

# Early Jurassic (Pliensbachian–Toarcian) Ammonoids from Limestone Tectonic Boulders in the Lozovoe Quarry (Simferopol, Central Crimea)

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**Abstract**—This study deals with the lower Jurassic (Pliensbachian–Toarcian) ammonites collected from tectonically isolated boulders of carbonate rocks excavated in the Lozovoe Quarry south of Simferopol (Crimea). We have identified 29 ammonoid species belonging to 20 genera and seven families, many of which are reported from Crimea for the first time: these are members of the subfamily Hildoceratinae (represented by the genus *Hildoceras*), genera *Nodicoeloceras* (family Dactylioceratidae), *Pseudaptetoceras* (subfamily Hammatoceratinae), *Perilytoceras* (subfamily Megalytoceratinae), *Pseudolioceras* and *Polyplectus* (subfamily Harpoceratinae), as well as a number of species representing the genera *Phylloceras*, *Calliphylloceras*, *Alocolytoceras*, *Harpoceras*, *Osperleioceras*, *Grammoceras*, *Dumortieria*, *Pleydellia*, and *Erycites*. Another find, *Amaltheus stokesi*, is the first confirmed record of late Pliensbachian ammonites in the region. The studied assemblage, both in its taxonomic composition and in the significant number of phyllo- and lytoceratids, is close to the coeval assemblages of Hungary, Italy and other Mediterranean regions. Analysis of the stratigraphic distribution of the recognized taxa allows eight ammonite assemblages to be provisionally established in Crimea, corresponding to the known stratigraphic units (zones, subzones and biohorizons) in the stratigraphic scales of the upper Pliensbachian–upper Toarcian of Western Europe.

**Keywords:** Crimea, ammonoids, biostratigraphy, tectonic melange, paleobiogeography, Pliensbachian, Toarcian

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## INTRODUCTION

The Lozovoe quarry, where crushed stone and quarry stone are produced, is located on the southern outskirts of Simferopol, on the right bank of the Salgir River in the upper reaches of the Simferopol Reservoir (3.5 km southeast of its dam) (Fig. 1). The nearest settlements are the villages of Lozovoe (formerly Eski-Orda) and Fersmanovo (formerly Totaykoy). The quarry extends in a northeasterly direction from the Salgir River to the foot of Mount Bayrakly for a distance of over one kilometer and reaches a width of approximately 500 m at its widest, southwestern sector.

The Lozovoe Quarry is developed within the magmatic rocks (gabbro-norite-dolerites) of the “Totaykoy Eruptive” (Yuzhnaya..., 1937; Muratov, 1959; Lebedinsky and Shalimov, 1961). In the literature it was also referred to as the “Main Totaykoy Quarry” (Prokopenko, 1928), the “Totaykoy (Eski-Orda) Quarry” (Moiseev, 1932), the “Totaykoy Quarry” (Zaika-Novatsky et al., 1976), and the “Fersman Quarry” (Mileev et al., 1989; Spiridonov et al., 1990).

In the 1990s, numerous boulders of limestone were exposed at the northeastern end of the quarry; these were clayey, pelitomorphous, and often crinoidal, ranging in color from brownish-red and pink to yellowish-gray, and containing interlayers of brecciated limestone. These boulders occurred along the periphery of an igneous massif, embedded within tectonically sheared mudstones of the Simferopol Melange (Yudin, 1993). A diverse Toarcian fauna was discovered within the limestones, including numerous belemnites, aulacocerids, nautiloids, bivalves, brachiopods, and crinoids, as well as an ammonite assemblage comparable to the Upper Toarcian assemblages of Hungary and Italy (Ippolitov et al., 2008).

New material makes it possible to improve our understanding of the taxonomic diversity of ammonoids from the Lozovoe Quarry and to refine the age of the limestone boulders. The latter are interpreted as exotic boulders originating from a buried shelf/epicontinental carbonate massif formed on the northern margin of the Tethys Ocean (Yudin, 2011)

that were brought to the surface within a tectonic melange. As no in-situ outcrops of Lower Jurassic limestones have yet been discovered in Crimea, the study of tectonic boulders found within the melange remains the sole source of information on the region's geological history during the Early Jurassic.

This study examined ammonoid specimens obtained from carbonate boulders by B.A. Zaitsev (2000–2024), M.A. and An.M. Rogov (2024), A.P. Ippolitov (2007–2009; all kept in Moscow, Earth Science Museum (MZ) of Moscow State University, coll. 149), D.B. Startsev (1998; Simferopol, M.I. Globenko Zoological Museum of the Taurida Academy, Crimean Federal University; specimens CFU-un-numbered), and A.I. Tishchenko (1990s–2000s; Simferopol, collections of the Central Museum of Taurida (specimens marked as “Pnv” below) and the N.I. Andrusov Geological Museum at the Taurida Academy, Crimean Federal University (specimens GM-1424–1454, GM-1503, GM-2132–2146, and GM-4913–4917)). In total, over 300 specimens were examined. The ammonoids were prepared and identified by B.A. Zaitsev and M.A. Rogov, and the belemnites by A.P. Ippolitov. A Triassic bivalve specimen was identified by V.A. Gavrilova (Karpinsky Institute, St. Petersburg).

#### HISTORY OF THE STUDY OF THE LOZOVUE QUARRY AND THE LOCAL GEOLOGICAL CONTEXT

The Lozovoe Quarry and the surrounding areas have been studied for over 150 years. Outcrops of igneous rocks on the right bank of the Salgir River were first depicted on a geological cross-section compiled by Romanovsky (1867, p. 78; text-fig. VI, no. 16). The massif of “crystalline rocks at the Kessler estate” was studied by Russian geologists in the late 19th and early 20th centuries (Sokolov, 1883; Golovkinsky, 1905; Fersman, 1906, and others.). It was reported that a number of quarries were already laid there at that time (Sokolov, 1883, p. 326; Fersman, 1908, p. 110).

Small, isolated limestone outcrops located to the north and northwest of the quarries also attracted the attention of researchers. In 1899, K.K. Vogdt was the first to establish a Paleozoic age for some of them (Vogdt, 1901, p. 303; Dvoychenko, 1926, p. 19). Vogdt believed that the limestones were *in situ* and formed

the core of an ancient “Meso-Tauric Ridge,” although V.D. Sokolov (1883, p. 331) had previously suggested that they were rootless bodies. Subsequently, the rootless nature of the limestone occurrences was confirmed by Moiseev (1930), and a Liassic (Vogdt, 1901; Dvoychenko, 1926) and Late Triassic (Moiseev, 1930, 1932) age was established for some of them.

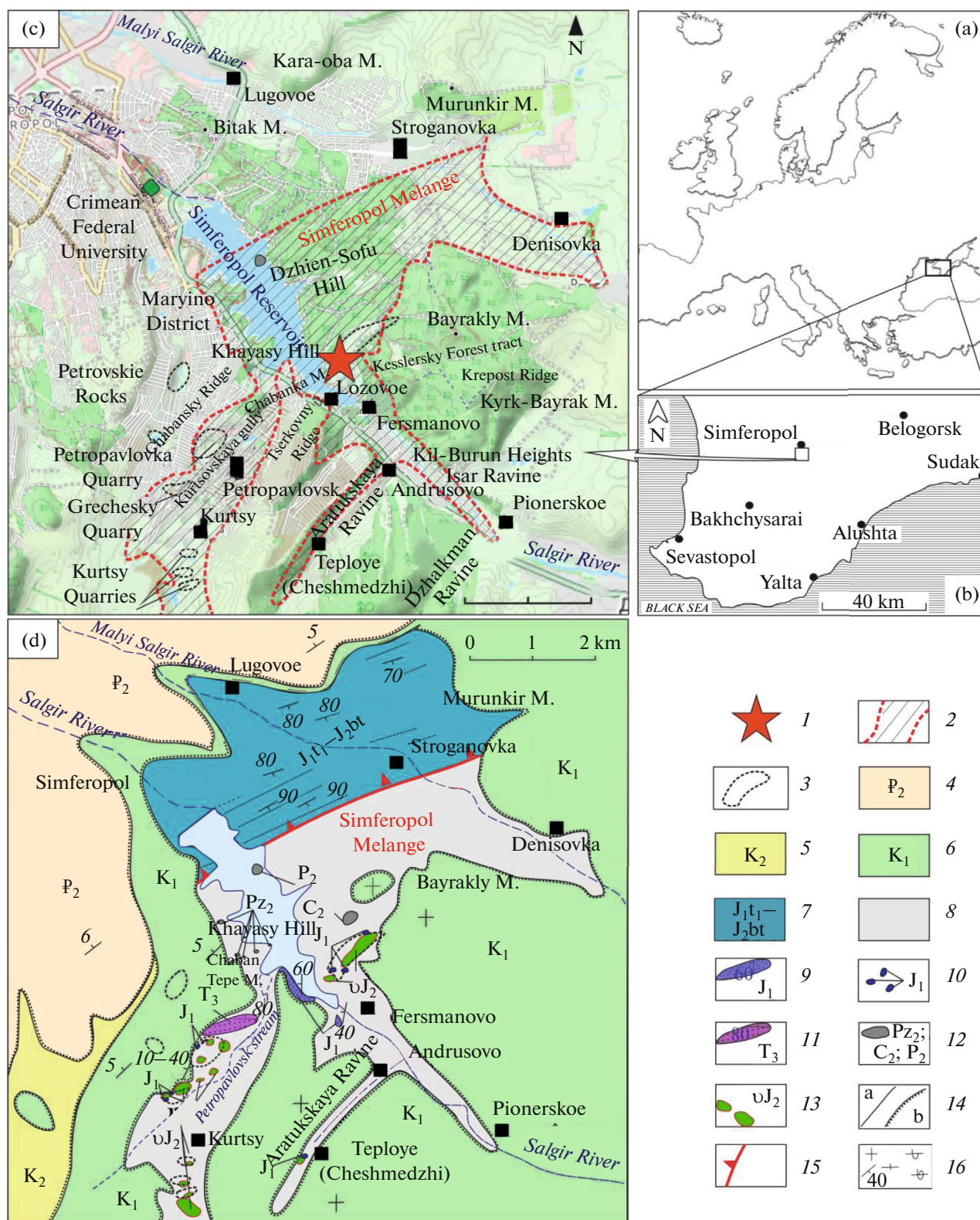
The discovery of the *Monotis* bivalves in “clayey-sideritic shales” at the site now occupied by the Lozovoe Quarry enabled Vogdt to establish, for the first time, the presence of Triassic deposits in Crimea (Vogdt, 1901, p. 303; Dvoychenko, 1926, p. 20; Prokopenko, 1928, p. 388). This finding attracted specialists from various disciplines to the area. During the first decade of the 20th century, staff members from the Department of Geology at Taurida University (Simferopol), including V.I. Vernadsky, P.A. Dvoychenko, V.A. Obruchev, S.P. Popov, G.F. Weber, and D.I. Shcherbakov—visited the quarry to sample for fossils (Vernadsky, 1997, pp. 72–73).

Later, A.S. Moiseev discovered “dark-gray micaceous shales containing the bivalves *Halobia* and rare cephalopods (*Arcestes* sp.)” in one of the quarries within the area now occupied by the Lozovoe Quarry (Moiseev, 1930, p. 11; 1932, p. 593). He dated these rocks as Carnian, thereby refining the stratigraphic range of the Triassic in Crimea (Moiseev, 1939). This Triassic locality, one of the few on the peninsula, was shown to the participants of the 17th International Geological Congress in 1937 (Yuzhnaya..., 1937, p. 27; Lebedinskiy and Shalimov, 1961, p. 199).

After examining outcrops of coarse-grained quartz sandstones near Eski-Orda village on the left bank of the Salgir River, Moiseev (1932, pp. 593, 604; 1944, p. 30) designated them as the “Eski-Orda unit” and determined their age as “transitional from the Triassic to the Liassic” (Moiseev, 1932, pp. 593, 604; 1944, p. 30). Moiseev (1932) noted that boulders (1–2 m across) of gray and reddish bioclastic-brecciated limestones with Liassic fauna occur within these sandstones. Subsequently, Pchelintsev (1937, p. 14) noted that the “sandstones of the Eski-Orda Formation also occur everywhere as scattered boulders.”

Later, A.I. Shalimov (in Krimholz and Shalimov, 1961, p. 74) described boulders of crinoidal limestone near Lozovoe village. He emphasized that these boulders

**Fig. 1.** Locations of Early Jurassic ammonoids in the Simferopol Melange within the Salgir River basin: (a, b) on small-scale maps; (c) on a topographic map (base: OpenStreetMap.org, Cycle map); (d) on a geological map (Yudin, 2018, modified). 1—Pliensbachian–Toarcian fauna locality at the Lozovoe Quarry; 2—outcrop area of Simferopol Melange rocks; 3—quarries; 4—Lower–Middle Eocene nummulitic limestones and carbonate clays; 5—Upper Cretaceous: Campanian and Maastrichtian marlstones; 6—Lower Cretaceous: clays, limestones, sandstones, and conglomerates; 7—Bitak Formation (Lower Toarcian–Bathonian; age adopted from Mileev et al. (1989)): conglomerates, gravelites, sandstones, and siltstones with carbonaceous interlayers; 8—Simferopol Melange rocks; 9—sandstone boulders in the melange assigned by A.S. Moiseev to the “Eski-Orda” Formation (Moiseev, 1932; Pchelintsev, 1937) and their attitude elements; 10—carbonate rock boulders in the melange containing Early Jurassic (Sinemurian, Pliensbachian, Toarcian) cephalopods; 11—Triassic psephite boulder in the melange near the village of Petropavlovka and its attitude elements; 12—Late Paleozoic (Carboniferous and Permian) carbonate rock boulders in the melange; 13—Bajocian igneous rocks: gabbro-norite-dolerites; 14—stratigraphic boundaries (a—conformable, b—unconformable); 15—thrusts and strike-slip thrusts; 16—structural orientation elements.



ders were redeposited and contained fauna of various ages, including ammonites Early Pliensbachian (“*Uptonia* sp.”) and Toarcian (“*Coeloceras crassum* (Phillips, 1829)”). Subsequently, Kamyshan (in Zolotarev, 1968, p. 910) identified Early Jurassic brachiopods from boulders of light-gray limestone. L.D. Kiparisova also noted the presence of “blocks and small masses... of Triassic and Liassic limestones” in the Lozovoe area (Kiparisova et al., 1969, p. 181).

Finds of the bivalve *Daonella lommeli* (Wissmann) in argillites within the northwestern part of the Lozovoe Quarry enabled L.D. Kiparisova to demonstrate the presence of terrigenous Upper Triassic and also Ladinian (Middle Triassic) rocks (Kiparisova et al., 1969). Subsequently, an ammonoid *Gymnotoceras*, a genus characteristic of the Middle Triassic in Eurasia and North America, was discovered in a “clay-siltstone” boulder at the Lozovoe Quarry (Astakhova, 1976). It was suggested that the aggregation of boulders varying in composition and age (ranging from Carboniferous to Liassic) is associated with the contact zone between igneous and terrigenous rocks (Kiparisova et al., 1969; Astakhova, 1976, p. 131). The lithological characteristics of the Triassic rocks and the stratigraphic ranges of fossils (including ammonoids) of this age from the vicinity of the Lozovoe Quarry are discussed in detail by Astakhova (1971).

Since 1955, the area around the newly created Simferopol Reservoir has served as the primary site for field geological practice for students from the Faculty of Geology at Kyiv University (Zaika-Novatsky et al., 1976, p. 3). Since then, most researchers have mapped the controversially interpreted “Eski-Orda” unit in this area, classifying it variously as a formation, a series, or a member (Barkhatov, 1955; Muratov, 1959, 1973; Shalimov, 1969; Zaika-Novatsky et al., 1976; Chernov, 1981; Slavin, 1982; Slavin et al., 1983; Permyakov et al., 1991, etc.); the history of its study has been examined in detail by Yudin and Zaitsev (2020a).

At the same time, a number of researchers identified the “Lozovoe thrust zone” (Shalimov in: Kiparisova et al., 1969), a “series of tectonic blocks of Upper Triassic rocks with varying spatial orientations” (Teslenko et al., 1978, p. 72), a “series of steeply dipping (65°–80°) thrusts” (Dekhtyareva et al., 1983, p. 42), a “local tectonic melange” (Zaika-Novatsky, 1981), and the “Eski-Orda mixtite” (Zaika-Novatsky and Solovyev, 1986, 1988) at the southeastern extremity of the reservoir. In some cases, the same researchers identified a stratigraphic unit in certain publications, while designating it as a thrust zone or melange in others (e.g., A.I. Shalimov, V.S. Zaika-Novatsky).

Finally, based on work on the first geodynamic model and a balanced geological map of Crimea, Yudin (1993) substantiated the existence of the Simferopol Melange—a frontal, polymictic thrust-related melange associated with the foreland collisional suture. It constitutes a regional chaotic complex of

endogenic origin, is characterized by nine features distinguishing it from olistostromes. It was mapped by Yudin at various scales within a zone over 50 km long and 1–6 km wide, to the north–northwest of the area where the Taurida flysch crops out. The most significant surface exposures of the Simferopol Melange occur where it intersects the valleys of the Salgir, Alma, and Bodrak rivers, as well as on the Bodrak–Alma interfluvium. Its tectonotype was designated in the southeastern part of the Simferopol Reservoir (Yudin, 1993, 2011, 2014, 2018). The structure of the mixtite within a small area of the tectonotype was examined in a recent study (Yudin and Zaitsev, 2020b).

It should be noted that some researchers continue to recognize units based on the study of isolated outcrops, preserved within large, structurally intact blocks of the sedimentary sequence, that retain their primary (bedded) depositional structure (Panov, 2002, 2015; Stafeyev et al., 2015; Praktika..., 2020; Bryantseva, 2021; Romanovskaya, 2021, etc.). These outcrops look like a continuous Lower Jurassic succession; in reality, however, they are nothing but allochthonous bodies embedded in a sheared matrix (boulder-in-matrix fabric characteristic of a melange; Yudin and Zaitsev, 2020a).

#### UPPER PLIENSBACHIAN–TOARCICAN FOSSILS FROM THE SIMFEROPOL MELANGE

The Simferopol Melange contains a various-sized boulders (ranging from tens of centimeters to hundreds of meters across), composed of rocks of diverse composition and age. Fossils spanning a wide stratigraphic range ( $C_1v$ ,  $C_{1s}$ ,  $C_2$ ,  $P_2kz$ ,  $T_2l$ ,  $T_3$ ,  $J_1s-t$ ,  $J_2a?$ ) have been described from these boulders (Tuman-skaya, 1916, 1931; Moiseev, 1926; Miklukho-Maklay and Muratov, 1958; Kazakova, 1962; Astakhova, 1976; Korchagin et al., 2003; Basistova, 2006; Ippolitov et al., 2008, 2015; Mychko, 2012; Repin, 2017; Zaitsev, 2021; Zaitsev and Ippolitov, 2023, etc.).

The presence of the Upper Pliensbachian in some of these boulders was indicated by Moiseev (1944) and Permyakov (1969) based on ammonite finds. Unfortunately, none of these ammonites were illustrated, and they are currently considered lost (Zaitsev, 2023, p. 73). Later, Klikushin mentioned the widespread occurrence of Lower Jurassic Ammonitico Rosso facies within the limestone boulders (including those at the Lozovoe Quarry). Based on the study of crinoid remains, he also suggested that some of the boulders belonged to the Upper Pliensbachian (Klikushin, 1987, 1988, p. 74).

The earliest reference to the discovery of Toarcian fauna in rocks belonging to the Simferopol melange appears in the works of M.V. Muratov, who reported that in 1958, V.A. Melnichuk gave him a specimen from the Alma River valley that had been tentatively identified as *Grammoceras saemanni* (Dumortier)

(Muratov, 1959, p. 39; 1960, p. 26). This specimen comes from the terrigenous rocks of the Simferopol Melange, which Muratov (1960, 1969) assigned to the “Taurida Group” as the “Eski-Orda Formation.” Later, G.Ya. Krimholz re-examined the specimen and confirmed Muratov’s preliminary identification (Krimholz and Shalimov, 1961, plate, fig. 5). Unfortunately, this specimen’s whereabouts is currently unknown, and it is impossible to verify the identification based solely on the published image. This taxon is interpreted in various ways (cf. Denckmann, 1887; Buckman, 1890, 1902; Janensch, 1902) and should be considered a *nomen dubium* (Rulleau in Alm  ras et al., 1998, p. 54). However, if the broadest possible interpretation is adopted, it can be associated with some species of *Grammoceras* or *Podagrosites* from Thouarsense Zone of the European Upper Toarcian (Metodiev, 2002).

Around the same time, during a geological survey conducted between 1955 and 1958, Toarcian ammonites *Grammoceras subquadratum* (Buckman) and *G. cf. thouarsense* (d’Orbigny)—as well as the belemnite *Mesoteuthis rhenana* (Oppel), were discovered in the Alma River valley south of the Karagach village (now Kizilovoe); these fossils were found in “clay shales” likely belonging to the Simferopol Melange. Descriptions and illustrations of the specimens were published by G.Ya. Krimholz and A.I. Shalimov (1961). Then, Permyakov (1962, p. 63) recorded Toarcian *Dactylioceras* ex gr. *commune* (J. Sowerby) and *Grammoceras quadratum* Haug “in shales along the Bodrak River,” though without specifying the exact locality or providing descriptions or illustrations of the specimens.

In the terrigenous rocks of Simferopol Melange, the Toarcian fossils were first discovered by O.V. Snegireva in the Salgir River basin nearby Lozovoe village, where she has identified a microfauna “from shales” (Shalimov, 1960, p. 1410; Krimholz and Shalimov, 1961, p. 74). Subsequently, Toarcian macrofauna, primarily bivalves (Komarova and Dekhtyarova, 1982) as well as the Early Toarcian ammonite *Dactylioceras tenuicostatum* (Young et Bird) (Permyakov, 1969; Slavin, 1982), were repeatedly recorded in the mudstones and sandstones between Lozovoe and Petropavlovka villages. Finally, Ippolitov et al. (2015) described and illustrated poorly preserved Late Toarcian–?Early Aalenian belemnites from the melange matrix on the left bank of the Bodrak River near the Trudolyubovka village (the Tatyana Gorka locality).

In the carbonate rock bodies of Simferopol Melange the Toarcian fauna was first discovered by A.I. Shalimov, who had found a *Catacoeloceras crassum* (Young et Bird) specimen in a limestone boulder near the Lozovoe village (Krimholz and Shalimov, 1961, p. 74). This specimen was not illustrated. Shortly thereafter, a lecturer at Kyiv University V.M. Neroedenko, identified Toarcian belemnite species in boulders of red limestone at the nearby Petropavlovka Quarry (Dekhtyareva et al., 1978; Furdui and Zagorodnyuk, 1987), and in the early 2000s, an assemblage of Toarcian foraminifera was described from the same locality (Bragin and Kuznetsova, 2004).

Ippolitov et al. (2008, 2009) published the most detailed description of the Toarcian–Aalenian cephalopod assemblage (ammonites, belemnites, and aulacocerids). They illustrated several specimens collected by A.I. Tishchenko and A.P. Ippolitov from “boulders of cherry-red crinoidal limestones from a sequence of tectonically re-worked dark-gray mudstones” at the Lozovoe Quarry (Ippolitov et al., 2008, p. 43). Among these finds, ammonoids identified by M.A. Rogov and A.S. Beko, included *Calliphyloceras supraliasicum* (Pompeckj), *Lytoceras* cf. *cornucopia* (Young et Bird), *Pseudogrammoceras fallaciosum* (Bayle), *Dumortieria brancoi* Benecke, *Pleydellia* spp., *Hammatoceras* cf. *victorii* Bonarelli, *Erycites* cf. *barodiscus* (Gemmelaro), *Pleydellia* (*Cotteswoldia*) cf. *paucicostata* (Buckman) and *Pseudammatoceras clocheri* Rulleau et Elmi. Among the listed taxa, several species marks narrow stratigraphic intervals: *P. fallaciosum* – the Fallaciosum Subzone of the Thouarsense Zone in Europe (Page, 2003); *D. brancoi* – the Levesquei Subzone of the Pseudoradiosa Zone (Schulbert, 2001); and *P. (C.) paucicostata* – the Mactra Subzone of the Aalensis Zone (Upper Toarcian) (Rulleau et al., 2001). Subsequently, the presence of *Bredya brancoi* (Benecke) and *Catacoeloceras* cf. *crassum* (Young et Bird)—the latter characteristic of the Crassum Subzone of the Bifrons Zone (Lower Toarcian<sup>1</sup>; cited in the original text as the “upper part of the Middle Toarcian”), was also recorded from the limestones of the Lozovoe Quarry (Ippolitov et al., 2010, p. 100). All the ammonites mentioned have been revised and re-illustrated in the present work.

Limestone boulders containing Upper Toarcian belemnites, lithologically identical to the boulders in the Lozovoe Quarry, have also been described in the Bodrak River basin on the northern slope of Malyi Kermen Mountain (Ippolitov et al., 2015).

## LOCALITY DETAILS

The Lozovoe Quarry is situated within the “Lozovoe diabase deposit” (Lyubomirsky and Fedorin, 2021, p. 330). Operations there target igneous rocks belonging to the island-arc picrite-gabbro-norite-dolerite formation, part of the Pervomaysk-Ayudag Intrusive Complex, which is presumed to be of Early Bajocian age (Spiridonov et al., 1990, 2018). Originally, before the onset of intensive quarrying, the

<sup>1</sup> Following the resolutions of the Interdepartmental Stratigraphic Committee and its permanent commissions (Krymholts, 1978; Sostoyanie..., 2008), as well as the scheme proposed in Zony... (1982), a twofold subdivision of the Toarcian Stage is adopted herein.



**Fig. 2.** Location of spoil heaps containing boulders of Lower Jurassic limestone at the Lozovoe Quarry. Satellite imagery from Google Earth (imagery date: 05.07.2019).

igneous rock outcrop was present in relief as a “small ridge, slightly over a kilometer in length, which... extends northeastward, with a gentle northwestern slope and a steep southeastern slope” (Popov, 1938, p. 34).

The igneous rocks are surrounded by crushed and brecciated sedimentary rocks of varying age and composition (Figs. 3, 4, 5). In the northwestern and central parts of the quarry, these consist of boulders of dark-gray mudstone (sometimes containing siltstone fragments) of Middle Triassic age, with the bivalve *Daonella lommeli* (Wissmann) and the ceratitid *Gymnotoceras crimicus* Astakhova (Zolotarev, 1968; Astakhova, 1971, 1976), as well as mudstone of Late Carnian–Early Norian age containing the bivalve *Primalobio (?) austriaca* (Mojsisovics) (Fig. 4a). Boulders of sandstone and gravelstone lacking identifiable fauna occur less frequently (Fig. 3g).

Boulders of carbonate rocks of varying size, composition, and age occur within a matrix of sheared, tectonically reworked mudstones and siltstones. Large boulders of Paleozoic limestones located to the north and northwest of the quarry are well known (Vogdt, 1901; Miklukho-Maklay, 1969; Amelichev et al., 2005). One of these, the “Totaykoy boulder” (according to Dvoychenko, 1926, p. 19), with an abandoned “artisanal quarry” in its southern section (Tishchenko, 2015,

pp. 66, 279), is located 180 m from the northeastern wall of the Lozovoe Quarry (Figs. 1b, 2).

Another large boulder of gray metamorphosed limestone, with no macrofauna and lithologically similar to the Totaykoi limestone boulder—is exposed in the northeastern wall of the active quarry (Fig. 4b, c). Bodies of Paleozoic limestone (0.2–7 m across) can be observed on the left bank of the Salgir River, 1–2 km northwest of the Lozovoe Quarry: on Khayasy Hill, along the roadside of the Yalta Highway (44°55′12.10″ N; 34°8′48.10″ E), and on the northwestern slope of Mount Choban-Tepe (Fig. 1), where some of them were revealed by drilling (Technical..., 1993). Boulders of Upper Triassic (Moiseev, 1930, 1932) and Sinemurian–Pliensbachian (Dvoychenko, 1926; Krimholz and Shalimov, 1961) limestone are also present nearby the Lozovoe Quarry.

In the northeastern wall of the quarry, limestone boulders containing Toarcian fauna—likely fragments of a formerly continuous larger body—are partially preserved in their original position within the melange (Figs. 3a–3c). An ammonite of the genus *Dumortieria* was found in one of these limestone fragments, and a *Harpoceras* specimen in another. This section was first exposed during the quarry expansion in the 1990s and is the source of the finds previously described in the literature (Ippolitov et al., 2008, 2010). Its geological

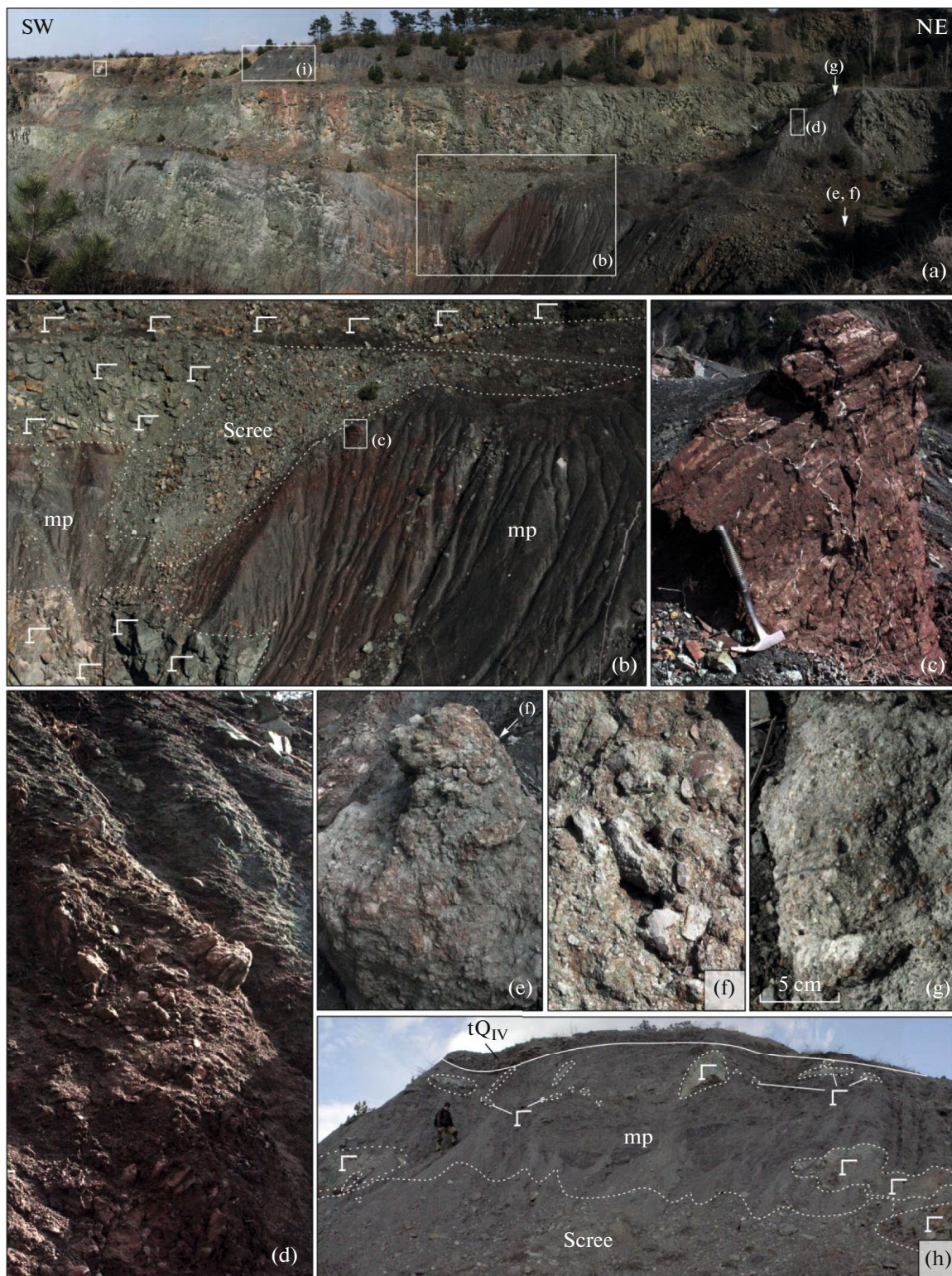


**Fig. 3.** General view of the northeastern extremity of the quarry and the mode of occurrence of boulders within the melange. (a) general view of the northeastern part of the quarry (panorama); (b) relationship between the melange rocks and the igneous body; (c) boulder of red Toarcian limestone with preserved bedding sequence; (d) outcrops of sheared sedimentary rocks (crushed black mudstones with fragments of red limestone); (e), (f) boulder of brecciated limestone containing abundant juvenile ammonoids: (e) general view, (f) close-up fragment; (g) boulder of quartz-rich gravelstone with carbonate cement; (h) tectonically reworked gabbro-dolerite fragments incorporated into the melange.  $\Gamma$ —gabbro-dolerites; mp—polymictic melange matrix.

