

## Rediscovery of a classic Middle Triassic fossil site of the Balaton Highland (Transdanubian Range, Hungary): cephalopods, brachiopods and vertebrate remains from the Akol Hill at Barnag

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### *A Balaton-felvidék egyik klasszikus középső triász ősmaradvány-lelőhelyének újrazvizsgálata: a barnagi Akol-domb cephalopoda-, brachiopoda- és gerinces faunája*

#### Összefoglalás

A jelen cikk a Balaton-felvidék talán legrégebb óta ismert, ugyanakkor eddig részletes feldolgozás nélkül maradt középső triász ősmaradvány-lelőhelyének ammonitesz-, brachiopoda- és gerinces faunáját ismerteti, kitérve annak rétegtani és ökoszisztémái jelentőségére is.

A barnagi Akol-domb (1. és 2. ábra) a Balaton-felvidék klasszikus ősmaradvány-lelőhelye, amely Böckh Jánosnak, a Bakony úttörő földtani térképezőjének az 1870-es években végzett felvételezése idején már évek óta ismert volt. A „nagyvászsonyi lelőhely” Mojsisovics klasszikus munkáiban is szerepel, több ammonitesz-fajt innen írt le először. Lóczy monográfiájában szintén tett említést a lelőhelyről, és az addig gyűjtött faunát is közölte. Ezt követően a lelőhelyről újabb őslénytani adatok csak szórványosan kerültek elő, részben a Bakony, részben a Balaton-felvidék földtani térképezéséhez kapcsolódóan. Az elmúlt években zajló gyűjtések során azonban olyan új és gazdag cephalopoda-, brachiopoda- és gerinces fauna került elő a terület anisusi rétegsorából, amelynek vizsgálata alapján több szempontból is árnyaltabb kép rajzolható a terület középső triász ökoszisztémái viszonyairól.

Az Akol-dombon és környékén a felszínre bukkanó legidősebb triász képződmény az alsó anisusi Megyehegyi Dolomit (2. és 3. ábra), amelyben viszonylag gyakoriak a krinoidea váztöredékek (4. ábra, a). Fölötte 1–2 méter vastag, világosszürke mészkő következik, amelyre jellemzőek a bekérgezett szemcsék, de elvétve brachiopoda és apró ammonitesz is előfordul benne (4. ábra, b). Ez a sekélytengeri platform fáciesű Tagyoni Formáció, amely a Balaton-felvidék középső anisusi medence kifejlődését, a Felsőörsi Mészkövet helyettesíti heteropikusan (1. ábra). A formáció azonban lényegesen vékonyabb az Akol-domb környékén (Barnagi-platform), mint a Balaton-felvidék középső részén (Tagyoni-platform), illetve a Veszprémi-fennsík (Kádártai-platform), ahol vastagsága eléri a 80–100 métert is.

A Tagyoni Formáció fölött települ a Vászolyi Formáció 2–3 méter vastag, biogén mészkőből álló rétegsora (4. ábra, c–d), ebből került elő a cikk tárgyát képező szokatlanul gazdag ősmaradvány-együttes. Az árkolásban feltárt rétegsor alsó két padját lilás szürke, kemény mészkő alkotja, fölötte vörös, sárgafoltos, gumós mészkő következik alsó szakaszán fekete vasas-mangános bevonatú ősmaradványokkal. A fauna döntő részét ammoniteszek alkotják, amelyek kőzetalkotó mennyiségben jelennek meg. A megtartási állapotra jellemző, hogy a túlnyomó részben héjas példányok egyik oldala részben vagy teljesen visszaoldott, ami lassú, kondenzált üledékképződésre utal. A példányok jelentős része töredékesen ágyazódott be, ami felveti az áthalmazódás lehetőségét. A fauna jellegzetes elemei (pl. *Proavites hueffeli*, *Beyrichites cadoricus*) (1. tábla) a pelsoi Balatonicus Zóna felsőbb részéből ismertek. A legnagyobb példányszámban, és legjobb megtartási állapotban az illyri Trinodosus Zóna legfőbb szubzónáját igazoló *Lardaroceras*-fajok (II. tábla 5–8; III. tábla) kerültek elő. A számos *Kellnerites* példány (IV. tábla) a Reitzi Zóna jelenlétét bizonyítja. A Barnagi-platform megfulladása tehát már a pelsoi korszak során bekövetkezett (Balatonicus Zóna). A Balaton-felvidéki középső anisusi platformokon települő legidősebb medencefáciesű üledékek korábbi biosztratigráfiai vizsgálatai szerint ugyanakkor a Tagyoni- és a Kádártai-platform ebben az időben még aktívan épült, megfulladásuk csak később, az illyri közepén következett be (Trinodosus Zóna, Camunum szubzóna).

A barnagi Akol-dombon az ammoniteszek mellett nautiloideák, brachiopodák (VII. tábla), elvétve csigák és gerinces maradványok fordulnak elő. Utóbbiak között (VIII. tábla) vannak halmaradványok: egy Hybodontoida úszótövis, egy *Polyacrodus* sp., valamint egy közelebről meg nem határozható cápa fog, továbbá *Birgeria* sp. fogmaradványa. Ezek megtartása és kis száma, valamint az e taxonokkal kapcsolatos ismeretek hiányosságai nem teszik lehetővé ökoszisztémái következtetések levonását. Ugyanakkor tengeri hiüllök maradványai is előkerültek, négy Ichthyosauria-csigolya, egy szintén halgyíktól származó fogtöredék és egy bordatöredék. A csigolyák közül egy háti csigolya cf. *Cymbospondylus* sp.-ként

sorolható be – a diapophysis helyzete és alakja alapján, míg a másik három feltételesen sorolható a középső triászban gyakori Cymbospondyliidae családba. A csigolyák legalább két, körülbelül 3,3 m illetve 4,5 m testhosszúságú egyedtől származhatnak, míg a fogtöredék egy akár ennél is nagyobb példánytól. A Cymbospondyliidae-család tagjai világszerte elterjedtek voltak az anisusiban és a ladinban, előfordulásuk a Balaton-felvidéki tengeralatti hátságok környékén egyáltalán nem meglepő, ugyanakkor a család első hazai előfordulását jelentik.

*Kulcsszavak: középső triász platform, cephelopodák, brachiopodák, tengeri hüllők, halak*

## Abstract

Recent collecting of the classic Middle Anisian site of the Akol Hill at Barnag (Nagyvázsony Plateau, Balaton Highland) yielded abundant fossils and significant new palaeontological data. The Middle Anisian platform carbonate succession (Tagyon Formation) is overlain by 2–3 m thick red, nodular, crinoidal limestone (Vászoly Formation) that contains a very rich fossil assemblage with ammonoids, nautiloids and brachiopods. The ammonoid fauna of the lower thin limestone bed above the Tagyon Formation contains elements reworked from the Balatonicus Zone. The overlying beds contain a rich early Illyrian ammonoid fauna which is more diverse than the equivalent faunas of the Tagyon and Kádárta Platforms. The ammonites of the Balatonicus Zone in the basal part of the Vászoly Formation prove that the drowning of the Barnag Platform occurred already during the Pelsonian, earlier than in the case of the Tagyon and the Kádárta Platforms where the oldest deeper marine sediments above the drowning surface are mid-Illyrian (Camunum Subzone of the Trinodosus Zone).

Some vertebrate fossils were also found in the Vászoly Formation. Besides ichthyosaurian remains, such as four vertebrae, a piece of a rib and a tooth crown fragment, as well as fish remains have been found. This locality provided the first known occurrence of the ichthyosaur *Cymbospondylus* in the Middle Triassic of the Balaton Highland. This predatory marine reptile probably dwelled mostly in deep marine environments but also might have been well adapted for hunting in shallow environments of submarine highs.

*Keywords: Middle Triassic platform, cephalopods, brachiopods, marine reptiles, fishes*

## Introduction

The Middle Triassic ammonoid fauna of the Akol Hill, north of Barnag is one of the oldest known fossil sites of the Balaton Highland. The first brief palaeontological review of the ammonite fauna at “Vaszony” was given by HAUER (1866). The stratigraphic succession and the collected fossil-assemblage of the “Nagy-Vázsony” site was published later by BÖCKH (1872, pp. 78–79) during the first detailed geological mapping project of the South Bakony. He already identified that the fossiliferous red yellow-spotted limestone succession, which was exposed in small abandoned quarries at that time, is underlain by dolomite (“megyehegy dolomite”) and is overlain by red cherty nodular limestone (“Tridentinus limestone” = Buchenstein Formation, in modern terms). MOJSISOVICS (1882) described and illustrated several ammonite species from the Nagyvázsony site. LÓCZY (1913, p. 93) mentioned this site as Kiserdőhegy at Magyarbarnag in his monograph and gave a list of the collected brachiopods and ammonoids. BÖCKH and LÓCZY classified this ammonite-bearing “barnag limestone” as “alpine Muschelkalk” of the Balaton Highland (=Felsőors Formation, in modern terms); however, they noted the lithological differences between the two lithofacies.

The next period of investigation of the area was related to uranium exploration in the Balaton Highland in the late 1960s. Trenches were excavated and boreholes were drilled to obtain more information about the Triassic succession. SZABÓ (1971) briefly described what he called “ammonitico rosso”-type Upper Anisian limestone of the Barnag area and correlated it with the strongly condensed “Bulog limestone” of Hydra Island in Greek. Later, these data were taken into

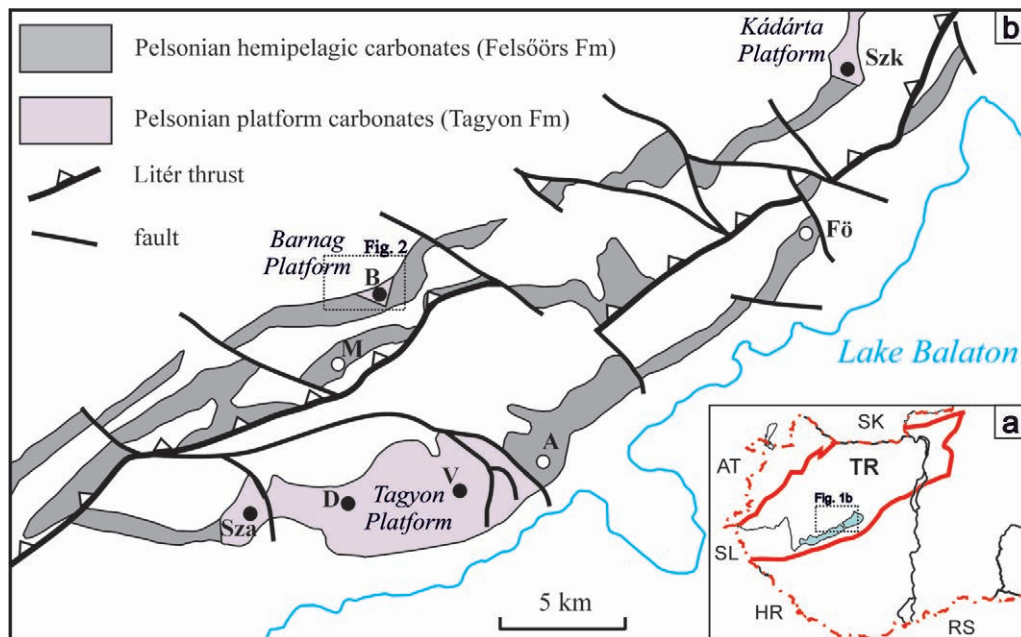
account in the geological mapping project of the Bakony Mountains. The Middle Triassic formations of the Nagyvázsony area were described by SZABÓ based on artificial trenches and the cores of Nagyvázsony Nv–11 and Barnag Bg–1 (SOLTI & SZABÓ 1975).

During the most recent detailed mapping project of the Balaton Highland, the Nagyvázsony area was revisited. The geological profile of the Akol Hill was presented by BUDAI & CSILLAG (1998) while the collected poor ammonoid fauna was inventoried by VÖRÖS (1998). Based on the stratigraphic and sedimentologic studies of the different Middle Anisian lithofacies of the Balaton Highland, the Akol Hill area was interpreted as a part of an isolated platform (earlier it was named as Vöröstó Platform, here it is referred to as the Barnag Platform, *Figure 1, b*) that was formed by extensional tectonics in the Pelsonian and later was drowned during the Late Anisian (VÖRÖS et al. 1997, BUDAI et al. 1999b, BUDAI & VÖRÖS 2006).

During the last two years, a new exploration was performed at the Akol Hill by amateur collectors (co-authors of this paper), and a well-preserved, abundant and highly diverse ammonoid assemblage was collected, containing also previously unknown forms, together with vertebrate fossils. In this paper we present these new palaeontological results together with some considerations on the platform evolution.

