

# Földtani Közlöny



154/2

A Magyarhoni Földtani Társulat folyóirata  
Bulletin of the Hungarian Geological Society



Budapest, 2024

**Felelős kiadó**

M. TÓTH Tivadar, az MFT elnöke

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(Stuttgart),  
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EPA, MTA REAL (Budapest)**Tartalom — Contents**

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## Rövidített útmutató a Földtani Közlöny szerzői számára

Kérjük olvassa el részletes útmutatónkat a [www.foldtanikozlony.hu](http://www.foldtanikozlony.hu) weboldalon.

A Földtani Közlönybe a földtudományok széles köréből várunk a Kárpát–Pannon térség földtani felépítésével foglalkozó magyar vagy angol nyelvű kéziratokat. Magyar nyelvű cikkek esetében annak címét, kulcsszavait, összefoglalóját, az ábrák és táblázatok címét, feliratait angol nyelven is meg kell adni, angol nyelvű cikkek esetén fordítva. Az angol nyelvű szövegek elkészítése a szerző feladata.

**A kéziratot bírálatra pdf formátumban, egyetlen fájlként kell benyújtani**, a szöveg mögé sorrendben elhelyezett számoszott ábraanyaggal. A fájl neve a szerző nevéből és a cikk témáját lefedi néhány szóból álljon (pl. szujo\_etai\_villanyi\_kavicsok). Kéziratok a fenti honlapon keresztül küldhetők be. Bármilyen technikai probléma esetén forduljon a technikai szerkesztőhöz (piros.olga@mbfsz.gov.hu) vagy a főszerkesztőhöz (sztano.orsolya@gmail.com).

Az értekezések eddig publikálattan adatokat, új eredményeket következtetéseket közölnek, széles tudományterületi képhez helyezve. A rövid közlemények célja az adatközlés, adatmentés, vagy az új eredmény gyors közzététele. A szemle széleskörű, szakmailag közérthető áttekintést nyújt egy tudományterület új eredményeiről, vagy kevessé ismert, új módszereiről, annak alkalmazásáról. Vitárat a vitatott cikk megjelenésétől származtatott hat hónapon belül küldhető be. A vitatott cikk szerzője lehetőséget kap arra, hogy válasza a vitázó cikkkel együtt jelenjen meg. A gyakorlati rovatba a földtani kutatással – bányászattal kapcsolatos kéziratok kerülnek, melyek eredménye nem elsősorban tudományos értékű, hanem a szakközösséggel tájékoztatását, szolgálja. A **tömör fogalmazás, az állításokat alátámasztó adatszolgáltatás, a szabatos szaknyelv használata és a nem specialistika olvasók érdekében a közérthetőség mindegyik műfajban alapkövetelmény**.

A KÉZIRAT TAGOLÁSA ÉS AZ EGYES FEJEZETEK JELLEMZŐI (kötelező, javasolt)

a) **Cím (magyarul, angolul)** Rövid, informatív és tárgyra törő, utal a fő mondanódra.

b) **Szerző(k), munkahelye, postacímmel (e-mail cím)**

c) **Összefoglalás (magyarul, angolul)** Kizárolág a tanulmány célját, az alkalmazott módszereket, az elérte legfontosabb új eredményeket és következtetéseket tartalmazza, így önállóan is megállja a helyét. Hossza legfeljebb 300 szó. Az angol nyelvű összefoglaló lehet bővebb a magyarnál (max. 1000 szó).

d) **Tárgyszavak (magyarul, angolul)** Legfeljebb 8 szó / egyszerű kifejezés e) Bevezetés A munkához kapcsolódó legfontosabb korábbi szakirodalmi eredmények összefoglalása, és ebből következően a tanulmány egyértel- műen megfogalmazott célja.

f) **Anyag és módszerek** A vizsgált anyag, esetleg korábbról származó adatok, a mérési, kiértékelési eszközök és módszerek ismertetése. Standard eljárások esetén csak a hivatkozott módszertől való eltérést kell megfogalmazni.

g) **Eredmények** Az új adatok és kutatási eredmények ismertetése, dokumentációja ábrákkal és táblázatokkal.

h) **Diszkusszió** A kapott eredményeknek a saját korábbi eredményekkel és a szakirodalmi ismeretekkel való összevetése, beágyazása a tágabb tudományos környezetbe.

i) **Következtetések** Az új következtetések tézisszerű, rövid ismertetése az eredmények és a diszkusszió ismétlése nélküli.

j) **Köszönnetnyilvánítás**

k) **Hivatkozott irodalom** Csak a szövegközi, az ábrákhoz és táblázatokhoz kapcsolódóan megjelenő hivatkozásokat foglalja magába (se többet, se kevesebbet).

l) **Ábrák, táblázatok és fényképtáblák (magyar és angol felirattal)** A szemléltetni kívánt jelenség, vagy összefüggés megértéséhez szükséges mennyiségek.

m) **Ábra-, táblázat- és fényképmagyarázatok (magyarul és angolul)** Az illusztrációk rövid, összefogott, tartalmában érdemi magyarázata.

### FORMAI KÖVETELMÉNYEK

Értekezés, szemle maximális összesített **terjedelme** 20 nyomdal oldal (szöveg, ábra, táblázat, fénykép, tábla együttesen). Ezt meghaladó tanulmány csak abban az esetben közhelyet, ha a szerző a többletoldal költségének téritésére kötelezettséget vállal. A rövid közmények összesített terjedelme maximálisan 4 nyomdal oldal.

A **szöveg doc, docx vagy rtf** formátumban készüljön. Az alcímeknél ne alkalmazzanak automatikus számozást vagy ábécés jelölést, csak a tipografiával jelölje a címrendet. A hivatkozásokban, irodalomjegyzékben a SZERZŐK nevét kis kapitalissal, ősmaradványok faj- és nemzetiségeinek dölt betűvel, fajok leírót szintén kis kapitalissal kell írni. A kézirat szövegében az ábrára és a táblázatokra számoszásuk növekvő sorrendjében a megfelelő helyen hivatkozni kell.

A szövegközi **hivatkozások** formája RADÓCZ 1974, vagy GALÁCZ & VÖRÖS 1972, míg három vagy több szerző esetén KUBOVICS et al. 1987. Több hivatkozás felsorolásakor ezek időrendben kövessék egymást. Az irodalomjegyzék tételei az alábbi minta szerint készüljenek, szoros ábécében, ezen belül időrendben álljanak. Kérjük a folyóiratok teljes dölt betűvel történő kiírását. Ezen kívül, ha a hivatkozott műnek van DOI száma, azt meg kell adni teljes URL formátumban. Hivatkozott egyedi kiadványok esetén a mű címét kérjük dölt betűvel szedni. Magyar szerzők idegen nyelvű publi-kációs esetén a vezetéknél után vesszőt kell tenni.

CSONTOS, L., NAGYMAROSY, A., HORVÁTH, F. & KOVÁC, M. 1992: Tertiary evolution of the intra-Carpathian area: A model. — *Tectonophysics* **208**, 221–241. [http://dx.doi.org/10.1016/0040-1951\(92\)90346-8](http://dx.doi.org/10.1016/0040-1951(92)90346-8)

JÁMBOR Á. 1998: A Tiszai nagyszerkezeti egység karbon üledékes képződményei rétegtanának ismertetése. — In: BÉRCZI I. & JÁMBOR Á. (szerk.): *Magyarország geológiai képződményeinek rétegtana*. MOL Rt. — MÁFI kiadvány, Budapest, 173–185.

VARGA A. 2009: A dél-dunántúli paleozoos–alsós-triász szilikiklasztos kőzetek kőzettani és geokémiai vizsgálatának eredményei. — PhD értekezés, ELTE Kőzettan–Geokémiai Tanszék, Budapest, 150 p.

WEAVER, C. E. 1989: *Clays, Muds, and Shales*. — Developments in Sedimentology 44, Elsevier, Amsterdam, 819 p. [http://dx.doi.org/10.1016/s0070-4571\(08\)x7036-0](http://dx.doi.org/10.1016/s0070-4571(08)x7036-0)

A **ábrákat** a szerzőknek kell elkészíteni, nyomdakész állapotban és minőségen a tükörméretbe (170×240 mm) álló, vagy fekvő helyzetben beilleszthetően. A fotótábla maximális magassága 230 mm lehet. Az ábrákon a vonalvastagság 0,3 pontnál, a betűméret 6 pontnál ne legyen kisebb. Az illusztrációkat X4-nél nem frissebb CorelDraw ábrákat, az Excel táblázatokat és diagramokat word vagy cdr formátumban tudjuk elfogadni. Egyéb esetben a fekete és színes vonalas ábrákat 1200 dpi felbontással, tif kiterjesztéssel, a szürkeárnyalatos fényképeket 600, a színes fényképeket 300 dpi felbontással, tif vagy jpg kiterjesztéssel kérjük beküldeni. A színes illusztrációkat a megfelelő nyomdal minden erdékelésében CMYK színprofilallal kérjük előállítani, ezért az online megjelenő pdf esetén előfordulhat némi színállítózás. A színes ábrák, fotótáblák nyomtatási költségeit a szerzőknek kell fedezniük. Ha a költséget a szerzők nem tudják vállalni, már benyújtáskor szürkeárnyalatos illusztrációkat használjanak.

A cikk benyújtásakor, kérjük a szerzőket, hogy **nevezzenek meg legalább négy olyan szakértőt**, akik annak tartalmáról érdemi véleményt adhatnak, és adják meg e-mail címüket. A bírálatot követően a szerzőtől egy vagy két hónapon belül várjuk vissza a javított változatot, ekkor még minden egyetlen összesített pdf-ben (eredeti fájl név\_átdolgozott megjelöléssel). E mellé kérünk csatolni egy **tételes jegyzéket**, melyben bemutatják, hogy lektoraik megjegyzéseit, tanácsait hogyan vették figyelembe, valamint esetleges egyet nem értéseknek milyen szakmailag alátámasztható indokai vannak.

A közlésre elfogadott kéziratok szövegét, ábráit, táblázatait egyesével kérjük a szerkesztési felület megfelelő menüpontját használva feltölteni. Tördelést követően a szerzők feladata a korrekciózás. Különlenyomatokat még külön költségért sem tudunk biztosítani.

## Rendhagyó köszöntő Galácz András és Vörös Attila barátaim 80. születésnapjára

Olyan volt, mintha évfolyamtársak lettünk volna. Ők ugyan egy évvel fölöttek jártak, de mivel akkor az évfolyam-leírások kicsik voltak (max. 15–20 fő), s az egyetemi busz (mert akkor még ilyen is létezett!) kihasználtsága akkor teljesült, ha benne minden ülés foglalt volt; az évközi tanulmányi kirándulásokra (mert akkor még ez is szerves része volt a képzésnek) többnyire együtt ment a két évfolyam. De előfordult, hogy kötelező tantermi foglalkozásokban is közösen részesültünk, így pl. a *Műszaki földtan* előadásokat közösen hallgattuk. Mindemellett volt a geológus hallgatóknak egy kedvenc helye: az *Optikai gyakorló terem*, ahol a kőzetmikroszkópia, az ércmikroszkópia és esetenként az ásványhatározás gyakorlatok is zajlottak, s ahol szabad délutánjainkon (ha a terem nem volt épp foglalt) megengedett volt a gyakorlati feladatok megoldására való felkészülés, a mikroszkópi vizsgálatok önkéntes gyakorlása. A gyakorló „előszobájából” nyílt az Ásványtani és Kőzettani gyűjtemény amely ugyancsak találkozóhelye/tanulószobája volt a mindenkorai geológus hallgatóknak I.-től akár V. évesig. Ez a közeg eredményezte azt, hogy a geológushallgatók, kicsik/nagyok vegyesen olyasféle közösséget képeztek a TTK-n belül, mint valami nagy család. Ismertük egymás érdeklődési körét; ha az órákon elhangzottakkal kapcsolatban kérdések merültek fel, a kicsik segítséget kérhettek és kaptak a nagyoktól (ezt ma „mentorálásnak” hívják – lám-lám, nincs új a nap alatt). Életünk e nagy közösségen zajlott: lubickoltunk a szakmában, vártuk a jövőt, amikor majd diplomával a kézben valódi geológusként kezdhetünk dolgozni.

András és Attila már akkor jóbarátok voltak. Mint afféle a paleontológia iránt érdeklődő „fosszília-vadászok”, ők többszörre az Őslénytani Tanszék környékén voltak fellelhetők, s már hallgatóként bekapcsolódtak a tanszéken folyó tudományos kutatásokba. Mindkettőjük mestere GÉCZY Barnabás volt, következésképp mindenkiten az ő kedvenc témaájában, a juraidőszak ősmaradványainak körében kezdték kutakodni: András az ammoniteszek, Attila a brachiopodák iránt mutatott különös érdeklődést. Fő vadászterületük a Bakony hegység volt. Én – a „kicsi” – mindenkorai áhítattal szemléltetem munkálkodásukat, hiszen ők már „nagyok” voltak. Igyekeztem a példát követni – mint ők, így én is – irányt vettetem a Tudományos Diák-kör felé (érdeklődési területeimnek megfelelően az Ásványtan-Ércteleptan területén). Azt akkor még nem sejtettem, hogy „felnőtt geológus”-ként tudományos érdeklődésünk egyszercsak konvergálni kezd majd. Az ő alapvetően mezozoos sztratigráfiai/szedimentológiai irányultságú kutatásai meg az én, ugyancsak mezozoos, de inkább ásványtani/geokémiai/szedimentológiai munkásságom össze fog érni, s barátságunk, közös gondolkodásunk a tethysi régió legszebb, legizgalmasabb színterén, Dél-Itáliában fog „szárba szökenni” (közös publikációt eredményezni).

Végzés után a sors egy időre szanaszét szórt bennünket: András és Attila az Őslénytani Tanszék, ill. a Természettudományi Múzeum kötelékében folytatták klasszikus alaputatásnak minősülő tevékenységüket, engem azonban egy kis Ásványtani tanszéki kitérőt követően a gyakorlati „alkalmazott” kutatás vont bűvkörébe: csaknem tíz hosszú évre „beszippantott” az alumíniumipar s ezen belül a bauxitkutatás. A szakmai/baráti kapcsolat azonban ezalatt sem szakadt meg, s mikor a ’80-as évek elején visszakerültem Budapestre az egyetemre, könnyű volt visszailleszkedni a tudományos szférába.

Ott akkor pezsgő élet folyt. Megindult az addigra már általánosan elfogadott lemeztektonikai elmélet globális kereteibe illeszthető regionális, sőt lokális ősföldrajzi rekonstrukciók kidolgozása. Ebben úttörő szerepe volt András és Attila mestereinek, GÉCZY Barnabásnak aki paleobiogeográfiai megfontolások alapján jutott arra a következtetésre, hogy a Dunántúli-középhegységi és a Mecsek-Villányi szerkezeti zónák a jura időszakban a Tethys ellentétes oldalain kellett legyenek, s jelenlegi helyzetük nagyrányú lemeztektonikai mozgásokat igazol (GÉCZY B. 1973, *Acta Geol. Hung.* **17/4**, 421–428). Ez az akkor merésznek mondható feltételezés nemzetközi (főként olasz–magyar, de részben egyéb, a környező országok, így pl. Ausztria, Csehország részvételével folyó) összefogást eredményező kutatássorozatot indított el. E sorozat célja a mai Pannon-medencét alkotó terrénumok mezozoikumtól máig tartó történetének az új globális tektonika alapján való értelmezése volt. A munka vezéregyéniségei akkor magyar részről STEGENA Lajos professzor úr és a geofizikus HORVÁTH Ferenc voltak s ebbe tudtunk bekapcsolóni – mi is – ki-ki a maga témajával. Attila volt az első, aki hosszabb időt eltöltvén Szicíliában, voltaképp megalapoza azt a máig tartó eleven szakmai kapcsolatot, amelynek részeként évekig, minden nyáron lehetőségünk nyílt megismerkedni a Középső- és Déli-Appenninek mezozoos rétegsoraival (ami engem illet: a rétegsorokat megszakító unkonformitásokkal). És persze ezek az utak azért is nagyszerűek voltak, mert mindenkorban a geológiai látni- és megtapasztalnivalók („divertimenti geologici”) környezetében fellelhető történelmi és művészettörténeti hagyományokat is megcsodálhattuk (ez utóbbiak tekintetében szakavatott „idegenvezetőnk” mindig András volt).

A finanszírási hárteret itáliai geológiai kalandozásainkhoz az Magyar–Olasz TÉT (kormányközi tudományos és technológiai együttműködési megállapodás), továbbá egyes tudományos intézetek (így pl. MTA–CNR) közötti, ill. egyetemközi együttműködési programok biztosították. Olasz részről a program vezetője B. D’ARGENIO (a Nápolyi Egyetem professzora) és R. CATALANO (a Palermói Egyetem professzora) volt, akiket – mindenkor egyetemen – kiváló, fiatalabb kollégákból álló csapat vett körül. A velük való együttműködés, a szébbnél-szebb itáliai feltárási meglátogatása, az értékes szakmai diskurzusok és az egészhez háttérként a hamisítatlan mediterrán környezet mindenhangsára egészen különleges inspirációt jelentett. Nagyszerű volt megtapasztalni, hogy a paleontológia, paleoökológia, biosztratográfia mellett a szedimentológia és az unkonformitásokhoz kapcsolódó ásványtani/geokémiai jelenségek (tenger alatt a keményfelszínek; szárazföldi környezetben a paleokarsztosodás, bauxitos és nem bauxitos paleotalajok képződése) is érdemben tudnak hozzájárulni az egykor üledékképződési folyamatok rekonstrukciójához, s hogy mindenkor végsőfokon visszavezethetők az egykor lemeztektonikai környezetre.

Legizgalmasabb témaink közé tartozott a szicíliai Monte Kumeta különleges, mangánoxiddal bekérgezett, kora jura szubmarin unkonformitásának és a Középső-Appenninek (Mte Matse, Campo Sauro), valamint Puglia bauxitos paleokarsztjának tanulmányozása. Ezekkel kapcsolatos cikkeink (pl. VÖRÖS, A., GALÁCZ, A., CATALANO, R. 1987, *Rend. Soc. Geol. It.* **9** (1986), 243–248; DI STEFANO, P. GALÁCZ, A., MALLARINO, G., MINDSZENTY, A., VÖRÖS, A. 2002, *Facies* **46**, 273–298; D’ARGENIO, B. & MINDSZENTY, A. 1995, *Ecl. Geol. Helv.* **88/3**, 453–499; CSOMA, A. E., GOLDSTEIN, R. H., MINDSZENTY, A., SIMONE, L. 2004, *Journ. Sed. Res.* **74/6**, 889–903) máig a kedvenceink közé tartoznak.

Szép lassan ugyan megöregedtünk, de lelkesedésünk, a geológia szépsége iránti fogékonyunk mitsem változott. Máig jó visszagondolni itáliai kalandozásainkra, az Itáliában látott és Magyarországról ismert Tethys D-i peremi rétegsorok hasonlóságára, arra, hogy sok minden, amit annak idején az egyetemen tanultunk, igazán mélyen ezeknek a kalandozásoknak az eredményeként érthettünk meg.

Kedves András és Attila! Köszönöm, hogy magatok közé fogadtatok, hogy együtt örülhettünk annak, hogy geológus lett belőltünk! Erre a jeles jubileumra pedig szeretettel kívánom nektek, hogy még sokáig gyönyörködhessetek mindabban, amit a geológia kínál azoknak, akik értő szemekkel tekintenek reájuk.

MINDSZENTY Andrea



Sorrento, 1988

## Reconstruction of Middle Triassic platform drowning and basin evolution of the Balaton Highland: new micropaleontological constraints

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### A Balaton-felvidéki középső triász platformok megfulladásának és medencefejlődésének rekonstrukciója új mikropaleontológiai adatok alapján

#### Összefoglalás

A Balaton-felvidék és a Veszprémi-fennsík területén az anisusi emelet középső részét egymással heteropikus fáciessű képződmények alkotják (*1. és 2. ábra*): a sekélytengeri, karbonátplatform-fáciessű Tagyoni Formáció és a hemipelágikus medencefáciessű Felsőörsi Mészkő. A két heteropikus fáciessű elterjedése alapján három pelsoi szigetplatform rekonstruálható: a Balaton-felvidék középső részén lévő Tagyoni-platform, az attól északra lévő Barnagi-platform és a Veszprémi-fennsíkon lévő Kádártai-platform (*9. ábra, A*). A korábbi részletes ammonitesvizsgálatok szerint (VÖRÖS 1998, 2018; VÖRÖS & BUDAI 1993a, b; VÖRÖS et al. 1996, 2003a, b) a közöttük lévő medence üledékképződése folyamatos volt, a Felsőörsi Mészkő és Vászolyi Formáció rétegsorában elkülöníthető az összes ammoniteszárona a középső anisusitól (Balatonicus Z.) a ladin elejéig (Curionii Z.). Ezzel szemben a pelsoi platformok területén üledékhézag és jelentős fáciess változás figyelhető meg a Tagyoni Formáció sekélytengeri, ciklusos rétegsora és a fölötte éles határral települő, felső anisusi medencefáciessű karbonátokból és vulkanitból álló Vászolyi F. között (BUDAI & HAAS 1997, VÖRÖS et al. 1997, BUDAI et al. 1999b), ami a platformok megfulladásaként értelmezhető (BUDAI & VÖRÖS 2006).

A platformok megfulladását előidéző folyamatok korának pontosabb meghatározása céljából mikropaleontológiai vizsgálatot végeztünk mindenáron platform egy-egy szelvényében. Az Akol-domb rétegsorában (*4. ábra*) a Tagyoni F.-ra települő Vászolyi F. krinoideás mészkővének conodontá-együttese a Paragondolella bulgarica Zónába tartozik, ami igazolja a Barnagi-platform peremi részének késő pelsoi megfulladását. A fölötté települő ammoniteses mészkő (VÖRÖS et al. 2022) conodontá-együttese késő illyr korú, az ostracoda-együttes mély neritikus környezetre utal. A szentkirályszabadai köfejtőben (*7. ábra*) a Tagyoni F.-t metsző neptuni telér *Paragondolella bulgarica*, *P. bifurcata* és *P. hanbulogi* conodontá-együttese a Balaton-felvidéki kora anisusi karbonátrámpa feldarabolódását eredményező, extenziós tektonikai esemény pelsoi korát igazolja. Itt a Tagyoni Mészkő fölött éles határral települő Vászolyi F. bázisrétegeiből *P. bifurcata*, *P. hanbulogi* és *Ne. cornuta* conodontá-együttes került elő, amely a Kádártai-platform peremi részének kora illyr megfulladását támasztja alá (BUDAI & HAAS 1997, VÖRÖS 1998). A Dörgicse Drt-1 térképező fúrás a Tagyoni-platform rétegsorát reprezentálja (*8. ábra*), amelyben a Tagyoni F.-ra települő krinoideás mészkő conodontá-együttese a platform kora illyr megfulladására utal.

A platformok megfulladásának árnyalatba értelmezése céljából az új adatokat együtt elemztük a korábban publikált Balaton-felvidéki és alpi-dinári kutatási eredményekkel. Megállapítottuk, hogy a három Balaton-felvidéki platform – illetve azokon belül egyes részterületek megfulladásának időpontja területenként bizonyos fokú eltérést mutat (*9. ábra, A, B*), és ezt igyekeztünk összefüggésbe hozni a lehetséges kiváltó okokkal. A legkorábbi megfulladási esemény a pelsoi idejére rögzíthető a Barnagi-platform peremén (*10. ábra, A*). Ezzel egy idejű a Kádártai-platform peremi részén feltárt neptuni telér felnyílása, továbbá megegyezik az Aggtelek-Rudabányai-egység (VELLEDITS et al. 2011, PÉRÓ et al. 2015), az Északi-Mészkőalpok (VELLEDITS et al. 2017, GAWLICK et al. 2021), a Dolomitok (FARABEGOLI & GUASTI 1980) és a Dinaridák (SUDAR et al. 2013) legidősebb középső triász telérjeinek korával. Ez az esemény tehát egyértelműen kapcsolatba hozható a Neotethys nyugati selfjének számos részén megfigyelt, extenziós blokktektonikával (*11. ábra*). A Tagyoni-platform mindenáron korábban vizsgált szelvényében (Szentantalfa, Dörgicse, Vászoly) a pelsoi sekélytengeri karbonát fedőjében települő, legidősebb medenceüledék középső illyr korú (Trinodosus kron, Camunum szubkron) az ammonitesek alapján (VÖRÖS & BUDAI 1993a, b; VÖRÖS 1998). A Dörgicse Drt-1 esetében a conodontafauna ennél valamivel idősebb, kora illyr körjelel. Időpontját és jellegét tekintve ez a megfulladási esemény egyértelmű korrelációt mutat az Ag-

telek–Rudabányai-egység Steinalmi-rámpájának megfulladásával (Szár-hegy; VÖRÖS 2010). A Kádártai-platform DNy-i pereme (Szentkirályszabadja) ugyancsak a Camunum szubkron idején fulladt meg (BUDAI & HAAS 1997), a platform belsőbb részei felé azonban a folyamat kezdete fiatalodást mutat (9. ábra, A, B; 10. ábra, B). A kádártai kőfejtő szelvényében a medencefáciesű rétegsor legidősebb conodontá-együttese az illyr végét jelzi (Paragondolella trameri Z.; KARÁDI et al. 2022). Ez összhangban van a hajmáskér–sólyi területen tapasztaltakkal, ahol a megfulladási felszín fölötti legalsó rétegek ammoniteszfaunája a Reitzi Zóna legfelső, Avisanum szubzónájába tartozik (VÖRÖS 1998, BUDAI et al. 2001). Értelmezésünk szerint a megfulladási esemény időbeli eltolódása elsősorban a Kádártai-platform ÉK felé terjeszkedő tektonikus feldarabolódásával magyarázható, de a megfulladást elősegítette a tengerszint eusztatikus emelkedése és az egyre intenzívebb váló vulkanizmus is a késő illyr során (10. ábra, B). Az ostracoda-együttesek szerint mély, neritikus, tenger alatti hátsági környezet alakult ki a platformok illyr megfulladását követően. A ladin során az üledékgýűjtőtovábbi mélyülését igazolja a batiális (ún. „psychrosferikus”) ostracoda-taxonok megjelenése és arányának növekedése az együttesekben.

## Ajánlás

Jelen publikációt a szerzők Vörös Attila és Galácz András paleontológusok tiszteletére ajánlják, akik úttörők voltak a szinszediment tektonikai események felismerése és rekonstrukciója terén a Dunántúli-középhegység mezozoos fejlődéstörténetében.

*Kulcsszavak:* extenziós tektonika, platformmegfulladás, medencefejlődés, conodont, kagylósrák

## Abstract

Three Middle Anisian carbonate platforms (Barnag, Tagyon and Kádárta Platforms) surrounded by the hemipelagic Felsőörs Basin have been reconstructed in the Balaton Highland. The truncated surface of all platforms is covered by basinal carbonates and volcanic rocks of the Vászoly Formation. Based on conodont investigations these platforms were subject to drowning at different times. The earliest drowning was recognized in the late Pelsonian on the southern edge of the Barnag Platform (Paragondolella bulgarica Zone). This date correlates well with the opening of a neptunian dyke encountered near the southwestern margin of the Kádárta Platform and also with the age of the dykes cutting through Pelsonian platforms in the Northern Calcareous Alps, Aggtelek Hills, Dinarides and Dolomites. Drowning of the Tagyon Platform and the marginal area of the Kádárta Platform occurred in the early Illyrian (Paragondolella bifurcata and Neogondolella constricta Zones). However, the Kádárta Platform shows a trend of decreasing age for the timing of the drowning from the edge towards the inner parts of the platform during the late Illyrian. This can be explained by tectonically forced backstepping of the downfaulted marginal blocks and/or by eustatic sea-level rise accompanied by increasing volcanic activity that may have caused the decrease of transparency of the sea-water. Later on, as a result of intensifying sea level rise bathyal environment formed during the Ladinian that can be confirmed by the appearance and increasing dominance of deep-water ‘psychrosphaeric’ forms in the ostracod assemblage.

## Dedication

The authors dedicate the present publication in honor of paleontologists Attila Vörös and András Galácz, who were pioneers in the recognition and reconstruction of synsedimentary tectonic events in the Mesozoic history of the Transdanubian Range.

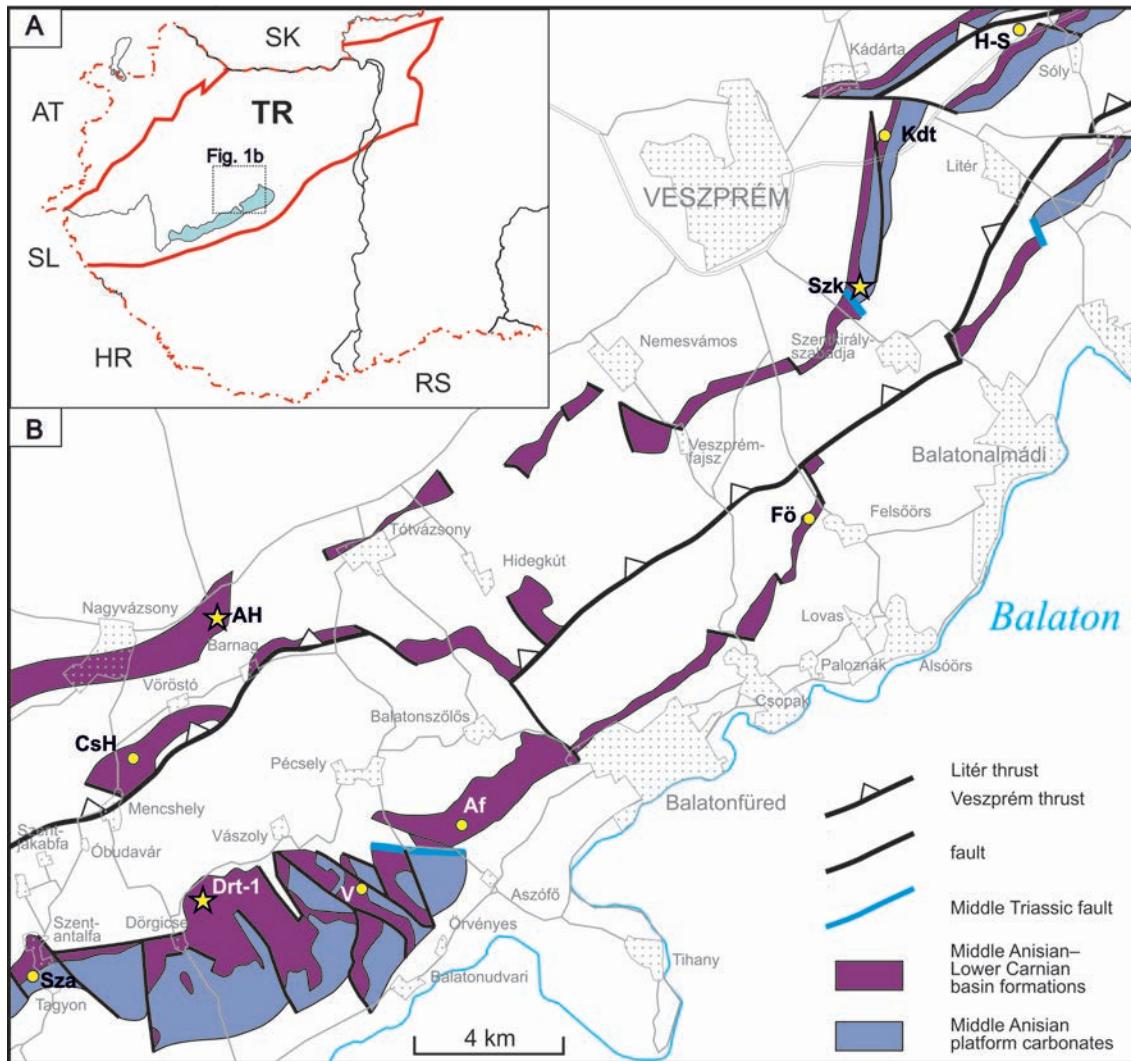
*Keywords:* extensional tectonics, platform drowning, basin evolution, conodonts, ostracods

## Introduction

During the last geological mapping project of the Balaton Highland several sections were sampled for micropaleontological investigations but only a few of the results on the conodont and ostracod studies were published (KOVÁCS 1993, 1994; KOVÁCS in VÖRÖS 2003b; MONOSTORI 1995; MONOSTORI & TÓTH 2013; TÓTH & MONOSTORI 2015; KARÁDI et al. 2022). In the last years micropaleontological investigations continued to produce important stratigraphic and paleoecologic data. The aim of this paper is to display these results and based on these new inferences to provide a more accurate reconstruction of the evolution of the Middle Triassic carbonate platforms and basins than the previous ones (BUDAI & VÖRÖS 1992, VÖRÖS et al. 1997, BUDAI & VÖRÖS 2006).

## Geological setting

The Balaton Highland is located on the southeastern limb of the SW–NE oriented syncline of the Transdanubian Range. It is made up of a very low to low grade metamorphic Paleozoic suite that is unconformably overlain by Permian and Triassic formations. This succession is cut through by the SW–NE oriented Litér thrust; the main structural element of the Balaton Highland. The Middle Anisian formations occur on both the northwestern and southeastern sides of this thrust (*Fig. 1*) showing significant lateral facies change. In a predominant part of the northern thrust-sheet the Middle Anisian is represented by hemipelagic cherty limestones of the Felsőörs Fm. and by the shallow marine platform carbonates of the Tagyon Fm. on the Veszprém Plateau (it was referred to as Szentkirályszabadja Platform



**Figure 1.** Geographic position of the Transdanubian Range Unit (A) and simplified Pre-Cenozoic geological map of the Balaton Highland (B) showing the areal extension of the Middle Anisian platform carbonates (Tagyon Fm.) and the Middle Anisian-lowermost Carnian basinal formations (Felsőörs, Vászoly, Buchenstein and Füred formations) (after BUDAI et al. 1999a, 2000). Studied localities (yellow asterisks): AH: Akol Hill, Barnag; Drt-1: Dörögics well; Szk: airport quarry, Szentkirályszabadja. Referred localities (yellow dots): Af: Aszófő; CsH: Cser Hill, Mencshely; Fö: Felsőörs, Forrás Hill; Kdt: Kádárta quarry; H-S: Hajmáskér–Sóly; Sza: Szentantalfa; V: Vászoly, Öreg Hill

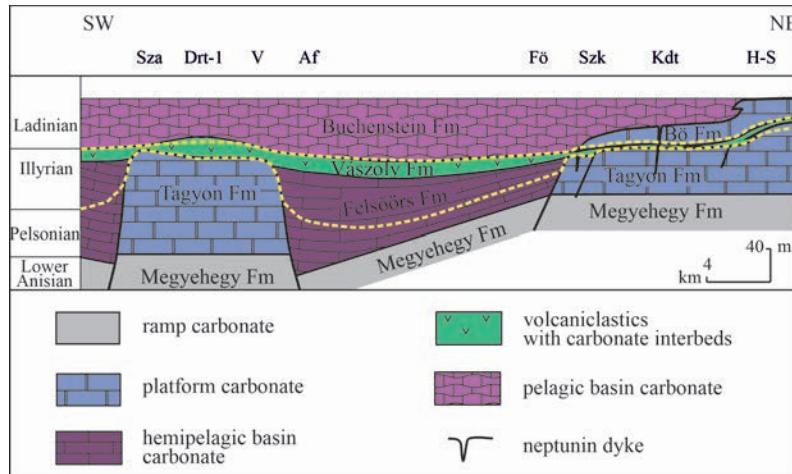
**1. ábra.** A Balaton-felvidék prekainozoos földtani térképének helyzete a Dunántúli-középhegységi-egység (TR) területén (A). A középső anisusi platformkarbonátok (Tagyon Fm.) és a középső anisusi – alsó karni medencefájcsú képződmények (Felsőörsi Mészkö, Vászolyi F., Buchenstein F., Füredi Mészkö) elterjedése (B). A vizsgált (sárga csillag) és hivatkozott szélvénnyek (sárga pötty) helyének feltüntetésével (BUDAI et al. 1999a, 2000 nyomán)

by BUDAI & VÖRÖS 2006, HAAS et al. 2014; and as Kádárta Platform by KARÁDI et al. 2022). A very small part of another platform was also encountered near Barnag (it was referred to as Vöröstó Platform by BUDAI & VÖRÖS 2006; and as Barnag Platform by VÖRÖS et al. 2022). In the area of the southern range the Middle Anisian is represented by platform carbonates in the middle part of the Balaton Highland (Tagyon Platform, BUDAI & VÖRÖS 2006, HAAS et al. 2014), and partly by coeval hemipelagic carbonate deposits (lower part of the Felsőörs Fm.). Based on the increasing thickness of the Felsőörs Fm. from the NE to the SW (Fig. 2) a tectonically controlled halfgraben basin was reconstructed for the Pelsonian to early Illyrian (BUDAI & VÖRÖS 1993, 2006; BUDAI & HAAS 1997; BUDAI et al. 1999b). The Pelsonian platforms are covered by Middle–Late Illyrian pelagic carbonates and volcanic tuffs of the Vászoly Fm. Deep marine

nodular cherty limestones and radiolarite of the Buchenstein Fm. were formed both above the previous platform and basin areas in the Ladinian (BUDAI et al. 1999b, 2017).

## Material and methods

For conodont biostratigraphic investigations three samples from the dolomite of the airport quarry at Szentkirályszabadja (Szk in Figs 1 and 2) and four samples from the lilac-red carbonate of the Akol Hill section were collected (AH in Fig. 1). The samples weighed 3 kg each, and were dissolved in hot acetic acid at 10% dilution in the Department of Palaeontology at the Eötvös Loránd University (Budapest). The washing residue was collected using a 125 µm mesh-size sieve. All seven samples contained conodont ele-



**Figure 2.** Simplified geological profile from the Veszprém Plateau (NE) to the middle part of the Balaton Highland (SW), showing the lateral and vertical relationship of the Middle Anisian–Ladinian formations (after BUDAI & VÖRÖS 2006, simplified). For abbreviations see Fig. 1. Bö Fm: Budaörs Dolomite Fm

**2. ábra.** Vázlatos földtani szelvény a Veszprémi-fennsíktól a Balaton-felvidék középső részéig a középső anisusi – ladin litosztratigráfiai egységek feltüntetésével (BUDAI & VÖRÖS 2006 nyomán, egyszerűsítve). Rövidítéseket lázd az 1. ábrán. Bö Fm: Budaörsi Dolomit Formáció

ments along with fish remains (teeth and placoid scales). Ostracods were recovered from one conodont sample of Szentkirályszabadja. For additional ostracod studies of Akol Hill, the samples (200–300 g air-dried hard limestones) were treated by acetolysis following a protocol originally developed by LETHIERS & CRASQUIN-SOLEAU (1988) with a slight modification to extract the calcareous microfauna. Only one sample provided suitable ostracod fauna along with few foraminifers, gastropods, bivalves, echinoderm fragments and fish teeth.