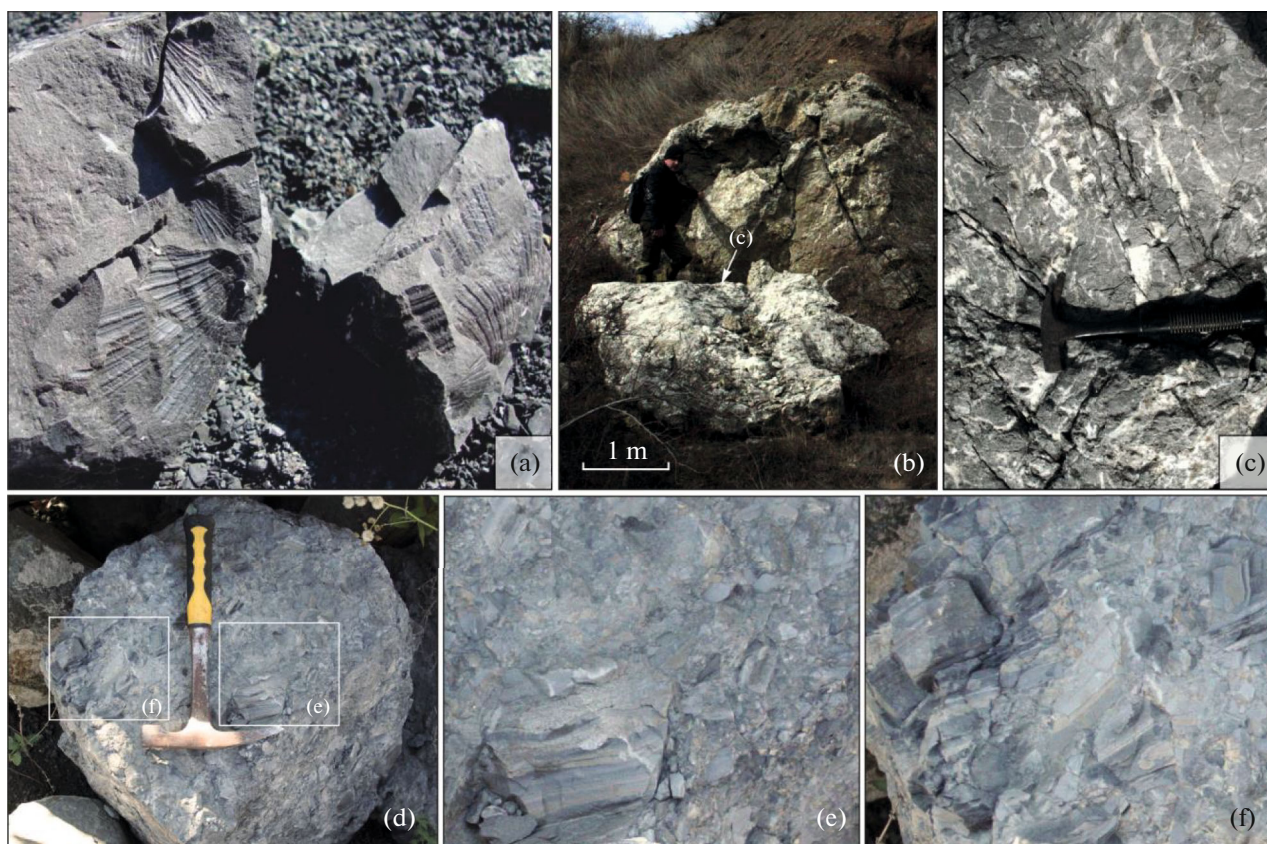


**Fig. 4.** Boulders of Paleozoic and Triassic rock, as well as rock of uncertain age, encountered in the Lozovoe Quarry. (a) dark gray mudstones containing the bivalves *Primahalobia* (?) *austriaca* (Mojsisovics, 1874) of Late Carnian–Early Norian age (identified by V.A. Gavrilova) in the northwestern part of the Lozovoe Quarry; (b, c) boulder of gray metamorphosed limestone lacking macrofauna (Carboniferous–?Permian): (b) general view, (c) close-up; (d–f) boulder of uncertain age composed of breccia with angular mudstone and siltstone fragments: (d) general view, (e, f) details.

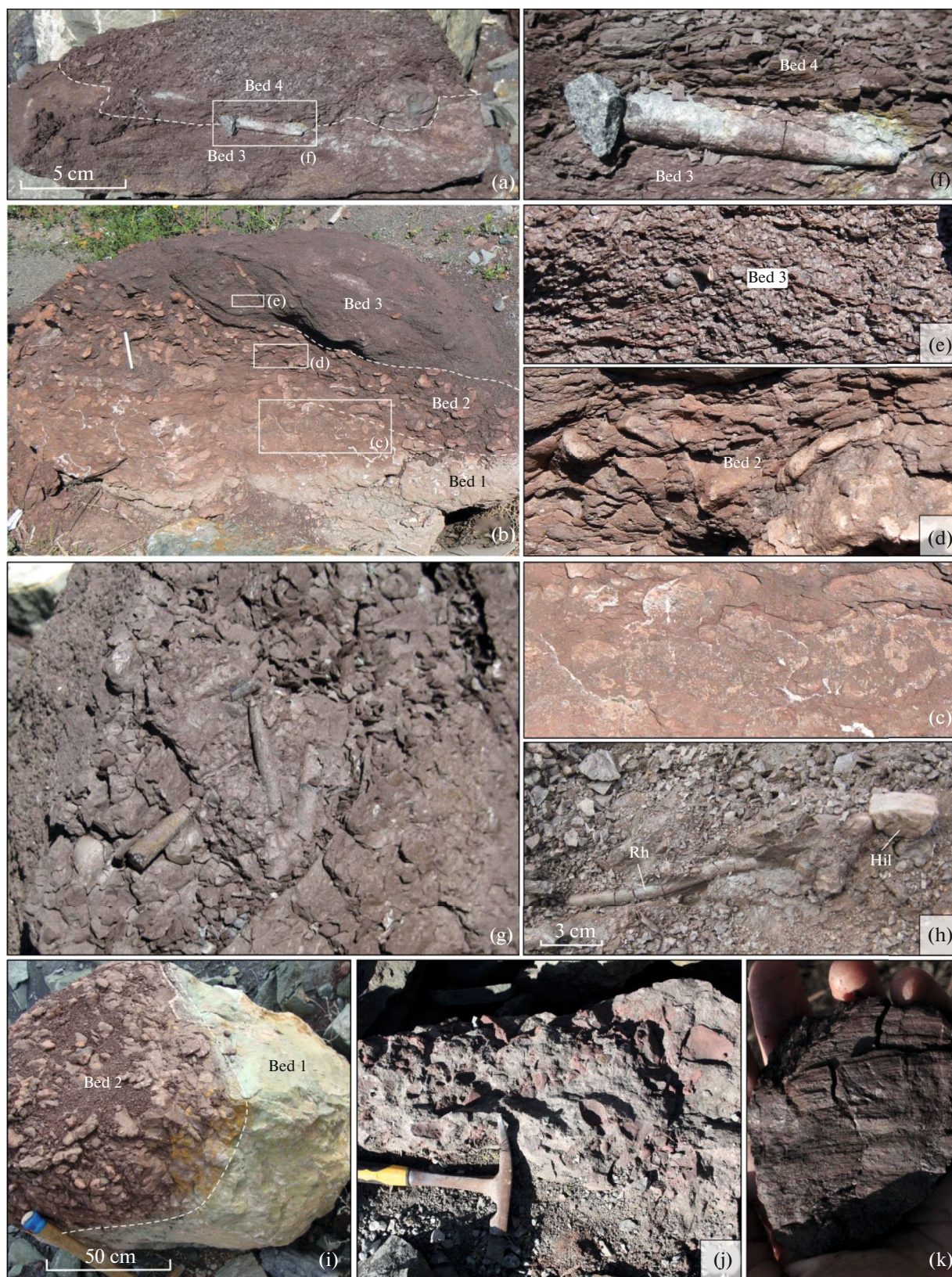
structure is discussed in Yudin (2017, p. 134). Fragments of fine-grained intrusive rocks (Fig. 3h) and a few boulders of gravelite (Fig. 3g) occur here amidst sheared black mudstones. Gravelites of similar composition were observed on the southern slope of Khayasy Hill, 1.5 km northwest of the quarry (Yudin and Zaitsev, 2020b).

Currently, the fragments of carbonate boulders excavated from the northeastern part of the quarry can be observed primarily in two spoil heaps located near the southwestern edge of the active quarry; most ammonites described in this paper originate from these piles. Additionally, in 2002, B.A. Zaitsev observed a single boulder of dark red, nodular argillaceous limestone

with *Grammoceras penestriatulum* Buckman in the eastern wall of the active quarry. The locations of ammonite-bearing boulders within the quarry, as well as the sites of the spoil heaps from which specimens were collected, are shown in Fig. 2.

In addition to red limestones, the spoil heaps contain boulders of argillite-siltstone breccia composed of randomly oriented, angular fragments (Figs. 4d–4f), confirming intense tectonic reworking of the rocks within the melange. Furthermore, both the spoil heaps and the quarry face contain boulders of dark gray and black argillites exhibiting numerous discordant slickensides on their surfaces. Slickensides are also frequently

**Fig. 5.** Boulders of red limestone in the spoil heaps of the Lozovoe Quarry and their main geological features. (a, e) Boulder with the contact between beds 3 and 4 preserved; see text for description: (a) general view, (e) close-up of the contact, with the belemnite *Acrocoelites* cf. *banzensis* Kolb (Upper Toarcian) resting upon it; (b–d) boulder with the sequence of Beds 1–3 preserved; see text for description: (b) general view of the boulder; (c, d, e) close-ups of Beds 1, 2, and 3; (g) accumulation of belemnite rostra at the base of Bed 4; (h) argillaceous limestone with the Late Toarcian belemnite *Rhabdobelus exilis* (d'Orbigny) (Rh) and a rounded internal mold of the Late Toarcian ammonite *Hildoceras* sp. (Hil), base of Bed 4 (?); (i) boulder in which the layer consists of a light-colored limestone variety; (j) boulder of carbonate conglomerate (rounded limestone clasts up to 5 cm along the long axis); (k) limestone fragment with a slickenside surface.



present within the boulders of red Toarcian limestone (Fig. 5k).

Based on individual large boulders of cherry-red limestone found in the spoil heaps, which have preserved their primary bedding, it is possible to reconstruct the original structure of the stratigraphic section (prior to tectonic fragmentation). At least four beds can be recognized within these boulders (observations by A.P. Ippolitov, 2008):

1. Cherry-red, pelitomorphous limestone conglomerate with a micritic matrix and accumulations of crinoid ossicles (Fig. 5c). The rock consists of numerous moderately to poorly rounded limestone pebbles up to 8–10 cm along the long axis; these are typically flattened and oriented parallel to the bedding plane. In places, the rock is weakly marmorized, while elsewhere it takes on a green color with scattered bright red patches; lenses of crinoidal limestone are also present. Thickness is at least 0.4 m. Aulacocerid phragmocones and bivalves were found at the contact with Bed 2.

2. Limestone conglomerate with carbonate-siltstone cement (Fig. 5d). Similar to Bed 1 but less strongly cemented, with a higher proportion of pebble-sized material and a greater abundance of crinoid ossicles (occurring in the matrix mostly as isolated elements, though sometimes articulated). Internal molds of ammonites, bivalves, and gastropods, as well as brachiopod shells, also occur in the bed. Thickness: 0.1–0.3 m.

3. Cherry-red, crinoid limestone, almost without a micritic component, with rare limestone pebbles (Fig. 5e). The apparent thickness is 0.2 m. The quarry dumps also contain lithologically similar green-gray crinoid limestones, which sometimes occur in the form of large “spots” within brown-red crinoid limestones.

4. Crinoidal marl (Fig. 5f). Equivalent to Bed 3 but more argillaceous, ranging in color from brown to chocolate-brown. Clusters of cemented belemnite rostra—often showing signs of breakage, dissolution, and rounding—occur at the base. Up the section, the unit grades into pure mudstones. The transition from the underlying bed is gradual but was observed in only one boulder. Thickness is uncertain.

Scree from the upper “argillaceous” part of Bed 4 contained cylindrical belemnite fragments with a strongly developed ventral sulcus, which can be identified as *Holcobelus* cf. *tschegemensis* (Krimholz). The genus *Holcobelus* is characteristic of the Aalenian–early Bajocian of Europe (Weis et al., 2012); notably, the scree from Bed 4 lacks the Toarcian belemnites *Acrocoelites* and *Odontobelus*, large numbers of which were collected from other intervals. Therefore, regardless of the precise age interpretation of the upper part of Bed 4 (Toarcian or Aalenian), it is certainly the youngest part of the described sequence.

The fossil fauna found in the limestones comprises numerous brachiopods, crinoids, belemnites, aulacocerids, nautiloids, ammonoids, and bivalves. Almost the entire ammonite assemblage described below likely comes from the basal horizons of Bed 4, although the majority of the material was collected without a clear association with the “section” of boulders described above. In addition, a rounded limestone fragment of an internal mold of the ammonite *Hildoceras* sp., characteristic of the Lower Toarcian (Bifrons Zone) of Europe, was found in the mudstones alongside the belemnite *Rhabdobelus exilis* (d’Orbigny), which is characteristic of the Upper Toarcian starting from the Thouarsense Zone (Schlegelmilch, 1998) (Fig. 5h). Thus, it can be argued that the rounded limestone clasts at least in part are redeposited and may be somewhat older than the enclosing terrigenous rocks. Nevertheless, it has been established that the belemnites found in various boulders and lithotypes form consistent assemblages and appear to originate from several stratigraphic levels. Consequently, the rock succession within the boulders can be viewed as a sequentially condensed section rather than a single horizon of heterochronous condensation. At the same time, it cannot be shown that the structural features observed in individual boulders characterize the entire material under study; lateral variations in the succession and bedding of the section are quite possible but cannot be determined through the study of the boulders alone.

#### OTHER TOARCIAN MACROFAUNA LOCALITIES IN THE LIMESTONES OF THE SIMFEROPOL MELANGE

Limestone boulders lithologically similar to those from the Lozovoe Quarry are frequently found south of Simferopol, although they do not always contain ammonoid remains. In addition to the Lozovoe Quarry, red limestone boulders with Toarcian cephalopods (ammonites and belemnites) can be observed 2.5 km to the southwest, in the northwestern wall of the New Petropavlovka Quarry. Some of these boulders are outlined in photographs in a study by V.V. Yudin (2017, p. 129). The large limestone boulders are oriented predominantly along a WSW–ENE axis, which likely corresponds to the general direction of tectonic material transport within the melange. The quarry face also exposes small siltstone fragments, boulders of black and greenish mudstone (which laterally grade in places into brownish-red mudstone), and occasional boulders composed of a flysch-like alternation of mudstone and siltstone. A Toarcian microfaunal assemblage has previously been described from the mudstones (Bragin and Kuznetsova, 2004), and belemnites are also occasionally found within them (A.P. Ippolitov, unpublished data).

In addition, lithologically similar rocks—though lacking cephalopod remains—are known from the left

bank of the Salgir River, 35 m north of the Petropavlovsky Pond dam (44°54'04" N, 34°09'05" E; observations by B.A. Zaitsev); the Grechesky Quarry (44°53'35" N, 34°08'10" E; Zaitsev and Ippolitov, 2023, p. 8); the western corner of the excavation pit for a school under construction in the Maryino-2 micro-district (44°54'26" N, 34°08'32" E; observations by B.A. Zaitsev); and other locations south of Simferopol.

In addition, large limestone boulders (more than one meter across) of similar lithological composition with numerous brachiopods—were encountered by B.A. Zaitsev and S.K. Sukhoruchenko (KrymGIINTIZ Institute) 1.5 km south of the Lozovoe Quarry. These boulders were found within the boulder-pebble conglomerates of the Bayrakly Formation (Tithonian–Valanginian age; Kabanova, 1964) near Andrusovo village (44°54'03.3" N; 34°10'14.3" E) and elsewhere.

A large red limestone boulder with Late Toarcian fauna is also known from the Bodrak River valley, in the forest on the northern slope of Mount Bolshoy Kermen (Ippolitov et al., 2008, 2015). Unfortunately, this boulder is currently located on private property and is inaccessible for further study.

In general, the Toarcian limestone boulders contain an abundant nektonic fauna (belemnites and ammonoids, with a predominance of oceanic phyllocerids and lytocerids) alongside relatively rare benthic fauna. There is evidence of transport and/or redeposition affecting at least part of the faunal assemblage (fragmentation of some belemnite rostra; abraded, corroded, and partially dissolved ammonite internal molds); and the presence of carbonate pebbles and terrigenous admixture in certain beds. The sedimentary sequence within the boulders is generally condensed. Some authors have referred to such limestones in Crimea as “Ammonitico Rosso” (Klikushin, 1987); however, this designation appears not entirely accurate. The classic “Ammonitico Rosso” facies, according to the modern interpretation by sedimentologists (Martire et al., 2006, p. 228), consist of nodular, condensed, horizontally bedded pelagic limestones formed on submarine highs in a low-energy setting, with a near-total absence of terrigenous input, save for minor amounts of suspended clay. In our case, the initial section consisted of carbonate-terrigenous deposits of the outer deep shelf, formed in high-energy environments and containing carbonate conglomerates and faunal remains showing signs of transport.

## SYSTEMATIC PALEONTOLOGY

The following notations are used in the description:

\* – first description of the taxon meeting the criteria of availability; D – shell diameter; Du – umbilicus diameter; H – height of the last whorl; W – width of the last whorl.

## ORDER PHYLLOCERIDA SCHINDEWOLF, 1923

### SUPERFAMILY PHYLLOCERATOIDEA ZITTEL, 1884

#### FAMILY PHYLLOCERATIDAE ZITTEL, 1884

#### SUBFAMILY PHYLLOCERATINAE ZITTEL, 1884

#### Genus *Phylloceras* Suess, 1865

#### *Phylloceras heterophyllum* (J. Sowerby, 1820)

Plate 1, figs. 2a, 2b, 3a–3c; Plate 2, figs. 5a–5c

*Ammonites heterophyllus*: J. Sowerby, 1820\* in Sowerby, 1818–1821, p. 119, pl. 266; d’Orbigny, 1845 in d’Orbigny, 1842–1851, p. 339, pl. 109, figs. 1–4.

*Phylloceras heterophyllum*: Arkell in Treatise..., 1957, p. L187, text-figs. 218.5a–218.5b; Krimholz, 1961, p. 19, pl. 1, figs. 1–2; Joly in Fischer, 1994, p. 97, pl. 32, figs. 4, 5a, 5b, 6, text-fig. 29; Joly, 2000, p. 43, pl. 5, figs. 1, 2, pl. 6, figs. 1, 2a, 2b, 3, text-figs. 72–78; Rulleau et al., 2001, p. 46, pl. 1, figs. 1a, 1b; Fauré, 2002, p. 694, pl. 1, fig. 2; Rulleau, 2006, p. 45, text-fig. 10.1, pl. 1, figs. 1–2; Kovács, 2011, p. 8, pl. I, figs. 1–4; Metodiev et al., 2013, p. 69, figs. 2.a–2.d; Repin, 2016, pl. 1, figs. 1a, 1b; Fossils..., 2019, p. 42, text-figs. 6.1A–1B; Howarth, 2020, p. 2, text-figs. 2a–2c; Arp et al., 2021, text-fig. 11.5; Benzaggagh, 2023, p. 6, text-figs. 8A–8C.

**H o l o t y p e.** By monotypy, illustrated by J. Sowerby (1818–1821, pl. 266), Toarcian of the Whitby area (North Yorkshire, England), specimen NHMUK 43879 (Natural History Museum, London). Re-illustrated in Treatise... (1957, figs. 218.5a–218.5b; Howarth, 2020, figs. 2a–2c).

**S h e l l s h a p e.** The shell is involute, small to medium-sized, and of moderate thickness. The whorls are elliptical in cross-section, with weakly convex flanks and a narrow, rounded venter. The umbilicus is narrow and funnel-shaped. The umbilical shoulder is gently rounded. The umbilical wall is steep.

**O r n a m e n t a t i o n.** The available internal molds lack ornamentation.

**D i m e n s i o n s i n m m a n d r a t i o s i n %:**

| Specimen no. | D  | H  | Du  | W   | H/D  | W/D  | Du/D | H/W |
|--------------|----|----|-----|-----|------|------|------|-----|
| GM-1427      | 23 | 13 | 3.5 | 7.5 | 56.5 | 32.6 | 15.2 | 173 |
| MZ 149/1     | 40 | 23 | 5   | ≈13 | 57.5 | 32.5 | 12.5 | 177 |
| MZ 149/2     | 72 | 44 | 7   | 29  | 61.1 | 40.3 | 9.7  | 152 |

**C o m p a r i s o n.** It differs from *Phylloceras dodereleinianum* (Catullo) in the noticeably narrower, elliptical cross-section and a narrower venter.

**O c c u r r e n c e.** The Toarcian and Lower Aalenian of Europe (Hungary, Bulgaria, France, Great Britain, Italy, Germany, Greece, etc.), North Africa, the Caucasus, and Northeastern Russia.

**M a t e r i a l.** Three specimens (nos. GM-1427, MZ-149/1, and MZ-149/2), as well as several fragments that can be assigned to this species based on their cross-section shape.

*Phylloceras doderleinianum* (Catullo, 1853)

Plate 1, figs. 1a–1c; Plate 2, figs. 4a–4c

*Ammonites doderleinianus*: Catullo, 1853\*, p. 19, pl. I, figs. 3a–3c (non figs. 3d–3e).*Ammonites (Phylloceras) doderleinianus*: Meneghini, 1875a, p. 87, pl. XVII, fig. 5; Meneghini, 1875b, p. 106 (pro pars. Catullo, 1853).*Phylloceras borni*: Prinz, 1904, p. 33, pl. XXVI, figs. 1–2, pl. XXXVI, fig. 1; Géczy, 1967b, p. 14, text-fig. 7, pl. III, fig. 3, pl. LXIII, fig. 6.*Phylloceras gajarii*: Prinz, 1904, p. 36, pl. XXVI, fig. 3 (originally spelled “gajarii”); Géczy, 1967b, p. 14, text-fig. 6, pl. I, fig. 2, pl. II, fig. 3, pl. LXIII, fig. 5, pl. LXV, fig. 80.*Phylloceras loczyi*: Prinz, 1904, p. 38, pl. XXVI, fig. 4, pl. XXXVI, fig. 3; Géczy, 1967b, p. 18, text-fig. 12, pl. I, fig. 3, pl. LXIII, fig. 9.*Phylloceras bockhi*: Prinz, 1904, p. 32, pl. XXVI, fig. 5–6, pl. XXXVI, fig. 2 (originally spelled “böckhi”).*Phylloceras* sp.: Géczy, 1967b, p. 15, text-fig. 9, pl. II, fig. 2, pl. LXIII, fig. 7.*Phylloceras doderleinianum*: Principi, 1915, p. 431, pl. XV, fig. 7; Zanzucchi, 1963, p. 108, pl. 13, figs. 1, 4; Géczy, 1967b, p. 16, text-fig. 10, pl. I, fig. 4, pl. LXIII, fig. 8; Pinna, 1969, p. 17, text-fig. 1 (=Meneghini, 1875a; pl. XVII, fig. 5); Galácz et al., 2010, p. 324, pl. 1, fig. 4; Kovács, 2011, p. 8, pl. I, figs. 5–6, pl. II, figs. 5–6; Benzaggagh, 2023, p. 7, figs. 8D–8G.

**Syntypes.** Illustrated in Catullo, 1853 (pl. I, figs. 3a–3e). They originate from the Toarcian oolitic limestones of the Vicenza province (Italy). However, modern researchers (Galácz et al., 2010; Kovács, 2011) follow the view of Meneghini (1875a, 1875b), asserting that only one of the two Catullo specimens (Catullo, 1853, pl. I, figs. 3a–3c) belongs to this species.

**Shell shape.** The shell is involute, medium or large, of medium width. The whorls are moderately increasing, with a wide oval or rounded rectangular section. The flanks are slightly convex. The venter is rounded, rather wide and low. The umbilicus is narrow, deep, and funnel-shaped.

**Ornamentation.** The internal mold is smooth. Occasionally, weakly developed, irregularly spaced constrictions may be present on the flanks of the inner whorls (Pl. I, fig. 1).

**Dimensions in mm and ratios in %:**

| Specimen no. | D    | H    | Du | W  | H/D  | W/D  | Du/D | H/W |
|--------------|------|------|----|----|------|------|------|-----|
| GM-2143      | 153  | ≈91  | —  | 60 | 59.5 | 39.2 | —    | 152 |
| MZ-149/3     | 50.5 | 24.8 | 7  | 18 | 49.1 | 35.6 | 13.9 | 138 |

**Comparison and remarks.** It differs from *Ph. heterophyllum* (J. Sowerby) in a broader cross-section, oval or rounded-rectangular, with a lower and wider ventral side, and from *Hantkeniceras hantkeni* (Schloenbach) in a narrower and higher cross-section.

**Occurrence.** It is a characteristic species of Toarcian Mediterranean phyllocerids: Italy (Zanzucchi, 1963; Pinna, 1969), Greece, Albania, Montenegro, Austria, and Hungary (Géczy, 1967b; Kovács, 2011), and Morocco (Benzaggagh, 2023).

**Material.** Two specimens nos. GM-2143 and MZ-149/3).

*Phylloceras? perplanum* Prinz, 1904

Plate 1, figs. 8a–8c; Plate 3, figs. 7a–7c

*Phylloceras perplanum*: Prinz, 1904\*, p. 35, pl. XXVII, fig. 3–4, pl. XXVI, fig. 6.*Phylloceras perplanum*: Géczy, 1967b, p. 21, text-fig. 16, pl. IV, figs. 1, 5, 6, pl. LXIII, figs. 16–18.

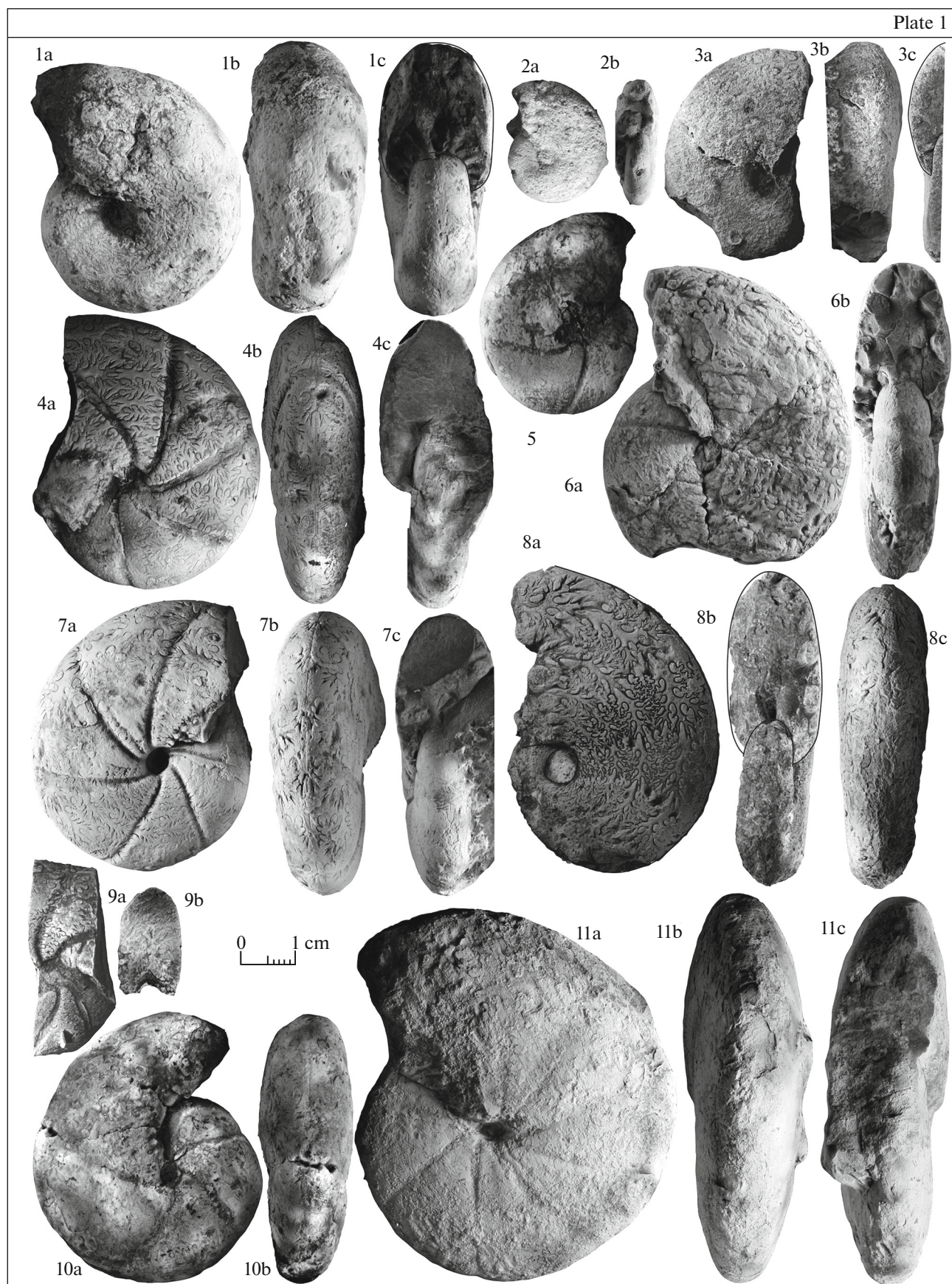
No type specimen has been designated. In addition to specimens from the Gyula Prinz collection, the type series includes specimens exhibited by the German paleontologist M. von Hantken at the 1873 World's Fair in Vienna, which were mentioned by Prinz in the original description (Prinz, 1904, p. 35). The specimens from the Prinz's collection are kept in the Geological Institute of Hungary (Budapest) and originate from the Aalenian of Hungary (Bakony Mountains); among them, specimen no. J.1057 is illustrated (Prinz, 1904, pl. XXVII, figs. 3–4).

**Shell shape.** The shell is medium-sized, involute, flattened. The whorls are elliptical, strongly compressed, with flattened subparallel flanks and a narrow, narrowly rounded venter. The umbilicus is narrow, funnel-shaped. The umbilical wall is subvertical, the umbilical bend is rounded-rectangular.

**Ornamentation.** A well-preserved specimen no. MZ-149/5 (Pl. 3, fig. 7a), shows faint, fine, closely spaced striations crossing the venter.

**Suture.** The suture has a deep and broad lobe L. The external saddle (V/L) is bipartite at its termination; the L/U1 saddle is broad and tripartite. The remaining saddles visible on the flanks are bipartite (Pl. I, fig. 8a).

**Plate 1.** Phylloceratidae. Here and in Plates II–VII, all figures are shown at natural size, unless otherwise indicated. *Phylloceras doderleinianum* (Catullo), specimen no. MZ-149/3: (1a) lateral view, (1b) ventral view, (1c) cross-section; (2, 3) *Phylloceras heterophyllum* (J. Sowerby), (2) specimen no. GM-1427: (2a) lateral view, (2b) cross-section; (3) specimen no. MZ-149/1: (3a) lateral view, (3b) ventral view, (3c) cross-section; (4, 7, 9) *Calliphylloceras capitantoi* (Catullo): (4) specimen no. MZ-149/10: (4a) lateral view, (4b) ventral view, (4c) cross-section; (7) specimen no. MZ-149/9: (7a) lateral view, (7b) ventral view, (7c) cross-section; (9) specimen no. MZ-149/11: (9a) lateral view, (9b) cross-section; (5–6, 10) *Calliphylloceras nilssoni* (Hébert), (5) specimen no. MZ-149/14: lateral view; (6) specimen no. MZ-149/12: (6a) lateral view, (6b) cross-section; (10) specimen no. MZ-149/13: (10a) lateral view, (10b) ventral view; (8) *Phylloceras? perplanum* Prinz, specimen no. MZ-149/4: (8a) lateral view, (8b) cross-section, (8c) ventral view; (11) *Calliphylloceras supraliasicum* (Pompeckj), specimen no. GM-2137: (11a) lateral view, (11b) ventral view, (11c) cross-section.



## Dimensions in mm and ratios in %.

| Specimen no. | D    | H    | Du | W    | H/D  | W/D  | Du/D | H/W |
|--------------|------|------|----|------|------|------|------|-----|
| MZ-149/4     | 57.5 | 32.5 | 5  | 17.5 | 56.5 | 30.4 | 8.7  | 186 |
| MZ-149/5     | 54   | 30.5 | 6  | 16   | 56.5 | 29.6 | 13   | 191 |

**Comparison and remarks.** It differs from *Ph. heterophyllum* (J. Sowerby) in the higher and narrower cross-section, as well as in the more flattened flanks. It differs from *Ph. prinzi* (Géczy) in the narrower cross-section.

Besnosov (1958) assigned this species to the genus *Calliphylloceras* based on the triphyllitic lateral saddle (L/U1). However, in the present study, the material is assigned to the genus *Phylloceras* because the internal mold completely lacks the constrictions characteristic of *Calliphylloceras*.

**Occurrence.** Aalenian of Hungary (Géczy, 1967b), Lower Aalenian of Argentina (Joly et al., 2023). The species is also reported from the Bajocian of Hungary (Galácz, 2015), the Aalenian of Turkey (Ankara region) (Türkünal, 1959), and the Lower Aalenian of Italy (Central Apennines) (Kälin, Ureta, 1987; Ferretti, 2017).