## Geological setting

The Barnag area is situated on the Nagyvázsony Plateau that belongs to the northern part of the Balaton Highland (*Figure 1, a*). The Balaton Highland forms the south-eastern



**Figure 1.** a) Position of the geological map (b) in the Transdanubian Range Unit (TR); b) Areal extent of the Middle Anisian–Ladinian formations of the Balaton Highland, distinguishing the areas where the Middle Anisian is represented by shallow marine platform carbonates (Pelsonian platforms) and/or hemipelagic basinal carbonates (after BUDAI & VÖRÖS 2006). Rectangle shows the position of the geological map of Figure 2. A – Aszófő, Pelsonian stratotype section; B – Barnag, Akol Hill; D – Dörgicse, Drt-1 drill core; Fö – Felsőörs, stratotype section; M – Mentshely, Cser Hill; Sza – Szentantalfa; Szk – Szentkirályszabadja, military airport; V – Vászoly, Öreg Hill

**I. ábra.** a. Az 1b. ábrán szereplő földtani térkép helyzete a Dunántúli-középhegységi-egység (TR) területén. b. A középső anisusi – ladin képződmények elterjedése a Balaton-felvidéken, eltérő színnel jelezve azokat a területeket, ahol a középső anisusi rétegsort platform-karbonát (pelsoi platformok), illetve medencekifejlődés alkotja (BUDAI & VÖRÖS 2006 nyomán). A pontozott vonalú négyyszög a 2. ábrán szereplő földtani térkép helyzetét mutatja

limb of the SW–NE oriented syncline structure of the Transdanubian Range where the most significant compressional Alpine structure is the Litér thrust (Figure 1, b).

The Nagyvázsöny Plateau is situated north of the Litér thrust (Figure 1, b) where the Triassic rocks crop out in relatively small patches from below Upper Miocene lacustrine sediments and Quaternary deposits (Figure 2). The area is very poorly exposed but some small artificial pits and trenches allow the Triassic succession to be studied. The general dip of the Triassic formations is about 20° to the W–NW.

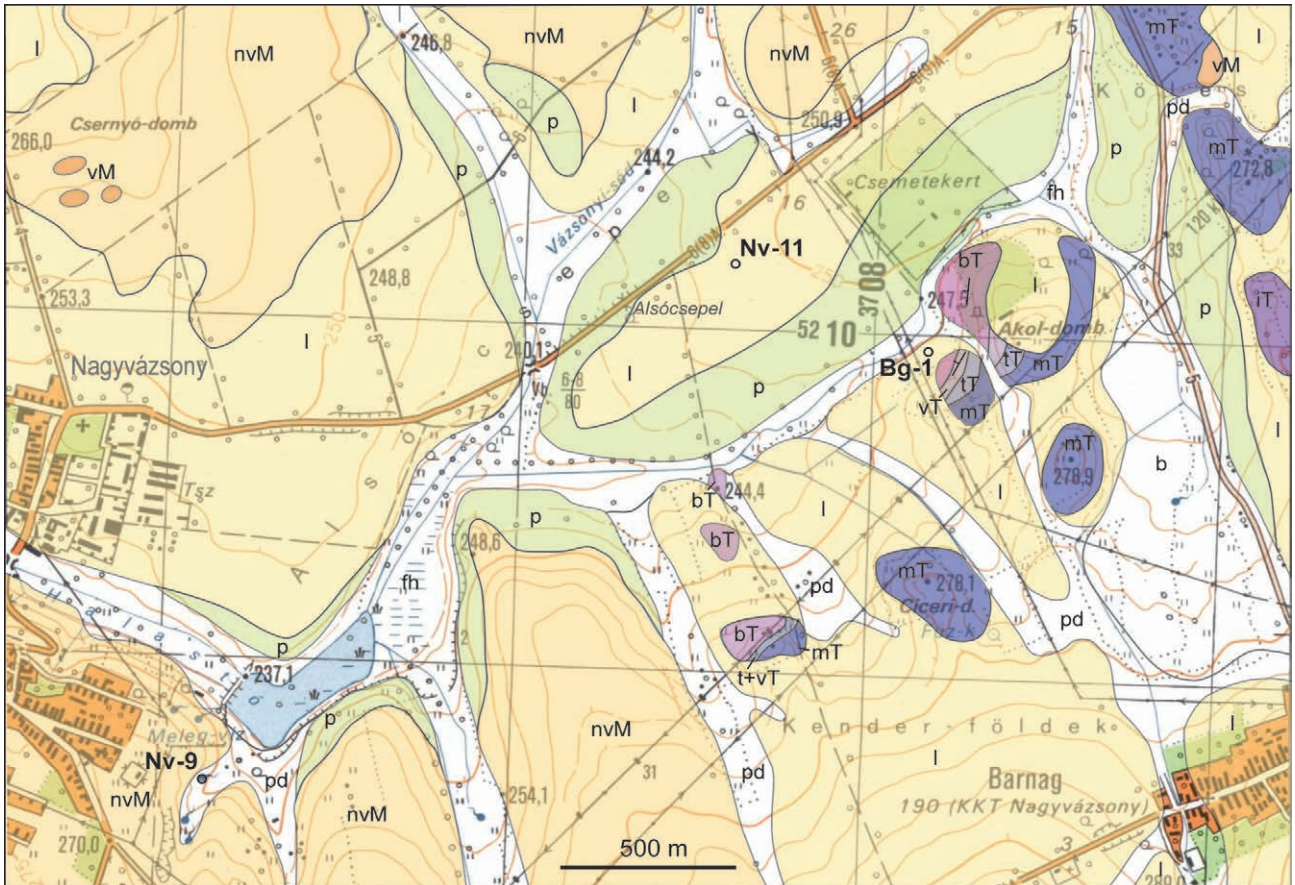
Two facies types are distinguished in the Middle Anisian succession of the Nagyvázsöny–Barnag area (Figure 1, b). In the major part of the area hemipelagic basinal succession of the Felsőörs Limestone occurs, which was penetrated by several boreholes at Nagyvázsöny (Nv–9) and between Vöröstó and Barnag (Vöt–1, Vöt–2 and Vöt–8;), close to the southern edge of the map (Figure 2). In this area of the Nagyvázsöny Plateau the Felsőörs Formation crops out at the Cser Hill (Cser-tető), between Mentshely and Nagyvázsöny (site M in Figure 1, b), where it has previously been studied in detail (BUDAI et al. 1991, VÖRÖS & BUDAI 1993, VÖRÖS 1998, VÖRÖS et al. 2003, VÖRÖS 2018). The thickness of the formation reaches 20–30 m.

North of Barnag, at the Akol Hill and in its surroundings (site B in Figure 1, b), the Felsőörs Formation is missing (Figure 2). Here, the Middle Anisian succession consists of the shallow marine carbonate sequence of the Tagyon

Formation. Combination of our field observations at the Akol Hill and drill core data made the reconstruction of the stratigraphic column of the area possible (Figure 3). Based on the geological description (SOLTI & SZABÓ 1975), the site of the Nagyvázsöny Nv–11 borehole that penetrated the Lower Anisian–Ladinian succession was near Alsócsapel, whereas the Barnag Bg–1 borehole was drilled at the west side of the Akol Hill (Figure 2).

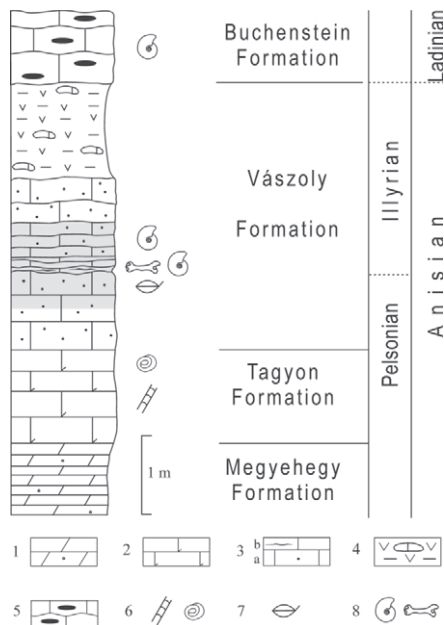
The lowermost part of the Middle Triassic succession of the Akol Hill is represented by a thin-bedded, slightly bituminous grey dolomite (Megyehegy Dolomite – mT) containing a few crinoid fragments (Figure 4, a). It is overlain by a 1–2 m-thick limestone, which contains microbially coated grains and a shallow marine microfossil assemblage. Minute brachiopods and embryonic ammonites also occur scarcely. A characteristic bioclastic, oncoidal boundstone microfacies type is displayed in Figure 4, b. Based on the sedimentary features and the Dasycladalea flora near Tótvázsony (*Physoporella pauciforata*, *Oligoporella*, det. PIROS O. in BUDAI & CSILLAG 1998) this Pelsonian platform carbonate succession can be assigned to the Tagyon Formation (tT in Figure 2).

The Tagyon Formation is overlain by a purple-grey or red, yellow-spotted limestone. It contains a very rich fossil assemblage with ammonoids, nautiloids, gastropods and crinoid fragments, locally in rock-forming quantity. Characteristic microfacies types (bioclastic wackestones and/or



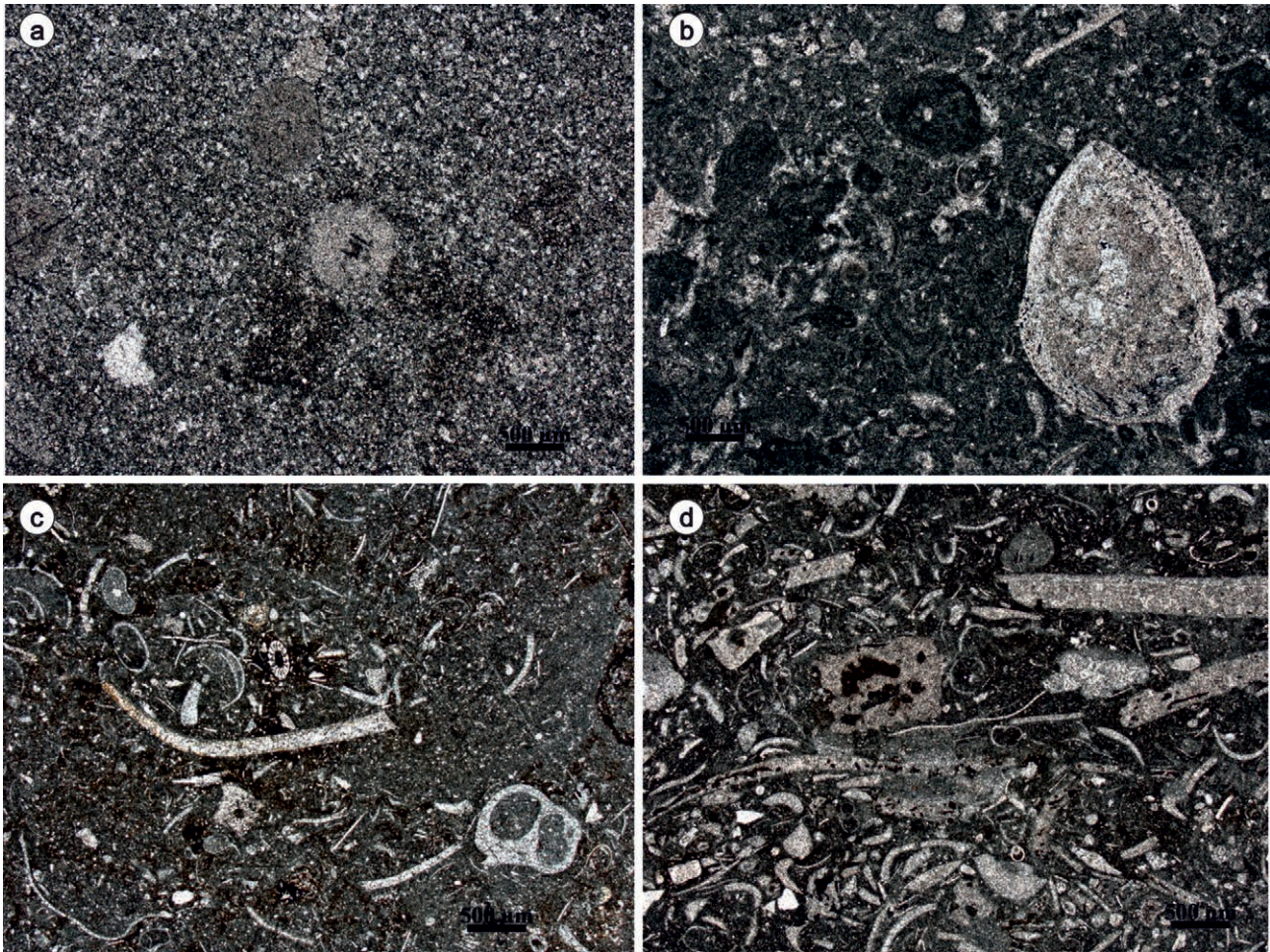
**Figure 2.** Geological map of the Akol-domb (Akol Hill) area, north of Barnag (based on unpublished manuscript map of I. SZABÓ, G. SOLTI and G. CSILLAG and the geological map of the Balaton Highland, BUDAI et al. 1999a). Locality of the collection site is marked by dip sign in the SW part of the Akol Hill. Quaternary sediments: b - paludal; fh - fluvial; p - proluvial; pd - proluvial-déluvial; l - loess.; Miocene sediments: nvM - freshwater limestone (Nagyvázasony Fm); vM - bauxitic red clay (Vöröstó Fm). Middle Triassic formations: iT - Iszkahegy Limestone Fm (Lower Anisian); mT - Megyehegy Dolomite Fm (Lower Anisian); tT - Tagyon Fm (Middle Anisian); vT - Vászolyi Fm (Middle-Upper Anisian); bT - Buchenstein Fm (Ladinian)