Scanning electron micrographs were taken of selected specimens at the Szentágóthai Research Centre of the University of Pécs and at the Department of Petrology and Geochemistry of the Eötvös Loránd University. All recovered specimens are stored at the Department of Palaeontology of the Eötvös Loránd University. The microfossils from the Dörgicse Drt-1 core (*Figs 1 and 2*) were studied in the Hungarian Natural History Museum where the material is housed. Conodonts were present in 19 samples and ostracods in 6 samples. Other faunal elements in the samples are represented by foraminifers, holothuroid sclerites, echinoid spines and warts, inarticulated brachiopods, fish teeth and placoid scales. The palaeoecological interpretation of ostracods is based mainly on the qualitative analyses and the semi-quantitative (percentage distribution) analyses of the specimens of the different taxa or groups.

## Results

The studied sections yielded abundant and well preserved conodont faunas characterized by a CAI value of 1 that indicates negligible thermal alteration. Biostratigraphic evaluation of the conodonts was based on the studies by KOVÁCS et al. (1980), KOVÁCS (1993, 1994, 2011), KOZUR (2003)

and BRACK et al. (2005). Nomenclature of KOZUR (2003) and MUTTONI et al. (2004) is followed here. Conodont zones were correlated with the ammonite zonation (*Fig. 3*) of VÖRÖS (1998, 2018) and VÖRÖS et al. (2003). Conodont zones and correlation is mainly based on KOZUR (2003) with slight modifications. The *Paragondolella trammeri praetrammeri* and the subsequent *Paragondolella trammeri trammeri* zones of KOZUR (2003) are merged, because even KOZUR (2003: 61) notes that the differences between the two subspecies are not easy to recognise. Therefore, the suitability of *P. trammeri praetrammeri* as an index fossil is debatable. There is an option for distinguishing a *Neogondolella pseudolonga* zone with a base correlatable to the Avisianum Subzone of the Reitzi Zone where the nominal taxon first appears (KOZUR 2003: 61), but *N. pseudolonga* is stated to be a rare species in the conodont assemblages (KOZUR 2003) and thus it is not included in the present zonal scheme. *Neogondolella prae-hungarica* is often used as marker conodont species for the base of the Ladinian, however, the FAD of this taxon is recorded already in the upper Secedensis Zone (KOZUR 2003: 59; BRACK et al. 2005).

The ostracod specimens are represented by articulated carapaces suggesting ‘in situ’ preservation according to BOOMER et al. (2003). In hard limestones, the preservation potential of the carapaces strongly depends on the diagenetic processes. The extracted ostracod carapaces from the studied Triassic samples are moderately preserved, recrystallized and sometimes broken.

Age Ma	Stage/ Substage	Ammonoid Zone / Subzone	Conodont Zone
240			<i>Budurovignathus hungaricus</i>
241	Ladinian Fassanian	Curionii	<i>Neogondolella prae-hungarica</i>
242		Secedensis	<i>Paragondolella trammeri</i>
		Crassus	
		Avisianum	
		Reitzi	
		Liepoldti	
243	Anisian Illyrian	Felsoeoversensis Pseudohungaricum	<i>Ne. mesotriassica</i>
244		Trinodosus	<i>Neogondolella constricta</i>
		Camunum	
		Trinodosus	<i>P. bifurcata</i>
245	Pelsonian	Binodosus	<i>P. bulgarica</i>
		Balatonicus	<i>Nicoraella kockeli</i>
		Zoldianus	
		Cadoricus	
		Balatonicus	
		Ottonis	

**Figure 3.** Middle Anisian-Lower Ladinian biostratigraphy of the Balaton Highland after VÖRÖS et al. (2003), VÖRÖS (2018) and KARÁDI et al. (2022)

**3. ábra.** A Balaton-felvidéki középső anisusi – alsó ladin biosztratigráfiai tagolása VÖRÖS et al. (2003), VÖRÖS (2018) és KARÁDI et al. (2022) nyomán

### Barnag, Akol Hill

The Akol Hill at Barnag (AH in Fig. 1; N46°59.419'; E017°44.180') is located north of the Litér thrust where the Middle Anisian succession is unusually thin (Fig. 4). The Lower Anisian bituminous dolomite of the Megyehegy Fm. is overlain by a few-metres-thick shallow marine limestone containing oncoids and dasycladalean algae (*Physoporella pauciforata*, *Oligoporella* sp.) that can be assigned to the Tagyon Fm. (VÖRÖS et al. 2022). It is overlain by the beds of a purple-grey crinoidal hard limestone with a few brachiopods, forming the basal part of the Vászoly Fm. Above it follows a reddish, slightly clayey limestone that contains ammonoids and nautiloids in a rock-forming quantity. In the Illyrian ammonite assemblage (Camunum and Pseudohungaricum Subzones) some species of the Pelsonian Balatonicus Zone also occur in the lower layers. Detailed description of the succession and the cephalopod fauna, together with some vertebrate remains were recently published by VÖRÖS et al. (2022).

In the Akol Hill section the lowermost samples (Ad-7, Ad-6) from the crinoidal limestone (lower part of the Vászoly Fm.) contained the conodonts *Paragondolella bulgarica*, *P. bifurcata*, *P. hanbulogi*, *Nicoraella germanica* and *Ni. kockeli*. This assemblage (Fig. 5) is indicative of the late Pelsonian. The species *Neogondolella cornuta* and *P. excelsa* from sample Ad-3 suggest Illyrian age. The fauna characterized by *Ne. cornuta*, *Ne. pseudolonga*, *Ne. mesotriassica* and *P. liebermani* from sample Ad-4 places this level in the late Illyrian.

The sample Ad-4 yielded benthic ostracod assemblage

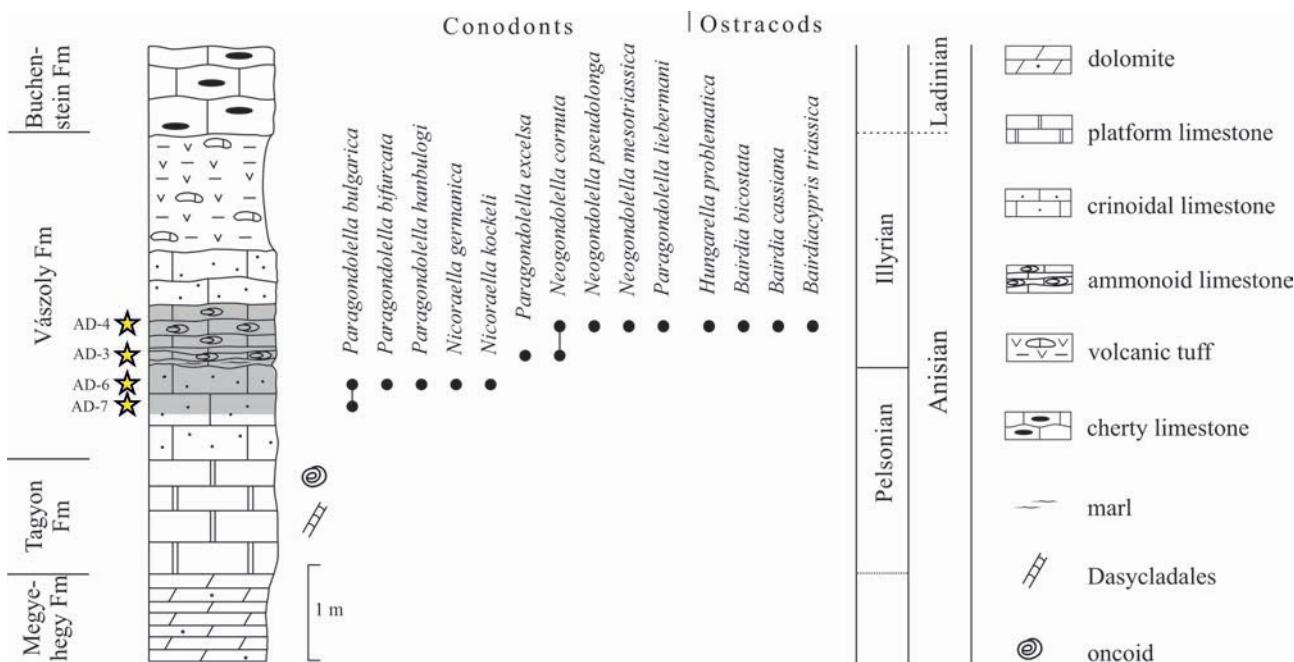
in low abundance. Four taxa (*Hungarella problematica*, *Bairdia bicostata*, *B. cassiana* and *Bairdiacypris triassica*) were identified (Fig. 6). The presence of smooth healdoids such as *Hungarella* in the fauna indicate water depth below 30–50 m (KOZUR 1991). The composition of the ostracod assemblage (smooth healdoids and bairdioids), the absence of shallow neritic forms (e.g., ornate bairdiids) and ‘paleopsychrosphaeric’ ostracods suggest most probably open marine deep neritic depositional environment below the storm wave base (according to KARÁDI et al. 2022).

### Szentkirálysabadjai, airport quarry

North of the Litér thrust on the rim of the Veszprém Plateau at Szentkirálysabadjai a small abandoned quarry (Szk in Fig. 1) exposes the shallow marine cyclic platform carbonate of the Tagyon Fm. (BUDAI et al. 1993, 1999b, 2001). Subtidal beds, containing dasycladalean algae (*Physoporella* div. sp., *Anisoporella*, *Pontecella*, *Teutloporella*), gastropods and oncoids, alternate with peritidal stromatolites and pisoidic intercalations. A lucky find of *Balatonites balatonicus* in a subtidal bed (Fig. 7, A) proves early Pelsonian age (Balatonicus Zone) of the formation (BUDAI & HAAS 1997, VÖRÖS et al. 2003).

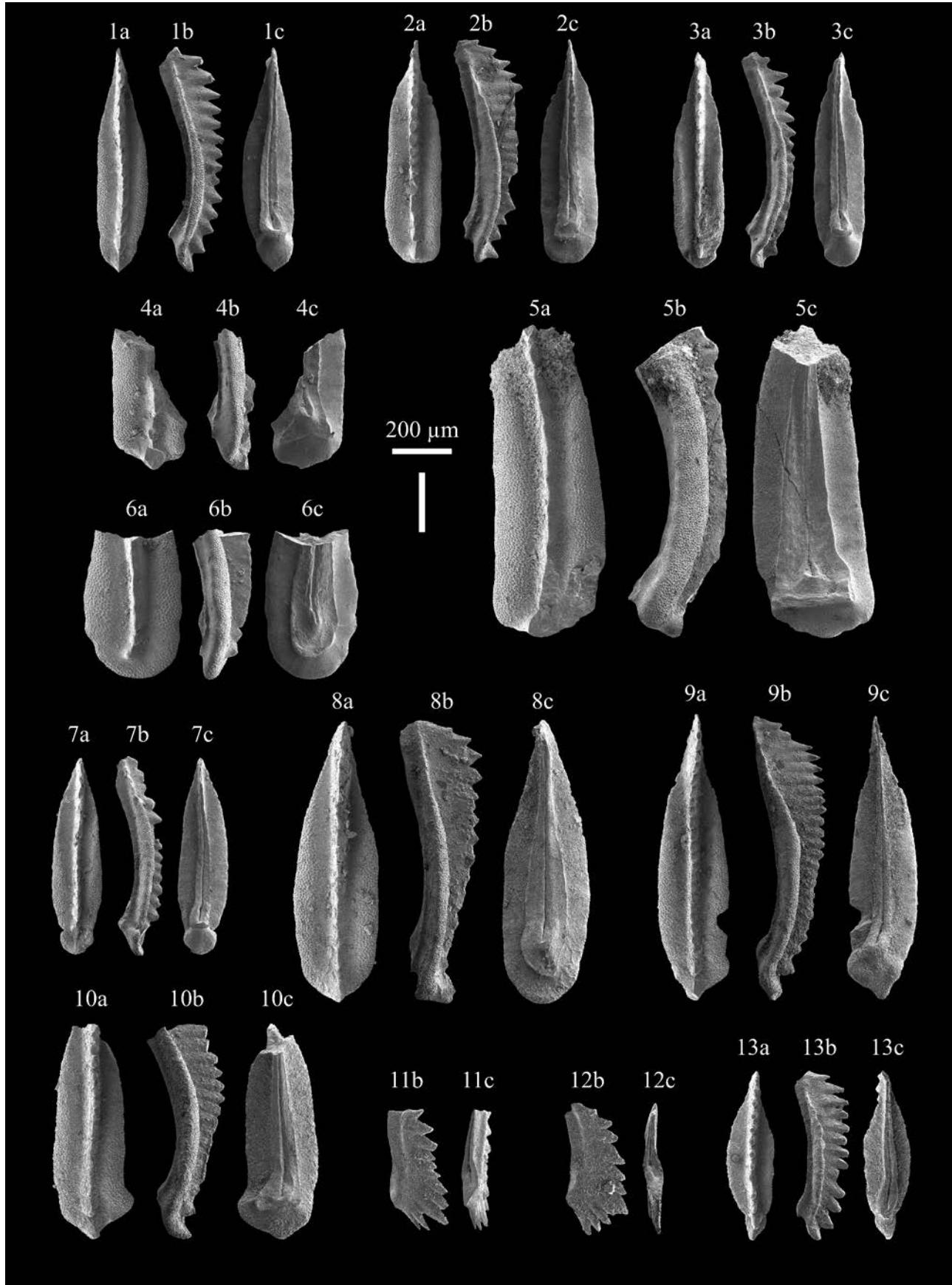
The Tagyon Fm. is cut by a nearly vertical neptunian dyke (Fig. 7, a, b) in the southern yard of the quarry (N 47°04'22.36", E 17°57'29.22"). It is filled by reddish micritic crinoidal packstone (VÖRÖS et al. 1997).

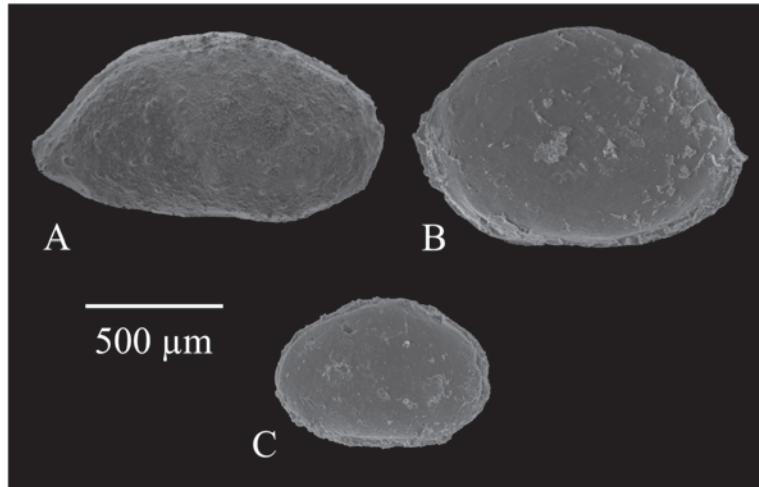
To determine the age of the opening of the dyke a sample was taken for micropaleontological study from the dolomitized crinoidal packstone of the neptunian dyke (Szk-3 in



**Figure 4.** Stratigraphic column of the Akol Hill at Barnag (after VÖRÖS et al. 2022) with the sites of micropaleontological samples (yellow asterisk). Grey shading marks the exposed and studied part of the site

**4. ábra.** A barnagi Akol-domb rétegzsövö (VÖRÖS et al. 2022 nyomán) a mikropaleontológiai minták feltüntetésével (sárga csillagok). A rétegsor feltárt, vizsgált részét a szürke kiemelés mutatja





**Figure 6.** Ostracods from the Akol Hill and the Szentkirályszabadja airport quarry. A) *Bairdia cassiana*, carapace in right view, Akol Hill, sample Ad-4; B) *Hungarella problematica*, carapace in left view, Szentkirályszabadja, sample Szk-2; C) *Hungarella* sp., carapace in right view, Szentkirályszabadja, sample Szk-2

**6. ábra.** Kagylósrákok a barnagi Akol-domb szelvényéből és a szentkirályszabadjai repülőtéri kőfűtőből. A) *Bairdia cassiana*, kettősteknő jobb oldali nézetben, Akol-domb, Ad-4 minta; B) *Hungarella problematica*, kettősteknő bal oldali nézetben, Szentkirályszabadja, Szk-2 minta; C) *Hungarella* sp., kettősteknő jobb oldali nézetben, Szentkirályszabadja, Szk-2 minta

*Fig. 7).* The infilling of the dyke contained the conodont species *P. bulgarica*, *P. bifurcata* and *P. hanbulogi*. This assemblage is Pelsonian in age.

In the northern yard of the quarry ( $N\ 47^{\circ}04'25.03''$ ,  $E\ 17^{\circ}57'25.66''$ ) the Tagyon Formation is overlain by a reddish-brown dolomite with a sharp boundary (basal beds of Vászoly Fm., *Fig. 7, A*), that contains a relatively poor ammonite assemblage of the lower Illyrian Camunum Subzone (VÖRÖS 1998, 2018). We took samples (SzK-1, SzK-2) just above the sequence boundary from the basinal dolomite to specify the age of the drowning event. In sample SzK-1 *P. bifurcata*, *P. hanbulogi* and *Ne. cornuta* were found. This assemblage is characteristic for the lowermost Illyrian. *Neogondolella cornuta* and *P. liebermani* from sample SzK-2 are indicative of the Illyrian (but not lowermost Illyrian). This latter sample also yielded ostracods (*Fig. 6*). Only a few specimens of *Hungarella* were found in the sample from the Vászoly Fm. suggesting a depositional environment below 30–50 m water depth (KOZUR 1991).

←**Figure 5.** Conodonts from the Akol Hill section. 1) *Neogondolella pseudolonga*, sample AD-4; 2) *Paragondolella liebermani*, sample AD-4; 3) *Neogondolella cornuta*, sample AD-4; 4) *Neogondolella mesotriassica*, sample AD-4; 5) *Neogondolella cornuta*, sample AD-3; 6) *Paragondolella excelsa*, sample AD-3; 7) *Neogondolella cornuta*, sample AD-3; 8) *Paragondolella hanbulogi*, sample AD-6; 9) *Paragondolella bulgarica*, sample AD-6; 10) *Paragondolella bifurcata*, sample AD-6; 11) *Nicoraella germanica*, sample AD-6; 12) *Nicoraella kockeli*, sample AD-6; 13) *Paragondolella bulgarica*, sample AD-7. a: upper view, b: lateral view, c: lower view. Scale bar: 200 µm

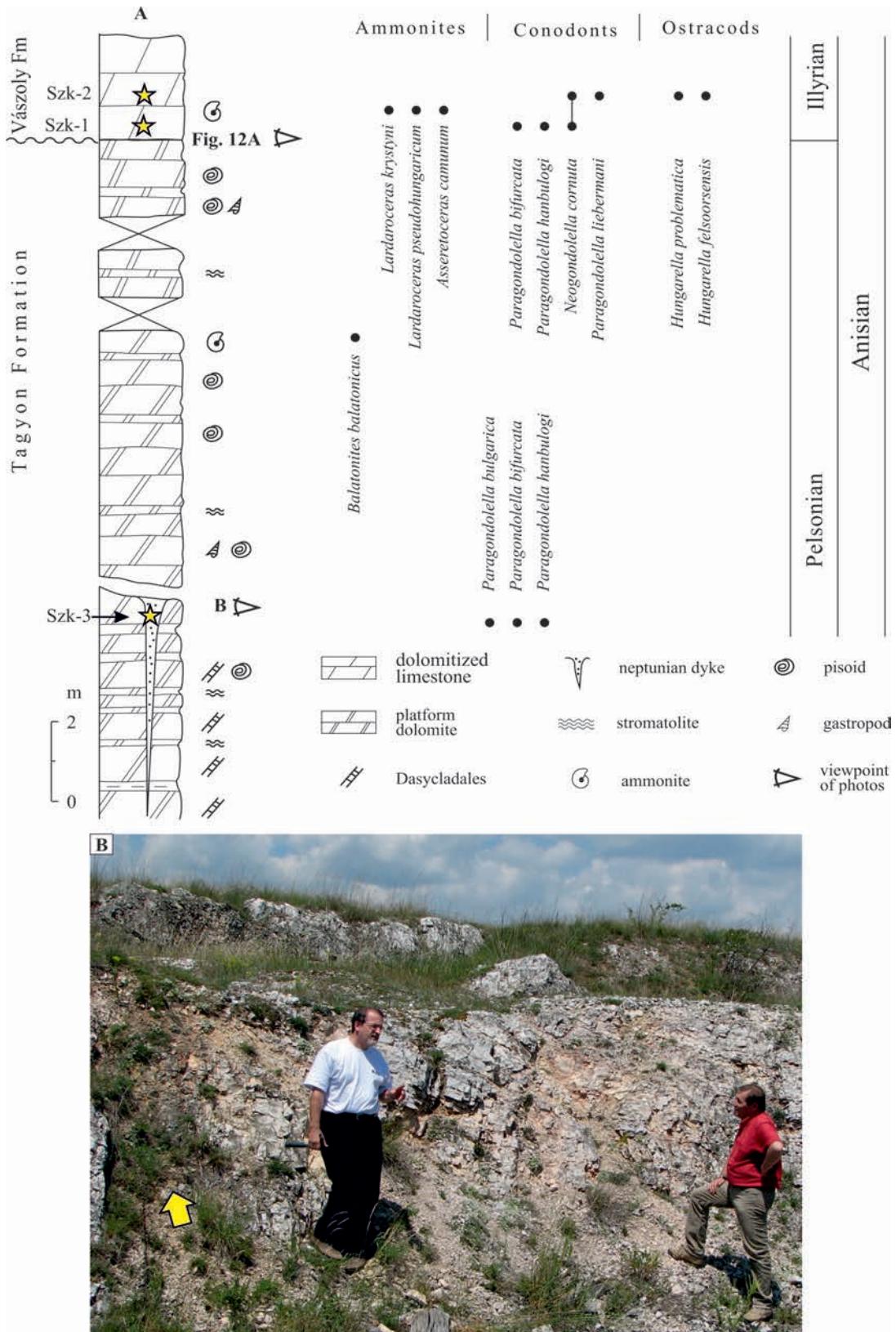
←**5. ábra.** Az Akol-domb szelvényének conodontái. 1) *Neogondolella pseudolonga*, AD-4 minta; 2) *Paragondolella liebermani*, AD-4 minta; 3) *Neogondolella cornuta*, AD-4 minta; 4) *Neogondolella mesotriassica*, AD-4 minta; 5) *Neogondolella cornuta*, AD-3 minta; 6) *Paragondolella excelsa*, AD-3 minta; 7) *Neogondolella cornuta*, AD-3 minta; 8) *Paragondolella hanbulogi*, AD-6 minta; 9) *Paragondolella bulgarica*, AD-6 minta; 10) *Paragondolella bifurcata*, AD-6 minta; 11) *Nicoraella germanica*, AD-6 minta; 12) *Nicoraella kockeli*, AD-6 minta; 13) *Paragondolella bulgarica*, AD-7 minta. a: felülnézet, b: oldalnézet, c: alulnézet. Skála: 200 µm

### Dörgicse Drt-1 well

The Dörgicse Drt-1 well ( $N\ 46^{\circ}55'31.68''$ ,  $E\ 17^{\circ}43'45.93''$ ) exposed the Middle Anisian to lowermost Carnian succession of the middle part of the Balaton Highland (Drt in *Fig. 1*). The cyclic platform carbonate of the Tagyon Fm. is overlain with a sharp contact by a light brownish crinoidal limestone of the Vászoly Fm. (*Fig. 8*), which contains ammonites of the lower Illyrian Camunum/Pseudohungaricum Subzone (VÖRÖS 1998, 2018). It is overlain by a colourful (green reddish or lilac) tuffitic limestone and volcanic tuff (“pietra verde”). The upper part of the formation consists of bedded light grey limestone (“Vászoly Limestone Mb”, VÖRÖS et al. 1997). The overlying Buchenstein Fm. is formed by a colourful (reddish, greenish or lilac) succession of nodular limestone with chert nodules and marl intercalations, alternating with volcanic tuff layers. Radiolarians in the upper part of the formation (*Fig. 8*) belong to the Upper Ladinian (Longobardian) *Muelleritortis cochleta* Zone (DOSZTÁLY 1993). The Füred Limestone Fm. is made up of light grey micritic limestone, with a 10-centimetre-thick marly interlayer in the lower part, containing many thin-shelled bivalves (e.g. *Halobia*) on the bedding surface.

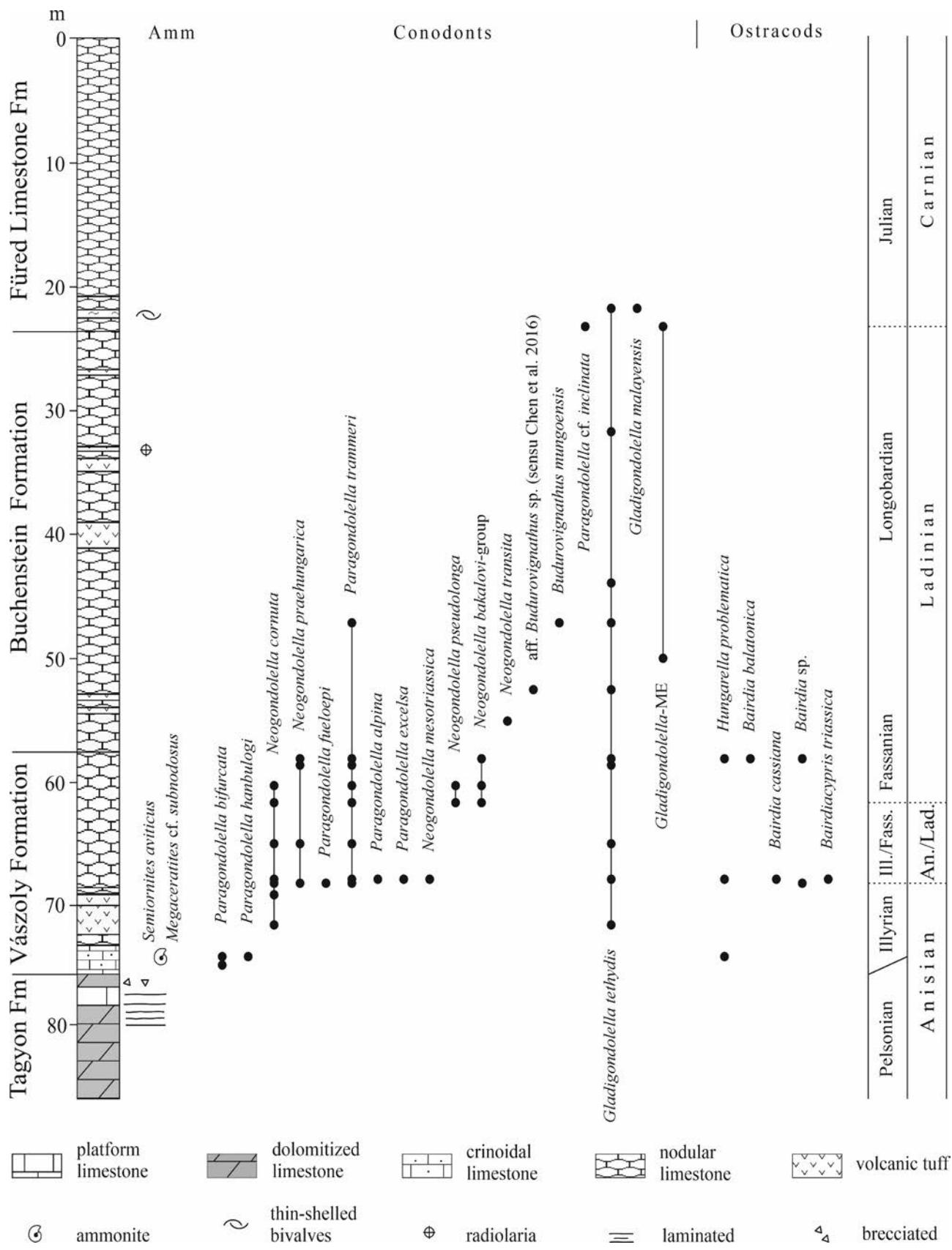
The lowest samples (75.4–75.2 m, 74.6–74.4 m) from the Vászoly Fm. of the Drt-1 core (*Fig. 8*) yielded a conodont fauna characterized by *P. bifurcata* and *P. hanbulogi*. This assemblage is either uppermost Pelsonian or lowermost Illyrian. Somewhat higher, from the samples at 72.8–72.6 m and 69.2–69.0 m a rather poor assemblage was recovered consisting of the species *Ne. cornuta* and *Gladigondolella tethydis*, which indicates Illyrian substage. The following interval (from 68.8 to 61.8 m) can be assigned either to the uppermost Illyrian or to the lowermost Fassanian based on the conodonts *Ne. praehungarica*, *Ne. cornuta*, *Ne. mesotriassica*, *P. fueloepi*, *P. trammeri*, *P. alpina*, *P. excelsa* and *Gl. tethydis*. The lower part of the Fassanian is represented by *Ne. cornuta*, *Ne. pseudolonga*, the *Ne. bakalovi*-group, *Ne. praehungarica*, *Ne. transita*, *P. trammeri* and *Gl. tethydis* from 61.8 m to 55.6 m. In the sample at 53.6–53.4 m a conodont specimen assignable to the genus aff. *Budurovignathus* sensu CHEN et al. (2016) was found. The sample at 47.7–47.4 m contained an assemblage consisting of *P. trammeri*, *Budurovignathus mungoensis* and *Gl. tethydis*, which suggests uppermost Fassanian or Longobardian substage. The conodont *Paragondolella cf. inclinata* in sample at 23.7–23.5 m is indicative of the Longobardian or the Julian (Lower Carnian). In the highest positive sample of the core (22.4–22.1 m) only long-ranging *Gl. tethydis* and *Gl. malayensis* were found.

The ostracod fauna found in the samples between 74.6 to 57.4 m from the nodular limestone of Vászoly Fm. is very similar to the assemblage of Akol Hill. Smooth healdoids



**Figure 7.** Stratigraphic column (A) of the airport quarry at Szentkirályszabadja (after BUDAI et al. 2001) indicating the sites of the samples for micropaleontology (yellow asterisk). Ammonoid data after VÖRÖS (1998, 2018) and VÖRÖS et al. (2003). Photograph (B) shows the two jubilant paleontologists in 2007 on a field-trip, studying the neptunian dyke (yellow arrow) that penetrates the Tagyon Fm. (photo: Zs. KERCSMÁR)

**7. ábra.** A szentkirályszabadjai repülőtéri kőfejtő rétegoszlopja (A) (BUDAI et al. 2001 nyomán), feltüntetve a mikropaleontológiai minták helyét (sárga csíkkal). Ammoniteszadatok VÖRÖS (1998, 2018) és VÖRÖS et al. (2003) nyomán. A fényképen (B) a két ünnepelt paleontológus látható egy kiránduláson 2007-ben a Tagyon Formációt harántoló neptúni telér (sárga nyíll) tanulmányozása közben (fotó: KERCSMÁR Zs.).



**Figure 8.** Stratigraphic column of Dörgicse Drt-1 drill core (after BUDAI et al. 1993, 1999b) showing the stratigraphic position of the conodont and ostracod taxa. Ammonoid data are based on VÖRÖS (1998)

**8. ábra.** A Dörgicse Drt-1 fúrás rétegoszlopá (BUDAI et al. 1993, 1999b nyomán), feltüntetve a conodonta és ostracoda taxonok rétegtani elterjedését. Ammoniteszadatok VÖRÖS (1998) nyomán

(*Hungarella problematica*), smooth bairdiacypridiids (*Bairdiacypris anisica*) and bairdiids (*Bairdia cassiana*) form the ostracod assemblage. The fauna suggests open marine deep neritic depositional environment below the storm wave base like in the Akol Hill section. Unrepresented numbers of *Hungarella problematica* and *Bairdia* sp. were recovered from the samples (23.7–23.5 m and 22.4–22.1 m) of Füred Limestone.

## Discussion

In the studied region, the Pelsonian platform carbonates (Tagyon Fm.) are directly overlain by ammonite bearing crinoidal limestone/dolomite beds representing the basal part of a deeper-water hemipelagic basin succession (Vászoly Fm.). Accordingly, examples for the platform drowning could be encountered and studied here and the new micro-paleontological investigations provided new data for the ex-

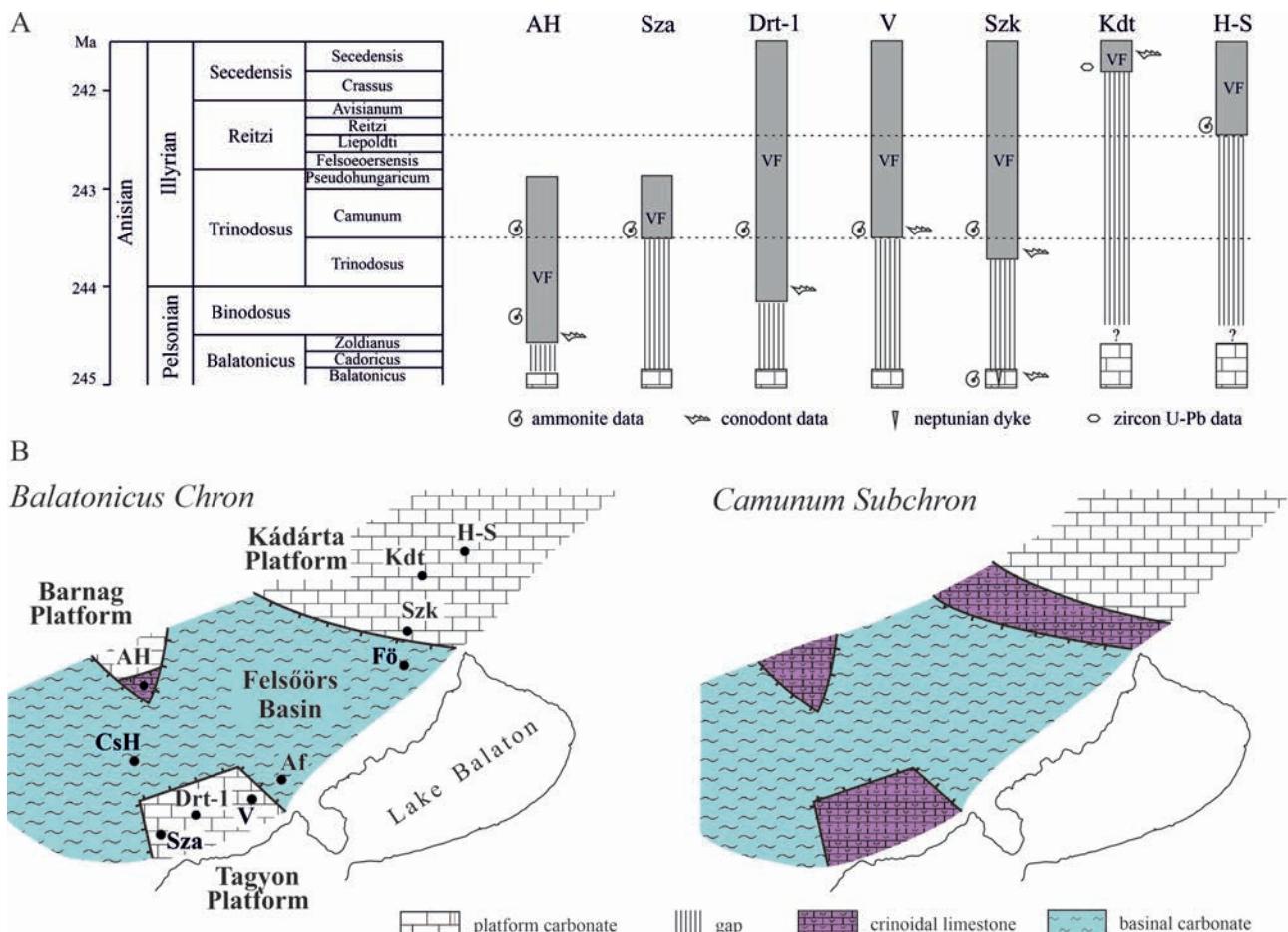
act dating and better understanding the process of this drowning event.

The previously published biostratigraphic data (VÖRÖS et al. 1997, VÖRÖS 1998, BUDAI & VÖRÖS 2006, VÖRÖS 2018, KARÁDI et al. 2022) and our new conodont stratigraphic results confirmed that ages of the base of the post-drowning successions above the Pelsonian platforms are different (Fig. 9, A).

Three Pelsonian platforms were recognised in our study area (Barnag, Tagyon and Kádárta Platforms; Fig. 9, B and Fig. 10) although only a small part of the Barnag platform was explored.