**Material.** Two well-preserved specimens (nos. MZ-149/4 and MZ-149/5).

**Genus *Calliphylloceras* Spath, 1927*****Calliphylloceras supraliasicum* (Pompeckj, 1893)**

Plate 1, figs. 11a–11c; Plate 2, fig. 6

*Ammonites heterophyllum jurensis*: Quenstedt, 1885 in Quenstedt, 1882–1885, p. 313, pl. 40, fig. 2, p. 401, pl. 51, fig. 1.

| Specimen no. | D   | H  | Du | W    | H/D  | W/D  | Du/D | H/W | Number of constrictions per whorl |
|--------------|-----|----|----|------|------|------|------|-----|-----------------------------------|
| GM-2137      | 72  | 41 | 2  | 21.5 | 56.9 | 29.9 | 2.8  | 191 | 9                                 |
| MZ-149/6     | 117 | 67 | —  | —    | 57.3 | —    | —    | —   | —                                 |

**Comparison.** It differs from other *Calliphylloceras* species in its high, spear-shaped cross-section, as well as numerous shallow, almost straight constrictions that wedge out towards the venter.

**Occurrence.** Lower Toarcian of Villebois (Ain Department, France (Joly, 2000)). Upper Toarcian

*Phylloceras supraliasicum*: Pompeckj, 1893\*, p. 29, text-fig. 5, pl. IV, fig. 1, 1a.

*Xeinophylloceras xeinus*: Buckman, 1921 (sp. nov.), pl. CCLXVIa, figs. 1–2.

*Calliphylloceras supraliasicum planulatum*: Géczy, 1967b (subsp. nov.), p. 41, text-fig. 39, pl. XI, pl. LXIII, fig. 43.

*Calliphylloceras supraliasicum hastaesimile*: Géczy, 1967b (subsp. nov.), p. 42, text-fig. 40, pl. X, fig. 2, pl. LXIII, fig. 44, pl. LXIV, fig. 1.

*Calliphylloceras supraliasicum*: Krimholz, 1961, p. 22, pl. I, fig. 3; Nutsubidze, 1966, p. 58, pl. XI, figs. 1–2; Géczy, 1967b, p. 40, text-fig. 38, pl. X, fig. 3, pl. LXIII, fig. 42; Schlegelmilch, 1992, p. 27, pl. 1, Fig. 3; Rulleau, 1998, p. 4, pl. 2, figs. 3–4; Joly, 2000, p. 89, pl. 20, figs. 3, 4, pl. 21, fig. 1, text-figs. 184–187; Cresta in Pavia and Cresta, 2002, p. 55, fig. 22; Rulleau, 2006, p. 50, text-fig. 10.7, pl. 3, fig. 1; Delsate and Weis, 2010, pl. 4, fig. 3.

*Calliphylloceras* aff. *mediojurassicum*: Rulleau, 1998, p. 31, pl. 4, fig. 6.

**Lectotype.** The lectotype was designated by Joly (2000, p. 89: Quenstedt, 1885 [1882–1885], pl. 40, fig. 2). It is kept at the University of Tübingen, Germany (specimen IGPT, Ce 5/4012). Upper Toarcian (“*Lytoceras jurensis* Zone” (= entire Upper Toarcian) (Oppel, 1856)), near Reutlingen (Swabian Alb). Reillustrated in Schlegelmilch, 1992 (Pl. 1, fig. 3).

**Shell shape.** The shell is discoidal, medium- to large-sized. The compressed high-oval whorls with a lanceolate cross-section. The maximum width point is located in the periumbilical third (Fig. 6). The flanks are weakly convex. The venter is rather narrow. The umbilicus is very narrow and funnel-shaped.

**Ornamentation.** The flanks bear a number (five per half-whorl) of shallow, weakly curved (almost straight), somewhat prorsiradiate constrictions. They reach their maximum depth in the periumbilical region. The constrictions become weaker as they approach the venter (especially on the outer whorls).

## Dimensions in mm and ratios in %.

(Pseudoradosa Zone) east of Lyon in southeastern France (Rulleau, 2006). Upper Toarcian (Fallaciosum Zone) of the Urup River valley (Northern Caucasus (Krimholz, 1961)). Upper Toarcian (Variabilis Zone) of Luxembourg (Delsate, Weis, 2010). Upper Toarcian (Pseudoradosa Subzone) of Stoford (Somerset, UK

**Plate 2.** Phylloceratidae, Lytoceratidae (all specimens shown at 0.5 scale). *Perilytoceras perlaevis* (Denckmann), specimen no. MZ-149/18: (1a) lateral view, (1b) ventral view, (1c) cross-section; (2, 3) *Alocolytoceras* ex gr. *germaini* (d’Orbigny): (2) specimen no. GM-2146: (2a) lateral view, (2b) ventral view, (2c) cross-section; (3) specimen no. MZ-149/15: (3a) lateral view, (3b) cross-section; (4) *Phylloceras doderleinianum* (Catullo), specimen no. GM-2143: (4a) ventral view, (4b) lateral view, (4c) cross-section; (5) *Phylloceras heterophyllum* (J. Sowerby), specimen no. MZ-149/2: (5a) lateral view, (5b) ventral view; (6) *Calliphylloceras supraliasicum* (Pompeckj), specimen no. MZ-149/6, lateral view.



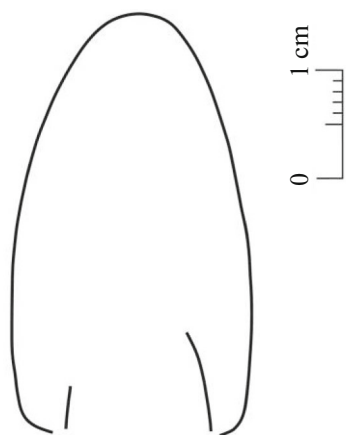


Fig. 6. Cross-section of *Calliphyloceras supraliasicum* (specimen no. GM-2137), D = 72 mm.

(Buckman, 1921)). Upper Toarcian (possibly Aalensis Zone) of the Swabian Alb (southwestern Germany (Quenstedt, 1885)). Upper Toarcian (Pseudoradiosa and Aalensis Zones) and Lower Aalenian of Belmont, northeastern France (Rulleau, 1998; Joly, 2000). Upper Toarcian (Pseudoradiosa and Aalensis Zones) and Lower Aalenian of the Bakony Mountains (Hungary (Géczy, 1967b)). Lower Aalenian of Sicily (Pavia and Cresta, 2002). Base of the Middle Aalenian (Opalinoides Subzone) (*Calliphyloceras* aff. *mediojurassicum* (Prinz) in Rulleau, 1998). Additionally, the species is mentioned without illustration from the Lower Toarcian (upper part of the Bifrons Zone) of Lombardy (northern Italy) (Mitzopoulos, 1930).

**Material.** One well-preserved internal mold (GM-2137) from the reddish-brown mudstones of the Lozovoe Quarry. Several other fragments of large *Calliphyloceras* specimens, featuring shallow and poorly defined constrictions, likely also belong to this species.

***Calliphyloceras spadae* (Meneghini, 1875a)**

Plate 3, figs. 1a–1c, 10a, 10b

*Ammonites* (*Phylloceras*) *spadae*: Meneghini, 1875a\*, p. 93, pl. XIX, figs. 1–4.

*Phylloceras spadae*: Meneghini, 1875b, p. 106; Fucini, 1901, p. 46, pl. VI, fig. 11; Prinz, 1904, p. 39, pl. XXVIII, fig. 3–4, pl. XXXVI, fig. 7; Principi, 1915, p. 433, pl. XV, figs. 3–5; Negri, 1936, p. 13, pl. 2 fig. 1.

*Phylloceras spadae* var. *chiesai*: Negri, 1936 (nov. var.), p. 15, pl. 2, figs. 2–3.

*Calliphyloceras spadae chiesai*: Géczy, 1967b (subsp. nov.), p. 29, text-fig. 23, pl. VII, fig. 5, pl. LXIII, fig. 26; Pinna, 1969, text-fig. 2.

*Calliphyloceras spadae praenuntius*: Géczy, 1967b (subsp. nov.), p. 28, text-fig. 21, pl. VII, fig. 4, pl. LXIII, fig. 23.

*Calliphyloceras spadae*: Géczy, 1967b, p. 28, text-fig. 22, pl. VII, figs. 2–3, pl. LXIII, figs. 24–25; Pinna, 1969, pl. VI, fig. 10; Panuzi, 1970, p. 73, pl. 5, figs. 4–6; Kovács, 2011, p. 12, pl. III, fig. 3, pl. IV, figs. 1–2.

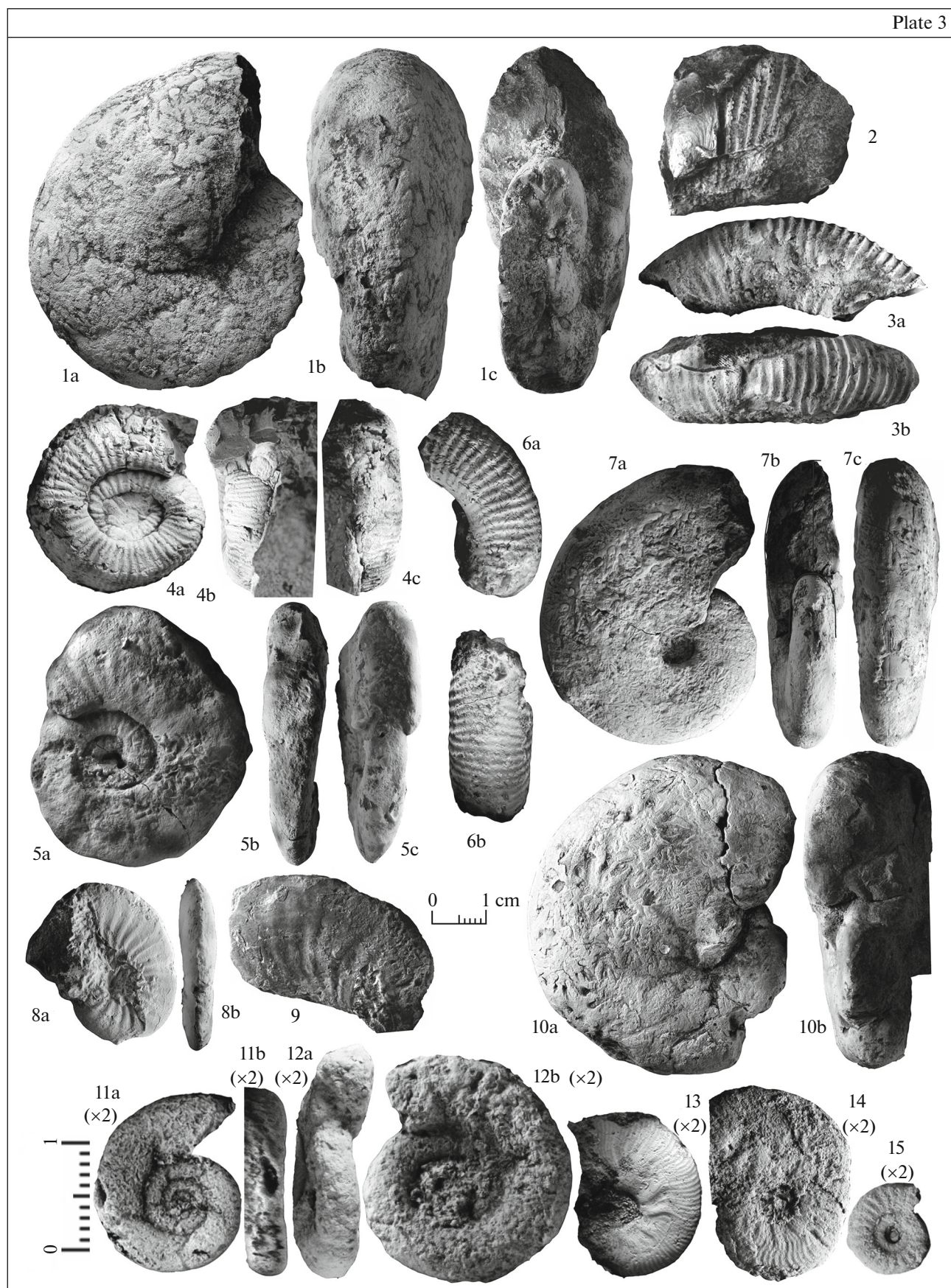
*Calliphyloceras* cf. *spadae*: Macchioni in Pavia and Cresta, 2002, p. 53, fig. 21.

The status of the type specimen is questionable. The type series originates from several Toarcian sections in the Central Apennines. One of the specimens, from the Frazione Cesi locality in the municipality of Terni, northern Italy (Meneghini, 1875a, pl. XIX, figs. 1a, 1b), was re-illustrated and labelled as the “holotype” by Pinna (1969, pl. VI, fig. 10). However, this is merely one of the specimens available to Meneghini, did not explicitly state that he was selecting it as the name-bearing type from the syntype series. Therefore, Pinna’s use of the term “holotype” cannot be regarded as a valid lectotype designation under Article 74.5 of the ICZN, contrary to the interpretation adopted by later authors (e.g. Kovács, 2011). We were unable to examine all earlier literature to determine whether Pinna (1973) was in fact the first author to designate this specimen as the lectotype. Such a designation could nevertheless be valid if it had been made by the earlier author in accordance with the requirements of Article 74.5 of the ICZN.

**Shell shape.** The shell is medium-sized, involute, and inflated. The whorls are fairly broad, oval or rounded-rectangular, with a wide, convex venter (Fig. 7). The flanks are moderately convex. The umbilicus is funnel-shaped, with a gentle, arcuate umbilical shoulder. The umbilical wall is convex.

**Ornamentation.** The flanks bear a large number (8–10 per whorl) of shallow, narrow, and distinctly concave constrictions. The constrictions originate at the umbilical shoulder, where they are relatively deep and sub-rectiradial. They then rapidly become prorsiradial, leaning increasingly forward and becoming shallower as they approach the venter. On the outer whorls, the constrictions may completely disappear within the ventral half of the flanks (specimen MZ-149/8).

**Plate 3.** Phylloceratidae, Lytoceratidae, Dactylioceratidae, Grammoceratinae. (1, 10) *Calliphyloceras spadae* (Meneghini): (1) specimen no. MZ-149/7: (1a) lateral view, (1b) ventral view, (1c) cross-section; (10) specimen no. MZ-149/8: (10a) lateral view, (10b) cross-section; (2) *Lytoceras* sp., specimen no. MZ-149/44, lateral view; (3, 6) Dactylioceratidae gen. et sp. indet.: (3) specimen no. MZ-149/45: (3a) lateral view, (3b) ventral view; (6) specimen no. MZ-149/46: (6a) lateral view, (6b) ventral view; (4) *Nodicoeloceras fonticulum* (Simpson), specimen no. Pnv-1877: (4a) lateral view, (4b) cross-section, (4c) ventral view; (5, 8–9) *Pleydellia* (*Pleydellia*) *leura* (Buckman), (5) specimen no. MZ-149/39: (5a) lateral view, (5b) ventral view, (5c) cross-section; (8) specimen no. MZ-149/40: (8a) lateral view, (8b) ventral view; (9) specimen no. MZ-149/41, lateral view; (7) *Phylloceras*? *perplanum* Prinz, specimen no. MZ-149/5: (7a) lateral view, (7b) cross-section, (7c) ventral view; (11, 12) *Alocolytoceras* sp., specimen no. MZ-149/16: (11a) lateral view,  $\times 2$ , (11b) ventral view,  $\times 2$ ; (12) specimen no. MZ-149/17: (12a) cross-section,  $\times 2$ , (12b) lateral view,  $\times 2$ ; (13, 14) *Pleydellia* (*Cotteswoldia*) cf. *subcompta* (juv.) (Branco): (13) specimen no. Pnv-1948, lateral view,  $\times 2$ ; (14) specimen no. GM-2132, lateral view,  $\times 2$ ; (15) *Grammoceras* sp. juv., specimen no. MZ-149/52, lateral view,  $\times 2$ .



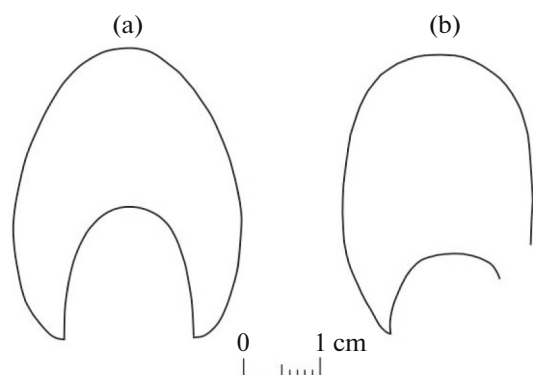


**Fig. 7.** Cross-section of *Calliphyloceras spadae*: (a) specimen no. MZ-149/7 (D = 65 mm); (b) specimen no. MZ-149/8 (D = 59 mm).

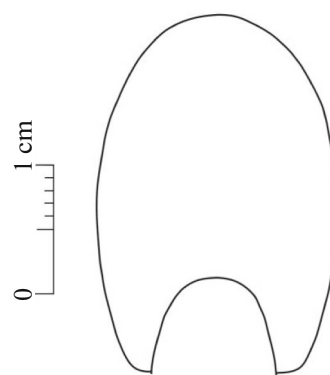


**Fig. 8.** Cross-section of *Calliphyloceras capitanoi*, specimen no. MZ-149/9, D = 52 mm.

#### Dimensions in mm and ratios in %.

| Specimen no. | D  | H  | Du | W    | H/D  | W/D  | Du/D | H/W | Number of constrictions per whorl |
|--------------|----|----|----|------|------|------|------|-----|-----------------------------------|
| MZ-149/7     | 65 | 35 | 8  | 27   | 53.9 | 41.5 | 12.3 | 129 | 8                                 |
| MZ-149/8     | 59 | 32 | 8  | 24.5 | 54.2 | 41.6 | 13.6 | 131 | 10                                |

**Comparison and remarks.** It differs from *C. supraliasicum* (Pompeckj) in a significantly wider and lower cross-section with a much broader venter, as well as by significantly more curved and less strongly developed constrictions. It differs from *C. capitanoi* (Catullo) and *C. nilssoni* (Hébert) in a wider and lower cross section, as well as by more numerous and shallower constrictions that become markedly fainter on the outer whorls in the ventral part of the flanks.

The Crimean sample includes specimens that differ in cross-sectional shape and correspond to Géczy's (1967b) concepts of several subspecies: the nominate subspecies with a rounded-rectangular section; *C. spadae chiesai* (Negri), distinguished by a particularly broad venter; and *C. spadae praenuntius* Géczy, with a sub-oval section. In the present study, all of these are treated as synonyms of *C. spadae*.

**Occurrence.** Toarcian of Sicily (Pavia and Cresta, 2002), Italy (Pinna, 1969) and Greece, subzone "Struckmanni" (Fallaciosum) of the Thouarsense Zone of North Tyrol (Austria (Fischer, 1966)); Pliensbachian–Toarcian, ?Aalenian of Hungary (Géczy, 1967b), *H. pseudoserpentinum* Biohorizon of the Bakony and Gerecse Mountains (Bakony Mts; Gerecse Mts) in northwestern Hungary (Galácz et al., 2010; Kovács, 2011). In addition, the species *C. cf. spadae* (Meneghini)

is mentioned without description or image from the Toarcian of Northern Turkey (Alkaya, 1983, p. 70).

**Material.** Two nearly complete inner molds (nos. MZ-149/7 and MZ-149/8).

#### *Calliphyloceras capitanoi* (Catullo, 1847)

Plate 1, figs. 4a–4c, 7a–7c, 9a, 9b

*Ammonites capitanei*: Catullo, 1847\*, p. 5, pl. 12, figs. 4a–4c.

*Ammonites capitanei*: Catullo, 1853, p. 38, pl. 4, figs. 4a–4c.

*Phylloceras capitanei*: Meneghini, 1875a, p. 94, pl. 18, figs. 4–6.

*Calliphyloceras capitanoi*: Pinna, 1969, pl. VI, figs. 4, 11.

*Calliphyloceras capitanei*: Macchioni in Pavia, Cresta, 2002, p. 46, fig. 15; Kovács, 2011, p. 10, pl. II, figs. 1–2, pl. III, figs. 5–6; Đaković et al., 2021, text-fig. 7A.

**Holotype.** By monotypy; figured by Catullo (1847, p. 5, pl. 12, figs. 4a–4c). Toarcian of the Venetian Alps (Alpi Venete) (Italy).

**Shell shape.** The shell is medium-sized, involute, and of moderate thickness. The whorls have an elliptical cross-section, with the point of maximum width located approximately at the mid-height of the whorl (Fig. 8). The flanks are weakly convex, and the venter is convex. The umbilicus is narrow and funnel-shaped.

**Ornamentation.** The flanks of the mold bear regularly spaced, concave, prorsiradiate constrictions (7 constrictions per whorl at D = 50 mm) that cross the venter with slight weakening.

#### Dimensions in mm and ratios in %.

| Specimen no. | D    | H    | Du  | W  | H/D  | W/D  | Du/D | H/W | Number of constrictions per whorl |
|--------------|------|------|-----|----|------|------|------|-----|-----------------------------------|
| MZ-149/9     | 52   | 27.5 | 5   | 17 | 52.9 | 32.7 | 9.6  | 162 | 7                                 |
| MZ-149/10    | 53.2 | 31   | 3.5 | 19 | 58.3 | 35.7 | 6.6  | 163 | 7                                 |
| MZ-149/11    | 36   | 21   | 2.5 | 15 | 58.3 | 41.7 | 6.9  | 140 | —                                 |

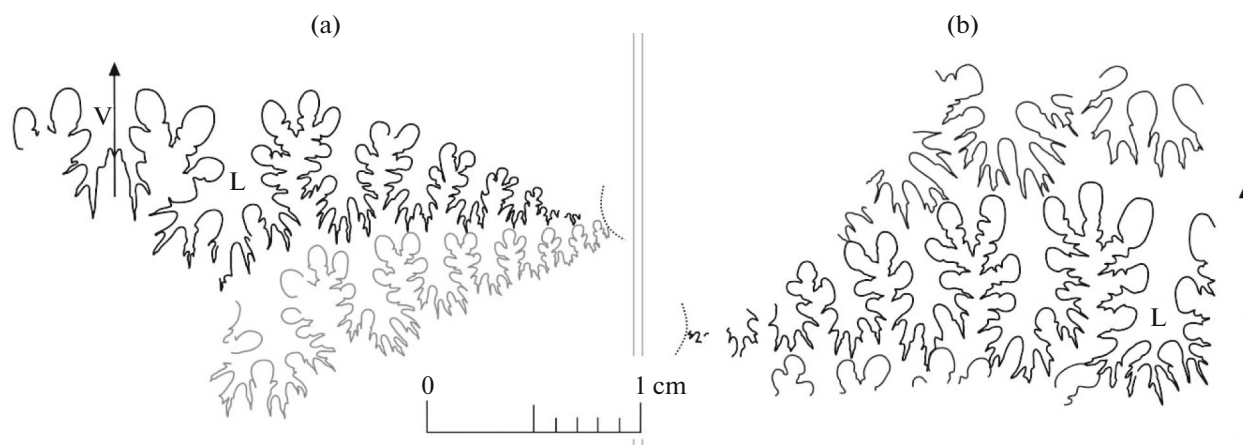


Fig. 9. Suture of *Calliphyloceras capitanoi*: (a) Specimen no. MZ-149/9 (D = 40 mm); (b) specimen no. MZ-149/10 (D = 45 mm).

**Suture.** The ventral lobe is shallow and narrow (its depth is approximately twice its width). The lateral lobe is wide, deep, and somewhat asymmetrical, approximately 1.5 times as deep as the ventral lobe. The V/L saddle is bipartite at its termination, while the L/U<sup>1</sup> saddle is tripartite. All subsequent saddles have a diphyletic termination (Fig. 9).

**Comparison.** It differs from the closely related *C. nilssoni* (Hébert) in having a greater number of constrictions, which are deeper. Furthermore, the constrictions of this species are less curved and are spaced more regularly and closely together. There are also differences in the cross-section shape; that of *C. capitanoi* is broader and typically has more convex flanks.

It differs from *C. beatricis* (Bonarelli) in a larger shell, as well as in somewhat narrower and more concave constrictions.

**Occurrence.** Toarcian of Italy, Greece, Austria, Albania, Algeria, and (?) Turkey; in Hungary, it is reported from the Serpentinum–Bifrons zonal interval of the Lower Toarcian (Kovács, 2011); Bifrons Zone of the Dinaric Alps (Montenegro).

**Material.** Three well-preserved internal molds (Nos. MZ-149/9, MZ-149/10, and MZ-149/11), as well as about 10 internal mold fragments. Specimens of this species have also been found at the Petropavlovka Quarry (unpublished data).

#### *Calliphyloceras nilssoni* (Hébert, 1866)

Plate 1, figs. 5, 6a, 6b, 10a, 10b

*Ammonites calypso*: d'Orbigny, 1845 in d'Orbigny, 1842–1851, p. 342, pl. 110, figs. 1–3; non d'Orbigny, 1841 [1840–1842], p. 167, pl. 52, figs. 7–9 (= *Leiohyloceras calypso* (d'Orbigny, 1841), after Arkadiev, 2002).

#### Dimensions in mm and ratios in %.

| Specimen no. | D  | H    | Du  | W  | H/D  | W/D  | Du/D | H/W | Number of constrictions per whorl |
|--------------|----|------|-----|----|------|------|------|-----|-----------------------------------|
| MZ-149/12    | 60 | 32.5 | 5   | 17 | 54.2 | 28.3 | 8.3  | 191 | 5                                 |
| MZ-149/13    | 50 | 28   | 2.5 | 17 | 56   | 34.0 | 5.0  | 165 | 5                                 |
| MZ-149/14    | 39 | 20.5 | 4.5 | 14 | 52.6 | 35.9 | 11.5 | 146 | 4                                 |

*Ammonites nilssoni*: Hébert, 1866\*, p. 527, fig. 3 (nom. nov. pro pars. *Ammonites calypso* d'Orbigny, 1845); Dumortier, 1874, p. 106.

*Phylloceras aveyronense*: Meneghini, 1875a (subsp. nov.), p. 93.

*Phylloceras nilssoni*: Schröder, 1927, p. 127, pl. VII (I), figs. 7a–7c, 8.

*Calliphyloceras aveyronense*: Géczy, 1967b, p. 36, text-fig. 32, pl. V, figs. 6, 7, pl. LXIII, figs. 34–35.

*Phylloceras nilssoni altisulcata*: Prinz (subsp. nov.), 1904, p. 40, pl. XXVIII, fig. 5, pl. XXVII, fig. 5.

*Calliphyloceras nilssoni*: Pannuzi, 1970, p. 66, pl. 4, figs. 1–12; Joly in Fischer et al., 1994, p. 97, text-fig. 30, pl. 32, figs. 3a–3c; Alméras et al., 1998, p. 90, pl. 15, figs. 1a–1b (= Dumortier, 1874, p. 106); Joly, 2000, p. 85, pl. 19, figs. 6a–6b, 7, 8a–8b, text-figs. 177–181; Kovács, 2011, p. 10, pl. II, figs. 3–4; Fauré, 2013, p. 22, pl. 1, figs. 10–11; Bardin et al., 2014, p. 11, figs. 4G–4H.

*Calliphyloceras* aff. *capitanei*: Benzaggagh, 2023, p. 8, figs. 9C–9G.

**Lectotype.** Designated by B. Joly (Fischer et al., 1994, p. 97, pl. 32, figs. 3a–3c). Originally illustrated in d'Orbigny, 1842–1851 (pl. 110, figs. 1–3). Housed in the Gallery of Paleontology and Comparative Anatomy of the Paris Museum of Natural History (Galerie de paléontologie et d'anatomie comparée, Muséum national d'Histoire naturelle (MNHN), specimen no. MNHN F R00518 (d'Orbigny collection no. 1926 D-1)). Comes from the Occitanie region, Aveyron Department, southern France.

**Shell shape.** The shell is of medium size, flattened or of moderate thickness, with flattened or weakly convex flanks and a narrow, strongly convex venter. The whorls are high, suboval (Fig. 10). The umbilicus is narrow or nearly closed, funnel-shaped.

**Ornamentation.** The flanks bear relatively widely spaced, shallow constrictions (4–5 per whorl). The constrictions are strongly curved: rectiradiate near the umbilical margin and strongly projected forward on the flanks. They cross the venter with reduced relief, curving forward.

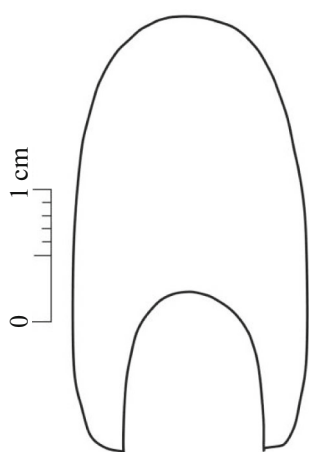


**Fig. 10.** Cross-section of *Calliphylloceras nilssoni*, specimen no. MZ-149/12, D = 60 mm.

**Suture.** It is preserved only fragmentarily in the available specimens (Fig. 11).

**Comparison.** It differs from *C. capitatioi* (Catullo) in having fewer constrictions, a more pronounced prorsiradiate constrictions, which are generally shallower and less distinct. Furthermore, it is distinguished by flatter flanks, a narrower and higher cross-section, and a stronger forward curvature of the constrictions as they cross the venter. It differs from *C. pompeckji* (Hug) in having more strongly prorsiradiate constrictions.

**Occurrence.** Toarcian of Europe (Slovakia, Germany (Schröder, 1927), France (Fischer et al., 1994; Alméras et al., 1998; Fauré, 2013), Italy (Pannuzi, 1970), Spain, Hungary (Géczy, 1967b; Kovács, 2011)), North Africa (Morocco (Bardin et al., 2014; Benzaggagh, 2023), Tunisia (Soussi et al., 1998)), Turkey (Türkunal, 1959), Iran, North America, and

Japan. It is recorded, without illustration, from Toarcian–Aalenian red bioclastic limestones of the Ammonitico Rosso facies in the Caucasus (near the village of Martotubani, Imereti, Georgia (Topchishvili et al., 2006)). In Europe, the species is common in Alpine regions and rare in Euro-Boreal regions.

**Material.** Three nearly complete internal molds (nos. MZ-149/12–MZ-149/14) and numerous mold fragments. Specimens of this species have also been found at the Petropavlovka Quarry (unpublished data).

## ORDER LYTOCERIDA

HYATT, 1889

## SUBORDER LYTOCERINA

HYATT, 1889

## SUPERFAMILY LYTOCERATOIDEA

NEUMAYR, 1875

## FAMILY LYTOCERATIDAE NEUMAYR, 1875

## SUBFAMILY ALOCOLYTOCERATINAE

SPATH, 1927

## Genus *Alocolytoceras* Hyatt, 1900

*Alocolytoceras* ex gr. *germaini* (d'Orbigny, 1845)

Plate 2, figs. 2a, 2c, 3a, 3b

**Shell shape.** The shell is large and inflated. The whorls are broad, with their maximum width at the umbilical shoulder. The cross-section of the inner whorls is broadly rounded. During ontogeny, the whorls increase rapidly in width. The umbilicus is stepped, moderately wide and deep. The umbilical shoulder is rounded. The umbilical wall is clearly defined, high, and slightly convex.

**Ornamentation.** Five broad, shallow constrictions are present on the outer whorl. The constrictions cross the venter with slight weakening. Ribs are absent on the preserved whorls.

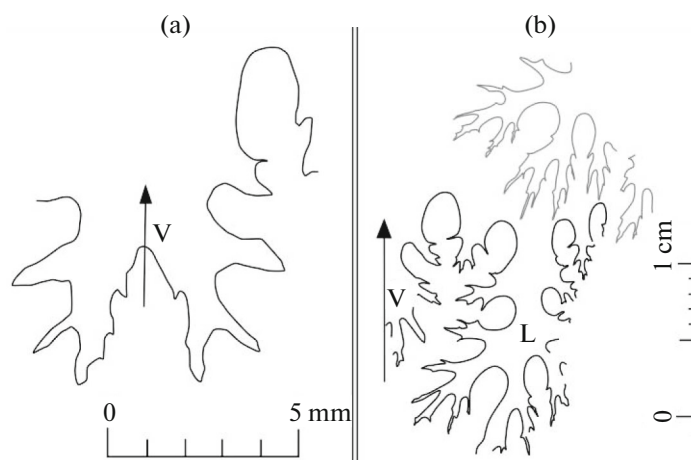


**Fig. 11.** Suture of *Calliphylloceras nilssoni*: (a) Specimen no. MZ-149/12, D = 51 mm, ventral lobe; (b) specimen no. MZ-149/12, D = 55 mm, lateral lobe.