**2. ábra.** A barnagi Akol-domb környezetének földtani térképe (SZABÓ I., SOLTI G. és CSILLAG G. kéziratoss térképe, valamint BUDAI et al. 1999a nyomán). A begyűjtött feltárás helyét dőlés jel mutatja az Akol-domb DNy-i részén. Kvarter képződmények: b - mocsári; fh - fluvialis; p - proluviális; pd - proluviális-déluviális; l - lösz. Miocén képződmények: nvM - édesvízi mészkő (Nagyvázasonyi F.); vM - bauxitos vörös agyag (Vöröstói F.). Középső triász formációk: iT - Iszkahegyi Mészkő F. (alsó anisusi); mT - Megyehegyi Dolomit F. (alsó anisusi); tT - Tagyoni F. (középső anisusi); vT - Vászolyi F. (középső - felső anisusi); bT - Buchenstein Fm (ladin)



**Figure 3.** Stratigraphic column of the Middle Triassic succession of the Akol Hill area (based on the geological profile by BUDAI & CSILLAG 1998 and data of Nagyvázasony Nv-11 and Barnag Bg-1 drilled cores). The stratigraphic position of the newly exposed and collected section is marked by grey shading. 1. dolomite, crinoidal dolomite; 2. oncoidal limestone; 3. a. massive crinoidal limestone, b. nodular limestone with dark Fe-Mn coating; 4. tuffitic clay with limestone nodules; 5. bedded nodular limestone with chert; 6. green algae; oncoids; 7. brachiopods; 8. ammonites, vertebrate remains

**3. ábra.** Az Akol-domb középső triász képződményeinek rétegoszlopa (BUDAI & CSILLAG 1998 földtani szelvénye, valamint a Nagyvázasony Nv-11 és a Barnag Bg-1 fúrás rétegsora alapján). Az újonnan feltárt és gyűjtött szelvény rétegtani helyzetét szürke kiemelés jelzi a rétegoszlopon. 1. dolomit, krinoideás dolomit; 2. onkoidos mészkő; 3. a. tömör krinoideás mészkő, b. gumós mészkő, vasas-mangános fekete bekérgezéssel; 4. tufás agyag mészkő-gumókkal; 5. pados, gumós tüköves mészkő; 6. zöldalga; onkoid; 7. brachiopoda; 8. ammonitesz, gerinces maradvány



**Figure 4.** Characteristic microfacies of the Middle Triassic formations of the Akol Hill (photomicrographs and description by J. HAAS). a) finely crystalline dolomite (Megyehegy Fm) with recognisable remnants of crinoids; b) boundstone (Tagyon Fm); bioclasts (a brachiopod and fragments of thin-shelled bivalves), oncooids and microbial nodules occur in micritic matrix (automicrite) and finely crystalline mosaic calcite cement fills in the small pore; c) bioclastic wackestone (Vászoly Fm) with fragments of thin-shelled bivalves, gastropods, ostracods, and a holothurian sclerite; d) wackestone-packstone (Vászoly Fm) with mm-sized fragments of molluscs, thin-shelled bivalves, ostracods and crinoids (traces of bioerosion are visible on some of the thick mollusc shells and a crinoid ossicle)

**4. ábra.** Az Akol-domb középső triász formációinak jellemző mikrofaciése (fotó és szöveg: HAAS J.). a) finomkristályos dolomit (Megyehegyi F.), crinoidea vázelemekkel; b) boundstone (Tagyoni F.), a mikrites mátrixban bioklasztok (egy brachiopoda-metszet és vékony héjú kagylótöredékek), onkoidok és mikrobiális gumók fordulnak elő; c) bioklasztos wackestone (Vászolyi F.) vékony héjú kagylók töredékeivel, csigákkal, ostracodákkal és holothuroidea szklerittel; d) wackestone-packstone (Vászolyi F.), vékony héjú kagylók, ostracodák és crinoideák mm-es nagyságú töredékeivel (egy molluszka vastag héjú töredékén és egy crinoidea-vázelemen bioeróziós nyomok láthatók)

packstones) are shown in *Figure 4, c–d*. The ammonites are commonly partly dissolved and have a blackish Fe-Mn encrustation. This sequence is assigned to the lower part of the Vászoly Formation (vT in *Figure 2*), which is widespread and well-documented in the Balaton Highland (VÖRÖS et al. 1997, BUDAI et al. 1999b) and on the Veszprém Plateau (BUDAI et al. 2001). Tuffitic layers, that typically occur in the Vászoly Formation elsewhere, are subordinate in the Akol Hill area.

To collect fossils, a shallow trench was excavated at the southwestern corner of a small forest on the Akol Hill (coordinates: N46°59.419'; E17°44.180'), and a shallow pit was also excavated a few metres away in dip direction. The stratigraphic log of the investigated section is presented in *Figure 3*. The lowermost two layers of the succession consists of purple-red, hard limestone. This is overlain by

clayey, yellow spotted limestone in a thickness of about 10 cm, pinching out within the outcrop, characterized by black iron-manganese crusts and coatings on fossils (*Figure 5*). More massive, red, purple-red, yellow spotted limestone was also exposed in the shallow pit (*Figure 6*). Similar limestones, which likely represent a somewhat higher part of the Vászoly Formation, were excavated in another pit to the north from the shallow pit. There is no continuity between the two exposures.

The red siliceous cherty nodular bedded limestone above the Vászoly Formation is assigned to the Ladinian Buchenstein Formation (bT in *Figure 2*). This unit was quarried in small pits on the Akol Hill and was penetrated in a thickness of 10 m by the Nagyvázsöny Nv-11 drill core (SOLTI & SZABÓ 1975). Triassic units younger than Ladinian are not known in the Akol Hill area.



**Figure 5.** Typical slab from the condensed bed of Akol Hill Section. Yellowish-red, clayey limestone (Vászoly Fm) with ferro-manganese crusts and coatings on fossils (*Beyrichites cadoricus* and a nautilid).

5. ábra. Jellegetes kézipéldány az Akol-domb szelvényének kondenzált rétegéből. Sárgás-vörös, agyagos mészkő (Vászolyi F.) vas-mangán kérgekkel és bekérgezett ősmaradványokkal (*Beyrichites cadoricus* és egy nautilida)



**Figure 6.** Typical bedding surface of the yellow spotted red limestone (Vászoly Fm) with partly dissolved ammonite shells (size of the slab is 25×15 cm)

6. ábra. A vörös, sárga foltos mészkő (Vászolyi F.) jellegetes rétegfelvétele felül visszaidott ammonitesz vázak tömegével (a kézipéldány mérete 25×15 cm)

## Material and methods

Recent collecting efforts by private collectors G. FÖLDVÁRI, M. BERCSÉNYI and Zs. PINTÉR produced abundant fossils and a wealth of new palaeontological data from the Vászoly Formation in the locality of Akol Hill. Ammonoids were found in the greatest number (342 specimens); other cephalopods were represented by 35 specimens, and brachiopods by 25 specimens. A few specimens of gastropods and echinoderms were also encountered. Special attention

was given to the rare vertebrate fossils: three fish teeth and six pieces of reptile remains were found.

The collectors worked in three different excavations separated by about ten metres distance. Some of these pits exposed distinct limestone layers with different fossil contents; these layers were traced along their strike but in dip direction the sequence of beds was not recorded.

Because of the poor exposure and the perturbation caused by the previous quarrying activities, a systematical bed-by-bed collecting was not possible, although certain trends could be recognized in the ammonite succession.

Partly for this reason, a comprehensive taxonomical analysis of the invertebrate fauna was not intended in the present paper. Our aim was only to give overall information on this extraordinarily large and well-preserved fossil material. Therefore, we selected the most representative specimens from the invertebrate assemblages: 38 ammonoid, eight other cephalopod, and four brachiopod specimens were identified at the species level, and were illustrated by photographs. This limited selection from the studied material represents a diverse invertebrate fauna, comprising 17 ammonoid, 8 other cephalopod and 3 brachiopod taxa. Nevertheless, this database is inadequate for detailed studies on taxonomic diversity and intraspecific variability.

In contrast to the invertebrates, the vertebrate fossils of Akol Hill are comprehensively described and discussed in the present paper.

## Results

### *The invertebrate assemblages*

This section deals with the taxa of cephalopods and brachiopods and considers their stratigraphic distribution, as well. Occurrences of these taxa are listed in *Tables I* and *II*. A few specimens of gastropods and echinoderms were also encountered; they will not be discussed herein.

### *Cephalopod taxa*

#### *Proavites hueffeli* ARTHABER, 1896 (Plate I, Figures 1–3)

This characteristic species with narrow umbilicus and bicarinate and wide, flat or even concave venter has simple goniatitid sutures, an indication of its Palaeozoic ancestry. Occurrences of this species are listed in *Tables I* and *II*.

#### *Balatonites egregius jovis* ARTHABER, 1896 (Plate I, Figure 4)

A single specimen in the collection of G. FÖLDVÁRI, shows the characteristic lateral ornamentation of *B. jovis* ARTHABER, 1896. As a result of their thorough morphometric analysis, HOHENEGGER & TATZREITER (1992) synonymized it with another species *B. egregius* ARTHABER, 1896, and this was accepted by VÖRÖS (2003). Occurrences of this species are listed in *Tables I* and *II*.

**Table I.** Occurrence of ammonoid species of the Akol Hill fauna at other localities of Hungary

**I. táblázat.** Az akol-dombi ammoniteszfauna előfordulása magyarországi lelőhelyeken

	Szentbékállá	Köveskál	Monoszló	Szentanatólfá	Mencshely	Tótvázsony	Vászoly	Aszófő	Felsőörs	Szentkirályszabadja	Vörösbereány	Rudabánya, Szár-hegy
<i>Proavites hueffeli</i>		+						+				
<i>Balatonites egregius jovis</i>								+				
<i>Beyrichites cadoricus</i>					+			+				
<i>Paraceratites trinodosus</i>		+	+	+					+		+	
<i>Asseretoceras camunum</i>	+			+	+		+		+	+	+	+
<i>Lardaroceras barrandei</i>				+			+		+		+	
<i>Lardaroceras krystyni</i>	+	+		+		+	+		+	+	+	+
<i>Lardaroceras pseudohungaricum</i>	+	+		+	+		+		+	+	+	+
<i>Kellnerites bosnensis</i>	+				+		+		+	+	+	
<i>Kellnerites cf. bispinosus</i>									+			+
<i>Hyarpadites cf. liepoldti</i>					+				+	+		
<i>Epikellnerites cf. bagolinensis</i>												
<i>Epikellnerites aff. tamasi</i>									+			
<i>Ptychites cf. oppeli</i>	+	+							+		+	+
<i>Discoptychites megalodiscus</i>					+				+		+	+
<i>Flexoptychites studeri</i>							+					+
<i>Flexoptychites cf. angustumbilicatus</i>	+	+		+	+		+		+		+	+

**Table II.** Stratigraphic distribution of the ammonoid species of the Akol Hill fauna

**II. táblázat.** Az akol-dombi ammoniteszfajok rétegtani elterjedése

Species	Stage		Anisian							
	Substages		Pelsonian		Illyrian					
	Zones		Balatonicus		Trinodosus			Reitzi		
	Subzones	Balatonicus	Cadoricus	Zoldianus	Binodosus	Trinodosus	Camunum	Pseudohungaricum	Felsoeorsensis	Liepoldti
<i>Proavites hueffeli</i>		+	+	+						
<i>Balatonites egregius jovis</i>		+	+							
<i>Beyrichites cadoricus</i>			+							
<i>Paraceratites trinodosus</i>						+	+			
<i>Asseretoceras camunum</i>							+	+		
<i>Lardaroceras barrandei</i>							+	+	+	
<i>Lardaroceras krystyni</i>							+	+	+	
<i>Lardaroceras pseudohungaricum</i>								+	+	
<i>Kellnerites bosnensis</i>									+	
<i>Kellnerites cf. bispinosus</i>									+	
<i>Hyarpadites cf. liepoldti</i>										+
<i>Epikellnerites cf. bagolinensis</i>										+
<i>Epikellnerites aff. tamasi</i>										+
<i>Ptychites cf. oppeli</i>						+	+	+	+	
<i>Discoptychites megalodiscus</i>					+	+	+	+	+	+
<i>Flexoptychites studeri</i>							+	+	+	+
<i>Flexoptychites cf. angustumbilicatus</i>							+	+	+	+

*Beyrichites cadoricus* (MOJSISOVICS, 1869)  
(Plate I, Figures 5–8)

By their compressed shape, narrow umbilicus, weak falcooid ribbing and rounded venter, the specimens of *Beyrichites* somewhat resemble *Flexoptychites*. However, they have ceratitic sutures in contrast to the ammonitic sutures of the ptychitids. Occurrences of this species are listed in *Tables I* and *II*.

