Chronostratigraphic overview of the Toarcian (Early Jurassic) ammonite fauna from the Mecsek Mountains (Hungary)

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(Manuscript received January 12, 2023; accepted in revised form June 2, 2023; Associate Editor: Ján Schlögl)

Abstract: Many localities worldwide yielded rich Toarcian (Early Jurassic) ammonoid faunas whose diversity history enhanced our understanding of global events and their geographic distribution aided paleogeographic and paleoceanographic reconstructions. However, major differences remain in the intensity of studies as some areas have received significantly less attention, yet their study would improve regional and global correlations and reconstructions. The Toarcian faunas of the Mecsek Mts (SW Hungary) represented one such knowledge gap that is filled herein on the basis of the large Hetényi Collection and other material, totaling more than 5000 specimens. The Toarcian Ammonitina assemblages are outlined, documenting the occurrence of 43 species, of which 14 stratigraphically important species are described systematically. The studied assemblages bear a close affinity to the NW European faunal province, hence the standard ammonite chronostratigraphic scale is conveniently applicable for subdividing the Toarcian sequence of the Mecsek Mts. All of the Toarcian zones and most subzones are documented by their index taxa and the ranges established from NW European localities allow chronostratigraphic assignment of the ammonite-bearing localities in the Mecsek Mts. A comparison with other coeval faunas from the widespread spotted marl facies reveals that taxon richness here is comparable with that recorded from other parts of the Tisza Mega-Unit in the Apuşeni Mts and the Eastern Carpathians in Romania. Temporal patterns of diversity changes, with peaks in the Bifrons and Thouarsense zones, may be interpreted in the framework of biotic changes in the aftermath of the Jenkyns Event.

Keywords: Ammonitina, chronostratigraphy, Jurassic, Mecsek Mts, paleobiogeography, Toarcian

Introduction

The Toarcian is arguably the most intensively studied stage within the Jurassic, for its rich faunas and a growing interest in the hyperthermal Jenkyns Event (often referred to as the Toarcian Oceanic Anoxic Event, T-OAE) and related climatic, environmental and biotic changes before, during, and after the event. Recently, the JET (Early Jurassic Earth System and Timescale) project (Hesselbo et al. 2013) has stimulated research and generated much new data (e.g., Storm et al. 2020). Historically, epicontinental marine successions from Northwest Europe provided the bulk of the available stratigraphic data, followed by adjacent basins of the Northwestern Neotethys. However, there still remain relatively less studied areas, such as the Mecsek Mts in southern Hungary, the focus of this study. Although several studies have been published on different aspects of the Toarcian and the local expression of the Jenkyns Event (Dulai et al. 1992; Monostori 2008; Raucsik & Varga 2008; Baranyi et al. 2016; Müller et al. 2017; Ruebsam et al. 2018), much less has been known about the ammonoid faunas of the Mecsek Mts and their biostratigraphy. Here we aim to provide an overview of the Toarcian ammonite assemblages of the Mecsek Mts and their chronostratigraphic significance, on the basis of a large collection newly available for study. Most of the previously published studies on the Jurassic of the Mecsek Mts focused primarily on the early Toarcian Serpentinum Zone in the context of the Jenkyns Event or T-OAE. The only available Jurassic chronostratigraphic summary was published 50 years ago and lacked a taxonomic treatment and illustration of the fossil assemblages (Fülöp 1971). In that work, the Toarcian stage was subdivided into only three chronozones (Harpoceras falcifer, Hildoceras bifrons, and Grammoceras thouarsense, in ascending order). This requires revision in light of the most recent NW European chronostratigraphic scale (Page 2003; Hesselbo et al. 2020). All Toarcian standard zones and most subzones are documented in the Mecsek for the first time based on the occurrences of well-known standard index taxa.

For the research presented here, existing museum collections and materials of private fossil collectors were studied, and new field surveys of some key localities were carried out. Beside the important but small assemblages collected by Galácz (1991) and Dulai et al. (1992), the backbone of this study is the voluminous collection of Rudolf Hetényi (1933–2003). Hetényi worked as a mapping geologist in the Mecsek Mts during the 1960's and 1970's with the Hungarian Geological Institute, where he served as deputy director from 1981 to 1993 (Brezsnyánszky 2004). Hetényi acquired a collection of more than 15000 Pliensbachian–Callovian ammonoid specimens. This material has been only available for research since the 2010's and provided the main motivation for our work. Together with the minor collections mentioned above, it opened an excellent opportunity for a detailed revision and an updated chronostratigraphic study presented here. Our results serve as a chronostratigraphic basis for other paleontological, geochemical, sedimentological, and paleoenvironmental studies in the area. In addition, a comparison of ammonoid fossil records from similar spotted marl ("Fleckenmergel") facies in other regions will contribute to our understanding of the transitional areas between the Northwest European epicontinental sea and the Neotethys ocean basin.

Geological, stratigraphical and paleogeographical setting

The Mecsek is an isolated mountain range in SW Hungary composed of mainly Permian and Mesozoic sedimentary rocks. Jurassic strata, including the Toarcian deposits, crop out in the eastern part of the Mecsek. Now located in the southern part of the Pannonian Basin, it forms part of the Mecsek Zone of the Tisza Mega-Unit that in the Late Palaeozoic and Early Mesozoic belonged to the European continental passive margin. Its separation from the margin started with the Middle Jurassic rifting and subsequent tectonic movements in the Neotethys. The Mecsek Zone reached its present-day position only in the Neogene, after a complex tectonic evolution within the Alpine orogenic system (Csontos et al. 2002; Csontos & Vörös 2004; Haas & Péró 2004; Császár et al. 2013; Fig. 1). The Late Triassic to Early Jurassic sedimentary evolution of the Mecsek Basin was controlled by a half-graben system related to continental rifting between the Tisza Mega-Unit and the European margin (Nagy 1968; Császár et al. 2013). This depocenter first accumulated a thick series of fluvio-lacustrine to parallic coal-bearing deposits (Mecsek Coal Formation), then gradual deepening in the late Sinemurian–early Pliensbachian led to the deposition of the Hosszúhetény Calcareous Marl Formation in an increasingly open marine basin (Fig. 2). The overlying upper Pliensbachian–middle Toarcian Mecseknádasd Sandstone Formation consists of spotted marl with intercalated sandstone and limestone beds. Within this formation, the lower Toarcian organic-rich siltstone, marlstone and an approx. 12 m thick black shale succession is distinguished as a separate lithostratigraphic unit, the Rékavölgy Siltstone Formation (Főzy 2012). The organic-rich, laminated black shale lithofacies indicate anoxic conditions in the Mecsek Basin during the early Toarcian Serpentinum Zone and is regarded as the local stratigraphic expression of the Jenkyns Event (Dulai et al. 1992; Müller et al. 2017; Ruebsam et al. 2018). The overlying strata, the middle Toarcian–Bajocian spotted marl facies is assigned to the Komló Calcareous Marl Formation (Főzy 2012). Note that the lower to middle Toarcian marly unit was assigned to the Óbánya Siltstone Formation in the earlier literature (e.g. in Raucsik & Varga 2008). The total thickness of the Toarcian deposits is approx. 200 m in the Mecsek Mts (Hetényi 1968).

From a paleobiogeographical point of view, the Toarcian ammonite assemblages in Hungary represent two different faunal provinces (Géczy 1984). The northern part of the country belongs to the ALCAPA Mega-Unit (Haas 2012; Fig. 1), where the ammonite faunas of the Transdanubian Mountain Range (Bakony, Vértes and Gerecse mountains) are typical of the Mediterranean Province of the Tethyan Realm (Page 2008; Kovács et al. 2020). In the southern part of the Pannonian Basin, the Villány–Bihor and the Mecsek zones of the Tisza Mega-Unit (Mecsek Mts and Villány Hills in Hungary, Bihor region, Apuşeni Mts and SE-SW Carpathians in Romania) are represented by NW European ammonite faunas (Géczy 1984, 1990a, b), therefore the standard Toarcian ammonite chronostratigraphy is applicable here.

Material and methods

The studied Ammonitina assemblages are housed in the collections of (i) the Hungarian Natural History Museum, Budapest (temporarily, the Hetényi Collection), (ii) the József Attila City Library and Museum Collection of Komló (MK), (iii) the Eötvös University, Budapest (Department of Geology, and Department of Paleontology), and (iv) in the private collection of László Sövér (Bonyhád). The approximate number of specimens included in this study is 4800 from the Hetényi Collection, 20 from the museum in Komló, 190 from the Eötvös University, and 30 from the Sövér Collection. The bulk of the Hetényi Collection originates from spot localities identified on the 1:10,000 geological maps, stratigraphic superposition can only be unambiguously established for drillcore samples. Only the collections at the Eötvös University originate from measured stratigraphic sections.

The fossiliferous localities of the Hetényi Collection presented herein are labeled by numbers in the 1:10,000 scale geological maps of the Mecsek Mts published by the Geological Institute of Hungary: Komló (K) (1969), Kisújbánya (KU; 1975), Zengővárkony (ZV; 1975), and Hosszúhetény N (HE; 1976) (for details see Geological Maps in References). The map of the Óbánya region (OB) remained unpublished (available from the State Geological, Geophysical and Mining Data Archive, Budapest).

The Toarcian chronostratigraphic scheme applied here is based on Elmi et al. (1997), Page (2003), Hesselbo et al. (2020) and Rulleau et al. (2020). The chronozones and subchronozones are recognized with confidence on the basis of the documented assemblages. However, no attempt is made here to achieve higher resolution because most of the studied material was not collected bed-by-bed in stratigraphic succession. Even though some taxa present may be indicative of faunal horizons recognized elsewhere (Page 2004; Boomer et al. 2021), the local reproducibility of their sequence known from the British successions cannot be proven in the Mecsek Mts without new collections.

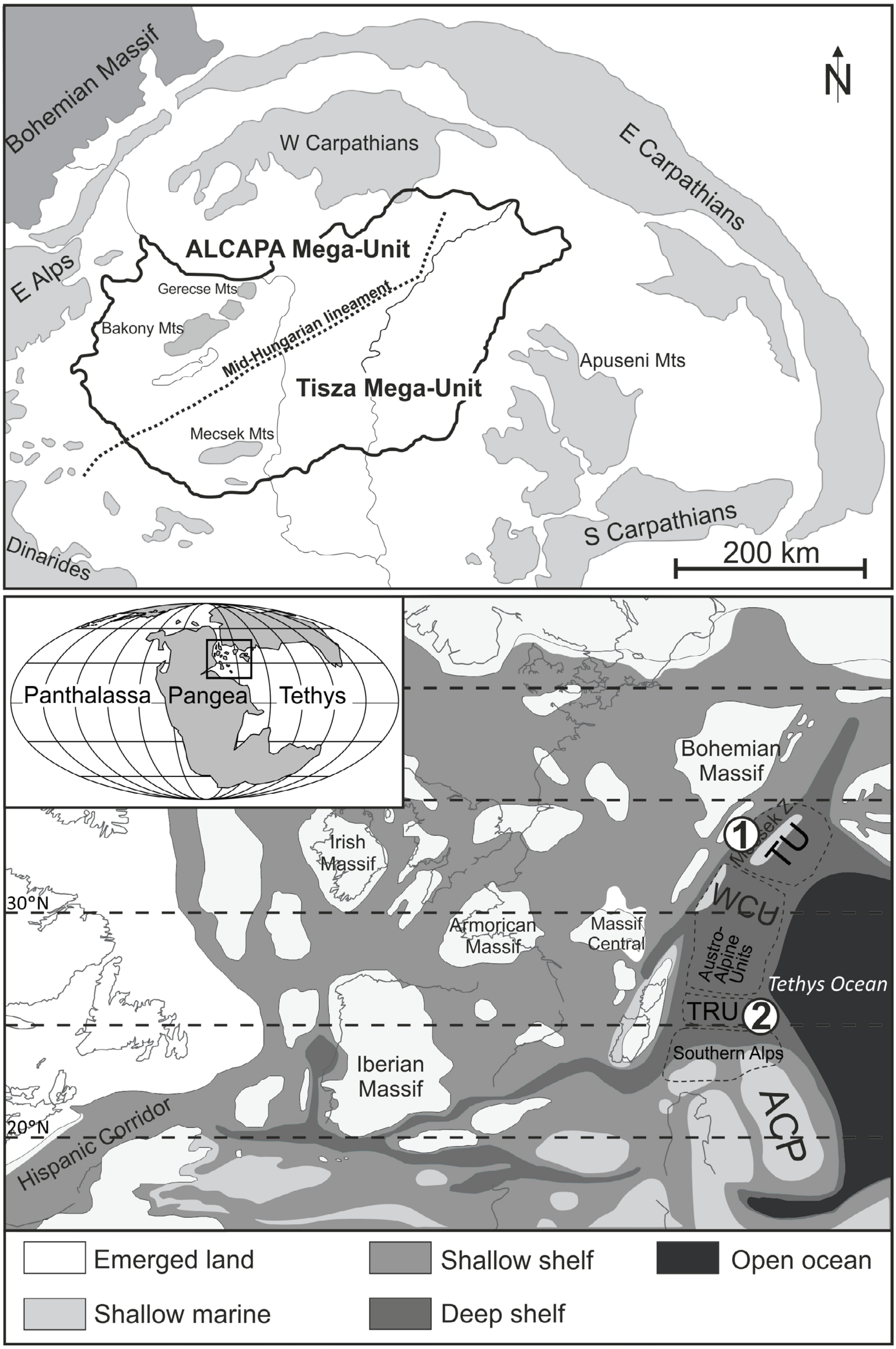

Fig. 1. The Mecsek Mountains in the Carpathian Basin (above), and its paleogeographical position during the Toarcian (below). 1: Mecsek Basin; 2: Bakony and Gerecse basins. WCU – Western Carpathian Units; TU – Tisza Mega-Unit; TRU – Transdanubian Unit; ACP – Adriatic Carbonate Platform (modified from Müller et al. 2021, based on Thierry & Barrier 2000).