## Dimensions in mm and ratios in %.

| Specimen no. | D   | H  | Du | W  | H/D | W/D  | Du/D | H/W  | Number of constrictions per whorl |
|--------------|-----|----|----|----|-----|------|------|------|-----------------------------------|
| GM-2146      | 134 | 59 | 45 | 64 | 44  | 47.8 | 33.6 | 92.2 | 5                                 |
| MZ-149/15    | —   | 43 | —  | 63 | —   | —    | —    | 68.3 | —                                 |

**Comparison and remarks.** The Crimean specimens are characterized by broad, depressed outer whorls with a well-defined umbilical wall and sparsely located broad and shallow constrictions. In their shape, by the number of constrictions, and cross-section, they closely resemble *A. germaini* (d'Orbigny) (lectotype designated by Mouterde in Fischer, 1994, p. 89), differing in having a somewhat broader whorl section ( $H/W = 68\text{--}92\%$ ). *A. sp.* (Rulleau, 1991, pl. 14, figs. 3–5; 1998, fig. 10.5, pl. 23, fig. 4; 2006, fig. 13.5) from the Dispansum Zone of the Upper Toarcian in France also appears to be similar.

According to Rulleau (2006), the *A. gr. germaini* (d'Orbigny) group comprises a series of closely related forms linked by a continuous morphological transition. Consequently, they can be regarded either as morphotypes of a variable species or as distinct species (or subspecies). For this reason, the identification here is presented using open nomenclature.

It differs from *Pleurolytoceras hircinum* (Schlotheim) in its larger size and having a fewer constrictions, and from *A. coarctatum* (Pompeckj) in the larger size of the adult shell and the wider cross-section.

## Dimensions in mm and ratios in %.

| Specimen no. | D  | H   | Du  | W   | H/D  | W/D  | Du/D | H/W | Number of constrictions per whorl |
|--------------|----|-----|-----|-----|------|------|------|-----|-----------------------------------|
| MZ-149/16    | 17 | 6.2 | 6.5 | —   | 36.5 | —    | 38.2 | —   | 6                                 |
| MZ-149/17    | 22 | 7.5 | 9   | 5.1 | 34.1 | 23.2 | 40.9 | 147 | 6                                 |

**Comparison and remarks.** The molds are strongly evolute at the juvenile stage and are characterized by the absence of fimbriate ribs as well as possess well-defined, curved, regularly spaced constrictions, which distinguishes them from *Lytoceras* Suess. They differ from *Pleurolytoceras* Hyatt in the significantly more widely spaced constrictions and their curved shape.

The material is assigned to the genus *Alocolytoceras* based on the presence of well-defined constrictions, a feature that distinguishes this genus from contemporaneous lytocerids.

**Occurrence.** The genus *Alocolytoceras* is known from the Lower Toarcian (Bifrons Zone, “Sublevisoni” [=Commune] Subzone) to the Lower Bajocian in both the Mediterranean region (Italy, Hungary, southeastern France, North Africa [Algeria, Morocco]) and northwestern Europe (southern Germany, Great Britain).

**Occurrence.** From the terminal Fallaciosum Subzone of the Thouarsense Zone to the top of the Dispansum Zone of the Upper Toarcian of France (Rulleau, 2006), in the Upper Toarcian of Germany (Sudetes) (Schlegelmilch, 1992) and Great Britain (Buckman, 1905b, p. 145).

**Material.** A well-preserved internal mold (specimen no. GM-2146) from the reddish-brown argillites of the Lozovoe Quarry, as well as several fragments from limestone boulders.

*Alocolytoceras* sp. juv.

Plate 3, figs. 11a, 11b, 12a, 12b

**Shell shape.** The shell is ophioconic, small, and flattened. The whorls are weakly overlapping, with an elliptical cross-section. The flanks are convex; the venter is narrow and convex. The umbilicus is wide, bowl-shaped, and shallow.

**Ornamentation.** The flanks bear six narrow, deep, concave, prorsiradiate constrictions per whorl. The constrictions reach their maximum depth near the umbilical shoulder and, weakening towards the venter, cross it with a slight backward curve. Ribs are entirely absent on the preserved internal molds.

**Material.** About 10 internal molds and their fragments from limestone boulders from the Lozovoe and Petropavlovka quarries.

## SUBFAMILY MEGALYTOCERATINAE SPATH, 1927

Genus *Perilytoceras* Rulleau, 1997*Perilytoceras perlaevis* (Denckmann, 1887)

Plate 2, figs. 1a–1c

*Ammonites perlaevis*: Denckmann, 1887\*, p. 45, pl. II, figs. 5, 5a. *Perilytoceras perlaevis*: Rulleau, 1997, p. 455, text-figs. 3/1, 4b, pl. 1, fig. 2; Rulleau, 1998, p. 54, text-figs. 8-1, 9-2, pl. 17, fig. 3, pl. 19, figs. 1–2; Rulleau, 2006, p. 56, text-fig. 12-1, pl. 7, figs. 3a, 3b; Benzaggagh, 2023, p. 9, figs. 10A–10C.

*Perilytoceras* ex gr. *perlaevis* (Denckmann): Fauré, 2002, p. 696, pl. 2, figs. 1–2; Fauré, 2007, p. 40, figs. 6.1–6.3.

**Holotype.** By monotypy. Figured by Denckmann, 1887 (pl. II, figs. 5, 5a). The *Grammoceras striatulus* level at the base of the Thouarsense Zone (Upper Toarcian) of Dörnten (municipality of Liebenburg, Lower Saxony, Germany).

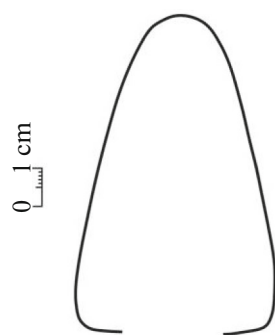


**Fig. 12.** Cross-section of *Perilytoceras perlaevis*, specimen no. MZ-149/18, D = 180 mm.

**Shell shape.** The shell is large and flattened. The whorls are slightly overlapping and compressed, with the point of maximum width near the umbilical shoulder; the cross-section is rounded-triangular, and whorl height increases rapidly during ontogeny (Fig. 12). The body chamber is extremely compressed. The flanks, convex on the inner whorls and flattened on the body chamber, gradually transiting into a narrowly rounded venter. The umbilicus is moderately wide and stepped. The umbilical shoulder is well-defined and rounded. The umbilical wall is subvertical.

**Ornamentation.** The internal mold is completely smooth.

**Dimensions in mm and ratios in %:**

| Specimen<br>no. | D   | H  | Du | W  | H/D | W/D | Du/D | H/W |
|-----------------|-----|----|----|----|-----|-----|------|-----|
| MZ-149/18       | 202 | 85 | 64 | 54 | 42  | 27  | 32   | 157 |

**Comparison.** This species differs from *P. jurensis* (Zieten) in the higher, rounded-triangular whorl section, which are significantly more compressed, as well as by a more evolute shell. It differs from *P. denckmanni* (Ernst) in having a vertical umbilical wall, whereas in *P. denckmanni* the wall is beveled (at an angle of about 45°) relative to the flanks. It is distinguished from *P. belmontense* Rulleau by a noticeably narrower whorl section and a narrower venter.

**Occurrence.** This species is the earliest representative of the genus *Perilytoceras*; it is known from the Thouarsense Zone (Striatulum Subzone) of Great Britain, France, and Germany, as well as from the Upper Toarcian of Morocco (Benzaggagh, 2023). The forms from Lyon described by Rulleau are likely somewhat older (Bingmanni Subzone) (Rulleau, 2006, p. 31; Fauré, 2007, p. 40).

**Material.** One large specimen (no. MZ-149/18).

## ORDER AMMONITIDA HAECKEL, 1866

### SUBORDER PSILOCERINA SEHIDEWOLF, 1923

#### SUPERFAMILY EODEROCERATOIDEA SPATH, 1929

#### FAMILY AMALTHEIDAE HYATT, 1867

#### Genus *Amaltheus* de Montfort, 1808

Subgenus *Amaltheus* de Montfort, 1808

#### *Amaltheus (Amaltheus) stokesi* (J. Sowerby, 1818)

Plate 4, figs. 1a, 1b

*Ammonites stokesi*: J. Sowerby, 1818 in Sowerby, 1818–1821\*, p. 205, pl. CXCI.

*Ammonites clevelandicus*: Young, Bird, 1822 (sp. nov.), p. 253, pl. XIII, fig. 11.

*Ammonites clevelandicus*: Simpson, 1843, p. 39; Simpson, 1884, p. 118.

*Amaltheus margaritatus*: Wright, 1882, p. 397, pl. LVI, fig. 15; Krimholz, 1961, p. 34, pl. I, fig. 8.

*Amaltheus clevelandicus* Young et Bird: Buckman, 1918 in Buckman, 1909–1930, pl. CIX.

*Amaltheus stokesi*: Spath, 1935, p. 396, pl. XVIII, fig. 2; Howarth, 1958, p. 3, pl. 1, figs. 5, 7, 12–14, pl. II, figs. 1, 3, 10, text-figs. 4–5; Stefanov, 1960, p. 272, pl. I, fig. 2 (figs. 6, 9?); Frebold, 1964a, p. 9, pl. II, figs. 2–6; Frebold, 1964b, pl. VI, figs. 6, 7, 13; Stankevich, 1964, p. 18, pl. II, fig. 5; Frebold, 1966, pl. I, figs. 1–4; Frebold et al., 1967, p. 14, pl. I, figs. 1–3, 5, 7; Repin, 1968, p. 108, pl. 36, fig. 2; Frebold, 1970, p. 441, pl. III, fig. 1; Elmi et al., 1974, p. 32, fig. 17.5, pl. I, figs. 2–3; Repin, 1974, p. 55, pl. I, fig. 4–9, text-fig. 2; Frebold, 1975, p. 10, pl. 4, figs. 3, 4; Wiedenmayer, 1980, p. 51, pl. 2, Fig. 11; Sey and Kalacheva, 1980, p. 71, pl. 1, fig. 4, 6–8, 11, 13; Imlay, 1981, pl. 10, figs. 27–28; Dommergues et al., 1983, pl. 3, fig. 9; Meister, 1988, pl. 1, fig. 1; Poulton, 1991, p. 18, pl. 8, figs. 2, 7–8; Smith in The Jurassic..., 1992, pl. 3, fig. 11, pl. 5, fig. 9; Jakobs and Pálffy, 1994, pl. 1, figs. 8–9; Smith and Tipper, 1996, p. 51, pl. 19, fig. 1, pl. 20, fig. 3, text-figs. 36a–36b; Biostratigraphie..., 1997, pl. 7, figs. 14–15; Géczy and Meister, 1998, p. 102, pl. 6, fig. 10; Meister and Friebe, 2003, p. 49, pl. 16, figs. 9, 14; Schubert, 2004, pl. 1, fig. 6; Callomon and Gradinaru, 2005, p. 56, pl. 2, fig. 2; Topchishvili et al., 2006, pl. 11, fig. 4; Fauré, 2006, fig. 8.5; Mouterde et al., 2007, p. 75, pl. 1, figs. 9, 14; Shirmohammad et al., 2011, pl. 1, fig. 14; Nützel et al., 2016, fig. 2; Nakada et al., 2021, p. 1009, fig. 4; Bohain et al., 2023, pl. 11, figs. 5, 6a, 6b, 7a, 7b, pl. 12, figs. 1a–1c; Bohain, 2024, pl. 15, figs. 11–12, pl. 16, figs. 2a–2c, 3a, 3; Geist et al., 2025, p. 6, Figs. 3D, 3E.

*Amaltheus* cf. *nudus*: Imlay, 1955, p. 87, pl. 10, fig. 5.

*Amaltheus* cf. *margaritatus*: Repin, 1968, p. 108, pl. 35, fig. 3.

*Amaltheus* sp. cf. *A. stokesi*: Hirano, 1971, p. 101, pl. 17, figs. 11a, 11b.

*Amaltheus (Proamaltheus) stokesi*: Dagys, 1976, p. 21, pl. X, fig. 5–7.

*Amaltheus (Amaltheus) stokesi*: Krimholz et al., 1988, pl. 2, fig. 1;

Hoedemaeker, 2012, p. 78, pl. 17, fig. L; Repin, 2016, pl. IV, fig. 4–5.

*Amaltheus (Amaltheus) cf. stokesi*: Meledina and Shurygin, 2001, p. 38, pl. I, fig. 2.

*Amaltheus* cf. *stokesi*: Seyed-Emami et al., 2008, p. 245, fig. 4B.

**Holotype.** By monotypy. Figured by J. Sowerby (1818, p. 205, pl. 191); refigured by Howarth (1958, pl. I, fig. 7), and on the website GB3D Type Fossils Online: <https://www.3d-fossils.ac.uk/fossilType.cfm?typSampleId=15000506>. Stored in the Oxford University Museum of Natural History (William Buckland collection, specimen no. OUM J.02248). Comes from the Upper Pliensbachian (*Amaltheus stokesi* Subzone) of Great Britain (Bridport, Dorset, near Eype Mouth).

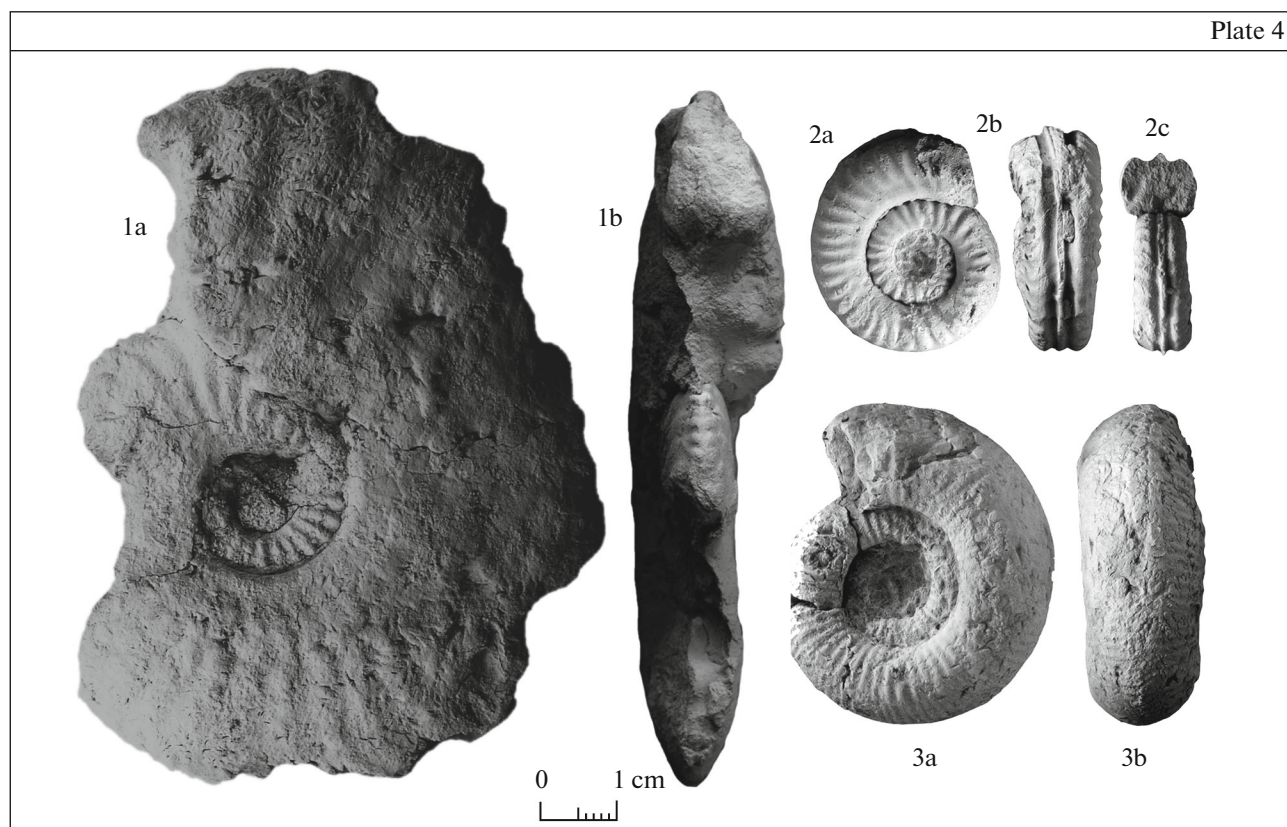


**Plate 4.** Amaltheidae. (1) *Amaltheus (Amaltheus) stokesi* (J. Sowerby), specimen no. MZ-149/19: (1a) lateral view, (1b) cross-section; (2) *Hildoceras laticostum* Bellini, specimen no. MZ-149/29: (2a) lateral view, (2b) ventral view, (2c) cross-section; (3) *Nodicoeloceras* ex gr. *crassoides* (Simpson), specimen no. MZ-149/22: (3a) lateral view, (3b) ventral view.

**Shell shape.** The shell is large, oxyconic. The whorls are high, strongly compressed, and lanceolate in cross-section, with a rounded umbilical shoulder. Each successive whorl overlaps approximately half of the preceding one.

**Ornamentation.** The ribs on the flanks are rectiradial, broad, and have no nodes, exhibiting a slight sigmoidal curvature. The ribs bifurcate or trifurcate near the venter, continuing as riblets (“chevrons”) that cover the blunt keel.

#### Dimensions in mm and ratios in %.

| Specimen no. | D | H    | Du | W | H/D | W/D | Du/D | H/W | Number of primary ribs per ½ whorl |
|--------------|---|------|----|---|-----|-----|------|-----|------------------------------------|
| MZ-149/19    | — | 43.8 | 24 | — | —   | —   | —    | —   | 16                                 |

**Comparison.** This species differs from *A. bifurcus* Howarth in having less coarse ribbing and lacking nodes on the ribs. It differs from *A. margaritatus* (Montfort) in having nearly straight, somewhat sigmoid ribs that transition directly into ventral “chevrons,” whereas in *A. margaritatus* the rib terminations fade and become barely discernible, and the keel, covered with riblets inclined toward the aperture, is separated from them by a distinct smooth band. It differs from *A. talrosei* Repin in having a narrower umbilicus and fewer whorls at the same size.

**Occurrence.** The species is characteristic of the basal Upper Pliensbachian (Stokesi Subzone of the Margaritatus Zone) and has an almost worldwide distribution across the Boreal, Euroboreal, Tethyan, and Pacific paleobiogeographic realms.

Upper Pliensbachian, Margaritatus Zone of the Northern Caucasus (Stankevich, 1964) and Georgia (Topchishvili et al., 2006); Stokesi Subzone of the Margaritatus Zone in Great Britain (Howarth, 1958), Canada (Frebold, 1966), Alaska (Imlay, 1981), British Columbia and Yukon (Imlay, 1968), the Canadian

Arctic Archipelago (Borden Island; Frebold, 1975), Bulgaria (Stefanov, 1960), the Romanian Carpathians (Callomon and Gradinaru, 2005), the Czech Republic (Western Carpathians; Geist et al., 2025), Portugal (Mouterde et al., 2007), northwestern Germany (Schubert, 2004), the Netherlands (Hoedemaeker, 2012), the Northern Calcareous Alps of Austria (Meister and Friebe, 2003), France (Meister, 1988; Biostratigraphie... 1997; Fauré, 2006; Bohain, 2024), the Bakony Mountains (Romania; Dommergues et al., 1983), Algeria (Elmi et al., 1974), Japan (Nakada et al., 2021), the Russian Far East and northern Siberia (Viliga, Sededema, and Bolshoy Anyuy rivers, as well as Transbaikalia and the Bureya River; Meledina and Shurygin, 2001; Repin, 2016); Stokesi Zone in Iran (Seyed-Emami et al., 2008) and Yakutia (Krimholz et al., 1988); Kunae Zone in British Columbia, Canada (Shirmohammad et al., 2011).

**Material.** One large specimen (no. MZ-149/19) from reddish-brown limestones. The juvenile specimen no. MZ-149/20, identified here as *Amaltheus* sp. juv. (Pl. 5, figs. 10a, 10b), possibly belongs to the same species.

#### Dimensions in mm and ratios in %.

| Specimen no. | D  | H  | Du | W  | H/D  | W/D  | Du/D | H/W | Number of primary ribs per ½ whorl |
|--------------|----|----|----|----|------|------|------|-----|------------------------------------|
| MZ-149/21    | 40 | 11 | 19 | 10 | 27.5 | 25.0 | 47.5 | 110 | 34                                 |

**Comparison and remarks.** It differs from *Zugodactylites braunianus* (d'Orbigny) in having significantly less developed nodes at the bifurcation point, as well as its lower position; from *D. (D.) athleticum* (Simpson) by the absence of a ventral rib curvature (sinus); and from typical *D. (D.) commune* by denser ribbing at all growth stages—a feature that accounts for its designation in open nomenclature. The absence of apertural modifications in dactylioceratids complicates the identification of microconchs and macroconchs within this group. It is possible that these ammonites exhibit morphotypes of varying sizes, a phenomenon frequently observed in certain Late Jurassic and Early Cretaceous ammonites that also lack specific apertural modifications (Rogov, 2021). The specimen described here is similar in size to mac-

#### FAMILY DACTYLIOCERATIDAE HYATT, 1867

##### SUBFAMILY DACTYLIOCERATINAE HYATT, 1867

#### Genus *Dactylioceras* Hyatt, 1867

##### Subgenus *Dactylioceras* Hyatt, 1867

#### *Dactylioceras (Dactylioceras) ex gr. commune* (J. Sowerby, 1815)

Plate 5, figs. 6a–6c

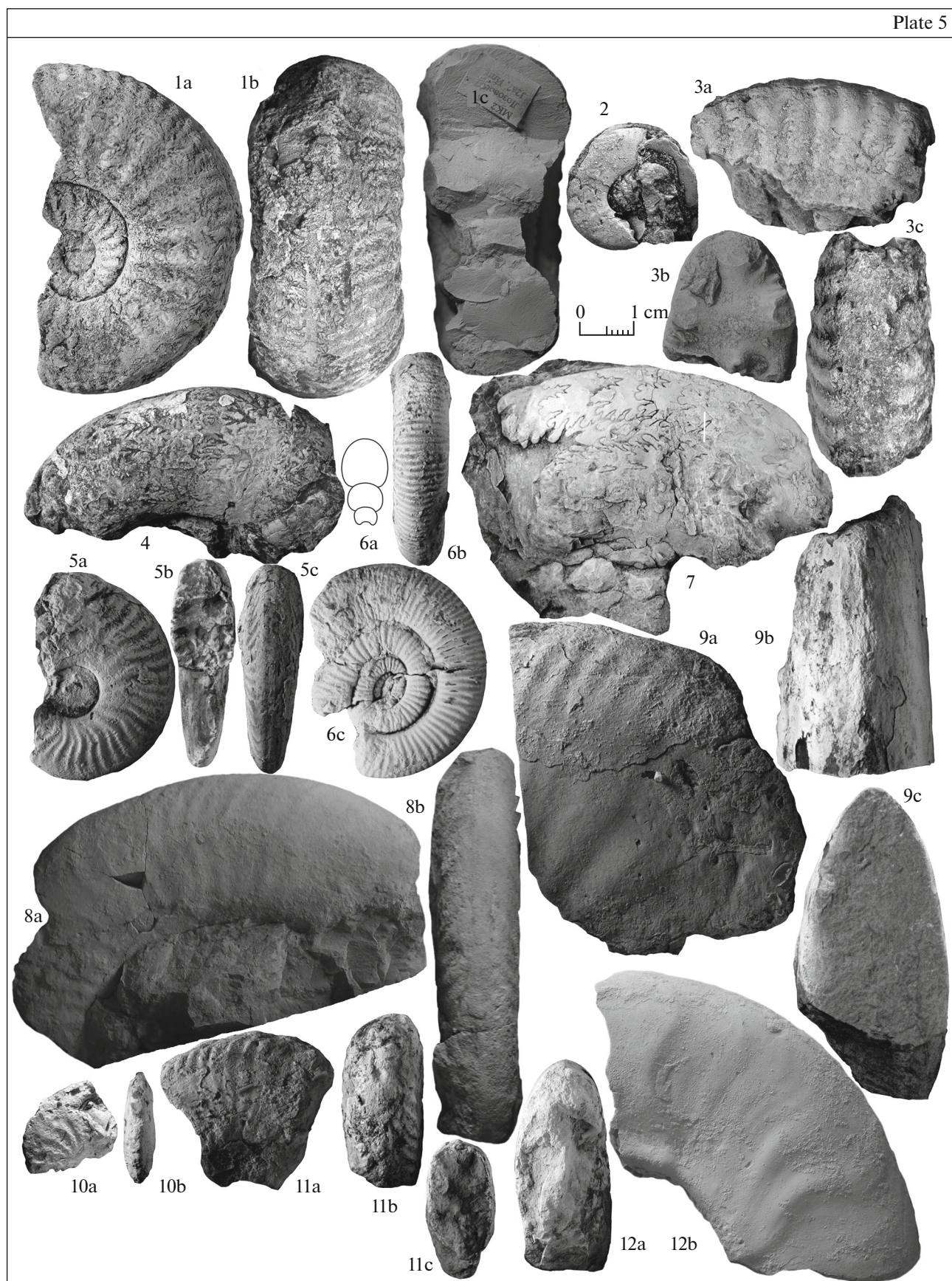
**Shell shape.** The shell is evolute, ophioconic, and small-sized. The cross-section of the outer whorl is slightly compressed, while the inner whorls are depressed (Pl. 5, fig. 6a). The flanks are slightly convex, the ventrolateral shoulder is not differentiated; the flanks gradually transit into a smoothly rounded venter. The umbilicus is wide and shallow.

**Ornamentation.** The ornamentation consists of a relatively regular alternation of simple and bifurcating ribs, with the branching point located in the perisiphonal third of the whorl. A weak node is sometimes present at the bifurcation point. The ribs are rectiradiate, slightly barely sigmoidal, and relatively closely spaced; they cross the venter without bending. Crowding of ribbing can be seen on the last half of the outer whorl.

roconchs from the Commune Zone of Spitsbergen (Rogov and Lutikov, 2022, text-figs. 3A–3B, 3D–3F, 3H–3I, 4D–4F, 4H). Another potential indicator suggesting this specimen is a macroconch is the ornamental elements crowding on the terminal body chamber, which is not typical of microconchs.

**Occurrence.** Ammonites of this group have been described in Crimea from the Taurida flysch near Prokhladnoe village (Zaitsev and Arkadiev, 2019, Pl. 1, fig. 14) and from conglomerates of the Bitak Formation nearby the Stroganovka village (Dovgal and Paryshev, 1979, p. 130, fig. 1). Furthermore, occurrences of *D. (D.) ex gr. commune* are reported from the “Skalturashi Formation” flysch on the southern slopes of Skalturashi Mount (Permyakov et al., 1991) and from terrigenous rocks near the Tru-

**Plate 5.** Erycitidae, Hildoceratidae, Lytoceratidae, Dactylioceratidae, Hammatoceratidae. (1) *Erycites* ex gr. *barodiscus* (Gemellaro), specimen no. MZ-149/48 (illustrated in Ippolitov et al., 2008, pl., fig. 1a, 1b): (1a) lateral view, (1b) ventral view, (1c) cross-section; (2) *Osperleioceras* sp., specimen no. MK2488, lateral view; (3) *Bredya* sp., specimen no. MZ-149/50: (3a) lateral view, (3b) cross-section, (3c) ventral view; (4) *Lytoceras* cf. *francisci* (Oppel), specimen no. MZ-149/53, lateral view; (5) *Osperleioceras* cf. *beaulizienae* (Monestier), specimen no. MZ-149/26: (5a) lateral view, (5b) cross-section, (5c) ventral view; (6) *Dactylioceras (Dactylioceras) ex gr. commune* (J. Sowerby), specimen no. MZ-149/21: (6a) cross-section sketch, (6b) ventral view, (6c) lateral view; (7) ? *Pseudolillia* sp., specimen no. MZ-149/49, lateral view; (8, 11) *Crestaites* cf. *meneghinii* (Bonarelli): (8) specimen no. MZ-149/47: (8a) lateral view, (8b) ventral view (depicted in Ippolitov et al., 2008, pl., fig. 3); (11) specimen no. MZ-149/42: (11a) lateral view, (11b) ventral view, (11c) cross-section; (9) “*Pseudaptetoceras*” cf. *christianae* (Elmi et Mouterde, 1997), specimen no. MZ-149/43: (9a) lateral view, (9b) ventral view, (9c) cross-section; (10) ? *Amaltheus* sp. juv., specimen no. MZ-149/20: (10a) lateral view, (10b) ventral view; (12) *Pleydellia (Cotteswoldia)* cf. *paucicostata* Buckman, specimen no. MZ-149/51 (illustrated in Ippolitov et al., 2008, pl., fig. 2): (12a) cross-section; (12b) lateral view.



dolyubovka village along the Bodrak River (Permyakov, 1962, p. 63); however, there are no illustrations, descriptions, or repository information.

The species *D. commune* (J. Sowerby) is the index species for the *D. commune* Biohorizon—part of the eponymous subzone within the Bifrons Zone of the European Lower Toarcian (Page, 2003); however, in Mediterranean sections, forms of the *D. commune* group also occur in the overlying *D. athleticum* Biohorizon.

**Material.** One well-preserved specimen (no. MZ-149/21).

SUBFAMILY NODICOELOCERATINAE VENTURI  
ET FERRI, 2001

**Genus *Nodicoeloceras* Buckman, 1926**

***Nodicoeloceras fonticulum* (Simpson, 1855)**

Plate 3, figs. 4a–4c

*Ammonites fonticulum*: Simpson, 1855\*, p. 57.

*Coeloceras fonticulum*: Buckman, 1912 in Buckman, 1909–1930, p. 59b, pl. LIX, figs. 1–2.

*Dactyloceras fonticulum*: Maubeuge, 1957, p. 220, pl. XXX, fig. 62.

*Catacoeloceras fonticulum*: Sapunov, 1963, p. 126, pl. VI, fig. 2a, 2b

*Peronoceras* cf. *fonticulum*: Géczy, 1967b, p. 98, text-fig. 95, pl. XXVI, fig. 2.

*Catacoeloceras crassum*: Kovács, 2011, p. 18, pl. V, figs. 3–4.

*Nodicoeloceras crassoides* morphotype *fonticulum*: Kovács, 2014 p. 54, pl. 4, fig. 1.

**Holotype.** By monotypy. Figure by Buckman (1909–1930, pl. LIX, figs. 1, 2). It apparently comes from the Exaratum Subzone (Serpentinum Zone) nearby Whitby (Yorkshire, England). Repository: Whitby Museum (Whitby, England), specimen WHITM:SIM496.

**Shell shape.** The shell is evolute and planorbic. The whorls increase moderately during ontogeny and have a rounded-trapezoidal cross-section, with the point of maximum width at the ventrolateral shoulder. The whorls are depressed (whorl width significantly exceeds whorl height). The flanks are strongly convex. The venter is broad and gently rounded. The ventrolateral shoulder is angular and well-defined on the inner whorls but becomes more rounded on the outer whorls. The umbilicus is deep, wide, and bowl-shaped. The umbilical wall is wide and convex.

**Ornamentation.** The flanks have well-defined rectoradiate ribs with irregularly fabulation (loops on the inner whorls). On the inner whorls, the ribs bifurcate at the ventrolateral shoulder, forming a distinct node at the bifurcation point. During ontogeny, the nodes become irregular and indistinct, and isolated single ribs also appear.

Dimensions in mm and ratios in %.

| Specimen no. | D  | H  | Du | W  | H/D  | W/D  | Du/D | H/W | Number of primary ribs per ½ whorl |
|--------------|----|----|----|----|------|------|------|-----|------------------------------------|
| Pnv-1877     | 36 | 12 | 15 | 15 | 33.3 | 41.6 | 41.7 | 80  | 22                                 |

**Comparison and remarks.** It differs from *N. tuberculatum* (Kottek) in having a wider whorl section and regularly spaced ribs. It differs from *Catacoeloceras crassum* (Young et Bird) in the presence of looped ribs, the irregular arrangement of nodes on the outer whorls, and tighter ribbing.

**Occurrence.** Lower Toarcian, Serpentinum Zone (starting from the middle of the Exaratum Subzone) Bifrons Zone of England (Buckman, 1912), France and Luxembourg (Maubeuge, 1957), Germany, Bulgaria (Sapunov, 1963), Italy, Greece, Spain, Hungary (Kovács, 2014), and the Caucasus.

**Material.** One specimen (no. TsMT Pnv-1877).

Dimensions in mm and ratios in %.

| Specimen no. | D  | H  | Du | W  | H/D  | W/D  | Du/D | H/W  | Number of primary ribs per ½ whorl |
|--------------|----|----|----|----|------|------|------|------|------------------------------------|
| MZ-149/22    | 40 | 14 | 18 | 16 | 35.0 | 40.0 | 45.0 | 87.5 | 24                                 |

**Comparison and remarks.** The species *N. crassoides* is the type species of the genus and is characterized by significant variability in whorl proportions, rib density, and the presence (or absence) of nodes at rib-bifurcation points. Furthermore, the

***Nodicoeloceras* ex gr. *crassoides* (Simpson, 1855)**

Plate 4, figs. 3a, 3b

**Shell shape.** The shell is evolute, small, and inflated. The whorls are depressed with the broadly oval section (width exceeds height at all growth stages), and the relative whorl height increases during ontogeny. The flanks are convex. The venter is broadly rounded. The umbilicus is wide, moderately deep, and bowl-shaped, with a convex umbilical wall (Fig. 13).