### Extensional tectonics

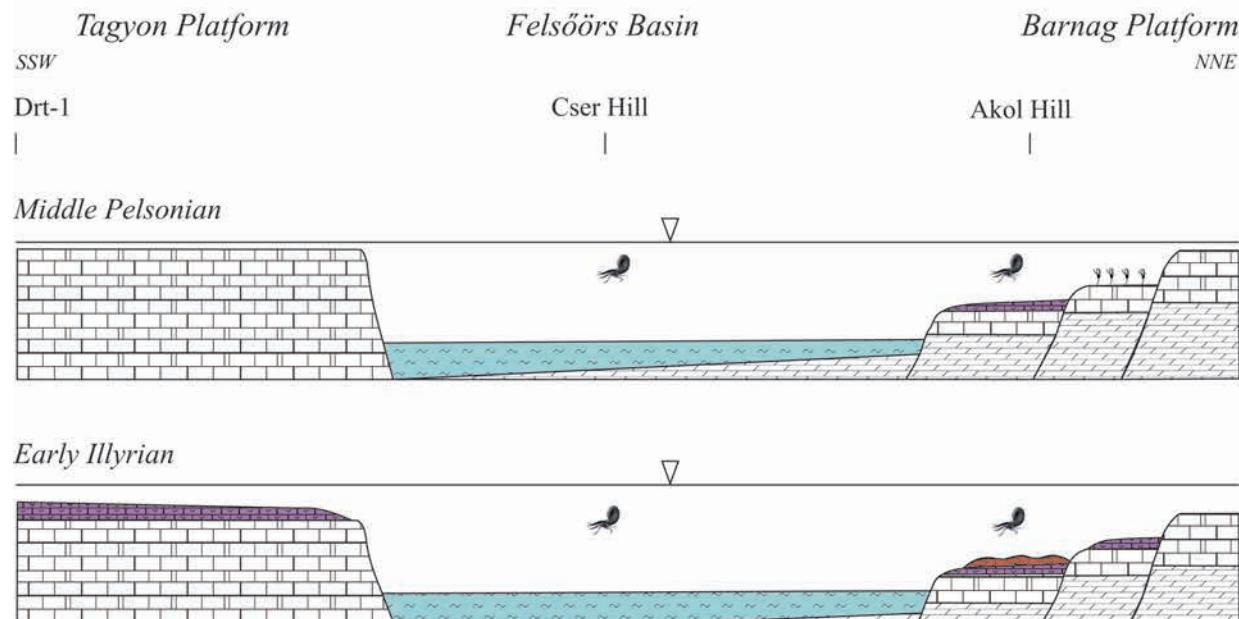
To determine the timing of the extensional tectonic activity we obtained data from the margin of the Kádárta Platform. The conodont fauna of the neptunian dyke in the Szentkirályszabadja quarry (Fig. 7) proves Pelsonian age.



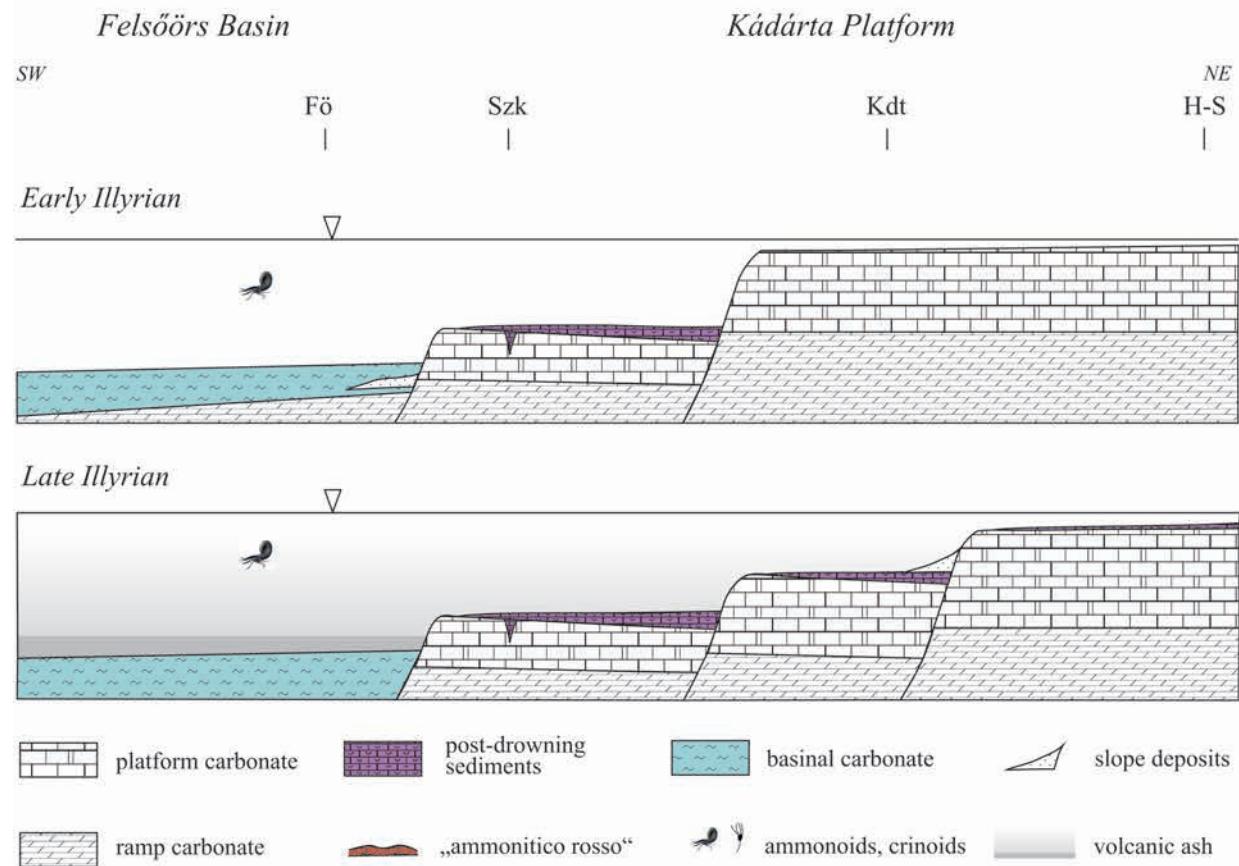
**Figure 9.** A) Simplified stratigraphic charts of the studied sections showing the gap between the Pelsonian platform carbonate (Tagyon Fm.) and the overlying oldest basin sediments (VF – Vászoly Fm.). AH: Akol Hill (VÖRÖS et al. 2022); Sza: Szentantalfa (VÖRÖS 2018); Drt-1: Dörgicse drill core (VÖRÖS 2018; conodonts this paper); V: Vászoly (VÖRÖS 2018; conodonts Kovács 1994); Szk: Szentkirályszabadja (VÖRÖS 2018; conodonts this paper); Kdt: Kádárta (KARÁDI et al. 2022); H-S: Hajmáskér-Sóly (VÖRÖS 2018). B) Palaeogeographic sketch of the Balaton Highland for the Pelsonian and for the early Illyrian showing the reconstructed position of the three isolated carbonate platforms and the hemipelagic basin between them (after BUDAI & VÖRÖS 2006; modified).

**9. ábra.** A) A vizsgált és hivatkozott szelvények egyszerűsített rétegtani táblázata, a pelsoi platformkarbonátok és a legidősebb medencefáciésű fedő üledékek (VF – Vászolyi F) közötti üledékhézag feltüntetésével. B) A Balaton-felvidék ösföldrajzi vázlata a pelsoi és a kora illír korszakban, a három karbonátplatform és a közöttük lévő, hemipelágikus medence rekonstruált helyzetével (BUDAI & VÖRÖS 2006 nyomán, módosítva)

A



B



**Figure 10.** Palaeogeographic profile A) between the Barnag and Tagyon platforms through the Felsőörs Basin and B) across the transition of the Felsőörs Basin and the Kádárta Platform. For the name of the studied/referred sections see Fig. 1.

**10. ábra.** Ősföldrajzi szelvény A) a Barnagi- és a Tagyon-i-platform között, a Felsőörsi-medencén keresztül; valamint B) a Felsőörsi-medence és a Kádárta-i-platform érintkezésén keresztül. A vizsgált/hivatalos szelvények nevét lásd az 1. ábrán

This date corresponds well with adjacent parts of the western Neotethys shelf (*Fig. 11*). In the Monte Rite area of the Southern Alps (SA in *Fig. 11*) FARABEGOLI & GUASTI (1980) reported three generations of neptunian dykes that penetrate the Pelsonian Upper Serla Platform. In the Aggtelek–Rudabánya Unit (A–R in *Fig. 11*) the Middle Anisian Steinalm Ramp is dissected by neptunian dykes, filled by red pelagic limestone rich in fragments of thin-shelled bivalves (“filaments”). Based on conodont assemblages, Late Pelsonian and Early–Middle Illyrian dyke generations were identified (VELLEDITS et al. 2011). Similar dual dyke generations were observed in the Schreyeralm area of the Northern Calcareous Alps (Austroalpine Units in *Fig. 11*; VELLEDITS et al. 2017; GAWLICK et al. 2021). In the Dinarides (OD in *Fig. 11*) the neptunian dykes that penetrate the Pelsonian platform carbonate (Ravni Fm.) started to form in the Late Pelsonian (SUDAR et al. 2013). In the Late Illyrian the tectonic activity intensified again and the dykes cross-cut not only the platform carbonates but the older post-drowning basinal deposits (Bulog Limestone), as well (GAWLICK et al. 2023).

### Platform drowning

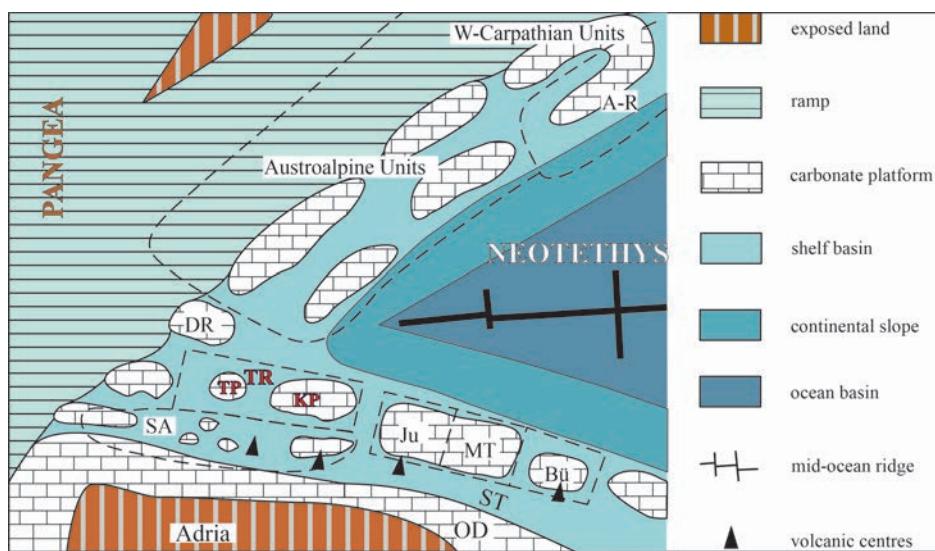
In the Akol Hill section at Barnag (*Fig. 4*, AH in *Fig. 9, A, B*) above the extremely thin Tagyon Limestone the conodont fauna constrains Pelsonian age for the basal crinoidal limestone beds. This indicates a relatively early flooding above the block-faulted margin of the Barnag Platform in the Middle Anisian (*Fig. 10, A*). The Early Illyrian ammonite fauna of the overlying condensed “ammonitico rosso” limestone also contains Pelsonian forms (VÖRÖS et al. 2022). The dissolved specimens coated by Fe–Mn oxide crust suggest

very slow and episodic sedimentation in a current dominated environment.

In the area of the Tagyon Platform, on the basis of the ammonite fauna, the basal beds can be assigned to the Early Illyrian (Camunum Subchron, VÖRÖS 1998; BUDAI & VÖRÖS 2006; VÖRÖS 2018) in both the Szentantalfa (Sza in *Fig. 9, A, B*) and in the core Dörgicse Drt–1 (*Figs 8 and 9, A, B*). It has to be mentioned that in the case of conodonts the Early Illyrian age of the lowermost layers of the Vászoly Fm. in Dörgicse Drt–1 core is only based on the lack of the Pelsonian *P. bulgarica*. However, this can easily be a bias caused by the very limited material available for conodont investigation. Since *P. bifurcata* and *P. hanbulogi* are also present prior to the Illyrian, a Late Pelsonian age of the basal beds cannot be excluded. In the marginal Vászoly section (V in *Fig. 9, A, B*) the age of the oldest post-drowning sediment is Early Illyrian (Camunum Subchron) based on ammonoids (VÖRÖS 1998, 2018) and conodonts (KOVÁCS 1994), as well.

In the Szentkirályszabadja section (*Fig. 7*, Szk in *Figs 9, A, B* and *10, B*), which may have been located near the western margin of the Kádárta Platform, the basal post-drowning hemipelagic carbonate beds (*Fig. 12, A*) can be assigned to the Early Illyrian (Camunum Subchron). However, conodonts found in the dyke prove earlier, Late Pelsonian drowning as a result of downfaulting of the platform margin. In the section of the Kádárta quarry (*Fig. 12, B*), representing the internal part of this platform (*Fig. 9, B*), based on conodont and zircon age data (*Fig. 9, A*; KARÁDI et al. 2022) latest Illyrian age (Secedensis Chron) of the volcaniclastic beds of the Vászoly Fm. was pointed out. In the internal platform area at Hajmáskér–Sóly, based on ammonoid data (VÖRÖS 2018), somewhat older age (Reitzi Subchron) was determined for the oldest post-drowning sediments.

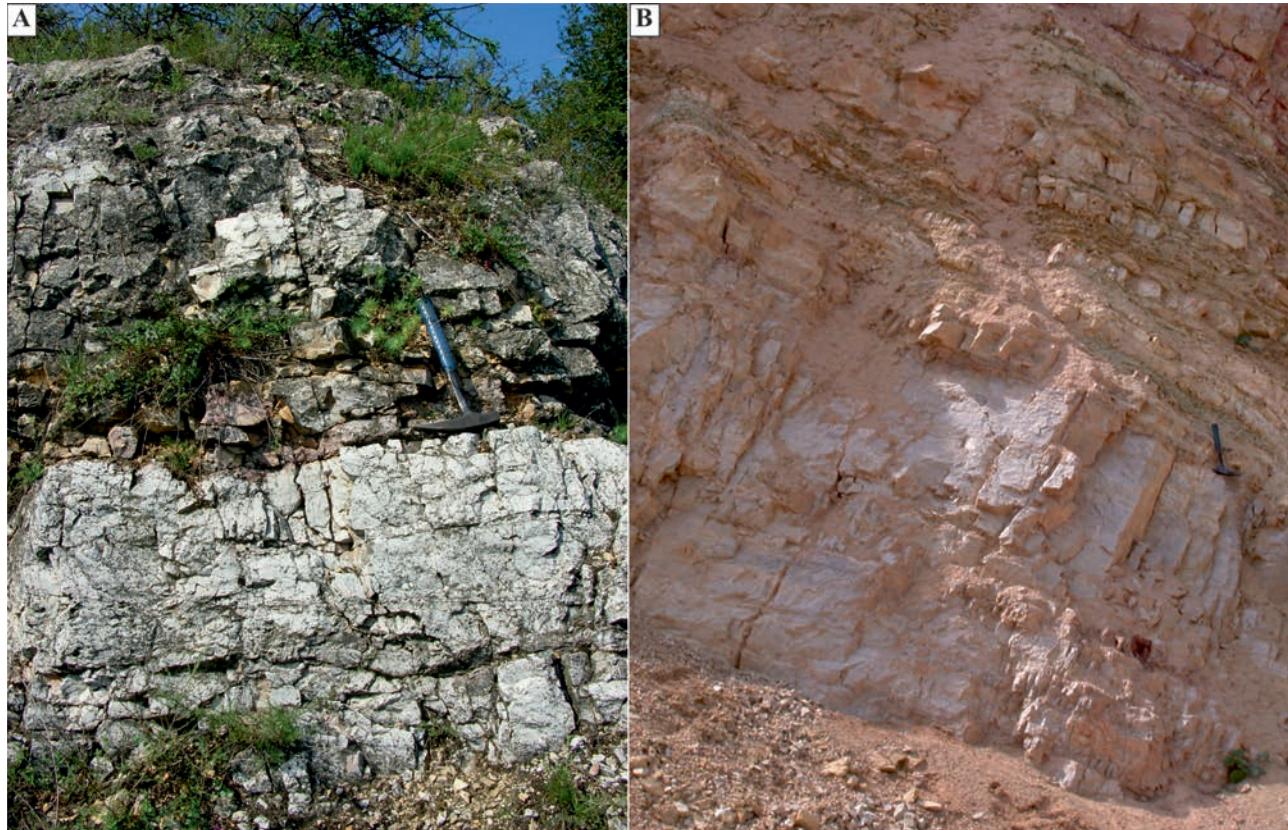
We must note that the age data for the base of the post-drowning succession provide information on the age of first record of the post-drowning deposition, which is not necessarily identical to the timing of the drowning event. In many cases the drowning is followed by a period of non-deposition leading to a short- or long-term stratigraphic gap (READ 1982, 1985; SCHLAGER 1989, 1991, 2005). The drowning is commonly preceded by sub-aerial exposure and erosion of the platform that resulted in the apparent increase in the duration of the gap. Various factors (in many cases combination of several factors) may lead to the drowning of carbonate platforms. In exten-



**Figure 11.** Palaeogeographic setting of the Tagyon Platform (TP) and the Kádárta Platform (KP) within the Transdanubian Range Unit (TR) during the Middle Triassic in the western part of the Neotethys (BUDAI et al. 2017, KARÁDI et al. 2022)

A–R: Aggtelek–Rudabánya Unit; Bü: Bükk Unit; DR: Drau Range; Ju: Julian Alps; MT: Mid-Transdanubian Unit; OD: Outer Dinarides; SA: South-Alpine Units; ST: Slovenian Trough

**11. ábra.** A Tagyon-i-platform (TP) és a Kádárta-i-platform (KP) középső triász ősföldrajzi helyzete a Dunántúli-középhegységi-egységen (TR) belül a Neotethys nyugati selfjén (BUDAI et al. 2017, KARÁDI et al. 2022)



**Figure 12.** Drowning unconformity on the top of the Pelsonian Tagyon Fm. (at the hammer), that is covered by A) dolomitized ammonitic Lower Illyrian limestone (Camunum Subzone) in the quarry at Szentkirálysabadjá; and B) uppermost Illyrian volcaniclastic layers (Sectedensis Zone) in the quarry at Kádárta

**12. ábra.** Megfulladási diszkordancia felszín a pelsói Tagyoni Fm. felső határán (kalapács a képeken), amelyre A) ammoniteszes, dolomitosodott alsó illyr mészkő (Camunum Szubzóna) települ a szentkirálysabadjai kőfejtőben; és B) legfelső illyr vulkanoklasztit rétegsor (Sectedenis Zóna) települ a kádártai kőfejtőben

sional structural regimes the tectonically forced retrograding of the margin may result in an exceptionally fast subsidence of the downfaulted blocks and, accordingly, the end of the production of the euphotic carbonate factory (*Fig. 10, B*). Coeval acceleration of subsidence and an intense eustatic sea level rise may also lead to drowning. Decreasing water transparency and, consequently, the shallowing of the light-saturated zone may also be a dominant factor in the drowning or may contribute to this phenomenon. Influx of large amount of suspended terrigenous material (clay and/or fine organic material) or extreme proliferation of planktonic organisms may be responsible for the reduced transparency.

At the beginning of the Pelsonian, the Akol Hill section was located in the external belt of the Barnag Platform (*Fig. 9, B*). Here, the Pelsonian drowning can be attributed to downfaulting of the platform margin when a fault-controlled and probably step-like slope may have come into being (*Fig. 10, A*). The drowning was likely followed by a period of non-deposition due to high-energy currents. Resedimented fragments of crinoids in the basal bed of the post-drowning succession may have been derived from higher terraces of the slope (*Fig. 10, A*), similar to the sedimentation model proposed by GALÁCZ & VÖRÖS (1972) and GALÁCZ (1988) for the Early Jurassic deposition of the Hierlatz-type limestones. The overlying condensed bed-set with a rich but partly reworked, mixed ammonite fauna reflects high-ener-

gy depositional conditions allowing only ephemeral sediment deposition and preservation.

In the area of the Tagyon Platform the drowning took place prior to the Early Illyrian (Camunum Subchron) both in near margin setting that is represented by the Vászoly sections (V in *Fig. 9, A, B*), and also in the central part of the isolated platform that is represented by the Szentantalfa section (Sza in *Fig. 9, A, B*) and the Dörgicse Drt-1 drill core (*Fig. 9, A, B* and *Fig. 10, A*). To determine the cause of the drowning we must take into account the facies of the basal beds of the post-drowning succession. They are made up of carbonate layers rich in radiolarians, fragments of thin-shelled bivalves, crinoids, ammonites and brachiopods and volcanic tuff interlayers. This bed set is punctuated by phosphoritic horizons along the NE platform margin represented by the Vászoly section (BUDAI et al. 2017). These litho- and biofacies characteristics suggest that along with the accelerated subsidence of this block and the coeval eustatic sea-level rise the reduced transparency as a result of enhanced productivity and input of volcanic dust might have played a critical role in the drowning. The radiolarians are indicators of high productivity of the surface waters, which depends on the fertility controlled by the availability of limiting nutrients (e.g. P, Si) (DE WEVER & BAUDIN 1996, DE WEVER et al. 2014). Due to common abundance of radiolarians in pyroclast-bearing successions, the role of input of volcanic dust

in the fertilization of sea-surface was also put forward (LIN et al. 2011, ABDI et al. 2016). Considering the palaeogeographic constrains, a monsoon-driven local upwelling and/or the input of volcanic material seems to be the source of the limiting nutrients along the margin of the Tagyon Platform (BUDAI et al. 2017).

In the marginal area of the Kádárta Platform (Szentkirályszabadja quarry, Szk in Fig. 9, A, B and 10, B) pedogenic crusts or stromatolitic horizons (akin to those in the core Drt-1) occur between the thick beds of the platform carbonate containing a rich shallow marine fossil assemblage. Accordingly, this succession reflects periodically changing depositional conditions; shallow marine lagoon and peritidal environments alternated as a consequence of the high frequency sea-level oscillation (HAAS et al. 2014). In contrast, in the inner part of the Kádárta Platform (Kádárta quarry, Kdt in Fig. 9, A, B and 10, B) at least in the upper part of the Tagyon Formation, the peritidal horizons are subordinate suggesting permanency of the subtidal depositional setting even during the periods of lowest sea level (HAAS et al. 2022). According to biostratigraphic constrains, the age of the basal part of the post-drowning succession is Illyrian in both sections (Fig. 9, A); however, it does not mean that the drowning took place at the same time. It is more probable that, due to downfaulting of the platform margin zone, the drowning happened earlier in the Szentkirályszabadja area (Figs 9, A and 10, B), although on the top of the downfaulted block the intense current activity hindered sediment deposition for a while, which could only accumulate in the fissures. Conversely, in the more internal part of the platform, which is represented by the Kádárta quarry section, the shallow marine conditions may have been prolonged during the Early Illyrian, although there are no exact biostratigraphic data for this. Nevertheless, the latest Illyrian was already characterized by deep-water sedimentation in this area as well (Figs 9, A and 10, B; KARÁDI et al. 2022). The thick sedimentary breccia bed set, occurring above the post-drowning pelagic tuffaceous dolomite layers, can be interpreted as a platform foreslope deposit indicating the presence of the coeval platform margin near this place (Fig. 9, C). Further northeast in the Hajmáskér–Sóly sections (H-S in Figs 9, A, B and 10, B) the oldest post-drowning layers are somewhat older; based on ammonoid biostratigraphic data they belong to the Reitzi Subzone of the Reitzi Zone (VÖRÖS 2018). In this area the intense volcanic activity, i.e. the related reduced water transparency, may have been the major controlling factor of the drowning since thick tuff layers were deposited at that time in the Felsőörs basin (BUDAI & VÖRÖS 1993, BUDAI et al. 2001). However, the role of tectonic retrograding cannot be excluded either, which continued even during the Ladinian as it was proven by a neptunian dyke in the Litér quarry containing a Ladinian ammonite assemblage (BUDAI et al. 2001, BUDAI & VÖRÖS 2006).

Drowning of the Middle Triassic platforms may have taken place at different times also in other parts of the western Neotethys shelf (KARÁDI et al. 2022 and references therein). For example, in the Aggtelek–Rudabánya Unit (AR

in Fig. 11) the Steinalm Limestone is overlain by the post-drowning sequence of the Schreyeralm Limestone of Late Pelsonian age in the Baradla Cave section (VELLEDITS et al. 2011, PERÓ et al. 2015), while the basal part of the red pelagic ammonitic limestone belongs to the lower Illyrian Trinodosus Zone in the Szár Hill section (VÖRÖS 2010). On the southern shelf of the rifting Neotethys (Fig. 11) the volcanic activity was much more intense (VELLEDITS 2009) and, accordingly, it played a more decisive role in the basin evolution from the Pelsonian until the Ladinian (SMIRCIC et al. 2020, KUKOC et al. 2023).

The palaeoenvironmental reconstruction based on ostracod palaeoecology reflects well the deepening of the Felsőörs Basin (KOZUR 1970, MONOSTORI 1995) and the flooding of the Middle Anisian isolated platforms during the Late Anisian. Very similar ostracod faunas (dominance of smooth bairdiids, bairdiacypridids and healdoids) were identified above the platform carbonates in the Illyrian beds (Vászoly Fm.) of the studied sections in Szentkirályszabadja quarry, Akol Hill and the Drt-1 core. The ostracod assemblages indicate deep neritic open shelf environment with water depth below 30–50 m (below the storm wave base) supporting the deepening of the basin above the former Kádárta, Barnag and Tagyon platforms during the Illyrian. The appearance of the thin-shelled ‘palaeopsychrophaeric elements’ with long spines such as bairdiid *Acratia*, beecherellid *Acanthoscapha*, tricorninid *Nagyella* and macrocypridid *Praemacrocypris* in the Ladinian ostracod fauna of the Litér and Kádárta quarries suggests the climax of the deepening of the basin with water depth below 200 m (upper bathyal zone). This represents the maximum flooding of the Kádárta Platform during the Longobardian (MONOSTORI & TÓTH 2013, KARÁDI et al. 2022).

## Conclusions

Drowning of the Middle Anisian platforms of the Balaton Highland was mostly controlled by the onset of block-faulting during the Pelsonian. Accordingly, the earliest drowning and post-drowning deposition may have taken place in the Pelsonian at the edge of the Barnag Platform (Akol Hill).

On the Tagyon Platform (Szentantalfa, Dörgicse and Vászoly), where the first post-drowning basinal layers were deposited during the Late Pelsonian or Early Illyrian, the drowning was probably governed by the accelerated relative sea-level rise, although the reduced water transparency, triggered by enhanced productivity in the upwelling zone and input of volcanic dust, may also have played some role in it.

The marginal area of the Kádárta Platform (Szentkirályszabadja) faulted down in the Pelsonian, however, the post-drowning deposition occurred in the Early Illyrian. In the inner parts of this platform (Kádárta and Hajmáskér–Sóly area) pelagic sediments deposited from the Late Illyrian indicating a step-by-step faulting of the platform.

During the Ladinian bathyal environment was established everywhere in the study area as a result of continuing sea level rise.

## Acknowledgement

The authors greatly appreciate the reviewers' (F. VELLEDITS and H. J. GAWLICK) meticulous proofreading work, which significantly improved the quality of the manuscript.

Present research was supported by the National Research, Development and Innovation Office (NKFIH K 124313 and NKFIH FK 134229 grants). Emőke TÓTH was also supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences.

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Manuscript received: 27/11/2023

## Disparity, diversity and body size changes of the Toarcian Spiriferinides (Brachiopoda, Lower Jurassic) in the westernmost Tethys

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*Diszparitás, diverzitás és méretváltozás a toarci Spiriferinidákban (alsó jura, Brachiopoda)  
a Tethys legnyugatabbi területein*

### Összefoglalás

Az Ibériai-masszívumot körülvevő spanyol és portugál medencék Spiriferinida-szukcessziója világviszonylatban is a csoport egyik legteljesebb és legjobban ismert fosszilis rekordját jelenti. Annak ellenére, hogy a csoporton belüli faji diverzitás alacsony, az Ibériai-masszívumot körülvevő medencékből a paleozoikum utáni fontosabb morfotípusok ismeretek. Ilyen módon ezek az alakok közvetlenül a kora toarci tömeges kihalási esemény előtt „az elveszett Éden” utolsó képviselőinek tekinthetők. A brachiopodák morfológiai és testméretváltozásait a tömeges kihalás idejének megfeleltethető késő pliensbach – kora toarci során a *Liospiriferina*-nemzetseg réteg szerint gyűjtött maradványain vizsgáltuk. A cél a morfológiai változások vizsgálata volt az adott időszakra jellemző hipertermális esemény tükrében. A példányok az Ibériai-hegység két szelvényéből származnak. Az eredmények azt mutatják, hogy a csoport diverzitásának kezdeti hanyatlása és a korai méretcsökkenés a toarci elején bekövetkezett első komolyabb felmelegedési epizóddal állítható párhu-zamba. A nemzetseg utolsó képviselőinél megjelenő nagy méretű formák pedig feltehetően a tengervíz rövid ideig tartó, de erős lehűléstől kapcsolatosak. Ez a lehűlés két jelentős felmelegedési szakasz közé ékelődött, és ez lehetett a Spiriferinida-klád kihalásának kiváltó oka.

Tárgyszavak: *brachiopoda, Spiriferinida, Liospiriferina, jura, toarcia, Tethys, Ibériai-masszívum*

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### Abstract

The fossil record of the Order Spiriferinida in the Toarcian basins surrounding the Iberian Massif (Spain and Portugal) is exposed as one of the most well-known, complete, and continuous worldwide. Despite the low specific diversity intrinsic to this group, the peri-Iberian basins include representatives of the main different morphological types recognized throughout the post-Paleozoic history of the group, representing the ultimate “Lost Eden” for this clade before its definitive demise in the Early Toarcian Mass Extinction Event (ETMEE). The changes in morphology and body size observed during the latest Pliensbachian–earliest Toarcian, corresponding to the Extinction interval of the ETMEE, are analyzed in specimens of the genus *Liospiriferina* carefully recorded bed by bed in two stratigraphical sections of the Iberian Range, in order to establish their detailed relationship with the evolution of the seawater temperature during this hyperthermal event. This analysis has revealed an initial decrease in diversity and size coinciding with the first important warming episode at the beginning of the Toarcian, while the big sizes observed in the last representatives of this genus probably correspond with a short but intense event of seawater cooling, intercalated in the severe warming episode that most probably was the main triggering factor of the spiriferinide clade extinction.

Keywords: *Brachiopoda, Spiriferinida, Liospiriferina, Jurassic, Toarcian, Tethys, Iberian Massif*

## Introduction

The Lower Jurassic spiriferinides (Order Spiriferinida IVANOVA, 1972) together with the ultimate representatives of the Order Athyridida BOUCOT et al., 1964, constituted the only spire-bearing groups recorded in the Mesozoic in contrast with the extraordinary proliferation of these clades in the Paleozoic times. These orders became extinct coinciding with the last clade (or “fatal”) extinction (*sensu* VÖRÖS et al. 2019) in the evolutionary history of brachiopods, occurred in a timespan with critical perturbations in the environmental conditions of marine ecosystems, culminating ca. 183 Ma in the so-called Early Toarcian Mass Extinction Event (ETMEE). Remarkably, the extinction of the Paleozoic spire-bearing brachiopods also coincided with preceding events matching with the concept of “fatal extinctions” introduced by VÖRÖS et al. (2019) to denote those episodes of synchronous extinction of high-grade taxa. It can therefore be stated that the last three fatal extinctions in the history of brachiopods especially affected the spire-bearing groups (VÖRÖS et al. 2016, 2019), i.e., the Devonian crisis extinguishing Atrypida; the End-Permian extinction affecting Spiriferida; and the ETMEE where Spiriferinides and Athyrididae became extinct (VÖRÖS 2002; GARCÍA JORAL et al. 2011; BAEZA-CARRATALÁ et al. 2015, 2017; VÖRÖS et al. 2016, 2019), excluding those from New Zealand attributed to *Spiriferina* by MACFARLAN (2023), occurring in the Bifrons Zone, c.a. 1 Ma post-ETMEE. No other order of brachiopods became extinct since this last event.

On the other hand, another of the many inspired ideas put forward by Attila Vörös throughout his prolific career was to consider the Jurassic spiriferinides (along with the athyrididae) as a “Dead Clade Walking” (*sensu* JABLONSKI 2002), alluding to their low diversity after surviving the severe end-Triassic extinction event and remaining in decline in the Early Jurassic (VÖRÖS et al. 2016, 2019) up to their total extinction in the critical perturbation of the ETMEE. Thus, representatives of the Order Spiriferinida are profusely and widely recorded throughout the Western Tethys in the Early Jurassic but, despite their conspicuous occurrences, they have been arranged only in a very few long-established genera (e.g., ROUSSELLE 1977; MANCEÑIDO 1981, 2004; DULAI 2003; VÖRÖS et al. 2003; CARTER & GOURVENNEC 2006; COMAS-RENGIFO et al. 2006; VÖRÖS 2009; MANDL et al. 2010; HE et al. 2015; BAEZA-CARRATALÁ et al. 2016c) denoting a relatively low supraspecific taxonomic diversity in contrast to their great abundance.

Likewise, another awe-inspiring concept put forward by VÖRÖS was to consider the Western Tethys Ocean as the “Lost Eden” for brachiopods (VÖRÖS 1993, 2005; VÖRÖS et al. 2016) representing the most important refuge for this epibenthic biota during the different Mesozoic biotic crises, including that of the ETMEE in which the spire-bearing groups finally became extinct.

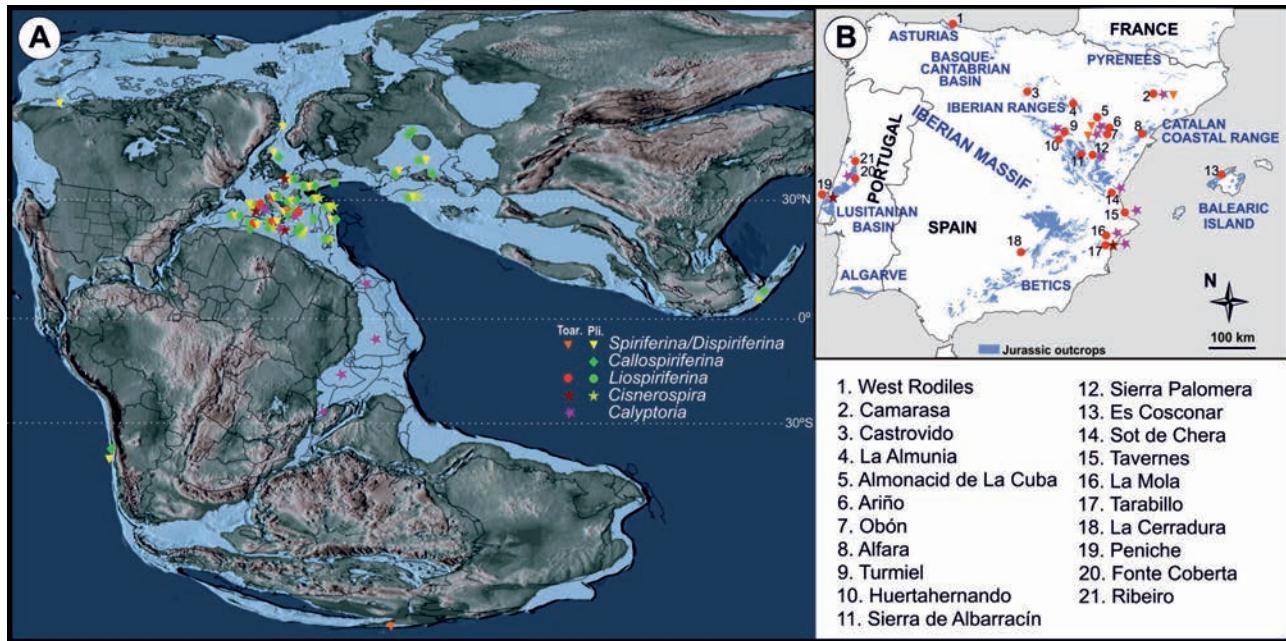
These three aforementioned concepts introduced and developed by Attila VÖRÖS over the last decades have become a paradigm that supports outstanding interpretations

on the paleobiogeographic distribution and on the different adaptive strategies undertaken by different Jurassic brachiopod groups, especially around the ETMEE. In the framework of these precepts, the present work analyzes the changes and adaptations experienced by the last spiriferinides in the westernmost part of the Tethys Ocean during the Early Toarcian. The morphology and body size variations of representatives of this clade over time around ETMEE are quantified and their morphospaces are explored on the basis of the dataset derived from the marginal peri-Iberian platforms system, where spiriferinides have exposed the most complete record preceding their definitive extinction, postulating the sea-water temperature oscillations as a primary factor of environmental control just prior to the hyperthermal maximum recorded in the basal part of the Serpentium Chronozone (GARCÍA JORAL et al. 2011; GÓMEZ & GOY 2011; CARUTHERS et al. 2013; DANISE et al. 2013; BAEZA-CARRATALÁ et al. 2015, 2017; KRENCKER et al. 2020; RUEBSAM et al. 2020; FERNANDEZ et al. 2021; BUCUR & REOLID 2023), just coinciding with the spiriferinides global demise.

## Paleobiogeographic distribution of Jurassic spiriferinides

Jurassic spiriferinides have a worldwide distribution from the Hettangian to the early Toarcian, although most of their known records are comprised in the Western Tethys. In the Pliensbachian, a very high number of spiriferinide species have been described in basins belonging to different bioprovinces of this area (e.g., ALMÉRAS & FAURÉ 2000, COMAS-RENGIFO et al. 2006, ELMI et al. 2007, VÖRÖS 2009, BAEZA-CARRATALÁ 2013, BENZAGGAGH 2023). However, they disappeared in the Toarcian in many basins of the Mediterranean Province, which typically includes more epioceanic areas than the Euro-Boreal one (cf. VÖRÖS & ESCARGUEL 2019). The westernmost part of the Tethys Ocean and its connection with the proto-Atlantic, together with the North-Gondwanan Paleomargin, seems to have represented a last refuge (the final relict of the “Lost Eden”) for spiriferinides in the Early Toarcian (Fig. 1A).