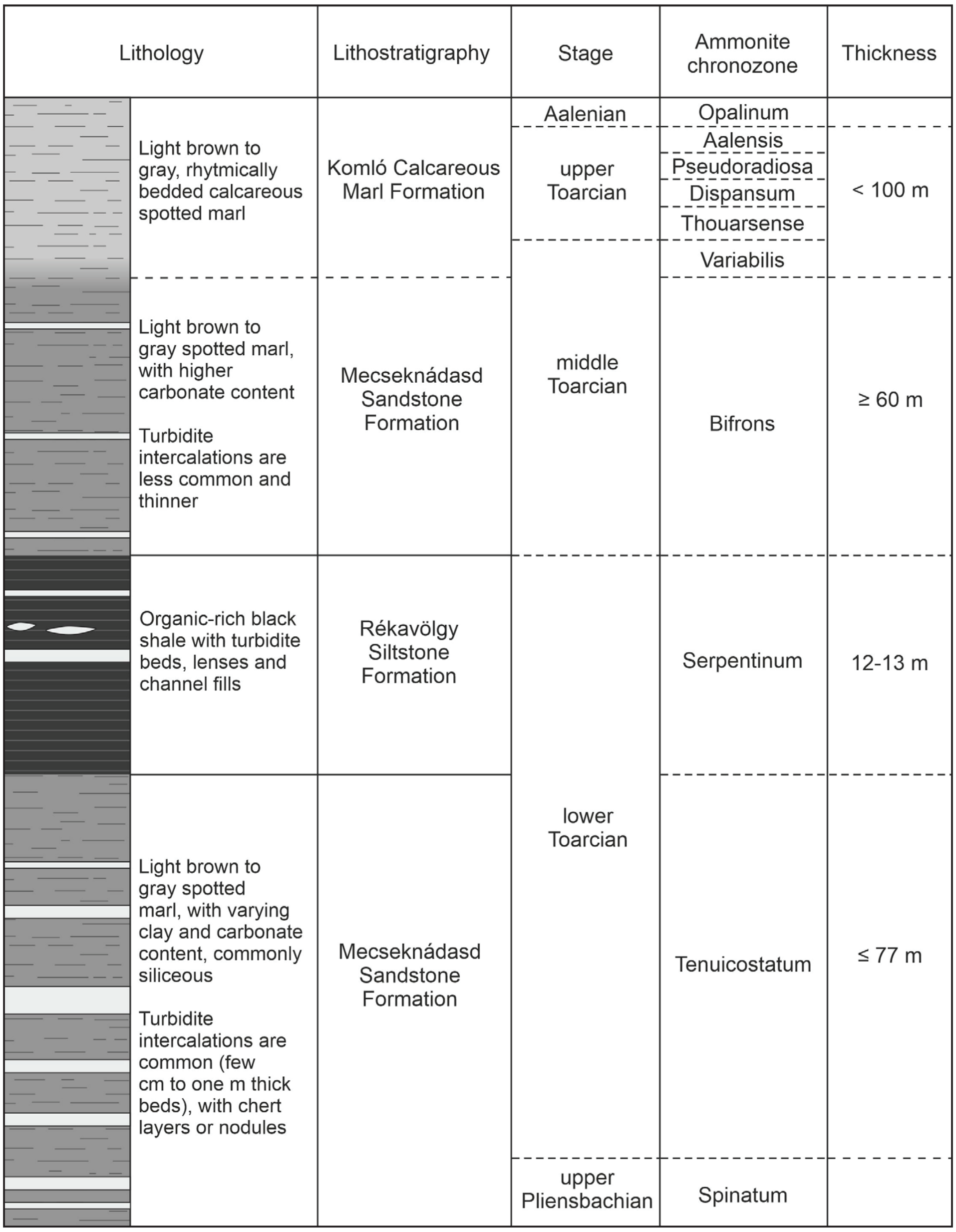

Fig. 2. Schematic stratigraphic overview of the Toarcian strata of the Mecsek Mts. Lithostratigraphy is based on Főzy (2012). Thicknesses are estimated on the basis of Galácz (1991) and Főzy (2012). Ammonite chronozones are as suggested in this study. Dashed horizontal lines mark uncertain boundaries.

Previous studies on Toarcian ammonoids from the Mecsek Mts

Reconnaissance geological research of the Mecsek Jurassic was started by Peters (1863) who described the Upper Liassic marl and shale deposits of the Réka Valley (*Réka-völgy*) south of Óbánya for the first time (Fig. 3). He recorded the occurrence of three Toarcian ammonite species from this area (valid names are listed here on the basis of our taxonomic revision, followed by the original identification in parentheses):

Dactylioceras (*Dactylioceras*) *commune* (J. Sowerby) (= *Ammonites communis* Sow.)

Pseudolioceras lythense (Young & Bird) (=*Ammonites lythensis* Young & B. Phill. [sic])

Pseudogrammoceras fallaciosum (Bayle) (=*Ammonites radians* d'Orb.)

Concerning the last taxon, in fact, *Ammonites radians* Schlotheim [=*Nautilus radians* Reinecke] was recorded by d'Orbigny (1845: 226, pl. 59, figs 1–3), and the identification of this specimen was revised by Gabilly (1976).

The research was continued by Vadász (1914) who reproduced Peters' records in his monographic work on the Mecsek Mts (Vadász 1935) and added numerous other Toarcian species on the basis of newly collected material:

Calliphylloceras cf. *nilssoni* (Hébert) (=*Phylloceras* cf. *nilssoni* Héb.)

Lytoceras cornucopiae (Young & Bird)

Alocolytoceras aff. *germaini* (d'Orbigny) (=*Lytoceras* sp. aff. *germaini* Orb.)

Dactylioceras (*Dactylioceras*) cf. *anguinum* (Reinecke) [=*Coeloceras* (*Dactylioceras*) cf. *anguinum* Rein.]

Porpoceras subarmatum (Young & Bird) [=*Coeloceras* (*Paroniceras*) *subarmatum* Sow.]

Mucrodactylites cf. *mucronatus* (d'Orbigny) (=*Coeloceras* cf. *mucronatum* Orb.)

Hildaites cf. *murleyi* (Moxon) (=*Hildoceras* cf. *levisoni* Simpson)

Hildoceras bifrons (Bruguière)

Cleviceras exaratum (Young & Bird) (=*Harpoceras exaratum* Y. & B.)

Harpoceras cf. *falciferum* (J. Sowerby) (=*Harpoceras* cf. *falciferum* Opp.)

Harpoceras serpentinum (Reinecke)

Harpoceras subplanatum (Oppel)

Grammoceras cf. *thouarsense* (d'Orbigny)

Grammoceras striatulum (J. Sowerby) (=*Harpoceras striatum* Sow.)

Pseudogrammoceras cf. *fallaciosum* (Bayle) (=*Grammoceras* cf. *subfallaciosum* Bayle; *Grammoceras radians* Br[onn]; *Grammoceras radians* Br. var. *fallaciosum* Bayle; *Grammoceras* cf. *cotteswoldiae* Buckm.)

Pleydellia cf. *aalense* (Zieten) (=*Grammoceras* cf. *aalense* Ziet.)

In a geological overview of the vicinity of Komló, Noszky (1952) described Upper Liassic greenish and grey marl deposits in the Cseresnyák Hill area east of Komló and mentioned a rich Grammoceratinae assemblage.

The next major contribution to the knowledge of the regional Toarcian paleontology was based on extensive field and drilling surveys as well as fossil collection campaigns which were carried out in the 1960's and 1970's as parts of the geological mapping projects conducted by the Hungarian Geological Institute. However, despite of the new, large Jurassic ammonite material, Vadász's list was complemented by only a single Toarcian species, *Grammoceras seamanni* (Dumortier non Oppel), in the subsequent literature (Fülöp 1971; Földi et al. 1977; Hetényi 1978; Nagy et al. 1978). From all the above-listed taxa, only one species was illustrated previously in the 19–20th century ("*Harpoceras radians* Rein.", in Lóczy 1910, fig. 48), and none of them was described taxonomically. Moreover, the newly collected material of Rudolf Hetényi was not accessible for other researchers for decades, and thus it was unavailable for paleontological studies until the 2010's.

The next chapter of the Toarcian paleontological research started with new field surveys of geology students in the 1980's. The lithological and biostratigraphic description of a Pliensbachian–Oxfordian section at Ófalu was presented

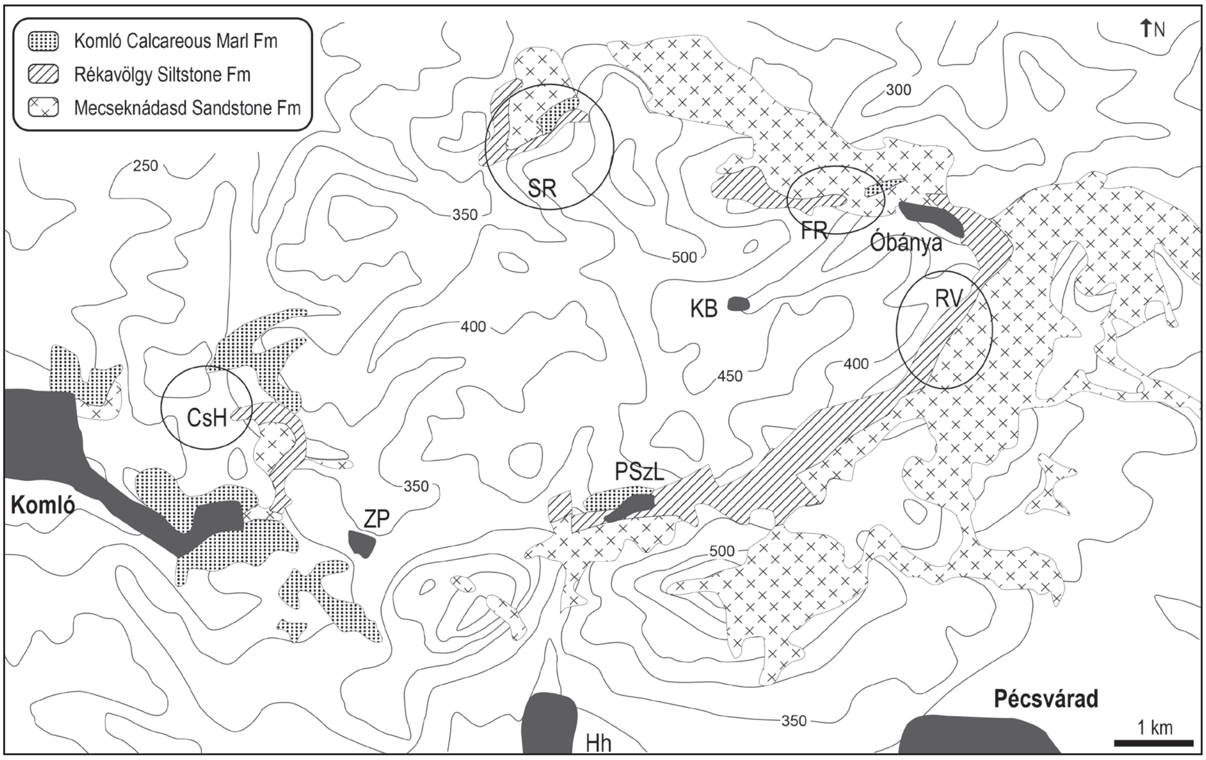

Fig. 3. Toarcian deposits in the eastern Mecsek Mountains and the fossiliferous areas mentioned in the text. CsH – Cseresnyák Hill; FR – Farkas Ravine; Hh – Hosszúhetény; KB – Kisújbánya; PSzL – Püspökszentlászló; RV – Réka Valley; SR – Somosi Ravine; ZP – Zobákpuszta (modified from the 1:100,000 geological base map available at https://map.mbfsz.gov.hu/fdt100).

by Pataki et al. (1982), whereas the stratigraphic, sedimentological and organic geochemical analyses of the Lower Toarcian laminated, organic-rich black shale (Rékavölgy Siltstone) were carried out by Dulai et al. (1992). Based on index fossils (e.g., the genus *Hildaites*) the latter study verified the early Toarcian age (Falciferum/Serpentinum Zone) of the deposit and established its connection with the T-OAE.

At this same time, a manuscript report was produced by Galácz (1991) with contributions of Barnabás Géczy, Miklós Monostori and István Szente from the Department of Paleontology at Eötvös University. This report described two measured stratigraphic sections in the Réka Valley. A 138 m thick section was referred to as B-1, and another, 48 m thick one as B-2. Both sections contain the approximately 12 m thick "black shale" unit now assigned to the Rékavölgy Siltstone Formation (Fig. 2). The sections consist of successions of well-bedded marl and sandstone beds with clay intercalations below and above the laminated black shale strata. This field survey was the first one that carried out a bed-by-bed fossil collection in the Mecsek Mts. Based on macrofossils, this work also proved that the black shale unit indeed belongs to the Falciferum/Serpentinum Zone. The authors attempted to locate the Pliensbachian–Toarcian boundary in Section B-1. Due to the lack of ammonites in the lower part of the section, ostracod biostratigraphy was used, which placed the Pliensbachian–Toarcian boundary around 90 m of the section, approximately 30 m from the base of the black shale unit (Monostori 2008).

The following ammonite taxa were identified by Géczy in Galácz (1991) from the Réka Valley:

Pleuroceras sp.

Phylloceras sp. [=*Lytoceras* cf. *siemensi* (Denckmann)]

Calliphylloceras sp.

Dactylioceras s.l. sp.

Cleviceras cf. *exaratum* (Young & Bird) [=*Harpoceras* cf. *exaratum* (Young & Bird)]

Harpoceras cf. *falciferum* (J. Sowerby)

Hildaites cf. *murleyi* (Moxon) [=*Hildaites* cf. *levisoni* (Simpson)]

Hildaites cf. *forte* (Buckman) [=*Hildaites* cf. *gyralis* (Buckman)]

Hildaites sp.

In contrast to the scarcity of Lower Jurassic ammonite studies, the Middle and Upper Jurassic ammonite faunas of the Mecsek Mts were treated in numerous papers over the last 30 years (Főzy 1993; Galácz 1993, 1995, 2012, 2015). There may be two main reasons for the lack of new paleontological investigations concerning the Early Jurassic (Sinemurian, Pliensbachian, and Toarcian) ammonoids. On one hand, fieldwork is rather difficult in the area that is affected by subsequent faulting, and where marly lithologies predominate within the very thick and commonly poorly exposed successions, in which the ammonite specimens are scarce and of mediocre to poor preservation. On the other hand, the extensive ammonite material assembled by Hetényi's team was inaccessible for research for a long time and it was not obtained using bed-by-bed collecting methods, therefore the material is not suitable for modern biostratigraphic analysis. Nevertheless, this material is still extremely valuable as a suite of representative collections for the faunal composition of a large number of localities, not reproducible today partly for deteriorating outcrop conditions, and partly for a lack of manpower and resources available for a similar effort. The scientific value of the Hetényi collection lies in the fact that the standard Toarcian chronostratigraphic scheme can be applied for the Mecsek Mts based on the presence of well-established index taxa. In addition, the ammonite record, summarized in Fig. 4, may contribute to our knowledge of the paleogeographical distributions of these species.

Results of revised chronostratigraphy

Here we present a chronostratigraphic overview of the studied material as considered representative for the Mecsek Mts. From oldest to youngest, we establish the presence of biochronozones and their subzones on the basis of local occurrences of diagnostic taxa with known ranges from Northwest Europe, where the standard zonation of the Toarcian was developed.

Tenuicostatum Chronozone

The zone is defined by the occurrence of the subgenus *Dactylioceras* (*Orthodactylites*) in the study area. The presence of this chronostratigraphic unit was first documented by Galácz (1991) for the lowermost Toarcian zone in the Mecsek Mts. The Tenuicostatum Zone is characterized by relatively thin strata of spotted marl (Galácz 1991). In the Réka Valley Section B-1, sandstone and clayey marl beds (Mecseknádasd Sandstone Formation) of approx. 30 m are assigned to the Tenuicostatum Zone, between the last Pliensbachian marly layers and the Serpentinum Zone black shale unit. Due to the scarcity of macro- and microfossils, however, neither the lower nor the upper boundary of the zone can be defined exactly. From the two subchronozones (Paltus and Semicelatum, in ascending order) only the Semicelatum Subzone is represented by poorly to moderately preserved internal molds of *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) (Fig. 5.1).

Serpentinum Chronozone

The zone is defined by the occurrences of the genera *Eleganticeras*, *Harpoceras* and *Hildaites*. It corresponds to the "Falciferum Zone" that nomenclature was widely used in the previous literature. Based on index taxa both subchronozones (the older Elegantulum and the younger Falciferum) can be identified.