**Ornamentation.** Consists primarily of regularly spaced rectoradiate ribs that bifurcate near the ventrolateral shoulder, without nodes, well as occasional simple ribs. Looped ribs are absent. Rib density increases during ontogeny.

presence or absence of the shell layer results in a different visible ribbing pattern: high, sharp-edged ribs with nodes on the shell versus low, rounded ribs on the internal mold (Howarth, 1978, p. 258). The Crimean specimen is quite similar to the holotype illustrated by

Buckman (1913 in Buckman, 1909–1930, pl. LXXXIX), which comes from the Exaratum Subzone (Falciferum Zone) of the Yorkshire coast and is housed in the Whitby Museum (no. WM 126).

In a number of studies (Pinna and Levi-Setti, 1971; Kovács, 2014), forms similar to *N. crassoides* from the Falciferum (Serpentinum)–Bifrons zonal interval of the Mediterranean region are assigned to the genus *Mesodactylites* Pinna et Levi-Setti (e.g., *M. mediterraneus* (Renz) and *M. sapphicus* (Renz), which have a subcircular whorl section). However, according to Howarth (2013), *Mesodactylites* is a junior synonym of *Nodicoeloceras* Buckman, a view adopted in the present study. Representatives of *Mesodactylites* are typically characterized by a somewhat lower rib furcation point than that observed in the Crimean specimen.

It differs from *Dactylioceras semiannulatum* Howarth and other representatives of the genus *Dactylioceras* by the significantly greater width of the whorls and their broadly oval cross-section (width exceeds height at all growth stages).

**Occurrence.** The species *N. crassoides* is characteristic of the Falciferum (Serpentinum) Zone (subzones Falciferum and Exaratum) in Great Britain (Howarth, 1978) and Poland (Myczyński, Jach, 2009); the Bifrons Zone, Lusitanicum Subzone in Bulgaria (Metodiev, 2008); and the interval from the Serpentinum Zone to the base of the Bifrons Zone in Luxembourg (Guérin-Franiatte et al., 2010). It is also known from the Falciferum Zone of the Mediterranean paleobiogeographic province: Greece (Kottek, 1966) and Italy (Pinna and Levi-Setti, 1971); the interval from the Serpentinum Zone to the base of the Bifrons Zone in France (Rulleau, 2006); the Serpentinum Zone (*H. serpentinum* Biohorizon) in Spain (Goy et al., 2023); and the interval spanning the Serpentinum Zone (Falciferum Subzone) to the Bifrons Zone (*Hildoceras semipolitum* Biohorizon) in Hungary (Kovács, 2014). The species is also known from North Africa, Pakistan, Iran, Indonesia, and North and South America.

**Material.** A single internal mold with a well-preserved outer whorl (specimen no. MZ-149/22).

#### SUPERFAMILY HILDOCERATOIDEA HYATT, 1867

##### FAMILY HILDOCERATIDAE HYATT, 1867

##### SUBFAMILY HARPOCERATINAE NEUMAYR, 1875

##### Genus *Harpoceras* Waagen, 1869

##### *Harpoceras falciferum* (J. Sowerby, 1820)

Plate 6, figs. 1a–1c, 2a, 2b, 3a–3c, 5a, 5b, 8

*Ammonites falcifer*: J. Sowerby, 1820\* in Sowerby, 1818–1821, p. 99, pl. 254, fig. 2.

*Ammonites mulgravius*: Young and Bird, 1822 (sp. nov.), p. 251, pl. XIII, fig. 8.

*Harpoceras mulgravius*: Thompson, 1909, pl. XIV, fig. 3, pl. XV; Popa and Patruilus, 1996, pl. 4, fig. 9, pl. 5, fig. 4.

*Harpoceras fellenbergi*: Hug, 1898 (sp. nov.), p. 10, pl. 2, Fig. 6, pl. 4, Fig. 3.

*Phaularmites exiguus*: Buckman, 1928 in Buckman, 1909–1930 (sp. nov.), pls. 775A, 775B.

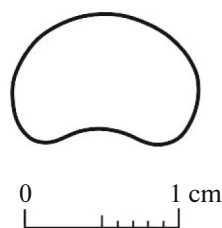


Fig. 13. Cross-section of *Nodicoeloceras* ex gr. *crassoides*, specimen no. MZ-149/22, D ≈ 25 mm. Key:

*Harpoceras falcifer*: Arkell, 1956, pl. 33, fig. 5; Dean et al., 1961, p. 479, pl. 72, fig. 3; Pinna, 1968, p. 34, p. IV, figs. 1, 1a; Dagys, 1974, p. 38, pl. IX, fig. 1–5; Urlichs, 1977, pl. 5, fig. 2; Maubeuge, 1984, p. 85, fig. 58; Krimholz et al., 1988, pl. 3, fig. 7; Schlegelmilch, 1992, p. 98, pl. 45, fig. 4; Bendík, 2012, pl. 3, figs. a–h.

*Harpoceras falciferum*: Thompson, 1909, text-figs. a, b, pl. XIV, fig. 1; Buckman, 1928 in Buckman, 1909–1930, pls. 764, 764A; Riegraf et al., 1984, S. 134, pl. 8, Fig. 8, fig. 39; Howarth, 1992, p. 119, pl. 18, fig. 3, pl. 19, figs. 2–4, pl. 20, figs. 1–11, text-figs. 18F, 19B, 27–34; Metodiev, 1997, p. 14, pl. I, fig. 8; Biostratigraphie..., 1997, pl. 9, figs. 9–10; Kment, 1998, S. 191, pl. 4, Fig. 3, pl. 6, Fig. 3; Neige and Rouget, 2002, p. 769, fig. 3c; Bécaud, 2002, pl. V, figs. 1–3; Knyazev et al., 2003, pl. 1, fig. 3; Rulleau, 2006, p. 68, pl. 18, figs. 1, 3; Bécaud, 2006, p. 61, pl. 19, figs. 1a–1c, pl. 20, figs. 1a–1c, pl. 24, figs. 2a–2b, pl. 26, figs. 1, 2a–2c, 3a–3c, 4a–4c, pl. 27, figs. 1a–1b, 2, pl. 32, figs. 2a, 2b, 4a, 4b; Howarth, 2013, p. 74, text-figs. 50.2a–50.2b; Fauré, 2013, p. 27, pl. 3, fig. 1; Repin, 2016, pl. V, fig. 12; Fauré et al., 2017, p. 56, pl. 2, fig. 16; Bardin et al., 2017, Fig. 1(b); Fossils..., 2019, p. 73, text-figs. 6.11G–H; Salazar-Ramírez et al., 2020, Fig. 4–d; Benzaggagh et al., 2022, p. 10, figs. 9G, 10A–10C; Kovács et al., 2023, p. 225, Figs. 5.4, 5.7; Benzaggagh, 2023, p. 11, figs. 11A–11D; Goy et al., 2023, p. 11/49, text-fig. 7a.

*Harpoceras* ex gr. *falciferum*: Kazakova, 1987, p. 93, pl. I, fig. 4; Myczyński and Jach, 2009, p. 32, figs. 5D–5F.

(?) *Harpoceras* sp. indet.: Atabekyan et al., 1997, p. 111, pl. 31, fig. 1.

**H o l o t y p e.** By monotypy. Figured by J. Sowerby (1818–1821, pl. CCLIV, fig. 2). Re-illustrated in (Thompson, 1909, pl. XIV, fig. 1; Buckman, 1909–1930, pl. DCCLXIV; Arkell, 1956, pl. 33, fig. 5; Dean et al., 1961, pl. 72, fig. 3; Pinna, 1968, p. IV, figs. 1, 1a; Schlegelmilch, 1992, pl. 45, fig. 4; Howarth, 1992, pl. 19, 2; 2013, text-figs. 50.2a–50.2b). Repository: Natural History Museum, London (UK), specimen no. NHMUK 43946. Provenance: Thorncombe Beacon (Dorset, England), Lower Toarcian, Falciferum (Serpentinum) Zone, Falciferum Subzone.

**S h e l l s h a p e.** The shell is large, discoidal, and moderately evolute. During ontogeny (at D > 100 mm), it becomes increasingly evolute: the last whorl overlaps less than one-third of the penultimate one. The whorls are high and laterally compressed (Fig. 14). The flanks are flattened. The venter is narrow and weakly convex. The umbilical shoulder is well-defined and angular. The umbilical wall is low and vertical, although on the outer whorl of some specimens, it is slightly beveled toward the umbilicus. The umbilicus is wide and stepped.

**O r n a m e n t a t i o n.** The shell has a well-developed ventral keel bordered by shallow sulci. The flanks bear numerous crescent-shaped ribs: straight and distinctly prorsiradiate in the umbilical half, approximately in the mid-flank, the ribs bend sharply back-

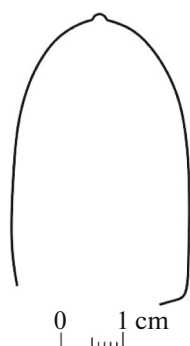


Fig. 14. Cross-section of *Harpoceras falciferum*, specimen no. MZ-149/23, D ≈ 125 mm.

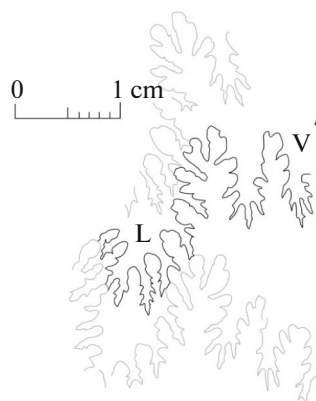


Fig. 15. Suture of *Harpoceras falciferum*, specimen no. MZ-149/24.

ward, in the ventral half they are concave, arched. In the ventral half of the flank, the ribs are more prominent than in the umbilical half. On the inner whorls, the ribs are coarser and sparsely spaced than on the outer ones. When  $D \leq 40$  mm, the ribs often bifurcate,

and sometimes there are inserted ribs. With a large diameter, the ribs are mostly single. Approximately in the mid-flank of the outer whorl, a line of shallow wavy depressions is noticeable, which do not connect with each other and do not form a continuous spiral groove.

#### Dimensions in mm and ratios in %.

| Specimen no. | D    | H    | Du   | W  | H/D  | W/D  | Du/D | H/W | Number of ribs per ½ whorl |
|--------------|------|------|------|----|------|------|------|-----|----------------------------|
| MZ-149/23    | ≈125 | ≈51  | 48   | 25 | 42.2 | 20   | 38.4 | 204 | —                          |
| Pnv-1875     | 46.5 | 22.2 | 14.5 | 12 | 47.7 | 25.8 | 31.2 | 185 | ≈30                        |

**Suture.** The ventral lobe is narrow and shallow. The V/L saddle is very wide and is divided into two unequal parts by a deep adventive lobe. The depth of the adventive lobe is only slightly less than that of the ventral lobe. The lateral lobe is deep and relatively wide (Fig. 15).

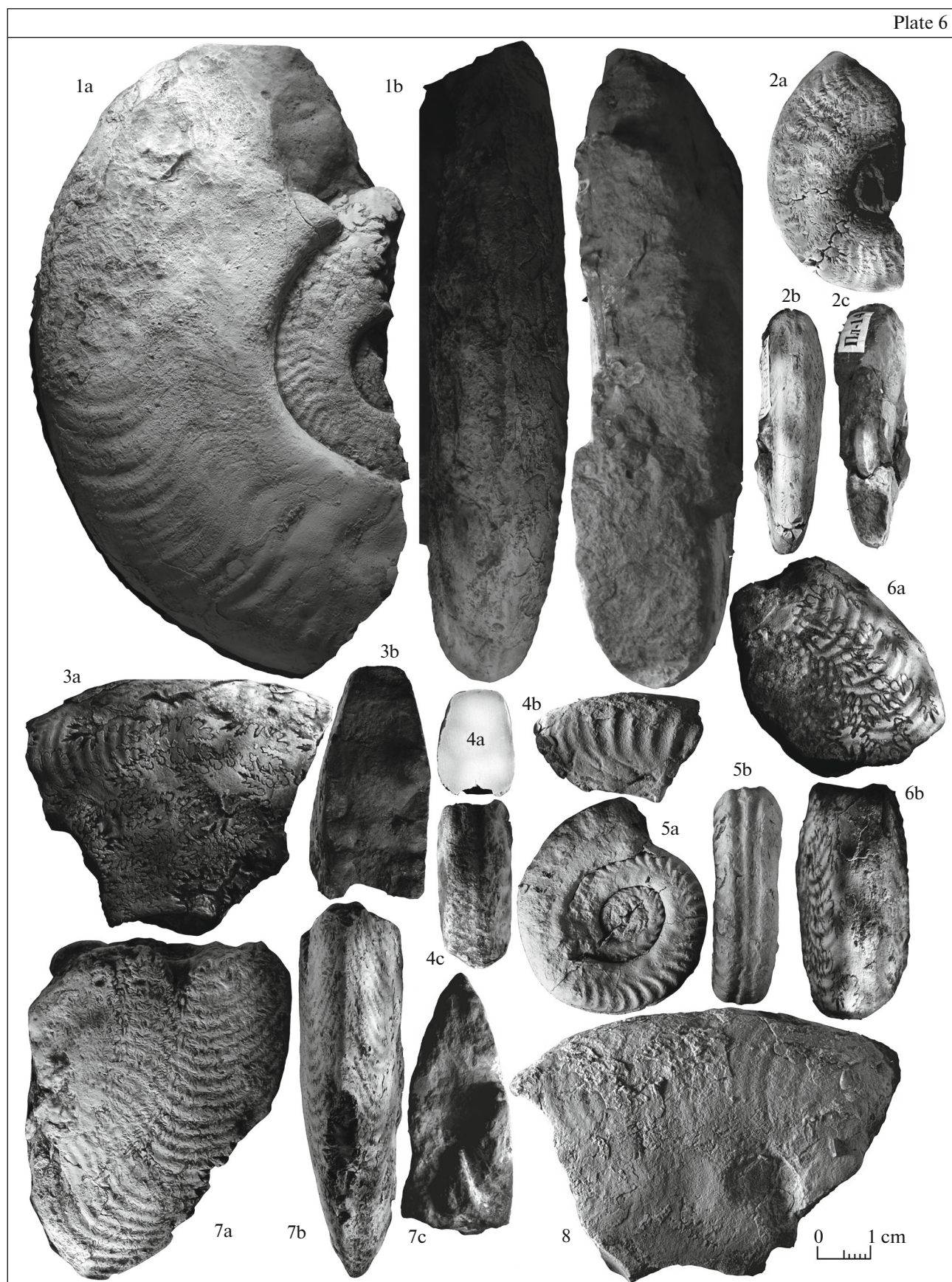
**Comparison and remarks.** It differs from the ancestral *H. serpentinum* (Schlotheim) in the shape of the umbilical wall. In *H. serpentinum*, the wall slopes toward the umbilicus at all ontogenetic stages, whereas in *H. falciferum* it may be vertical or undercut. Furthermore, there are differences in the ribbing pattern. The periumbilical sections of the ribs in *H. falciferum* are straight and more pronounced, while in *H. serpentinum* they are typically curved and interrupted. *H. falciferum* shells are, on average, larger than those of *H. serpentinum*. Despite this, the shell proportions of the two species do not differ significantly.

A fragment of a body chamber identified by Yu.S. Repin as *Harpoceras* sp. indet. and originating from the Taurida flysch (sensu Yudin, 2011) near Solnechnoselye village in the Bodrak River basin

(Atabekyan et al., 1997, pl. 31, fig. 1) possibly belongs to this species.

**Occurrence.** The Falcifer Zone of Yakutia (Krimholz et al., 1988); the Falciferum [= Serpentinum] Zone (Falciferum Subzone) Bifrons Zone (Commune Subzone) of England (Howarth, 1992), Luxembourg (Guérin-Franiatte et al., 2010, p. 25), Hungary (Kovács et al., 2023), Germany (Hanover (Weitschat, 1973), Württemberg (Riegraf et al., 1984), Sudetenland (Schlegelmilch, 1992)), Switzerland (Hug, 1898), Austria (Kment, 1998), Greece (Kottek, 1966), Bulgaria (Metodiev, 2008), Italy (Pinna, 1968), Spain (Goy et al., 2023), Romania (Popa, Patrulius, 1996), the North Caucasus (Karachay-Cherkessia (Kazakova, 1987)), NE Siberia (Repin, 2016), New Zealand (Speden, Keyes, 1981), Poland (Myczyński, Jach, 2009), and Ukraine (Transcarpathia (Wierzbowski et al., 2012)); the Bifrons Zone, *H. lusitanicum* Biohorizon of France (Fauré, 2013); the Falcifer Biozone of the Lower Toarcian in Slovakia (Bendík, 2012); and presumably the Sublevisoni Subzone of Morocco (Benzaggagh, 2023).

**Plate 6.** Hildoceratidae. (1–2, 6, 8) *Harpoceras falciferum* (J. Sowerby): (1) specimen no. MZ-149/23: (1a) lateral view, (1b) ventral view, (1c) cross-section; (2) specimen no. Pnv-1875: (2a) lateral view; (2b) ventral view; (2c) cross-section; (6) specimen no. MZ-149/24: (6a) lateral view; (6b) ventral view; (8) specimen no. MZ-149/25, lateral view; (3) *Osperleioceras* sp., specimen no. MZ-149/27: (3a) lateral view, (3b) cross-section; (4–5) *Hildoceras lusitanicum* Meister, specimen no. MZ-149/30: (4a) polished cross-section (photo), (4b) lateral view, (4c) ventral view; (5) specimen no. CFU-unnumbered: 5a) lateral view; 5b) ventral view; (7) *Polypilectus discoides* (Zieten), specimen no. GM-2145: (7a) lateral view, (7b) ventral view, (7c) cross-section.



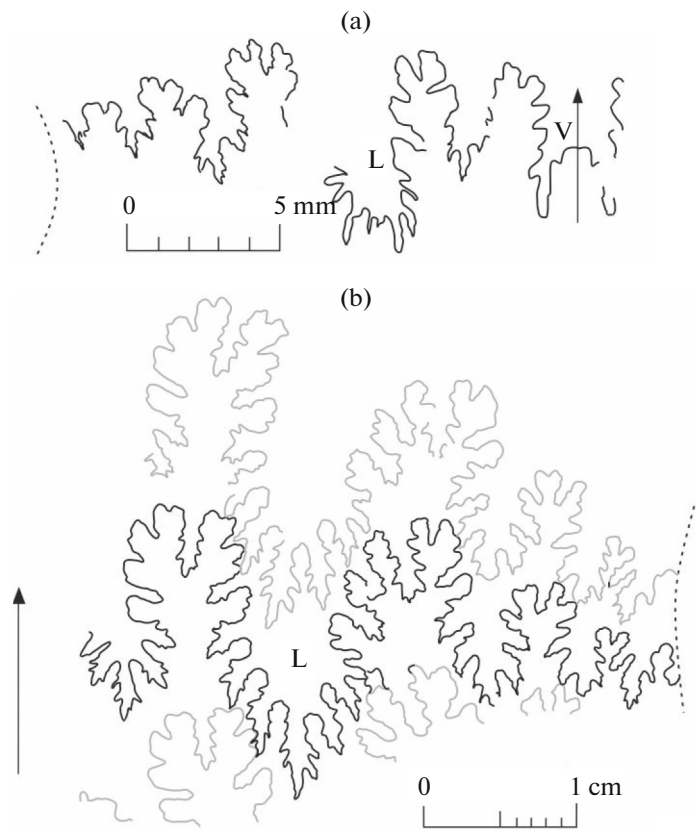


Fig. 16. Suture of *Osperleioceras* (*Osperleioceras*) cf. *beauliense*: (a) specimen. no. MZ-149/26, D = 35 mm; (b) ex. no. MZ-149/27.

**Material.** Four incompletely preserved specimens (nos. Pnv-1875, MZ-149/23, MZ-149/24, MZ-149/25).

**Genus *Osperleioceras* Krimholz  
in Krimholz et Tazikhin, 1957**

Subgenus *Osperleioceras* Krimholz  
in Krimholz et Tazikhin, 1957

***Osperleioceras* (*Osperleioceras*) cf. *beauliense* (Monestier, 1921)**

Plate 5, figs. 5a–5c

**Shell shape.** The shell is small-sized, moderately involute, and flattened. The whorls are high, compressed, and sub-trapezoidal in cross-section, with the point of maximum width located in the peri-

umbilical third. The flanks are slightly convex, sloping gently from the point of maximum whorl width toward the venter. The venter is narrow, flattened, and clearly delimited. The ventrolateral shoulder is angular. The umbilicus is moderately narrow, shallow, and bowl-shaped. The umbilical shoulder is gently rounded.

**Ornamentation.** The ribbing is regular, consisting of fine ribs that are paired in the periumbilical third of the whorl and do not extend onto the venter (fading out at the ventrolateral shoulder). The ribs are falcoïd: straight and rursiradiate in the periumbilical third of the whorl, but curving gently forward in the periventral region. The venter bears a low, well-defined keel that is not flanked by ventral sulci.

**Dimensions in mm and ratios in %.**

| Specimen no. | D  | H    | Du | W    | H/D | W/D  | Du/D | H/W | Number of ribs per ½ whorl |
|--------------|----|------|----|------|-----|------|------|-----|----------------------------|
| MZ-149/26    | 39 | 19.5 | 9  | 10   | 50  | 25.6 | 23.1 | 195 | 20                         |
| MZ-149/27    | —  | 45   | —  | 20.1 | —   | —    | —    | 224 | —                          |

**Suture.** The suture is preserved incompletely. It has a broad, asymmetric V/L saddle (the inner part is higher and narrower than the outer part) with a deep adventive lobe and a deep, deeply incised L lobe that is deeper than the ventral lobe (Fig. 16).

**Comparison and remarks.** The subgenus *O.* (*Osperleioceras*) comprises ammonites that retain their ancestral ornamentation—consisting of widely spaced, falcoïd ribs—throughout most of their ontogeny; this distinguishes them from *O.* (*Pseudopolyplectus*)

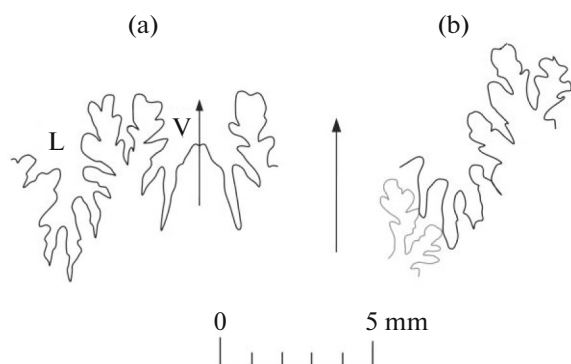


Fig. 17. Suture of *Pseudolioceras* (*Pseudolioceras*) cf. *boulbiense*, specimen no. MZ-149/28a, D = 25 mm,  $\times 4$ ; (b) D = 30 mm,  $\times 4$ .

Mattéi, which enter a stage of dense ribbing at diameters greater than 15 mm (Bécaud, 2006). Species of the genus *Osperleioceras* exhibit significant morphological variability, even within a single population (Mattei, 1969, p. 18). Consequently, reliable differentiation requires extensive material (Morard and Guex, 2003). The Crimean specimen can be compared to the type species of the genus, *O. (O.) beauliziense*, which is characterized by regular ribbing, consisting of sigmoidally curved ribs, and laterally compressed whorls. The lectotype of *O. (O.) beauliziense* (Monestier, 1921, pl. I, fig. 1)—proposed and re-illustrated by Howarth (2013, p. 76, text-figs. 49, 3a)—collected from the

Thouarsense Zone of the Upper Toarcian at Cornus (Aveyron, France).

**Occurrence.** Toarcian of Crimea. The species *O. (O.) beauliziense* and the closely related *O. (O.) rivierense* (Monestier) are known in Europe from the stratigraphic interval spanning the Variabilis Zone to the Thouarsense Zone (Fallaciosum Subzone) of the Upper Toarcian (Howarth, 1992, p. 155).

**Material.** One well-preserved specimen (no. MZ-149/26). A fragment of the outer whorl (no. MZ-149/27), identified here as *Osperleioceras* sp. (Pl. 6, fig. 3), may also belong to the same species.

### Genus *Pseudolioceras* Buckman, 1889

Subgenus *Pseudolioceras* Buckman, 1889

*Pseudolioceras* (*Pseudolioceras*) cf. *boulbiense* (Young et Bird, 1922)

Plate 7, figs. 7a–7d

**Shell shape.** The shell is small, moderately involute, and of medium thickness. The whorls are suboval, with the greatest width at the umbilical bend. The flanks are slightly convex, the ventral side is narrow, strongly convex. The umbilicus is moderately narrow, the umbilical wall is beveled, slightly beveled.

**Ornamentation.** The ribs are low-relief and sickle-shaped; they reach their maximum width and height near the ventrolateral shoulder but do not extend onto the venter. On the inner half of the flanks, the ribs are weak, straight, and prorsiradiate.

### Dimensions in mm and ratios in %.

| Specimen no. | D    | H  | Du | W  | H/D  | W/D  | Du/D | H/W | Number of ribs per $\frac{1}{2}$ whorl |
|--------------|------|----|----|----|------|------|------|-----|----------------------------------------|
| MZ-149/28    | 32.5 | 15 | 7  | 10 | 46.2 | 30.8 | 21.5 | 150 | 17                                     |

**Suture.** Preserved incompletely. Broad V-lobe; asymmetric V/L saddle, divided into two parts by a deep supplementary lobe. Deep, asymmetric L-lobe (Fig. 17).

**Comparison and remarks.** Based on the slightly beveled umbilical wall, and the ribs, which are rather abruptly wedging out without extending onto the venter, the ammonite described here can be compared to *P. (P.) boulbiense*; however, the state of preservation does not allow for a definitive identification. It differs from *P. (Pseudolioceras) lythense* (Young et Bird) in having a narrower umbilicus and lacking a forward curvature of the ribs on the ventrolateral shoulder.

**Occurrence.** The species *P. (P.) boulbiense* is recorded within the stratigraphic interval spanning the Lower Toarcian (Bifrons Zone, Crassum Subzone) to the Upper Toarcian (Thouarsense Zone, Fallaciosum Subzone) in Great Britain, France, Germany, Switzerland, northwestern Canada, and Spitsbergen. In Russia, it is also known from the Upper Toarcian

(?Thouarsense Zone) of northeastern Siberia (as *Pseudolioceras wuerttenbergeri* (Denckmann); Knyazev et al., 2003, p. 46).

**Material.** One internal mold (phragmocone) of satisfactory preservation (MZ-149/28).

### SUBFAMILY POLYPLECTINAE VENTURI, 1991

### Genus *Polyplectus* Buckman, 1890

*Polyplectus discoides* (Zieten, 1831)

Plate 6, figs. 7a–7c

*Ammonites discoides*: Zieten, 1831\* in Zieten, 1830–1833, p. 21, pl. XVI, fig. 1; d'Orbigny, 1845 in d'Orbigny, 1842–1851, p. 356, pl. 115, figs. 1–4; Oppel, 1856, p. 365; Quenstedt, 1858, p. 283, pl. 40, fig. 7; Quenstedt, 1885 in Quenstedt, 1882–1885, p. 426, pl. LIII, fig. 9.

*Lioceras discoides*: Bayle, 1878, pl. LXXXVIII, figs. 2–5.

*Ammonites capellinus jurensis*: Quenstedt, 1885 in Quenstedt, 1882–1885 (subsp. nov.), p. 417, pl. LIII, figs. 1, 3–5.

*Harpoceras* (*Polyplectus*) *discoides* var. *apenninica*: Haas, 1913 (var. nov.), p. 118 [182].

*Polyplectus capellinus*: Rostovtsev, 1965, p. 53, pl. 1, fig. 1.

*Polyplectus discoides*: Buckman, 1891, p. 215, pl. XXXVII, figs. 1–5; Renz, 1912, pl. VI, Fig. 3; Krimholz, 1947, p. 171, pl. XXIX, fig. 5–6; Krimholz, 1958, p. 71, pl. XXVII, figs. 9a, 9b; Krymholz, 1961, p. 94, pl. II, fig. 4; Stankevich, 1964, p. 23, pl. II, fig. 8–10, pl. IV; Rostovtsev, 1965, p. 52, pl. I, fig. 2, 3; Nutschidze, 1966, p. 94, pl. VII, figs. 2–4; Guex, 1975, p. 115, pl. VII, fig. 8; Topchishvili, 1990, p. 38, pl. XIV, fig. 3, 4; Schlegelmilch, 1992, p. 102, pl. 47, fig. 8; Rostovtsev and Krimholz, 1992, p. 39, pl. 15, fig. 5; Jakobs, 1997, p. 52, Pl. 3, figs 10–11; Pl. 4, figs. 14, 15; Howarth, 1992, p. 153, pl. 28, figs. 6–8; Mouterde and Gabilly in Fischer, 1994, p. 102, pl. 35, figs. 3a, 3b; Bernad and Martínez, 1996, p. 10, lam. 2, fig. 2; Metodiev, 1997, p. 15, pl. I, fig. 7; Fauré, 2002, p. 718, pl. 31, fig. 11; Myczyński, 2004, p. 53, Fig. 23: 1; 24: 3; Topchishvili et al., 2006, pl. 15, fig. 5–7; Bécaud, 2006, p. 55, pl. 4, figs. 2a–2c; Rulleau, 2006, p. 68, pl. 20, figs. 7–8; Fauré, 2007, fig. 6.8; Metodiev, 2008, figs. 5.r–5.s; Énay, 2011, fig. 7c; Bendík, 2012, p. 293, pl. 5, figs. a–d; Howarth, 2013, p. 76, figs. 51.4a–51.4b; Benzaggagh, 2023, p. 13, figs. 12D–12E.

*Polyplectus* cf. *discoides*: Topchishvili, 1969, p. 88, pl. VI, fig. 3.

**H o l o t y p e.** By monotypy, comes from the Toarcian sandstones at Reichenbach im Täle (municipality of Heiningen, Württemberg, Germany). Natural History Museum (London, UK), specimen no. BMNH 62568. Re-illustrated by Howarth (1992, pl. 28, fig. 7; 2013, figs. 51.4a–51.4b).

**S h e l l s h a p e.** The shell is large, involute, and oxyconic. The cross-section is high, narrow, and triangular, with the greatest width in the periumbilical third of the whorl. The flanks are slightly convex and converge toward the venter, meeting to form an acute angle. The venter is not differentiated.

**Or n a m e n t a t i o n.** The flanks bear densely spaced, falcate ribs that are wider than the intercostal spaces. The ribs are low and narrow, slightly expanding as they approach the venter. No distinct ventral keel is observed on the outer and penultimate whorls.

**D i m e n s i o n s i n m m a n d r a t i o s i n %.**

| Specimen no. | H  | W  | H/W |
|--------------|----|----|-----|
| GM-2145      | 48 | 20 | 240 |

**S u t u r e.** The lateral lobe is deep and deeply dissected (with a large number of additional elements).

**C o m p a r i s o n.** The absence of a distinct keel at all ontogeny stages distinguishes the species from the ancestral *P. pluricostatum* (Haas).

**O c c u r r e n c e.** Upper Toarcian of the Northern Caucasus (Krimholz, 1961; Nutschidze, 1966), Germany (Schlegelmilch, 1992), Italy and Portugal (Renz, 1912); Thouarsense Zone (Bingmanni and Fascigerum subzones) to Insigne Zone (*H. insignis* Bioho-

rizon) of the central sector of the Pyrenees, NE Spain (Goy, Martínez, 1990); Variabilis Zone, Illustris Subzone, *H. illustris* Biohorizon to Vitiosa Subzone of the Cantabrian Mountains in Northern Spain (Goy et al., 2023); Thouarsense Zone (Striatulum and Regale subzones) of the Western and Northwestern Caucasus (basins of the Belaya, Bolshaya and Malaya Laba, Khodz, Pkhiya, Bzdykh, Pshekha, and other rivers (Rostovtsev, 1965)); Toarcian of Oman (Énay, 2011); Thouarsense Zone of Georgia (Topchishvili, 1990; Topchishvili et al., 2006); Variabilis Zone of Slovakia (Bendík, 2012); Thouarsense Subzone of Bulgaria (Metodiev, 2008); Crassica and Gillerbrandti zones of North America (Jakobs, 1997); Thouarsense Zone (Fascigerum and Fallaciosum subzones) and Dispansum Zone (Insigne and Gruneri subzones) of Southern France (Causse Plateau) (Guex, 1975); Levesquei Subzone of the Pseudoradiosa Zone of Western France, Poitou (Gabilly, 1976a, 1976b); the Thouarsense terminal Zone – Aalensis basal Zone of northeastern France (Belmont) (Almeras et al., 1998); the Fibulatum Subzone of the Bifrons Zone in Austria (Fischer, 1966); the Thouarsense Zone (Fallaciosum Subzone) and Levesquei Zone (Dispansum Subzone) in Great Britain (Howarth, 1992); the Fallaciosum Subzone of the Thouarsense Zone in southern Poland (Western Carpathians) (Myczyński, 2004); and the presumably Bifrons Zone in Morocco (Benzaggagh, 2023).

**M a t e r i a l.** One incompletely preserved specimen (no. GM-2145).

#### SUBFAMILY HILDOCERATINAE HYATT, 1867

##### Genus *Hildoceras* Hyatt, 1867

##### *Hildoceras laticostum* Bellini, 1900

Plate 6, figs. 2a–2c

*Ammonites levisoni*: Dumortier, 1874, p. 49, pl. IX, figs. 3, 4 [=Almeras et al., 1998, p. 46, pl. 6, fig. 3].