As representatives of this ultimate refuge, the specimens herein analyzed derive from the Lower Jurassic peri-Iberian platforms system, constituted by different basins surrounding the Iberian Massif which, in paleogeographical and geotectonic terms, was operating as an isolated microplate during most of the Mesozoic times. The Jurassic peri-Iberian platforms system constituted, together with the Southern Betic unities (corresponding to the Alborán microplate margins) and the North-African margins, the westernmost marine environments and sub-environments of the Tethys Ocean. In the late Early Jurassic, the proto-Atlantic seaway connected this part of the Tethys with the Arctic and the Panthalassa via the Viking and the Hispanic Corridors (e.g., POULTON & CALLOMON 1977; SMITH 1983; MANCEÑIDO 1990, 2002; MANCEÑIDO & DAGYS 1992; DAMBORENEA 2000; BJERRUM et al. 2001; ABERHAN 2001; SHA 2002; GARCÍA



**Figure 1.** (A) Paleobiogeographic distribution of the Pliensbachian (greenish symbols) and Toarcian (reddish symbols) genera of spiriferinides. Data from the Paleobiology Database, consulted in December 2023, supplemented with data after ALMÉRAS & FAURÉ (2000), ALMÉRAS et al. (2007), VÖRÖS (2009), BAEZA-CARRATALÁ (2008, 2013), and BENZAGGAGH (2023). Paleomap after SCOTSE (2013). (B) Toarcian spiriferinide genera recorded in selected localities from the peri-Iberian basins. Data sources after COMAS-RENGIFO (1982), FERNÁNDEZ-LÓPEZ et al. (1998), COMAS-RENGIFO et al. (1999, 2006, 2013, 2015, 2018a, 2018b), GARCÍA JORAL & GOY (2009), GARCÍA JORAL et al. (2011, 2022), BAEZA-CARRATALÁ et al. (2016a, 2016b, 2017, 2018). Symbols as in (A)

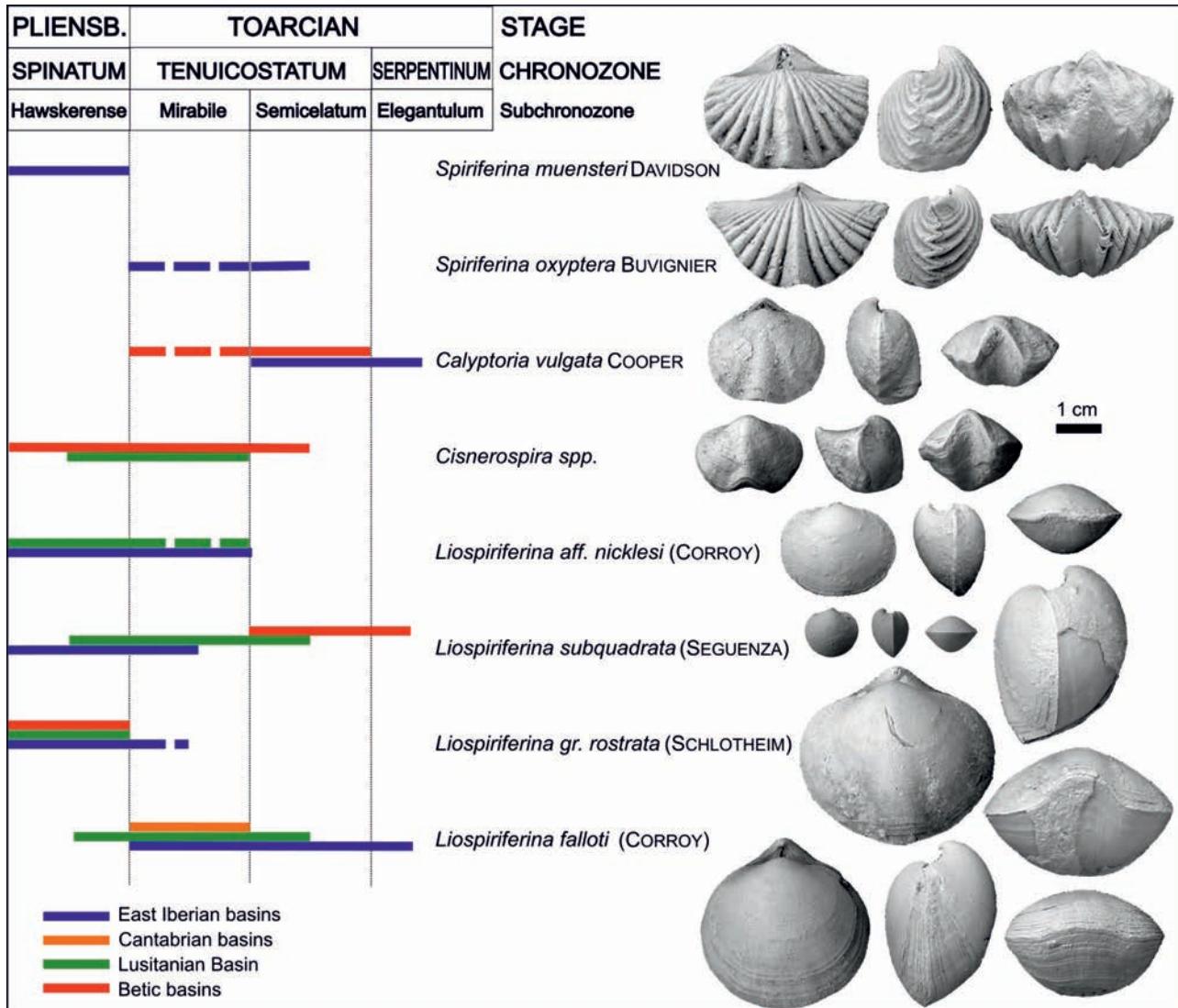
**1. ábra.** (A) A Spiriferinida-nemzetségek paleogeográfiai elterjedése. A pliensbachi előfordulások zöld színnel, a toarciai vörössel jelölve. Az adatokat a Paleobiology Database-ból 2023 decemberében töltöttük le, és kiegészítettük ALMÉRAS & FAURÉ (2000), ALMÉRAS et al. (2007), VÖRÖS (2009), BAEZA-CARRATALÁ (2008, 2013) és BENZAGGAGH (2023) adataival. A paleogeográfiai térképet SCOTSE (2013) nyomán készült. (B) Toarcia Spiriferinida nemzetségek néhány lelőhelye a Peri-Iberiai-medencében. Az adatok COMAS-RENGIFO (1982), FERNÁNDEZ-LÓPEZ és társai (1988), COMAS-RENGIFO és társai (1999, 2006, 2013, 2015, 2018a, 2018b), GARCÍA JORAL & GOY (2009), GARCÍA JORAL és társai (2011, 2022), BAEZA-CARRATALÁ és társai (2016a, 2016b, 2017, 2018) nyomán. Jelkulcs, mint az (A) ábrán

JORAL et al. 2011). The most relevant localities containing Early Toarcian spiriferinides in these basins have been indicated in the figure 1B.

Interestingly, the spiriferinide genera that settled in this area show a morphological disparity in accordance with that shown by the group throughout the Early Jurassic. In this sense, VÖRÖS et al. (2016), taking into account the outline and global shape, differentiated three basic morphogroups among the Lower Jurassic spiriferinides: biconvex, winged, and cyrtiniform. On the other hand, COMAS-RENGIFO et al. (2006), bearing in mind the ribbing pattern of the shell, considered a different arrangement based on the record of this group derived from the northern and eastern peri-Iberian basins, discriminating the fully ribbed, smooth, and sparsely ribbed (including capillate) morphogroups. Combining both criteria, it can be deduced that all the four resulting morphogroups recorded throughout the Early Jurassic are also systematically represented during the Early Toarcian in the peri-Iberian basins (Fig. 2), i.e., *Cisnerospira* (smooth-cyrtiniform), *Spiriferina* (ribbed-winged), *Liospiriferina* (smooth-biconvex), and *Calyptoria* (capillate or scarcely ribbed-biconvex). In fact, this disparity is basically the same as that observed among spiriferinides in the Triassic, when the group expanded and filled the vacant eco- and morphospaces left after the disappearance of their Paleozoic relatives Spiriferides after the Permian-Triassic mass extinction (GUO et al. 2020).

### Geological framework and chronostratigraphic record of spiriferinides around the Iberian paleomargins

In most of the peri-Iberian basins, the Lower Toarcian deposits are arranged in expanded stratigraphic sequences in which spiriferinides have been widely and profusely reported since the 18th century (e.g., TORRUBIA 1754; DESLONGCHAMPS 1863; JIMÉNEZ DE CISNEROS 1921, 1923; DUBAR 1931; DELANCE 1969; COMAS-RENGIFO & GOY 1975; ROUSSELLE 1977; CALZADA 1979; GOY et al. 1984; ARIAS et al. 1992; FERNÁNDEZ-LÓPEZ et al. 1998; GARCÍA JORAL & GOY 2000, 2009; GAHR 2002; COMAS-RENGIFO et al. 2006, 2013, 2015; GARCÍA JORAL et al. 2011, 2022; BAEZA-CARRATALÁ 2011, 2013; BAEZA-CARRATALÁ et al. 2016a, 2016b, 2017, 2018). For the sake of consistency, the well-established record of spiriferinide taxa along the Tenuicostatum (Poly-morphum)-Serpentinum chrono-zones in the peri-Iberian basins have been summarized in four regions on the basis of their paleobiogeographic situation and differences among depositional environments: i.e., those forming part of the East-Iberian Platforms System (*EIPS*: Iberian Range, Catalonian Coastal Range and the Balearic Basin); the Northern-Cantabrian paleomargin (Asturias and Basque-Cantabrian Basins); the Atlantic paleomargin (Lusitanian Basin); and the South-Iberian paleomargin (Subbetic-Alborán regions).



**Figure 2.** Chronostratigraphic distribution of the spiriferinides in the peri-Iberian basins. Photographs refigured from COMAS-RENGIFO et al. (2006) except for *L. subquadrata* (from COMAS-RENGIFO et al. 2013) and *Cisnerospira* spp. (from COMAS-RENGIFO et al. 2015)

**2. ábra.** A Spiriferinidák időbeli elterjedése a peri-Iberiai-medencékben. Fotók: COMAS-RENGIFO et al. (2006) nyomán, kivéve *L. subquadrata* (COMAS-RENGIFO et al. 2013) és *Cisnerospira* spp. (COMAS-RENGIFO et al. 2015)

The chronostratigraphical range of the main recorded taxa in the four established regions is shown in *Figure 2*.

**EIPS** – Representatives of Spiriferinida in this region are recorded in the Iberian Range within the Turmiel Fm., in a depositional environment representing a shallow epicontinental platform. These deposits consist of an alternation of well-bedded grey/yellowish marl and micritic mudstone beds arranged into deepening and shallowing-upwards sequences (GÓMEZ & GOY 2000). These marly facies are deposited overlying the red bioclastic grainstone-packstone beds of the Upper Pliensbachian-lowermost Toarcian Barahona Fm. where spiriferinides are recorded as well. In the Catalonian Coastal Range and Mallorca Island, spiriferinides are recorded in a lithostratigraphical framework comparable to that of the Iberian Range, in the last levels of the Barahona Fm. and the first levels of the El Caregol Mb. of the Sant Blai Fm. (FERNÁNDEZ-LÓPEZ et al. 1998), and in the

Es Cosconar Fm. and the lower part of Gorg Blau Fm. (ROSALES et al. 2018, GARCÍA JORAL et al. 2022) respectively.

**South-Iberian Paleomargin** – In the easternmost Betic Range (East Spain) spiriferinides are recorded in the Pliensbachian–lowermost Toarcian sediments from the epioceanic External Subbetic area (BAEZA-CARRATALÁ 2013), which is characterized by pelagic seamount facies. Most of the taxa are recorded in the upper part of the Gavilán Fm. (late Pliensbachian), consisting of red crinoidal grainstone beds, and the marly levels of the Zegrí Fm. (uppermost Pliensbachian–lowermost Toarcian), consisting of marls and marly/sandy marlstone deposits. In the innermost part of the External Subbetic (La Cerradura, Jaen), the Zegrí Fm. was deposited in a deeper subsiding trough area with an expanded sedimentation and greater cumulative thickness (REOLID et al. 2014, BAEZA-CARRATALÁ et al. 2017). Lower Toarcian spiriferinides have been also recorded in the transitional

areas of the Prebetic-Subbetic domains (La Mola, Alicante, E-Spain; BAEZA-CARRATALÁ et al. 2016b).

**Atlantic paleomargin** – In the Lusitanian Basin, spiriferinides are found mainly in Toarcian sediments from the Rabaçal-Condeixa and the Peniche regions. They are recorded in the Coimbra area (Ribeiro and Fonte Coberta sections) in the São Gião Fm. (COMAS-RENGIFO et al. 2013) as whitish gray marly beds. In Peniche, occurred in the lower member of the Cabo Carvoeiro Fm. (ALMÉRAS et al. 1996, COMAS-RENGIFO et al. 2015). Both formations correspond to low-energy, distal homoclinal ramps, deeper to the west/northwest, typified by hemipelagic sequences and organic-matter-rich facies, where an alternation of marlstone and argillaceous limestone beds prevailed (DUARTE 2007).

**Northern-Cantabrian paleomargin** – Toarcian spiriferinides have not yet been recorded in the Basque-Cantabrian Basin, and are scarce in Asturias, where they come from the Santa Mera Member of the Rodiles Fm., composed of rhythmic alternations of micritic and marly limestones with an episode punctually enriched in organic matter (black shales), interpreted as deposited on a hemipelagic carbonate ramp (GARCÍA JORAL & GOY 2009).

The lithostratigraphic differences and environmental scenarios among the different peri-Iberian basins influenced the characteristics of the spiriferinide record (Fig. 2). In the EIPS, which correspond to the best oxygenated areas, this record is more diverse and abundant. In the less oxygenated areas of the north and west of the Iberian Massif, the record basically consists of small specimens of *Liospiriferina*, together with few specimens of *Cisnerospira* and *Calyptoria* in the Lusitanian Basin. In the shallower epioceanic areas of the South-Iberian margin, such as the Subbetic Domain and the transitional zones to the more proximal areas, the record is also diversified throughout the Early Jurassic, similarly to that which took place in the EIPS, with standard-sized *Spiriferina*, *Callospiriferina*, *Dispiriferina*, *Liospiriferina*, and *Cisnerospira* as the main representative genera, but only *Cisnerospira* and *Calyptoria* persisted up to the uppermost Early Toarcian record, while the more restricted Betic troughs became deeper refuges, promoting the development of small *Liospiriferina* species and specimens just like those occurring in the Cantabrian and Lusitanian basins.

### Evolutionary patterns of the last peri-Iberian spiriferinides

As previously stated, peri-Iberian spiriferinides preserve a remarkable morphological disparity in the Early Toarcian. Therefore, diversity dynamics in this group seems to have experienced significant changes, with a notable reduction if compared to the Pliensbachian diversity maximum (COMAS-RENGIFO et al. 2006).

The earliest important change took place concurring with the initial episode of the biotic crisis, which was considered by several previous authors as a multi-phase event (cf. LITTLE 1996; MACCHIONI & CECCA 2002; WIGNALL &

BOND 2008; DERA et al. 2010; CARUTHERS et al. 2013; ARIAS 2013; BAEZA-CARRATALÁ et al. 2015, 2017; RITA et al. 2016; REOLID et al. 2021). This earlier episode occurred at the beginning of the Tenuicostatum Chronozone, in a period of changes in long-term environmental conditions prior to the ETMEE boundary. In this first phase, while spiriferinides virtually disappeared in a great number of basins of the Mediterranean Bioprovince (VÖRÖS 2005, BAEZA-CARRATALÁ 2013), in some peri-Iberian areas, as the EIPS, Pyrenees, or in the Northwestern African basins, spiriferinides still occurs, but their diversity decreased (cf. COMAS-RENGIFO et al. 2006). Simultaneously, in less oxygenated habitats, such as the Cantabrian and the Lusitanian basins, only some small-sized species thrived (ALMÉRAS et al. 1996; GARCÍA JORAL & GOY 2009; COMAS-RENGIFO et al. 2013, 2015).

The second phase of the biotic crisis is recorded in the last stratigraphic levels prior to the extinction boundary, in the uppermost Semicelatum Subchronozone and the first levels of the Elegantulum Subchronozone. The spiriferinides recorded in this interval (Fig. 2) correspond only to the biconvex *Liospiriferina*, considered as the most conservative and generalist morphotype (cf. VÖRÖS et al. 2019), and *Calyptoria*, an immigrant who arrived just at this time from lower latitude areas (BAEZA-CARRATALÁ et al. 2018).

This decline in diversity follows the same global dynamics documented for all brachiopod clades in the Toarcian. In the Mediterranean Bioprovince, brachiopod diversity was not recovered until the Aalenian–Bajocian times (VÖRÖS 2005, VÖRÖS & DULAI 2007, BAEZA-CARRATALÁ 2013, ANDRADE et al. 2016). In the extinction interval some typical groups of this bioprovince show strategies to escape from unfavorable environmental conditions established in their homeland areas, moving towards deep refugia, such as the southernmost subsiding troughs in deeper-water settings of the Subbetic domain (BAEZA-CARRATALÁ et al. 2017), or migrating from the most intra-Tethyan areas up to some NW-European epicontinental seas (VÖRÖS 2002, BAEZA-CARRATALÁ et al. 2015), where they found a suitable habitat to colonize. In other westernmost Tethys shallower regions (EIPS, Pyrenees, or several basins in the southern and western France), taxa of the NW-European Province persisted, although they underwent a remarkable renewal at species-level, entailing in some cases a size reduction stage (GARCÍA JORAL et al. 2011, BAEZA-CARRATALÁ et al. 2015, PIAZZA et al. 2020a).

Several of these new species survived up to the last stratigraphic levels prior to the extinction, when all the brachiopod species (and most of the genera) disappeared from the peri-Iberian basins and many other Western Tethys areas. Recovery and repopulation with new species, adapted to much warmer conditions (ULMANN et al. 2020), begun in several basins after a relatively short delay (cf. GARCÍA JORAL et al. 2011, ANDRADE et al. 2016).

Climate changes, and more specifically seawater temperature variations, were likely the most important triggering factors for these evolutionary patterns. Seawater temperature variations have been linked by GUO et al. (2020) to

the diversity fluctuations among Triassic spiriferinides, so that major cooling events of seawater temperatures in the Anisian and Carnian seem to have facilitated the recovery of the spiriferinides and their radiation in the Triassic, and their noticeable diversification in the Late Pliensbachian coincides with another major cooling (icehouse) interval as well (PRICE 1999, GÓMEZ et al. 2008, GÓMEZ & GOY 2011, RODRIGUEZ SALES et al. 2018, RUEBSAM et al. 2020). The brachiopod migration and dispersal movements observed at the Pliensbachian–Toarcian boundary can be correlated with the first warming pulse of the Early Toarcian Biotic crisis (BAEZA-CARRATALÁ et al. 2015, 2017), estimated to be approximately in 5 °C (RUEBSAM et al. 2020, FERNANDEZ et al. 2021) and can be interpreted as the probable response of most species to the geographic shift in their thermal optimum due to this global warming episode.

After a relative sea-water temperature cooling in the mid-Tenuicostatum Chronozone, a drastic rise of 10° C occurred concomitantly with the onset of the Early Toarcian Oceanic Anoxic Event near the Tenuicostatum–Serpentinum chronozones boundary (RUEBSAM et al. 2020). The variation in the oxygen-isotope ratios ( $\Delta^{18}\text{O}$ ) recorded in many basins of the Western Tethys corresponding with this severe warming episode shows the most negative excursion values in basins located at latitudes above 30°N, and the least negative (or even positive) values in lower latitude basins, such as the peri-Iberian and North African basins (FERNANDEZ et al. 2021, GAMBACORTA et al. 2024). These variations should reflect not only temperature variations, but also a strong North–South salinity gradient, possibly due to the southward currents flow through the Viking Corridor of brackish waters derived from the Arctic (BJERRUM et al. 2001) and the progressive increase in runoff and fresh-water inputs to the epicontinental basins and sub-basins of northern Europe in correspondence with the general increase in temperature (GAMBACORTA et al. 2024). Thus, either because the water temperature was even higher in the areas located north of the peri-Iberian basins, or because they had too low levels of salinity or oxygen, the surviving spiriferinides (like the rest of the brachiopod species in these basins) did not manage to escape the hyperthermal event by moving to places further north.

### Morphology, size changes and seawater temperature in the Toarcian *Liospiriferina* from the Iberian Basin

Analyzing the body-size changes in the brachiopods recognized in the Extinction interval prior to the ETMEE from the peri-Iberian basins, GARCÍA JORAL et al. (2018) found two crossing trends involving not only latitudinal and temporal gradients but also environmental factors. On one hand, a diminishing tendency in the brachiopods body size is noticed from shallower and well-oxygenated regions to the muddy and oxygen-depleted bottoms, in line with what was observed in the Western Tethys as a whole in the first

phase of the biotic crisis. On the other hand, an increasing-size trend over time is revealed in some species in all the peri-Iberian basins. The first tendency affected the taxonomic composition of the assemblages, so that the larger species are recorded to the east of the Iberian Massif whereas the smaller ones occurred in the northern and western peri-Iberian platforms.

The increasing-size trend over time is related to within-species changes affecting the intraspecific size of individuals throughout the extinction interval. This increase is revealed in the most profusely recorded taxa and it is independent of their standard size, affecting both the large spiriferinides in the most favorable habitats prevailing in the Iberian Basin and the small rhynchonellides and koninckinides in more adverse conditions from the Cantabrian and Lusitanian basins (GARCÍA JORAL et al. 2018).

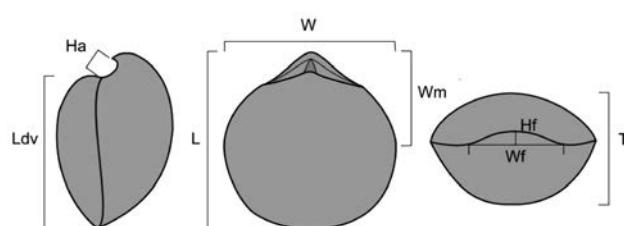
Regarding this size increasing trend, experienced, among others, by the last representatives of the genus *Liospiriferina* in the Iberian Range, it seems to be inconsistent with the customary global postulation expecting an inverse relationship between size and temperature in numerous organism groups, the so-called “Bergmann’s Rule” or the temperature-size rule (TSR). According to this “rule” ectotherm organisms acquire the mature ontogenetic conditions at smaller adult body size in warmer conditions (ATKINSON 1994), although compliance with this rule is not so evident in the case of brachiopods (cf. PECK & HARPER 2010).

In this way, PIAZZA et al. (2020a, 2020b) carried out a comprehensive analysis on the bivalve and brachiopod body size variation from a single lower Toarcian locality of the Iberian Basin, concluding that a decreasing-size pattern of benthic communities was linked to the increasing of the sea-water temperatures during the extinction interval, admitting a more manifest relationship when analyzed in bivalves and less statistically evidenced in brachiopods. These authors also remarked that the key factor of size reduction was a decrease in the occurrence and abundance of larger species rather than a within-species change in size. In the case of brachiopods, this trend is supported by the presence of *Soaresirhynchia bouchardi*, which is an opportunistic taxon that colonized the basin from deeper and warmer waters after the ETMEE (cf. BAEZA-CARRATALÁ et al. 2017, ULMANN et al. 2020). However, in other areas, such as the Lusitanian Basin, *S. bouchardi* shows larger size than those brachiopods occurring prior to the extinction boundary (cf. COMAS-RENGIFO et al. 2013, 2015; PIAZZA et al. 2019). Excluding *S. bouchardi*, the coupling of brachiopod size changes with the increasing of sea-water temperatures is not statistically significant along the Tenuicostatum Zone (PIAZZA et al. 2020a).

In order to better understand the effect of the sea-water temperature in the brachiopod body sizes, a more detailed comparative analysis has been now performed taking into account not only the changes in body size, but also morphological patterns and morphospace occupation recorded in the Iberian Basin among the spiriferinide representatives assigned to the genus *Liospiriferina*, which represents the

only of the four genera with a certified continuous record in the peri-Iberian paleomargins during the uppermost Pliensbachian – lower Toarcian interval. Simultaneously, these changes are interrelated with the paleotemperature pattern derived from the sea-water temperature curves estimated by the different authors for this basin.

A total number of 345 specimens of *Liospiriferina* ROUSSELLE, 1977 were included in the analysis, all of them collected and studied bed-by-bed in the Almonacid de la Cuba (after COMAS-RENGIFO et al. 2010) and the Ariño localities (after GOY et al. 1998, GARCÍA JORAL et al. 2011), spanning the uppermost Pliensbachian – lower Toarcian deposits throughout the Hawskerense, Mirabile, and Semicelatum subzones. The extensive record of spiriferinides in the Semicelatum Subzone, that probably represents a longer time interval than that of the Mirabile subzone, have been divided in two parts (lower and upper part of the Subzone) for a more detailed analysis. All specimens analyzed are deposited at the Department of Geodynamics, Stratigraphy and Paleontology (Universidad Complutense de Madrid, Spain; DPUCM). With the purpose of analyzing the morphologic variability and the size changes over time, the main biometric parameters suggested by MANCEÑIDO (1981) for the characterization of the spiriferinides were directly measured on the 252 complete available specimens (Fig. 3): total length (L), width (W), thickness (T), dorsal valve length (Ldv), distance from the apex to the maximum width of the shell (Wm), height of the cardinal area (Ha), width of the dorsal median fold (Wf), and maximum height of the fold in the anterior commissure (Hf). Subsequently, Principal Component Analysis (PCA) was conducted as exploratory method for variable reduction (HAMMER & HARPER 2006) using a correlation matrix instead of variance-covariance, considering that there is a great difference in the width of the range of values between some variables and others. The correlation matrix is more appropriate when the ranges of values are different because it standardizes the data so that all variables contribute equally to the analysis. These analyses and successive statistical explorations were carried out by means of the PAST 3.22 software package (HAMMER et al. 2001). The labelling of the specimens studied at each



**Figure 3.** Main biometric parameters measured on *Liospiriferina* specimens from Almonacid de la Cuba and Ariño localities: L: total length; W: width; T: thickness; Ldv: length of the dorsal valve; Wm: length from the apex to the maximum width; Ha: Height of the cardinal area; Hf: height of the dorsal anterior fold; Wf: width of the dorsal anterior fold. **3. ábra.** Az Almonacid de la Cuba és az Ariño lelőhelyekről származó *Liospiriferina*-példányokon mért fontosabb méretek. L: teljes hosszúság; W: szélesség; T: vastagság; Ldv: a dorzáris teknő hossza; Wm: a csúcstól a legnagyobb szélességgig mért távolság; Ha: a cardinális terület magassága; Hf: a dorzáris anterior kiemelkedés magassága; Wf: a dorzáris anterior kiemelkedés szélessége.

stratigraphic level and their measurements are included as supplementary material. Correlation of size, diversity, and disparity changes with seawater paleotemperatures are based on temperature curves published by different authors. The ammonoid chronostratigraphic zonal scheme is based on the standard zones proposed by ELMI et al. (1997), and PAGE (2003) for the Tethys Realm.

By correlating all the main biometric parameters using a correlation matrix (Table I), it can be deduced that all of them are closely related ( $p < 0.05$ ). The lowest correlation values are observed for the height of the cardinal area (Ha) and the height of the dorsal median fold (Hf), these revealed as the most independent parameters, and consequently being responsible for the greatest shape variations non-aligned with the body-size.

The PCA plot (Fig. 4) also reveals that morphospaces occupation varied over time, mainly along the PC2 axis. The specimens recorded in the uppermost Pliensbachian (Hawskerense Subzone of the Spinatum Zone) occupied a much greater range along this axis than those recorded in the Tenuicostatum Zone (Mirabile and Semicelatum subzones) from the lowermost Toarcian. This wide-range variability in the PC2 scores corresponds to the great morphological variability observed among spiriferinides from the Late Pliensbachian of the Iberian Range, that have led to the taxonomic determination of several species assigned to the genus *Liospiriferina*, such as *L. rostrata* (SCHLOTHEIM), *L. terebratuloides* (SEGUENZA), *L. hartmani* (ZIETEN), *L. falloti* (CORROY) and some other taxa (cf. COMAS-RENGIFO et al. 2006) which have been grouped as *Liospiriferina* gr. *rostrata* in the Figure 2.

However, the morphological variability of the *Liospiriferina* specimens from the Mirabile and Semicelatum sub-zones is considerably lower than in the Hawskerense Sub-zone, as indicated by the reduction in the morphospaces occupied in the PCA plot, so that, in our opinion, all these specimens can be assigned to a single species, *L. falloti*, which corresponds to a simplified morphology, less folded and with the cardinal area less curved, among the *L. rostrata* group. The decrease in variability is concurring in the Mirabile Subzone and in the lower part of the Semicelatum Subzone with a significant reduction in size of the individuals, indicated by the contraction of the PC1 scores. This miniaturization has been related in the Iberian Basin to the first episode of the ETMEE, that as previously explained, consists of the replacement of some species of brachiopods by other smaller ones within the same genus (e.g. *Lobothyris*, *Aulacothyris*, *Quadratirhynchia*, *Gibbirhynchia*), also involving the genus *Liospiriferina* (cf. GARCÍA JORAL & GOY 2000, GARCÍA JORAL et al. 2011). On the other hand, while the variation in the morphological variability between the specimens of the two Toarcian subzones can be interpreted as scarce from the wide-ranging PC2 scores, the size of the specimens (estimated, given the rounded style of the shells, as the volume of an ellipsoid whose three axes correspond to the main dimensions of the shell: length, width and thickness, as proposed by GUO et al., 2022) changed noticeably,

**Table I.** Below, colored: Linear correlation coefficient ( $r$ ) between the measured dimensions. Above:  $p$  (uncorrected) values of normality. In red boxes  $r$  values lower than 0.5; in orange boxes  $r$  values between 0.5 and 0.7. All  $p$  values are lower than 0.05. Biometric abbreviations as in Figure 3

*I. táblázat. Alul, színesben: a mért értétek közötti lineáris korrelációs együttható ( $r$ ). Fent:  $p$  (nem korrigált) normalitás értékek. Piros dobozokban a 0,5-nél alacsonyabb  $r$  értékek; narancssárga dobozokban a 0,5 és 0,7 közötti  $r$  értékek. minden p-érték 0,05-nél alacsonyabb*

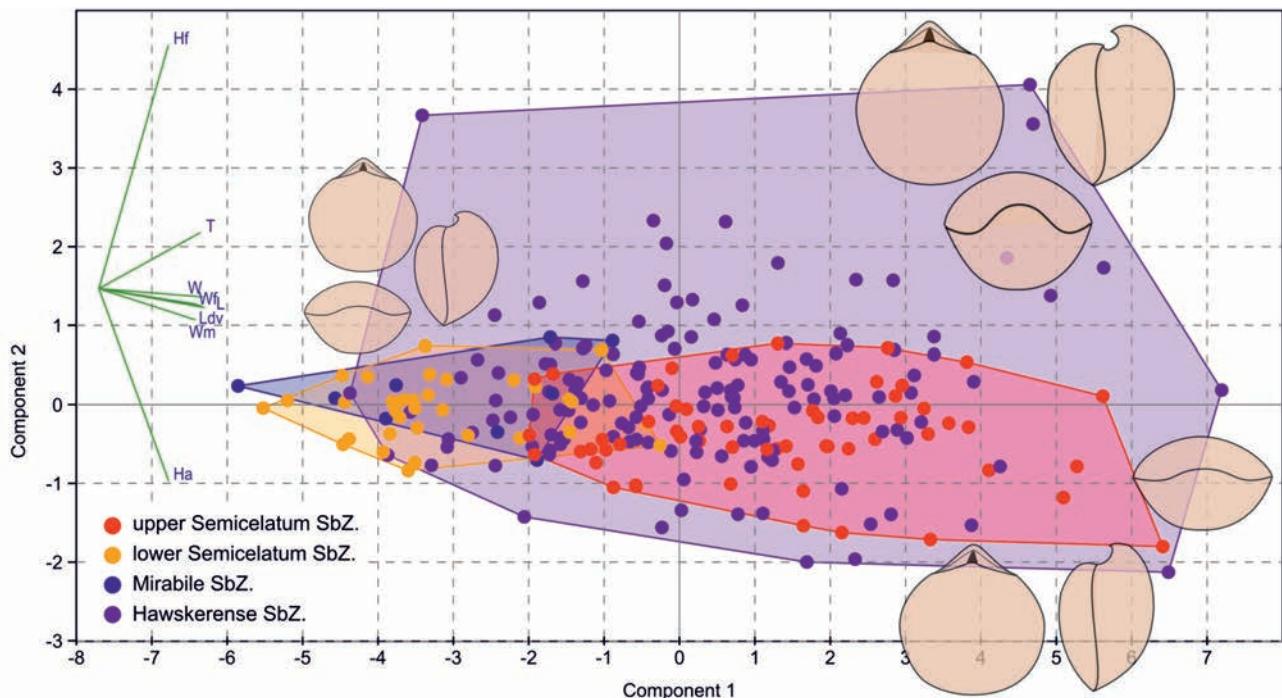
	<b>W</b>	<b>L</b>	<b>T</b>	<b>Ha</b>	<b>Ldv</b>	<b>Wm</b>	<b>Hf</b>	<b>Wf</b>
<b>W</b>		4.62E-100	2,3213E-85	3,6902E-28	3,0854E-95	2,05E-63	5,7695E-25	4,1407E-67
<b>L</b>	0.91422		3.9224E-88	7.741E-25	1.5811E-127	2.2496E-78	5.5253E-21	7.2435E-76
<b>T</b>	0.88588	0.8919		9.7245E-17	2.5313E-81	2.1232E-65	1.7226E-30	7.9129E-49
<b>Ha</b>	0.62002	0.5881	0.4916		1.4863E-18	5.651E-15	5.9645E-07	2.4674E-22
<b>Ldv</b>	0.90584	0.94919	0.87646	0.51608		1.1784E-69	9.2537E-17	1.2457E-65
<b>Wm</b>	0.82325	0.86905	0.83023	0.46578	0.8442		5.2912E-12	2.2602E-47
<b>Hf</b>	0.58939	0.54603	0.64043	0.30833	0.4919	0.41666		3.0369E-20
<b>Wf</b>	0.83601	0.86238	0.7607	0.56146	0.83103	0.75316	0.53722	

decreasing in the Mirabile Subzone and in the lower part of the Semicelatum Subzone and increasing in the upper part of the Semicelatum Subzone (Fig. 5).

Thus, the restriction of the morphological variability detected in the *Liospiriferina* individuals from the morphospace occupation resulting in the PCA analysis (Fig. 4), as well as the size decreasing episode identified in the Mirabile Subzone (Fig. 5), can be related to the first stages of the Early Toarcian Biotic Crisis. However, size-changes pattern in the rest of the Tenuicostatum Zone probably needs a further interpretation.

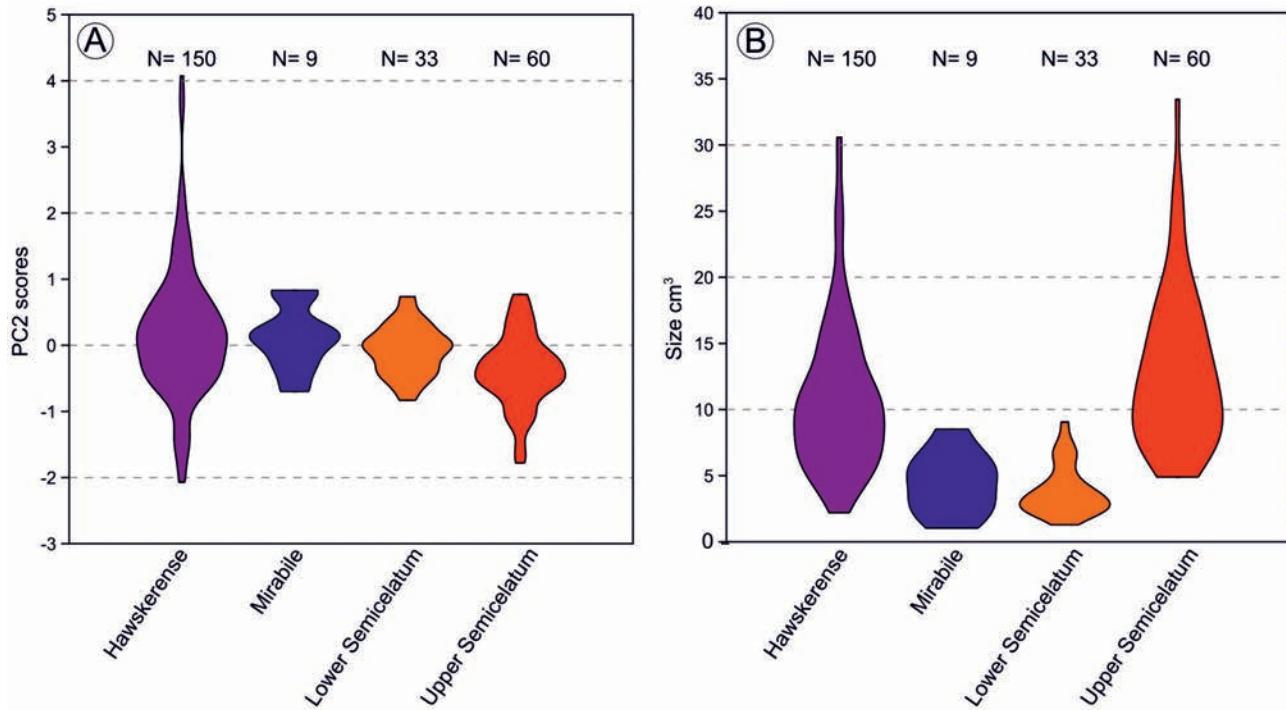
Regarding the sea-water paleotemperatures, a number of

previous authors have profusely studied their oscillations in this timespan through different methods and techniques, both globally and regionally in the peri-Iberian platforms system (BAILEY et al. 2003; ROSALES et al. 2004, 2018; McELWAIN et al. 2005; GÓMEZ et al. 2008; COMAS-RENGIFO et al. 2010; GÓMEZ & GOY 2011; DANISE et al. 2019; PIAZZA et al. 2019, 2020a; RUEBSAM et al. 2019, 2020; FERNANDEZ et al. 2021). Most of these works were based on the changes in the O<sup>16</sup>/O<sup>18</sup> isotopic ratio analyzed in belemnites rostra, and bivalves or brachiopods shells. Recently, the oscillation curve presented by RUEBSAM et al. (2020), based on the TEX86 paleotemperature proxy (SCHOUTEN et al. 2004) provides a



**Figure 4.** Morphometric scatter diagram of the analyzed representatives of *Liospiriferina* from the Iberian Basin, showing the morphospaces defined by the first two axes of the Principal Component Analysis (PCA). Clusters take into account the distribution over time. Dimensional vectors have been plotted to show the main discriminating factors

**4. ábra.** Az Ibériai-medencéből származó *Liospiriferina*-példányok morfometriai szórásdiagramja; a morphospace-t a főkomponens-analízis első két tengelye határozza meg. A klaszterek az időbeliséget érzékelhetik. A dimenziós vektorok a fő megkülönböztető faktorokat mutatják



**Figure 5.** Spindle diagrams of the PCA2 scores (A) and size (B) (estimated volume in  $\text{cm}^3$ ) of the measured specimens of *Liospiriferina* in the studied time intervals. Width of the spindles correspond to the proportion of individuals of each interval of values within the same temporal interval

**5. ábra.** Az adott időszakban vizsgált *Liospiriferina*-példányok főkomponens-analízisének dobozdiagramja. A: méreteloszlás; B: becsült térfogat  $\text{cm}^3$ -ben. A dobozok szélessége arányos az egyes értékintervallumokban szereplő egyedek számával

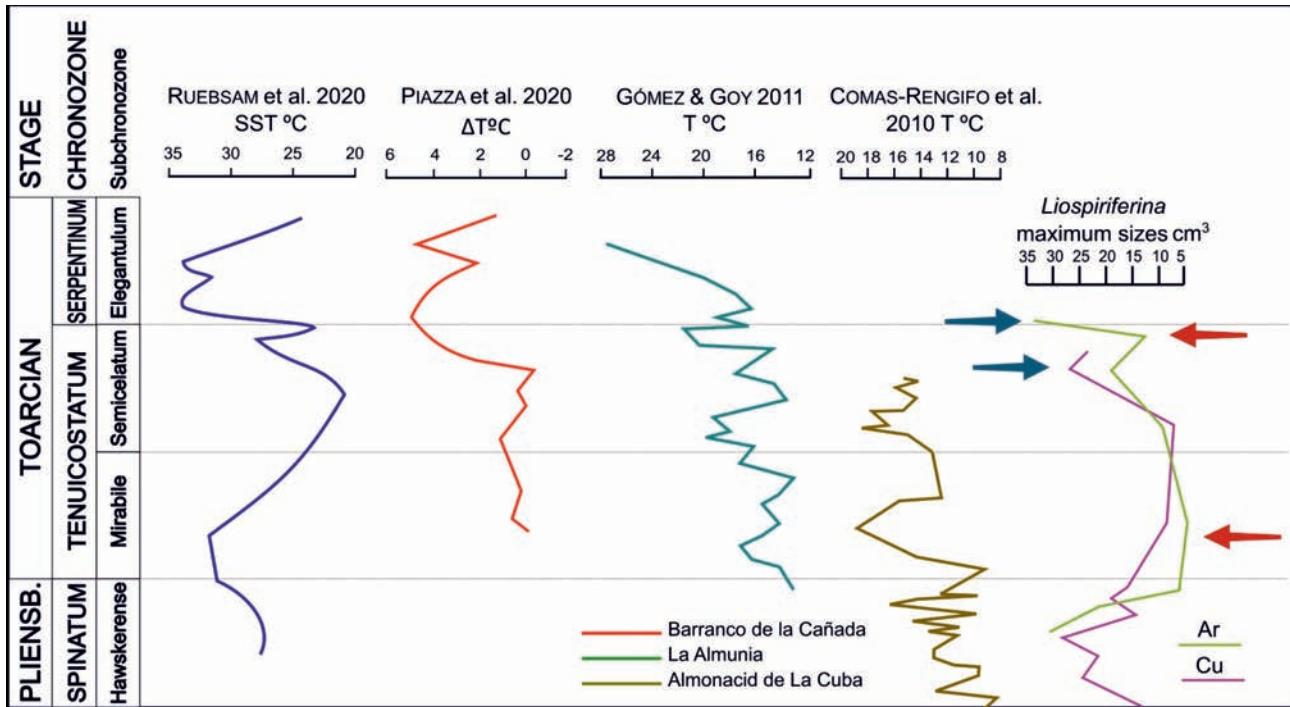
different perspective and seems to be useful to explain generalized climate change episodes at a regional scale.