*Paraceratites trinodosus* (MOJSISOVICS, 1882)  
(Plate II, Figures 1–3)

This well-known species is a zonal index and a good guide fossil. Various morphotypes of *P. trinodosus* were collected at the Akol Hill locality. Occurrences of this species are listed in *Tables I* and *II*.

*Asseretoceras camunum* (ASSERETO, 1963)  
(Plate II, Figure 4)

The genus *Asseretoceras* was introduced by BALINI (1992) for a type species *camunum*, what was previously attributed to *Bulogites* by ASSERETO (1963). However, BALINI (1992) recorded this species in Lombardy in a stratigraphic level much higher than the range of *Bulogites*. Occurrences of this species are listed in *Tables I* and *II*.

*Lardaroceras barrandei* (MOJSISOVICS, 1882)  
(Plate II, Figures 6, 7)

This ammonoid species was originally described from Nagyvázsony by MOJSISOVICS (1882). From the point of view of its lateral ornamentation (weak ribbing, and lateral nodes), *L. barrandei* is transitional between *L. krystyni* (without lateral nodes) and *L. pseudohungaricum* (with strong lateral nodes and strong ribbing). Occurrences of this species are listed in *Tables I* and *II*.

*Lardaroceras krystyni* BALINI, 1992  
(Plate II, Figure 5)

This is a less strongly ornamented species of the genus *Lardaroceras*, without lateral nodes. Occurrences of this species are listed in *Tables I* and *II*.

*Lardaroceras pseudohungaricum* BALINI, 1992  
(Plate II, Figure 8; Plate III, Figures 1–6)

The coarsely ornamented, large, well-preserved specimens of this species are particularly attractive for the collectors and this is reflected also by the profuse illustrations given here. The strength and density of the lateral ribbing and nodes are variable; in some cases the lateral ornamentation may resemble the genus *Kellnerites*, but a definite ventral keel is always missing in *L. pseudohungaricum*. It is the index species of the uppermost part of the Illyrian Trinodosus Zone (*Pseudohungaricum* Subzone). Occurrences of this species are listed in *Tables I* and *II*.

*Kellnerites bosnensis* (HAUER, 1887)  
(Plate IV, Figures 2–6; Plate V, Figure 1)

This is the other most attractive ammonite, from the collectors' point of view, at Akol Hill. The definite ventral keel and the ventrolateral row of nodes, or even spines, give the most important differences from the coarsely ornamented specimens of *Lardaroceras pseudohungaricum*. The lateral nodes are near the inner third of the flank, whereas in *K. felsoeersensis* they are around the middle. Occurrences of this species are listed in *Tables I* and *II*.

*Kellnerites* cf. *bispinosus* (HAUER, 1896)  
(Plate IV, Figure 1)

This smaller species of the genus *Kellnerites* differs from *K. bosnensis* and *K. felsoeersensis* by its more depressed whorls. Occurrences of this species are listed in *Tables I* and *II*.

*Hyparpadites* cf. *liepoldti* (MOJSISOVICS, 1882)  
(Plate V, Figure 2)

A single specimen vaguely shows the distinctive double rows of nodes on its lateral flank. The conch shape and the partially preserved fastigate venter support its attribution to the species *liepoldti*, which is taken as the index species of the Liepoldti Subzone in the lower part of the Illyrian Reitzi Zone at the Balaton Highland. Occurrences of this species are listed in *Tables I* and *II*.

*Epikellnerites* cf. *bagolinensis* (BRACK & RIEBER, 1993) (Plate V, Figure 3)

A single fragment of a body chamber, from the collection of G. FÖLDVÁRI, portrays the strongly ornamented lateral flank with two distinct rows of nodes; one closer to the umbilicus and another, closer to the venter. This fits rather well with the species *bagolinensis* described by BRACK & RIEBER (1993) from the Bagolino Section (the type section of the base of the Ladinian Stage) from the level corresponding to the Liepoldti Subzone of the Felsőörs Section (VÖRÖS et al. 2009). This species was not previously recorded from the Balaton Highland.

*Epikellnerites* aff. *tamasi* VÖRÖS, 2018  
(Plate V, Figure 4)

A single fragment in the collection of G. FÖLDVÁRI, akin to *Epikellnerites tamasi* VÖRÖS, 2018, but considerably larger and more inflated than that species. It is even more similar to the specimen described and illustrated from Felsőörs by MOJSISOVICS (1882) as "*Ceratites* nov. forma indet. aff. *hungarico*", and refigured by VÖRÖS (2018, pl. VII, Figure 5) as *E.* aff. *tamasi*.

*Protrachyceras* sp. (Plate V, Figures 5, 6)

The occurrence of a well-preserved small specimen of this genus (Plate V, Figure 5) in the trench of Akol Hill is unexpected and can be explained by artificial mixing caused by previous quarrying activity in the area. A poorly preserved fragment of *Protrachyceras* sp. (Plate V, Figure 6) was found



in the adjacent forest, where the Ladinian Nemesvámos Limestone (Buchenstein Formation) was exposed in small abandoned quarries. Both specimens resemble other specimens from the upper Ladinian fauna of Nemesvámos (VÖRÖS 1998).

*Ptychites* cf. *oppeli* MOJSISOVICS, 1882  
(Plate VI, Figure 1)

A similar specimen of this species was illustrated by VÖRÖS (2018, pl. XLI, Figure 6) from the Illyrian Trinodosus Zone from Szentbékállá. Occurrences of this species are listed in *Tables I* and *II*.

*Discoptychites megalodiscus* (BEYRICH, 1867)  
(Plate VI, Figures 2, 3)

This is the largest ammonoid found at Akol Hill; this size (125 mm in diameter) and the characteristic discoidal shape are unmistakable characteristics for identification. The smaller, incomplete specimen (*Plate VI, Figure 3*) probably represents the inner whorls of an even larger *Discoptychites*. Occurrences of this species are listed in *Tables I* and *II*.

*Flexoptychites studeri* (HAUER, 1857)  
(Plate VI, Figure 4)

This species was first reported by HAUER (1866, p. 632) from Nagyvázsöny (“Vaszony”). Occurrences of this species are listed in *Tables I* and *II*.

*Flexoptychites* cf. *angustoumbilicatus* (BÖCKH, 1872) (Plate VI, Figure 5)

This species is widespread in the whole Illyrian at the Balaton Highland. The single fragment, illustrated here, shows the diagnostic elements of the lateral flank, where the primary folds are intercalated by weaker falcoid secondary folds. Occurrences of this species are listed in *Tables I* and *II*.

*Parasturia* ? sp. (Plate VI, Figure 6)

A single half specimen is deceptively similar to one of the *Beyrichites* species in shape and partly in ornamentation. However, its well-preserved suture lines are clearly ammonitic, with phylloid lobes, in sharp contrast with the ceratitic sutures of *Beyrichites*. The specimen belongs most probably to the genus *Parasturia*, which was recorded previously from the Reitzi Zone at the Balaton Highland (Mencshely).

*Mojsisovicsteuthis* sp. (Plate VI, Figure 7)

A straight and conical phragmocone is the single specimen found to represent the subclass Coleoidea. Better preserved specimens in the Ladinian “Grenzbitumenzone” (RIEBER 1973) possess very reduced rostra (guard).

*Michelinoceras* ? sp. (Plate VII, Figure 6)

This orthocone cephalopod represents the order Orthocerida. The very elongate, subconical specimens easily break in parts along the concave septa of the phragmocone which show the trace of the siphuncle at the center. Probably

this taxon was reported by HAUER (1866, p. 620) as “*Orthoceras*” sp.

*Germanonautilus salinarius* (MOJSISOVICS, 1882)  
(Plate VII, Figure 3)

This very widespread and well-known nautiloid species was recorded by VÖRÖS (2001) in the uppermost (lower Illyrian) part of the Aszófő Section.

*Trachynautilus* cf. *nodulosus* (ARTHABER, 1896)  
(Plate VII, Figure 4)

The characteristic ornamentation of this species consists of weak longitudinal strigation and rursiradiate riblets, with fine nodes at the points of intersection. It was described by VÖRÖS (2001) also from the uppermost (lower Illyrian) part of the Aszófő Section.

*Pleuronautilus* cf. *mosis* MOJSISOVICS, 1882  
(Plate VI, Figure 8; Plate VII, Figure 5)

The rather evolute conch has a complex ornamentation with numerous prorsiradiate ribs and ventrolateral nodes which are divided from the ribs by a narrow longitudinal furrow. It was recorded by VÖRÖS (2001) in the lower, Pelsonian part of the Aszófő Section.

*Anoploceras* cf. *esinense* (MOJSISOVICS, 1882)  
(Plate VII, Figure 2)

The most important distinctive character of this species is the rursiradiate ribbing. It has not been reported previously from the Balaton Highland.

*Anoploceras* cf. *pichleri* (HAUER, 1866)  
(Plate VII, Figure 1)

This typical *Anoploceras* is similar to *A. esinense* but differs by its less numerous and nearly straight ribs.

*Brachiopod taxa*

*Volirhynchia vivida* (BITTNER, 1890)  
(Plate VII, Figure 10)

This distinctive rhynchonellid species has three deflexions in its high uniplication. It was recorded and described in detail by PÁLFY (1988) from several Pelsonian localities in the Balaton Highland.

*Mentzelia mentzeli* (DUNKER, 1851)  
(Plate VII, Figures 8, 9)

This smooth spiriferinid species has rather depressed ventral beak and nearly straight anterior commissure. It was recorded in great number by PÁLFY (2003) from several Pelsonian localities in the Balaton Highland but it occurs in the Illyrian as well.

*Koeveskallina koeveskalyensis* (STUR, 1865)  
(Plate VII, Figure 7)

It is rather similar to *Mentzelia mentzeli*, except that it has very fine and dense radial costulation. It was also

described in detail by PÁLFY (2003) from several Pelsonian localities in the Balaton Highland but it occurs in the Illyrian as well.

### ***The vertebrate assemblage***

Together with the rich invertebrate assemblage some vertebrate remains were also collected in the red limestone succession of the Vászoly Formation, including different types of teeth, vertebrae and a rib fragment. Among these, the marine reptiles are especially valuable additions to similar previous finds. So far, mostly placodonts have been described in detail from the Triassic of the Balaton Highland: *Paraplacodus broilii* from the upper Anisian of Felsőörs (GERE et al. 2020), *Placochelys placodonta* from the Carnian of Veszprém (JAEKEL 1902), and *Placochelyidae* indet. from the Norian–Rhaetian of Rezi (BÖCKH & LÓCZY 1912, GERE et al. 2020). However, more importantly, some associated ichthyosaur vertebrae were found in the upper Anisian of Dörgicse (SZABÓ 1972) and were assigned as *?Mixosaurus* by KRETZOI (SZABÓ I. personal communication), their study is currently in progress. Lastly, an unpublished ichthyosaur vertebra was also found recently in the Triassic near Veszprém (M. SEGESDI personal communication).

### ***Fishes***

Altogether three fish teeth have been found at the Akol Hill site, two of them belong to chondrichthyans, and one to osteichthyans.