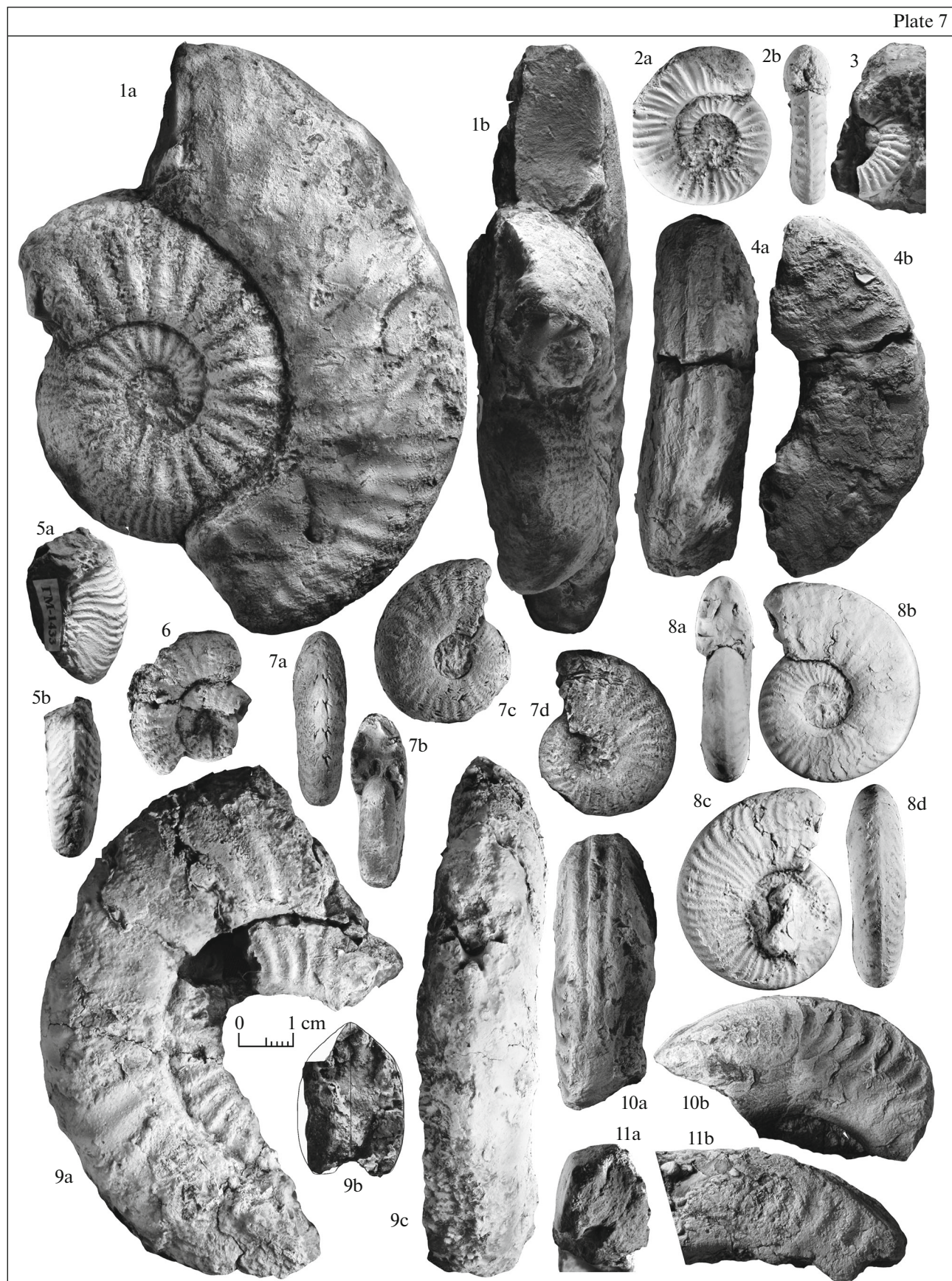
*Hildoceras levisoni*: Haug, 1885, p. 641, pl. XII, fig. 7.

*Hildoceras bifrons*: Bellini, 1900, p. 144, fig. 10 [=Ridente, 2023, fig. 9.10]; Pinna, 1969, p. 10, p. 1, fig. 1.

*Hildoceras bifrons* var. *laticosta*: Bellini, 1900\*, p. 145, fig. 12 [=Ridente, 2023, fig. 9.12].

*Hildoceras sublevisoni*: Fucini, 1919, p. 182; Mitzopoulos, 1930, s. 48, pl. 4, fig. 8; Merla, 1933, p. 51, p. VII, fig. 1; Zanzucchi, 1963, p. 124, p. XVI, figs. 5–7, 12, 13, pl. 17, figs. 1–3, 5; Géczy, 1967b, p. 130, text-fig. 129, pl. XXIX, fig. 11, pl. XXX, fig. 4, pl. LXIV, fig. 45; Géczy, 1967a, p. 127, pl. 3, fig. 4; Guex, 1972, p. 639, pl. VI, fig. 2; Elmi et al., 1974, p. 61, pl. 2, figs. 2, 4; Popa et al., 1976, pl. V, fig. 2; Biostratigraphie..., 1997, pl. 9, figs. 13–14; Parisi et al., 1998, pl. 3, fig. 1, text-fig. 7.2, text-fig. 8.9; Rulleau et al., 2001, pl. 6, fig. 2; Neige and Rouget, 2002, p. 772, figs. 4C–4E,

**Plate 7.** Erycitidae, Hildoceratidae. (1) *Erycites gerecsensis* Kovacs et Géczy, specimen no. GM-2138: (1a) lateral view, (1b) cross-section; (2–3) *Dumortieria levesquei* (D'Orbigny), (2) specimen no. MZ-149/38: (2a) lateral view, (2b) cross-section; (3) specimen no. GM-2134, lateral view; (4, 10–11) *Hildoceras lusitanicum* Meister: (4) specimen no. MZ-149/32: (4a) ventral view, (4b) lateral view; (10) specimen no. MZ-149/33: (10a) lateral view, (10b) lateral view; (11) specimen no. MZ-149/31: (11a) cross-section, (11b) lateral view; (5, 8) *Pseudogrammoceras fallaciosum* (Bayle): (5) specimen no. GM-1433: (5a) lateral view, (5b) ventral view; (8) specimen no. MZ-149/36: (8a) cross-section, (8b, 8c) lateral view, (8d) ventral view; (6, 9) *Grammoceras penestriatulum* Buckman: (6) specimen no. MZ-149/35 (juv.), lateral view, (9) specimen no. MZ-149/34: (9a) lateral view, (9b) cross-section, (9c) ventral view; 7 – *Pseudolioceras* (*Pseudolioceras*) cf. *boulbiense* (Young et Bird), specimen no. MZ-149/28: 7a) ventral view, (7b) cross-section, (7c, 7d) lateral view.



8D–8F; Bécaud, 2002, pl. VII, figs. 1–5; Rulleau, 2006, p. 71, pl. 21, fig. 4; Bécaud, 2006, p. 85, pl. VII, figs. 1–5; Géczy and Szente, 2006, p. 230, pl. I, figs. 1–2, pl. II, figs. 1–2; Myczyński and Jach, 2009, p. 35, text-fig. 6, figs. 5G–5O; Guérin-Franiatte et al., 2010, pl. 2, fig. 7; Fauré, 2013, p. 31, pl. 4, fig. 2; Salazar Ramírez et al., 2020, fig. 4–H; Benzaggagh, 2023, p. 14, figs. 13F–13H; Goy et al., 2023, p. 13/49, Fig. 6d; Lesti et al., 2024, fig. 5.12. *Hildoceras sublevisoni* var. *raricostata*: Mitzopoulos, 1930 (var. nov.), s. 49, pl. IV, figs. 9a–9c; Merla, 1933, p. 51, pl. 7, fig. 4. *Hildoceras caterinii*: Merla, 1933 (sp. nov.), p. 53, p. VII, figs. 5; Pinna, 1969, p. 10, p. 1, fig. 5; Bécaud, 2006, p. 86, pl. 40, figs. 3a, 3b, pl. 43, figs. 1a–1c. *Hildoceras graecum sublevisoni*: Kottek, 1966, p. 67, pl. IV, fig. 2, fig. 24. *Hildoceras* (*Orthildaites*) *sublevisoni*: Behmel and Geyer, 1966, p. 23, pl. 1, fig. 1, pl. 4, fig. 8. *Arietoceras* cf. *falciplicatum*: Behmel, Geyer, 1966, p. 20, pl. 3, fig. 7, pl. 6, fig. 7. *Hildoceras* (*Orthildaites*) *ambiguum*: Behmel, Geyer, 1966, p. 23, pl. 1, fig. 3, pl. 6, fig. 12. *Hildoceras sublevisoni raricostatum*: Géczy, 1967a, p. 128, pl. 3, fig. 3. *Hildoceras caterinii*: Pinna, 1969, p. 10, p. 1, fig. 5. *Hildoceratoides levisoni*: Dagys, 1974, p. 58, pl. IX, fig. 6–9, pl. X, fig. 5. *Hildoceras laticosta*: Howarth, 1992, p. 178, pl. 34, figs. 4–6; Ridente, 1996, pp. 178, 179, pl. 1, figs. 1–6, text-fig. 4; Metodiev, 1997, p. 15, pl. II, fig. 1; Metodiev, 2008, figs. 4o, 4p; Ridente, 2016, p. 27, figs. 3a, 4a. *Hildoceras* cf. *sublevisoni*: Wierzbowski et al., 2012, p. 38, pl. 3, fig. 1; Lesti et al., 2024, figs. 5–18. *Hildoceras* gr. *sublevisoni* Fucini: Fauré et al., 2017, p. 58, pl. 2, fig. 24.

#### Dimensions in mm and ratios in %.

| Specimen no. | D    | H | Du   | W  | H/D  | W/D  | Du/D | H/W  | Number of ribs per ½ whorl |
|--------------|------|---|------|----|------|------|------|------|----------------------------|
| MZ-149/29    | 29.1 | 9 | 14.9 | 11 | 30.9 | 37.8 | 51.2 | 81.8 | 18                         |

**Comparison and remarks.** It differs from *H. lusitanicum* Meister by a significantly narrower, weakly defined smooth band in the periumbilical region of the flanks (or even its absence), the complete absence of periumbilical relief, and less curved, sigmoid ribs that usually originate at the umbilical margin.

In all works published prior to 1992, as well as in numerous later publications, the name *H. laticostum* Bellini, 1900 is not treated as a nomen oblitum; instead, the name *H. sublevisoni* Fucini, 1919, based on a lectotype designated by Merla (1933, p. 51) and illustrated by Dumortier (1874, pl. IX, fig. 3), is applied to the species in question. However, Howarth (1992, Pt. 2, p. 180) convincingly demonstrated that the specific name *H. laticostum* cannot be considered a nomen oblitum under the current International Code of Zoological Nomenclature (1999). Consequently, the name *H. sublevisoni* should be regarded as a junior subjective synonym of *H. laticostum*. Nevertheless, the name “*H. sublevisoni*” continues to be used in works by some modern authors to facilitate the correct correlation of stratigraphic schemes.

**Occurrence.** The *H. sublevisoni* (*H. laticostum* provs.) biohorizon of the Bifrons Zone in the Lower Toarcian of France (Rulleau et al., 2001) and Germany; the Sublevisoni Subzone of the Bifrons

**Holotype.** The holotype originates from the Toarcian “Ammonitico Rosso” facies of Monte Subasio in the province of Perugia (Central Italy), near Assisi. It is stored in the Paleontology Museum of the University of Naples. It is illustrated in a drawing by Bellini (1900, p. 146, fig. 12). This drawing was later reproduced in Ridente (2023, fig. 9.12). A photograph of the holotype is provided in Ridente (1996, p. 179, text-fig. 4).

**Shell shape.** The whorls are broad and evolute, with their point of maximum width approximately at the mid-whorl. The flanks are flattened. The venter is broad, flattened, and tricarinate, with a high, acute central keel flanked by wide ventral sulci. The umbilical wall is rounded slightly beveled.

**Ornamentation.** The ribs are sigmoid; in the periumbilical quarter of the whorl, they are low and weakly defined. In the periventral half of the whorl, the ribs become high and coarse, then smooth out near the ventrolateral shoulder, curving forward in an arc. On inner whorls, the ribs start from the umbilical margin, whereas on the outer whorl, they nearly fade out near it, forming a narrow smooth strip adjacent to the umbilical wall. Periumbilical relief (such as sulci, a furrow, or a periumbilical ridge) is absent on the flanks.

Zone in Luxembourg (Guérin-Franiatte et al., 2010), Italy (Parisi et al., 1998), Spain (Goy et al., 2023), Portugal, Greece (Kottek, 1966), Austria, Hungary (Géczy, 1967a), Romania, Poland (Myczyński and Jach, 2009), Morocco (Benzaggagh, 2023), Algeria (Elmi et al., 1974), and possibly Western Ukraine (Wierzbowski et al., 2012); the Falciferum Subzone of the Falciferum Zone in Bulgaria (Metodiev, 2008); the Falciferum Subzone of the Falciferum (Serpentinum) Zone and the Commune Subzone of the Bifrons Zone in England (Somerset and North Dorset (Howarth, 1992)); the Laticostum [= Sublevisoni] Subzone of the Bifrons Zone in the Apennines (Italy) (Ridente, 2022, text-fig. 6.c); and the Bifrons Zone of the Lower Toarcian in the Kuban region (North Caucasus). Furthermore, the species is known from northern Siberia (Dagys, 1974) and is mentioned in open nomenclature from the Bifrons Zone of Georgia (Topchishvili, 1978, 1996).

**Material.** One well-preserved specimen (no. MZ-149/29).

#### *Hildoceras lusitanicum* (Meister, 1913)

Plate 6, figs. 4a–4c, 5a, 5b;

Plate 7, fig. 4a, 4b, 10a, 10b, 11a, 11b

*Hildoceras bifrons* var. *lusitanica*: Meister, 1913\*, p. 548, pl. XII, fig. 3

*Hildoceras lusitanicum*: Elmi, 1967, p. 234, fig. 45.1; Popa et al., 1976, pl. VI, fig. 2, pl. VII, figs. 3, 3a; Maubeuge, 1984, p. 88, figs. 59–61; Howarth, 1992, pl. 34, fig. 7, pl. 35, figs. 1–4, pl. 36, figs. 1–3, text-fig. 42; Faraoni et al., 1994, p. 249, p. XIII, fig. 4; Ridente, 1996, p. 180, pl. 1, figs. 7–10, pl. 2, figs. 1–10, pl. 3, figs. 1–8; Metodiev, 1997, p. 16, pl. II, fig. 2; Kment, 1998, p. 194, fig. 23–24; Parisi et al., 1998, pl. 3, fig. 13, text-fig. 7.4; Rulleau et al., 2001, pl. 9, fig. 1, pl. 10, fig. 2; Seyed-Emami et al., 2005, p. 356, Fig. 4D; Rulleau, 2006, p. 71, pl. 22, fig. 1; Bécaud, 2006, p. 88, pl. 44, figs. 1a–1b, 3a–3c, pl. 45, figs. 1a–1b, 3a–3c, pl. 46, figs. 2a–2b, 5a–5c, pl. 48, figs. 3a–3b; Géczy et al., 2008, pl. I, fig. 17; Metodiev et al., 2013, p. 71, figs. 2.n–2.o, fig. 4.a; Ridente, 2016, p. 27, figs. 3b, 4b–4c, 7a–7c, 8a–8c, 9a–9c; El Hammichi et al., 2016, pl. IV, figs. 2–5; Fauré et al., 2017, p. 58, pl. 2, figs. 22–23; Ridente, 2023, figs. 2a–2b, figs. 5.1, 6a; Kovács et al., 2023, p. 226, figs. 6.3, 6.6; Goy et al., 2023, p. 13/49, Fig. 6f.

*Hildoceras sublevisoni* var. *sulcosa*: Mitzopoulos, 1930 (var. nov.), p. 58, pl. V, figs. 1a–1c; Faraoni et al., 1994, p. XIII, figs. 10, 21.

*Hildoceras sublevisoni* var. *acarnanica*: Mitzopoulos, 1930 (var. nov.), p. 43, pl. 4, fig. 5.

*Hildoceras sublevisoni* var. *lombardica*: Mitzopoulos (var. nov.), 1930, p. 44, pl. 4, fig. 6.

*Hildoceras sublevisoni* var. *crassa*: Mitzopoulos, 1930 (var. nov.), s. 45, pl. 4, figs. 7a–7b.

*Hildoceras sublevisoni*: Donovan, 1958, p. 50; Zanzucchi, 1963, p. 124, p. XV, figs. 3, 6–8, pl. 16, figs. 2, 4, 8–11; Elmi, 1967, p. 231, fig. 44.3; Géczy, 1967a, p. 130, pl. XXIX, fig. 11, pl. XXX, fig. 4, pl. 64, fig. 45; Popa, 1971, p. 58, pl. I, figs. 1, 5; Elmi et al., 1974 p. 61, pl. 2, fig. 5; Riegraf et al., 1984, S. 117, pl. 6, Fig. 5, fig. 32; Kazakova, 1987, p. 101, pl. 2, figs. 6–7; Schlegelmilch, 1992, p. 96, pl. 43, fig. 6; Jattiot et al., 2016, text-fig. 4.A.

*Hildoceras bifrons*: Zanzucchi, 1963, p. 120, p. XIV, fig. 10, pl. 15, figs. 1, 4, 9, pl. 16, fig. 3; Topchishvili, 1969, p. 83, pl. V, fig. 7a–7b; Pinna, 1969, p. 10, p. 1, figs. 1, 4, 11; Howarth, 1992, pl. 37, fig. 8; Topchishvili et al., 2006, pl. 16, fig. 1a–1b.

*Hildoceras bifrons* f. *crassa*: Zanzucchi, 1963, p. 122, p. XV, fig. 10.

*Hildoceras bifrons* f. *evoluta*: Zanzucchi, 1963, p. 123, p. XVII, figs. 9, 11.

*Hildoceras* cf. *semicosta*: Zanzucchi, 1963, p. 126, p. XIV, fig. 11, pl. 15, fig. 5.

*Hildoceras bifrons tethysi*: Géczy, 1967a, p. 126, pl. 4, fig. 6.

*Hildaites* aff. *serpentiniformis*: Géczy, 1967b, p. 128, pl. XXX, fig. 2.

*Hildoceras* cf. *bifrons* ?*quadratum*: Géczy, 1967b, p. 129, pl. XXIX, fig. 5.

*Hildaites* ?*acarnanicus*: Géczy, 1967b, p. 128, pl. XXIX, fig. 8, pl. XXX, fig. 3.

*Hildoceras* aff. *lusitanicum*: Elmi et al., 1974, p. 62, pl. 2, fig. 6.

*Hildoceras crassum*: Gabilly, 1976b, p. 143, pl. 23, figs. 1–5, pl. 124, figs. 1, 2, pl. 25, figs. 1, 2; Rulleau, 2006, p. 71, pl. 21, fig. 6; Bécaud, 2006, p. 87, pl. 42, figs. 3a–3c, pl. 43, figs. 2a–2c; Wierzbowski et al., 2012, pl. 3, fig. 3; El Hammichi et al., 2016, pl. III, fig. 10, pl. IV, fig. 1; Benzaggagh, 2023, p. 14, figs. 13A–13C.

*Hildoceras (Hildoceras) sublevisoni*: Riegraf et al., 1984, p. 117, pl. 6, fig. 5, figs. 32, 33b.

*Hildoceras* gr. *sublevisoni*: Faraoni et al., 1994, p. 252, p. XIII, figs. 7, 11, 13, 20.

*Hildoceras graecum*: Faraoni et al., 1994, p. 249, p. XIII, fig. 19.

*Hildoceras* gr. *acarnanicum*: Faraoni et al., 1994, p. 249, p. XIII, fig. 8.

*Hildoceras tethysi*: Bécaud, 2006, p. 87, pl. 44, figs. 2a–2b, pl. 45, figs. 2a–2b; El Hammichi et al., 2016, pl. III, figs. 7–9; Goy et al., 2023, p. 13/49, Fig. 6e.

*Hildoceras* ex gr. *Lusitanicum* – *tethysi*: Wierzbowski et al., 2012, pl. 3, fig. 2.

*Hildoceras* cf. *lusitanicum*: Arp et al., 2021, fig. 12.2.

**H o l o t y p e.** The holotype is illustrated by E. Meister (Meister, 1913, p. 548, pl. XII, fig. 3) and comes from the Bifrons Zone of Marmeleira, Portugal.

**S h e l l s h a p e.** The whorls are high and evolute, with a square or subtrapezoidal cross-section; the point of maximum width lies in the periumbilical third of the whorl. The flanks are flattened. The venter is broad, flattened, and tricarinate, with the high, acute central keel flanked by broad ventral sulci. The umbilical shoulder is well-defined, and the umbilical wall is weakly convex and slightly beveled toward the umbilicus (Fig. 18).

**O r n a m e n t a t i o n.** The ribs are concavo-falcate and do not extend onto the venter, smoothing out near the ventrolateral shoulder. The width of the intercostal spaces are almost twice as much as the ribs width. On the periumbilical part of the lateral flanks, the ribs gradually fade, leaving the periumbilical quarter of the whorl completely smooth. A periumbilical ridge and a lateral groove on the flanks are absent.

#### Dimensions in mm and ratios in %.

| Specimen no. | D    | H    | Du   | W    | H/D  | W/D  | Du/D | H/W | Number of ribs per ½ whorl |
|--------------|------|------|------|------|------|------|------|-----|----------------------------|
| CFU-unnumb.  | 41.5 | 12   | 19.5 | 12   | 28.9 | 28.9 | 50   | 100 | 21                         |
| MZ-149/30    | —    | 20   | —    | 14.5 | —    | —    | —    | 138 | —                          |
| MZ-149/31    | —    | 22.5 | —    | 19.0 | —    | —    | —    | 118 | —                          |
| MZ-149/32    | —    | 23   | —    | 16   | —    | —    | —    | 144 | —                          |
| MZ-149/33    | —    | 25   | —    | 20   | —    | —    | —    | 125 | —                          |

**Comparison and remarks.** The falcate ribbing and their absence in the periumbilical region of the flanks are diagnostic features of this species. It differs from *H. bifrons* (Bruguère) primarily by the absence of a lateral groove on the flanks. It differs from *H. laticostum* Bellini by the presence of a wider, well-defined smooth band in the periumbilical region of the flanks, as well as by less coarse ribbing. Specimens with somewhat coarser ribbing found in the Crimean sample (Pl. 7, fig. 11), which are sometimes regarded

as distinct species, *H. tethysi* and *H. crassum*, are here included in *H. lusitanicum* (sensu Howarth, 1992).

**Occurrence.** Bifrons Zone in Portugal (Meister, 1913), Montenegro (Metodiev et al., 2013), Georgia (Topchishvili, 1969; Topchishvili et al., 2006), and Morocco (Benzaggagh, 2023); Commune Subzone of the Bifrons Zone in Southern Germany (Arp et al., 2021); Falciferum Subzone of the Falciferum [= Serpentinum] Zone and Commune Subzone of the

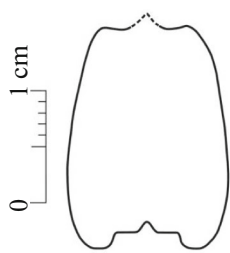


Fig. 18. Cross-section of *Hildoceras lusitanicum*, specimen no. MZ-149/30.

Bifrons Zone in Great Britain (Howarth, 1992) and Austria (Kment, 1998); Bifrons Zone (presumably the upper part of the “Sublevisoni” Subzone) in Iran (Seyed-Emami et al., 2005); “Sublevisoni” Subzone of the Bifrons Zone in Southern Switzerland (Donovan, 1958), France (Bécaud, 2006), Luxembourg (Guérin-Franiatte et al., 2010), Algeria (Elmi et al., 1974), the North Caucasus (middle part of the Dzhi-giata Formation (Kazakova, 1987)), and Western Ukraine (Wierzbowski et al., 2012); *Lusitanicum* Subzone of the Bifrons Zone in Bulgaria (Metodiev, 2008) and the Apennines (Italy) (Parisi et al., 1998; Ridente, 1996); Bifrons Zone, “Sublevisoni” Subzone, and *H. lusitanicum* Biohorizon in France (Rulleau et al., 2001) and Spain (Goy et al., 2023); and the stratigraphic interval of the *H. lusitanicum*–*H. bifrons* biohorizons of the Bifrons Zone in Hungary (Géczy et al., 2008; Kovács et al., 2023).

**Material.** Numerous mold fragments.

#### SUBFAMILY GRAMMOCERATINAE BUCKMAN, 1905

##### Genus *Grammoceras* Hyatt, 1867

##### *Grammoceras penestriatulum* Buckman, 1902

Plate 7, figs. 6, 9a–9c

*Grammoceras striatulum*: Buckman, 1890, p. 173, pl. XXVIII, figs. 16–17, pl. A, figs. 43–44.

#### Dimensions in mm and ratios in %.

| Specimen no. | D  | H   | Du | W   | H/D  | W/D  | Du/D | H/W | Number of ribs per ½ whorl |
|--------------|----|-----|----|-----|------|------|------|-----|----------------------------|
| MZ-149/34    | 99 | 30  | 48 | ≈19 | 30.3 | 19.2 | 48.5 | 158 | 21                         |
| MZ-149/35    | 29 | 8.5 | 14 | 5   | 29.3 | 17.2 | 48.3 | 170 | ≈19                        |

**Comparison and remarks.** This species differs from *G. striatulum* (J. de C. Sowerby) in having significantly coarser and more widely spaced ribbing. It is distinguished from the closely related *G. thouarsense* (d’Orbigny) by a more evolute shell with a noticeably wider umbilicus, as well as a narrower whorl section. In Russian literature, the species *G. thouarsense* and *G. penestriatulum* were long undifferentiated, with both more and less evolute specimens tradition-

*Grammoceras thouarsense*: Buckman, 1890, p. 169, pl. XXVIII, figs. 4–13, pl. XXXIV, fig. 12; Buckman, 1904, p. CXXXII; Buckman, 1928 in Buckman, 1909–1930, pl. DCCCLXXIV, figs. 1–2; Krimholz, 1947, p. 168, pl. XXVIII, fig. 1–2; Krimholz, 1961, p. 51, pl. 2, fig. 8.

*Grammoceras audax*: Buckman, 1902, p. 3.

*Grammoceras penestriatulum*: Buckman, 1902\*, p. 3 (nomen nov. pro pars *Grammoceras striatulum*: Buckman, 1890, p. 173, pl. XXVIII, figs. 16–17); Buckman, 1904, p. CXXXII; Gabilly, 1973, p. 186, text-figs. 21, 23, pl. XXX, figs. 3–4, pl. XXXI, figs. 3–4, pl. XXXII, figs. 6–7; Urlichs, 1977, pl. 5, fig. 3; Goy, Martínez, 1990, pl. 3, fig. 2; Metodiev, 1997, p. 19, pl. III, fig. 4; Alméras et al., 1998, pl. 7, fig. 5; Metodiev, 2002, p. 173, text-figs. 5, 6a–6b, pl. 1, fig. 7; Neige and Rouget, 2002, p. 777, figs. 7G, 8N; Fauré, 2002, p. 725, pl. 18, fig. 3; Rulleau, 2006, p. 86, fig. 22–7, pl. 42, fig. 1; Rulleau, 2010, pl. 1, fig. 3; Guérin-Franiatte et al., 2010, p. 31, pl. 3, fig. 9; Kovács, 2013, p. 128, pl. 2, figs. 6–7, tab. 3, figs. 6–7; Weis et al., 2018, fig. 8-A; Fauré and Guibbert, 2021, p. 108, Fig. 3E; Kovács et al., 2023, p. 227.

*Costigrammoceras costigerum*: Buckman, 1926 in Buckman, 1909–1930 (sp. nov.), pl. DCLXXXVI, figs. 1–2, Figs. 7.7, 7.9.

**Holotype.** The holotype by monotypy is illustrated in (Buckman, 1890, pl. XXVIII, figs. 16–17) as “*Grammoceras striatulum*”. Later, this specimen (the only one from the sample in Buckman, 1890) was renamed *G. penestriatulum* by Buckman (1902, p. 3). The specimen comes from the “Striatulum-beds, Stinchcombe Hill”, Gloucestershire, England. Sedgwick Museum of Earth Sciences (University of Cambridge), specimen no. SM J 6270. Re-illustrated on the GB3D Type Fossils Online website: <https://www.3d-fossils.ac.uk/fossilType.cfm?typSampleId=20006210>

**Shell shape.** The shell is evolute, discoidal, medium-sized. The whorls expand moderately and have a sub-oval cross-section. The flanks are weakly convex, and the venter is narrow and tectiform. The umbilicus is wide, shallow, and bowl-shaped. The umbilical wall is narrow and convex.

**Ornamentation.** The venter has a low but well-defined keel bordered by smooth stripes. The ribs are sigmoid and curve sharply forward as they pass onto the venter. The width of the ribs is slightly less than the width of the intercostal spaces.

ally assigned to *G. thouarsense* (Krimholz, 1961; Gasanov, 1967; et al.).

The Crimean specimens resemble the holotype in shape and proportions but are characterized by somewhat more widely spaced and coarser ribbing. The average rib density per whorl at comparable diameters is very similar to that of *G. thouarsense*. However, similar rib density values are reported for *G. penestriatulum* from France (Gabilly, 1973, p. 188). The same

applies to certain specimens from Germany (Urlichs, 1977, pl. 5, fig. 3) and the Northern Caucasus (Krimholz, 1961, pl. 2, fig. 8).

**Occurrence.** The Striatulum and Fascigerum subzones of the Thouarsense Zone (Upper Toarcian) in the Northern Caucasus (Krimholz, 1961), Bulgaria (Metodiev, 2002, 2008), Hungary (Kovács et al., 2023), France (Fauré, 2007, p. 44; Fauré, Guibbert, 2021), Germany (Urlichs, 1977), Luxembourg (Guérin-Franiatte et al., 2010), Great Britain (Buckman, 1904), Italy, Spain (Goy, Martínez, 1990), North Tyrol (Austria (Fischer, 1966)), and possibly the Upper Toarcian of Morocco (El Arabi et al., 1999).

**Material.** One large, partially preserved specimen (no. MZ-149/34) and numerous mold fragments of the inner whorls.

### Genus *Pseudogrammoceras* Buckman, 1901

#### *Pseudogrammoceras fallaciosum* (Bayle, 1878)

Plate 7, figs. 5a, 5b, 8a–8d

*Grammoceras fallaciosum*: Bayle, 1878\*, pl. LXXVIII, figs. 1–2; Rosenberg, 1909, S. 299 [107], pl. XV (VI), figs. 11a–11c, 12, fig. 8; Urlichs, 1977, pl. 6, fig. 1; Schlegelmilch, 1992, p. 95, pl. 42, Fig. 8. *Harpoceras fallaciosum*: Haug, 1885, p. 616, pl. XII, fig. 1c.

*Ammonites radians*: Quenstedt, 1885 in Quenstedt, 1882–1885 (sp. nov.), p. 403, pl. LI, fig. 4, pl. LIV, fig. 56.

*Ammonites cf. radians*: Quenstedt, 1885 in Quenstedt, 1882–1885, p. 406, pl. LIII, fig. 13.

*Ammonites radians depressus*: Quenstedt, 1885 in Quenstedt, 1882–1885, (subsp. nov.), p. 406, pl. LII, fig. 6.

*Grammoceras fallaciosum* var. *cotteswoldiae*: Buckman, 1889 (var. nov.), p. 204, pl. XXXV, figs. 4–7, Meister, 1913, p. 566, pl. XIV, fig. 2.

*Pseudogrammoceras cotteswoldiae*: Buckman, 1904, p. CXLIX, pl. XXV, figs. 4–6; Stankevich, 1964, p. 28, pl. VII, fig. 2–4; Rostovtsev, 1965, p. 61, pl. VI, fig. 2; pl. IX, fig. 1; Popa, 1967, p. 43, pl. II, fig. 2, pl. III, fig. 3; Topchishvili, 1990, p. 47, pl. XVI, figs. 2, 2a; Topchishvili, 2006, pl. 19, figs. 1a, 1b.

*Pseudogrammoceras expeditum*: Buckman, 1904 (sp. nov.), p. CXLVIII, pl. XXXIV, figs. 10–11; Elmi, 1967, text-fig. 48.

*Pseudogrammoceras subfallaciosum*: Buckman, 1904 (sp. nov.), p. CXLVII, pl. XXXIII, figs. 17–18; Stankevich, 1964, p. 27, pl. VII, fig. 5; Popa, 1967, p. 43, pl. II, fig. 3, pl. III, fig. 1.

*Pseudogrammoceras pedicum*: Buckman, 1904 (sp. nov.), p. CXLVII, text-fig. 140; Rostovtsev, 1965, p. 63, pl. VIII, fig. 1.

*Pseudogrammoceras regale*: Buckman, 1904 (sp. nov.), p. CXLV, text-fig. 134, suppl. pl. III (p. CLXVI), fig. 138; Stankevich, 1964, p. 31, pl. VIII, fig. 1; Rostovtsev, 1965, p. 64, pl. V, fig. 1, pl. VII, fig. 1.