To further refine the comparison between size and temperature in the studied *Liospiriferina*, their changes in body size have been confronted in the *Figure 6* with the most detailed temperature curves obtained in the Iberian Range and the SST (Sea Surface Temperature) curve calculated by RUEBSAM et al. (2020), which is considered to reflect the annual mean temperature in the upper mixed layer of the ocean on a regional scale. Despite the differences in the temperature data revealed in these studies, and although in the case of the Almonacid de la Cuba stratigraphic section the data do not reach the upper part of the Semicelatum Subzone, a general paleotemperature pattern can be extracted for the Iberian Basin. It seems that, after the important warming episode occurred in the lowermost early Toarcian, fluctuation of cooling and warming periods took place at the time corresponding to the upper part of the Mirabile Subzone and the lower part of the Semicelatum Subzone, followed by a hyperwarming event in the uppermost part of this last Subzone, which may have been of 10 to 15 °C until the end of the Elegantulum Subzone (cf. GÓMEZ & GOY 2011). In La Almunia section, where the more detailed curve was obtained, this severe warming episode is disrupted by a short cooling event coinciding with the Tenuicostatum–Serpentinum zones boundary, which is also recorded in other peri-Iberian and North-European basins (GÓMEZ & GOY 2011, fig. 11) and in the SST curve calculated by RUEBSAM et al. (2020).

The significant seawater warming occurred at the begin-

ning of the Mirabile Subzone can be reasonably linked to the decrease in size in the studied *Liospiriferina* representatives (*Fig. 6*). The subsequent significant change in size is an increase recorded in the upper part of the Semicelatum Subzone, which is also observed in other brachiopod genera (cf. BAEZA-CARRATALÁ et al. 2017, GARCÍA JORAL et al. 2018). This increase can be correlated with the cooling pulse that has been inferred for this time in the sections of the Iberian Basin shown in *Figure 6*. The SST curve of RUESBAM et al. (2020) does not differentiate the two subzones of the Tenuicostatum Zone, but it also indicates an important cooling phase within this zone that possibly coincides in age with that deduced for the Iberian Basin. After this relative cooling, the second and most severe phase of the hyperthermal event took place. The rapid initial warming is correlated in the Ariño section with a notable decrease in size in the last layer belonging to this subzone, immediately followed by an even more notable increase in size in the overlying level already belonging to the Elegantulum Subzone of the Serpentinum Zone, that coincides with the sudden cooling previously commented. These biggest *Liospiriferina* individuals, together with the standard-sized *Calyptoria* recorded in the same levels in Ariño and in some other localities of the peri-Iberian basins, are the last known representatives of the spiriferinidines in the Western Tethys.

Therefore, the tendency to increase in size in certain resilient species of brachiopods exposed in our previous work (GARCÍA JORAL et al. 2018), analyzed at Sub-chronozone level, can now be qualified with the more detailed analysis carried out in this work in light of the more accurate



**Figure 6.** Temperature curves for the extinction interval of the Early Toarcian Biotic Crisis compared with the maximum sizes of the *Liospiriferina* specimens measured in the studied sections. More explanations in the text. Ar: Ariño section; Cu: Almonacid de La Cuba Section

**6. ábra.** A kora toarci biotikus krízis idejére eső hőméréséklei görbék és a *Liospiriferina*-példányok maximális méreteinek összehasonlítása. További magyarázatok a szövegben. Ar: Ariño-szélvénnyel; Cu: Almonacid de La Cuba-szélvénnyel

temperature and body size data achieved from the Iberian basin. The big size in the *Liospiriferina* specimens – as well as in other representatives of several species – reached in the upper Semicelatum Subzone, could correspond to the cooling episode prior to the maximum hyperthermal event, whereas the even larger size of the last spiriferinides could represent the last heyday of the scarce survivors to the rapid onset of the seawater warming, taking advantage of the short cooling episode around the zonal boundary.

Finally, the severe warming that took place at the beginning of the Serpentinum Chronozone, when the sea-water temperature increased very noticeably (HU et al. 2020, RUEBSAM et al. 2020) seems to have been unbearable for these resilient species.

The Early Toarcian Hyperthermal Event has been related to the widespread occurrence of black shales in many basins around the globe, evidencing a global anoxic event (the so-called Early Toarcian Anoxic Event or “Jenkyns Event”). Anoxia has been recurrently invoked to explain the extinction of the last spire-bearer brachiopods in the Early Toarcian (VÖRÖS 2002). As exposed by AGER (1987) and VÖRÖS et al. (2016), the passive feeding mechanism of spire-bearing brachiopods with fixed lophophores becomes less effective under adverse conditions of oxygenation than the ciliate active feeding of the more adaptable rhynchonellides and terebratulides, and this could have been a factor influencing the extinction of spiriferinids and the survival of the other orders. However, there are no evidence of anoxic environments in most of the peri-Iberian basins, precluding this interpretation in this region (GÓMEZ et al. 2008, GARCÍA JORAL et al. 2011, GÓMEZ & GOY 2011, PIAZZA et al. 2020b).

The severe warming is the most feasible cause of the clade or “fatal extinction” (*sensu* VÖRÖS et al. 2019) that brachiopod fauna experienced at this time, an extinction that is among the most important in the post-Paleozoic history of this phylum and represents, as previously mentioned, the disappearance of the Order Spiriferinida (GARCÍA JORAL et al. 2011; VÖRÖS et al. 2016, 2019). The survival, for a short time, of spiriferinides in the cold seawater habitats of the high latitudes from New Zealand is also consistent with this postulate. As can be seen in *Figure 1A*, the few Pliensbachian spiriferinide records known outside the Western Tethys region are mainly representatives of the “ribbed/winged” morphotype, arranged into the genus *Spiriferina*, which have been considered as the best adapted to the high latitude environments (cf. GUO et al. 2020 and references therein). This is the same morphotype of the last recorded spiriferinides in the New Zealand region (cf. MACFARLAN 2023).

Subordinately to the present analysis, it can be also corroborated that brachiopods were unmistakably more sensitive to the sea-water temperature increase (at least in the post-Paleozoic times) than other groups of benthic epibionts, such as bivalves; this is clearly manifested in the different intensity of extinction if both groups are compared in the Early Toarcian (PIAZZA et al. 2019, 2020a, 2020b).

## Conclusions

The significant environmental changes that occurred in the early Toarcian biotic crisis seriously affected the brachiopod fauna, especially to the Order Spiriferinida, whose

diversity was previously quite restricted to the point of having been considered as a “Dead Clade Walking”. In the lowermost Toarcian, the earlier phase of this crisis entailed a first significant seawater warming episode, leading to the greatly constricted paleobiogeographic distribution of this clade, being limited to the westernmost corner of the Tethys Ocean, in contact with the “Viking” and the “Hispanic” corridors. In this area, the spiriferinides preserved a morphological disparity like that revealed throughout the entire Early Jurassic, although represented by very few species. Furthermore, these species suffered a generalized reduction in size, more noticeable in the more oxygen-starved areas. In the second phase of this ecological crisis, occurred at the basal Serpentinium Chronozone, a new and even more intense warming episode could not be overcome by the few spiriferinide species remaining in this region, thus representing the “fatal extinction” of the Order Spiriferinida.

The abundant and continuous record of spiriferinides in the basins surrounding the Iberian Massif, in Spain and Portugal, allows us to study in detail the changes experienced by the group during this crisis. The analysis of morphology and size changes in individuals of the best represented genus (*Liospiriferina*) in the Iberian Basin, where their record is the most abundant and continuous, reveals a drastic decrease in both features as a consequence of the first marine warming phase, while the only resilient inhabitant species of the genus (*L. falloti*), maintained or even increased their size until the last moment. These size changes may be related to the more or less intense water temperature fluctua-

tions, so that the last big sizes observed are possibly an ultimate response to a short cooling event, intercalated within the very intense warming that is very probably the main cause responsible for the extinction of the spiriferinide clade, together with paleogeographic conditions preventing escape to colder waters environments.

## Acknowledgments

This research is a contribution to the Research Groups PBM 3491 (Complutense University of Madrid) and VIGROB-167 (University of Alicante), and to the Project IGCP-710 Western Tethys meets Eastern Tethys. Authors thank V.F. FERRERO SAN ROMÁN helping with the biometric measurements used in this work as part of his End-Course Work for the master’s degree (Complutense University of Madrid). The critical reviews and helpful comments of reviewers M.O. MANCEÑIDO and A. DULAI and editors have clearly improved the quality of the paper. We would strongly acknowledge Attila VÖRÖS for his extensive career and his research activity on post-Paleozoic brachiopods, becoming a great reference for all the researchers working on this discipline. The results of his studies have inspired, without any doubt, topics of palaeobiogeographical and taxonomical relevance on the macroevolutionary history of Brachiopoda, being the pioneer to suggest many innovative postulates and theories.

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## Early Jurassic thecideids (Thecideidae, Brachiopoda) and associated fossils from Tivoli near Rome, Italy

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*Kora jura Thecideida brachiopodák és velük együtt előforduló egyéb ősmaradványok  
a Róma (Olaszország) melletti Tivoliból*

### Összefoglalás

A dolgozat elsőként ismerteti az Appenninek alsó toarci rétegeiből a *Moorellina parca* (RAU), 1905, *Davidsonella sinuata* (DESLONGCHAMPS) és a *Suessia liasina* (DESLONGCHAMPS) brachiopoda fajokat. A begyűjtött 460, többségében töredékes ammonitesz segítségével a brachiopodákban és krinoidea-maradványokban gazdag réteget a toarci bázisát jelző Polymorphum Zónába sorolhatjuk. A Colle Vecchio toarci szelvényét – a lelőhely egyedi és sajátos őslénytani értékei alapján – javasoljuk felvenni a földtani örökség regionális jegyzékébe.

*Kulcsszavak:* alsó jura, Középső-Appenninek, brachiopoda, ammonitesz, belemnitesz, Polymorphum Zóna, földtani örökség

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### Abstract

The aim of this paper is to point out the first reporting of *Moorellina parca* (RAU), *Davidsonella sinuata* (DESLONGCHAMPS) and *Suessia liasiana* (DESLONGCHAMPS) in the Apenninic Lower Toarcian beds. The sampling of 460 specimens of ammonites (mainly fragmentary specimens) allowed us to correlate the fossiliferous level known in the literature for the rich associations with brachiopods and crinoids in the basal Toarcian, Polymorphum Zone. Due to its uniqueness and paleontological value, we propose the Toarcian fossil deposit of Colle Vecchio to be included in the regional list of Geosites for the conservation of the geological heritage.

*Keywords:* Lower Jurassic, Central Apennines, Brachiopods, Ammonites, Belemnites, Polymorphum Zone, Geological heritage

### Introduction

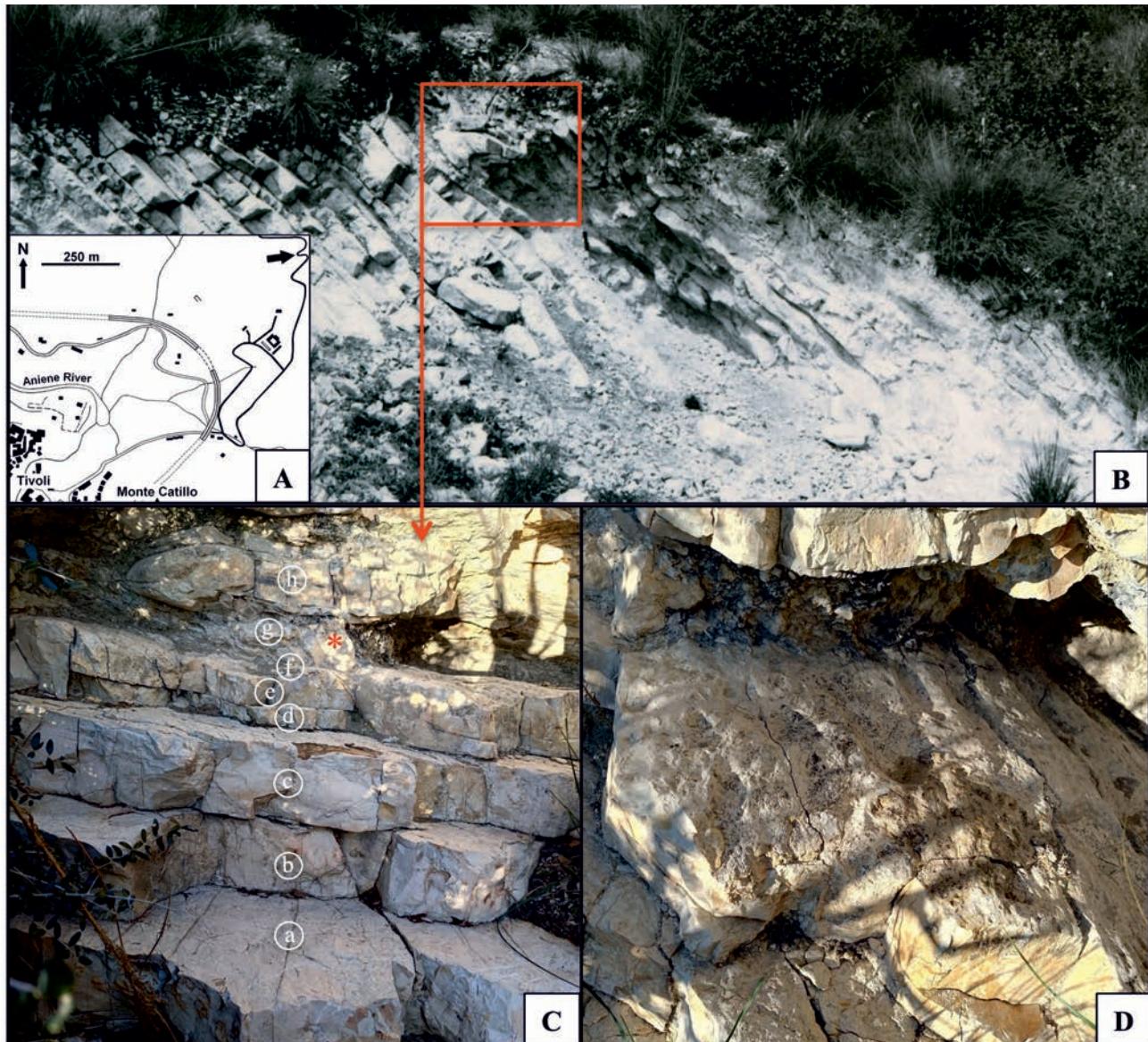
The brachiopod fauna of the Colle Vecchio outcrop was studied by VÖRÖS (2002); however, he did not report these micromorphic species of encrusting. Their recognition in a retrospect is due to the passion and patience of the second author (G. A.) who, during the preparation of the dossier relating to the formalization of the outcrop in the regional catalog of Geosites (CRESTA et al. 2005), recognized the species encrusted on other fossils and present in the microfauna associated with the level of *Koninckella* already known in the literature.

The present volume dedicated to the scientific activity of Attila VÖRÖS provides an excellent opportunity to inform the scientific community of this occurrence.

### Geological and stratigraphic framework

As pointed out by MANNI & DI NARDO (2021 and references therein), the Colle Vecchio outcrop (*Figure 1, A*) is part of the Apennine Jurassic pelagic succession included in the “Monte Catillo” Regional Nature Reserve. Our attention, motivated by the opportunity to include the outcrop in the Regional Catalogue of Geosites, was focused on the layers within which the fossil association known in the literature originates.

The sampled section (*Figure 1, B*) is 7 meters thick and consists of white and light grey micritic limestones with chert lenses and nodules from the topmost portion of the Corniola Formation corresponding regionally to the basal Toarcian. The authors have highlighted two different scenar-



**Figure 1.** A) location of the Colle Vecchio outcrop (from MANNI & DI NARDO 2021); B) stratigraphic succession of the topmost part of the Corniola Formation; C) sampled stratigraphic interval: bed a - micritic limestones (20 cm, macrofossils not found); bed b - micritic limestones (18 cm, macrofossils not found); bed c - micritic limestones (18 cm) with an irregular surface on the top covered by a marly layer of variable thickness (1–2 cm) macrofossils not found; bed d - micritic limestones (5 cm) with a firm ground on the top, macrofossils not found; bed e - micritic limestones (14 cm) with a hard-ground erosion surface on the top containing indeterminate brachiopods; bed f - marly level of variable thickness (2–5 cm) with re-sedimented ammonites, belemnites and brachiopods; bed g - marl and marly clays (25–30 cm), richly fossiliferous, from which the specimens described in the literature come (MANNI & NICOSIA 1990, VÖRÖS 2002, MANNI & DI NARDO 2021); bed h - slumping level (130 cm), followed by recent debris cover that hides the stratigraphic succession; D) detail of bed e top surface in which the depressions filled by marls containing ammonites, brachiopods and re-sedimented belemnites can be seen

**1. ábra.** A) a Colle Vecchio lelőhely (MANNI & DI NARDO 2021 nyomán); B) a Corniola Formáció felső részének rétegsora; C) a begyűjtött szelvény: a réteg - finomszemcsés mészkő (20 cm, makrofaunát nem szolgáltatott); b réteg - finomszemcsés mészkő (18 cm, makrofaunát nem szolgáltatott); c réteg - finomszemcsés mészkő (18 cm, egvenetlen felső felszínén 1–2 cm vastag, makrofaunamentes márgaréteggel); d réteg - finomszemcsés mészkő (5 cm) tetején keményfelszínnel, makrofaunamentes; e réteg - finomszemcsés mészkő (14 cm) tetején keményfelszínnel, meghatározhatatlan brachiopoda-maradványokkal; f réteg - változó vastagságú márgás réteg (2–5 cm) áthalmozott ammoniteszekkel, belemniteszekkel és brachiopodákkal; g réteg - márga és márgás agyag (25–30 cm), össmaradványokban gazdag, (MANNI & NICOSIA 1990; VÖRÖS 2002; MANNI és DI NARDO 2021); h réteg - rogyott réteg (slump), (130 cm) felső részén törmelékkel fedve; D) az e réteg felső részének részlete; a mélyedéseket ammoniteseket, belemniteseket és áthalmozott brachiopódákat tartalmazó márga tölti ki

ios of lithostratigraphic evolution between this Formation and the above.

In the Pelagic Carbonate Platform areas (SANTANTONIO 1994; GALLUZZO & SANTANTONIO 2002; BALDANZA et al. 2022 and references therein) a hard-ground formed prior to the resumption of sedimentation with the nodular lime-

stones and marls of the Umbrian Marche Ammonitico Rosso Formation; in the most depressed basin areas there is a transition between the micritic sediments of the Corniola Formation to the predominantly marly-clayey sediments of the Marne di Monte Serrone Formation.

In addition to these two main typologies, there are cases,

like the one described here, in which tectonic and/or palaeogeographic evidence points to local variations. The peculiarity of this outcrop is the presence of a slumped level in contact with a surface with elements that suggest a slowing/stopping of sedimentation and the formation of a hard-ground whose clastic components (fragments of ammonites belonging to the Polymorphum Zone) are also found in the marl portion above, squeezed by gravitational sliding.

In detail, we found that in the upper part (beds a, b, c, d, e) the limestone layers are interspersed with thin marly and calcareous-marly layers of cm-thickness (*Figure 1, C*). The bank below the fossiliferous level (beds d-e) is divided by a “sharp surface” and has a hard-ground on the roof whose trace is represented by morphological depressions that form niches (*Figure 1, D*).

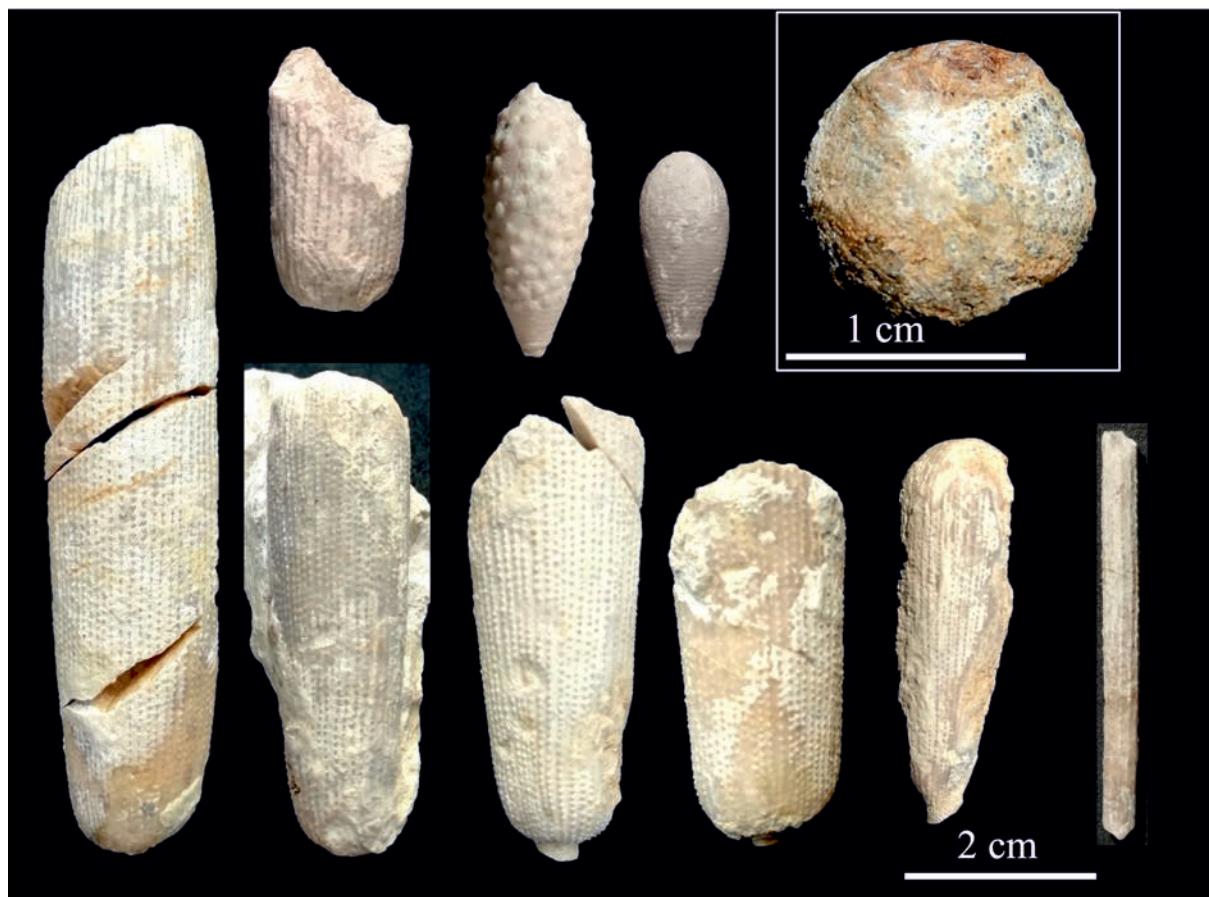
These depressions are filled by fossiliferous marls (*Figure 1, C*, bed f) in which the specimens of ammonites and belemnites displayed in *Plate II* have been found (*Figure 1, D*): some specimens show signs of resedimentation. Above, squeezed into calcareous and calcareous-marly levels bent by sliding, a chaotic level (bed g, 20–35cm) emerges consisting of fragments of micritic limestone in a richly fossiliferous marly-clayey matrix from which most of the known fossils come (MANNI & NICOSIA 1990, MARIOTTI 1994, VÖRÖS 2002, VENTURI 2006, MANNI & DI NARDO 2021).

## Paleontological framework

Although the fossil association of this outcrop is known in the literature, in order to construct a dossier necessary for the proposal of a Paleontological Geosite we considered it necessary to resample the succession to constitute a reference collection, still under study, which is temporarily hosted by the second author (G. A.).

Fifty kg of fossiliferous marl from bed g was sieved and the subsequent count of the specimens found (1176) gave the following result: 460 ammonites (mostly in a fragmented state); 25 belemnites; 4 gastropods; 25 regular echinoids spines plus 3 specimens less than 1 cm in size (*Figure 2*); 200 crinoid cups (of genera already known in literature); 450 brachiopods, of which 200 belong to the groups Terebratulidae and Rhynchonellidae and 250 to Koninckinidae, in addition to the Thecididae covered by this report encrusted on 30 organic bases (belemnites, crinoids, brachiopods). Specimens belonging to the genera *Suessia* and *Davidsonella* have also been found (*Plate II*); 50 fragments of problematic attribution (sponge spicules, corals?) and approximately one thousand of columnaria crinoids articles (with minimum size 2 mm).

Some ammonites and belemnites figured in *Plate II* came from the marly layer covering the eroded depre-



**Figure 2.** Regular echinoid remains from bed g. The figured specimens will be housed in the Piobbico Geo-Paleontological Museum collections  
**2. ábra.** A g rétegből származó echinoidea-maradványok. A példányok a piobbicói földtani és öslénytani gyűjteményben lesznek elhelyezve

sions on the top of the last bed of the Corniola Formation (bed f).

Since the purpose of this report is to integrate our finds with an already extensive and well-determined paleontological dossier (MANNI & NICOSIA 1990, MARIOTTI 1994, VÖRÖS 2002, VENTURI 2006, MANNI & DI NARDO 2021), we provide a limited illustration of the specimens and a brief descriptions in the captions of the same to promote the knowledge of the association.

## Conclusions

The ammonite faunas found both at the top of the Corniola Formation (bed f) and in the sieved fossiliferous level (bed

f) allow the attribution of the fossiliferous assemblages known in the literature to the basal Toarcian, Polymorphum Zone (FARAONI et al. 1994, CRESTA et al. 1995, PARISI et al. 1998).

The discovery of numerous Thecideidae referred to the species *Moorellina parca* (RAU) and *Davidsonella sinuata* (DESLONGCHAMPS) encrusted on belemnites, brachiopods and crinoids cup allows the extension of the palaeobiogeographical distribution area of this group to the central Apennines. A similar update can be made for *Suessia liasiana* (DESLONGCHAMPS).

The occurrence of this highly diversified fossiliferous concentration is a perfect motivation to propose the inclusion of the Colle Vecchio Toarcian outcrop in the geosites catalogue for the conservation of the Lazio region geological heritage.

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Manuscript received: 01/01/2024

### Plate I – I. tábla

Fig. 1. *Davidsonella sinuata* (DESLONGCHAMPS) (CP020): a) cemented on a crinoid cup; b) c) d) a loose ventral valve in three different views: anterior, posterior and lateral.

Fig. 2. a) *Moorellina* sp. (C021) cemented on a *Linguithyris aspasia* (ZITTEL); b–c) enlarged views of the ventral valve.

Fig. 3. *Moorellina parca* (RAU) (CP022) (a) cemented on a *Koninckella gibbosula* (GEMMELLARO); b) enlarged view of the ventral valve.

Fig. 4. *Moorellina parca* (RAU) (CP023) two cemented remain valves (perimeter walls) on a columnaria; b) enlarged, c) interior view of one of the pedicle valve highlighted with red circle.

Fig. 5. *Suessia liasiana* (DESLONGCHAMPS) (CP024): a) dorsal view, b) brachial view; c–d) same specimen, photos taken with back light to show the internal preservation of the brachidium; e) oblique view of hinge margin with foramen f) commissure view.

Fig. 6. *Ismenia suessia* (DESLONGCHAMPS) (CP025).

The figured specimens will be housed in the Piobbico Geo-Paleontological Museum collections. All specimens come from bed g.

1. ábra. *Davidsonella sinuata* (DESLONGCHAMPS) (CP020): a) a példány egy krinoidea-kehelyhez tapadva; b), c), d), a ventrális teknő elülső, hátulsó és oldalsó nézetben.

2. ábra. a) *Moorellina* sp. (C021) *Linguithyris aspasia* (ZITTEL) példányára tapadva: b), c) a ventrális teknő nagyítva.

3. ábra. *Moorellina parca* (RAU) (CP022): a) *Koninckella gibbosula* (GEMMELLARO) példányára cementálva, b) a ventrális teknő nagyítva.

4. ábra. *Moorellina parca* (RAU) (CP023) két cementált példány krinoidea-nyelen: b) nagyítva, c) a pediculáris teknő belső nézete.

5. ábra. *Suessia liasiana* (DESLONGCHAMPS) (CP024): a) dorsális nézet, b) brachiális nézet; (c-d) ugyanaz a példány hátulról megvilágítva, hogy a kartámasztó váz látható legyen; e) a zárosperem nézete a forámennel; f) a commissura felőli nézet.

6. ábra. *Ismenia suessia* (DESLONGCHAMPS) (CP025).

Valamennyi maradvány a g rétegből származik. A példányok a piobbicói földtani és őslénytani gyűjteményben lesznek elhelyezve.

**Plate I – I. tabla**

## Plate II – II. tábla

Fig. 1. *Dactylioceras (Eodactylites) pseudocommune* (FUCINI) (bed f, CP003); the asterisk indicates the beginning of the body chamber.

Fig. 2. *Atractites* sp. (bed g, CP005).

Fig. 3. *Canavaria retroPLICata* GEMMELLARO (bed f, CP002): (a) ventral view, (b) lateral view.

Fig. 4. *Harpophylloceras (Juraphyllites) eximium* (HAUER) (bed g, CP013); (a) ventral view, (b) lateral view.

Fig. 5. *Acroelites* sp. LISSAJOUS (bed f, CP012).

Fig. 6. *Protogrammoceras bassanii* (FUCINI) (bed g, CP009): (a) ventral view, (b) lateral view.

Fig. 7. *Emaciaticeras* sp. (bed g, CP004): (a) ventral view, (b) lateral view.

Fig. 8. *Lioceratoides* sp. (bed g, CP014).

Fig. 9. *Dactylioceras (Eodactylites) pseudocommune* (FUCINI) (bed g, CP007), inner whorls.

Fig. 10. *Calaiceras calais* (MENEGRINI) (bed g, CP008), inner whorls.

Fig. 11. *Fontanelliceras fontanellense* (GEMMELLARO) (bed g, CP009).

Fig. 12. *Simpsonibelus expansus* (SIMPSON) (bed f, CP011): (a) lateral profile, (b) ventral profile.

Fig. 13. *Acroelites* sp. LISSAJOUS (bed f, CP010): (a) lateral profile, (b) ventral profile.

Fig. 14. *Canavaria retroPLICata* GEMMELLARO (bed f, CP001): (a) ventral view, (b) lateral view; the asterisk indicates the beginning of the body chamber.

All specimens are figured in original size and will be housed in the Piobbico Geo-Paleontological Museum collections.

1. ábra. Dactylioceras (Eodactylites) pseudocommune (FUCINI) (frétek, CP003); a csillag a lakókamra kezdetét jelöli.

2. ábra. Atractites sp. (g rétek, CP005).

3. ábra. Canavaria retroPLICata GEMMELLARO (frétek, CP002): (a) ventrális nézet, (b) laterális nézet.

4. ábra. Harpophylloceras (Juraphyllites) eximium (HAUER) (g rétek, CP0013) (a) ventrális nézet, (b) laterális nézet.

5. ábra. Acroelites sp. LISSAJOUS (frétek, CP012).

6. ábra. Protogrammoceras bassanii (FUCINI) (g rétek, CP009) (a) ventrális nézet, (b) laterális nézet.

7. ábra. Emaciaticeras sp. (g rétek, CP004) (a) ventrális nézet, (b) laterális nézet.

8. ábra. Lioceratoides sp. (g rétek, CP014).

9. ábra. Dactylioceras (Eodactylites) pseudocommune (FUCINI) (g rétek, CP007) belső kanyarulatok.

10. ábra. Calaiceras calais (MENEGRINI) (g rétek, CP007) belső kanyarulatok.

11. ábra. Fontanelliceras fontanellense (GEMMELLARO) (g rétek, CP009).

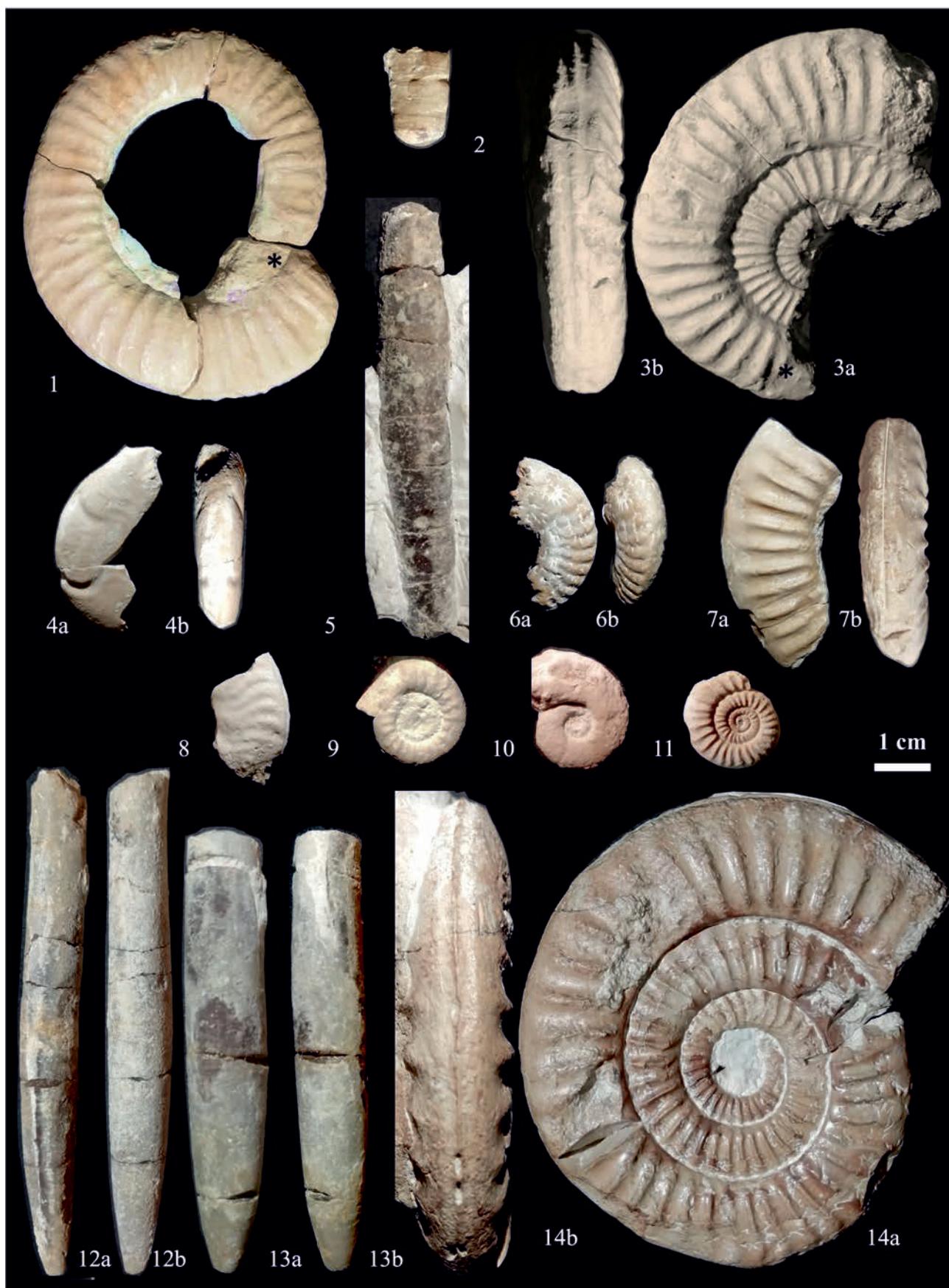
12. ábra. Simpsonibelus expansus (SIMPSON) (frétek, CP011) (a) ventrális nézet, (b) laterális nézet.