A fin spine is referred to an indeterminate Hybodontoida (*Plate VIII, Figure 1*). The spine is still embedded in rock. It is apically narrowing and slightly curved posteriorly. The lateral surface bears numerous fine striae, longitudinal with its long axis. One series of denticles occurs in the posterior edge of the fin spine. Following the poorly known level of inter- and intraspecific variability of hybodontoid fin spines, this isolated fin spine is not referred to on a lower taxonomical rank herein. A morphologically similar Hybodontoida fin spine from the early Triassic of the Spitzbergen has been published by BRATWOLD et al. (2018, Figure 16).

One of the chondrichthyan tooth remains (*Plate VIII, Figure 2*) shows great similarity to those of the hybodontiform genus *Polyacrodus* (see CAPPETTA 2012, SZABÓ et al. 2019). This tooth is incomplete, the whole root and a large part of the crown is missing. The preserved portions of the crown are low and richly ornamented. The ornamentation consists of a central ridge, running along the mesiodistal axis of the occlusal midline, with smaller, diverging ridges, running to the crown base. Some faint remains of the base of a labial apron are visible. We tentatively refer this specimen to the genus *Polyacrodus*. Though the validity of *Polyacrodus* is debated (e.g. REES 2008, REES & UNDERWOOD 2008, STUMPF et al. 2022), its remains have been found in Europe, Russia and Greenland, ranging from the Lower

Triassic to the Upper Cretaceous (CAPPETTA 2012). The genus is regarded as a generalist predator, preying on fish and hard-shelled prey items (BLANGER 2005).

The other chondrichthyan tooth remain consists of the crown only (*Plate VIII, Figure 3*). The crown is flattened and blade-like with smooth cutting edges. The crown faces bear apicobasal striae vanishing towards the tip. This tooth morphology is generally similar to that of many Triassic chondrichthyans (e.g. Hybodontidae – see BÖTTCHER 2015; CAPPETTA 2012; SZABÓ et al. 2019). Because of the poor preservation (e.g., missing root, fragmentary crown), a closer identification is not possible.

The osteichthyan tooth (*Plate VIII, Figure 4*) is triangular in labial and lingual views, it consists of the apical part of the tooth only, whereas the tooth base is missing. Both sides of the preserved tooth bear irregularly arranged, apicobasally running striation not reaching the cutting edges. The basal-most portion has a much finer striation, which most likely continued on the tooth base. This specimen is almost identical to those previously published as *Birgeria* sp. teeth (see SZABÓ et al. 2019, Figure 7). The genus *Birgeria* is known from Triassic marine deposits worldwide (ROMANO & BRINKMANN 2009). Members of the genus were large-sized predatory fishes (ROMANO et al. 2017, NI et al. 2019).

### ***Marine reptiles***

Besides fishes, marine reptiles are also present in the fauna. Four vertebral centra, a tooth crown fragment, as well as a piece of a rib have also been found.

The four vertebrae (*Plate VIII, Figures 5–6*) were found in the red nodular limestone, characterized by black Fe-Mn coating (*Figure 5*). All these vertebral remains are centra without the neural arches, exhibiting only the articulation facets on their dorsal side. They are fish-like, being much shorter anteroposteriorly than wide laterally and deeply amphicoelous, as typical for ichthyopterygians (MCGOWAN & MOTANI 2003).

One of them is 33 mm high and 37 mm wide, and it is a dorsal (*Plate VIII, Figure 5*), as indicated by the subcircular outline of the centrum in anterior-posterior views, as well as the absence of ventral structures such as haemapophyses (MCGOWAN & MOTANI 2003). Its most diagnostic feature is the position of the diapophyses on the lateral sides of the centrum. They start to emerge at the lateral edge of the articulation surface of the neural arch and extend anteroventrally right onto the lateral margin of the anterior face of the centrum. This “truncated” condition is considered as a distinctive character of the genus *Cymbospondylus* (e.g. MERRIAM 1908, von HUENE 1916, SANDER 1992), though some authors suggested this being plesiomorphic for all ichthyopterygians (MCGOWAN & MOTANI 2003).

The three other vertebrae appear to be caudals from different regions based on their shape and the presence of haemapophyses (MCGOWAN & MOTANI 2003). One has a height and width both about 40 mm and seems to be an

anterior caudal (*Plate VIII, Figure 6*), as indicated by the slightly hexagonal outline in anterior-posterior views. The second specimen is probably a mid-caudal (*Plate VIII, Figure 7*), being more hexagonal and dorsoventrally elongated (37 mm high and 32 mm wide, 1.16:1) in anterior-posterior views. The third specimen is a distal caudal (*Plate VIII, Figure 8*), 35 mm high and 25 mm wide (with an aspect ratio of 1.4:1) thus the caudal centrum is also hexagonal but more compressed laterally than the previous one, similarly to *Cymbospondylus* and *Shonisaurus* (MASSARE & CALLAWAY 1990, SANDER 1992: Figure 5).

The tooth crown fragment (*Plate VIII, Figure 9*) is 11 mm high, 10 mm wide but only 4 mm thick, it is likely a surface fragment rather than a complete section of the crown. Its surface bears apico-basal ridges that curve 'backwards' (supposedly in lingual-distal direction) and diverge basally, suggesting a congruent curvature of the original tooth. One of the ridges, which is situated in the middle part of the preserved position, appears to be more pronounced, being reminiscent of a slight lingual-mesial carina.

The rib fragment (not figured) is about 65 mm long and is about 15 mm in diameter. Its cross-section is somewhat heart-shaped, being wider on the medial side. A single groove apparently just appears on the distal end of the medial side of the preserved portion, whereas two grooves run entirely along the lateral surface of the fragment. This seems to differ from the ribs described for *Cymbospondylus* having "a prominent posterior groove and a less pronounced anterior one" (SANDER 1992).

## Discussion

The stratigraphy of the Akol Hill area (Barnag Platform) shows similarities in several aspects to that of the well-studied Tagyon Platform of the Balaton Highland and the Kádárta Platform of the Veszprém Plateau (*Figure 1, b*) but there are marked differences, as well. The Lower Anisian carbonate ramp facies of the Megyehegy Dolomite is overlain by carbonate platform facies of the Middle Anisian Tagyon Formation; however, the thickness of the latter unit is very much reduced (to only a few metres) in the area of the Barnag Platform, in contrast to the 80–100 m thick cyclic platform carbonate succession of the Tagyon and the Kádárta Platforms (BUDAI et al. 1999b, BUDAI et al. 2001, BUDAI & VÖRÖS 2006). (It should be noted, however, that we know only a very small segment of the Barnag Platform, while the other two platforms are exposed in significant areas and much more studied.) The stratigraphy and lithology of the overlying Upper Anisian Vászoly Formation and the Ladinian Buchenstein Formation are almost the same in all the three platform areas.

The ammonoid fauna of the Akol Hill locality may be subdivided into two assemblages. The yellowish, clayey red limestone bed, that rests directly on a massive limestone bank, and contains black iron-manganese coated fossils (*Figures 3 and 5*) can be considered a lag deposit. This thin bed pinching

out within the outcrop is actually a lens-shaped rock body. It contains characteristic elements of the Balatonicus Zone (*Proavites hueffeli*, *Balatonites egregius jovis*, *Beyrichites cadoricus*), together with Illyrian taxa. Consequently, this fauna is interpreted as a reworked and mixed assemblage partly derived from the Pelsonian deposits. This is a unique phenomenon, which has no similar occurrence known from elsewhere in the Balaton Highland.

The early Illyrian ammonoid fauna of the Akol Hill (Barnag Platform) is probably more diverse than the equivalent faunas of the Tagyon Platform and the Kádárta Platform (VÖRÖS 2018). Sixteen species were recorded at Szentantalfa, 13 at Vászoly (Tagyon Platform), and 16 in the coeval layers of the Szentkirályszabadja Section (Kádárta Platform). On the other hand, 17 ammonoid species are presented and illustrated in the current paper from the Akol Hill locality. However, it should be kept in mind that we provide here a only a selection; in fact, the complete ammonoid fauna was probably much more diverse. For the same reason, a detailed comparison between the taxonomic composition of the above presented fauna, and that of other early Illyrian faunas would be misleading. However, it is important to note that the diagnostic species *Lardaroceras krystyni*, *L. pseudohungaricum* and *Asseretoceras camunum* were recorded in all mentioned localities (VÖRÖS 1998, 2018).

Despite the partly reworked fossils, the preservation state of the ammonoids is excellent on the Akol Hill, much better than in any other coeval localities in the Balaton Highland. It pertains particularly to the large and nearly complete conchs of *Lardaroceras pseudohungaricum*; specimens of this species were collected only as half-whorls or fragments at Szentantalfa, Vászoly and Szentkirályszabadja. This might be the consequence of the thin ferruginous clayey coating on the specimens.

The nautiloid assemblage is also diverse. Nautiloids are almost absent from the coeval faunas of the Tagyon Platform (Szentantalfa, Vászoly). The Szentkirályszabadja Section (Kádárta Platform) yielded a few nautiloids (VÖRÖS 1998, 2018), but the abundance and diversity of that assemblage are far from those of the Akol Hill.

The overall high taxonomic diversity of both cephalopod groups may perhaps be related to the stratigraphic and palaeoenvironmental position of the fossiliferous layers. The site of deposition was on the top of a drowned isolated platform (submerged pelagic plateau), near the steep slope of a bordering synsedimentary fault.

The low number and poor preservation of the fish remains do not allow any specific inferences regarding the paleoenvironment. All recovered fish taxa are common elements of Triassic faunas across Europe, including Hungary, where a Triassic fish fauna is known from Villány (SZABÓ et al. 2019).

As for the marine reptile remains, based on their characters, the dorsal vertebra are referred to as cf. *Cymbospondylus* sp., whereas the caudals are tentatively assigned to Cymbospondylidae. On the other hand, the tooth fragment seems to differ from those of *Cymbospondylus*. While there were some contemporary large marine reptiles present in the

Middle Triassic, such as nothosaurs, these mostly piscivorous reptiles had relatively small heads with more apicobasally elongated, procumbent teeth (RIEPEL 2000). This more robust crown morphology of the tooth found at Akol Hill locality with strong ridges and with the possible presence of a weak carina suggest a grasping/smashing function of the tooth and a diet of shelled cephalopods and vertebrates (MASSARE 1987). These prey items would also be more fitting to relatively large ichthyosaurs like *Cymbospondylus*, as opposed to the above mentioned mostly piscivorous groups such as nothosaurs. Most ichthyosaurs have sturdy, lingually curved conical teeth (MCGOWAN & MOTANI 2003). If a similar original morphology of the Barnag tooth fragment is assumed with a subcircular cross-section, the diameter of the crown might have been at least around 15 mm, as indicated by the curvature of its surface outline in basal view, if the fragment was from the widest basal part of the crown. If it was from the apical part, and thus a substantial basal portion is completely missing, the original size of the tooth might have been even larger. Based on comparisons with other species (e.g., KLEIN et al. 2020: figure 2H) it is safe to assume a body length of at least ~4.3 metres for the individual found at Barnag. However, if our extrapolation for the original diameter to 15 mm is accepted as valid, then the crown fragment from Akol Hill refers to a ~6.45-metre-long animal. On the other hand, if a labiolingually strongly flattened tooth is assumed as opposed to a more 'regular' ichthyosaurian tooth, then it is possible that the tooth came from an individual only ~4.3 m long. If so, then it refers to a highly specialized (though smaller) macropredatory ichthyosaur like the large *Thalattoarchon saurophagis*, which, uniquely among ichthyosaurians, was equipped with highly compressed teeth extremely suitable for cutting (FRÖBISCH et al. 2013).

Regardless, dental features in ichthyosaurians can exhibit a variance even in the same individual, thus they must be used cautiously for taxonomic purposes (MCGOWAN & MOTANI 2003). Therefore, the tooth fragment from Akol Hill is referred to as Ichthyosauria indet. The rib fragment, as it differs from the ones described for *Cymbospondylus*, might belong to another marine reptile taxon and is referred to as Sauropsida indet. However, it is uncertain whether it was a placodont, a nothosaur, or another ichthyosaur within this group.