*Pseudogrammoceras fallaciosum*: Buckman, 1904, p. CLII, text-figs. 150a–150c; Krimholz, 1947, pl. XXVIII, fig. 1; Krimholz, 1958, p. 71, pl. XXVIII, figs. 1a–1b; Krimholz, 1961, p. 63, pl. 4, figs. 3, 4a, 4b; Rostovtsev, 1965, p. 62, pl. VI, fig. 1; Nutsbidze, 1966, p. 101, pl. XXII, figs. 3–5, 5a; Popa, 1967, p. 42, pl. II, fig. 1; Gasanov, 1967, p. 167, pl. V, figs. 1–2; Seyed-Emami, 1971, pl. 5, fig. 5; Kazakova, 1971, p. 11, pl. 1, figs. 5–6; Barfety et al., 1972, pl. I, fig. 6; Gabilly, 1973, p. 234, pl. XLII, figs. 1–6, 8–9, pl. XLIII, fig. 4, pl. XLIV, figs. 1–2; Guex, 1975, p. 101, pl. III, figs. 2, 6, pl. IV, fig. 5; Gabilly, 1976b, pl. 30, figs. 1–4; Popa et al., 1976, pl. IX, fig. 3; Krimholz et al., 1988, pl. 3, fig. 5; Goy and Martínez, 1990, pl. 3, fig. 4; Topchishvili, 1990, p. 45, pl. XVII, fig. 3; Rostovtsev, Krimholz, 1992, c. 40, pl. 17, fig. 1; Biostratigraphie..., 1997, pl. 11, figs. 1–2; Metodiev, 1997, p. 20, pl. III, fig. 6; Rulleau et al., 2001, pl. 13, figs. 4, 6; Fauré, 2002, p. 724, pl. 18, figs. 16–17, pl. 20, figs. 1–2; Metodiev, 2002, p. 183, pl. IV, figs. 2–6, pl. V, figs. 1–5; text-figs. 7/1a, b–10a, b; Neige, Rouget, 2002, p. 776, figs. 7C, 8M; Rulleau, 2003, p. 139; Seyed-Emami et al., 2005, p. 357, Figs. 5B, 5C; Topchishvili et al., 2006, pl. 17, fig. 8, pl. 18, fig. 1; Fauré, 2007, p. 42, figs. 7.18–20; Seyed-Emami et al., 2008, p. 250, fig. 5/N1–3; Metodiev, 2008, Fig. 5.z; Galácz et al., 2010, p. 329, pl. 4, fig. 3, pl. 5, fig. 3; Galácz et al., 2012, pl. I, fig. 6.

*Pseudogrammoceras* aff. *expeditum*: Popa, 1967, p. 45, pl. II, figs. 4a–4b, pl. III, fig. 2.

*Pseudogrammoceras* ex gr. *fallaciosum*: Rulleau, 2006, p. 83, figs. 21–15, pl. 38, fig. 4, pl. 39, figs. 3–5, pl. 40, fig. 1; Kovács et al., 2020, p. 148, pl. I, fig. 8, pl. II, figs. 1–3; 2023, p. 226, figs. 7.12, 8.1–2.

*Pseudogrammoceras* cf. *fallaciosum*: Ippolitov et al., 2008, pl. 1, fig. 4.

**Holotype.** The holotype is illustrated in Bayle (1878, pl. LXXVIII, figs. 1–2) and comes from Urweiler (Rhine basin, Lorraine); Upper Toarcian, Thouarsense Zone; its repository is cited inconsistently in various works (cf. Metodiev, 2002, 2008); it is re-illustrated in Gabilly (1976b, pl. 30, figs. 1–4).

**Shell shape.** The shell is small and compressed. The whorls expand moderately and are weakly overlapping, becoming more involute at early growth stages. The cross-section is high sub-oval, with maximum width at the umbilical shoulder. The flanks are weakly convex; the venter is narrow, convex, and carinate. The umbilicus is wide, and the umbilical shoulder is distinct and rounded.

**Ornamentation.** The ribs are single and sigmoidal; they extend to the ventral keel and are closely spaced at the umbilical bend. Along their length, the ribs exhibit two gentle flexures: a backward curve in the periumbilical third of the whorl and a forward curve in the periventral quarter of the lateral flanks. The venter bears a distinct, narrow keel bordered by shallow, weakly developed ventral grooves.

#### Dimensions in mm and ratios in %.

| Specimen no. | D    | H  | Du  | W   | H/D  | W/D  | Du/D | H/W | Number of ribs per ½ whorl |
|--------------|------|----|-----|-----|------|------|------|-----|----------------------------|
| MZ-149/36    | 38.5 | 15 | 15  | 10  | 39   | 26   | 39   | 150 | 27                         |
| MZ-149/37    | 31   | 14 | 8.5 | 9.5 | 45.2 | 30.7 | 27.4 |     |                            |
| GM- 1433     | —    | 13 | —   | 10  | —    | —    | —    | 130 | —                          |

**Comparison and remarks.** Based on a revision of the genus (Gabilly, 1976b), several taxa described by S. Buckman (*P. cotteswoldiae*, *P. expeditum*, *P. subfallaciosum*, *P. regale*, and *P. pedicum*) were synonymized with *P. fallaciosum*; which was characterized for significant morphological variability, by the

*tum*, *P. subfallaciosum*, *P. regale*, and *P. pedicum*) were synonymized with *P. fallaciosum*; which was characterized for significant morphological variability, by the

presence of different morphotypes with a narrower umbilicus (compared to other representatives of the genus); high and strongly compressed whorls, and a rib configuration that remains constant throughout all growth stages.

It differs from the morphologically similar *P. pinnai* García-Gómez et Rivas by the convex shape of the ventral side (which is tectiform in *P. pinnai*) and by the absence of the inclination trend of ribbing during ontogeny.

**Occurrence.** In Northwest Europe, *P. fallaciosum* used as an index for the eponymous subzone and biohorizon within the Thouarsense Zone of the Upper Toarcian. It is also used as an index species for the corresponding subzone in the Mediterranean-Caucasian Province. However, according to Page (2003), the Fallaciosum Subzone of the Mediterranean Province may not be the precise temporal equivalent of the eponymous Northwest European unit. The Fallaciosum Subzone of the Mediterranean-Caucasian Province should perhaps be interpreted more broadly, encompassing the temporal equivalent of the upper part of the Northwest European Fascigerum Subzone as well (Biostratigraphie..., 1997, p. 27, pl. IV; Page, 2003, p. 50, fig. 7).

The species is widely distributed in Bulgaria, France, Germany, Hungary, Spain, northern Iran, the North Caucasus, and Transcaucasia.

**Material.** One small-sized specimen (no. MZ-149/36) and several fragments.

#### Genus *Dumortieria* Haug, 1885

##### *Dumortieria levesquei* (d'Orbigny, 1844)

Plate 7, figs. 2a, 2b, 3

*Ammonites solaris*: Zieten, 1831, p. 19, pl. XIV, figs. 7a–7c (=non *A. solaris* Phillips, 1829)

*Ammonites levesquei*: d'Orbigny, 1844\* in d'Orbigny, 1842–1851, p. 230, pl. 60, figs. 1–4 (inscription on the plate “*A. solaris* Phillips”).

#### Dimensions in mm and ratios in %.

| Specimen no. | D    | H   | Du   | W | H/D  | W/D  | Du/D | H/W | Number of ribs per ½ whorl |
|--------------|------|-----|------|---|------|------|------|-----|----------------------------|
| MZ-149/38    | 29.4 | 8.5 | 14.1 | 8 | 28.9 | 27.2 | 48   | 106 | 24                         |
| GM-2134      | 22   | 7.0 | 10.0 | — | 31.8 | —    | 45.5 | —   | 14                         |

**Comparison.** It differs from *D. nicklesi* Benecke and *D. striatulocostata* (Quenstedt) by the broader whorl section, and from *D. suevica* Haug in a more evolute shell.

**Occurrence.** Lower part of the Pseudoradiosa Zone (Levesquei Subzone) of the Upper Toarcian in Western Europe (Great Britain, Germany, Luxembourg, France, Bulgaria, Spain); Levesquei Zone of Georgia, Azerbaijan, and the North Caucasus.

**Material.** Three specimens, including one well-preserved mold of the inner whorls. (no. MZ-149/38).

*Harpoceras levesquei*: Haug, 1885, p. 662, pl. XI, fig. 5.

*Ammonites falcofila*: (pars) Quenstedt, 1885 in Quenstedt, 1882–1885, p. 430, pl. 54, Fig. 28 (non pl. 54, fig. 30–31).

*Dumortieria levesquei* (d'Orbigny): Haug, 1887, p. 129; Rostovtsev, 1965, p. 75, pl. XI, figs. 2a–2c; Nutschidze, 1966, p. 107, pl. XXIV, figs. 1–1a; Urlachs, 1977, pl. 6, fig. 4; Goy and Martínez, 1990, pl. IV, fig. 1; Schlegelmilch, 1992, p. 105, pl. 57, fig. 6; Rostovtsev and Krimholz, 1992, p. 41, pl. 16, fig. 6; Gabilly and Mouterde in Fischer, 1994, p. 58, pl. 36, figs. 3a, 3b; Biostratigraphie..., 1997, pl. 11, figs. 9–10; Metodiev, 1997, p. 20, pl. IV, fig. 2; Schulbert, 2001, p. 61, pl. 5, figs. 1–3, 10; Arp, 2010, p. 38, pl. 1, figs. 2–3; Howarth, 2013, p. 89, figs. 62 1a–1b; Di Cencio and Weis, 2020, p. 24, pl. 8, fig. c; Arp et al., 2021, figs. 14.11, 14.13.

*Dumortieria falcofila*: Schlegelmilch, 1992, p. 106, pl. 50, fig. 3.

**Lectotype.** The lectotype is illustrated in (d'Orbigny, 1842–1851, pl. 60, figs. 1–3), designated by J. Gabilly and R. Mouterde in (Fischer et al., 1994, p. 59); it presumably comes from the vicinity of Autun (Burgundy, France) and is housed in the Muséum national d'Histoire naturelle (Paris), specimen no. MNHN F B09769, d'Orbigny collection no. 1910-1; it is re-illustrated in (Fischer, 1994, pl. 36, figs. 3a, 3b; Biostratigraphie..., 1997, pl. 11, figs. 9–10; Howarth, 2013, figs. 62 1a–b).

**Shell shape.** The shell is small-sized and evolute. The whorls increase slowly in size during ontogeny and have a sub-elliptical cross-section (height slightly exceeding width). The umbilicus is wide and shallow. The flanks are sub-parallel and weakly convex. The venter is strongly convex and slightly acute. The umbilical and ventrolateral shoulders are gentle. The relative width of the umbilicus increases during ontogeny.

**Ornamentation.** The ribs are quite prominent and weakly curved, ranging from sub-rectiradial to weakly retroradial; they curve gently forward at the ventrolateral bend. On the outer whorl, the ribs are somewhat irregularly spaced and unequal in height. Starting at a diameter of 25 mm, the ribs exhibit a gentle backward curve on the periventral half of the flanks. Rib density increases with diameter. A distinct ventral keel is present.

#### Genus *Pleydellia* Buckman, 1899

Subgenus *Pleydellia* Buckman, 1899

##### *Pleydellia* (*Pleydellia*) *leura* (Buckman, 1890)

Plate 3, figs. 5a–5c, 8a, 8b, 9

*Grammoceras leura*: Buckman, 1890\*, p. 195, pl. XXXIII, figs. 5–7, 8–10.

*Pleydellia leura*: Buckman, 1902, p. 4; Buckman, 1904, p. CXXXVIII, suppl. pl. II (p. CLXV), fig. 115; Rostovtsev, 1965, p. 68, pl. X, fig. 1a–1b, 3a–3b; Nutschidze, 1966, p. 105, pl. XXIII, fig. 2; Kazakova, 1984, p. 77, pl. II, figs. 2–3, 5; Schlegelmilch, 1992, S. 108, pl. 51, Fig. 15; Schulbert, 2001, p. 96, pl. 13, fig. 6–7, 10–11, pl. 14, fig. 1; Metodiev, 2008, text-fig. 6.w; De Celis et al., 2017, fig. 3.h; Di Cencio and Weis, 2020, p. 64, pl. 28, figs. b, d.

*Pleydellia (Pleydellia) leura*: Rulleau et al., 2001, pl. 18, fig. 1; Rulleau, 2006, p. 94, pl. 55, fig. 4.

*Pleydellia* aff. *comata*: Kazakova, 1984, p. 73, pl. I, fig. 5.

? *Pleydellia caucasica*: Kazakova, 1984 (sp. nov.), p. 74, pl. I, figs. 6–8.

**Lectotype** (designated herein). illustrated by Buckman (1890, pl. XXXIII, figs. 8–10). This specimen was later designated as the “type” by Buckman (1904, p. CXXXVIII); according to the International Code of Zoological Nomenclature (1999, 72.4.7., 73.1.3.), if a specimen is designated in another work, it continues to be considered a syntype; therefore, it is selected here as the lectotype. Gloucestershire, England, “aalensis hemera” (according to S.S. Buckman’s terminology); Sedgwick Museum of Earth Sciences (University of Cambridge), specimen no. SM J 6406.

#### Dimensions in mm and ratios in %.

| Specimen no. | D  | H    | Du   | W    | H/D  | W/D  | Du/D | H/W | Number of ribs per ½ whorl |
|--------------|----|------|------|------|------|------|------|-----|----------------------------|
| MZ-149/39    | 49 | 21   | 15.5 | 11.5 | 42.9 | 23.5 | 31.6 | 183 | —                          |
| MZ-149/40    | 31 | 12.5 | 9.5  | 6.0  | 40.3 | 19.4 | 30.6 | 208 | 14                         |
| MZ-149/41    | —  | 22.5 | —    | 11   | —    | —    | —    | 205 | —                          |

**Comparison and remarks.** It differs from *P. aalensis* (Zieten) and *P. costulata* (Zieten) by having a more involute shell with a narrower umbilicus, as well as by the reduction of ribs on the outer whorls. It further differs from *P. costulata* in a narrower cross-section and in less prominent and more evenly spaced ribs. It is distinguished from *P. aalensis* by the absence of ribs that bifurcate at the umbilical shoulder. It differs from *P. buckmani* Maubeuge in the absence of rib bundles.

The Crimean material is closest to the specimen illustrated in (Buckman, 1890, pl. XXXIII, figs. 5–7). It has a similar cross-sectional shape and is also characterized by the presence of only simple ribs, which smooth out on the periventral half of the flanks and tend to become reduced on the outer whorls.

**Occurrence.** Upper Toarcian, Aalensis Zone of Europe and the Caucasus (Nutsbidze, 1966). In Central Spain, occurrences have been recorded in the Buckmani Subzone and even in the basal Aalenian (Goy et al., 2021).

**Material.** Two small specimens (Nos. MZ-149/39, MZ-149/40) and one fragment of the outer whorl (No. MZ-149/41).

Subgenus *Cotteswoldia* Buckman, 1902

*Pleydellia (Cotteswoldia)* cf. *paucicostata* (Buckman, 1904)

Plate 5, figs. 12a, 12b

*Pleydellia (Cotteswoldia)* cf. *paucicostata*: Ippolitov et al., 2008, pl. 1, fig. 2.

**Shell shape.** The whorl section is acutely oval. The flanks are weakly convex. The umbilical wall is

**Shell shape.** The shell is discoidal, flattened, and moderately involute, with moderately expanding whorls. The whorls are strongly compressed (height approximately twice the width). The cross-section is a high, laterally flattened, acute oval (Fig. 19). The flanks slope gently towards the venter and grade smoothly into a narrow, acute venter. The umbilicus is shallow and of moderate width.

**Ornamentation.** The ribs are single, thin, and sigmoidally curved, becoming somewhat closer together in the periumbilical region; they fade out on the periventral half of the flanks (shifting progressively closer to the umbilicus during ontogeny) and do not extend onto the venter. A low ventral keel is present.

low, rounded, and slightly beveled toward the umbilicus. The umbilical shoulder is well-defined. The point of maximum whorl width is located approximately at mid-height.

**Ornamentation.** The outer whorl bears weak, sigmoidal ribs, some of which are grouped into broad, ridge-like bundles spaced at relatively regular intervals. The ventral keel is low and acute.

**Comparison and remarks.** The specimen described here was previously illustrated by Ippolitov et al. (2008, pl. 1, fig. 2). The ornamentation and cross-section resemble those of the outer whorl of the *P. paucicostata* holotype (Buckman, 1904, p. 133; 1905a, Suppl., pl. XXIII, figs. 1–3a) and a specimen of *P. (C.) paucicostata* illustrated by Rulleau et al. (2001, pl. 17, figs. 1–2). However, due to its incomplete preservation, the Crimean material can be identified only in open nomenclature.

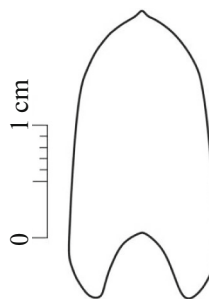


**Fig. 19.** Cross-section of *Pleydellia (Pleydellia) leura*, specimen no. MZ-149/39, D = 49 mm.

## Dimensions in mm and ratios in %.

| Specimen no. | H  | W    | H/W  |
|--------------|----|------|------|
| MK2495       | 24 | 20.5 | 1.17 |

**Occurrence.** The species *P. (C.) paucicostata* is characteristic of the Mactra Subzone of the Aalensis Zone of the upper Toarcian Pyrenees Mountains (Goy and Martínez, 1990), Britain (Buckman, 1904), and France (Rulleau et al., 2001); the lower part of the Aalensis Zone of Luxembourg (Di Cencio and Weis, 2020), Hungary (Kovács, 2010), Sicily (Pallini et al., 2004), the Caucasus (Nutschidze, 1966), and Iran (Seyed-Emami et al., 2005); the Aalensis Subzone of Bulgaria (Metodiev, 2008).

## Dimensions in mm and ratios in %.

| Specimen no. | D    | H   | Du  | W | H/D  | WW/D | Du/D | Number of ribs per ½ whorl |
|--------------|------|-----|-----|---|------|------|------|----------------------------|
| GM-2132      | 19   | 7.5 | 3.5 | — | 39.5 | —    | 18.4 | ≈23                        |
| Pnv-1948     | 15.5 | 7.2 | 3   | — | 46.5 | —    | 19.4 | —                          |

**Comparison.** The specimens are assigned to *P. (C.) cf. subcompta* based on the fasciculation of ribs in the periumbilical quarter of the whorl. However, the presence of only two juvenile specimens in the sample precludes their precise identification. *P. (C.) misera* Buckman is another closely related species with similar ornamentation. A similar juvenile form was identified by Myczyński (2004, fig. 23.7) as *P. cf. fluens* Buckman. Furthermore, the possibility that the Crimean sample belongs to the species *P. buckmani* Maubeuge—in which the ribs on the phragmocone also form bundles—cannot be ruled out.

**Occurrence.** The species *P. (C.) subcompta* is known from both northwestern Europe and the Mediterranean region: the Upper Toarcian (Mactra Subzone of the Aalensis Zone) in Sicily (Pallini et al., 2004), France (Rulleau et al., 2001), and Luxembourg (Di Cencio and Weis, 2020); the terminal Mactra Subzone to the basal Aalensis [=Mactra] Subzone in the Pyrenees (Goy and Martínez, 1990); the Aalensis Zone in Poland (Myczyński, 2004) and Hungary (Kovács, 2010); the Aalensis Subzone in Bulgaria (Metodiev, 2008); and the base of the Aalensis [=Mactra] Subzone in Germany (Arp, 2010; Arp et al., 2021). In Iran, this species has been recorded alongside *P. aalensis* (Schlotheim in Zieten) and *P. buckmani* Maubeuge (Seyed-Emami et al., 2005).

**Material.** Two juvenile specimens (Pnv-1948 and GM-2132).

**Material.** A fragment of the outer whorl (specimen no. MK2495).

*Pleydellia (Cotteswoldia) cf. subcompta* (Branco, 1879) [sp. juv.]  
Plate 3, figs. 13, 14

**Shell shape.** The shell is flattened, moderately involute, and small. The umbilicus is moderately narrow and shallow. The flanks are weakly convex and grade smoothly into a narrow venter. The cross-section is a tall oval, acute ventrally.

**Ornamentation.** The flanks are covered with fine, closely spaced, falcate ribs that may group into fan-like bundles (fasciculate) in the periumbilical region, forming a broad, primary-rib-like structure at the base. The venter bears a fine, distinct keel.

## FAMILY HAMMATOCERATIDAE ARKELL, 1957

## SUBFAMILY HAMMATOCERATINAE ARKELL, 1957

Genus *Crestaites* Rulleau et Elmi, 2001*Crestaites cf. meneghinii* (Bonarelli, 1899)

Plate 5, figs. 8a, 8b, 11a–11c

*Pseudammatoceras clocheri*: Ippolitov et al., 2008, pl. 1, fig. 3.

**Shell shape.** The shell is large and evolute. The whorls have a rounded-rectangular section with slightly convex flanks and a high, rounded venter. The umbilicus is wide. The umbilical and ventrolateral shoulders are gently rounded.

**Ornamentation.** On the smaller specimen, the ribs extend to the ventral keel. The ribbing is relatively dense, consisting of single ribs (predominant) and bifurcating ribs that branch in the periumbilical third of the whorl. The ribs are prorsiradiate, weakly sigmoidal, and lack nodes. On the venter, the ribs curve gently forward. A low ventral keel is present; on the larger specimen (MZ-149/47), it is well-defined and bordered by smooth bands.

## Dimensions in mm and ratios in %.

| Specimen no. | H     | W     | H/W   |
|--------------|-------|-------|-------|
| MZ-149/47    | 28.48 | 18.82 | 1.513 |
| MZ-149/42    | 20.50 | 15.20 | 1.349 |

**Comparison and remarks.** Specimen MZ-149/47 was previously published in (Ippolitov et al., 2008, pl. 1, fig. 3) as *Pseudammatoceras clocheri* Rulleau et Elmi. The material compares well with the holotype of *C. meneghinii* (Meneghini, 1874, p. 59, pl. XIII, figs. 1a–1c; Merla, 1933, p. 10, pl. 1, fig. 1;

Pinna, 1969, p. 4, text-fig. 11; Howarth, 2013, text-fig. 72.1), which is also characterized by strongly compressed whorls and closely spaced, prorsiradiate ribs without nodes. However, the fragmentary preservation allows the Crimean material to be identified only in open nomenclature.

**O c c u r r e n c e.** The species *C. meneghinii* is characteristic of the Mediterranean region, including the Southern Alps (Spain, Portugal, Italy, Sicily, Austria, Hungary, and Morocco). It occurs sporadically in northwestern Europe (Upper Toarcian of France and England). In southern Spain (Betic Cordillera). Sandoval (Sandoval et al., 2011, p. 244, text-fig. 8) defines the “*Geczyceras meneghinii*”<sup>2</sup> Biozone, which partially corresponds to the Meneghinii<sup>3</sup> and Aalensis chronozones, spanning the interval from the upper part of the Levesquei Subzone to the lower part of the Fluitans Subzone. The reported stratigraphic range of the biozone’s index species varies significantly across different regions. For example, in Portugal, it appears in the Speciosum Zone (Reynesi Subzone) and disappears in the upper part of the Meneghinii Zone (Elmi et al., 2007); in Iberia, it is distributed within the Insigne Subzone of the Dispansum/Speciosum Zone (Martínez, 1996), whereas in Hungary, it occurs within the Speciosum Zone (Kovács, 2009, 2020).

**M a t e r i a l.** Two incompletely preserved specimens.

#### ?Genus *Pseudaptetoceras* Géczy, 1966

“*Pseudaptetoceras*” cf. *christianae* (Elmi et Mouterde, 1997)

Plate 5, figs. 9a–9c

**S h e l l s h a p e.** The shell is large, flattened, discoidal, and involute. The whorls are high, with a high oval cross-section tapering toward the venter. The flanks are weakly convex, converging toward the keel in the outer half of the whorl. The venter is very narrow and practically undifferentiated.

**Ornamentation** weakly developed. It is characterized by broad, low primary ribs, bifurcating into two narrower, higher secondary ribs at approximately the mid-flank. In the periventral region, the secondary ribs curve smoothly forward. There are no nodes on the ribs. The venter bears a distinct keel.

**C o m p a r i s o n a n d r e m a r k s.** Based on its shape and cross-section, the Crimean specimen presumably belongs to the genus *Pseudaptetoceras*, proposed for Aalenian hammatoceratids characterized by a discoidal, compressed shell and an acute venter (Géczy, 1966, p. 78). Morphologically, the species

most similar to it is *P. christianae* (Elmi and Mouterde, 1997). However, some authors regard this as a junior synonym of *P. klimakomphalum* (Vacek, 1886), the type species of the genus (Rulleau et al., 2001). The fact that the Crimean sample contains only a single, fragmentarily preserved specimen makes a definitive identification impossible. The validity, taxonomic position, and composition of the genus remain matters of debate (Kovács, 2009, p. 55); notably, a recent review (Howarth, 2013, p. 104) assigns it to the Middle Aalenian, which is why the generic name is enclosed in quotation marks in the present study. The Crimean specimen differs from representatives of the genus *Euaptetoceras* Buckman by having a significantly more acute venter.

**O c c u r r e n c e.** The genus *Pseudaptetoceras* s.l. is known from the Upper Toarcian–Aalenian of Europe, Alaska, North Africa, and Argentina. “*P.*” *christianae* (Elmi et Mouterde) is known from the Upper Toarcian: the Aalensis Zone, Mactra and Buckmani [= Fluitans] subzones in Portugal (Elmi et al., 2007); the upper Lugdunensis [= Fluitans] Subzone of the Aalensis Zone in Tunisia (Sekatni et al., 2008); and the Aalensis Zone in Morocco (El Hammichi et al., 2008) and Sicily (Pallini et al., 2004).

**M a t e r i a l.** One segment (about a quarter) of the outer whorl (specimen no. MZ-149/43).

#### S U B O R D E R STEPHANOCERINA BESNOSOV, 1960

FAMILY STEPHANOCERATOIDEA NEUMAYR, 1875

FAMILY ERYCITIDAE SPATH, 1928

SUBFAMILY ERYCITINAE SPATH, 1928

Genus *Erycites* Gemmellaro, 1886

*Erycites gerecsensis* Kovacs et Géczy, 2008

Plate 7, figs. 1a, 1b

*Erycites gerecsensis*: Kovács and Géczy, 2008\*, p. 78, pl. 12, figs. 1–2; Sandoval et al., 2015, p. 86; text-fig. 2.

**H o l o t y p e.** The holotype is kept in the Natural History Museum of the Faculty of Sciences of Eötvös Loránd University, Budapest, Hungary, specimen no. EG31A; illustrated by Kovács and Géczy (2008, pl. 12, figs. 1–2); it comes from the Upper Toarcian Aalensis Zone, Kis-Gerece Quarry near Süttő in the Gerece Mountain region, northwestern Hungary.

**S h e l l s h a p e.** The shell is large; during ontogeny, its shape changes from evolute-spheroconic to serpenticonic. The whorls expand slowly during ontogeny. On the phragmocone, the whorls are moderately overlapping, whereas on the body chamber, they are barely overlapping. The whorls of the phragmocone are depressed ( $W > H$ ), while the outer whorl (body chamber) is compressed with elliptical cross-section ( $H > W$ ). The flanks are strongly convex on the phragmocone but become significantly less convex on the body chamber. The venter is broad and strongly convex. The umbilicus is shallow and bowl-shaped; its

<sup>2</sup> *Geczyceras* Martínez Gutiérrez, 1992 is currently regarded as a synonym of *Hammatoceras* Hyatt, 1867; in turn, *Hammatoceras meneghinii* Bonarelli, 1899 is the type species of *Crestaites* Rulleau et Elmi, 2001 (Howarth, 2013).

<sup>3</sup> The Zone was established in the Apennines based on the first appearance of *Dumortieria meneghinii* (Zittel) (Kälin and Ureta, 1987; Cresta et al., 1995).

relative width increases significantly during ontogeny: on the phragmocone, at a diameter (D) of 68 mm, the ratio of umbilical diameter to shell diameter (Du/D) is 17%, whereas at D = 115 mm, Du/D is 50%. The umbilical shoulder is gentle; the umbilical wall is convex.

**Ornamentation.** A narrow smooth strip is present along the center of the venter. The flanks bear coarse, broad primary ribs that are rounded in cross-section and exhibit a noticeable swelling at the bifurcation point on the body chamber. The primary ribs

divide into three secondary ribs that extend onto the venter but are interrupted at its center. On the phragmocone, the ribs are rectiradiate, with intercostal spaces approximately equal in width to the ribs themselves. On the body chamber, the ribs are prorsiradiate and more widely spaced, with intercostal spaces significantly wider than the ribs. On the phragmocone, the bifurcation point is located near the ventrolateral shoulder; meanwhile on the body chamber, it shifts toward the periumbilical third of the whorl.

#### Dimensions in mm and ratios in %.

| Specimen no. | D   | H    | Du   | ½ W | H/D  | Du/D | Number of primary ribs per ½ whorl |
|--------------|-----|------|------|-----|------|------|------------------------------------|
| GM-2138      | 113 | 32.5 | 57.5 | 13  | 28.8 | 50.9 | ≈14                                |

**Comparison.** It differs from the closely related *E. barodiscus* (Gemmellaro, 1886) by its compressed body chamber (no wider than the penultimate whorl) with a highly elliptical cross-section, as well as the body chambers ribbing with a lower bifurcation point of the ribs (in the umbilical half of the flanks).

**Occurrence.** The Aalensis Zone of the upper Toarcian in Hungary (Kovács and Géczy, 2008). However, a wider distribution of the species cannot be ruled out. It is possible that certain specimens described from other regions as *E. barodiscus* (Gemmellaro, 1886), which lack the body chamber, may belong to this species.

**Material.** A single specimen, no. GM-2138. It consists of an internal mold fragment comprising the preserved phragmocone and a portion (slightly less than half a whorl) of the body chamber, preserved in reddish-brown argillite from the Lozovoe Quarry.

#### Dimensions in mm and ratios in %.

| Specimen no. | D    | H    | Du    | H/D  | Du/D | Number of primary ribs per ½ whorl |
|--------------|------|------|-------|------|------|------------------------------------|
| MZ-149/48    | 64.4 | 22.8 | 21.52 | 35.4 | 33.4 | 13                                 |

**Comparison and remarks.** The specimen described here was previously illustrated by Ippolitov et al. (2008, pl. 1, figs. 1a, 1b). In its morphology and ribbing pattern, it closely resembles the lectotype of *E. barodiscus* (Gemmellaro, 1886) designated by Cresta (1997, p. 43) and illustrated by Pavia and Cresta (2002, fig. 129). However, as the specimen under study lacks a body chamber, it could belong to any of the following species: *E. barodiscus* (Gemmellaro), *E. subquadratus* (Géczy, 1966), or *E. gerecsensis* Kovács and Géczy, 2008. These species are distinguished by the morphology and ornamentation of the body chamber and are treated here as separate taxa, following Kovács and Géczy (2008). A coarsely ribbed specimen from Georgia (Nutschidze, 1966, pl. XXXV, figs. 1, 1a)—

#### *Erycites* ex gr. *barodiscus* (Gemmellaro, 1886)

Plate 5, figs. 1a–1c

*Erycites* cf. *barodiscus*: Ippolitov et al., 2008, pl. 1, figs. 1a, 1b

**Shell shape.** The shell is medium-sized, planorbicone, moderately evolute on the inner whorls and evolute on the outer ones. The whorls are broad, suboval, and depressed ( $W > H$ ). The outer whorl exceeds the inner ones in width. The flanks are convex (more so on the inner whorls than on the outer one). The venter is broad and convex. The umbilicus is wide, deep, and bowl-shaped. The relative diameter of the umbilicus increases as the shell grows. The umbilical wall is convex.

**Ornamentation.** The ribbing on the flanks is coarse, consisting of thick, somewhat prorsiradiate primary ribs that branch into two or three secondary ribs in the periventral third of the flanks. The secondary ribs extend onto the venter, curving smoothly forward, and fade out upon reaching a narrow smooth strip at its center.

identified by K.Sh. Nutschidze as *Erycites fallax* Benecke, a classification noted by Kovács (Kovács and Géczy, 2008, p. 77), also evidently belongs to this group. A specimen from Iran described as *Erycites* aff. *sphaeroconicus* Buckman (Seyed-Emami et al., 2008, p. 255, text-fig. 6 (1<sub>1</sub>–1<sub>2</sub>)) likely belongs to this same group as well.

It differs from the closely related *E. fallfax* Arkell, 1957 in its coarser and more widely spaced ribbing. It differs from *E. sutneri* Gemmellaro, 1886 in its coarser ribbing and wider whorl section.

**Occurrence.** The terminal part of the Meneghinii Zone (Upper Toarcian) Comptum Subzone of the Opalinum Zone (Lower Aalenian) of the Apennines,

Sicily, France, Spain, Hungary, Georgia (periphery of the Dzirula Massif), Great Britain, and possibly Iran.