13. ábra. Acroelites sp. (frétek, CP010) (a) laterális nézet, (b) ventrális nézet.

14. ábra. Canavaria retroPLICata GEMMELLARO (frétek, CP001) (a) ventrális nézet, (b) laterális nézet, a csillag a lakókamra kezdetét jelöli.

Minden példány eredeti nagyságban. A maradványok a piobbicói földtani és őslénytani gyűjteményben lesznek elhelyezve.

## Plate II – II. tábla



## Bajocian stephanoceratid ammonites and their stratigraphy from Dorset, UK, with reference to the work of András Galácz

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### *Bajoci stephanoceratid ammoniteszek és rétegtanuk Dorsetből (Egyesült Királyság) hivatkozással Galácz András munkásságára*

#### Összefoglalás

Az angliai Dorset területén felszínen lévő Inferior Oolite formációba tartozó alsó bajoci rétegekben rendszerint gyakoriak a stephanoceratid ammoniteszek, amelyek összehasonlíthatók a Dunántúli-középhegységből származó ammoniteszegyüttesekkel. Utóbbiakat – köztük a *Lokuticeras*okat – GALÁCZ András tanulmányozta. Dorsetben a „*Lokuticeras morfológiájú*” példányok a Sauzei és a Humphriesianum zónák számos rétegében elfordulnak, és meghatározható volt az ezen ammoniteszeket tartalmazó biohorizontok faji összetétele. Dorsetben a *Lokuticeras*ok a Humphriesianum zóna Blagdeni szubzónájában és a Humphriesianum szubzóná legtetején voltak a leggyakoribbak. A magyarországi maradványokkal való összehasonlítás érdekében három dorseti lelőhelyről ábrázoltunk példányokat. A *Lokuticeras rossbrunnense* típusfaj példányai gyakoriak a Humphriesianum és Blagdeni szubzónák határán. Az európai területekkel való párhuzamosítást segítendő, a Blagdeni szubzóna legalsó biohorizontjakként bevezettük a *Lokuticeras rossbrunnense* biohorizontot. A korábbi publikált példányok kritikai értékelését is elvégeztük.

Kulcsszavak: *bajoci, biosztratigráfia, Inferior Oolite, Lokuticeras, Stephanoceras*

#### Abstract

The Inferior Oolite Formation of Dorset includes Lower Bajocian strata often rich in stephanoceratid ammonites comparable with assemblages from the rocks of the Transdanubian Central Range (W Hungary) that are the subject of research by András GALÁCZ, specifically *Lokuticeras*. In Dorset the stratigraphical occurrence of the ‘*Lokuticeras* morphology’ can be traced over a range of strata from the Sauzei and Humphriesianum zones and the assemblage composition of the biohorizons in which they occur identified. *Lokuticeras* is most abundant in Dorset in the uppermost Humphriesianum and Blagdeni subzones of the Humphriesianum Zone. Specimens from three Dorset locations are figured facilitating comparison with the Hungarian specimens. Type species *Lokuticeras rossbrunnense* is common at the Humphriesianum–Blagdeni subzonal transition. A new biohorizon is erected *Lokuticeras rossbrunnense* nov. as the lowest biohorizon of the Blagdeni Subzone facilitating correlating some areas of Europe. A critical review is made of previously published specimens and their affinities.

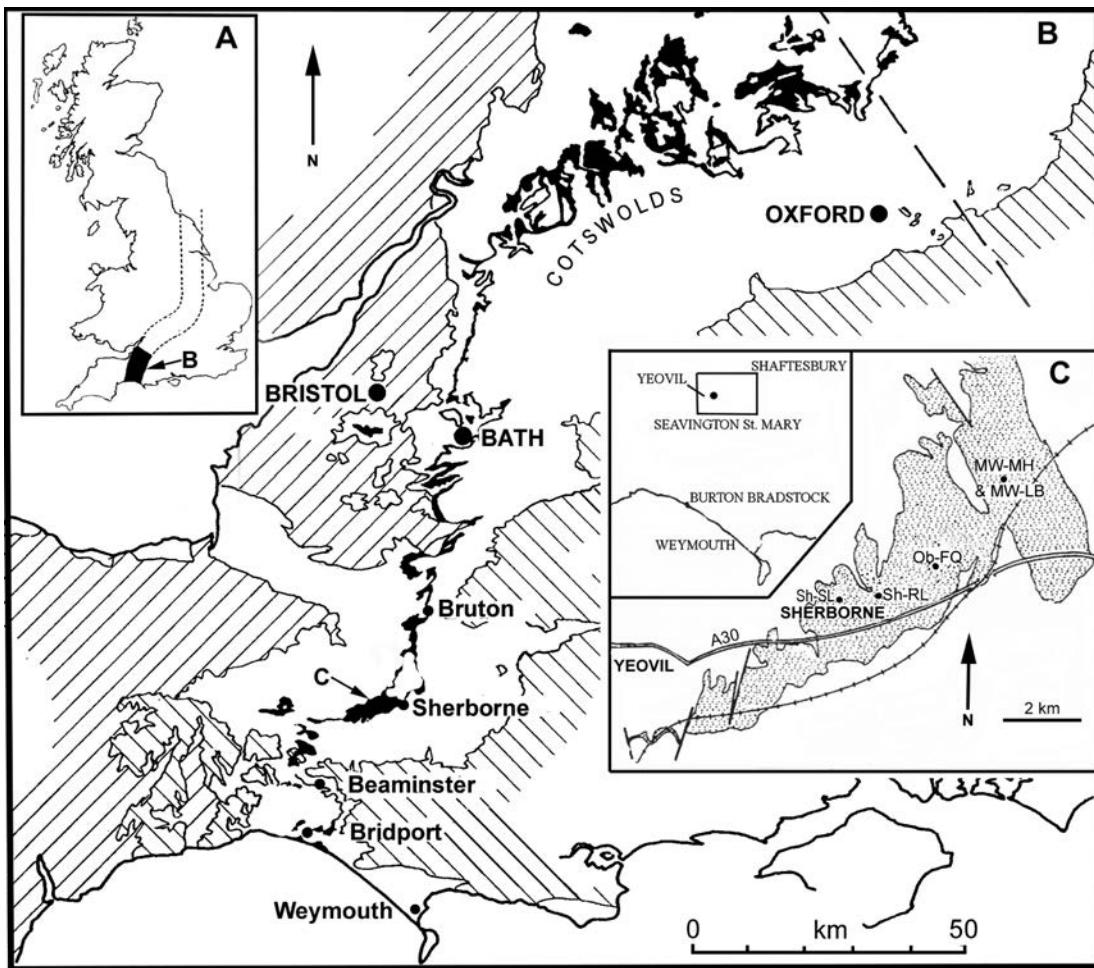
Keywords: *Bajocian, biostratigraphy, Inferior Oolite, Lokuticeras, Stephanoceras*

#### Introduction

Observations are presented regarding previously published data on some stephanoceratid ammonites from Hungary and England; the purpose is to present information from detailed field work in Dorset over the past thirty years that improves and clarifies the situation regarding the nomenclature, distribution in time, intraspecific variability and di-

morphism of this ammonite family in the Lower Bajocian. Ammonites from three Dorset localities are described.

The Sherborne area of England (*Fig. 1*) lies in a region of highly fossiliferous deposits of the Inferior Oolite Formation of the Aalenian to lowest Bathonian. Many abandoned quarries are present locally in a more or less east-west tract. The region is the source of numerous type species and genera, mostly ammonites described by S. S. BUCKMAN during



**Figure 1.** A. Sketch map of Britain (excluding Ireland) showing the outcrop of the Aalenian–lowest Bathonian of England. The solid black area is that shown in B. B. Outcrop of the Inferior Oolite Formation (solid) in southwest England. Diagonal shading to the west: pre-Jurassic rocks; diagonal shading to the east: post-Jurassic rocks. C. Outcrop of the Inferior Oolite Formation (dotted) in the Sherborne region. Localities are marked by a dot and code: Sh-SL Sherborne, Sandford Lane; Sh-RL Sherborne, Redhole Lane; Ob-FQ Oborne, Frogden Quarry; MW-MH Miller's Hill SSSI and MW-LB Little Bradley, Milborne Wick

**I. ábra.** A: Az aaleini – alsó bathi rétegek előfordulása Nagy-Britanniában. A feketével jelzett terület a B ábrán látható. B: Az Inferior Oolite formáció kibukkanása (fekete) Délnyugat-Angliában. Az áltós árnyékolás nyugat felé a juránál fiatallabb közeteket jelöli. Az áltós árnyékolás kelet felé a juránál fiatallabb közeteket mutatja. C: Az Inferior Oolite Formáció (pontozott terület) a Sherborne régióban. A lelőhelyeket pontok és kódok jelölik: Sh-SL Sherborne, Sandford Lane; Sh-RL Sherborne, Redhole Lane; Ob-FQ Oborne, Frogden Quarry; MW-MH Miller's Hill SSSI and MW-LB Little Bradley, Milborne Wick

his life (1860–1929). A zonal and biohorizon scheme is given here as *Fig. 2* for part of the Lower Bajocian.

The most westerly exposure included is at Sherborne, Redhole Lane, Clatcombe (ST 635 185) (Sh-RL) (*Fig. 3*) described by HUXTABLE (1999) and CHANDLER (2019) about which nearby locations were described by BUCKMAN (1893). Oborne, Frogden Quarry (ST 648 183) (Ob-FQ) (*Fig. 4*) is renowned from the researches of HUDLESTON & WOODWARD (1885); HUDLESTON (1887–1896) and BUCKMAN (1893, 1909–1930). The original quarry face is preserved as a Site of Special Scientific Interest (SSSI) (CHANDLER et al. 2013, 2014, 2017; LARWOOD & CHANDLER 2016). Milborne Wick, Miller's Hill (MW-MH) (ST 653 205) (*Fig. 5*), also an SSSI is along a heavily overgrown lane known as Miller's Hill Lane. Described here are specimens from Little Bradley (MW-LB) (ST 663 207) close to Miller's Hill (HUXTABLE 2005, CHANDLER 2019). The Frogden and Milborne Wick locations are

included in the Geological Conservation Review (GCR) (COX & SUMBLER 2002).

Ammonites of the family Stephanoceratidae have been carefully recorded from the Lower Bajocian of Dorset and the Transdanubian Central Range (W Hungary). This account concerns only those from the Sauzei and Humphriesianum zones of Dorset. GALÁCZ (1976, 1991, 1994) published on the occurrence and temporal distribution of lower Middle Jurassic ammonites, mainly stephanoceratids, and in particular the introduction of the genus *Lokuticeras* GALÁCZ, 1994, which is the primary subject of this paper. *Lokuticeras* from the Lower Bajocian, Humphriesianum Zone, Humphriesianum Subzone to the Niortense Zone, Banksii Subzone of the Upper Bajocian were described. The occurrence of morphologically identical examples from the Lower Bajocian of Dorset is reported here over part of that range.

Stage/Substage	Zone	Subzone	biohorizon
Bajocian	Lower Bajocian	Humphriesianum	<i>Teloceras coronatum</i>
			<i>Teloceras blagdeni</i>
			<i>Lokuticeras rossbrunnense</i> biohorizon nov.
			<i>Stephanoceras blagdeniforme</i>
			<i>Stephanoceras gibbosum</i>
		Humphriesianum	<i>Stephanoceras humphriesianum</i>
			<i>Pseudoteloceras labrum</i>
			<i>Chondroceras wrighti</i>
		Romani	<i>Chondroceras delphinum</i>
			<i>Nannina evoluta</i>
Sauzei	Hebridica	<i>Stephanoceras rhytum</i>	<i>Pseudoteloceras digbyi</i>
			<i>Stephanoceras kalum</i>
		Kumaterus	<i>Kumatostephanus kumaterus</i>

**Figure 2.** The stage, substage, zones and subzones of the Inferior Oolite Formation (pars). Ammonite biohorizons of the Lower Bajocian Sauzei–Humphriesianum zones of Dorset and Somerset, UK. Biohorizons are labelled by a characteristic guide fossil; the scheme is based on CALLOMON & CHANDLER (1990) amended here and introduces the rossbrunnense biohorizon nov.

**2. ábra.** Az Inferior Oolite Formáció egy részének emelet, zóna és szubzóna szintű tagolása a Dorset és Somerset területén használatos ammonitesz-biohorizontokkal. A biohorizontokat a jellegzetes vezéralakok neve jelöli. A jelen munkában a rossbrunnense új biohorizonttal kiegészített táblázatot eredetileg CALLOMON & CHANDLER (1990) publikálta

The distribution of Aalenian – lowest Lower Bathonian ammonites in Dorset and Somerset has achieved significant progress since the introduction of the scheme of faunal horizons (biohorizons) by CALLOMON & CHANDLER (1990), with extension of the scheme to cover the Upper Bajocian and Lower Bathonian by CALLOMON & COPE (1995). The methodology of erection of the biohorizon scheme has been repeatedly described (CALLOMON & CHANDLER 1990; CALLOMON 1994, 1995; CALLOMON & COPE 1995).

The stratigraphical succession of the Inferior Oolite Formation in Dorset is that of richly fossiliferous, thin beds with omissions of strata on a very localized scale. These strata are heterogeneously condensed units, assumed, based on the close reproducibility of their assemblages at distant locations to be, in most cases, biohorizons isolated within the beds that are close to isochronous and contain contemporary assemblages of fossils (e.g., CHANDLER & CALLOMON 2009; CHANDLER et al. 2017, 2023). Excluding obviously reworked elements, these rock units represent biohorizons containing what is likely the closest to a palaeobiospecies, a segment of the evolving lineage in question.

The Hungarian succession such as at the Bakony Mountains is reported by GÉCZY (1967) and GALÁCZ (1991, 1994) and consists of red nodular limestones in thin beds separated by gaps of unknown duration.

Specimens depicted in the figures herein are morpho-species; they are members of segments of evolving lineages labelled with suitable names rather than any attempt to re-classify them.

## Abbreviations

[M], [m] Macroconch, microconch respectively. Specimen prefixed 'J' is stored at the Sedgwick Museum, Cambridge, UK; \* type species, HT holotype, PT paratype; SSSI Site of Special Scientific Interest.

Locality codes and UK map references: Sherborne, Redhole Lane, Clatcombe (ST 635 185) (Sh-RL); Oborne, Frogden Quarry (ST 648 183) (Ob-FQ); Milborne Wick, Miller's Hill (MW-MH) (ST 653 205); Milborne Wick, Little Bradley (MW-LB) (ST 663 207). Map references are UK Ordnance Survey National Grid Reference System. ST refers to an area within which the locations are positioned. The six figure numerical reference locates a position to within 100 m.

## Palaeontology

Suborder Ammonitina FISCHER, 1882  
Superfamily Stephanoceratoidea NEUMAYR, 1875  
Family Stephanoceratidae NEUMAYR, 1875  
Genus *Stephanoceras* WAAGEN, 1869

\**Ammonites humphriesianus*  
J. de C. SOWERBY, 1825 [M]

It is not the aim here to offer any revision of the numerous generic and specific names introduced mostly by BUCKMAN (1909–1930) or to recommend how such taxa could be

## SHERBORNE, REDHOLE LANE (Sh-RL)

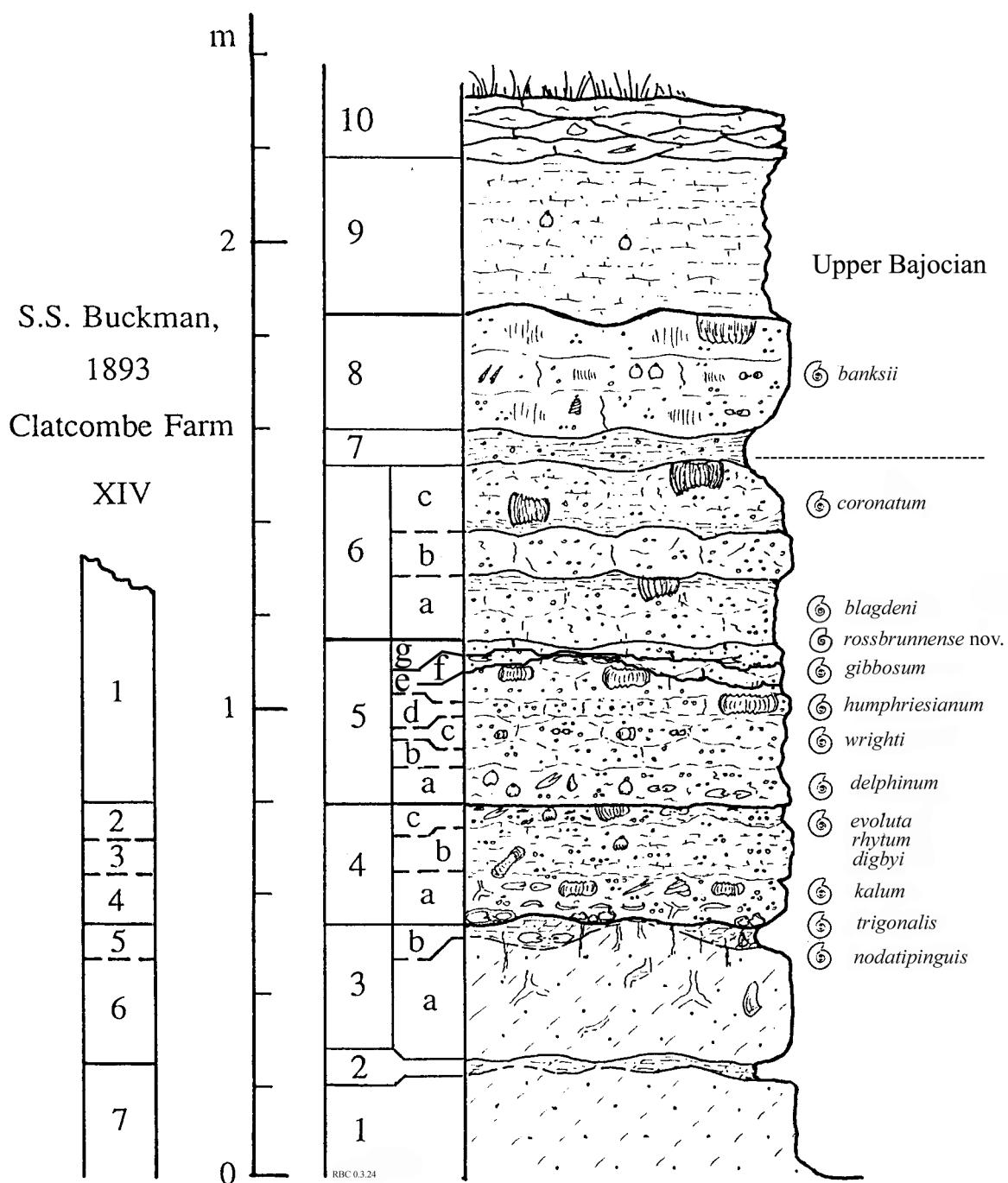


Figure 3. Diagrammatic representation through the Inferior Oolite at Lower Clatcombe, Redhole Lane (Sh-RL). Horizons in italics and given by species name. BUCKMAN's (1893) section is shown on the left

3. ábra. Az Inferior Oolite a Lower Clatcombe, Redhole Lane (Sh-RL) szelvényben. A horizontokat a dölttel szedett fajnevek jelölik. BUCKMAN (1893) szelvénye a bal oldalon

treated in a modern classification; however, it is now possible to state with certainty what occurs in each level representing the evolving family and what division, if any, is evident in the assemblages. Fig. 6 gives names of stephanoceratid, macroconch morphospecies found to date in the Dorset locations over part of the Sauzei to Humphriesianum zones. The difficulty in naming members of chronoclines

that have taxa with long-established morphogenetic names included in their assemblages has recently been discussed for the Graphoceratidae (CHANDLER et al. 2023). The listing of numerous synonyms is avoided as homoeomorphy is prevalent in stephanoceratids at different stratigraphical levels and would only serve to distort the direct field evidence other than for precisely stratigraphically located specimens.

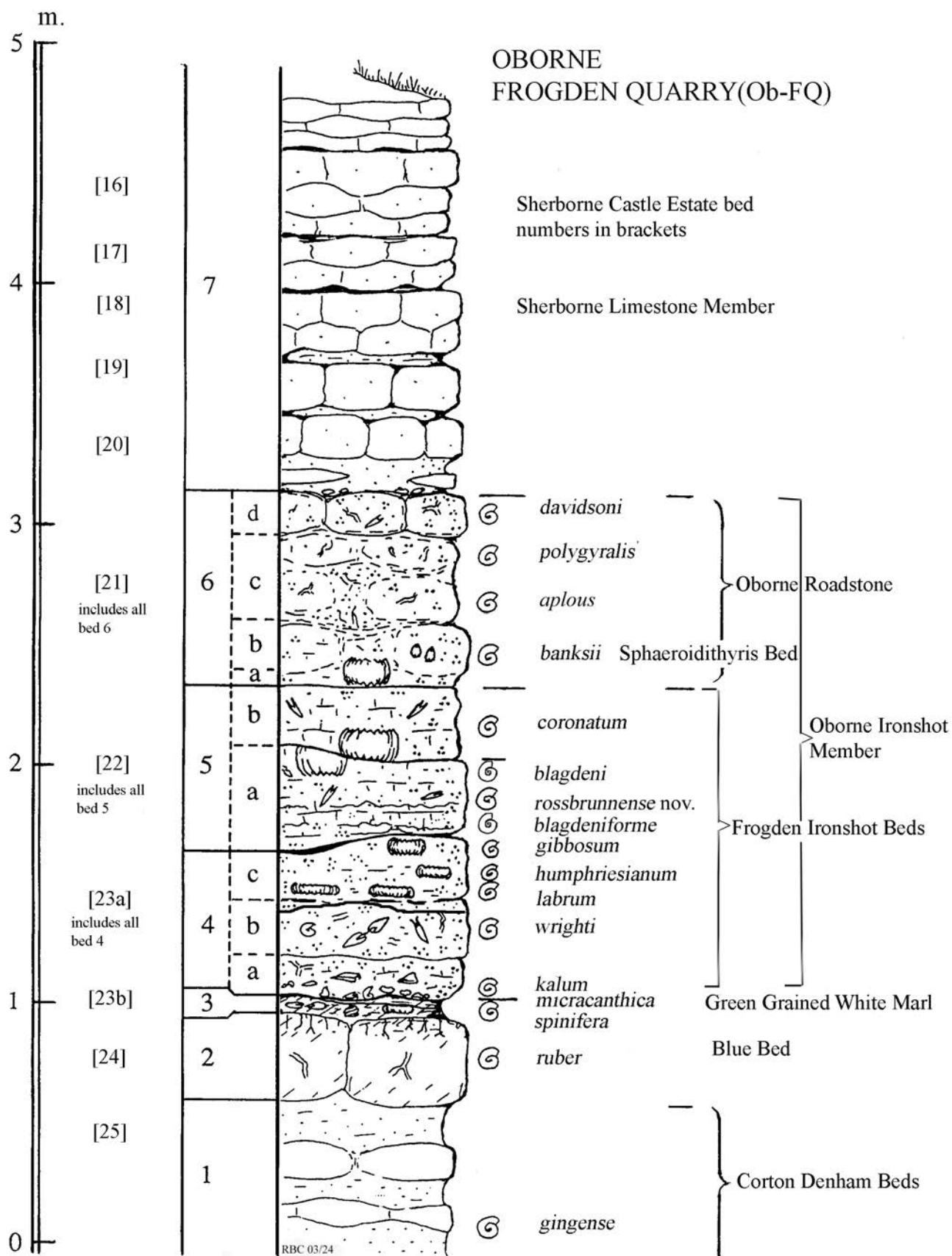


Figure 4. Diagrammatic representation through the Inferior Oolite at Frogden Quarry (Ob-FQ) after CHANDLER et al. (2014). Biohorizons in italics and given by guide species name. Sherborne Castle quarry numbers on left

4. ábra. Az Inferior Oolite a Frogden Quarry (Ob-FQ) szelvényben CHANDLER et al. (2014) nyomán. A biohorizontokat a dölttel szedett fajnevek jelölik. A Sherborne Castle Estate köfejtő számai a bal oldalon

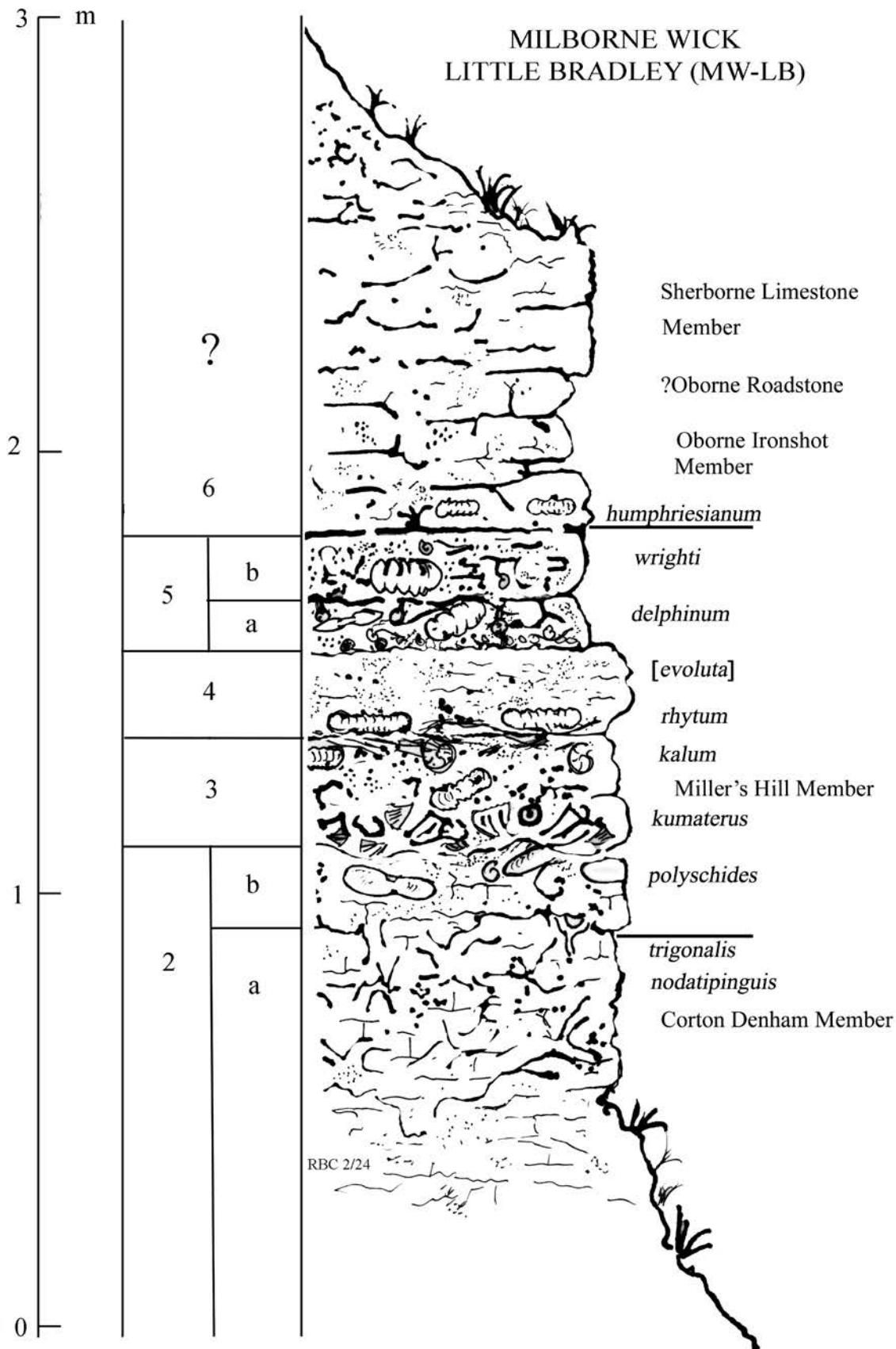


Figure 5. Diagrammatic representation through the Inferior Oolite at Little Bradley, Milborne Wick (MW-LB). The section is similar, but not identical to that at Miller's Hill (MW-MH) of Cox & SUMBLER (2002). Biohorizons in italics and given by guide species name

5. ábra. Az Inferior Oolite a Little Bradley, Milborne Wick (MW-LB) szelvényben. A szelvény hasonló, de nem azonos a Miller's Hill (MW-MH) Cox & SUMBLER (2002)félé szelvénnel. A biohorizontokat a dölttel szedett fajnevek jelölik

ZONE	SUBZONE	Macroconchs
Humphriesianum	Blagdeni	<i>Lokuticeras fredericiromani</i> (ROCHÉ) (R), <i>Stephanoceras (Stephanoceras) aff. sturanii</i> PAVIA (O), <i>Teloceras blagdeni</i> (SOWERBY) (C) <i>Lokuticeras rossbrunnense</i> GALÁCZ (O), <i>L. fredericiromani</i> (R), <i>S. sturanii</i> (O), <i>Stephanoceras leoniae</i> SCHMIDTILL & KRUMBEK (O), <i>Stephanoceras tenuicostatum</i> (HOCHSTETTER) (O), <i>T. blagdeni</i> (C)
	Humphriesianum	<i>Stephanoceras blagdeniforme</i> (ROCHÉ) (C), <i>L. rossbrunnense</i> & aff. (C), <i>L. fredericiromani</i> (R), <i>S. leoniae</i> (C), <i>Stephanoceras scalare</i> WEISERT (O), <i>Stephanoceras (Skirroceras) englandi</i> CHANDLER (O), <i>Stephanoceras zieteni</i> (QUENSTEDT) (O), <i>Stephanoceras gibbosum</i> (BUCKMAN) (C), <i>Stephanoceras humphriesianum</i> (J. DE C. SOWERBY) (C), <i>S. aff. sturanii</i> (O), <i>Stephanoceras triplex</i> WEISERT (O), <i>Kumatostephanus gibbosus</i> (BUCKMAN) (C)
	Romani	<i>L. aff. rossbrunnense</i> (O), <i>S. zieteni</i> (C), <i>St. (Sk.) aff. englandi</i> (O), <i>S. scalare</i> (C), <i>S. humphriesianum</i> (C), <i>S. aff. sturanii</i> (O), <i>Stephanoceras plicatissimum</i> (QUENSTEDT) (O), <i>Stephanoceras pyritosum</i> (QUENSTEDT) (C), <i>S. tenuicostatum</i> (O), <i>Stephanoceras hoffmanni</i> SCHMIDTILL & KRUMBEK (O), <i>Teloceras labrum</i> BUCKMAN (O), <i>Stephanoceras umbilicum</i> (QUENSTEDT) (C), <i>Stephanoceras mutabile</i> (QUENSTEDT) (C), <i>Stephanoceras plagioides</i> BUCKMAN (O)
Sauzei	Hebridica	<i>S. umbilicum</i> (QUENSTEDT) (O), <i>S. mutabile</i> (O), <i>S. aff. humphriesianum</i> (O), <i>S. scalare</i> (O), <i>S. aff. sturanii</i> (R), <i>S. zieteni</i> (O), <i>T. aff. labrum</i> (O) ? <i>Stephanoceras frechi</i> (RENZ), <i>S. aff. humphriesianum</i> (R) S. aff. sturanii (R), <i>Stephanoceras rochei</i> (MAUBEUGE) (O) <i>S. tenuicostatum</i> (R), <i>S. aff. scalare</i> (O), <i>Teloceras ellipticum</i> (MASCKE) (R)

**Figure 6.** The distribution of some stephanoceratid morphospecies from Redhole Lane, Frogden Quarry and Milborne Wick. Each Subzone is shown as an upper grey shaded part and a lower part without shading. The macroconch stephanoceratid morphospecies found from the three Dorset locations are shown by their occurrence in each part of the figure. The full name with author is given on first use only. Estimated abundance is indicated by (C) common, (O) occurs and (R) rare. It is to be stressed that the diagram only acts as a guide to what has been found based on comparison with published specimens. It is not a comprehensive list as much remains to be prepared and evaluated

**6. ábra.** Néhány stephanoceratid morphospecies a Redhole Lane, Frogden Quarry és Milborne Wick lelőhelyekről. A szubzónák felső része szürkével jelölve. A fajleíró nevét csak az első említéskor közöljük. Gyakorisági viszonyok: C: gyakori, O: előfordul, R: ritka

#### Genus *Lokuticeras* GALÁCZ, 1994

##### *Lokuticeras \*rossbrunnense* GALÁCZ, 1994

The type species is figured by GALÁCZ (1994, pl. 1, fig. 1), a specimen from Lókút, Bakony Mountains, from the Humphriesianum Zone, Blagdeni Subzone; it is identical to specimens from the Sherborne area of Dorset from the *Stephanoceras humphriesianum* and *Stephanoceras gibbosum* biohorizons (e.g., Pl. III, 4a–b; Pl. V, 3a–b). Common examples occur in the base of the Blagdeni Subzone at Redhole Lane, where to date, the group is best represented in Dorset. Close matches for the paratypes of GALÁCZ (1994, PT 1, pl. 1, fig. 2; PT 3, pl. 1, fig. 4; PT 2, pl. 2, fig. 1; PT 4, pl. 3, fig. 1) also occur and are depicted in Pls. II–V. The 4<sup>th</sup> paratype (J51767) is a Dorset specimen from Miller's Quarry Sherborne and is the most coarsely ribbed of the type series. The location of Miller's Quarry appears lost, but by matrix, it can only have come from a geographically restricted, narrow belt of strata, of the Oborne Ironshot Member, Frogden Ironshot Beds (CHANDLER et al 2014), Bed 4c belonging to the Humphriesianum Subzone, *humphriesianum* or *gibbosum* biohorizon from between Sherborne and Oborne. That specimen figured by GALÁCZ (1994, pl. 3, fig.

1) as paratype 4 is refigured here from new photographs as Pl. VI, 1a–b. Similar additional specimens from Dorset are demonstrated to range as low as the Sauzei Zone and up to the Banksii Subzone. Only examples from part of that range are included here as some specimens await preparation.

Included in *Lokuticeras* GALÁCZ, 1994 are macroconch species *Stephanoceras (Stephanoceras) sturanii* PAVIA, 1983 of the Humphriesianum/Niortense boundary and *Lokuticeras fredericiromani* (ROCHÉ, 1939) of the Blagdeni Subzone. The holotype of *St. sturanii* PAVIA is figured in PAVIA (1983 pl. 13, fig. 6; listed incorrectly in GALÁCZ 1994 as pl. 14). PAVIA figures additional specimens from Bayeux (pl. 13, fig. 2) and another from Chaudon (pl. 13, fig. 4). The Dorset specimens figured herein (Pl. IV, 3a–b; Pl. V, 2a–b) are slightly different; therefore these have been listed as aff. or as a transitional form.

The profile of the mouth-border of many of these ammonites is similar to that depicted by J. BUCKMAN (1881, p. 64, text fig. 6). The microconch partners of *Lokuticeras* are placed in *Masckeites* BUCKMAN, 1920 and include *Masckeites \*densus* BUCKMAN, 1920 of the Humphriesianum Zone and *Masckeites psilacanthoides* (SANDOVAL, 1983), Niortense Zone.

It should be clarified that the above are morphospecies that can be located to a specific range of biohorizons in Dorset at a number of locations. In all cases the observations of GALÁCZ (1994) can be confirmed with the qualifications made below.

## Discussion

This account is based on a large number of specimens collected *in situ*; however not all have yet been prepared in time for this work. Records of the stratigraphical distribution of '*Lokuticeras*' morphology in Dorset appears to begin lower in the succession than in Hungary, first occurring in the Sauzei Zone or below. This may be due to earlier examples not so far being identified in Hungary, stratigraphic omission or an ecological factor. It may also be the case that if this ammonite group arrived via the 'Hispanic Corridor' (SADKI & MOUTERDE 1994) morphs leading to *Lokuticeras* may have inhabited western Europe slightly earlier. Examples of what GALÁCZ considers included in *Lokuticeras* are quite widely reported across Europe (e.g., PAVIA 1983 for France, FERNÁNDEZ-LÓPEZ 1985 for Spain, CRESTA & GALÁCZ 1990 for Hungary and Italy). A specimen figured by DIETZE (2010, pl. 4, figs. 3–4) from southern Germany has similar ribbing on the inner whorls to (pl. 3, fig. 1) of GALÁCZ (1994) paratype 4 but has a broader whorl section and is less serepticonic. All the macroconchs figured by GALÁCZ (1994) lack a ventral view image therefore the interpretations here must take that into account.

In Dorset the first specimens collected to date that match the morphology of *Lokuticeras* [M & m] occur in the assemblage of the *rhytum* biohorizon of the upper part of the Sauzei Zone. They occur in the Romani Subzone and become relatively abundant in the lower Humphriesianum Subzone. They are most common (as observed by GALÁCZ) in the uppermost Humphriesianum Subzone and persist at least to the *polygyralis* biohorizon of the Niortense Zone.

All the specimens have fine close ribbing, coronate innermost whorls, short primary ribbing and lack pronounced tubercles, some have tiny sharp spines. The most notable feature is the abundance of small macroconchs (e.g., Pl. III, Figs. 1–4; Pl. IV, Figs. 2a–b, 3a–b; Fig. 5, 2a–b, 3a–b) that show the features of adults with well-developed mouth-borders and lacking lappets. Such specimens are what CHANDLER (2019) referred to as mesoconchs. Taking only the range of morphological variability of *Lokuticeras* as described by GALÁCZ in isolation, it is reasonable to consider, as GALÁCZ concluded, that *Lokuticeras* forms a separate evolutionary lineage within the Stephanoceratidae; however this interpretation must be judged, based on the information presented here.

