, Italy (RAMACCIONI, 1939, pl. 12, Fig. 13) [12]. Characteristically, this species exhibits planulate coiling and moderately sharp ornament that consists of regularly alternating single and biplicate ribs. Small marginal tubercles are visible at the points of bifurcation, but they seem to disappear with growth. Our specimen (70 mm diameter) is very similar in ornament, but slightly more evolute and less compressed than the holotype. It agrees very well in ribbing style and ratios of whorl and umbilical width against diameter (0.21 and 0.59 correspondingly) to the members of the association of *N. angelonii* from Passo del Furlo (Italy), described by Pinna, Levi-Setti [11].

Family HILDOCERATIDAE Hyatt, 1807. Subfamily HILDOCERATINAE Hyatt, 1867 (Fig. 2l–n; Fig. 4a–d). The brilliant monograph on the Hildoceratidae in Britain (HOWARTH) [13] gave the best treatment of this ammonite family and little can be added after that. On our material, we found two mid-members from the sequence of species of genus *Hildoceras*, accepted in this monograph: *H. lusitanicum* Meister (Fig. 2n, o; Fig. 4a) and *H. bifrons* (Bruguière) (Fig. 2l, m). The first was reported previously from Mihailovići [1], whereas the latter is newly recorded in the association. We also found one *Hildoceras*-allied taxon – *Cingolites* aff. *picens* Sassaroli & Venturi (Fig. 4b–d). It belongs to rare Tethyan genus evolved from the pre-*Hildoceras* genus *Hildaites* earlier than the Bifrons Zone and existing up to the middle of this zone [14]. Equally, *Hildoceras* and *Cingolites* show poorly serrated hildoceratid sutures with narrow ventral lobes, and wide and shallow lateral lobes.

The ammonites identified as *H. lusitanicum* are typical examples of the species, having evolute, subquadrate to subrectangular whorls, strongly keeled tricarinate-bisulcate venter, prominent dorsal smooth band of the sides and arcuate ribs that are reflexed backwards near the middle of the flanks. The ratios of whorl height and umbilical width against diameter exhibit minor variability ranging between 0.30 and 0.33, and from 0.40 to 0.43 respectively, and the whorl breadth proportion is 0.22.

One ammonite was referred to *H. bifrons* [$D = 62$ mm, $Wh = 22$ mm (0.35), $Wb = 11$ mm (0.18), $U = 29$ mm (0.47)]. It represents an early form of the species that reminds in ornament to *H. lusitanicum*. However, even less prominent, a clear mid-lateral spiral groove is developed at all stages of growth. This ammonite is more evolute, compressed, and bears too much reduced ribbing to be *H. lusitanicum*.

Cingolites has been a recently proposed genus with no record outside Italy (Apennines and Southern Alps) and Lefkas Island (Greece) until now [14]. Being in transitional position between these two areas, the Mihailovići locality was potentially expected to contain *Cingolites*. The genus displays specific morphology: subquadrate whorls with wide tricarinate-bisulcate venter bearing more or less deep sulci, and simple flexuous ribbing that reaches maximum relief on the marginal area, forming a prominent clavus-like segment. Thus the venter became coronate. The Italian authors propose four *Cingolites* species, and our example (Fig. 4b–d) seems to be closest to *C. picenus*. It is a medium-sized ammonite [$D = 67$ mm, $Wh = 21.4$ mm (0.32), $Wb = 18$ mm (0.27), $U = 31.5$ mm (0.47)]. It has the same whorl shape and identical whorl proportions as the holotype and the allied type-specimens that come from the Marconessa, Italy (SASSAROLI, VENTURI, pp. 106–108, Figs 6a–f, i–1, n; pl. 1, Figs 5–8; pl. 2, Figs 1–5, 9) [14]. However, our ammonite has more distant and sharp ornament and occurs higher than the last recorded occurrence of *C. picenus*, which is the base of the Bifrons Zone. Besides, it exhibits a vague but visible leaning towards umbilical tuberculation. Therefore, it was conditionally identified. *Cingolites stefaninii* (Merla) [14] that has the same stratigraphic position as our example displays essentially more evolute coiling, more crowded and more swollen ribbing.

Sassaroli and Venturi [14] noted that the *Cingolites* morphology had already existed in three hildoceratid genera (*Orthildaites*, *Hildaites*, and *Mercaticeras*), and linked them phylogenetically. The Italians assumed *Cingolites* evolving from *Hildaites* and giving rise to *Mercaticeras*. This hypothesis and the observed trend to umbilical tuberculation on the Mihailovići ammonite provoke the questions: which are the ancestors of *Cingolites-Mercaticeras* group, are they the Phymatoceratidae, what Tethyan area is the promising recorder of this event? That requires at least a detailed re-examination of the older Tethyan collections in order to reject the initial meaning that *Cingolites* is an endemic taxon [14].