In the studied region, the Serpentinum Zone is characterized by strata of spotted marl with intercalated limestone and sandstone beds, organic-rich siltstone and marlstone

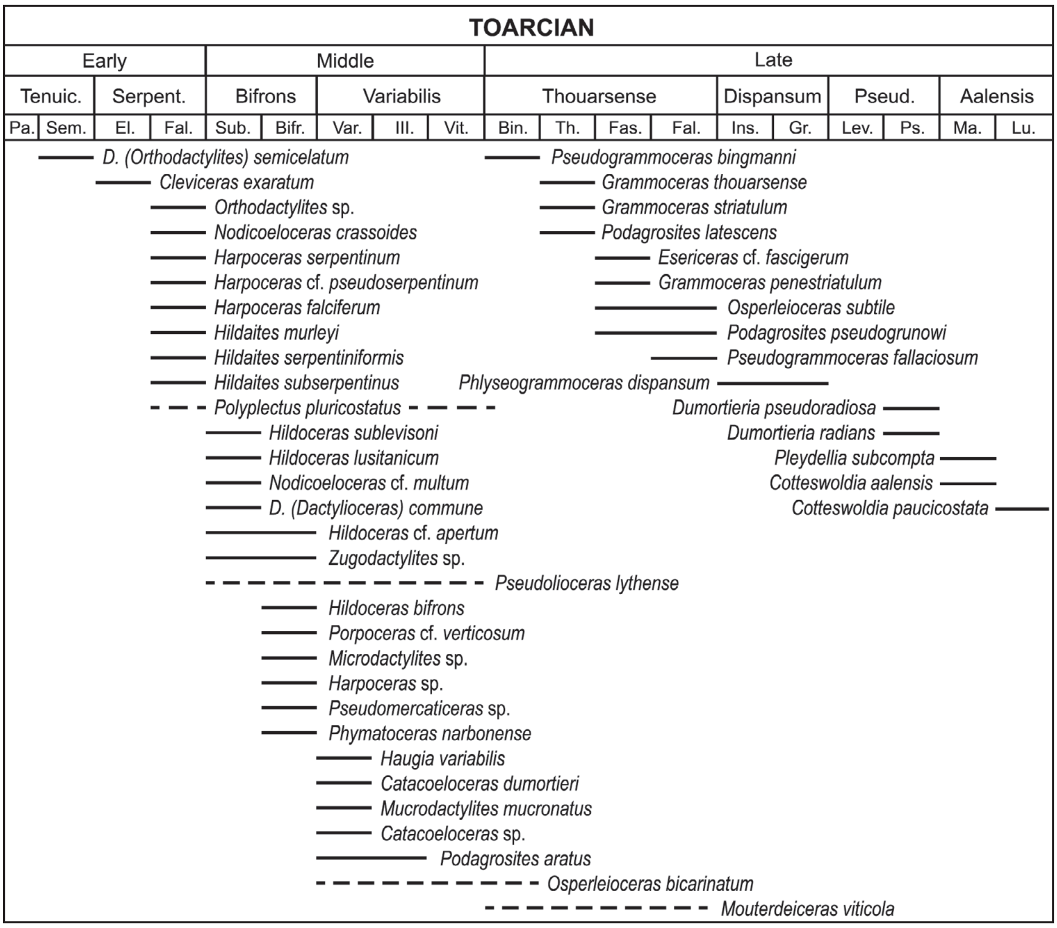

Fig. 4. Toarcian Ammonitina species from the eastern Mecsek Mountains with their known chronostratigraphic ranges (for literature see *Discussion*). Solid line: well-established ranges; dashed line: uncertain ranges. Zones and subzones follow Elmi et al. 1997. Tenuicostatum: Paltus, Semicelatum; Serpentinum: Elegantulum, Falciferum; Bifrons: Sublevisoni, Bifrons; Variabilis: Variabilis, Illustris, Vitiosa; Thouarsense: Bingmanni, Thouarsense, Fascigerum, Fallaciosum; Dispansum: Insigne, Gruneri; Pseudoradiosa: Levesquei, Pseudoradiosa; Aalensis: Mactra, Lugdunensis.

(Mecseknádasd Sandstone Formation), and an approx. 12 m thick laminated black shale succession (Rékavölgy Siltstone Formation). The latter deposits are widespread in the eastern Mecsek (Hetényi 1978), and its best exposures appear in the Réka Valley (Locality ZV-293), and around the Cseresnyák Hill (Galácz 1991). For macro- and microfossil sampling bed-by-bed method was carried out by two research teams (Galácz 1991; Dulai et al. 1992), and as a result, biostratigraphic data are available at least for the black shale strata. The ammonite material from the black shale consists of poorly preserved, flattened shells and moderately deformed internal molds in the overlying marlstone beds.

The Elegantulum Subzone is defined by the occurrence of *Cleviceras exaratum* (Young & Bird) in Section B-2 in the Réka Valley (Galácz 1991; Fig. 5.3). From the Falciferum Subzone *Orthodactylites* sp., *Nodicoeloceras crassoides* (Simpson), *Harpoceras serpentinum* (Schlotheim) (Fig. 6.1–2), *H.* cf. *pseudoserpentinum* Gabilly, *H. falciferum* (J. Sowerby) (Fig. 5.4, 5.7), *Hildaites murleyi* (Moxon) (Fig. 5.5), *H. serpentiniformis* Buckman, and *H.* cf. *subserpentinus* Buckman are recorded herein. *Dactylioceras* (*Orthodactylites*) *anguinum* (Simpson) and *Hildaites forte* (Buckman) reported in the previous literature have not been found in the studied material.

Bifrons Chronozone

The zone is defined by the occurrence of the genus *Hildoceras*. For the Jurassic of the Mecsek Mts, the name of this zone was first used by Fülöp (1971: fig. 11), and it corresponds to the ”Bifrons level” in Vadász (1935) and Hetényi (1978). Based on the occurrence of the subzonal index species of *Hildoceras,* both subchronozones (Sublevisoni and Bifrons) can be distinguished.

The clayey grey marl deposits assigned to this zone belong to the upper part of the Mecseknádasd Sandstone Formation. The best exposures are located in the eastern ravine of the Cseresnyák Hill (Locality K-75) yielded more than 2000 ammonite specimens, and in the Réka Valley (localities ZV-293, ZV-294, OB-408) where approximately 1000 specimens were

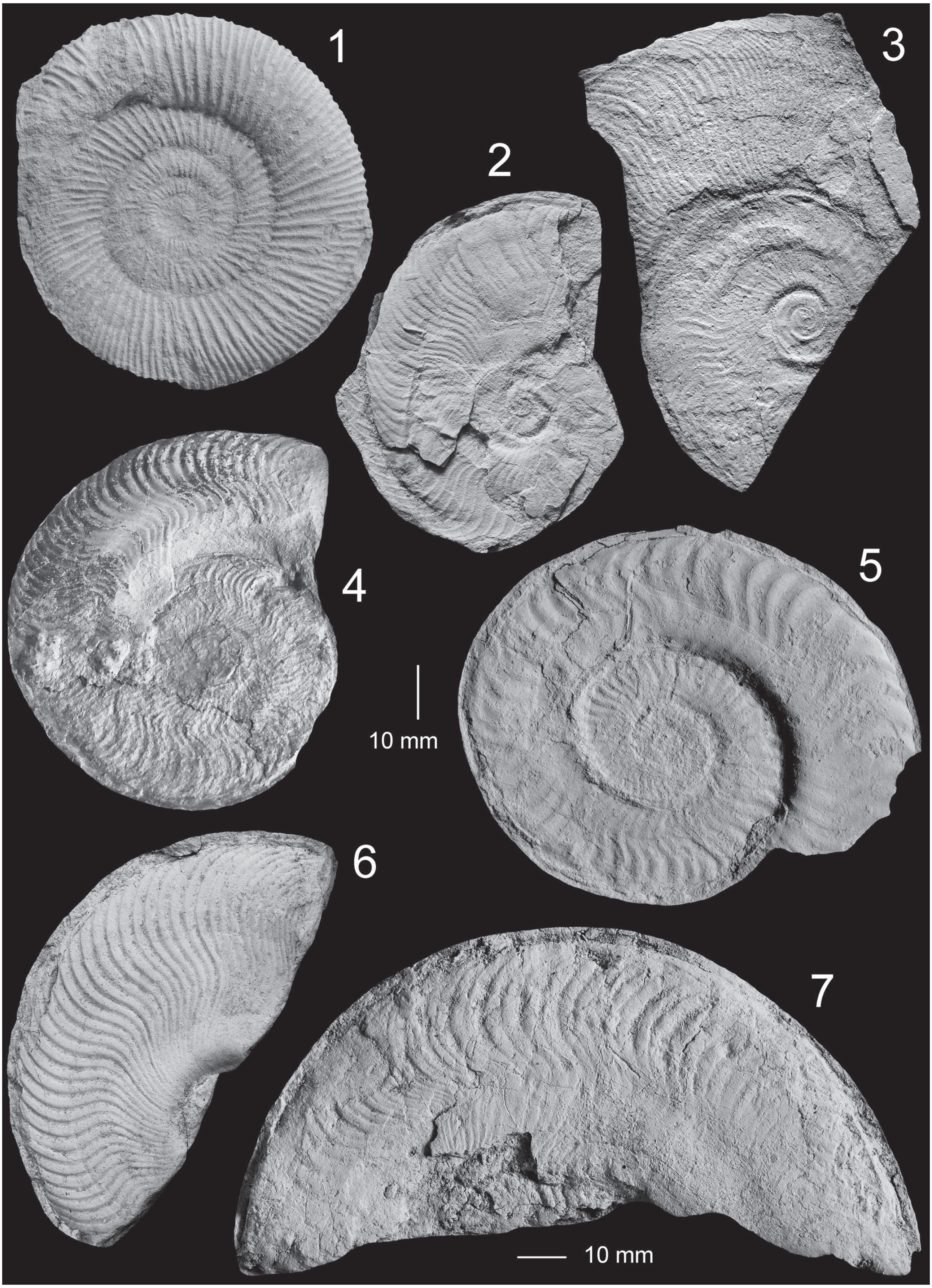
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Fig. 5. 1 – *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) (HC10169), D 68, Réka Valley, Locality ZV-294, Tenuicostatum Zone. **2** – *Cleviceras exaratum* (Young & Bird) (HC16388), D 68, Somosi Ravine, Locality KU-260, Serpentinum Zone. **3** – *Cleviceras exaratum* (Young & Bird), refiguration of Galácz (1991, pl. 4, fig. 2), D 89, Réka Valley, Section B2, Serpentinum Zone. **4** – *Harpoceras falciferum* (J. Sowerby) (MK 2020.154.1), D 74, Cseresnyák Hill, Serpentinum Zone (Photo: Tamás Henn). **5** – *Hildaites murleyi* (Moxon), refiguration of Galácz (1991, pl. 3, fig. 5), D 89, Réka Valley, Section B1, Serpentinum Zone. **6** – *Cleviceras exaratum* (Young & Bird) (HC16006), D 86, Réka Valley, Locality ZV-293, Serpentinum Zone. **7** – *Harpoceras falciferum* (J. Sowerby) (HC16093), D 140 (0.9×), Réka Valley, Locality ZV-293, Serpentinum Zone. Specimens coated with ammonium chloride and shown in natural size (except where otherwise indicated). Scale bars: 10 mm.

collected by Hetényi. The ammonite material consists of poorly to moderately preserved, slightly deformed internal molds.

The Ammonitina fauna is characterized by the mass occurrence of the genus *Hildoceras*. The most abundant species is *H. lusitanicum* Meister (Fig. 6.3, 6.6), whereas *H. sublevisoni* Fucini, *H.* cf. *apertum* Gabilly, and *H. bifrons* (Bruguière) are represented only by a few specimens. Another common species is *Dactylioceras* (*Dactylioceras*) *commune* (J. Sowerby) (Fig. 6.4). Besides these taxa, *Nodicoeloceras* cf. *multum* (Buckman), *Porpoceras* cf. *verticosum* Buckman, *Microdactylites* sp., *Zugodactylites* sp., *Harpoceras* sp., *Pseudomercaticeras* sp. and *Phymatoceras narbonense* (Buckman) (Fig. 6.7) appear rarely within the Bifrons Zone. *Porpoceras subarmatum* (Young & Bird) and *Harpoceras subplanatum* (Oppel) were reported by Vadász (1935) but they do not occur in the studied material.

Variabilis Chronozone

The zone is defined by the occurrence of *Haugia variabilis* (d'Orbigny) (Fig. 6.10), *Catacoeloceras dumortieri* (de Brun) (Fig. 6.5), *Mucrodactylites mucronatus* (d'Orbigny) (Fig. 6.8), and *Podagrosites aratus* (Buckman) (Fig. 6.11). From the Mecsek Mts, this zone was first documented by Galácz (1991). The first three taxa are typical of the Variabilis Subzone, whereas *Podagrosites aratus* ranges from the Variabilis to the Illustris subzones at the NW European localities (Rulleau et al. 2013, 2020). This unit corresponds to the lower part of the "Thouarsense Zone" in Fülöp (1971: fig. 11).

The grey calcareous marl matrix of the *Catacoeloceras dumortieri* specimen represents the Komló Calcareous Marl Formation which overlies the uppermost clayey marl layers of the Pliensbachian–middle Toarcian Mecseknádasd Sandstone Formation. Consequently, the appearance of the former lithostratigraphic unit can be documented as early as the upper part of the middle Toarcian.

One specimen of *Haugia variabilis* was collected in the Farkas Ravine (*Farkas-árok* in Hungarian, *Wolfsgraben* in German) west of Óbánya, and a *Catacoeloceras dumortieri* specimen came from the Somosi Ravine (*Somosi-csörge*) area NW to Kisújbánya, where Locality KU-259 yielded numerous Toarcian to Aalenian ammonite specimens. A *Mucrodactylites* specimen was found in the drill core Hosszúhetény Hh-68.

In addition to the above-mentioned taxa, single specimens of *Pseudolioceras lythense* (Young & Bird) and *Osperleioceras bicarinatum* (Zieten), and two specimens of *Catacoeloceras* sp. indet. belong to the ammonite material of the Variabilis Zone. Although *Pseudolioceras lythense* is characterized by a long stratigraphic range in the Bifrons–Variabilis zones, the calcareous marl matrix (Komló Calcareous Marl Formation) of the specimen differs from the clayey marl that is typical of the Bifrons Zone in the Mecsek Mts, so this specimen (Fig. 6.9) probably originates from the Variabilis Zone.

Thouarsense Chronozone

The zone is defined by occurrences of genera *Grammoceras* and *Pseudogrammoceras*. This unit corresponds to the middle part of the Thouarsense Zone in Fülöp (1971: fig. 11). All four subchronozones (Bingmanni, Thouarsense, Fascigerum and Fallaciosum) can be identified.

The ammonite fauna is far more diverse than in the previous and subsequent zones. The best exposures are located at Cseresnyák Hill (K-73–76), in the Farkas Ravine (localities KU-310, OB-128–130, OB-151), and in the Somosi Ravine (localities KU-254, KU-259, KU-261). Drill cores from the vicinity of Hosszúhetény (boreholes Hh-50 and Hh-68) also yielded abundant Grammoceratinae material. The ammonites are characterized by moderately to well-preserved internal molds in the Komló Calcareous Marl Formation.

The fauna in the Thouarsense Zone is dominated by specimens of genera *Podagrosites* and *Pseudogrammoceras;* the most abundant species are *Podagrosites pseudogrunowi* Guex (Fig. 7.1–2), and *Pseudogrammoceras fallaciosum* (Bayle) (Figs. 7.12, 8.1–2). Beside these taxa, the following species are recorded: *Polyplectus pluricostatus* (Haas), *Osperleioceras subtile* (Schirardin) (Fig. 7.6), *Podagrosites latescens* (Simpson) (Fig. 7.3–4), *Grammoceras thouarsense* (d'Orbigny) (Fig. 7.8), *G. striatulum* (J. Sowerby) (Fig. 7.10–11), *G. penestriatulum* Buckman (Fig. 7.7, 7.9), *Pseudogrammoceras bingmanni* (Denckmann), *Esericeras* cf. *fascigerum* (Buckman) (Fig. 8.3), and *Mouterdeiceras viticola* Elmi & Rulleau (Fig. 7.5).