The Dorset specimens from the upper Sauzei Zone constitute a continuum, a plexus of morphology and size variability centred on *Stephanoceras rhytum*, the type of which has fine close ribbing of the inner whorls and similarity to *Lokuticeras*. *Stephanoceras* (St.) aff. *scalare* (Pl. IV, 3a–b) has morphology intermediate to S. aff. *sturanii*. It is ar-

guable (as discussed by CHANDLER 2019) that the generic names *Skirroceras* or *Stephanoceras* can both be applied to the ammonites at this level as the plexus of variability ranges from stephanoceratids with depressed oval whorls sections approaching *Stephanoceras humphriesianum* to slender rather quadrate, very evolute *Skirroceras*. The line leading to *Stephanoceras* sensu stricto (\**Ammonites humphriesianus* J. de C. SOWERBY, 1825 [M]), is present in the *rhytum* assemblage, as part of a continuum that can be traced back to the Aalenian from *Riccardiceras*. Furthermore, some of the more coarsely ribbed morphospecies (e.g., *Kumatostephanus*) likely originate from a different ancestor.

The size variability of complete adult macroconchs in the *rhytum* biohorizon and above is staggering, with small macroconchs of around 80 mm existing alongside shells of 350 mm, all displaying features of adulthood. A mesoconch specimen with *Lokuticeras* morphology identified as *Stephanoceras* aff. *pyritosum* (QUENSTEDT) from the Sauzei Zone is given in Pl. V, 1a–b. A further observation is that the larger examples develop coarser, more distant ribbing on the later whorls and sometimes spines or tubercles on the body-chamber. In all cases the ribbing persists to a short distance before the aperture. The mouth-border is flared with a constriction preceding the peristome.

Collections from Dorset from the Sauzei Zone to Blagdeni Subzone includes the *Lokuticeras* morphs within the intraspecific variability of the assemblage. The *Lokuticeras* morphology attains maximum abundance in the lowest Blagdeni Subzone and is the dominant stephanoceratid (excluding teloceratids). In the *blagdeniforme* and *blagdeni* biohorizons *Lokuticeras* persists as the only serpenticonic/subserpenticonic stephanoceratid alongside abundant '*Teloceras-like*' forms. Further insight into the evolution of the morphogenus can be evaluated from specimens collected from three key Dorset locations

Redhole Lane is the most westerly exposure of strata of Humphriesianum Zone age relevant here. Further west, in a short distance at Sandford Lane (ST 628 178) the entire succession of the Humphriesianum Zone and almost all of the Niortense Zone is cut out beneath the Upper Bajocian. The outcrop at Redhole Lane is in an agricultural field and has been studied in temporary excavations (HUXTABLE 1999, CHANDLER 2019). Records from historical exposures nearby are by BUCKMAN (1893). Above the Sauzei Zone (Fig. 4) is a series of thin ironshot, oolitic limestones (Bed 5 & 6) representing the upper part of the Romani Subzone to the Humphriesianum Subzone; these are labelled 5a–g. Bed 6 is Blagdeni Subzone and contains common *Lokuticeras* in the lowest part. The beds are discontinuous across the area and are sometimes, locally, individually absent. New information regarding Beds 5 and 6 is now available shedding further clarity on the biostratigraphical division of this bed at Redhole Lane and Frogden Quarry. CHANDLER (2019, fig 13e) introduced the species *Stephanoceras* (*Skirroceras*) *englandi* HT, from Frogden Quarry, Bed 4c–5a transition (Fig. 4). The inner whorls of members of the type series closely resemble *Lokuticeras*; they are also close to GALÁCZ

(1991, pl. 1, fig. 3) referred to as *Stephanoceras* sp. A number of examples of *S. englandi* have now been collected *in situ* from Redhole Lane and Frogden Quarry and their levels of occurrence can now be separated. The lower level at which the stouter '*Skirroceras*' morphology of *S. englandi* is found is in the *humphriesianum* biohorizon (in the middle part of Bed 4c at Frogden) and includes large (300 mm +) *S. humphriesianum* and smaller *Lokuticeras*; this is the level of PT 4 of *L. \*rossbrunnense* GALÁCZ, 1994 with relatively common chorotypes of PT 4. The large *S. aff. englandi* are intermediate between *S. humphriesianum* and *Skirroceras* (*Pl. I, 1a–b*). Directly above at both Redhole Lane and Frogden Quarry is a bed of rotted limestone with specimens including some of the type series of *S. englandi*. These specimens are smaller than those below (c 150–250 mm or less) (*Pl. I, 2a–b*) and have rope-like narrow coiling and less pronounced close ribbing. They are accompanied by common *Lokuticeras* [M] at Redhole Lane (*Pl. III, 1–4; Pl. IV, 1a–b, 2a–b; Pl. V, 3a–b*) and lesser numbers at Frogden (*Pl. II, 1a–b, 2a–b, 3a–b*). They include diminutive examples (all c110 mm) of *L. rossbrunnense*, that themselves resemble small morphs of *S. englandi*. The same occurrence is seen at Frogden Quarry, but there *L. rossbrunnense* is less frequent and both *Kumatostephanus gibbosum* and *Teloceras* occur at the same level.

The microconch association remains more obscure. The specimen of *Masckeites densus* [m] (*Pl. I, 3a–b*) is a fairly common form throughout the upper Humphriesianum and Blagdeni subzones and *Gerzenites rugosus* WESTERMANN [m] (*Pl. V, Figs. 4a–b*) occurs in the Humphriesianum Subzone. Finely ribbed examples such as *Germanites bicostatus* (WESTERMANN) [m] (*Pl. IV, Fig. 4*) occur in the Sauzei Zone.

The occurrence of '*Skirroceras*-like *Lokuticeras*' in the Sauzei Zone in the plexus of forms in the *Stephanoceras rhytum* biohorizon (*Pl. V, 1a–b*) and in the Romani Subzone, *delphinium* biohorizon of Milborne Wick (*Pl. IV, 3a–b; Pl. V, 2a–b*) points to the origins of at least some *Lokuticeras* species in the Sauzei Zone from miniature members of the assemblage. Small macroconch ammonites (mesoconchs) are constituent members of stephanoceratid assemblages throughout the Bajocian and can also be identified in other families (e.g. sphaeroceratids, otoitids, perisphinctids). The smallest collected so far is *Pl. II, 3a–b* at 50 mm, smaller than some contemporary microconchs. They are paedomorphic members of the palaeobiospecies at the levels sampled, each being a miniature version of the normal size population. At some levels (e.g., *humphriesianum* biohorizon) there is indication of a trimodal size distribution (macroconchs, mesoconchs and microconchs). Testing this reliability, statistically, is challenging without knowing how many generations of ammonites are present in the time duration of a biohorizon. It is also likely that these ammonites could represent the extreme end of a highly variable palaeobiospecies with respect to size. FERNÁNDEZ-LÓPEZ & PAVIA (2016) have presented biological mechanisms to explain such size discrepancies. The upper levels of the occurrence of *Lokuticeras* are still in the early stage of study in Dorset;

*L. rossbrunnense* and spp. aff. rather than splitting-off towards the top of the Humphriesianum Zone evolve as surviving stephanoceratids with morphological changes including both an increase in size of the larger end members and evolution of others to *Cadomites* (see GALÁCZ 1991, fig. 1). *L. rossbrunnense* occupies a stratigraphical position in Dorset where it is a common, characteristic, guide fossil in the uppermost Humphriesianum Subzone and lower Blagdeni Subzone. This range of occurrence is similar in Hungary and close matches to specimens that can be attributed to *Lokuticeras* can now be confirmed from collections made in Hungary (GALÁCZ 1991, 1994), Hungary and Italy (CRESTA & GALÁCZ 1990), Spain (FERNÁNDEZ-LÓPEZ 1985), Germany (DIETZE 2010), SE France (PAVIA 1983) and recently western France at La Grande Palisse, Nanteuil (Deux-Sèvres) in Bed 19b of the Blagdeni Subzone (LA-CROIX pers. comm.). Typical specimens centre on *L. rossbrunnense* which here is erected as the lowest biohorizon of the Blagdeni Subzone of the Humphriesianum Zone and included in the table of biohorizons (*Fig. 2*).

## Conclusion

In Dorset the morphology of *Lokuticeras* can be traced back to the Sauzei Zone and possibly earlier. The morphology of the genus in Dorset constitutes part of the total stephanoceratid assemblage of biohorizons of the Humphriesianum Zone and in minor numbers in the Sauzei Zone. It becomes the dominant ammonite in the upper Humphriesianum Subzone/lowest Blagdeni Subzone for which a *L. rossbrunnense* biohorizon is erected herein. Specimens included in *Lokuticeras* have been widely reported across parts of Europe. Its persistence into higher strata gives rise to *Cadomites*. Much still needs to be clarified regarding the relationship of diminutive, but mature, small macroconchs of a number of taxa.

## Acknowledgements

The author thanks Orsolya SZTANÓ (editor-in-chief) and István FÓZY (section editor) for their guidance in the preparation of this work. Thanks are given to professors J.C.W. COPE and G. PAVIA for their critical review of the manuscript and suggestions for its improvement. This work was made possible by the kind cooperation of Sherborne Castle Estates over many years. In particular the expert quarry management and skill of Martin DODGE. Robert and Peter HUNT are thanked as tenants of land on which Frogden and Redhole Lane are situated. Natural England gave consent to work in SSSI designated areas. In the field John H. CALLOMON (deceased) contributed much to the work at Redhole Lane. Much of the industrious effort in the collection of specimens was provided by Andy STEADMAN, Peter LANGHAM, Andy COWAP and Volker DIETZE. From earlier times great thanks are due to Andrew ENGLAND (deceased) name giver of S.

*englandi*, William JONES and John WHICHER. The late J.G. HUXTABLE first identified the site of investigation at Red-hole Lane. Information on specimens from La Grande Palisse is kindly provided by Pierre LACROIX (project geologist) and Jérôme CAILLET-LABASSE (owner Labasse et Fils Com-

pany). Matt RILEY of the Sedgwick Museum, Cambridge is thanked for providing images of J51767 housed in that collection. John FREDD is thanked for preparing some of the figured specimens.

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Manuscript received: 07/02/2024

## Plate I – 1. tábla

Fig. 1a-b. *Stephanoceras (Skirroceras) aff. englandi* CHANDLER [M] CT, WC6067, Bed 4c middle part, *humphriesianum* biohorizon.

Fig. 2a-b. *St. (Sk.) englandi* [M] CT, WC6066, Bed 4d, *gibbosum* biohorizon.

Fig. 3a-b. *Stephanoceras (Masckeites) aff. densus* (BUCKMAN) [m], WC0934, Bed 4c lower or middle part, *labrum* or *humphriesianum* biohorizon. Humphriesianum Zone, Oborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Oborne, Dorset.

Scale bar Figs. 1-2 is 120 mm and Fig. 3 is 40 mm. A black star marks the last preserved suture.

*Fig. 1a-b. Stephanoceras (Skirroceras) aff. englandi CHANDLER [M] CT, WC6067, 4c réteg, humphriesianum biohorizont középső része.*

*Fig. 2a-b. St. (Sk.) englandi [M] CT, WC6066, 4d réteg, gibbosum biohorizont.*

*Fig. 3a-b. Stephanoceras (Masckeites) aff. densus (BUCKMAN) [m], WC0934, 4c réteg, alsó vagy középső része a labrum vagy humphriesianum biohorizontnak. Humphriesianum zóna, Oborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Oborne, Dorset.*

Méretarány: Figs. 1-2: 120 mm és Fig. 3: 40 mm. A csillag az utolsó megőrződött szutúrát jelzi.

## Plate II – 2. tábla

Figs. 1-4. *Stephanoceras scalare* WEISERT [M]. 1a-b. WC0311, Bed 4c middle part, Humphriesianum Subzone, *humphriesianum* biohorizon. 2a-b. WC0032 & 3a-b. WC2397, Bed 4b, Romani Subzone, *wrighti* biohorizon. WC2397 is the smallest [M] specimen found to date. Humphriesianum Zone, Oborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Oborne, Dorset. 4a-b. WC6072 *St. (L.) scalare*.

Fig. 5a-b. WC6071 *Stephanoceras zieteni* (QUENSTEDT), both Bed 5a, *delphinum* biohorizon, Milborne Wick, Little Bradly, Humphriesianum Zone, Romani Subzone.

Scale bar is 40 mm. A black star marks the last preserved suture.

*Figs. 1-4. Stephanoceras scalare WEISERT [M]. 1a-b. WC0311, 4c réteg, Humphriesianum szubzóna középső része, humphriesianum biohorizont. 2a-b. WC0032 és 3a-b. WC2397, 4b réteg, Romani Szubzóna, wrighti biohorizont. WC2397 a legkisebb valaha talált [M] példány. Humphriesianum zóna, Oborne Ironshot Member, Frogden Ironshot Beds, Frogden Quarry, Oborne, Dorset. 4a-b. WC6072 St. (L.) scalare.*

*Fig. 5a-b. WC6071 Stephanoceras zieteni (QUENSTEDT), mindenkor az 5a rétegből, delphinum biohorizont, Milborne Wick, Little Bradly, Humphriesianum zóna, Romani szubzóna.*

Méretarány: 40 mm. A csillag az utolsó megőrződött szutúrát jelzi.

### Plate III – 3. tábla

Figs. 1-3. *Stephanoceras scalare* WEISERT & aff. [M]. 1a-b. WC0320 St. aff. scalare, Bed 5d, 2a-b. WC2396 Bed 5d, 3a-b. WC0033 Bed 5d, *humphriesianum* biohorizon.

Fig. 4a-b. *Lokuticeras rossbrunnense* GALÁCZ, Bed 5f, *gibbosum* biohorizon.

All Humphriesianum Zone, Humphriesianum Subzone, Sherborne, Clatcombe, Redhole Lane.

Scale bar is 40 mm. A black star marks the last preserved suture.

*Figs. 1-3. Stephanoceras scalare WEISERT & aff. [M]. 1a-b. WC0320 St. aff. scalare, 5d réteg, 2a-b. WC2396 5d réteg, 3a-b. WC0033 5 réteg, humphriesianum biohorizont.*

*Fig. 4a-b. Lokuticeras rossbrunnense GALÁCZ, 5f réteg, gibbosum biohorizont.*

*Minden példány Humphriesianum zóná, Humphriesianum szubzóná, Sherborne, Clatcombe, Redhole Lane.*

*Méretarány: 40 mm. A csillag az utolsó megőrződött szutúrát jelzi.*

### Plate IV – 4. tábla

Fig. 1a-b. *Lokuticeras aff. rossbrunnense* GALÁCZ [M] WC6070 Bed 5e, *gibbosum* biohorizon.

Fig. 2a-b. *L. rossbrunnense* [M] WC0598 Bed 5d, *humphriesianum* biohorizon. Both Humphriesianum Subzone, Sherborne, Clatcombe, Redhole Lane.

Fig. 3a-b. *Stephanoceras (St.) scalare trans. sturanii* PAVIA [M] WC2428 Bed 5a, *delphinum* biohorizon. Romani Subzone, Milborne Wick, Little Bradley.

Fig. 4a-b. *Germanites bicostatus* (WESTERMANN) [m] WC2223, Bed 4b, Sauzei Zone, Hebridica Subzone, *rhytum* biohorizon. Clatcombe, Redhole Lane. The specimen is attached to a specimen of *Dorsetenia*.

Scale bar is 40 mm. A black star marks the last preserved suture.

*Fig. 1a-b. Lokuticeras aff. rossbrunnense GALÁCZ [M] WC6070 5e réteg, gibbosum biohorizont.*

*Fig. 2a-b. L. rossbrunnense [M] WC0598 5d réteg, humphriesianum biohorizont. Mindkettő Humphriesianum szubzóná, Sherborne, Clatcombe, Redhole Lane.*

*fig. 3a-b. Stephanoceras (St.) scalare trans. sturanii PAVIA [M] WC2428 5a réteg, delphinum biohorizont. Romani szubzóná, Milborne Wick, Little Bradley.*

*Fig. 4a-b. Germanites bicostatus (WESTERMANN) [m] WC2223, 4b réteg, Sauzei zóná, Hebridica szubzóná, rhytum biohorizont. Clatcombe, Redhole Lane. A példány egy Dorsetenia példányával van összenöve.*

*Méretarány: 40 mm. A csillag az utolsó megőrződött szutúrát jelzi.*

### Plate V – 5. tábla

Fig. 1a-b. *Stephanoceras aff. pyritosum* (QUENSTEDT) [M] WC2670 Bed 4 Sauzei Zone, Hebridica Subzone, *rhytum* biohorizon.

Fig. 2a-b. *Stephanoceras (St.) aff. sturanii* PAVIA [M] WC2427 Bed 5a, *delphinum* biohorizon. Romani Subzone 1-2 Milborne Wick, Little Bradley.

Fig. 3a-b. *Lokuticeras rossbrunnense* GALÁCZ [M] WC2407 Bed 5g or 6a, *gibbosum* or *rossbrunnense* biohorizon, Sherborne, Clatcombe, Redhole Lane. A specimen of *Sphaeroceras* is adhering to the body-chamber.

Fig. 4a-b. *Gerizenites rugosus* WESTERMANN [m] WC0723 *humphriesianum* biohorizon, Oborne Wood adjacent to Frogden Quarry. 3-4: both Humphriesianum Zone and Subzone.

Scale bar is 40 mm.

*Fig. 1a-b. Stephanoceras aff. pyritosum (QUENSTEDT) [M] WC2670 4. réteg, Sauzei zóná, Hebridica szubzóná, rhytum biohorizont.*

*Fig. 2a-b. Stephanoceras (St.) aff. sturanii PAVIA [M] WC2427 5a réteg, delphinum biohorizont. Romani szubzóná 1-2 Milborne Wick, Little Bradley.*

*Fig. 3a-b. Lokuticeras rossbrunnense GALÁCZ [M] WC2407 5g vagy 6a réteg, gibbosum vagy rossbrunnense biohorizont, Sherborne, Clatcombe, Redhole Lane. A példány egy Sphaeroceras lakókamrájával van összenöve.*

*Fig. 4a-b. Gerizenites rugosus WESTERMANN [m] WC0723 humphriesianum biohorizont, Oborne Wood a Frogden Quarry szomszédságában. 3-4: Humphriesianum zóná és szubzóná. A csillag az utolsó megőrződött szutúrát jelzi.*

*Méretarány 40 mm.*

### Plate VI – 6. tábla

Fig. 1a-b. *Lokuticeras rossbrunnense* GALÁCZ [M] Sedgwick Museum, Cambridge J51767. 4th paratype of GALÁCZ, 1994. Monk Collection. Miller's quarry, Sherborne. See text for details.

Scale bar is 50 mm. A black star marks the approximate position of the last preserved suture.

*Fig. 1a-b. Lokuticeras rossbrunnense GALÁCZ [M] Sedgwick Museum, Cambridge J51767. 4th paratype of GALÁCZ (1994). Monk-gyűjtemény. Miller's quarry, Sherborne. Részletek a szövegben.*

*Méretarány: 50 mm. A csillag az utolsó megőrződött szutúra hozzávetőleges helyét jelzi.*

Plate I – 1. tábla

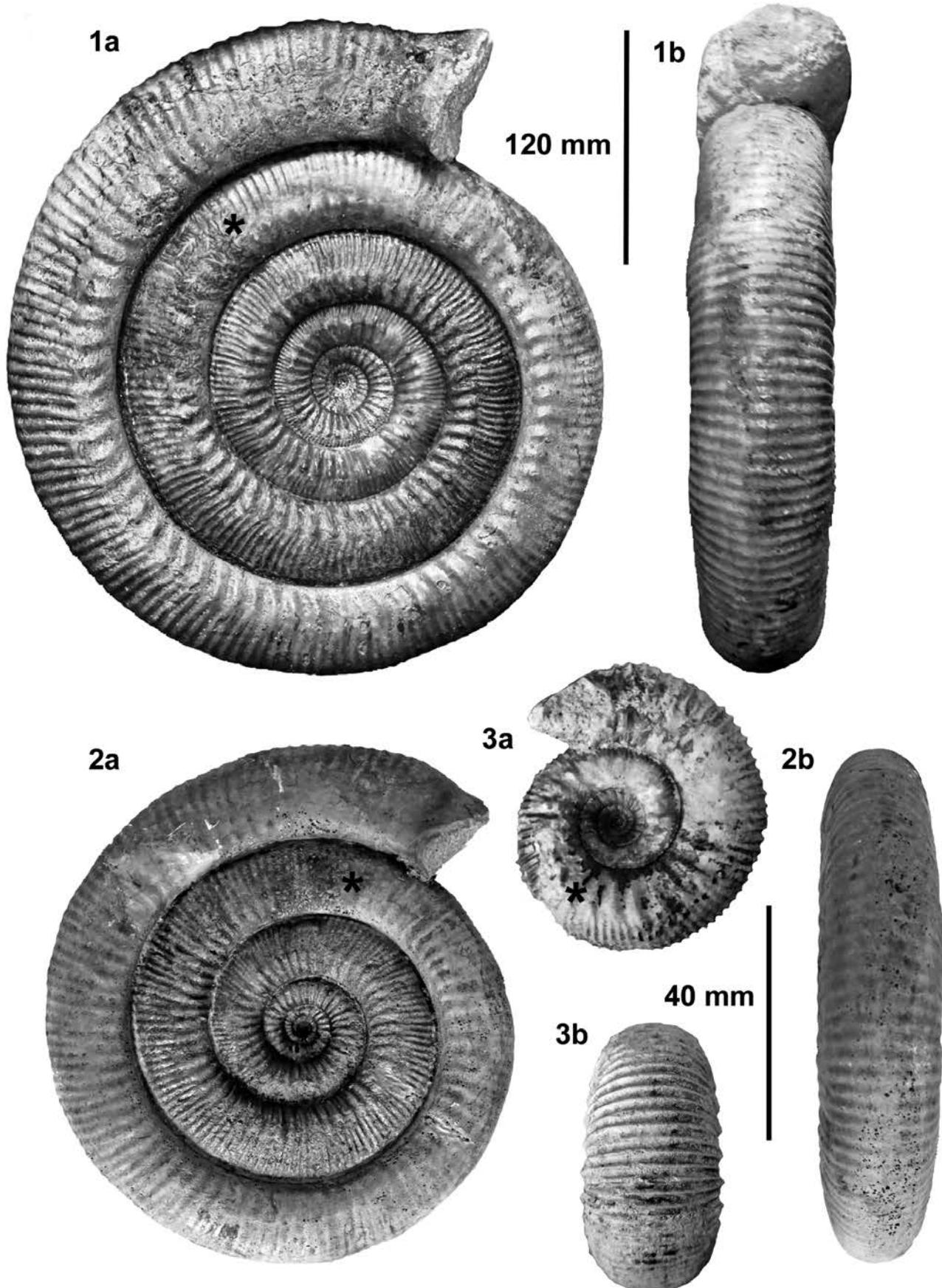


Plate II – 2. tábla

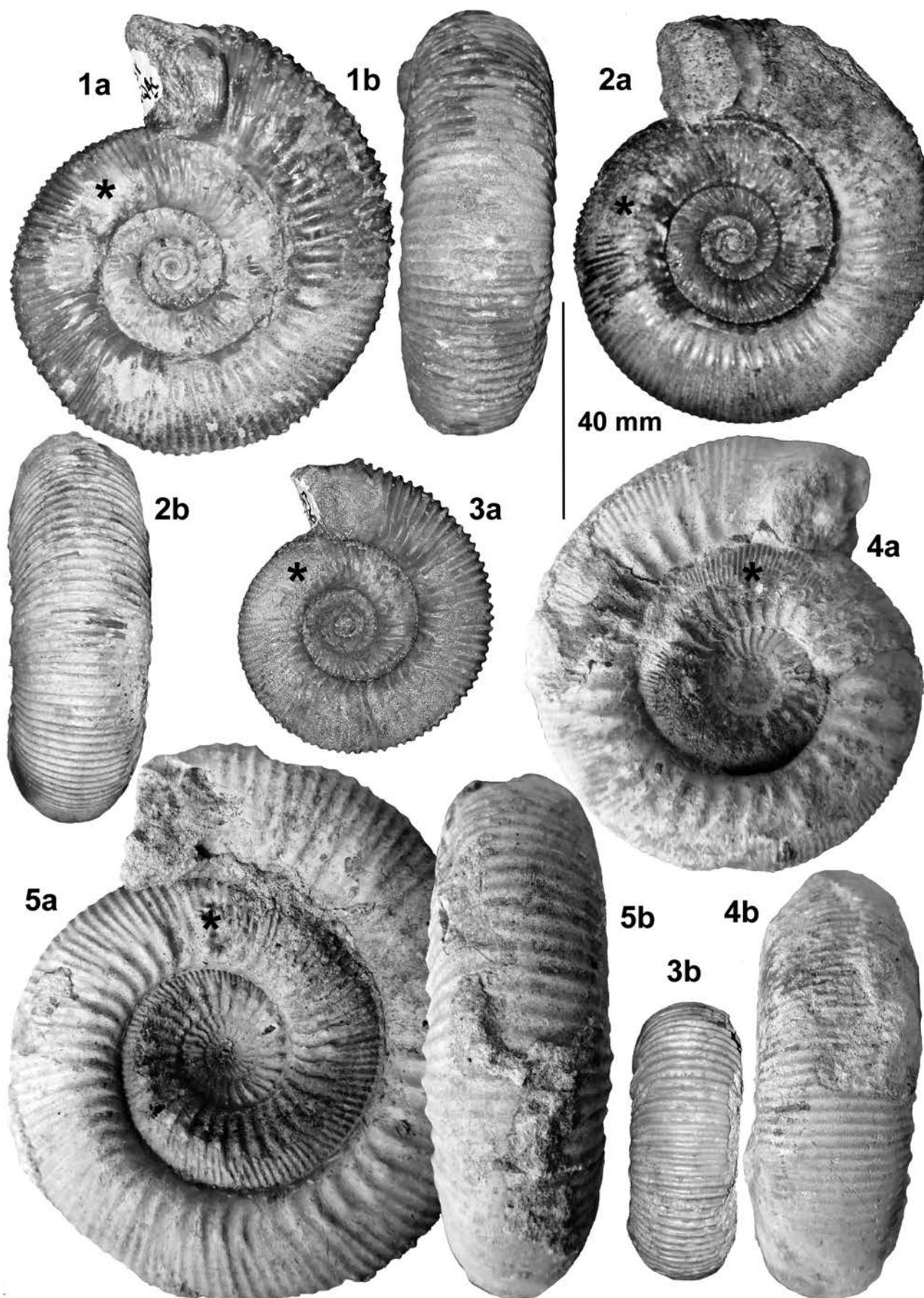
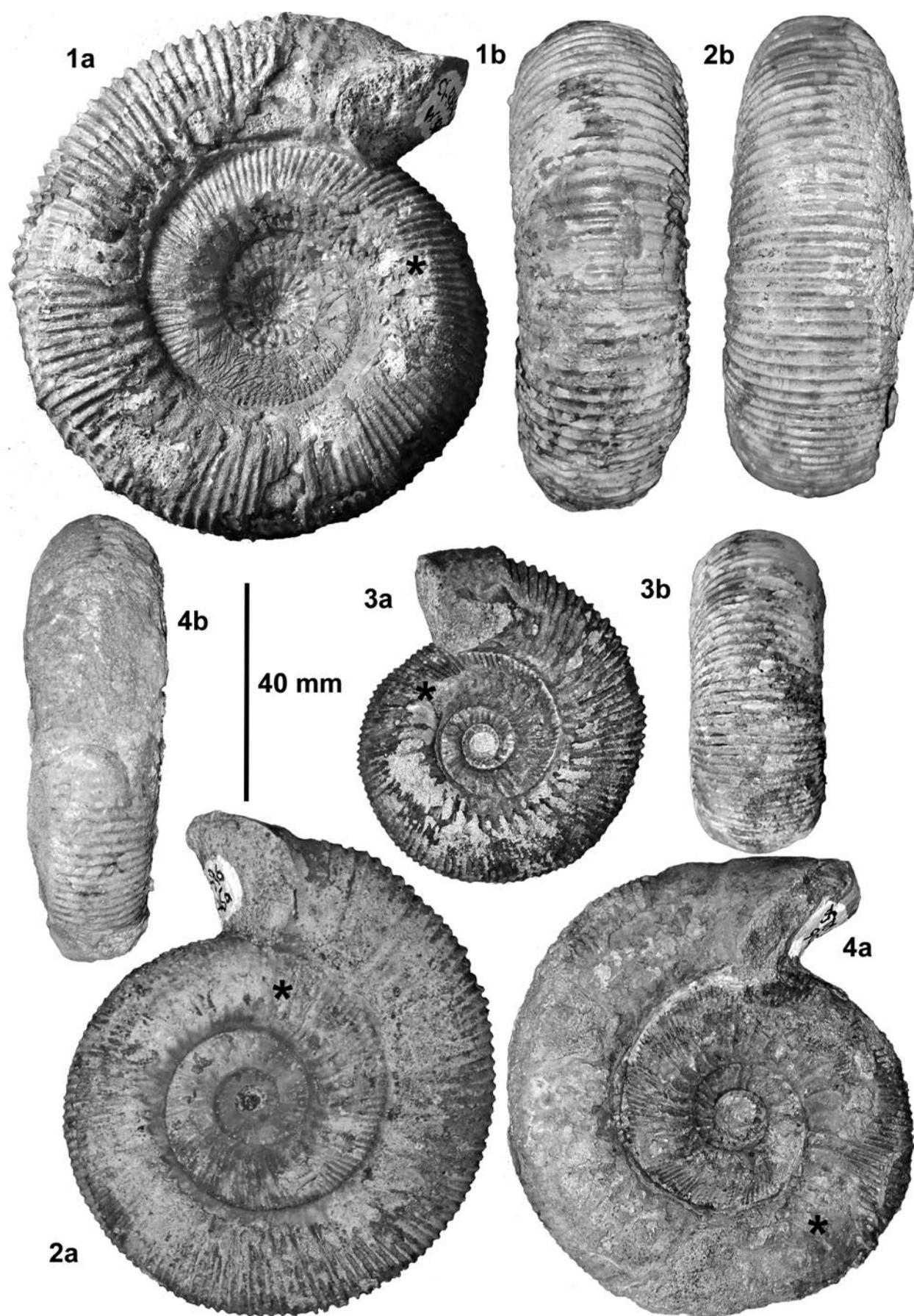


Plate III – 3. tábla



## Plate IV – 4. tábla

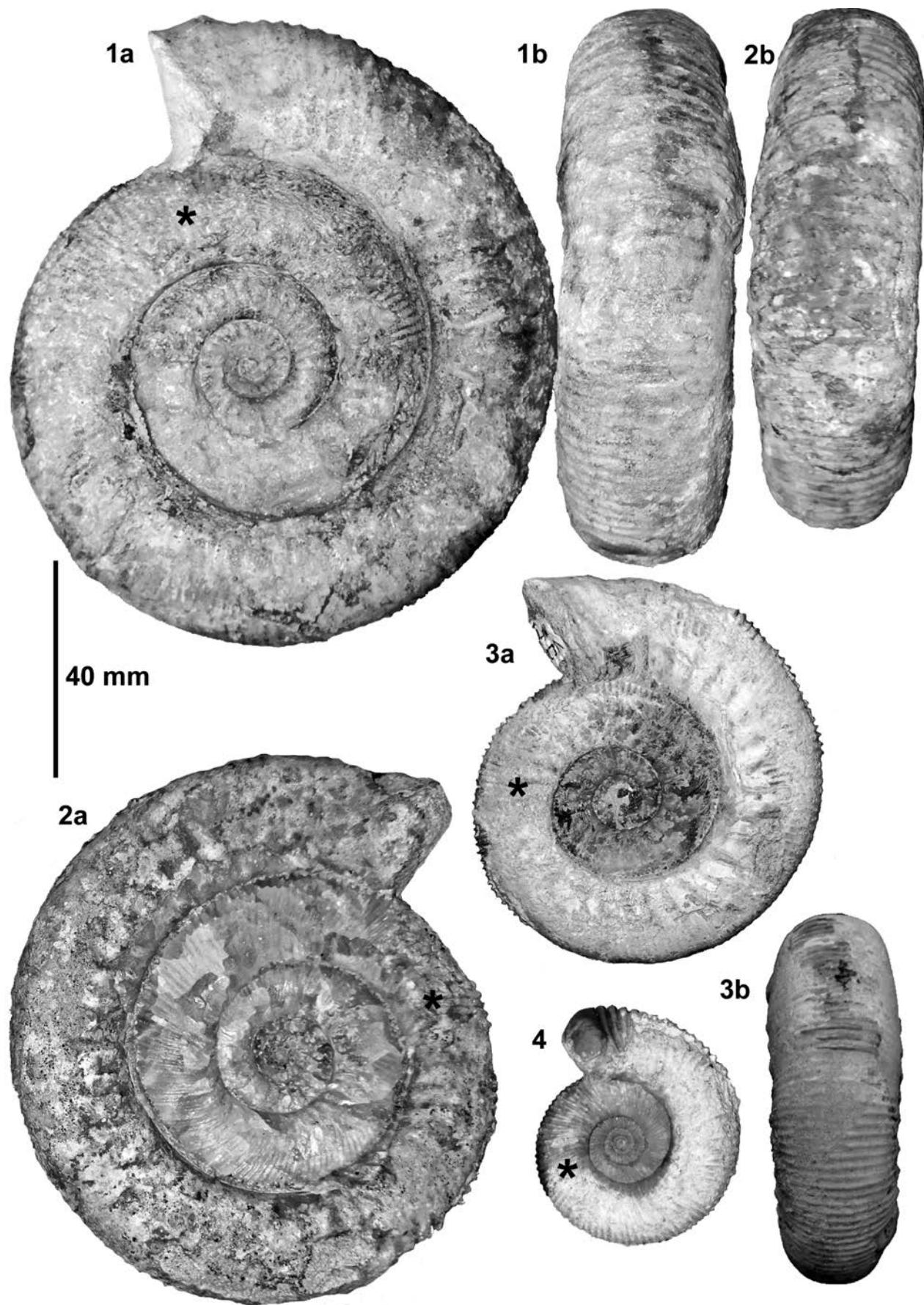
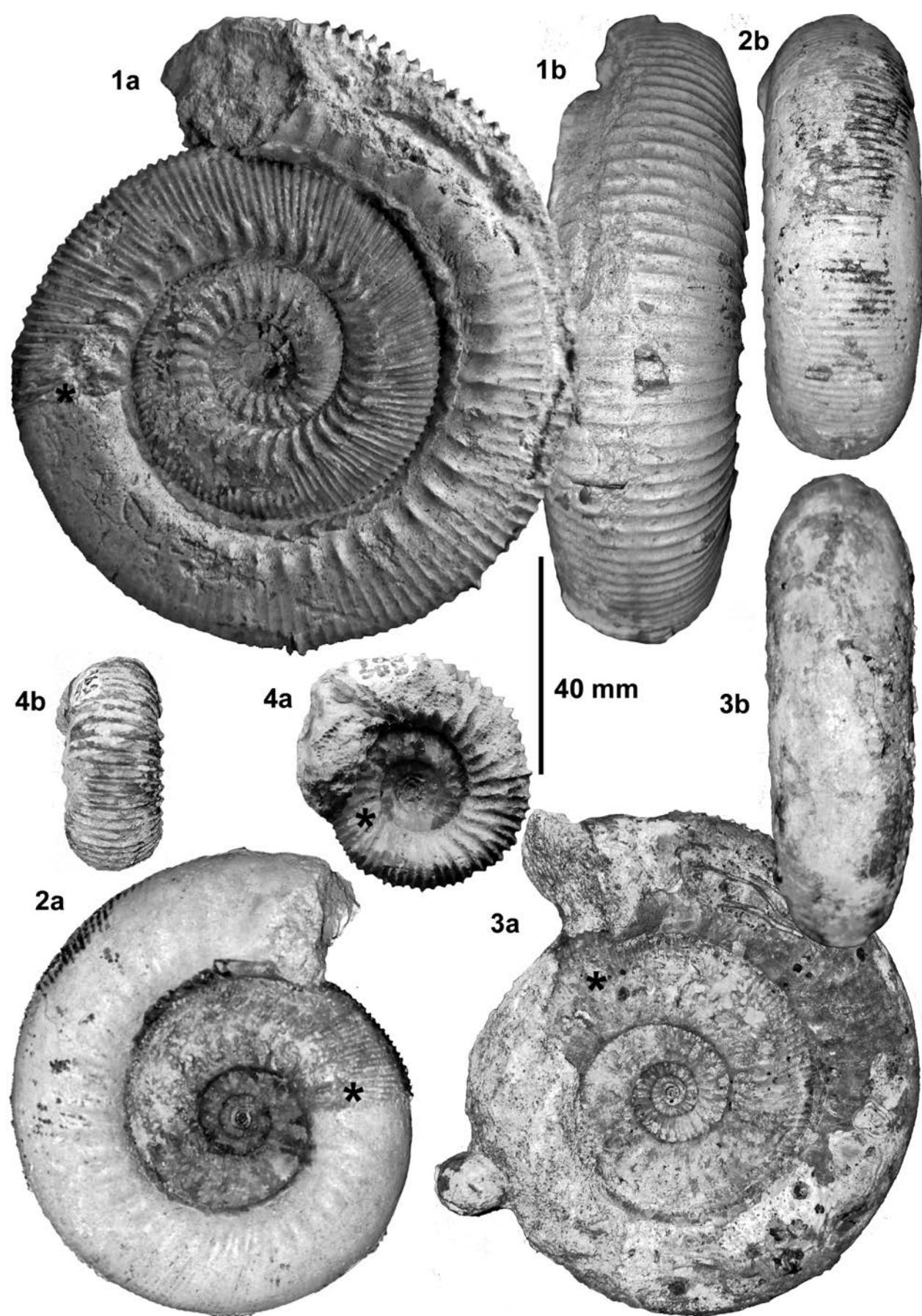
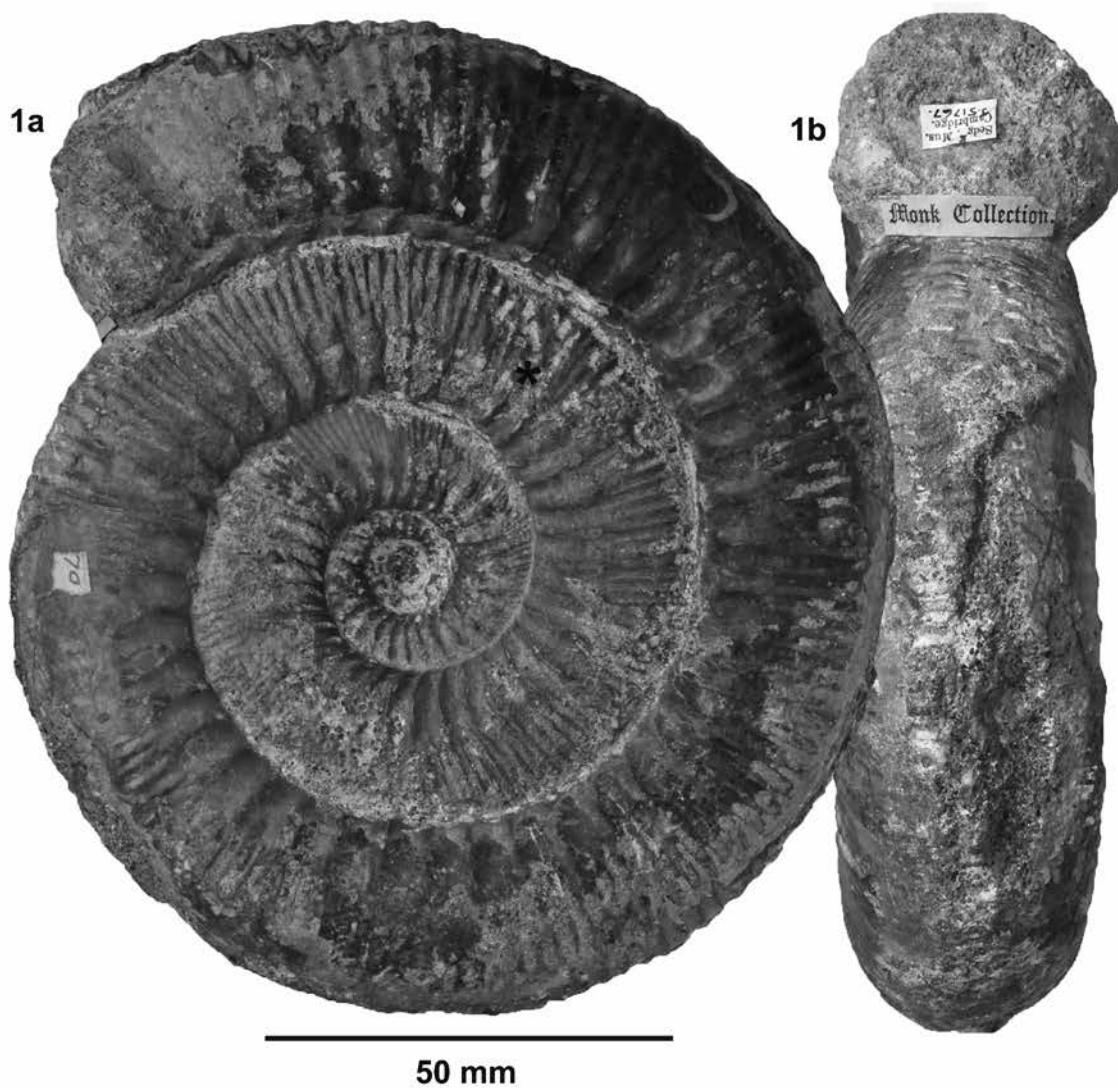


Plate V – 5. tábla



**Plate VI – 6. tabla**

## Two bivalve species, hitherto unrecorded, from the Upper Jurassic of the Transdanubian Range (Hungary)

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### Két, a Dunántúli-középhegység felső jurájából eddig nem dokumentált kagylófaj

#### Összefoglalás

A Dunántúli-középhegység felső jurájából a 2010-es évek elejéig előkerült kagylókat az utóbbi évtizedben megjelent két tanulmány ismerteti. A publikációk megjelenését követően a területről korábban nem ismert két faj egy-egy példánya került elő. Az antimarginális irányú redőkkel díszített teknőjű osztrigafélék közé tartozó *Actinostreon aff. gregareum* (J. SOWERBY, 1815) teknőjét a tatai Kálvária-dombon feltárt vörös, *Saccocoma*-maradványokban gazdag kimmeridgei mészkő egy 2015-ben, törmelékben talált darabja tartalmazza, míg a tágabb értelemben vett *Pholadomya*-féléket képviselő *Procardia aff. acuminata* (HARTMANN, 1830) példányá a hárskúti Közöskúti-árok vörös, gumós, ammoniteszes, tithon mészkövből 2022-ben került elő. Mindkét előfordulás a Pálihási Mészkő formációt képviseli.