Subfamily HARPOCERATINAE Neumayr, 1875 (Fig. 2g–k; Fig. 3l–o). Howarth [13] was right saying that: “after a long period of evolution in the British Isles area, the centre of evolution of the *Harpoceras* phylogeny moved southwards late in the Bifrons Zone to the Mediterranean”. However, our record suggests that it happened at least in the mid-Bifrons Zone times and affected not only the *Harpoceras* lineage, but also possibly more members of the subfamily of Harpoceratinae. The Mihailovići fossiliferous bed yielded interesting examples of the genera *Oesperleioceras* and *Harpoceras*. Rampnoux [1] reported previously an

Osperleioceras bicarinatum (Zieten) from this bed, but our ammonites are referred to another species. It is *O. subexaratum* (Bonarelli), which is distinguished from *O. bicarinatum* by its much more evolute whorls and less strong ornament. We have the first *Harpoceras* record in Mihailovići. It is apparent that our examples represent proper Tethyan *Harpoceras* taxa, which are distinct from these in NW Europe. We identified *Harpoceras mediterraneum* Pinna and *Harpoceras* sp. n. The latter does not match any species from the literature, but displays enough morphological features to be erected as a new species if more material appears.

Osperleioceras subexaratum (Bonarelli) is a Tethyan species recorded from a limited present-day geographic area around the Adriatic Sea: Greece, Albania, Italy [15], and now Montenegro. Some authors attribute it to *Harpoceras*, but it has distinctive triangular to bitriangular whorl section of maximum whorl breadth usually around the umbilical area, and flat sides converging towards a narrow and characteristically keeled venter. In addition, this species displays suture-line that is too highly incised and ornate to be *Harpoceras*. The holotype was figured by PINNA (pl. 1, Fig. 18) [16], and it comes from an unrecorded locality in Central Apennines. We have two moderately involute and compressed whole septates, attaining 83 mm diameter, having the same proportion of whorl height against diameter (0.48), and umbilical with/diameter ratio ranging from 0.23 to 0.25. One of them is figured in Fig. 2j, k. The greatest width of the whorls is slightly below the mid-flanks. Even leached, both ammonites exhibit weak sinuous ribbing bundled near the umbilical edge with often-intercalated secondaries up to 45 mm diameter. At larger sizes, ribs seem to be single and falcoid.

The Mihailovići examples of *O. subexaratum* completely agree with the holotype. KOTTEK [15] registered an abundant occurrence of this species in section near the Greek–Albanian border on the Adriatic Sea coast. He fixed the stratigraphic distribution of his specimens to a local ammonite zone that seems to be equivalent to the Bifrons Zone. This is in agreement with the position of our material and the Greek locality is the closest locality of the species to Mihailovići. Even being from condensed sequence, our data suggest that *O. subexaratum* is a pre-*bicarinatum* species in *Osperleioceras* phylogeny. This contradicts Howarth's assumption that *O. bicarinatum* is the ancestor of *Osperleioceras* lineage, descending from *Harpoceras subplanatum* (Opper) [13]. This phylogenetic transition seems to be problematic because both *O. bicarinatum* and *H. subplanatum* are species certainly occurring higher than *O. subexaratum*. Thus *O. subexaratum* is distant from the lineage, and another origin of *Osperleioceras* is needed.

Harpoceras mediterraneum Pinna is a Tethyan species of Falciferum–Bifrons Zone occurrence (Italy, Albania, Greece, Switzerland, and Morocco) [13, 17]. It has been proposed as subspecies of *H. falciferum* (J. Sowerby) [17] in order to combine a group of ammonites from the Falciferum Zone, that resemble the nominate subspecies, but differ in having more evolute and higher whorls, and denser ornament consisting of less flexuous ribbing with no spiral groove

at the mid-flank falcate bend of the ribs. Unlike *H. falciferum*, the ribs in *H. mediterraneum* display a falcoid trajectory that does not intersect the radial line. These morphological distinctions were found enough to be considered as proper Tethyan member of *Harpoceras* lineage [13]. Recently, *H. mediterraneum* has been recorded from the Bifrons Zone in Hungary [18], and now we figure two ammonites of the same occurrence from Montenegro (Fig. 2*g–i*, Fig. 3*l, m*). These examples are medium-sized and moderately evolute, with rather robust whorls, undercut umbilical walls and rounded sides converging towards a narrow venter with strong floored keel. The ratios of whorl height and umbilical width against diameter vary from 0.42 to 0.45, and from 0.27 to 0.31 respectively. Ribs dense, falcoid, bifurcating or with intercalated secondaries, at larger sizes single and weak on inner half of the whorls, with characteristic trajectory as stated above (see Figs 2*i*, 3*m*). Our ammonites agree in morphology with the holotype and the other specimens of the type-series of *H. mediterraneum* from Italy (PINNA, pl. 2, Fig. 10; pl. 3, Figs 5, 7, 8, 10; pl. 4, Fig. 7; pl. 5, Figs 1, 1*a*; pl. 6, Figs 2, 3) [17]. We suggest for the range of this species to be Tethyan biostratigraphic equivalent to the combined stratigraphic distribution of *Harpoceras falciferum* (J. Sowerby) and *H. soloniasense* (Lissajous) in NW Europe.