Dispansum Chronozone

The zone is defined by the occurrence of the zonal index genus *Phlyseogrammoceras*. This unit corresponds to the upper part of the Thouarsense Zone in Fülöp (1971: fig. 11). The species *Phlyseogrammoceras dispansum* (Lycett) is typical for the entire zone, therefore its subchronozones (Insigne and Gruneri) cannot be distinguished.

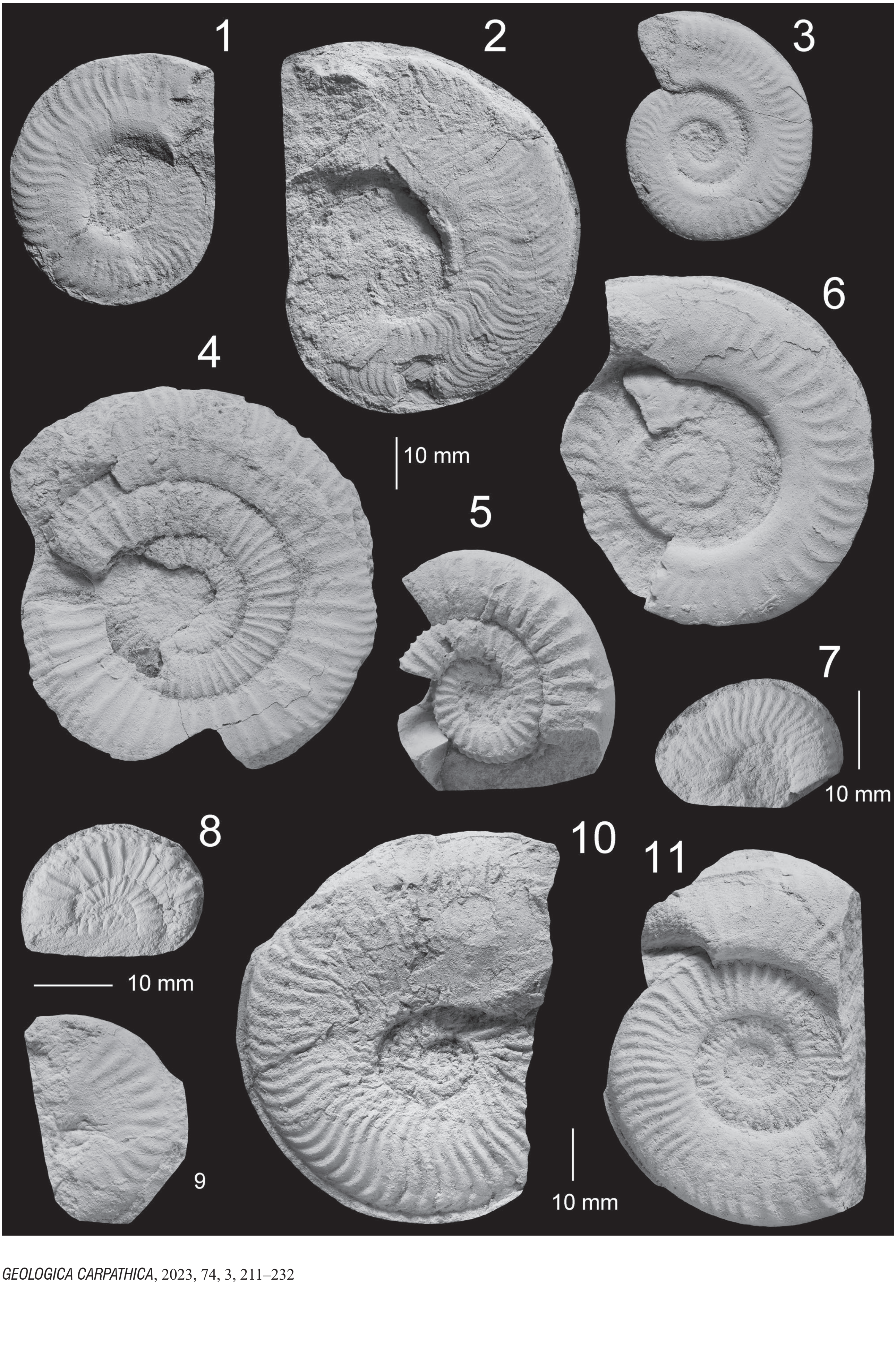
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Fig. 6. 1 – *Harpoceras serpentinum* (Schlotheim) (HC14520), microconch, D 48, Réka Valley, Locality ZV-293, Serpentinum Zone. **2** – *Harpoceras serpentinum* (Schlotheim) (HC16073), macroconch, D 71, Réka Valley, Locality ZV-293, Serpentinum Zone. **3** – *Hildoceras lusitanicum* Meister (HC12653), D 44, Réka Valley, Locality ZV-293, Bifrons Zone. **4** – *Dactylioceras* (*Dactylioceras*) *commune* (J. Sowerby) (HC11952), D 73, Réka Valley, Locality ZV-293, Bifrons Zone. **5** – *Catacoeloceras dumortieri* (de Brun) (HC11571), D 35 (1.5×), Somosi Ravine, Locality KU-259, Variabilis Zone. **6** – *Hildoceras lusitanicum* Meister (HC12757), D 67, Réka Valley, Locality ZV-293, Bifrons Zone. **7** – *Phymatoceras narbonense* (Buckman) (HC14348), D 24 (1.5×), Réka Valley, Locality OB-408, Bifrons Zone. **8** – *Mucrodactylites mucronatus* (d'Orbigny) (HC11789), D 23 (1.5×), Borehole Hosszúhetény Hh-68, Variabilis Zone. **9** – *Pseudolioceras lythense* (Young & Bird) (HC14770), D 26 (1.5×), Óbánya, Tél-hegy, Locality II/5, Variabilis Zone. **10** – *Haugia variabilis* (d'Orbigny), (HC9285), D 75, Farkas Ravine, Locality KU-310, Variabilis Zone. **11** – *Podagrosites aratus* (Buckman) (HC8544), D 72, Somosi Ravine, Locality KU-259, Variabilis–Thouarsense Zone. Specimens coated with ammonium chloride and shown in natural size (except where otherwise indicated). Scale bars: 10 mm.

Two poorly to moderately preserved specimens of *Phlyseogrammoceras dispansum* were found in the Hetényi Collection (HC23314: Fig. 8.4, and HC23318). Both came from the "Vadászház pataka" area of the Farkas Ravine (Locality OB-151) which yielded a rich late Toarcian material.

Pseudoradiosa Chronozone

The zone is defined by the occurrence of the zonal index genus *Dumortieria*. This unit cannot be correlated with any stratigraphical level in the previous literature. From the two subchronozones (Levesquei and Pseudoradiosa), only the presence of the Pseudoradiosa Subzone can be established.

Similarly to the Dispansum Zone, this unit is poorly represented by poorly preserved ammonites, of which only two taxa are recorded herein. Three specimens of *Dumortieria pseudoradiosa* (Branco) were found in the Hetényi Collection. Specimen HC8777 came from the "Dobogó" area close to the western part of the Farkas Ravine, whereas specimens HC14795 and HC14796 were collected from the "Vöröspart" area north of Püspökszentlászló. A single *Dumortieria radians* (Reinecke) specimen (Fig. 8.7) was identified in the Sövér Collection, originating from the "Lapát-vár" area of the Farkas Ravine.

Aalensis Chronozone

The zone is defined by occurrences of poorly to moderately preserved specimens of zonal index genera *Pleydellia* and *Cotteswoldia*. This unit corresponds to the Pleydellia aalensis Subzone in Fülöp (1971: fig. 11). Both subchronozones can be documented by occurrences of *Pleydellia subcompta* (Branco) (HC14043, Somosi Ravine, Locality KU-261) and *Cotteswoldia aalensis* (Zieten) (Fig. 8.9) (Mactra Subzone), and *Cotteswoldia paucicostata* Buckman (Fig. 8.8) (Lugdunensis Subzone).

Systematic paleontology

Here we provide conventional taxonomic descriptions of 14 ammonite species, each of them of different genera, that deserve detailed treatment either for their bio- and chronostratigraphic significance, first documentation from the area, or the opportunity to complement or knowledge of their intraspecific morphologic variations. We refrain from formally re-describing these species whose description can be found in multiple previous systematic paleontological works. However, we offer remarks to highlight diagnostic features and to make comparison with related forms. Abbreviations used: D (shell diameter) in mm.

Class Cephalopoda Cuvier, 1797
Order Ammonitida Fischer, 1882
Suborder Ammonitina Fischer, 1882
Superfamily Eoderoceratoidea Spath, 1929
Family Dactylioceratidae Hyatt, 1867
Subfamily Dactylioceratinae Hyatt, 1867
Genus *Dactylioceras* Hyatt, 1867
Subgenus *Orthodactylites* Buckman, 1926

Dactylioceras (*Orthodactylites*) *semicelatum* (Simpson, 1843)
Figure 5.1

1980 *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) – Howarth, p. 646, text-figs 2–3, pls 80–81, pl. 82, figs 11–12.
1996 *Dactylioceras semicelatum* (Simpson) – Popa & Patrulius, pl. 4, fig. 5.
2013 *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) – Rulleau et al., p. 72, pl. 4, figs 2–7.
2014 *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) – Bardin et al., p. 14, figs 6A–J.
2014 *Dactylioceras* (*Orthodactylites*) *semicelatum* (Simpson) – Kovács, p. 47, pl. 1, figs 1, 7.

Material: 4 specimens (Hetényi Coll.)

Remarks: The species is characterized by highly variable shell morphology (see Schmidt-Effing 1972; Howarth 1973, 1980). *Dactylioceras* (*Orthodactylites*) *semicelatum* differs from *D.* (*Eodactylites*) *mirabile* (Fucini) and *D.* (*O.*) *tenuicostatum* (Young & Bird) in oval whorl-section and more prorsiradiate ribs. *Orthodactylites crosbeyi* (Simpson) has more depressed, broader whorls, while *O. clevelandicum* Howarth is characterized by broader whorls with rectiradiate ribs. The shell of the specimen figured herein has moderately evolute coiling, compressed, oval whorls and dense, sharp, proverse ribs; the ribbing consists of mainly bifurcating primaries, and single ribs appear more rarely than on the type specimens (see Howarth 1980, pls 80–81).

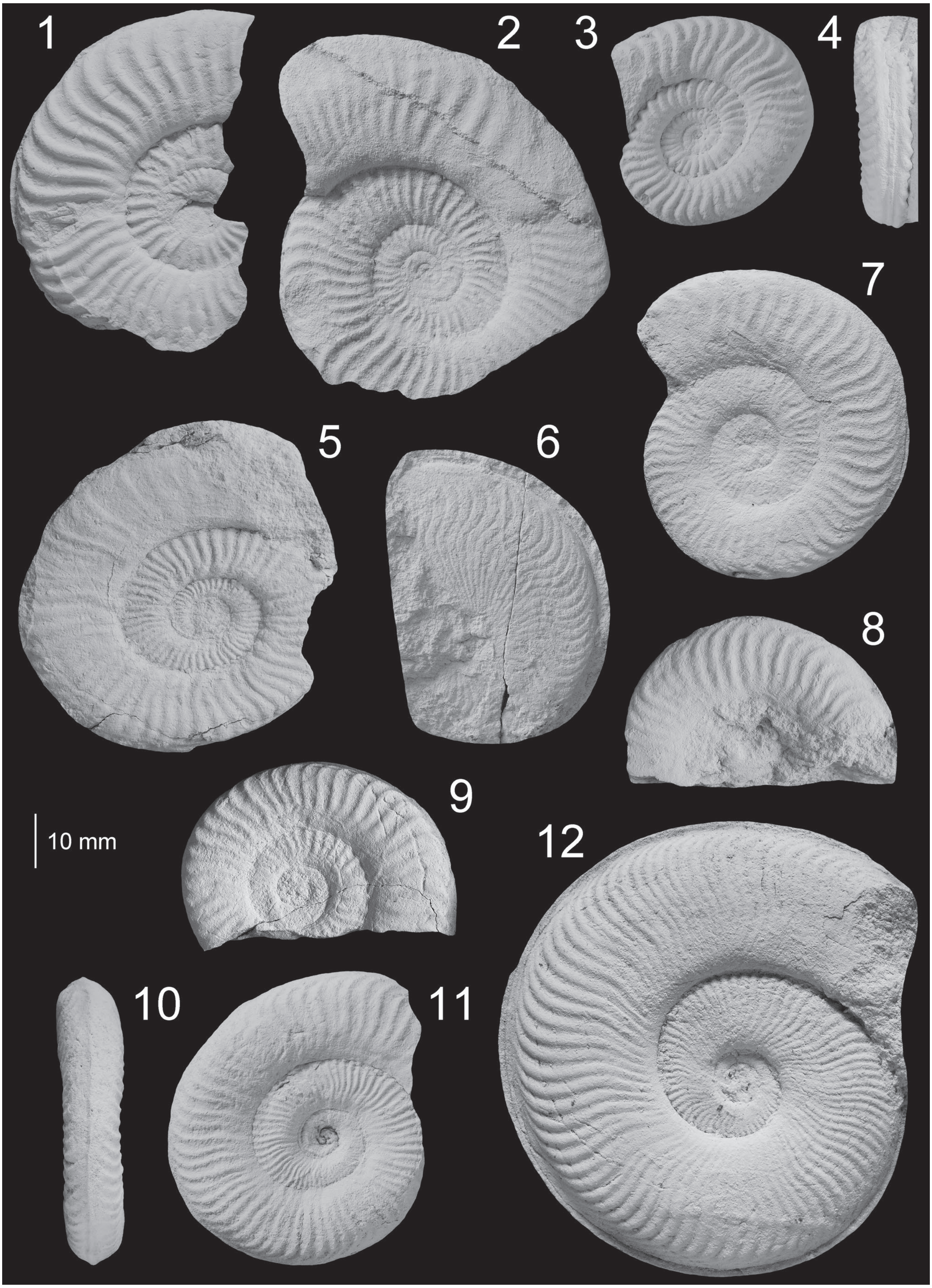
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Fig. 7. 1 – *Podagrosites pseudogrunowi* Guex (HC8770), D 63, Réka Valley, Locality OB-408, Thouarsense Zone. **2** – *Podagrosites pseudogrunowi* Guex (HC8752), D 65, Réka Valley, Locality OB-408, Thouarsense Zone. **3, 4** – *Podagrosites latescens* (Simpson) (HC12035), D 39, Somosi Ravine, Locality KU-261, Thouarsense Zone. **5** – *Mouterdeiceras viticola* Elmi & Rulleau (HC14733), D 64, Óbánya area, Locality OB-3/d, Thouarsense Zone. **6** – *Osperleioceras subtile* (Schirardin) (Coll. Sövér), D 58, Réka Valley, Variabilis–Thouarsense Zone. **7** – *Grammoceras penestriatulum* Buckman (HC9131), D57, Farkas Ravine, Locality KU-310, Thouarsense Zone. **8** – *Grammoceras thouarsense* (d'Orbigny) (HC8856), D 50, Somosi Ravine, Locality KU-261, Thouarsense Zone. **9** – *Grammoceras penestriatulum* Buckman (HC14657), D 50, Óbánya area, Locality OB-3/c, Thouarsense Zone. **10, 11** – *Grammoceras striatulum* (J. Sowerby) (HC8035), D 54, Somosi Ravine, Locality KU-261, Thouarsense Zone. **12** – *Pseudogrammoceras* gr. *fallaciosum* (Bayle) (HC9056), D 84, Óbánya area, Locality OB-3/c, Thouarsense Zone. Specimens coated with ammonium chloride and shown in natural size. Scale bar: 10 mm.