As evidenced by the size differences of the vertebrae, they originate from at least two separate individuals, of which the dorsal vertebra belonged to an individual with a total length of 3.3 m, while the anterior caudal might have originated from one at least 4–4.5 meters long. Cymbospondylids could even reach twice that size; thus, the presence of such large marine reptiles is not surprising in the area of the Akol Hill. The family also had a cosmopolitan distribution in the Anisian and the Ladinian, as the remains of its members have been found in various localities around the globe, e.g., Nevada (USA), Spitzbergen, various European localities (Germany, Switzerland and Italy), Guizhou (South China) and possibly Timor (Indonesia) (e.g., LEIDY 1868, HUENE 1936, SANDER 1989, SANDER 1992, MAISCH & MATZKE 2000, JI et al. 2015, RIEPEL 2019). The strati-

graphic position of *Cymbospondylus* remains of the Upper Anisian Prezzo Limestone in the Lombardian Alps (BALINI & RENESTO 2012) and of the Vászoly Formation at the Akol Hill area in the Balaton Highland is similar, i.e. within the Trinodosus Zone, below the Lardaroceras beds.

Large Triassic ichthyosaurs like *Cymbospondylus* are regarded as pelagic forms that only occasionally strayed into coastal waters, as opposed to smaller contemporary genera like *Mixosaurus* (SANDER 1992, SANDER 1997, FRÖBISCH et al. 2006, RIEPEL 2019). On the other hand, some authors argued that basal ichthyosaurs, like cymbospondylids, were ambush predators, since they had less dolphin-like bodies with a lesser degree of marine adaptation (BALINI & RENESTO 2012). Thus, they were probably more restricted to shallow marine environments than the more streamlined and better adapted taxa, like *Mixosaurus*, that were most likely pursuit predators in turn (MASSARE & CALLAWAY 1990).

## Conclusions

The lifespan of the Barnag Platform seems to be much shorter than that of the other two reconstructed Middle Anisian platforms of the Balaton Highland. The oldest ammonites, reworked from the Balatonicus Zone in the lower part of the Vászoly Formation prove that the drowning of the Barnag Platform took place already during the Pelsonian, earlier than in the case of the Tagyon and the Kádárta Platforms, where the oldest basinal sediments above the drowning unconformity are mid-Illyrian (Camunum Subzone of the Trinodosus Zone).

The ammonoid fauna of the Camunum and Pseudohungaricum subzones at the Akol Hill is probably the most diverse among the coeval assemblages of the Balaton Highland. This may be the consequence of the peculiar environmental conditions that prevailed during the deposition of the basal beds that onlap the rim of a submerged pelagic plateau.

The Akol Hill locality provided the first known occurrence of cymbospondylid ichthyosaurs in Hungary, predators that probably dwelled in mostly open marine environments but also might have been well-adapted for hunting in shallow environments like submarine highs.

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**Plate I – I. tábla**

*Middle Triassic ammonoids from Akol Hill (Barnag, Balaton Highland), collected by M. BERCSÉNYI, Zs. PINTÉR and G. FÖLDVÁRI. All figures are in natural size in the print version. The specimens are kept in the private collections of M. BERCSÉNYI (Nyúl), Zs. PINTÉR (Győr) and G. FÖLDVÁRI (Kővágóörs).*

Középső triász ammonoideák az Akol-dombról (Barnag, Balaton-felvidék), BERCSÉNYI M., PINTÉR Zs. és FÖLDVÁRI G. gyűjtése. Az ábrák természetes nagyságúak. A példányokat BERCSÉNYI M. (Nyúl), PINTÉR Zs. (Győr) és FÖLDVÁRI G. (Kővágóörs) magángyűjteménye őrzi.

1. *Proavites cf. hueffeli* ARTHABER, 1896; Akol Hill, Balatonicus + Trinodosus Zone; a: lateral view, b: ventral view (coll: M. BERCSÉNYI).
2. *Proavites cf. hueffeli* ARTHABER, 1896; Akol Hill, Balatonicus + Trinodosus Zone; a: lateral view, b: ventral view (coll: M. BERCSÉNYI).
3. *Proavites cf. hueffeli* ARTHABER, 1896; Akol Hill, Balatonicus + Trinodosus Zone; a: lateral view, b: ventral view (coll: G. FÖLDVÁRI).
4. *Balatonites egregius jovis* ARTHABER, 1896; Akol Hill, Balatonicus + Trinodosus Zone; lateral view (coll: G. FÖLDVÁRI).
- 5–8. *Beyrichites cadoricus* (MOJISOVICS, 1869); Akol Hill, Balatonicus + Trinodosus Zone; lateral views, 8b: ventral view (5, 6: coll. Zs. PINTÉR, 7, 8: coll. M. BERCSÉNYI)

**Plate II – II. tábla**

*Middle Triassic ammonoids from Akol Hill (Barnag, Balaton Highland), collected by M. BERCSÉNYI, Zs. PINTÉR and G. FÖLDVÁRI. All figures are in natural size in the print version. The specimens are kept in the private collections of M. BERCSÉNYI (Nyúl), Zs. PINTÉR (Győr) and G. FÖLDVÁRI (Kővágóörs).*

Középső triász ammonoideák az Akol-dombról (Barnag, Balaton-felvidék), BERCSÉNYI M., PINTÉR Zs. és FÖLDVÁRI G. gyűjtése. Az ábrák természetes nagyságúak. A példányokat BERCSÉNYI M. (Nyúl), PINTÉR Zs. (Győr) és FÖLDVÁRI G. (Kővágóörs) magángyűjteménye őrzi.

1. *Paraceratites cf. trinodosus* (MOJISOVICS, 1882); Akol Hill, Balatonicus + Trinodosus Zone; lateral view (coll: Zs. PINTÉR).
2. *Paraceratites trinodosus* (MOJISOVICS, 1882); Akol Hill, Balatonicus + Trinodosus Zone; lateral view (coll: M. BERCSÉNYI).
3. *Paraceratites trinodosus* (MOJISOVICS, 1882); Akol Hill, Balatonicus + Trinodosus Zone; lateral view (coll: G. FÖLDVÁRI).
4. *Asseretoceras camunum* (ASSERETO, 1963); Akol Hill, Trinodosus Zone; lateral view (coll: G. FÖLDVÁRI).
5. *Lardaroceras krystyni* BALINI, 1992; Trinodosus Zone; lateral view (coll: G. FÖLDVÁRI).
6. *Lardaroceras cf. barrandei* (MOJISOVICS, 1882); Akol Hill, Trinodosus Zone; lateral view (coll: M. BERCSÉNYI).
7. *Lardaroceras cf. barrandei* (MOJISOVICS, 1882); Akol Hill, Trinodosus Zone; a: lateral view, b: ventral view (coll: M. BERCSÉNYI).
8. *Lardaroceras pseudohungaricum* BALINI, 1992; Trinodosus Zone; lateral view (coll: G. FÖLDVÁRI).

**Plate III – III. tábla**

*Middle Triassic ammonoids from Akol Hill (Barnag, Balaton Highland), collected by Zs. PINTÉR and M. BERCSÉNYI. All figures are in natural size in the print version. The specimens are kept in the private collections of Zs. PINTÉR (Győr) and M. BERCSÉNYI (Nyúl).*

Középső triász ammonoideák az Akol-dombról (Barnag, Balaton-felvidék), PINTÉR Zs. és BERCSÉNYI M. gyűjtése. Az ábrák természetes nagyságúak. A példányokat PINTÉR Zs. (Győr) és BERCSÉNYI M. (Nyúl) magángyűjteménye őrzi.

- 1–5. *Lardaroceras pseudohungaricum* BALINI, 1992; Trinodosus Zone; a: lateral view, b: ventral view (coll: Zs. PINTÉR).
6. *Lardaroceras pseudohungaricum* BALINI, 1992; Trinodosus Zone; lateral view (coll: M. BERCSÉNYI).

**Plate IV – IV. tábla**

*Middle Triassic ammonoids from Akol Hill (Barnag, Balaton Highland), collected by G. FÖLDVÁRI and M. BERCSÉNYI. All figures are in natural size in the print version. The specimens are kept in the private collections of G. FÖLDVÁRI (Kővágóörs) and M. BERCSÉNYI (Nyúl).*

Középső triász ammonoideák az Akol-dombról (Barnag, Balaton-felvidék), FÖLDVÁRI G. és BERCSÉNYI M. gyűjtése. Az ábrák természetes nagyságúak. A példányokat FÖLDVÁRI G. (Kővágóörs) és BERCSÉNYI M. (Nyúl) magángyűjteménye őrzi.

1. *Kellnerites cf. bispinosus* (HAUER, 1896); Reitzi Zone, Felsőeoersensis Subzone; a: lateral view, b: ventral view (coll: G. FÖLDVÁRI).
2. *Kellnerites bosnensis* (HAUER, 1887); Reitzi Zone, Felsőeoersensis Subzone; lateral view (coll: M. BERCSÉNYI).
3. *Kellnerites bosnensis* (HAUER, 1887); Reitzi Zone, Felsőeoersensis Subzone; a: lateral view, b: ventral view (coll: M. BERCSÉNYI).
4. *Kellnerites bosnensis* (HAUER, 1887); Reitzi Zone, Felsőeoersensis Subzone; lateral view (coll: G. FÖLDVÁRI).
5. *Kellnerites bosnensis* (HAUER, 1887); Reitzi Zone, Felsőeoersensis Subzone; a: lateral view, b: ventral view (coll: G. FÖLDVÁRI).
6. *Kellnerites bosnensis* (HAUER, 1887); Reitzi Zone, Felsőeoersensis Subzone; lateral view (coll: G. FÖLDVÁRI).

### Plate V – V. tábla

*Middle Triassic ammonoids from Akol Hill (Barnag, Balaton Highland), collected by G. FÖLDVÁRI, Zs. PINTÉR, M. BERCSÉNYI and A. VÖRÖS. All figures are in natural size in the print version. The specimens are kept in the private collections of G. FÖLDVÁRI (Kővágóörs), Zs. PINTÉR (Győr), M. BERCSÉNYI (Nyúl) and in the collection of the Department of Palaeontology and Geology, Hungarian Natural History Museum.*

Középső triász ammonoideák az Akol-dombról (Barnag, Balaton-felvidék), FÖLDVÁRI G., PINTÉR Zs., BERCSÉNYI M. és VÖRÖS A. gyűjtése. Az ábrák természetes nagyságúak. A példányokat FÖLDVÁRI G. (Kővágóörs), PINTÉR Zs. (Győr) és BERCSÉNYI M. (Nyúl) magángyűjteménye, valamint a Magyar Természettudományi Múzeum Őslénytani és Földtani Tárának gyűjteménye őrzi.

1. *Kellnerites bosnensis* (HAUER, 1887); Reitzi Zone, Felsőeoersensis Subzone; a: lateral view, b: ventral view (coll: G. FÖLDVÁRI).
2. *Hyparpadites* cf. *liepoldti* (MOJSISOVICS, 1882); Reitzi Zone, Liepoldti Subzone; lateral view (coll: M. BERCSÉNYI).
3. *Epikellnerites* cf. *bagolinensis* (BRACK & RIEBER, 1993); Reitzi Zone, Liepoldti Subzone; a: lateral view, b: ventral view (coll: G. FÖLDVÁRI).
4. *Epikellnerites* aff. *tamasi* VÖRÖS, 2018; Reitzi Zone, Liepoldti Subzone; a: lateral view, b: ventral view (coll: G. FÖLDVÁRI).
5. *Protrachyceras* sp.; Ladinian, lateral view (coll: M. BERCSÉNYI).
6. *Protrachyceras* sp.; Ladinian, lateral view (coll: A. VÖRÖS).
7. *Flexoptychites flexuosus* (MOJSISOVICS, 1882); Trinodosus Zone (?); lateral view (coll: Zs. PINTÉR) (not described in the text)

### Plate VI – VI. tábla

*Middle Triassic cephalopods from Akol Hill (Barnag, Balaton Highland), collected by Zs. PINTÉR and M. BERCSÉNYI. All figures are in natural size in the print version. The specimens are kept in the private collections of Zs. PINTÉR (Győr) and M. BERCSÉNYI (Nyúl).*

Középső triász fejlábúak az Akol-dombról (Barnag, Balaton-felvidék), PINTÉR Zs. és BERCSÉNYI M. gyűjtése. Az ábrák természetes nagyságúak. A példányokat PINTÉR Zs. (Győr) és BERCSÉNYI M. (Nyúl) magángyűjteménye őrzi.