**Material.** One specimen no. MZ-149/48.

## STRATIGRAPHY AND CORRELATION

The studied fossils were collected not from continuous stratigraphic succession but from isolated boulders within a zone of tectonic fragmentation, a melange (Yudin and Zaitsev, 2020a). Within the limestone boulders of the Lozovoe Quarry, we identified ammonoid assemblages corresponding to specific biostratigraphic intervals of European ammonite-based zonal and subzonal scales (Figs. 20, 22). The studied xenolithic boulders represent melanged fragments of a formerly stratified rock sequence. In this case, as in the case of the discovery of fossils of varying ages in such deposits as moraines, paleontological data allow former presence of specific stratigraphic intervals at the site to be identified. Despite the absence of a continuous succession and the inability to trace precise positions of zonal boundaries, we can, with a certain degree of approximation, reconstruct the original stratigraphic sequence. This is how, for example, the discovery of Jurassic and Cretaceous fossils in boulders on Novaya Zemlya enabled the reconstruction of the zonal structure of a now-vanished rock sequence in that region (Bodylevsky, 1967; Cherkesov and Burdykina, 1981). Similarly, the presence of redeposited Pliensbachian–Aalenian fossils in the basal conglomerate of the Lower Bathonian on Spitsbergen provided the basis for describing assemblages characteristic of specific zones spanning the Lower–Middle Jurassic boundary (Ershova and Repin, 1983) and for inferring the former presence of these “zones” in the area (Harland and Kelly, 1997). Thus, based on the taxonomic composition of the ammonoid assemblages found in the red limestone boulders of the Lozovoe Quarry and data on the stratigraphic distribution of the identified taxa across various regions of Europe (Figs. 20, 22), it is possible to reconstruct the presence of eight successive ammonite biostratigraphic units of various ranks within the original Pliensbachian–Toarcian carbonate succession:

### Upper Pliensbachian

(1) *Amaltheus margaritatus* Zone Oppel, 1856; *Amaltheus stokesi* Subzone Lange, 1936, emend. Howarth, 1955

**Index species:** *Amaltheus (Amaltheus) stokesi* (J. Sowerby, 1818).

**Occurrence.** This unit is recognized as subzone or zone across the Northern Hemisphere: in Northwestern Europe, Bulgaria, Iran, Japan, Canada, and Alaska, as well as in the Caucasus, Transbaikalia, and the Northeast and Far East of Russia (Repin, 2016).

**Remarks.** This unit corresponds to the stratigraphic range of the index species. Only Harpoceratinae (which are not known in Crimea) allow for further subdivision (Biostratigraphie..., 1997, p. 20).

**Correlation.** Correlates with the lower part of the Lavinianum Zone of the Mediterranean scale (Biostratigraphie..., 1997).

**Characteristic ammonites in Crimea.** The index species is represented by a single specimen from the Lozovoe Quarry; in addition, a juvenile *Amaltheus* sp. was found, belonging to the same or a slightly later species. Some of the phyllocerids described in the present paper may also be of Late Pliensbachian age.

**Occurrences in Crimea.** The specimen of *Amaltheus* sp. reported from a limestone boulder nearby Koktebel village in southeastern Crimea (Permyakov, 1969, p. 104) may come from this or a closely related stratigraphic interval. However, none of V.V. Permyakov's works provide a description or illustration of this specimen, which makes its identification unverifiable (Zaitsev, 2023, p. 75). Thus, an identification error cannot be ruled out—specifically the scenario that V.V. Permyakov mistakenly identified some Middle Jurassic ammonite (possibly a member of the Hecticoceratinae) as the member of Pliensbachian genus *Amaltheus*.

### Lower Toarcian

*Hildoceras bifrons* Zone Reynès, 1868; “*Hildoceras sublevisoni* Subzone Donovan, 1958”<sup>4</sup>

**Occurrences in Crimea.** In addition to the carbonate rock boulders of the Simferopol Melange, finds of *Dactylioceras (Dactylioceras) ex gr. commune* (J. Sowerby) are also associated with the “Sublevisoni” Subzone. Apart from the Lozovoe Quarry in Crimea, these ammonites are known from the Upper Taurida Formation flysch of Mangush Ravine on the southeastern slope of Patil Mount (Zaitsev and Arkadiyev, 2019, p. 27). Judging by the faunal lists in published works, ammonites characteristic of this subzone are also present near Privetnoe village, a locality also cited for finds of “*D. ex gr. commune*” (Permyakov et al., 1991, p. 16). Furthermore, *Dactylioceras cf. commune* (J. Sowerby) has been illustrated and described from Bitak Formation conglomerates near Stroganovka village (Dovgal and Paryshev, 1979, p. 129). The Sublevisoni Subzone also includes a specimen of *Dactylioceras cf. athleticum* (Simpson, 1855) described from the Upper Taurida flysch on the northwestern slope of Sheludivaya Mount, near Prokhladnoe village (Turov et al., 2002, p. 25). A specimen of *Harpoceras*

<sup>4</sup> In the present work, following Howarth (1992), *Hildoceras sublevisoni* Fucini, 1919 is treated as a junior subjective synonym of *H. laticostum* Bellini, 1900. Consequently, units based on junior synonyms are enclosed in quotation marks, as they require renaming.

sp. indet. from the Upper Taurida Formation nearby Solnechnoselye village (Belbek River basin) may also belong to the Sublevisoni Subzone (Atabekyan et al., 1997).

### (2) *Hildoceras laticostum* provisional Biohorizon

**Index-species:** *Hildoceras laticostum* Bellini, 1900.

**Occurrence.** Recognized in France, Italy, Hungary, and Spain as the *Hildoceras sublevisoni* Biohorizon.

**Remarks.** The biohorizon was originally defined as *Hildoceras sublevisoni* in southeastern France (Gabilly, 1976a – “horizon VII”). This name is not used here because *H. sublevisoni* Fucini is invalid and should be considered a junior subjective synonym of *H. laticostum* Bellini. The biohorizon, now designated as *H. laticostum*, is currently regarded as provisional, as further study of the stratotype is required for its formal definition.

**Correlation.** It corresponds to the *Ovaticeras ovatum* Biohorizon at the base of the Commune Subzone of the Subboreal scale (Page, 2003).

**Characteristic ammonites in Crimea.** In addition to the index species, the finds of *Nodicoeloceras fonticulum* (Simpson), *N. ex gr. crassoides* (Simpson), and *Harpoceras falciferum* (J. de C. Sowerby) likely belong to this stratigraphic level.

### (3) *Hildoceras lusitanicum* Biohorizon Gabilly, 1976a

**Index-species:** *Hildoceras lusitanicum* Meister, 1913.

**Occurrence.** Central and Western France, Portugal, North Africa, Spain, Great Britain, Hungary.

**Remarks.** The assemblage of *Hildoceras laticostum* Bellini, *Harpoceras falciferum* (J. Sowerby), and *Dactylioceras* (*Dactylioceras*) ex gr. *commune* (J. Sowerby) is highly characteristic of the “Sublevisoni” subzone defined by Donovan (1958) for the Tethyan Realm. However, it should be noted that in Tethyan sections, the correlation of stratigraphic intervals, based on the succession of *Dactylioceras*, with units, based on the succession of *Hildoceras* species, remains a subject of debate. In particular, the *Dactylioceras commune* Biohorizon in Tethyan sections (where index species were selected based on the *Hildoceras* species succession but utilizing the *D. commune* horizon (Mouterde et al., 1971)) does not stratigraphically correspond to the eponymous biohorizon in Great Britain, where biohorizons are based strictly on the *Dactylioceratinae* succession (Biostratigraphie..., 1997, p. 29). Furthermore, in southwestern Germany, the “*H. sublevisoni*” Biohorizon has been observed above the *D. commune* Biohorizon—contrary to the order seen in Great Britain (Riegraf et al., 1984)—

“which clearly illustrates the difficulties of a scale based on index species whose evolution may proceed at vastly different rates and in very different ways” (Biostratigraphie..., 1997, p. 29).

**Correlation.** It is correlated with the upper part of the European “Sublevisoni” Subzone (Page, 2003). In a number of stratigraphic schemes in France (Biostratigraphie..., 1997; Bécaud, 2006), an *H. tethysi* Biohorizon is distinguished, underlying the *H. lusitanicum* Biohorizon. However, based on the interpretation of the species adopted in the present study, following Ridente (1996, 2016), *H. tethysi* Géczy is regarded as a junior subjective synonym of *H. lusitanicum*. Due to difficulties in correlating with stratigraphic intervals defined by the successive turnover of species of *Dactylioceras*, the use of sequences based on *Hildoceras* is preferable in Tethyan sections (Biostratigraphie..., 1997, p. 29).

**Characteristic ammonites in Crimea.** In addition to the index species, *Dactylioceras* (*Dactylioceras*) ex gr. *commune*, which co-occurs with *H. lusitanicum*, may also be assigned to this biohorizon.

## Upper Toarcian

*Grammoceras thouarsense* Zone Brasil, 1896;  
(4) *Grammoceras striatulum* Subzone Buckman, 1888

**Index-species:** *Grammoceras striatulum* (J. de C. Sowerby, 1823). Some authors use this species as the index for the *G. thouarsense* Subzone, distinguishing the Thouarsense Subzone (Brasil, 1896, emend. Gabilly, 1976a; Biostratigraphie..., 1997, p. 32).

**Occurrence.** North-Western Europe.

**Remarks.** The presence of the subzone in the boulders is established based on finds of the characteristic species *Perilytoceras perlaevis* (Denckmann) (Rulleau, 1997; Fauré, 2007). Finds of *Grammoceras penestriatulum* Buckman—a species associated with the Fascigerum Subzone of the Thouarsense Zone in northwestern Europe—indicate a similar age. In Hungary, according to Z. Kovács (Kovács, 2013), this species occurs alongside *Pseudogrammoceras mediterraneum* Garcia-Gómez et Rivas, 1980, within the interval designated as “*Pseudogrammoceras mediterraneum*”.

**Correlation.** It corresponds to the Thouarsense Subzone of Northwestern European scale and is correlated with the upper part of the Mediterranean Zone of the Mediterranean scale (Biostratigraphie..., 1997; Kovács, 2013).

**Occurrences in Crimea.** Boulders of terrigenous rocks in the Volkovskaya Balka Ravine on the left bank of the Alma River—located 1.5 km upstream from the ravine mouth and characterized by the ammonites *Grammoceras saemani* (Dumortier), *G. thouarsense* (d’Orbigny), and *G. subquadratum* (Buckman), likely correspond to this same stratigraphic interval (Muratov, 1959, p. 39; 1960, p. 26; Shalimov, 1960, p. 1409, pl. 1; Krimholz and Shalimov, 1961, pp. 76, 80). A similar

stratigraphic interval, characterized by finds of *Grammoceras* sp., can also be distinguished within the Bitak Formation in the Salgir River basin (Permyakov, 1962, p. 63; 1969, p. 106; Dovgal and Zagorodnyuk, 1985, p. 130; Permyakov et al., 1991).

*Pseudogrammoceras fallaciosum* Subzone Nicklès, 1907 emend. Howarth, 1980

(5) *Pseudogrammoceras fallaciosum* Biohorizon Gabilly, 1976a

**Index-species:** *Pseudogrammoceras fallaciosum* (Bayle, 1878).

**Occurrence.** SE France, Bulgaria, Spain, Portugal, Hungary, Georgia and Iran.

**Correlation.** Page (2003) distinguishes the Fallaciosum Subzone in both the Mediterranean and Northwest European scales but considers that it encompasses a somewhat different range in each.

**Characteristic ammonites in Crimea.** Index-species only.

**Occurrences in Crimea.** In addition to the carbonate rock boulders of Simferopol Melange, this same stratigraphic interval—characterized by the presence of the index species, has also been identified in borehole data from the Prysyvashya region (Orlova-Turchina et al., 1968; Permyakov et al., 1984, p. 46).

(6) *Dumortieria pseudoradiosa* Zone Haug, 1892;  
*Dumortieria levesquei* Subzone Benecke, 1901,  
emend. Spath, 1942

**Index-species:** *Dumortieria levesquei* (d'Orbigny, 1844).

**Occurrence and correlation.** The Levesquei Subzone is a part of the standard zonation for Northwestern Europe but is also widely recognized in other regions. It is identified in England, France, Bulgaria, Luxembourg, Hungary, and southern Germany. Equivalents of the subzone, based on the occurrence of *Dumortieria* spp., are also found in Chile and Argentina.

**Characteristic ammonites in Crimea.** Index-species only.

**Occurrences in Crimea.** In addition to the carbonate rock boulders of Simferopol Melange, this same or a similar stratigraphic interval—characterized by finds of *Dumortieria* sp.—is possibly present in the Bitak Formation of the Salgir River basin (Permyakov, 1962, p. 63; 1969, p. 106; Permyakov et al., 1991; Dovgal and Zagorodnyuk, 1985, p. 130).

*Pleydellia aalensis* Zone Reynès, 1868,  
emend. Dean et al., 1961

**Index-species:** *Pleydellia aalensis* (Zieten, 1832).

**Characteristic ammonites in Crimea.** *Pleydellia* (*Pleydellia*) cf. *subcompta*, *P. (P.) leura* (Buckman), *P. (Cotteswoldia)* cf. *paucicostata* (Buckman), *Erycites* ex gr. *barodiscus* (Gemmellaro) *E. gerecsensis* Kovács et Géczy, *Crestaites* cf. *meneghinii* (Bonarelli), "*Pseudaptetoceras*" cf. *christianae* (Elmi et Mouterde).

(7) *Pleydellia mactra* Subzone Mouterde, 1952,  
emend. Gabilly et al., 1971

**Index-species:** *Pleydellia mactra* (Dumortier, 1874).

**Occurrence and correlation.** The subzone is recognized in both the Mediterranean and Northwestern European scales (Biostratigraphie..., 1997; Page, 2003).

**Remarks.** In the type sections, the subzone is characterized by assemblages of *Pleydella* (*Cotteswoldia*) and *P. (Pleydella)* species lacking a distinct umbilical wall or rim (Biostratigraphie..., 1997). In Crimea, the presence of the subzone is established by the occurrence of characteristic species: *P. (Cotteswoldia)* cf. *paucicostata* (Buckman) and *P. (Pleydella)* cf. *subcompta* (Branco).

**Occurrences in Crimea.** In addition to the carbonate rock boulders of Simferopol Melange, the stratigraphic interval potentially corresponding to the European Mactra Subzone is present in the Bitak Formation of Crimea (Permyakov et al., 1991, p. 15); near the Stroganovka village, this interval is characterized by finds of *Grammoceras mactra* (= *Pleydellia mactra* (Dumortier, 1874)) (Dovgal and Zagorodnyuk, 1985, p. 130).

(8) *Pleydellia fluitans* Subzone Elmi et al., 1991,  
emend. 1994

**Index-species:** *Pleydellia fluitans* (Dumortier, 1874).

**Occurrence and correlation.** This subzone is recognized in both the Mediterranean and Northwest European scales (Page, 2003). In the Toarcian of northwestern Europe, the Lugdunensis Subzone (Biostratigraphie..., 1997) or the Aalensis Subzone (Bulgaria: Metodiev, 2008) is sometimes distinguished as the terminal subzone; these are entirely equivalent in scope to the Fluitans Subzone (Biostratigraphie..., 1997, p. 34).

**Remarks.** In Crimea, the presence of the subzone is determined by the occurrence of the characteristic species *Pleydellia leura* (Buckm.) (Fig. 20).

The described assemblage includes species known from both the Toarcian and the Aalenian, as well as certain taxa previously described only from the Aalenian (e.g., *Phylloceras? perplanum* Prinz) and belemnite species characteristic of the Aalenian. Therefore, the possible presence of the Lower Aalenian within the boulders at the Lozovoe Quarry cannot be ruled out.

| Stage    | Substage               | Europe (Page, 2003)           |                     |                                      |                                | <i>Nodicoeloceras fonticulium</i> | <i>Harpoceras falciferum</i>        | <i>Hildoceras laticosta</i> | <i>Hildoceras lusitanicum</i> | <i>Dactylioceras</i> ex gr. <i>commune</i> | <i>Perilytoceras perlaevis</i> | <i>Grammoceras penetratulum</i> | <i>Pseudogrammoceras fallaciosum</i> | <i>Onycheloceras</i> cf. <i>beaultiense</i> | <i>Polyplocus discoides</i> | <i>Dumortieria levesquei</i> | <i>Pleydellia</i> ( <i>Conteswoldia</i> ) cf. <i>paucicostata</i> | <i>Pleydellia</i> cf. <i>subcompta</i> | <i>Crestaites</i> cf. <i>meneghinii</i> | <i>Pleydellia leura</i> | <i>Erycites geresensis</i> | <i>"Pseudaptetoceras"</i> cf. <i>christianae</i> | Lozovoe Quarry (this study)        |                          |  |
|----------|------------------------|-------------------------------|---------------------|--------------------------------------|--------------------------------|-----------------------------------|-------------------------------------|-----------------------------|-------------------------------|--------------------------------------------|--------------------------------|---------------------------------|--------------------------------------|---------------------------------------------|-----------------------------|------------------------------|-------------------------------------------------------------------|----------------------------------------|-----------------------------------------|-------------------------|----------------------------|--------------------------------------------------|------------------------------------|--------------------------|--|
|          |                        | Zone                          | Subzone             | Biohorizons (Submediterranean scale) | Bio Horizons (Subboreal scale) |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  | Ammonoid biohorizons/ associations | Ammonite zones, subzones |  |
| Toarcian | Aalenian               | Lower                         | Leioceras opalinum  |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Pleydellia aalensis | Fluitans                             |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          | Mactra                 |                               |                     |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          | Upper                  | Dumortieria levesquei         | Pseudoradiosa       |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Levesquei           |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        | Phlyseo-grammoceras dispansum | Gruneri             |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Insigne             |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        | Grammoceras thouarsense       | Fallaciosum         | <i>fallaciosum</i>                   |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Fascigerum          | <i>fascigerum</i>                    |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Striatulum          | <i>thouarsense</i>                   |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Bingmanni           | <i>doernense</i>                     |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        | Haugia variabilis             | Vitiosa             |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Illustris           |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               | Variabilis          |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        | Lower                         |                     | Hildoceras bifrons                   | Bifrons                        | <i>semipolatum</i>                | <i>crassum</i> – <i>semipolatum</i> |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          | "Sublevisoni"          |                               |                     |                                      | <i>bifrons</i>                 | <i>crassum</i> – <i>bifrons</i>   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     |                                      | <i>apertum</i>                 | <i>braunianus</i>                 |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     |                                      | <i>lusitanicum</i>             | <i>athleticum</i>                 |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          | Harpoceras serpentinum |                               |                     | Falciferum                           | <i>tethysi</i>                 | <i>commune</i>                    |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     |                                      | "Sublevisoni"                  | <i>ovatum</i>                     |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     | Elegantulum                          | <i>Douvillci</i>               | <i>falciferum</i>                 |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     |                                      | <i>pseudoserpentinum</i>       |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          | Hildoceras bifrons     |                               |                     | Bifrons                              | <i>strangewayi</i>             | <i>elegans</i>                    |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     |                                      | <i>elegantulum</i>             | <i>exaratum</i>                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     | "Sublevisoni"                        | <i>elegantulum</i>             | <i>elegantulum</i>                |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |
|          |                        |                               |                     |                                      |                                |                                   |                                     |                             |                               |                                            |                                |                                 |                                      |                                             |                             |                              |                                                                   |                                        |                                         |                         |                            |                                                  |                                    |                          |  |

Fig. 20. Full ranges of stratigraphically important Ammonitida and Lytocerida species recorded from in the Lozovoe Quarry, in comparison with the zonal and infrazonal scales of the Toarcian of Europe.

The correlation of biostratigraphic units in the reconstructed limestone section of the Lozovoe Quarry with European stratigraphic scales is shown in Figs. 21 and 22.

## STRUCTURE OF TOARCIAN AMMONOID ASSEMBLAGES

The ammonoid assemblages of the Lozovoe Quarry exhibit a Tethyan character, dominated by the oceanic Phyllocerida and Lytocerida (comprising more than two-thirds of the total specimens). However, Lytocerida are significantly less abundant than Phyllocerida (Fig. 23). The various species of *Calli-phyloceras* are predominant among the latter. A high proportion of juvenile specimens—particularly within the Phylloceratinae, Lytoceratinae, and Grammocerotinae—is characteristic of the studied ammonoid assemblages.

The Early Toarcian Psilocerina of the Lozovoe Quarry are represented by two superfamilies: Eoderoceratoidea (family Dactylioceratinae, with the subfamilies Dactylioceratinae and Nodicoeloceratinae) and Hildoceratoidea (family Hildoceratinae, with the subfamilies Harpoceratinae and Hildoceratinae). Hil-

doceratinae (predominantly the genera *Harpoceras* and *Hildoceras*) are the most abundant group. A widely distributed across the Mediterranean and north-western Europe genus *Hildoceras* (subfamily Hildoceratinae) (Ridente, 2016) are particularly numerous, whereas only eight specimens belonging to the Dactylioceratinae (genera *Dactylioceras* and *Nodicoeloceras*) were found. A significant proportion of the Early Toarcian species discovered in Crimea had a nearly global distribution in epicontinental seas and along oceanic margins (particularly the Harpoceratinae and Dactylioceratinae; Dommergues, 1987, p. 274).

The Late Toarcian Psilocerina from the Lozovoe Quarry are represented by a single superfamily (Eoderoceratoidea) comprising two families: Hildoceratinae (subfamilies Harpoceratinae, Polyplectinae, and Grammocerotinae) and Hammatoceratinae (subfamily Hammatoceratinae). Hildoceratinae predominate numerically (39 specimens), whereas Hammatoceratinae are significantly less common (8 specimens). A substantial proportion of the identified species are characteristic primarily of the Mediterranean region and Central Europe: "*Pseudaptetoceras*" cf. *christianae* (Elmi et Mouterde), *Crestaites* cf. *meneghinii* (Bonarelli), *Polyplocus discoides* (Zieten), and others. The Late

| System<br>Series<br>Stage<br>Substage | N-W European Province<br>(Page, 2003; biostratigraphic..., 1997) | Mediterranean province<br>(Page, 2003; Elmi et al., 1994<br>biostratigraphic..., 1997) | Bulgaria<br>(Metodiev, 2008) | Transdanubian Mountains (Hungary)<br>(Kovacs, 2011, 2013, 2014, 2017) | Northern Caucasus<br>(Karakova, 1973, 1977;<br>Decision, 1984;<br>Rostovtsev et al., 1992) | Crimea              |                     |
|---------------------------------------|------------------------------------------------------------------|----------------------------------------------------------------------------------------|------------------------------|-----------------------------------------------------------------------|--------------------------------------------------------------------------------------------|---------------------|---------------------|
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            | Zone                | Subzone/<br>Lona    |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            | Zone                | Subzone/<br>Lona    |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            | Zone                | Subzone/<br>Lona    |
| Jurassic<br>Lower<br>Toarcian         | Subboreal                                                        | Sub-Mediterranean                                                                      | Biorhorizon                  | Subzone                                                               | Zone                                                                                       | Substage            | Zone                |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            |                     |                     |
| Upper                                 | Leioceras opalinum                                               | Leioceras opalinum                                                                     | Leioceras opalinum           | Leioceras opalinum                                                    | Leioceras opalinum                                                                         | Leioceras opalinum  | Leioceras opalinum  |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            |                     |                     |
| Lower                                 | Peydelia aalenensis                                              | Peydelia aalenensis                                                                    | Peydelia aalenensis          | Peydelia aalenensis                                                   | Peydelia aalenensis                                                                        | Peydelia aalenensis | Peydelia aalenensis |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            |                     |                     |
| Upper                                 | Leioceras opalinum                                               | Leioceras opalinum                                                                     | Leioceras opalinum           | Leioceras opalinum                                                    | Leioceras opalinum                                                                         | Leioceras opalinum  | Leioceras opalinum  |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            |                     |                     |
| Lower                                 | Peydelia aalenensis                                              | Peydelia aalenensis                                                                    | Peydelia aalenensis          | Peydelia aalenensis                                                   | Peydelia aalenensis                                                                        | Peydelia aalenensis | Peydelia aalenensis |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            |                     |                     |
| Upper                                 | Leioceras opalinum                                               | Leioceras opalinum                                                                     | Leioceras opalinum           | Leioceras opalinum                                                    | Leioceras opalinum                                                                         | Leioceras opalinum  | Leioceras opalinum  |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            |                     |                     |
| Lower                                 | Peydelia aalenensis                                              | Peydelia aalenensis                                                                    | Peydelia aalenensis          | Peydelia aalenensis                                                   | Peydelia aalenensis                                                                        | Peydelia aalenensis | Peydelia aalenensis |
|                                       |                                                                  |                                                                                        |                              |                                                                       |                                                                                            |                     |                     |

**Fig. 21.** Correlation of the biostratigraphic intervals of the reconstructed Toarcian section of Crimea with the stratigraphic scales of Europe.

| System<br>Series<br>Stage<br>Substage | Zone                   | Subzone  | Page, 2003; Biostratigraphic..., 1997 |                            | Meister, Blue, 2014; Meister et al., 2017 |                               | Species                       | Lozovoe Quarry<br>(this study) |
|---------------------------------------|------------------------|----------|---------------------------------------|----------------------------|-------------------------------------------|-------------------------------|-------------------------------|--------------------------------|
|                                       |                        |          | Subboreal Province                    | Sub-Mediterranean Province | Central Apennines                         | Austria, Hungary              |                               |                                |
|                                       |                        |          | Biorhorizon                           | Biorhorizon                | Biorhorizon                               | Biorhorizon                   |                               |                                |
|                                       |                        |          | Biorhorizon                           | Biorhorizon                | Biorhorizon                               | Biorhorizon                   |                               |                                |
| Jurassic<br>Lower<br>Pliensbachian    | Amaltheus margaritatus | Gibbosus | There is no name                      | There is no name           | Arieticeraster gr. algovianum             | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum  |
|                                       |                        |          |                                       |                            |                                           |                               |                               |                                |
| Upper (part)                          | Stokesi                | Stokesi  | There is no name                      | There is no name           | Arieticeraster gr. algovianum             | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum  |
|                                       |                        |          |                                       |                            |                                           |                               |                               |                                |
| Lower                                 | Stokesi                | Stokesi  | There is no name                      | There is no name           | Arieticeraster gr. algovianum             | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum  |
|                                       |                        |          |                                       |                            |                                           |                               |                               |                                |
| Upper                                 | Stokesi                | Stokesi  | There is no name                      | There is no name           | Arieticeraster gr. algovianum             | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum  |
|                                       |                        |          |                                       |                            |                                           |                               |                               |                                |
| Lower                                 | Stokesi                | Stokesi  | There is no name                      | There is no name           | Arieticeraster gr. algovianum             | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum | Arieticeraster gr. algovianum  |
|                                       |                        |          |                                       |                            |                                           |                               |                               |                                |

**Fig. 22.** Stratigraphic distribution of the species *Amaltheus stokesi* (J. Sowerby) and correlation of the Upper Pliensbachian of Crimea with the stratigraphic scales of Europe.

Toarcian Stephanocerina (Stephanoceratoidea, Erycitidae, Erycitinae) are represented by only two specimens belonging to the genus *Erycites*.

The presence of *Erycites gerecsensis* Kovács and Géczy and *Calliphylloceras spadae* (Meneghini) in Crimea is noteworthy. These species have a limited geographic distribution and are characteristic of the Toarcian of Austria, Hungary, Italy, and Greece. At

the same time, species more characteristic of north-western Europe—such as *Alocolytoceras* ex gr. *germaini* (d'Orbigny) and *Perilytoceras perlaevis* (Denckmann)—are found among the Lytocerida.

The ammonite assemblages encountered consistently show a resemblance, first and foremost, to coeval assemblages from the northwestern margin of Tethys. At the same time, the zonal scale based on

| Taxa                      | Number of specimens | %     |
|---------------------------|---------------------|-------|
| Phyllocerida              | 166                 | 46.76 |
| Lytocerida                | 77                  | 21.69 |
| Phyllocerida + Lytocerida | 243                 | 68.45 |
| Hildoceratidae            | 93                  | 26.20 |
| Hammatoceratidae          | 9                   | 2.54  |
| Dactylioceratidae         | 8                   | 2.25  |
| Erycitidae                | 2                   | 0.56  |
| Ammonitida                | 112                 | 31.55 |
| Total                     | 355                 | 100   |

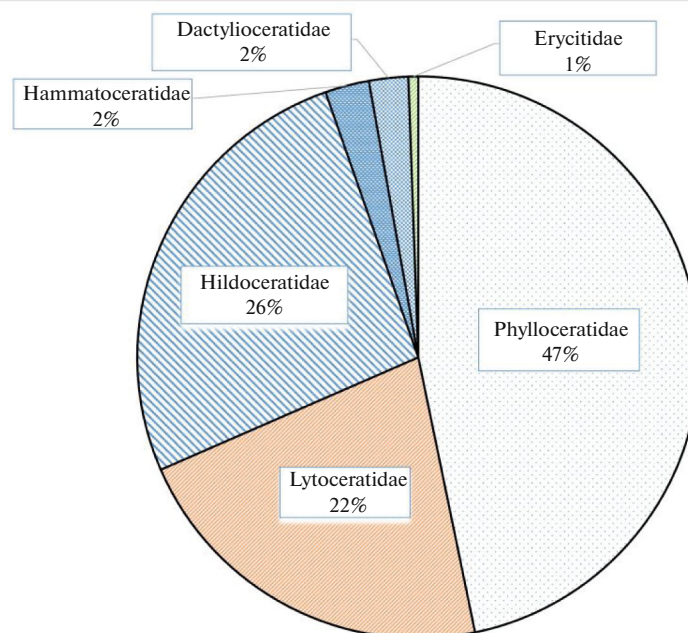


Fig. 23. General structure of the Toarcian ammonoid assemblage from the Lozovoe Quarry.

these ammonites is more similar to the scale of north-western Europe.

## CONCLUSIONS

The main results of studies on Pliensbachian–Toarcian ammonoids from limestone boulders at the Lozovoe Quarry, near Simferopol, are summarized below.

1. The understanding of Crimean Toarcian ammonoids taxonomic composition has been significantly expanded. The presence of 29 ammonoid species, belonging to 20 genera and 7 families, has been established. The presence of the subfamily Hildoceratinae (genus *Hildoceras*), two genera of the subfamily Harpoceratinae (*Pseudolioceras* and *Polyplectus*), the genera *Nodicoeloceras* (family Dactylioceratidae) and *Perilytoceras* (subfamily Megalytoceratidae), as well as a number of species of *Phylloceras*, *Calliphyloceras*, *Alocolytoceras*, *Harpoceras*, *Grammoceras*, *Dumortieria*, *Pleydellia*, and *Erycites*, has been recorded in Crimea for the first time.

2. The presence of Upper Pliensbachian ammonites in Crimea, previously recorded by Moiseev (1944) and Permyakov (1969), is confirmed, as is the presence of Lower Toarcian ammonites (Ippolitov et al., 2010, p. 100), from which species characteristic of the basal “Sublevisoni” Subzone of the European Bifrons Zone have been identified.

3. Analysis of the distribution of the identified ammonite species suggests the presence, within the reconstructed ammonite succession of the Lozovoe Quarry red limestones, of at least eight stratigraphi-

cally discrete, successive ammonite assemblages characteristic of biostratigraphic units of various ranks within European standard stratigraphic scales (in ascending order): (1) *Amaltheus stokesi* Subzone (*Amaltheus margaritatus* Zone); (2) *Hildoceras latirocostum provis* Biohorizon (*Hildoceras bifrons* Zone, “*H. sublevisoni*” Subzone); (3) *H. lusitanicum* Biohorizon (*H. bifrons* Zone, “*H. sublevisoni*” Subzone); (4) *Grammoceras striatulum* Subzone (*Grammoceras thouarsense* Zone); (5) *Pseudogrammoceras fallaciosum* Biohorizon (*Grammoceras thouarsense* Zone, *Pseudogrammoceras fallaciosum* Subzone); (6) *Dumortieria levesquei* Subzone (*Dumortieria pseudoradiosa* Zone); (7) *Pleydellia mactra* Subzone (*P. aalensis* Zone); and (8) *P. fluitans* Subzone (*P. aalensis* Zone). The presence of Lower Aalenian strata within the boulders at the Lozovoe Quarry may also be inferred (primarily based on finds of belemnite species characteristic of the Aalenian; A.P. Ippolitov, unpubl.).

4. By its taxonomic composition and structure, the ammonoid assemblage from the red limestones of the Lozovoe Quarry is most similar to assemblages from the Alps, the Northern Apennines, and other Mediterranean regions derived from limestones of the “Ammonitico Rosso” facies (Donovan, 1958; Géczy, 1976b; Géczy and Szente, 2006).

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#### AUTHOR CONTRIBUTION

The ammonite collections studied were assembled by B.A. Zaitsev, A.P. Ippolitov, A.I. Tishchenko, D.B. Startsev, M.A. Rogov, and A.M. Rogov; their paleontological analysis was conducted by B.A. Zaitsev and M.A. Rogov. The main sections of the manuscript were prepared by B.A. Zaitsev. The field description of the locality was compiled by A.P. Ippolitov, and the biostratigraphy section was written by B.A. Zaitsev. The photographic materials used were sourced from the archives of A.I. Tishchenko, B.A. Zaitsev, and A.P. Ippolitov. All authors participated in editing the manuscript and preparing the figures.

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#### CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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