Stratigraphic and geographic distribution: Tenuicostatum Zone – lowermost Serpentinum Zone (Striatus horizon in the Mediterranean Province) – Europe (e.g., Bulgaria, England, France, Germany, Hungary, Luxembourg, Portugal, Romania, Slovakia, Spain), N Africa (Algeria, Morocco), Iran, Japan.

Subgenus *Dactylioceras* Hyatt, 1867

Dactylioceras (*Dactylioceras*) *commune* (J. Sowerby, 1815)
Figure 6.4

2002 *Dactylioceras commune* (Sowerby in Buckman) – Fauré, p. 708, pl. 9, fig. 1.
2013 *Dactylioceras* (*Dactylioceras*) *commune* (Sowerby) – Rulleau et al., p. 78, pl. 7, figs 2–4, pl. 8, figs 1–2, pl. 9, figs 1–2, 5–6, pl. 13, figs 1–2.
2014 *Dactylioceras* (*Dactylioceras*) *commune* (Sowerby) – Kovács, p. 48, pl. 1, fig. 2.

Material: 212 specimens in the Hetényi Coll., 1 specimen in the Sövér Coll.

Remarks: The species differs from the closely related *Dactylioceras athleticum* (Simpson) by having a subcircular whorl-section, although transitional forms were illustrated by Rulleau et al. (2013). *Dactylioceras holandrei* (d'Orbigny) is also similar in size and morphology but differs by bearing well-defined tubercles at the bifurcation points of the ribs. The studied material is poorly preserved, and the specimens are somewhat flattened and deformed but specific morphological features are identifiable. *Dactylioceras commune* is abundant in layers of the Sublevisoni Subzone in the E Mecsek Mts, it is associated generally with *Hildoceras lusitanicum* Meister in the fauna.

Stratigraphic and geographic distribution: Bifrons Zone (Sublevisoni Subzone) – Europe (England, France, Germany, Hungary, Luxembourg, Poland, Slovakia), N Africa (Algeria), Iran, N Russia.

Genus *Catacoeloceras* Buckman, 1923

Catacoeloceras dumortieri (de Brun, 1932)
Figure 6.5

2008 *Catacoeloceras dumortieri* (de Brun) – Géczy et al., p. 37, pl. 1, fig. 11.
2013 *Catacoeloceras dumortieri* (de Brun) – Rulleau et al., p. 110, pl. 37, figs 2–3, 5–6, 8, pl. 38, figs 1–2
2014 *Catacoeloceras dumortieri* (de Brun) – Kovács, p. 51, pl. 2, fig. 6.

Material: 1 specimen (Hetényi Coll.)

Remarks: The species differs from *Catacoeloceras crassum* (Young & Bird) by having more evolute and narrower shell, and by bearing slightly more widely spaced ribs. *Catacoeloceras dumortieri* is typical of the NW European Province but sporadically appears in Mediterranean localities as well).

Stratigraphic and geographic distribution: Variabilis Zone – Europe (Austria, England, France, Germany, Hungary, Italy), N Africa (Morocco).

Superfamily Hildoceratoidea Hyatt, 1867
Family Hildoceratidae Hyatt, 1867
Subfamily Harpoceratinae Neumayr, 1875
Genus *Eleganticeras* Buckman, 1913
Cleviceras exaratum (Young & Bird, 1828)
Figure 5.2–3, 5.6

1992 *Cleviceras exaratum* (Young & Bird) – Howarth, p. 90, text-figs 10, 16, 18C, 19C, 20, 21, pl. 9, figs 2–6, pls 10–11, pl. 12, figs 1–5, pl. 13, figs 1– 2.
1996 *Harpoceras exaratum* (Young & Bird) – Popa & Patrulius, pl. 5, fig. 1.
2006 *Eleganticeras exaratum* (Young & Bird) – Bécaud, p. 50, pl. 6, fig. 2.
2011 *Eleganticeras exaratum* (Young & Bird) – Lacroix, p. 82, pl. 8, fig. 7, pl. 9, fig. 2.

Material: 11 specimens in the Hetényi Coll., 1 specimen in the Eötvös University Coll.

Remarks: The species differs from its ancestor, *Eleganticeras elegantulum* (Young & Bird) by possessing more involute coiling, broader whorls and rounded umbilical wall, while its descendant, *Cleviceras elegans* (J. Sowerby) has a much more involute shell. The co-existent *Harpoceras serpentinum* (Schlotheim) and *H. strangewaysi* (J. Sowerby) are more evolute forms. *Cleviceras exaratum* was recorded from the black shale strata of the Rékavölgy Siltstone Formation in the Réka Valley (Section B2) by Galácz (1991, pl. 4, fig. 2) as *Harpoceras* cf. *exaratum*.

Stratigraphic and geographic distribution: Serpentinum Zone (Elegantulum Subzone) – Europe (NW European Province:

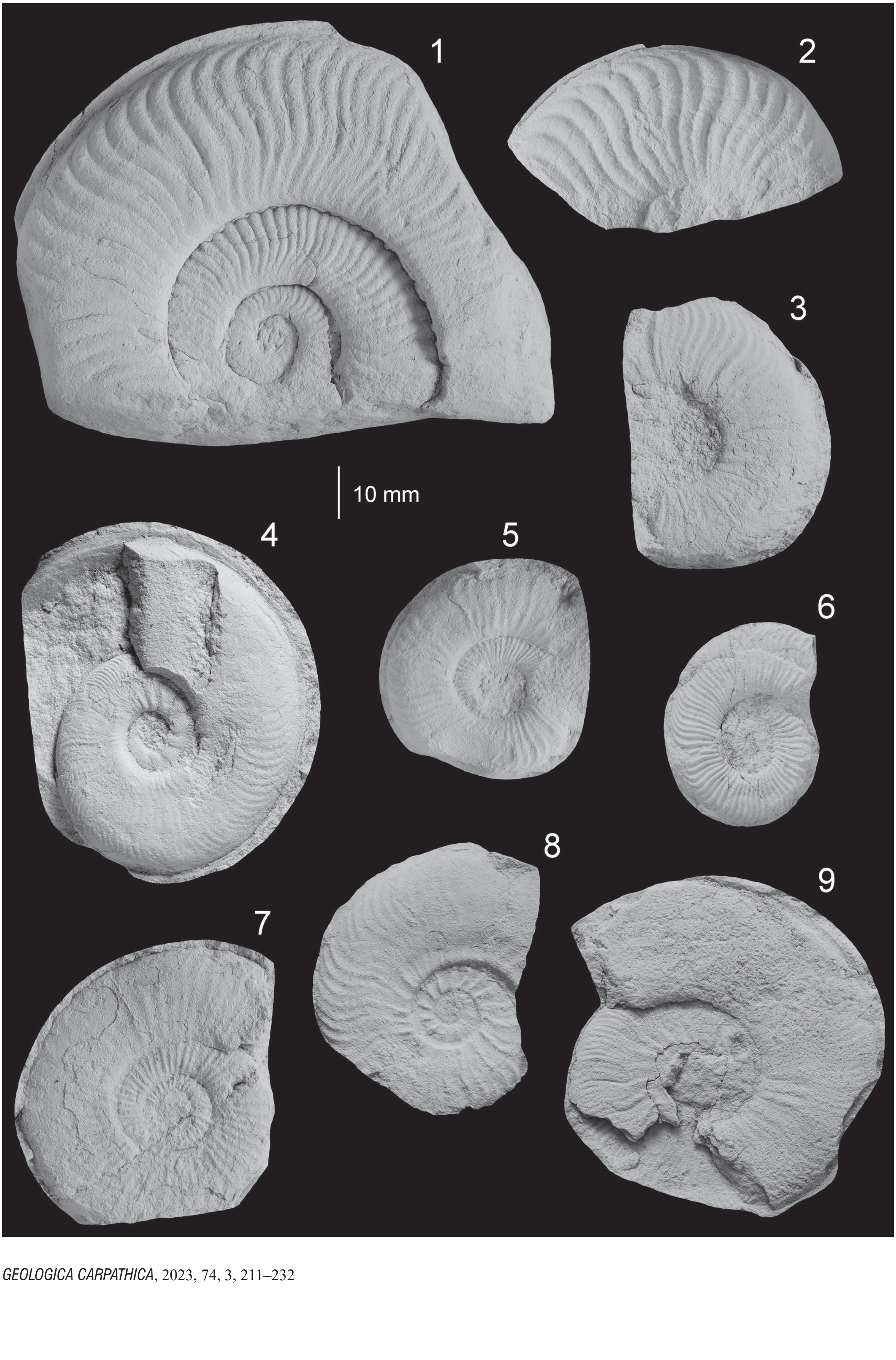
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Fig. 8. 1 – *Pseudogrammoceras* gr. *fallaciosum* (Bayle) morphotype *pedicum* Buckman (HC8453), D 104, Cseresnyák Hill, Locality K-102, Thouarsense Zone. **2** – *Pseudogrammoceras* gr. *fallaciosum* (Bayle) morphotype *cotteswoldiae* Buckman (HC8053), D 64, Somosi Ravine, KU-261, Thouarsense Zone. **3** – *Esericeras* cf. *fascigerum* (Buckman) (HC9280), D 52, Óbánya, Tél-hegy, Locality II/5, Thouarsense Zone. **4** – *Phlyseogrammoceras dispansum* (Lycett) (HC23314), D 67, Farkas Ravine, Locality OB-151, Dispansum Zone. **5** – *Dumortieria pseudoradiosa* (Branco) (HC8777), D 44, Farkas Ravine, Locality KU-310, Pseudoradiosa Zone. **6** – *Dumortieria pseudoradiosa* (Branco) (HC14795), D 38, Püspökszentlászló, Vöröspart area, Locality ZV-243, Pseudoradiosa Zone. **7** – *Dumortieria radians* (Reinecke) (Coll. Sövér), D 60, Farkas Ravine, Pseudoradiosa Zone. **8** – *Cotteswoldia paucicostata* Buckman (HC23016), D 52, Püspökszentlászló, Aalensis Zone. **9** – *Cotteswoldia aalensis* (Zieten) (HC16384), macroconch, D 66, Óbánya area, Locality OB-3/a, Aalensis Zone. Specimens coated with ammonium chloride and shown in natural size. Scale bar: 10 mm.

England, France, Germany, Hungary, Luxembourg, Romania, Slovakia, Switzerland), the Caucasus, Canada, NE Russia.

Genus *Harpoceras* Waagen, 1869

Harpoceras falciferum (J. Sowerby, 1820)
Figure 5.4, 5.7

1992 *Harpoceras falciferum* (J. Sowerby) – Howarth, p. 119, text-figs 18F, 19B, 27–34, pl. 18, fig. 3, pl. 19, figs 2–4, pl. 20, figs 1–11.
1996 *Harpoceras mulgravium* (Young & Bird) – Popa & Patrulius, pl. 4, fig. 9, pl. 5, fig. 4.
2006 *Harpoceras* (*Harpoceras*) *falciferum* (Sowerby) – Bécaud, p. 61, pl. 19, fig. 1, pl. 20, fig. 1, pl. 24, fig. 2, pl. 26, fig. 1, pl. 27, figs 1, 2, pl. 32, figs 2, 4.
2012 *Harpoceras* (*Harpoceras*) *falciferum* – Kovács, p. 28, pl. 7, fig. 2, pl. 11, fig. 1.

Material: 5 specimens in the Hetényi Coll., 3 specimens in the Eötvös University Coll., 1 specimen in the MK Coll.

Remarks: The species is characterized by notable variability in the style of coiling and ribbing but distinguishable from its ancestor, *Harpoceras serpentinum* (Schlotheim) (Fig. 6.1–2) mainly by its larger adult size, more involute shell, vertical or undercut umbilical wall, continuous mid-lateral groove, and falcate ribs. *Harpoceras pseudoserpentinum* Gabilly and *H. rulleaui* Bécaud are more evolute forms with falcoid ribs, while *H. subplanatum* (Oppel) (recorded in earlier literature from the region) has a discoidal, involute shell bearing fine and dense ribs. *Harpoceras* cf. *falciferum* was recorded by Galácz (1991, pl. 4, fig. 1) from a marly layer that overlies the black shale strata of Section B2 in the Réka Valley.

Stratigraphic and geographic distribution: Serpentinum Zone (Falciferum Subzone) – worldwide.

Genus *Osperleioceras* Krimholtz, 1957

Osperleioceras subtile (Schirardin, 1914)
Figure 7.6

2006 *Osperleioceras* (*Pseudopolyplectus*) *subtile* (Schirardin) – Bécaud, p. 71, pl. 31, fig. 1.
2007 *Osperlioceras subtile* (Schirardin) – Fauré, p. 40, fig. 6/9–10.

Material: 1 specimen in the Hetényi Coll., 1 specimen in the Sövér Coll.

Remarks: The species differs from the co-existent *Polyplectus discoides* (Zieten) by tabulate–carinate venter and broader, flattened and more falcoid ribs. The specimen figured here belongs to László Sövér's private collection, it came from the Réka Valley, and was associated with *Pseudogrammoceras* specimens (L. Sövér *pers. com.*). *Osperleioceras subtile* is closely allied to *O. bicarinatum* (Zieten) but is distinguishable in morphology by its larger size, more involute and, compressed shell, as well as its range at localities in France is typical of the middle–upper part of the Thouarsense Zone while *O. bicarinatum* ranged in the upper Bifrons Zone – lower Thouarsense Zone with acme in the Variabilis Zone.

Stratigraphic and geographic distribution: Thouarsense Zone (Thouarsense–Fascigerum subzones) – Europe (NW European Province: France, Hungary).

Subfamily Hildoceratinae Hyatt, 1867
Genus *Hildaites* Buckman, 1921

Hildaites murleyi (Moxon, 1841)
Figure 5.5

1992 *Hildaites murleyi* (Moxon) – Howarth, p. 168, pl. 30, figs 9–10, pl. 31, figs 1–8, pl. 32, fig. 4.
2008 *Hildaites murleyi* (Moxon) – Metodiev, fig. 4/k–l.
2011 *Hildaites murleyi* (Moxon) – Lacroix, p. 155, pl. 41, figs 2–3, pls 42–43.
2012 *Hildaites murleyi* (Moxon) – Kovács, p. 36, pl. 13, fig. 1, pl. 14, figs 1–2, pl. 15, figs 1–2.

Material: 12 specimens (Eötvös University Coll.)

Remarks: The species shows remarkable variability in morphology, so *Hildaites levisoni* (Simpson), *H. borealis* (Seebach), *H. propeserpentinus* (Buckman), and *Murleyiceras aptum* Buckman were considered as synonyms of *H. murleyi* by Howarth (1992), this arrangement is accepted herein. The species differs in morphology from its NW European congeners *Hildaites wrighti* (Spath) and *H. serpentiniformis* Buckman by bearing much stronger and more widely spaced ribs. *Hildaites forte* (Buckman) [= *Murleyiceras gyrale* Buckman] has a similar sculpture but is distinguishable by possessing a lower, subquadrate whorl section and lower rib density. *Hildaites subserpentinus* Buckman has a slightly more involute shell and bears finer, rectiradiate, and sinuous ribs. The *Hildaites murleyi* specimen figured herein came from the Réka Valley (Section B1), it was illustrated under the name *Hildaites* cf. *levisoni* by Galácz (1991, pl. 3, fig. 5).