1. *Ptychites* cf. *oppeli* MOJSISOVICS, 1882; Trinodosus Zone (?); lateral view (coll: Zs. PINTÉR)
2. *Discoptychites megalodiscus* (BEYRICH, 1867); Trinodosus Zone (?); lateral view (coll: M. BERCSÉNYI)
3. *Discoptychites* cf. *megalodiscus* (BEYRICH, 1867); Trinodosus Zone (?); a: lateral view, b: ventral view (coll: Zs. PINTÉR)
4. *Flexoptychites studeri* (HAUER, 1857); Trinodosus Zone (?); lateral view (coll: Zs. PINTÉR)
5. *Flexoptychites* cf. *angustoumbilicatus* (BÖCKH, 1872); Reitzi Zone (?); lateral view (coll: M. BERCSÉNYI)
6. *Parasturia* ? sp.; Reitzi Zone (?); lateral view (coll: M. BERCSÉNYI)
7. *Mojsisovicsteuthis* sp.; Reitzi Zone (?); (coll: M. BERCSÉNYI)
8. *Pleuronutilus* cf. *mosis* MOJSISOVICS, 1882; Balatonicus + Trinodosus Zone (?), lateral view (coll: Zs. PINTÉR)

### Plate VII – VII. tábla

*Middle Triassic cephalopods and brachiopods from Akol Hill (Barnag, Balaton Highland), collected by Zs. PINTÉR and M. BERCSÉNYI. All figures are in natural size in the print version unless otherwise stated. The specimens are kept in the private collections of Zs. PINTÉR (Győr) and M. BERCSÉNYI (Nyúl).*

Középső triász fejlábúak és pöregkarúak az Akol-dombról (Barnag, Balaton-felvidék), PINTÉR Zs. és BERCSÉNYI M. gyűjtése. Az ábrák természetes nagyságúak, kivéve a jelzett esetekben. A példányokat PINTÉR Zs. (Győr) és BERCSÉNYI M. (Nyúl) magángyűjteménye őrzi.

1. *Anoploceras* cf. *pichleri* (HAUER, 1866); lateral view (coll: M. BERCSÉNYI)
2. *Anoploceras* cf. *esinense* (MOJSISOVICS, 1882), 1882; lateral view (coll: Zs. PINTÉR)
3. *Germanonutilus salinarius* (MOJSISOVICS, 1882); a: lateral view, b: ventral view (coll: M. BERCSÉNYI)
4. *Trachynutilus* cf. *nodulosus* (ARTHABER, 1896); lateral view (coll: Zs. PINTÉR)
5. *Pleuronutilus* cf. *mosis* MOJSISOVICS, 1882; lateral view (coll: Zs. PINTÉR)
6. *Michelinoceras* ? sp.; (coll: Zs. PINTÉR)
7. *Koeveskallina koeveskalyensis* (STUR, 1865); ventral view (coll: M. BERCSÉNYI)
8. *Mentzelia mentzeli* (DUNKER, 1851); a: dorsal view, b: anterior view; magnified 2× (coll: Zs. PINTÉR)
9. *Mentzelia mentzeli* (DUNKER, 1851); a: dorsal view, b: anterior view, c: lateral view; magnified 2× (coll: Zs. PINTÉR)
10. *Volirhynchia vivida* (BITTNER, 1890); a: dorsal view, b: anterior view, c: lateral view; magnified 2× (coll: Zs. PINTÉR)

### Plate VIII – VIII. tábla

*Fish and marine reptile remains from the Middle Triassic of the Akol Hill (Barnag, Balaton Highland). Scale bars: 1., 5–8.: 10 mm; 2–4.: 0.6 mm; 9.: 5 mm.*



Középső triász hal- és tengeri hüllő maradványok az Akol-dombról (Barnag, Balaton felvidék). Méretarányok: 1., 5–8.: 10 mm; 2–4.: 0.6 mm; 9.: 5 mm.

1. Hybodontoida indet. fin spine, embedded in lateral view (coll: I. SZABÓ, SZTFH V 2016.62.1.)
2. ?*Polyacrodus* sp. tooth; a: occlusal view, b: labial view (coll: Zs. PINTÉR)
3. indeterminate chondrichthyan tooth (coll: M. BERCSÉNYI)
4. *Birgeria* sp. tooth; a: labial view, b: profile view (coll: Zs. PINTÉR)
5. cf. *Cymbospondylus* sp. dorsal vertebra; a: anterior view, b: right lateral view (coll: Zs. PINTÉR)
6. Cymbospondylidae indet. proximal caudal vertebra, anterior view (coll: M. BERCSÉNYI)
7. Cymbospondylidae indet. mid-caudal vertebra, anterior view (coll: Zs. PINTÉR)
8. Cymbospondylidae indet. distal caudal vertebra, anterior view (coll: M. BERCSÉNYI)
9. Ichthyosauria indet. tooth crown fragment; ?labial view (coll: M. BERCSÉNYI)