The ammonite figured in Fig. 3*n, o* did not match any species from the references cited below, as well as in the literature on similar topics. Certainly, it is a *Harpoceras* example, having falcate ribbing and harpoceratinaean suture with large division in the 1st lateral saddle and deep lateral lobe of trifold pattern (Fig. 3*n*). It is moderately involute and compressed wholly septate (83 mm diameter), with undercut umbilical walls and massive whorls. The ratios of whorl height and umbilical width against diameter are 0.48 and 0.23. The wide venter has thick and feebly sulcated keel. Ribs falcate, dense, with long prorsiradiate dorsal segment and short outer segment that sweeps forwards near the venter (Fig. 3*o*). At sizes up to 40 mm diameter, ribs seem often bifurcate, while at larger sizes ribs are single, with occasionally intercalated secondaries. Our specimen has more involute and more massive whorls than the ammonites referred to *H. mediterraneum*. Besides, it exhibits a rib trajectory which differs from that in *H. mediterraneum*. Both whorl shape and ribbing style differ from that in *H. falciferum*, where ribs are usually flat and broad on the outer half of the whorls. We believe that better-preserved material with more specimens of this morphology will put this form into the Tethyan *Harpoceras* lineage, but that requires a normally-developed sequence to be found.

Family PHYMATOCERATIDAE Hyatt, 1867 (Fig. 4*e, f*, 5*a–d*). It was due for some Phymatoceratidae to occur in Mihailovići ammonite association. First, it is the Bifrons Zone assemblage and, second, the members of this family exhibit a pronounced Tethyan affinity. Rampnoux [1] reported “*Chartronia* sp.” and “*Phymatoceras* sp.” from Mihailovići. Our collection contains ammonites

referred to three species of the genus *Phymatoceras*: *Ph. anomalum* MERLA, *Ph. gr. narbonense* Buckman and *Ph. cf. formosum* Rulleau & Elmi.

Phymatoceras anomalum Merla (Fig. 5b, c) identifies with single specimen (55.8 mm diameter). It is rather evolute and compressed, having tricarinate-bisulcate venter with shallow ventral furrows and low keel. Whorl proportions against diameter are 0.32 (whorl height), 0.26 (whorl breadth), and 0.54 (umbilical width). Ribs are prominent, sinuous and regularly bifurcated from thick and short prorsiradiate peri-umbilical primaries. This ammonite shows a very good agreement with the type of specimens from Central Apennines (MERLA, pl. 3, Figs 10a, b – the lectotype, pl. 3, Fig. 5 – paratype) [19]. The stratigraphic position and generic affiliation of this species remain yet unresolved in the literature. It is still not clear if it emerges in the Bifrons Zone or appears higher up in the next Gradata Zone [9, 18, 19]. The *Phymatoceras s.s.* include ammonites with septacriate whorls distributed from the middle to the top of the Bifrons Zone in NW Europe, but preceded in Tethyan areas by small tricarinate-bisulcate examples assigned to different generic or subgeneric names [9]. *P. anomalum* belongs to the second group. Some authors refer it to *Furloceras* [19], that is a Tethyan genus, but appearing no earlier than the top of the Bifrons Zone.

The poor state of preservation did not allow for two large ammonites to be determined more than *Phymatoceras gr. narbonense* Buckman (Figs 4e, f; 5a). Specimens attain diameters 206 mm (Fig. 4e, f) and 170 mm (Fig. 5a). The first has ratios of whorl height and umbilical breadth against diameter which are 0.36 and 0.45, whereas the second has ratios which are 0.25 and 0.54 respectively. Both are wholly septate and evolute, with slightly convex flanks, rounded marginal shoulder and low keel without sulci. Ribs are sinuous and usually arise in pairs from small umbilical tubercles. Single ribs occur in internal whorls as well, and tuberculation disappears quickly with coiling. Suture-line is moderately ornate, with deep lateral lobe. The smaller specimen has much more primary ribs on the inner whorls and seems to be closer to the holotype that comes from La Verpillière (Isère), France (RULLEAU et al., pl. 10, Figs 3a, b) [20]. It has equal whorl shape and whorl proportions, but the diagenetic leaching of the sides of the last preserved whorl does not allow to observe if the ribs are simple, robust and sinuous as on the holotype. The bigger specimen deviates in morphology from the holotype in being less evolute, but it shows a trend towards simple and sinuous robust ribbing up to 130 mm diameter.

Phymatoceras cf. formosum Rulleau & Elmi (Fig. 5d) consists of a fragment of two whorls ending at ~ 90 mm diameter. It is septate throughout, has a square whorl section with slope umbilical walls and ventral keel bordered by wide shallow furrows. Robust umbilical tubercles give rise to pairs of thick sinuous ribs, usually divided by single ribs in between and irregularly emphasized by shallow sinuous back-constrictions. This fragment matches in ornament the internal whorls of the holotype, from the Bifrons Zone at La Verpillière, France (Rulleau et al., pl. 11,

Figs 1a–b) [20]. Although the original diagnosis excludes the presence of ventral sulci, it seems that in earlier growth stages, ventral furrows exist and these quickly disappear during the coiling.

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