Stratigraphic and geographic distribution: Serpentinum Zone (Elegantulum Subzone, upper Elegantulum horizon – Falciferum Subzone, Douvillei horizon) – Europe (Austria, Bulgaria, England, France, Germany, Greece, Hungary, Slovakia, Spain, Switzerland), N Africa (Algeria, Morocco), Greenland, the Caucasus, N Russia, South and North America.

Genus *Hildoceras* Hyatt, 1867

Hildoceras lusitanicum Meister, 1913
Figure 6.3, 6.6

1996 *Hildoceras lusitanicum* (Meister) – Popa & Patrulius, pl. 6, figs 8–10.
2006 *Hildoceras lusitanicum* Meister – Bécaud, p. 88, pl. 44, figs 1, 3, pl. 45, figs 1, 3, pl. 46, figs 2, 5, pl. 48, fig. 3.
2008 *Hildoceras lusitanicum* Meister – Géczy et al., pl. 1, fig. 17.
2011 *Hildoceras lusitanicum* Meister – Lacroix, p. 173, pl. 64, fig. 3, pls 65–67, 70, pl. 68, figs 1–2, 4–6, pl. 69, figs 1–3, 5–6.
2016 *Hildoceras lusitanicum* Meister – Ridente, figs 7–9.

Material: 420 specimens (Hetényi Coll.)

Remarks: The species differs from the congeners by its narrower whorls with shallow lateral pseudogroove and finer ribs. *Hildoceras lusitanicum* is the most abundant species in the Bifrons Zone in the E Mecsek Mts, it is associated generally with *Dactylioceras commune* (J. Sowerby) in the fauna. *Hildoceras lusitanicum* is also the dominant species of the upper Sublevisoni – lower Bifrons subzones in the Mediterranean ammonite assemblages of the Gerecse Mts. *Hildoceras* is the only genus within the Toarcian biostratigraphy that allows the same zonal, subzonal and biohorizon subdivisions in both European faunal provinces.

Stratigraphic and geographic distribution: Bifrons Zone (Lusitanicum–Bifrons horizons) – Europe (Austria, Bulgaria, England, France, Germany, Greece, Hungary, Italy, Luxembourg, Poland, Portugal, Slovakia, Spain), N Africa (Algeria, Morocco, Tunisia), ? the Caucasus, Iran.

Subfamily Grammoceratinae Buckman, 1905
Genus: *Pseudogrammoceras* Buckman, 1901

Pseudogrammoceras gr. *fallaciosum* (Bayle, 1878)
Figures 7.12, 8.1–2

1996 *Pseudogrammoceras fallaciosum* (Bayle) – Popa & Patrulius, pl. 11, figs 6–7, pl. 12, figs 1–4, 7–8, pl. 13, figs 1–5, pl. 14, figs 2, 4.
2011 *Pseudogrammoceras fallaciosum* (Bayle) – Galácz et al., p. 329, pl. 4, fig. 3, pl. 5, fig. 3.
2020 *Pseudogrammoceras* gr. *fallaciosum* (Bayle) – Rulleau et al., p. 68, text-fig. 22/15, pl. 20, figs 1–6, pl. 21, figs 1–3, pl. 22, figs 1, 3, pl. 23, figs 1, 4, pl. 24, fig. 1.

Material: 404 specimens in the Hetényi Coll., 3 specimens in the Sövér Coll.

Remarks: The species group is characterized by highly variable shell morphology, so morphotypes, closely related nominal species and/or subspecies are recognized in the literature (Gabilly 1976; Kovács 2013; Rulleau et al. 2020). In the studied assemblages three morphotypes appear: the typical *Pseudogrammoceras fallaciosum* (Bayle) has a moderately evolute shell with fine ribs (Fig. 7.12), *P. pedicum* Buckman has a more evolute coiling and its ribs are moderately broader than that of *P. fallaciosum* (Fig. 8.1), whereas *P. fallaciosum cotteswoldiae* Buckman is a more involute form with broad ribs (Fig. 8.2). These species are relatively abundant in the eastern Mecsek Mts. *Pseudogrammoceras* gr. *fallaciosum* is typical of the NW European Province but it sporadically occurs in Mediterranean localities as well.

Stratigraphic and geographic distribution: Thouarsense Zone (Fallaciosum Subzone) – Dispansum Zone (lowermost Insigne Subzone) – Europe (Bulgaria, England, France, Germany, Hungary, Portugal, Romania, Slovakia, Spain), N Africa (Algeria, Morocco, Tunisia), the Caucasus, Iran.

Genus: *Podagrosites* Guex, 1973

Podagrosites pseudogrunowi Guex, 1975
Figure 7.1–2

1967 *Pseudogrammoceras saemanni raricostatum* n. subsp. – Géczy, p. 121, pl. 4, fig. 1.
1996 *Pseudogrammoceras latescens* – Popa & Patrulius, pl. 9, fig. 10, pl. 10, fig. 7 *only* (non Simpson)
2002 *Podagrosites* aff. *pseudogrunowi* Guex – Metodiev, p. 187, text-fig. 7/15–16, pl. 6, figs 6–7.
2005 *Podagrosites pseudogrunowi* Guex – Seyed-Emami et al., p. 357, figs 5/F, J.
2020 *Podagrosites pseudogrunowi* (Guex) – Rulleau et al., p. 81, text-figs 21/1, 4, 24/3–4, pl. 25, figs 2, 4–6, pl. 26, fig. 1.

Material: 70 specimens in the Hetényi Coll., 6 specimens in the Sövér Coll.

Remarks: The species differs from the co-occurring *Podagrosites latescens* (Simpson) (Fig. 7.3–4) by having a more involute shell with compressed and higher whorls, more rounded lateral walls, narrower venter with shallow sulci, and denser ribs. *Podagrosites aratus* (Buckman) (Fig. 6.11), which is typical of the Variabilis Zone, has narrower whorls, less rounded lateral walls, and a lower venter. The two "*Harpoceras radians* Reinecke" specimens from the "Radians-Schichten" of the Komló area (Lóczy 1910, fig. 48) are characterized by evolute coiling, bearing coarse, rectiradiate, simple ribs; the figured specimens probably represent *Podagrosites aratus*.

Based on taxonomical revisions of *Ammonites seamanni* Dumortier non Oppel and *Podagrosites pseudogrunowi* Guex by Rulleau et al. (2020), the *P. seamanni* reported in Géczy (1967) and Hetényi (1978) is revised herein as *Podagrosites pseudogrunowi*. The species was not described by Popa & Patrulius (1996) in their summary of the Toarcian ammonite assemblages of Romania. However, two "*Pseudogrammoceras latescens*" specimens with narrow venter (Popa & Patrulius 1996, pl. 9, fig. 10, pl. 10, fig. 7) differ in morphology from the type of *latescens* (refigured by Rulleau et al. 2020, pl. 26, fig. 2) and probably represent *Podagrosites pseudogrunowi*.

Stratigraphic and geographic distribution: Thouarsense Zone (Fascigerum–Fallaciosum subzones) – Europe (NW European Province: Bulgaria, England, France, Germany, Hungary, Poland, Portugal, Romania, Spain, Ukraine), N Africa (Algeria, Morocco), the Caucasus, Iran.

Genus: *Grammoceras* Hyatt, 1867

Grammoceras penestriatulum Buckman, 1902
Figure 7.7, 7.9

1976 *Grammoceras penestriatulum* Buckman – Gabilly, p. 119, text-figs 83, 103b, t. 17, pl. 18, figs 3–4, pl. 19, figs 3–4, pl. 20, figs 6–7.
2002 *Grammoceras penestriatulum* Buckman – Metodiev, p. 173, text-fig. 5/6, pl. 1, fig. 7.
2013 *Grammoceras penestriatulum* Buckman – Kovács, p. 129, pl. 2, figs 6–7, pl. 3, figs 6–7.
2020 *Grammoceras* gr. de *penestriatulum* (Buckman) – Rulleau et al., p. 93, text-figs 23/2, 25/6, pl. 29, fig. 4, pl. 30, fig. 5, pl. 31, figs 2, 6–8, pl. 32, fig. 1.

Material: 9 specimens in the Hetényi Coll., 2 specimens in the Sövér Coll.

Remarks: The species has a more evolute shell than that of *Grammoceras thouarsense* (d'Orbigny) (Fig. 7.8), and its ribs are stronger and more widely spaced than on *G. striatulum* (J. Sowerby) (Fig. 7.10–11). *Grammoceras penestriatulum* is typical of the NW European Province but rarely occurs in Mediterranean localities as well.

Stratigraphic and geographic distribution: Thouarsense Zone (Thouarsense–Fascigerum subzones) – Europe (Bulgaria, England, France, Germany, Hungary, Italy, Luxembourg, Spain), the Caucasus.

Genus *Phlyseogrammoceras* Buckman, 1901

Phlyseogrammoceras dispansum (Lycett, 1860)
Figure 8.4

2008 *Phlyseogrammoceras dispansum* (Lycett) – Metodiev, fig. 6/a.
2011 *Phlyseogrammoceras dispansum* (Lycett) – Lacroix, p. 308, pl. 148, fig. 1, pl. 149, figs 4–5.
2020 *Phlyseogrammoceras* gr. *dispansum* (Lycett) – Rulleau et al., p. 111, text-figs 28/1–2, 7, 9–10, pl. 42, fig. 3, pl. 45, fig. 3, pl. 46, figs 1–3, pl. 47, fig. 2, pl. 48, fig. 1, pl. 52, fig. 4.

Material: 2 specimens (Hetényi Coll.)

Remarks: The species is characterized by moderate morphological variability but is distinguishable from the other species of this genus [e.g., *Phlyseogrammoceras dispansiforme* (Wunstorf), *P. schneideri* Maubeuge, *P. metallarium* (Buckman)] by having a more involute and compressed shell with a sculpture of fine, strongly proverse, fasciculate ribbing. *Phlyseogrammoceras dispansum* is recorded from Hungary for the first time here.

Stratigraphic and geographic distribution: Dispansum Zone – Europe (NW European Province: Belgium, Bulgaria, England, France, Germany, Hungary, Luxembourg), N Africa (Algeria, Morocco), the Caucasus, ? South America.

Superfamily Hammatoceratoidea Schindewolf, 1964
Family Tmetoceratidae Spath, 1936
Subfamily Dumortieriinae Maubeuge, 1950
Genus *Dumortieria* Haug, 1885

Dumortieria pseudoradiosa (Branco, 1879)
Figure 8.5–6

2002 *Dumortieria pseudoradiosa* (Branco) – Fauré, p. 729, pl. 22, fig. 10.
2008 *Dumortieria pseudoradiosa* (Branco) – Metodiev, fig. 6/n.
2020 *Dumortieria pseudoradiosa* (Branco) – Di Cencio & Weis, p. 26, pl. 8, fig. b.

Material: 3 specimens (Hetényi Coll.)

Remarks: The species is distinguishable from the other species of this genus [e.g., *Dumortieria multicostata* Buckman, *D. rhodanica* Haug, *D.* gr. *subundulata* (Branco)] by bearing stronger and more flexuous ribs. The ribs of *Dumortieria radians* (Reinecke) are weaker, straight and rectiradiate (Fig. 8.7). Both species are new records in Hungary.

Stratigraphic and geographic distribution: Pseudoradiosa Zone (and Subzone) – Europe (NW European Province: Bulgaria, France, Germany, Hungary, Luxembourg, Spain), N Africa (Algeria), the Caucasus, Iran.

Genus *Cotteswoldia* Buckman, 1902

Cotteswoldia paucicostata Buckman, 1904
Figure 8.8

2008 *Pleydellia* (*Cotteswoldia*) *paucicostata* Buckman – Metodiev, fig. 6/x.
2011 *Cotteswoldia paucicostata* Buckman – Kovács, p. 358, pl. 6, fig. 3.
2020 *Cotteswoldia paucicostata* Buckman – Di Cencio & Weis, p. 45, pl. 15, fig. f.

Material: 1 specimen (Hetényi Coll.)

Remarks: *Cotteswoldia paucicostata* is a distinctive species, it differs from its congeners by bearing widely spaced and strong primary ribs on its inner whorls.

Stratigraphic and geographic distribution: Aalensis Zone – Europe (Bulgaria, England, France, Hungary, Italy, Luxembourg, Portugal, Spain), N Africa (Tunisia), Crimea, the Caucasus, Iran.

Discussion and comparison with other Toarcian ammonite faunas

In this study, 43 Ammonitina species are recognized from the Toarcian deposits of the eastern Mecsek Mts. The material consists of taxa that are typical for the late Early Jurassic NW European faunal province, hence the standard ammonite chronostratigraphy is applicable for the Toarcian of the Mecsek Mts and allows, for the first time, the recognition of the presence of all eight Toarcian chronozones and most of their contained chronozones.

Only a minor part of the studied material is derived from bed-by-bed collections (Galácz 1991; Dulai et al. 1992), whereas the exact stratigraphic position of most specimens in the extremely rich Hetényi Collection as well as in the Sövér Collection remains unknown. Therefore, the vast majority of this material is only suitable for chronostratigraphic, diversity, and paleobiogeographic analyses.

Although the preservation of the Toarcian specimens is generally poor to mediocre, the large material (more than 5000 ammonites) is regarded as an exceptionally representative sample for the area and time interval. We found that the diversity of the Toarcian Ammonitina in the Mecsek Mts is significantly lower than at fossiliferous localities in the NW European Province in England, France, Germany, N Spain, and Bulgaria (e.g., Goy & Martínez 1990; Howarth 1992; Schulbert 2001; Fauré 2002; Rulleau 2007, 2009; Metodiev 2008; Arp 2010; Goy et al. 2010; Lacroix 2011; Rulleau et al. 2013, 2015, 2020). In the studied material, many genera that are widespread and characteristic elsewhere and are considered zonal or subzonal indices occur rather rarely in this area (e.g., *Orthodactylites*, *Dactylioceras*, *Nodicoeloceras*, *Catacoeloceras*, *Haugia*, *Esericeras*, *Phlyseogrammoceras*, *Phymatoceras*, *Dumortieria*, and *Pleydellia*) or are missing altogether (e.g., *Peronoceras*, *Paltarpites*, *Maconiceras*, *Orthildaites*, *Paroniceras*, *Denckmannia*, *Pseudolillia*, *Hammatoceras*, and *Crestaites*).

The lithofacies, the characteristic spotted marl (*Fleckenmergel* or *Allgäu* facies in the German literature) is a widespread deposit in the Lower and Middle Jurassic in the northern Tethyan open shelf from the Betic Cordillera to the Eastern Carpathians (Müller et al. 2017). From the neighboring regions Toarcian ammonite faunas of this facies were described by Böse (1894) and Schröder (1927–1928) from the Bavarian Alps (S Germany), Jacobshagen (1965) from the Allgäu Alps (W Austria), and Rakús (1964) from the Fatra and Low Tatra Mts (Western Carpathians, Slovakia). Although these ammonite assemblages require taxonomic revision, it seems certain that diversity in all of these three regions is much lower than in the Mecsek Mts. Temporal distribution of this diversity is also uneven, with the Bifrons and Thouarsense zones being the richest, whereas the Serpentinum, Variabilis and the uppermost Toarcian zones are represented by only one or two species. The ammonite fauna of the Serpentinum Zone presented by Müller et al. (2020) from the spotted marly limestone, marl and black shale strata of the Skladaná Skala section (W Carpathians, Slovakia) is characterized by a similar faunal composition but displays somewhat higher diversity. The small Toarcian ammonite fauna documented by Wierzbowski et al. (2012) from the Ukrainian part of the Pieniny Klippen Belt also shows comparable faunal compositions and diversity.