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Plate I – I. tábla

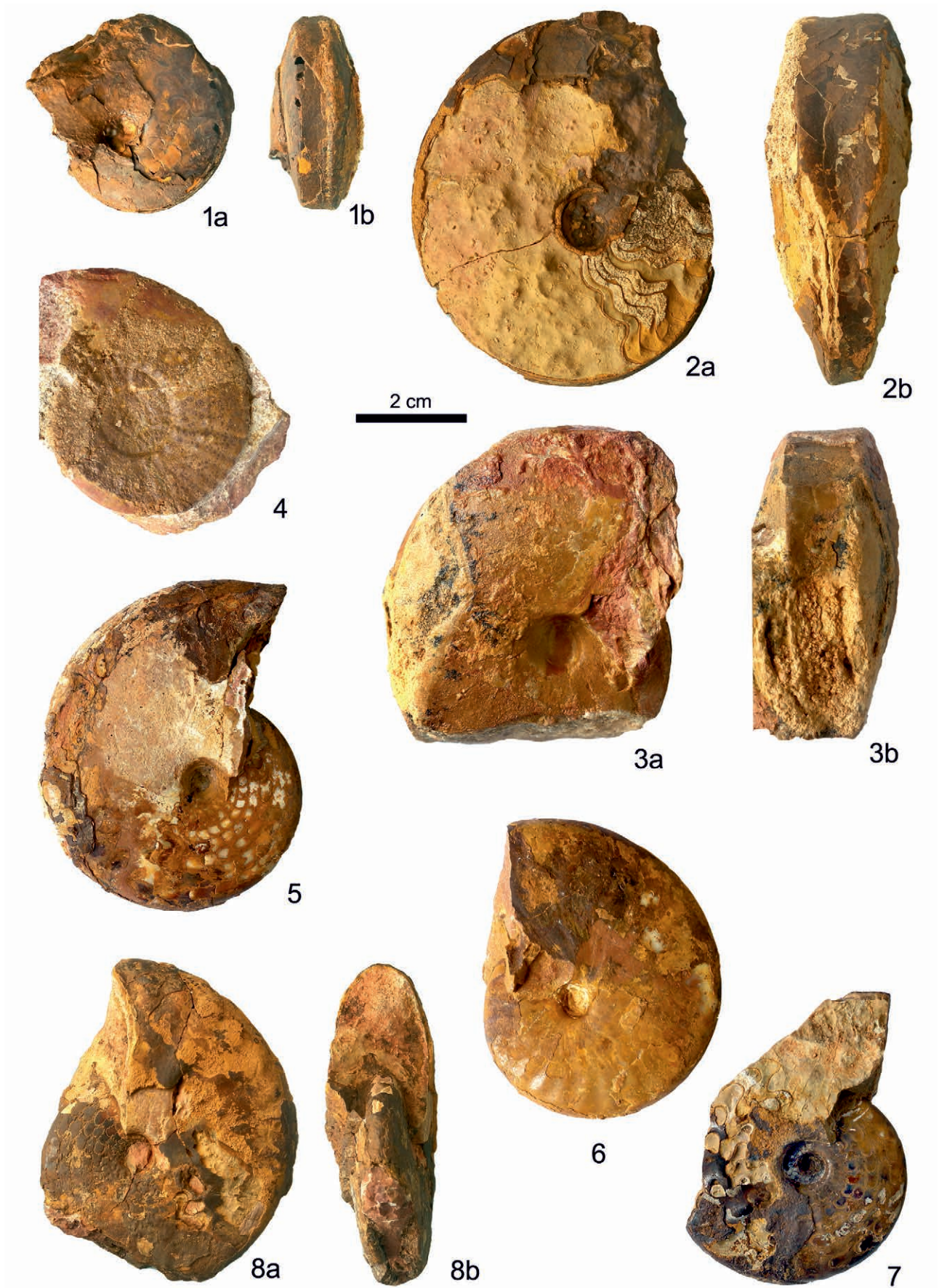


Plate II – II. tábla



2 cm



Plate III – III. tábla

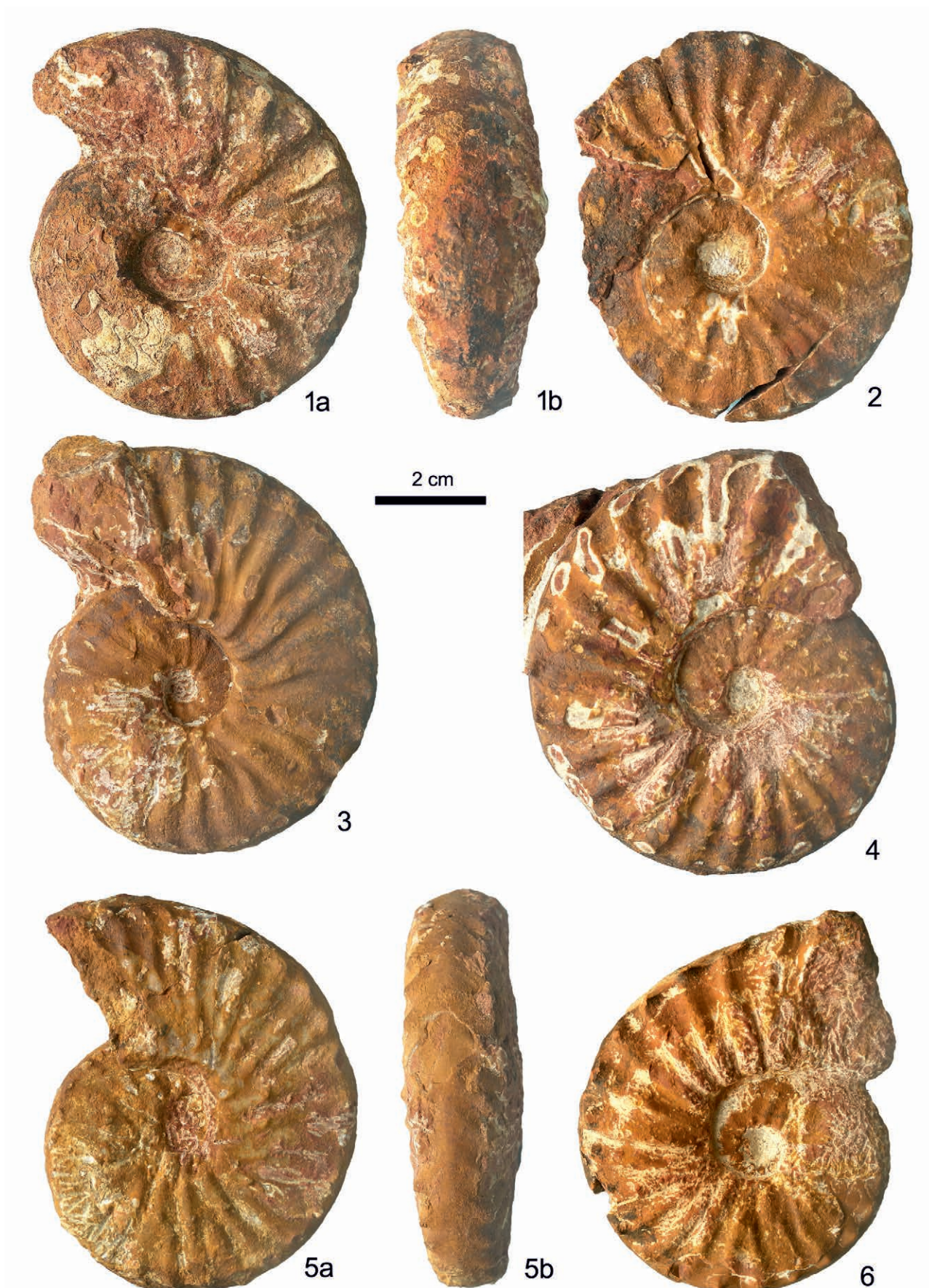


Plate IV – IV. tábla



1a



1b



2 cm

2



3b



3a



4



5a



5b



6

Plate V – V. tábla

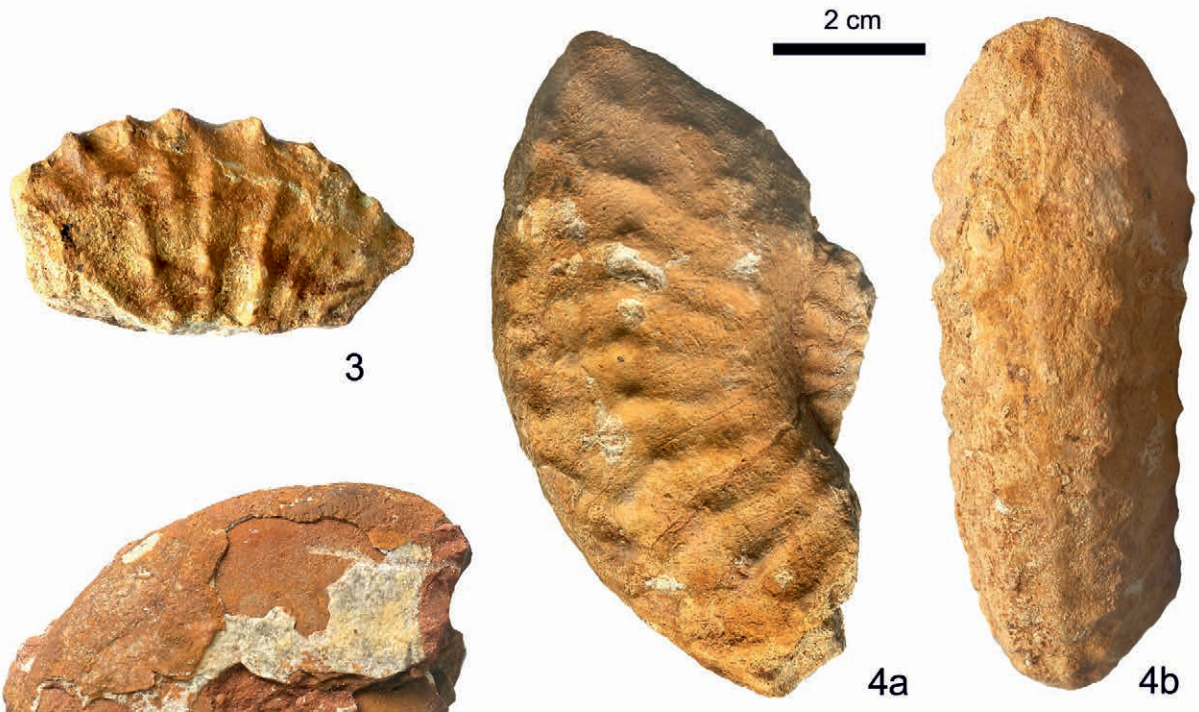
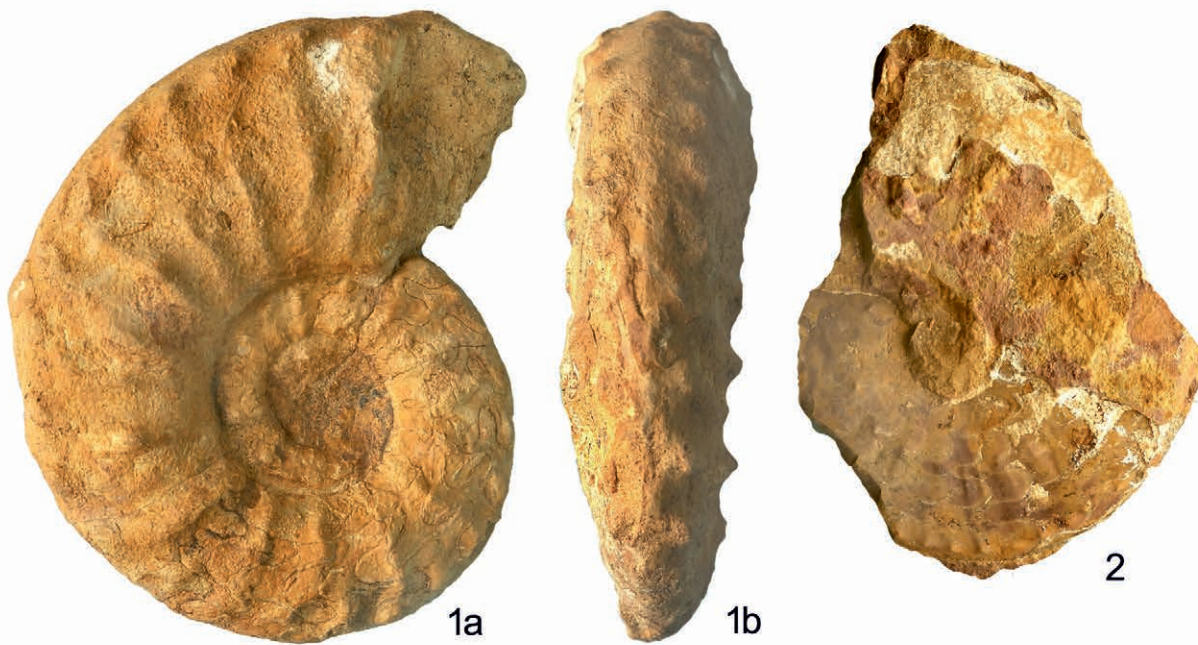


Plate VI – VI. tábla

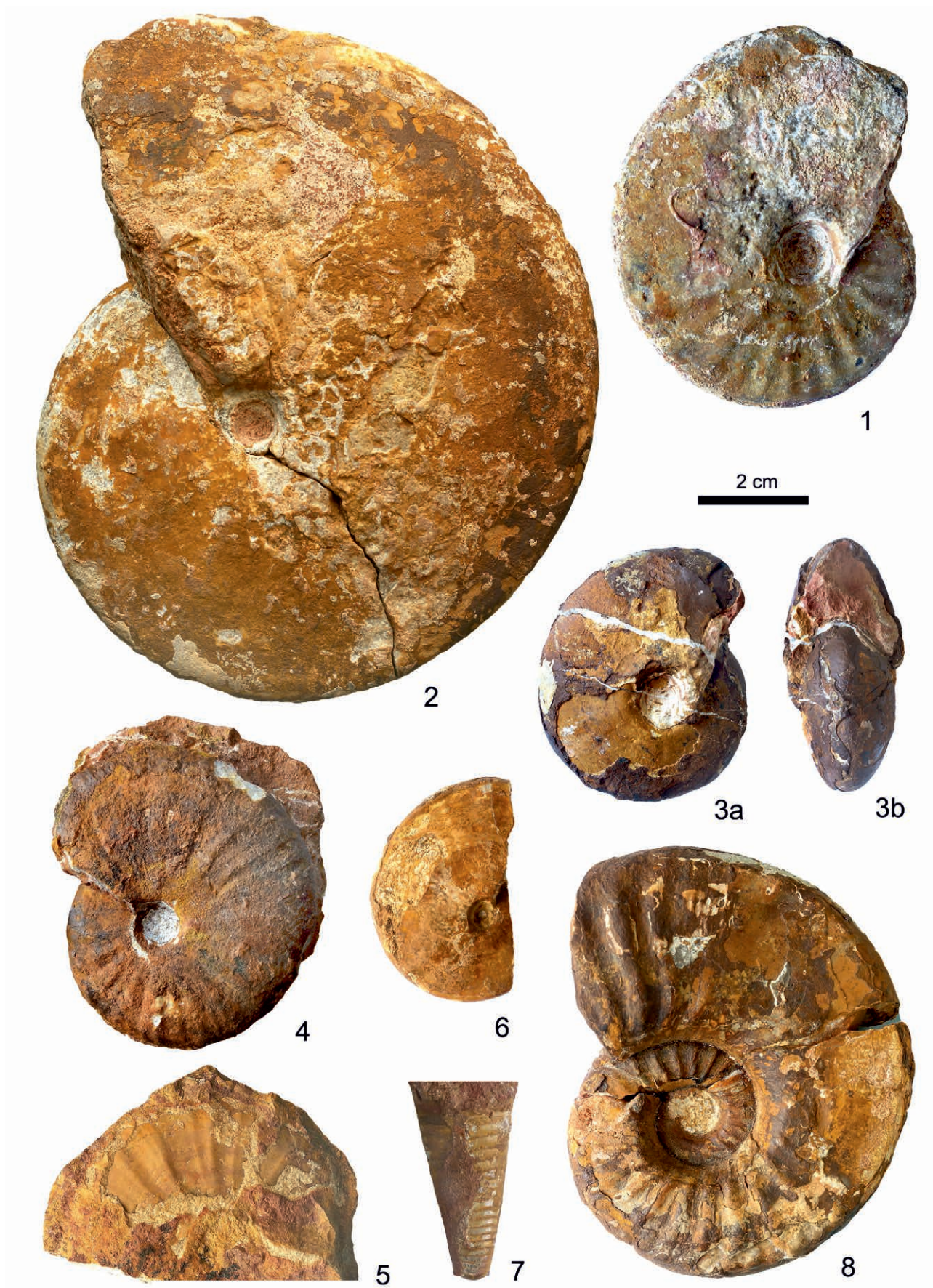


Plate VII – VII. tábla

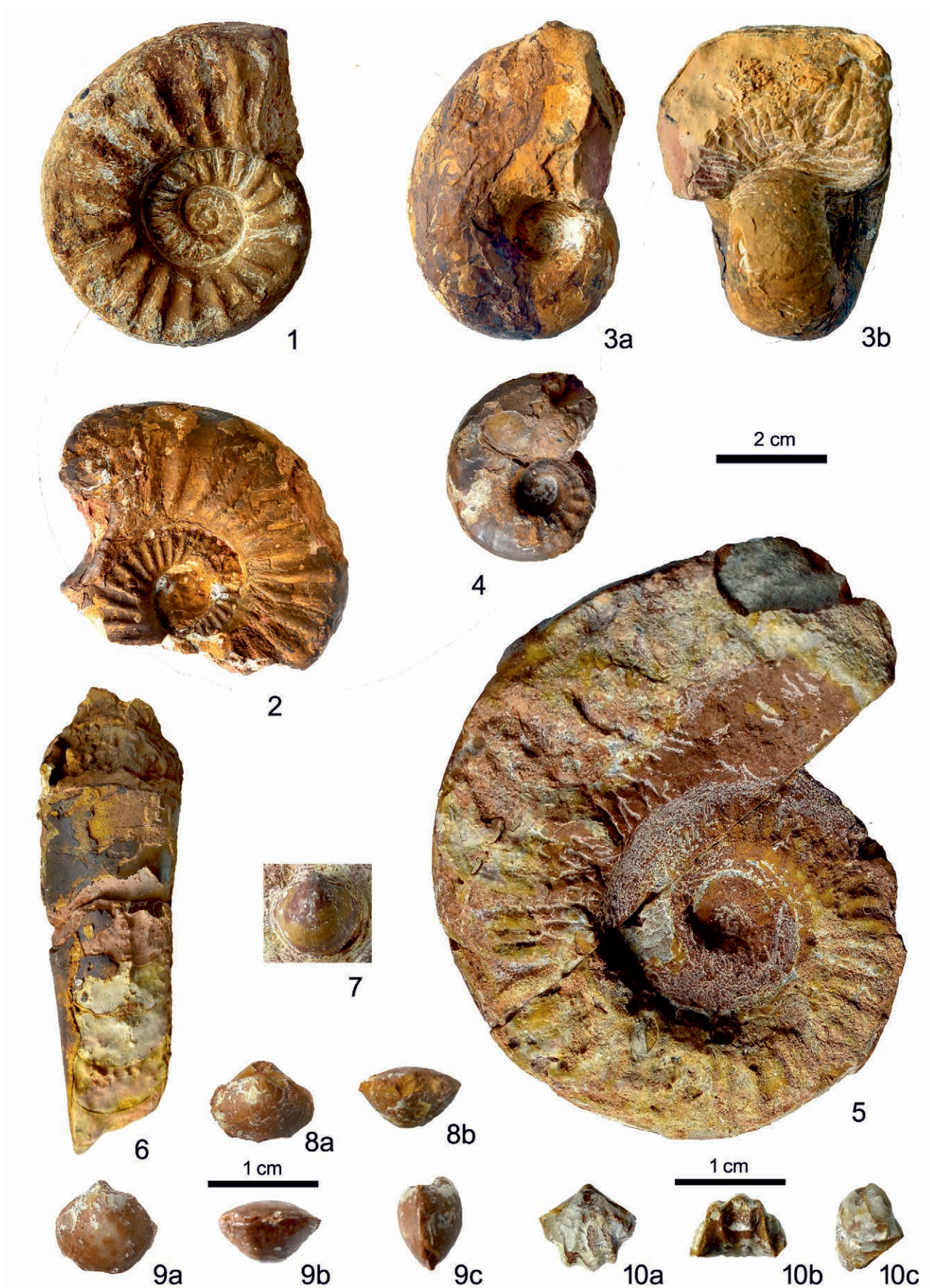




Plate VIII – VIII. tábla