On the other hand, Ammonitina assemblages that are remarkably similar to those from the Mecsek Mts were described by Popa & Patrulius (1996) from two regions in Romania: the Eastern Carpathians (Perşani Mts and the Braşov region), and the Apuşeni Mts. Not only the faunal composition with numerous common taxa and the relatively low species richness resembled that of the Mecsek region, but also the temporal pattern of diversity change. In both regions, a gradual growth is observed from the poorly diversified fauna of the Tenuicostatum Zone to the much richer Bifrons Zone, followed by a decline in the Variabilis Zone, and again a fauna of increasing diversity in the Thouarsense Zone. The Dispansum, Pseudoradiosa and Aalensis zones display again a radical decline both in the abundance and the species diversity. This close similarity may be explained by their paleogeographical proximity, since all three regions represent hemipelagic basins of the Tisza Mega-Unit, at the transition between the shallow epicontinental sea of the NW European faunal province and the open Tethys Ocean (Fig. 1) following the demise of peri-Tethyan carbonate platforms. The spatiotemporal trajectories of Toarcian ammonite diversity are expected to reflect the biotic response in the aftermath of the Jenkyns Event in the broad western peri-Tethyan region (Macchioni & Cecca 2002; Dera et al. 2011; Benzaggagh 2022). Thus, the new data presented here from Mecsek Mts may lead to improved faunal analyses in future studies.

Conclusions

A systematic study of more than 5000 Toarcian ammonite specimens from the Mecsek Mts, previously unavailable for research, revealed the presence of 43 species Although the majority of the material is from the Hetényi collection that was obtained during geological mapping and lacks precise stratigraphic context, it allows the unambiguous recognition of all eight standard chronozones and most of their contained subzones. The assemblages show affinity with those from the NW European faunas but are less diverse. Their diversity is comparable with other areas in the Early Jurassic facies belt of hemipelagic spotted marl. Temporal changes in diversity are characterized by distinct maxima in the Bifrons and Thouarsense Zones.

Acknowledgments: We are grateful to Gábor Botfalvai, András Galácz, Anna Somlyay and István Szente (Eötvös University, Budapest), Alfréd Dulai (HNHM, Budapest), Tamás Henn (MK, Komló), Olga Piros and Tímea Szlepák (Library of the Geological Institute of Hungary) for professional help and advice. Márta Hetényi kindly provided indispensable locality information on the ammonite material in the Hetényi Collection. Márton Szabó (HNHM) and Domonkos Verestói-Kovács (Budapest) contributed to the illustrations in this work. Private fossil collectors László Kanizsai (Komló) and László Sövér (Bonyhád) helped with our field surveys in the Cseresnyák Hill and the Farkas Ravine areas. László Sövér kindly made available his ammonite material for study and publication. Critical comments by Philippe Fauré (France) on an earlier version and constructive reviews by two anonymous journal reviewers helped to improve the manuscript. This study received funding by the National Research, Development and Innovation Office of Hungary (grants OTKA NN 128702 and K 135309). This is ELKH-MTM-ELTE Paleo contribution No. 372.

References

Arp G. 2010: Ammonitenfauna und Stratigraphie des Grenzbereichs Jurensismergel / Opalinuston-Formation bei Neumarkt i.d. Opf. (oberstes Toarcium, Fränkische Alb). *Zitteliana* A 50, 25–50. https://doi.org/10.5282/ubm/epub.11987

Baranyi V., Pálfy J., Görög Á., Riding J.B. & Raucsik B. 2016: Multiphase response of palynomorphs to the Toarcian Oceanic Anoxic Event (Early Jurassic) in the Réka Valley section, Hungary. *Review of Palaeobotany and Palynology* 235, 51–70. https://doi.org/10.1016/j.revpalbo.2016.09.011

Bardin J., Rouget I., Benzaggagh M., Fürsich F.T. & Cecca F. 2014: Lower Toarcian (Jurassic) ammonites of the South Riffian ridges (Morocco): systematics and biostratigraphy. *Journal of Systematic Palaeontology* 13, 471–501. https://doi.org/10.1080/14772019.2014.937204

Bayle M. 1878: Fossiles principaux des terrains. *Explication de la Carte géologique de la France* 4, pls 168.

Bécaud M. 2006: Les Harpoceratinae, Hildoceratinae et Paroniceratinae du Toarcien de la Vendée et des Deux-Sèvres (France). *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon* 162, 1–245.

Benzaggagh M. 2022: Toarcian terebratulides (brachiopods) and ammonites from the Central Unit of the South Riffian Ridges, northwestern Morocco. *Journal of African Earth Sciences* 196, 104625. https://doi.org/10.1016/j.jafrearsci.2022.104625

Boomer I., Copestake P., Page K., Huxtable J., Loy T., Bown P., Dunkley Jones T., O'Callaghan M., Hawkes S., Halfacree D., Reay H. & Caughtry N. 2021: Biotic and stable-isotope characterization of the Toarcian Ocean Anoxic Event through a carbonate–clastic sequence from Somerset, UK. *Geological Society, London, Special Publications* 514, 239–268. https://doi.org/10.1144/SP514-2020-263

Böse E. 1894: Ueber lieber liasische und mitteljurassische Fleckenmergel in den bayerischen Alpen. *Zeitschrift der Deutschen Geologischen Gesellschaft* 46, 703–768.

Branco W. 1879: Der untere Dogger Deutsch-Lothringens. *Abhandlungen zur Geologischen Spezialkarte von Elsass–Lothringen* 2, 1–155.

Brezsnyánszky K. 2004: Hetényi Rudolf emlékezete [In memoriam Rudolf Hetényi]. *A Magyar Állami Földtani Intézet Évi Jelentése (Annual Report of the Hungarian Geological Institute)* 2003, 43–52.

Brun P. de 1932: Étude géologique et paléontologique des environs de Saint-Ambroix (Gard) 3. partie: Lias supérieur. *Bulletin de la Société d'étude des Sciences Naturelles de Nimes* 46, 175–204; 47, 82–120.

Buckman S.S. 1887–1907: A monograph of the Inferior Oolite ammonites of the British Islands. *Monograph of the Palaeontographical Society. London*, 456+cclxii p., 103+24 supplementary pls.

Buckman S.S. 1902: Emendations of ammonite nomenclature. *Norman, Sawyer and Co.*, Cheltenham, 1–7.

Buckman S.S. 1909–1930: Yorkshire Type Ammonites (1, 2), Type Ammonites (3–7). *Wesley & Wesley*, London, pls 790.

Császár G., Szinger B. & Piros O. 2013: From continental platform towards rifting of the Tisza Unit in the Late Triassic to Early Cretaceous. *Geologica Carpathica* 64, 279–290. https://doi.org/10.2478/geoca-2013-0020

Csontos L. & Vörös A. 2004: Mesozoic plate tectonic reconstruction of the Carpathian region. *Palaeogeography Palaeoclimatology Palaeoecology* 210, 1–56. https://doi.org/10.1016/j.palaeo.2004.02.033

Csontos L., Benkovics L., Bergerat F., Mansy J.-L. & Wórum G. 2002: Tertiary deformation history from seismic section study and fault analysis in a former European Tethyan margin (the Mecsek-Villány area, SW Hungary). *Tectonophysics* 357, 81–102. https://doi.org/10.1016/S0040-1951(02)00363-3

Cuvier G. 1797: Tableau élémentaire de l'histoire naturelle des animaux. *Baudouin*, Paris, 1–710.

d'Orbigny A. 1845: Paléontologie française, terrains jurassiques. Volume I. Céphalopodes. *Masson*, Paris, 1–642, pls 234.

Dera G., Neige P., Dommergues J.L. & Brayard A. 2011: Ammonite paleobiogeography during the Pliensbachian-Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. *Global and Planetary Change* 78, 92–105. https://doi.org/10.1016/j.gloplacha.2011.05.009

Di Cencio A. & Weis R. 2020: Revision of upper Toarcian ammonites (Lytoceratidae, Graphoceratidae and Hammatoceratidae) from the Minette ironstones, southern Luxembourg. In: Di Cencio A., Sadki D. & Weis R. (eds): Paléontologie au Luxembourg (2). Les ammonites de la Minette. *Ferrantia* 83, 5–103.

Dulai A., Suba Zs. & Szarka A. 1992: Toarcian (Lower Jurassic) organic-rich black shale in the Réka Valley (Mecsek Hills, Hungary). *Földtani Közlöny* 122, 67–87 (in Hungarian with English abstract).

Elmi S., Rulleau L., Gabilly J. & Mouterde R. 1997: Toarcien. In: Cariou E. & Hantzpergue P. (eds): Biostratigraphie du Jurassique ouest-européen et méditerranéen. *Bulletin du Centre des Recherches, Elf Exploration Production Mémoires* 17, 25–36.

Fauré P. 2002: Le Lias des Pyrénées. *STRATA. Actes du Laboratoire de Géologie Sédimentaire et Paléontologie de l'Université Paul-Sabatier* [Mémoires] 39, 1–761.

Fauré P. 2007: La zone à Thouarsense (Toarcien supérieur, Jurassique inférieur) des Corbières (Aude, France): biostratigraphie et évolution sédimentaire. *Bulletin de la Société d'études scientifiques de l'Aude* 107, 31–46.

Fischer P.H. 1882: Manuel de conchyliologie et de paléontologie conchyliologique. *Librairie F. Savy*, Paris, 1–1369.

Földi M., Hetényi R., Nagy I., Bilik I. & Hámor G. 1977: Magyarázó a Mecsek hegység földtani térképéhez, 10,000-es sorozat. Hosszúhetény–É. [Explanations to the Geological Map of the Mecsek Hills, Scale 1:10,000, Hosszúhetény–North]. *Magyar Állami Földtani Intézet*, Budapest, 1–71.

Főzy I. 1993: Upper Jurassic ammonite biostratigraphy of the Mecsek Mts., southern Hungary. *Földtani Közlöny* 123, 195–205.

Főzy I. (Ed.) 2012: Jura. Magyarország litosztratigráfiai alapegységei. *Magyarhoni Földtani Társulat*, Budapest, 1–235.

Fülöp J. 1971: Les formations jurassiques de la Hongrie. *Annales de l'Institut Géologique de Hongrie* 54, 31–46.

Gabilly J. 1976: Évolution et systématique des Phymatoceratinae et des Grammoceratinae (Hildocerataceae, Ammonitina) de la région de Thouars, stratotype du Toarcien. *Mémoires de la Société géologique de France* 124, 1–196.

Galácz A. 1991: A Mecsek-hegységi toarci fekete pala őslénytani vizsgálata. [Paleontological research of the Toarcian black shale of the Mecsek Mts]. *Manuscript, Eötvös Loránd University, Department of Paleontology*, 1–31 (in Hungarian).

Galácz A. 1993: Comparison of Hungarian Bathonian (Middle Jurassic) ammonite assemblages: suggestions on habitats. *Őslénytani Viták* 39, 25–33 (in Hungarian with English abstract).

Galácz A. (Ed.) 1995: Bathonian Fossils from the Mecsek Mountains (Hungary). *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös nominatae, Sectio Geologica* 30 (1994), 1–238.

Galácz A. 2012: The Middle Jurassic ammonites of the Mecsek Mts (South Hungary) in the collection of the late Professor Lajos Kovács. *Földtani Közlöny* 142, 313–319 (in Hungarian with English abstract).

Galácz A. 2015: Macrocephalitid-bearing Lower Callovian (Middle Jurassic) beds in the Mecsek Mts (South Hungary). *Hantkeniana* 10, 73–88.

Galácz A., Császár G., Géczy B. & Kovács Z. 2011: Ammonite stratigraphy of a Toarcian (Lower Jurassic) section on Nagy-Pisznice Hill (Gerecse Mts, Hungary). *Central European Geology* 53 (2010), 311–342. https://doi.org/10.1556/CEuGeol.53.2010.4.1

Géczy B. 1967: Upper Liassic Ammonites from Úrkút, Bakony Mountains, Transdanubia, Hungary. *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös nominatae, Sectio Geologica* 10, 115–150.

Géczy B. 1984: Provincialism of Jurassic ammonites, examples from Hungarian faunas. *Acta Geologica Hungarica* 27, 379–389.

Géczy B. 1990a: La paleobiogeographie des ammonites du Toarcien. *Les Cahiers de L'institut Catholique de Lyon* 4, 63–71.

Géczy B. 1990b: Palaeobiogeographic evaluation of Toarcian Ammonoidea in the Mediterranean and stable European regions. *Általános Földtani Szemle* 25, 231–249 (in Hungarian with English abstract).

Géczy B., Kovács Z. & Szente I. 2008: Remarks on the Toarcian–Aalenian fossil assemblage of the Kis-Teke Hill, Gerecse Mts, Hungary. *Hantkeniana* 6, 33–55.

Geological Maps, 1:10,000, *Geological Institute of Hungary*. Hosszúhetény É (1976): Eds Hetényi R., Nagy I., Földi M., Hámor G. & Bilik I.; Kisújbánya (1975): Eds Nagy I., Hámor G., Hetényi R., Bilik I. & Földi M.; Komló (1969): Eds Földi M., Hámor G., Hetényi R., Nagy E., Nagy I. & Bilik I.; Zengővárkony (1975): Eds Hetényi R., Hámor G. & Nagy I.

Goy A. & Martínez G. 1990: Biozonación del Toarciense en el área de La Almunia de Doña Godina-Ricla (Sector Central de la Cordillera Ibérica). *Cuadernos de Geología Ibérica* 14, 11–53.

Goy A., Comas-Rengifo M.J., Gómez J.J., Herrero C., Suárez-Vega L.C. & Ureta S. 2010: Toarcian ammonite biohorizons in Astu rias. In: Ruiz-Omeñaca J., Piñuela L. & García-Ramos J. (eds): Comunicaciones del V Congreso del Jurásico de España. *Museo del Jurásico de Asturias (MUJA), Colunga, 8–11 de septiembre de 2010*, 94–102.

Guex J. 1973: Observations sur la répartition biostratigraphique des ammonites du Toarcien supérieur de l'Aveyron (France). *Bulletin des Laboratoires de Géologie, Minéralogie, Géophysique et du Musée géologique de l'Université de Lausanne* 207, 1–14.

Guex J. 1975: Description biostratigraphique du Toarcien supérieur de la bordure sud des Causses (France). *Eclogae geologicae Helvetiae* 68, 97–129.

Haug E. 1885: Beiträge zu einer Monographie der Ammonitengattung Harpoceras. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 3, 585–722.

Haas J. (Ed.) 2012: Geology of Hungary. *Springer-Verlag*, Berlin Heidelberg, 1–244.

Haas J. & Péró C. 2004: Mesozoic evolution of the Tisza Mega-unit. *International Journal of Earth Science* 93, 297–313. https://doi.org/10.1007/s00531-004-0384-9

Hesselbo S.P., Bjerrum C.J., Hinnov L.A., MacNiocaill C., Miller K.G., Riding J.B., Van De Schootbrugge B., Abels H., Belcher C., Blau J., Browning J., Cartwright J., Condon D., Daines S., Damborenea S., Dickson A., Fraguas A., Hilgen F., Hooker J., Huang C., Huesing S., Jenkyns H., Korte C., Krijgsman W., Lenton T., Little C., Manceñido M., Mattioli E., Meister C., Morgan R., Newton R., Pálfy J., Pienkowski G., Poulton S., Riccardi A., Robinson A., Ruhl M., Suan G., Smith N., Thibault N., Ullmann C., Wignall P., Williford K., Wonik T. & Xu W. 2013: Mochras borehole revisited: A new global standard for Early Jurassic earth history. *Scientific Drilling* 16, 81–91. https://doi.org/10.5194/sd-16-81-2013

Hesselbo S.P., Ogg J.G., Ruhl M., Hinnov L.A. & Huang C.J. 2020: The Jurassic Period. In: Gradstein F.M., Ogg J.G., Schmitz M.D. & Ogg G.M. (eds): Geologic Time Scale 2020. *Elsevier*, 955–1021. https://doi.org/10.1016/B978-0-12-824360-2.00026-7

Hetényi R. 1968: A Mecsek hegység részletes és átfogó földtani vizsgálata az összefoglalás szakaszában. *A Magyar Állami Földtani Intézet Évi Jelentése az 1966. évről*, 31–48.

Hetényi R. 1978: Bifrons, 3. Montagne de Mecsek; Posidonomya; Radians. In: Fülöp J. (Ed.): Hongrie. *Lexique stratigraphique international* Vol. I. Europe, fasc. 9: 100–101, 425–426, 430–431. *CNRS*, Paris, 1–666.

Howarth M.K. 1973: The stratigraphy and ammonite fauna of the Upper Liassic Grey Shales of the Yorkshire coast. *Bulletin of the British Museum (Natural History), Geology* 24, 235–277.

Howarth M.K. 1980: The Toarcian age of the upper part of the Marlstone Rock Bed of England. *Palaeontology* 23, 637–656.

Howarth M.K. 1992: The Ammonite Family Hildoceratidae in the Lower Jurassic of Britain. Part I et II. *Monograph of the Palaeontographical Society*, London, 1–200. https://doi.org/10.1080/25761900.2022.12131773

Hyatt A. 1867: The Fossil Cephalopods of the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology* 5, 71–102.

Jacobshagen V. 1965: Die Allgäu-Schichten (Jura-Fleckenmergel) zwischen Wettersteingebirge und Rhein *Jahrbuch der Geologischen Bundesanstalt* 108, 1–114.

Kovács Z. 2011: Tmetoceratidae (Ammonitina) fauna from the Gerecse Mts (Hungary). *Central European Geology* 53, 343–376. https://doi.org/10.1556/CEuGeol.53.2010.4.2

Kovács Z. 2012: Lower Toarcian Ammonitida fauna and biostratigraphy of the Gerecse Mountains (Hungary). *Fragmenta Palaeontologica Hungarica* 29, 1–48.

Kovács Z. 2013: Grammoceratinae (Ammonitina) fauna from the Gerecse Mts (Hungary) (Appendix: *Pseudolillia paralleliformis* nov. sp.). *Földtani Közlöny* 143, 123–144 (in Hungarian with English abstract).

Kovács Z. 2014: Toarcian Dactylioceratidae (Ammonitina) from the Gerecse Mts (Hungary). *Hantkeniana* 9, 45–77.

Kovács Z., Dunai M. & Evanics Z. 2020: Toarcian (Jurassic) Ammonitina fauna and stratigraphy from Bakonycsernye (Hungary). *Revue de Paléobiologie* 39, 141–181. https://doi.org/10.5281/zenodo.3936163

Krimholz G.Y. & Tazikhin N.N. 1957: New data concerning the stratigraphy of the Jurassic deposits of the Vilyui syncline. *Doklady Akademii Nauk SSSR* 116, 129–130 (in Russian)

Lacroix P. 2011: Les Hildoceratidae du Lias moyen et supérieur des domaines NW européen et téthysien. Une histoire de famille. *Chirat*, St-Just-La-Pendue, 1–659.

Lóczy L. von (Ed.) 1910: Führer durch das Museum der kön. ungar. Geologischen Reichsanstalt. *Kilian*, Budapest, 1–347.

Lycett J. 1860: On the sands intermediate the Inferior Oolite and Lias of the Cotteswold Hills, compared with a similar deposit upon the coast of Yorkshire. *Proceedings of the Cotteswold Naturalists' Field Club, Gloucester* 2, 142–149.

Macchioni F. & Cecca F. 2002: Biodiversity and biogeography of middle-late liassic ammonoids: implications for the Early Toarcian mass extinction. *Geobios Mémoire spécial* 24, 165–175. https://doi.org/10.1016/S0016-6995(02)00057-8

Maubeuge P.L. 1950: Nouvelles reserches stratigraphiques et paléontologiques sur l'Aalénien luxembourgeois. *Archives de la Section des Sciences naturelles, physiques et mathématiques de l'Institut Grand-Ducal de Luxembourg* 19, 365–397.

Meister E. 1913: Zur Kenntnis der Ammonitenfauna des portugiesischen Lias. *Zeitschrift der deutschen geologischen Gesellschaft* 65, 518–586.

Metodiev L. 2002: *Grammoceras*, *Pseudogrammoceras* et *Podagrosites* (Grammoceratinae, Ammonitina) du Toarcien supérieur dans la région du Balkan (Bulgarie). Taxonomie et biostratigraphie. *Geologica Balcanica* 32, 2–4, 165–189.

Metodiev L. 2008: The Ammonite zones of the Toarcian in Bulgaria – New evidence, subzonation and correlation with the standard zones and subzones in North-Western Europe. *Comptes rendus de l'Académie bulgare des Sciences* 61, 87–132.

Monostori M. 2008: Comparative study of the Pliensbachian and Toarcian ostracods in the Gerecse and Mecsek Mountains, Hungary. *Hantkeniana* 6, 17–31.

Moxon C. 1841: Illustrations of the characteristic fossils of British strata. *Bailliere*, London, 1–46.

Müller T., Price G.D., Bajnai D., Nyerges A., Kesjár D., Raucsik B., Varga A., Judik K., Fekete J., May Z. & Pálfy J. 2017: New multiproxy record of the Jenkyns Event (also known as the Toarcian Oceanic Anoxic Event) from the Mecsek Mountains (Hungary): Differences, duration and drivers. *Sedimentology* 64, 66–86. https://doi.org/10.1111/sed.12332

Müller T., Karancz Sz., Mattioli E., Milovský R., Pálfy J., Schlögl J., Segit T., Šimo V. & Tomašových A. 2020: Assessing anoxia, recovery and carbonate production setback in a hemipelagic Tethyan basin during the Toarcian Oceanic Anoxic Event (Western Carpathians). *Global and Planetary Change* 195, 10336617. https://doi.org/10.1016/j.gloplacha.2020.103366

Müller T., Price G.D., Mattioli E., Leskó M.Z., Kristály F. & Pálfy J. 2021: Hardground, gap and thin black shale: spatial heterogeneity of arrested carbonate sedimentation during the Jenkyns Event (T-OAE) in a Tethyan pelagic Basin (Gerecse Mts, Hungary). *Geological Society, London, Special Publications* 514, 269–289. https://doi.org/10.1144/sp514-2020-266

Nagy E. 1968: A Mecsek hegység triászidőszaki képződményei (Triasbildungen des Mecsek-Gebirges). *Annals of the Hungarian Geological Institute* 51, 1–198.

Nagy I., Hámor G., Hetényi R., Bilik I. & Földi M. 1978: Magyarázó a Mecsek hegység földtani térképéhez, 10.000-es sorozat. Kisújbánya [Explanations to the Geological Map of the Mecsek Hills, Scale 1:10.000, Kisújbánya]. *Magyar Állami Földtani Intézet*, Budapest, 1–88.

Neumayr M. 1875: Die Ammoniten der Kreide und die Systematik der Ammonitiden. *Zeitschrift der Deutschen geologischen Gesellschaft* 27, 854–942.

Noszky J. 1952: Conditions géologiques du territoire houiller des environs de Komló. *Rapport Annuel de l'Institut géologique de Hongrie sur l'année 1948*, 65–77 (in Hungarian with French and Russian abstracts).

Page K.N. 2003: The Lower Jurassic of Europe: its subdivision and correlation. *Geological Survey of Denmark and Greenland Bulletin* 1, 23–59. https://doi.org/10.34194/geusb.v1.4646

Page K.N. 2004: A sequence of biohorizons for the Subboreal Province Lower Toarcian in northern Britain and their correlation with a Submediterranean Standard. *Rivista Italiana di Paleontologia e Stratigrafia* 110, 109–114. https://doi.org/10.13130/2039-4942/6274

Page K.N. 2008: The evolution and geography of Jurassic ammonoids. *Proceedings of the Geologists' Association* 119, 35–57. https://doi.org/10.1016/S0016-7878(08)80257-X

Pataki N., Józsa S. & Dunkl I. 1982: The Jurassic sequence of Coal Valley (Kohl-Thal) at Ófalu. *Földtani Közlöny* 112, 383–394 (in Hungarian with English abstract).

Peters K.F. 1863: Über den Lias von Fünfkirchen. *Sitzungsberichte der Akademie der Wissenschaften mathematisch-naturwissenschaftliche Klasse* 46, 241–293.

Popa E. & Patrulius D. 1996: Lower Jurassic Ammonites in the Romanian Carpathians. *Memoirs of the Geological Institute of Romania* 36, 53–63.

Rakús M. 1964: Paläontologische Studien im Lias der Grossen Fatra und des Westteils der Niederen Tatra. *Sborník Geologických Vied, Západné Karpaty* 1, 95–156.

Raucsik B. & Varga A. 2008: Climato-environmental controls on clay mineralogy of the Hettangian–Bajocian successions of the Mecsek Mountains, Hungary: An evidence for extreme continental weathering during the early Toarcian oceanic anoxic event. *Palaeogeography, Palaeoclimatology, Palaeoecology* 265, 1–13. https://doi.org/10.1016/j.palaeo.2008.02.004

Ridente D. 2016: Heterochrony and evolution in some Toarcian ammonites. Speculations and insights. *Journal of Mediterranean Earth Sciences* 8, 25–37. https://doi.org/10.3304/JMES.2016.002

Ruebsam W., Müller T., Kovács J., Pálfy J. & Schwark L. 2018: Environmental response to the early Toarcian carbon cycle and climate perturbations in the northeastern part of the West Tethys shelf. *Gondwana Research* 59, 144–158. https://doi.org/10.1016/j.gr.2018.03.013

Rulleau L. 2007: Biostratigraphie et paleontologie du Lias supérieur et du Dogger de la région lyonnaise, Tome 1. *Section Géologie et Paléontologie du Comité d'Enterprise Lafarge Ciments*, Lozanne, 1–382.

Rulleau L. 2009: Les Hammatoceratidae et les Erycitidae NW européens et tethysiens du Lias et du Dogger. *Section Géologie et Paléontologie du Comité d'Enterprise Lafarge Ciments*, Lozanne, 1–285.

Rulleau L., Lacroix P., Bécaud M. & Pichon J.-P. 2013: Les Dactylioceratidae du Toarcien inférieur et moyen. Une famille cosmopolite. *Diffusion Dédale Éditions*, Lyon, 1–242.

Rulleau L., Lacroix P. & Pichon J.-P. 2015: Révision des Phymatoceratinae (Hildoceratidae, Ammonitina) du Toarcien moyen et supérieur en France et dans le monde. *Diffusion Dédale Éditions*, Lyon, 1–351.

Rulleau L., Lacroix P., Le Pichon J.-P. & Ové F. 2020: Les Grammoceratinae du Toarcien supérieur. *Diffusion Dédale Éditions*, Lyon, 1–292.

Schindewolf O.H. 1964: Studien zur Stammesgeshichte der Ammoniten. *Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse der Akademie der Wissenschaften und der Literatur, Mainz* 1963, 287–432.

Schirardin J. 1914: Der Obere Lias von Barr-Heiligenstein. *Mitteilungen des Geologischen Landesanstalt von Elsass-Lothringen* 8, 339–448.

Schmidt-Effing R. 1972: Die Dactylioceratidae, eine Ammoniten Familie des unteren Jura. *Münstersche Forschungen zur Geologie und Paläontologie* 25, 1–255.

Schröder J. 1927–1928: Die Ammoniten der jurassichen Fleckenmergel in den Bayrischen Alpen. *Palaeontographica* 68, 111–232, 1–110.

Schulbert C. 2001: Die Ammonitenfauna und Stratigraphie der Tongrube Mistelgau bei Bayreuth (Oberfranken). *Beihefte zu den Berichten der Naturwissenschaftlichen Gesellschaft Bayreuth* 4, 1–83.

Seyed-Emami K., Fürsich F.T., Wilmsen M., Schairer G. & Majidifard M.R. 2005: Toarcian and Aalenian (Jurassic) ammonites from the Shemshak Formation of the Jajarm area (eastern Alborz, Iran). *Paläontologische Zeitschrift* 79, 349–369. https://doi.org/10.1007/BF02991928

Simpson M. 1843: A monograph of the ammonites of the Yorkshire Lias. *Simpkin, Marshall, and Co.*, London, 1–60.
Sowerby J. 1812–1822: The Mineral Conchology of Great Britain. *Benjamin Meredith*, London. 1 (1812): 234 p., pls 1–9; (1813) pls 10–44; (1814) pls 45–78; (1815) pls 79–102. 2 (1815): 251 p., pls 103–114; (1816) pls 115–150; (1817) pls 151–186; (1818) pls 187–203. 3 (1818): 194 p., pls 204–221; (1819) pls 222–253; (1820) pls 254–271; (1821) pls 272–306. 4 (1821) 160 p., pls 307–318; (1822) pls 319–383.
Spath L.F. 1929: Corrections of cephalopod nomenclature. *The Naturalist* 871, 269–271.
Spath L.F. 1936: On Bajocian Ammonites and Belemnites from Eastern Persia (Iran). *Palaeontologia Indica* [n. s.] 22, 1–21.
Storm M.S., Hesselbo S.P., Jenkyns H.C., Ruhl M., Ullmann C.V., Xu W., Leng M.J., Riding J.B. & Gorbanenko O. 2020: Orbital pacing and secular evolution of the Early Jurassic carbon cycle. *Proceedings of the National Academy of Sciences* 117, 3974–3982. https://doi.org/10.1073/pnas.1912094117
Thierry J. & Barrier E. 2000: Middle Toarcian. In: Dercourt J. et al. (eds): Atlas Peri-Tethys, Paleogeographic Maps. *CCGM/CGMW*, Map 8.
Vadász E. 1914: A Zengővonulat és a környező dombvidék földtani viszonyai. *A Magyar királyi Földtani Intézet Évi Jelentése az 1913. évről*, 336–352.
Vadász E. 1935: A Mecsekhegység. (Das Mecsek-Gebirge.) Magyar tájak földtani leírása (Geologische Beschreibung ungarischer Landschaften) I. Budapest, 1–180.
Waagen W.H. 1869: Die Formenreihe des *Ammonites subradiatus* versuch einer Palaontologischen Monographie. In: Benecke E.W.: *Geognostisch-Paläontologische Beitrage* 2, 2. Oldenbourg, München, 179–256.
Wierzbowski A., Krobicki M. & Matyja B. 2012: The stratigraphy and palaeogeographic position of the Jurassic successions of the Priborzhavske-Perechin Zone in the Pieniny Klippen Belt of the Transcarpathian Ukraine. *Volumina Jurassica* 10, 25–46.
Young G. & Bird J. 1828: A geological survey of the Yorkshire Coast. Sec. ed., *Kirby*, Whitby, 1–360.