A jelen dolgozatban dokumentált formák kevés példánnal képviselt, kis diverzitású kagylófaunák elemei. Feltételezhető, hogy az *A. aff. gregareum* teknője sekelyebb vizű régióból, áthalmozódás útján került a beágyazódási helyére. A leletek egyben a két genus első ismert előfordulását jelentik a Dunántúli-középhegység jurájában. Mind az *Actinostreon*, mind a *Procardia* kifejezetten ritka a Földközi-tengert övező térség mélyebb vízi, pelágikus felső jurájában.

Tárgyszavak: *Mediterrán jura, kimmeridgei, tithon, Bakony, Tata, Ostreoidea, Pholadomyoidea*

#### Abstract

Upper Jurassic bivalves yielded by the Transdanubian Range until the early 2010s were documented in two papers published in the last decade. Following the publication of them, two specimens representing species previously unknown from the area have been found. The Kimmeridgian limestone of Kálvária Hill, located in the town of Tata has yielded the lophate oyster *Actinostreon aff. gregareum* (J. SOWERBY, 1815), while a specimen of the pholadomyidean *Procardia aff. acuminata* (HARTMANN, 1830) was collected from the Tithonian limestone exposed in the Közöskút Ravine, located near the village of Hárskút (Bakony Mts.). The new finds represent the first known occurrence of the genera *Actinostreon* and *Procardia* in the Jurassic of the Transdanubian Range. Both genera are particularly uncommon in the deeper water pelagic Upper Jurassic of the peri-Mediterranean region.

Keywords: *Mediterranean Jurassic, Kimmeridgian, Tithonian, Bakony, Tata, Ostreoidea, Pholadomyoidea*

#### Introduction

Bivalve fossils are remarkably rare in deeper water pelagic facies of the Mediterranean Late Jurassic (ZIEGLER 1971) and this statement applies to the Transdanubian Range as well. Based on a study of approx. 250 specimens accumulated in Hungary in public collections since the second half of the 19<sup>th</sup> century, however, a relatively diverse assemblage, altogether composed of around 30 species assigned to 17

genera, has recently been documented from the Gerecse Mts. and its surroundings including the Kálvária Hill of Tata, as well as from the Bakony Mts., by SZENTE (2013) and SZENTE (2022), respectively.

Since the publication of the afore-mentioned papers, two specimens representing two further species (as well as genera) have been found. In 2015, during the large-scale reconstruction of the ELTE Geological Garden located at the Kálvária Hill, a loose slab of the red Kimmeridgian limestone

assigned to the Pálhálás Limestone Formation, a unit displaying variable lithology and usually rich in *Saccocoma*-remains, ammonites as well as manganese-oxide nodules, was found to contain a lophate oyster identified as *Actinostreon* aff. *gregareum* (J. SOWERBY, 1815). In October of 2022, when participating in a field exercise for the course “Fossil collecting and preparation”, András SZABÓ, a geology student at the Eötvös University collected a specimen of the pholadomyoidean *Procardia* aff. *acuminata* (HARTMANN, 1830), yielded by red, nodular, ammonite-rich Tithonian limestone (Pálhálás Limestone Formation) of the HK-12 section, located in the Közöskút Ravine. Details on the locality, including data on fossil assemblages, can be found in FÜLÖP (1976) and in FÓZY et al. (2022). Since both genera are new for the Jurassic of the Transdanubian Range, these unique finds are worth documenting here.

### Remarks on the new finds

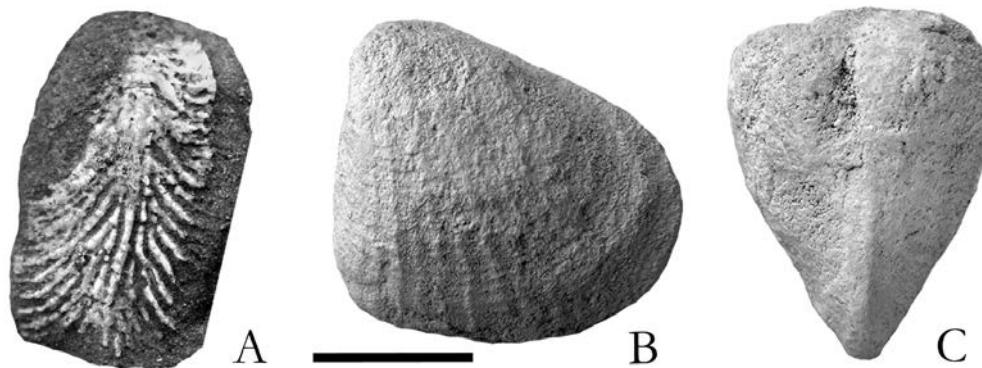
#### *Actinostreon* aff. *gregareum* (J. SOWERBY, 1815) (Figure 1, A)

The specimen is a slightly worn right valve exposed on the surface of a slab of dark red limestone. It bears around 35 plicae oriented in antimarginal direction. Their crest is composed of alternative swellings and depressions, presumably indicating the presence of empty shell chambers. On the basis of the afore-mentioned features, the specimen corresponds to the description of *Actinostreon gregareum* given recently by KOPPKA (2015). The only argument against this interpretation is the large number of plicae compared to the small size of the specimen (height = 14 mm, width = 8 mm). The number of plicae increases either by bifurcation or intercalation during ontogeny in *A. gregareum* and reaches a maximum of 35 in specimens considerably larger than the

one at Tata (up to 70 mm in height, KOPPKA 2015, see also MACHALSKI 1998). The specimen documented here is either a dwarf representative of *A. gregareum* or belongs to a new species.

As reviewed by KOPPKA (2015), *A. gregareum* was an ecologically tolerant and widely distributed form adapted to various marine environments ranging from reefs including the Tithonian Štramberk Limestone of Moravia (BOEHM 1883, REMEŠ 1903) to “relatively calm subtidal environments.” It forms shell beds, e.g., in the Kimmeridgian Coquina Formation of the Mesozoic Border of the Holy Cross Mountains of Poland, a unit deposited in “a relatively shallow-water setting” (MACHALSKI 1998, ZATOŃ & MACHALSKI 2013). There, two morphotypes reflecting different life positions (“mud-sticker” and “recliner” sensu SEILACHER 1984) occur. As indicated by its straight and elongated outline, the Tata specimen seems to represent the former mode of life.

In contrast to coeval shallow-marine rocks of Europe, however, this species – and, actually, lophate oysters in general – are extremely rare in deeper water Late Jurassic facies of the peri-Mediterranean region. Apparently, the only previously documented occurrence is the specimen identified as *Lopha* (*Lopha*) *solitaria* (J. DE C. SOWERBY, 1832) by MONARI (1995) from the Kimmeridgian “Calcaria Diasprigni” of the Terminilletto outcrop (Umbria-Marche Apennines, Italy), a section rich in re-deposited clasts of shallower-water origin (BARTOLINI et al. 1996). According to KOPPKA (2015) “*L. solitaria*” is a name applied by several authors to *A. gregareum*. *Actinostreon* was a cementing form attached to solid substrate by its left valve. The substrate is, however, unknown in both cases. Thus, it cannot be excluded that the specimens in question are allochthonous elements, re-deposited from areas covered by shallower-water. The Tata specimen forms part of a sparse and low-diversity bivalve fauna dominated by the byssally attached epifaunal *Campnectes*? sp. (SZENTE 2013).



**Figure 1.** Upper Jurassic bivalves from the Transdanubian Range. A) *Actinostreon* aff. *gregareum* (J. SOWERBY, 1815) from the Kimmeridgian of the Kálvária Hill (Tata); B, C) *Procardia* aff. *acuminata* (HARTMANN, 1830) from the Tithonian of the Közöskút Ravine (Hárskút, Bakony Mts). B: lateral view, C: dorsal view. B and C covered with ammonium-chloride. Scale bar represents 7 mm for (A) and 10 mm for (B) and (C). The specimens are housed in the collection of the ELTE Tata Geological Garden  
**1. ábra.** Felső jura kagylók a Dunántúli-középhegységből. A) *Actinostreon* aff. *gregareum* (J. SOWERBY, 1815) a Tatai Kálvária-domb kimmeridgei mészkövből; B, C) *Procardia* aff. *acuminata* (HARTMANN, 1830) a hárskúti (Bakony) Közöskút-i árok tithon mészkövből. B: oldalnézet, C: háti nézet. B és C ammónium-kloriddal van bevonva. A mérete 7 mm (A); 10 mm (B, C). A példányok az ELTE Tatai Geológus Kert gyűjteményében találhatók

***Procardia* aff. *acuminata* (HARTMANN, 1830)  
(Figure 1, B, C)**

The specimen is a small-sized (length = 22 mm, height = 19 mm) composite internal mould of rounded sub-triangular outline, bearing around 12 radial ribs. These features correspond to the description of “*Pholadomya (Pholadomya) acuminata*”, as given by DELVENE (2001). Ventral margin of the Hárskút specimen is, however, convex while that of *P. acuminata* figured in the literature is nearly straight.

Assignment of this relatively well-characterized species to *Procardia* MEEK, 1871 is, however, much more justified (e.g., SZTAJNER 2020). *Procardia* was treated either as a subgenus of *Pholadomya* (e.g., SZENTE 2003, SZTAJNER 2020), or as a separate genus (RUNEGGAR 1974, AMANO 2019, SZENTE 2022), and the latter view is shared here. Its systematic status is discussed in detail in AMANO (2019). According to BEU & RAINÉ (2009) *Procardia* belongs to the family Parilimyidae MORTON, 1981 and, consequently, to the order Poro-myida RIDWOOD, 1903, instead of the order Pholadomyida NEWELL, 1965. AMANO (2019), however, assigned Parilimyidae to the superfamily Pholadomyoidea KING, 1844, and this taxonomic opinion is shared here.

*Pholadomyoidean* bivalves sensu stricto (family Pholadomyidae GRAY, 1847) are widely distributed in the European epicontinental Upper Jurassic (e.g., MOESCH 1874) and occasionally considered emblematic fossils of lithostratigraphic units, such as the “*Pholadomyen*” of the Oxfordian of the Jura Mts. (e.g., ÉTALLON 1863). On the other hand, *Pholadomyoidean* bivalves as a whole are uncommon elements in fossil assemblages of the deeper water pelagic facies of the peri-Mediterranean region and seem to be confined to rare finds of *Procardia*. A single specimen of *P. acuminata*, along with a diverse ammonite fauna, was documented by NICOLIS & PARONA (1886) from the Upper Tithonian of near Verona (Southern Alps) and another one has been figured by REMEŠ (1903) from the Štramberk Limestone of Moravia. The faunal association of the latter is unknown.

*P. acuminata* was a deep-burrower, low level suspension-feeder form (DELVENE 2001, SZTAJNER 2020). Thus, it is considered an autochthonous element of the low-diversity Upper Jurassic bivalve fauna of the HK-12 section, consist-

ing nearly exclusively of species of the epibenthic *Rhynchomytilus* ROLLIER, 1914. It is worth mentioning that in the Lower Cretaceous of the Transdanubian Range another *Procardia* species identified as *P. malbosi* (PICTET, 1863) is widely distributed and represented by at least a dozen specimens in public collections (SZENTE 2003, 2022). The latter bears a close resemblance to *P. acuminata* and is probably identical with it. Further studies are, however, needed to answer this question.

## Conclusion

Since the publication of comprehensive papers on Upper Jurassic bivalves of the Transdanubian Range, two hitherto undocumented species represented by single specimens have been found and identified. These finds prove that extensively studied fossil localities occasionally yield unexpected, rare forms. Probably due to the relatively wide range of environments reflected by the lithological variety of the sections, as well as to the intensive collecting work carried out in the last one and a half century, the Transdanubian Range has yielded the most diverse bivalve assemblage of the deeper water pelagic Upper Jurassic of the peri-Mediterranean region.

## Acknowledgments

This paper is dedicated to Professors András GALÁCZ and Attila VÖRÖS, acknowledged scholars and teachers, on occasion of their 80<sup>th</sup> birthday. Due to their achievement and guidance, both Triassic and Jurassic research are nowadays prolific branches of geology in Hungary. Sincere thanks are due to István FÓZY, who encouraged me to prepare this paper and provided fundamental help in the identification of *Actinostreon* aff. *gregareum*. I am deeply grateful to András SZABÓ, who kindly donated the specimen of *Procardia* aff. *acuminata* he found. Constructive remarks and suggestions of reviewers Dr. Michał KROBICKI and Dr. Stefano MONARI, as well as thought-provoking questions of the editor Dr. Orsolya SZTANÓ are also gratefully acknowledged herein.

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Manuscript received: 16/01/2024

## First report of the Mid Barremian Event from the Transdanubian Range (Hungary) and associated Leptoceratoididae (Ammonoidea) fauna

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### A Középső Barremi Esemény felismerése a Dunántúli-középhegységben és az azzal egykorú Leptoceratoididae ammoniteszek revíziója

#### Összefoglalás

Jelen munkánkban a Leptoceratoididae-család kora és késő barremiben élt képviselőinek magyarországi elterjedését vizsgáltuk, valamint azokat a környezeti tényezőket igyekeztünk megkeresni, amelyek hatást gyakorolhattak a csoport gyakoriságára, diverzitására és paleoökológiájára. Ezen ammonitescsalád példányai két hazai lelőhelyről kerültek elő: a Bersek-hegy (Gerecse hegység) két szelvényéből és a Sümeg Süt-17 fúrásból (Déli-Bakony).

Legfontosabb rétegtani eredményünk a Bersek-hegy barremi rétegeiről készült korábbi rétegeszlopok adatainak integrálása és a Leptoceratoididae család képviselőinek eltérő rétegtani elterjedésének a demonstrálása. Az általunk létrehozott rétegeszlop korábbi szerzők rétegszámait korrelálja egymással, valamint saját geokémiai és nannofosszília mintáinkkal. Ez a kompozit rétegsor nagy pontossággal használható a *Toxancyloceras vandenheckii* Zónában, valamint megbízható a *Moutoniceras moutonianum* Zónában, viszont a *Kotetishvilia compressissima* Zóna alsó részében pontossága fenntartásokkal kezelendő. Taxonómiai vizsgálatunk eredményeképp megállapítottuk, hogy a *Karsteniceras*- és a *Leptoceratoides* nemzetiségek nem egymás szinonimái. A Bersek-hegy szelvényeiben a Leptoceratoididae családot három faj képviseli részben eltérő rétegtani elterjedéssel: a *Leptoceratoides balernaensis* a *M. moutonianum* Zónában, a *Leptoceratoides pumilus* főként a *T. vandenheckii* Zónában fordul elő. Rétegtani elterjedésük a *M. moutonianum* Zóna felső részén fed csak át. A *Karsteniceras ibericum* a leggyakrabban előforduló faj, a *K. compressissima* Zóna alsó részétől a *T. vandenheckii* Zóna aljáig terjedő rétegtani elterjedéssel. A Sümeg Süt-17 fúrásban a *L. pumilus* kizártlagos tömeges előfordulása mutatható ki. Azonban ez utóbbi rétegsorban a *M. moutonianum* Zóna rétegtani helyzete csak indirekt módon állapítható meg.

A vizsgált két lelőhely faunájának eltérését részben a rétegsorok eltérő ősföldrajzi helyzetével és ebből következően eltérő paleoceanográfiai paramétereivel magyarázzuk, vagyis a különböző ősföldrajzi helyzetű egykor medencék ammoniteszei eltérő módon reagáltak a környezetváltozásra, illetve eltérő környezeti igényekkel lehettek. Feltételezhetően ezek az apró ammoniteszek is különböző ökológiai igényekkel rendelkeztek, vagyis nem alkottak homogén csoportot. Taxonómiai eredményeinket őskörnyezeti keretbe helyezve arra a következetére jutottunk, hogy a Bersek-hegyi előfordulás kapcsán a különböző belemnitescsoportokon korábban mért stabil szénizotóp görbe hirtelen +1‰ kilengése a *M. moutonianum* Zónában a Középső Barremi Eseményt (KBE) jelzi. A gyors környezetváltozással összefüggő melegedésre utal a stabil oxigén izotóp -1,5‰ feletti változása is. Ekkor a szárazulatok felől a gerezsei üledékgyűjtőbe jutó megnövekedett szerves anyag mennyisége, és az ezt valószínűleg követő primer produktivitás növekedése dyzoxikus környezetet idézhetett elő a medence aljzatán. A megnövekedett szerves anyag mennyiségét a Leptoceratoididae család képviselői, valamint más epipelágikus zónában élő ammoniteszek jól tolerálhatták, míg bizonyos csoportok hiányoznak ebből a rétegösszletből.

Tárgyszavak: Leptoceratoididae; Középső Barremi Esemény, Dunántúli-középhegység, Magyarország

#### Abstract

Here the distribution of criocone members of the family Leptoceratoididae that proliferated during the early and late Barremian are investigated. We attempted to identify environmental factors that may have influenced the abundance, diversity and palaeoecology of the group. Specimens of this ammonite family were found at two Hungarian localities: the Bersek Hill (Gerecse Mountains) and the Sümeg Süt-17 drill core (Southern Bakony).

Our most important stratigraphic result is the integration of stratigraphic frameworks of different autors from the

Bersek Hill section which enabled us to precisely evaluate the stratigraphic distribution of this ammonite family. This integrated stratigraphy can be used with high accuracy for the *Toxancyloceras vandenheckii* Zone and is reliable for the *Moutoniceras moutonianum* Zone, but its accuracy for the lower part of the *Kotetishvilia compressissima* Zone is less stable. Our taxonomic analysis confirmed that *Karsteniceras* and *Leptoceratoides* should be kept as separate genera. In the Bersek Hill sections, family Leptoceratoididae is represented by *Karsteniceras ibericum* as the most common species found in basal *K. compressissima* to basal *T. vandenheckii* Zones. *Leptoceratoides balernaensis* occurs in the *M. moutonianum* and *Leptoceratoides pumilus* occurs mainly in the *T. vandenheckii* Zone. Their stratigraphic occurrence displays that only a few beds overlap at the top *M. moutonianum* Zone. In the Süt-17 borehole, the family is monospecific with *L. pumilus* occurrences. Unfortunately, the stratigraphic position of the *Moutoniceras moutonianum* Zone in Süt-17 borehole could only be inferred indirectly. Local response of Leptoceratoididae to the Mid Barremian Event shows spatial distribution patterns and resulted in different assemblage composition between the two localities. Discussion on lifestyle and paleoecology of criocone Leptoceratoididae ammonites is presented. Comparing our paleontologic findings to previously measured stable isotope data on belemnite rostra from Bersek Hill, we suggest that within the *Moutoniceras moutonianum* Zone, a sudden +1‰ shift in the stable carbon isotope excursion indicates the Mid Barremian Event (MBE). The -1.5‰ shift in the stable oxygen isotope excursion also indicates warming associated with rapid environmental change. During this time interval, increased organic matter might have entered into the Gerecse basin that could have induced increased primary productivity, hence dysoxic environment on the ocean floor. The increasing organic matter content was probably well tolerated by members of the family Leptoceratoididae and by other ammonite taxons that might have lived in the epipelagic zone, while certain groups of ammonites are missing from these strata.

**Keywords:** *Leptoceratoididae*; *Mid Barremian Event*, *Transdanubian Range, Hungary*

## Introduction

In the past few decades, several new achievements were accomplished on the investigation of Lower Cretaceous deposits and their fauna of the Transdanubian Range including the Bersek Hill quarry (FÓZY & FOGARASI 2002; FÓZY et al. 2002; JANSSEN & FÓZY 2003, 2004, 2005; FÓZY & JANSSEN 2009; FÓZY 2017, 2024; BAJNAI et al. 2017; LODOWSKI et al. 2022). These authors provided new additions to the classical geological compilations (FÜLÖP 1958, HAAS et al. 1985). Related to the Bersek Hill quarry, detailed faunal lists of the sequence were given, which defined its Valanginian–Barremian age. Paleontologic, geochemical and stratigraphic data were combined into multiproxy analysis, and the Valanginian Weissert Event was reported (Bajnai et al. 2017). Moreover, a detailed integrated bio- and chemostratigraphy was carried out on the Barremian strata, where stable  $^{18}\text{O}$  and  $^{13}\text{C}$  isotopes were measured from different belemnite taxa together with Mg/Ca ratios (PRICE et al. 2011).

Although the macrofauna of this locality is well documented (see references above), there are still faunal elements – including tiny heteromorph Leptoceratoididae – which are less investigated. During our previous work on Cretaceous deposits of Hungary (SZIVES et al. 2007) one of us encountered two sequences in the Transdanubian Range where enrichments of tiny heteromorphs of Barremian age were detected. Appearance of this group is linked to certain paleoenvironmental perturbations (LUKENEDER & TANABE 2002); however, their ecology and periodic mass occurrences in the paleontologic record is still obscure.

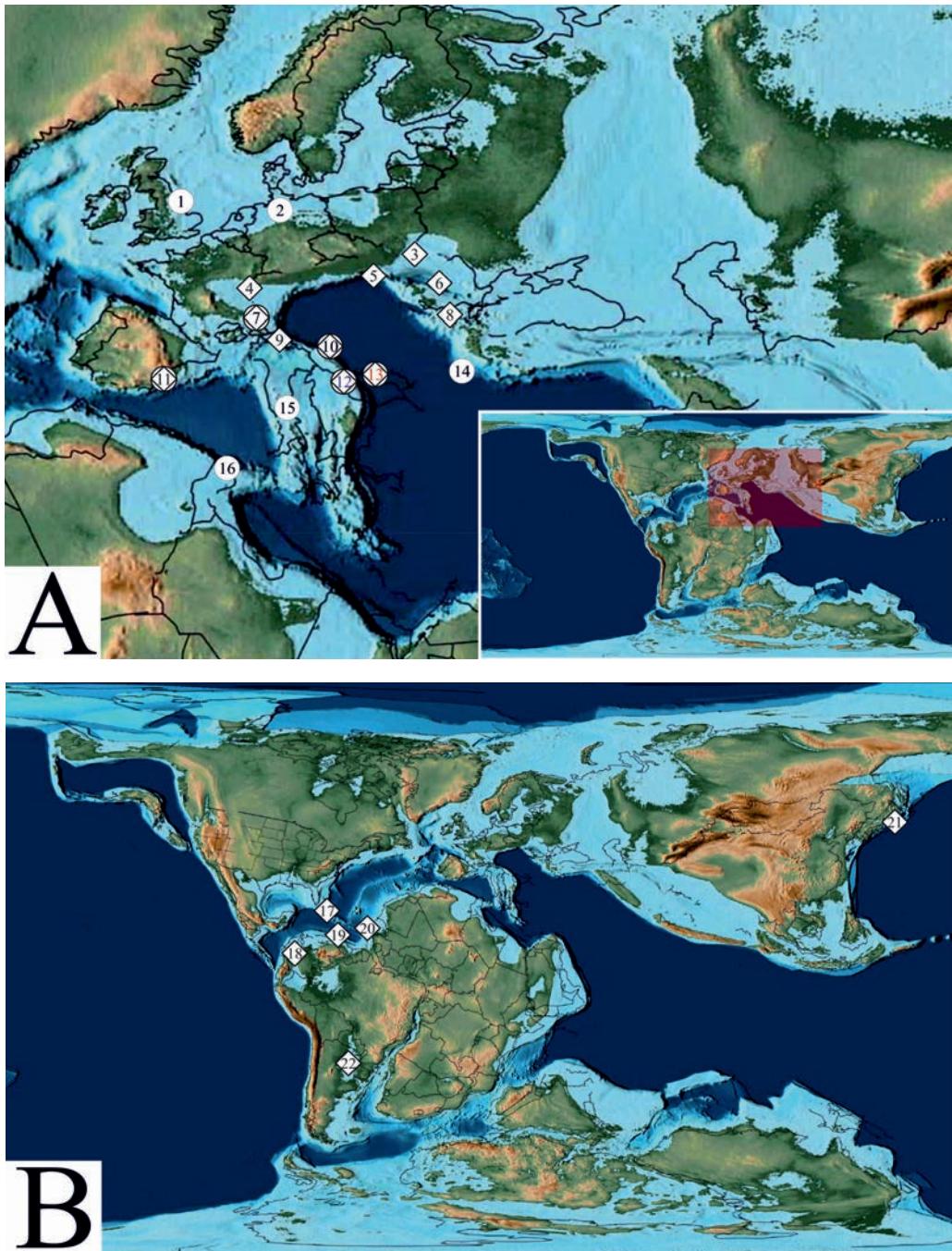
Scientific interest on global scale is focussed on the environmental and climatic changes of the Earth, and some of them can be traced in the deep past as well with the tools of geochemistry and paleontology. One of the less known environmental changes is called „Mid Barremian Event (MBE)” by COCCIONI et al. (2003), who documented a thin black shale level from the Umbria–Marche Basin (UMB, Italy)

and associated a 0.5 per mil positive shift in the carbon isotope values in addition to certain biotic turnovers. This observed event occurred in the *Moutoniceras moutonianum* standard Mediterranean ammonite Zone (SZIVES et al. 2023). Within this ammonite zone, a significant enrichment of tiny heteromorph ammonites (*Karsteniceras ternbergense* LUKENEDER & TANABE 2002) from family Leptoceratoididae of Barremian age was also observed first by LUKENEDER & TANABE (2002); however, reports on this family are very sporadic worldwide (Fig. 1). These enrichment levels are

→ **Figure 1.** Occurrences of family Leptoceratoididae (rectangle) and records of the MBE (circle) from the Tethyan and Boreal regions (A), and other paleogeographic realms (B) (Barremian paleomaps are modified after SCOTESE, 2014).

Numbers refer to the following localities: (A) 1, England (Speeton) (MUTTERLOSE et al. 2009); 2, North Germany (Letter, Gott, A39, Roklum) (MUTTERLOSE et al. 2009; MALKOC & MUTTERLOSE 2010); 3, Silesia (Czech Republik) (UHLIG 1883; VAŠÍČEK 1972, 1979, 1999; VAŠÍČEK & WIEDMANN 1994; VAŠÍČEK & KLAJMON 1998); 4, Veveyse (Switzerland) (OOSTER 1860; SARASIN & SCHÖNDEL-MAYER 1902; VAŠÍČEK & WIEDMANN 1994; BUSNARDO et al. 2003; VAŠÍČEK & HOEDEMAEKER 2003a); 5, Inner Carpathians (Slovakia) (VAŠÍČEK & WIEDMANN 1994); 6, Southern- and Eastern Carpathians (Romania) (AVRAM & KUSKO 1984; VAŠÍČEK & WIEDMANN 1994; AVRAM 1999); 7, SE France (Angles, Cluses) (VAŠÍČEK & WIEDMANN 1994; KAKABADZE & HOEDEMAEKER 1997; VERMEULEN 1998; WISSLER et al. 2002; BUSNARDO et al. 2003; GODET et al. 2006; BODIN et al. 2009; HUCK et al. 2013; MARTINEZ et al. 2023); 8, Kraptshene (Prebalkan Mts., Bulgaria) (MANOLOV 1962; DIMITROVA 1967; VAŠÍČEK & WIEDMANN 1994); 9, Swiss Alps and Southern Alps (RIEBER 1977; LUKENEDER & GRUNERT 2013); 10, Austria (WIEDMANN 1978; VAŠÍČEK & WIEDMANN 1994; LUKENEDER & TANABE 2002; LUKENEDER 2003, 2005, 2007); 11, SE Spain (FALLOT & TERMIER 1923; VAŠÍČEK & WIEDMANN 1994; VAŠÍČEK & HOEDEMAEKER 2003a; COMPANY et al. 2005; AGUADÓ et al. 2014, 2022; MATAMALES-ANDREU et al. 2019; MARTINEZ et al. 2020, 2023); 12, Sümeg Süt-17 drill core (Hungary) (HAAS et al. 1985); 13, Bersek Hill (Hungary) (FÜLÖP 1958; NAGY 1967; JANSSEN & FÓZY 2005; FÓZY & JANSSEN 2009); 14, Vezirhan (Turkey) (YILMAZ et al. 2012); 15, Italy (COCCIONI et al. 2003; SPROVERI et al. 2006; HUCK et al. 2013); 16, NE Tunisia (TALBI et al. 2021); (B) 17, Cuba (MYCZYNKI & TRIFF 1986; MYCZYNKI 1977; VAŠÍČEK & WIEDMANN 1994); 18, Colombia (ROYO Y GOMEZ 1945; ETAYO-SERNA 1968; VAŠÍČEK & WIEDMANN 1994; KAKABADZE & HOEDEMAEKER 1997; VAŠÍČEK & HOEDEMAEKER 2003b); 19, Trinidad (IMLAY 1954; VAŠÍČEK & WIEDMANN 1994); 20, Capo Verde (Maio) (STAHLCKER 1935; VAŠÍČEK & WIEDMANN 1994; CASSON et al. 2020); 21, Japan (YABE et al. 1927; MATSUKAWA 1987, 1988, 2019, 2022; VAŠÍČEK & WIEDMANN 1994; OBATA & MATSUKAWA 2007); 22, Argentina (Neuquén Basin) (AGUIRRE-URRETA & RAWSON 2012).

→ **1. ábra.** *Leptoceratoididae-család elterjedése (rombuszszal jelölve) és a Középső Barremi Esemény (körrrel jelölve) megjelenése a tethysi és a*



boreális területeken (A), valamint a Leptoceratoididae család Európán kívüli elterjedése (B) (barremi paleotérkép SCOTSESE 2014 után módosítva).

A számok a következő földrajzi elterjedéseket jelölik: (A) 1, Anglia (Speeton) (MUTTERLOSE et al. 2009); 2, Észak Németország (Letter, Gott, A39, Roklum) (MUTTERLOSE et al. 2009; MALKOC & MUTTERLOSE 2010); 3, Szílezia (Csehország) (UHLIG 1883; VÁSÍČEK 1972, 1979, 1999; VÁSÍČEK & WIEDMANN 1994; VÁSÍČEK & KLAJMON 1998); 4, Veveyse (Svájc) (OOSTER 1860; SARASIN & SCHÖNDELMAYER 1902; VÁSÍČEK & WIEDMANN 1994; BUSNARDO et al. 2003; VÁSÍČEK & HOEDEMAEKER 2003a); 5, Belső-Kárpátok (Szlovákia) (VÁSÍČEK & WIEDMANN 1994); 6, Déli- és Keleti-Kárpátok (Románia) (AVRAM & KUSKO 1984; VÁSÍČEK & WIEDMANN 1994; AVRAM 1999); 7, Délkelet-Franciaország (Angles, Cluses) (VÁSÍČEK & WIEDMANN 1994; KAKABADZE & HOEDEMAEKER 1997; VERMEULEN 1998; WİSSLER et al. 2002; BUSNARDO et al. 2003; GODET et al. 2006; BODIN et al. 2009; HÜCK et al. 2013; MARTINEZ et al. 2023); 8, Kraptshene (Balkán-hegység előtere, Bulgária) (MANOLOV 1962; DIMITROVA 1967; VÁSÍČEK & WIEDMANN 1994); 9, Svájci-Alpok és Déli-Alpok (RIEBER 1977; LUKENEDER & GRUNERT 2013); 10, Ausztria (WIEDMANN 1978; VÁSÍČEK & WIEDMANN 1994; LUKENEDER & TANABE 2002; LUKENEDER 2003, 2005, 2007); 11, Délkelet-Spanyolország (FALLOT & TERMIER 1923; VÁSÍČEK & WIEDMANN 1994; VÁSÍČEK & HOEDEMAEKER 2003a; COMPANY et al. 2005; AGUADO et al. 2014, 2022; MATAMALES-ANDREU et al. 2019; MARTINEZ et al. 2020, 2023); 12, Sümeg Sűt-17 fúrás (Magyarország) (HAAS et al. 1985); 13, Bersek-hegy (Magyarország) (FÜLÖP 1958; NAGY 1967; JÄNSSEN & FÓZY 2005; FÓZY & JÄNSSEN 2009); 14, Vezirhan (Törökország) (YILMAZ et al. 2012); 15, Olaszország (COCCIONI et al. 2003; SPROVIERI et al. 2006; HÜCK et al. 2013); 16, Északkelet-Tunézia (TALBI et al. 2021); (B) 17, Kuba (MYCZYNSKI & TRIFF 1986; MYCZYNSKI 1977; VÁSÍČEK & WIEDMANN 1994); 18, Kolumbia (ROYO Y GOMEZ 1945; ETAYO-SERNA 1968; VÁSÍČEK & WIEDMANN 1994; KAKABADZE & HOEDEMAEKER 1997; VÁSÍČEK & HOEDEMAEKER 2003b); 19, Trinidad (IMLAY 1954; VÁSÍČEK & WIEDMANN 1994); 20, Zöld-foki Köztársaság (Maio) (STAHLER 1935; VÁSÍČEK & WIEDMANN 1994; CASSON et al. 2020); 21, Japán (YABE et al. 1927; MATSUKAWA 1987, 1988, 2019, 2022; VÁSÍČEK & WIEDMANN 1994; OBATA & MATSUKAWA 2007); 22, Argentina (Neuquén-medence) (AGUIRRE-URRETA & RAWSON 2012).

named as “*Karsteniceras* Level” by LUKENEDER (2003, 2005) and are possibly linked to an environmental perturbation, which resulted in dysaerobic conditions. This is inferred from their age, which may fit the stratigraphic extent of the MBE (LUKENEDER & TANABE 2002; LUKENEDER 2007) within the *M. moutonianum* Zone. Organic-rich levels did not always form during the MBE, but they were recently interpreted as episodes of regional expansion of the oxygen minimum zone (MARTÍNEZ et al. 2020, FÖLLMI 2012).

The ecologic affinities of the family Leptoceratoididae of mainly Barremian age are not straightforward and their possible connection with the Mid Barremian Event is still unclear; however, their mass occurrence was observed to be in the middle Barremian (LUKENEDER 2003, 2005, 2007). RIEBER (1977) considered Leptoceratoididae to be a nekton, VÁŠÍČEK & WIEDMANN (1994) considered them to be a group living and grazing within the algal mats, while WESTERMANN (1996), due to the shape of the fragile small shell, suggested a pseudoplanktonic or planktonic lifestyle in contrast to feeding on the shallow neritic waters.

Based on these previous observations, we present the first complete account of Hungarian representatives of the family with a precise stratigraphy, together with giving a taxonomic revision of the fauna. Furthermore, we attempt to link Leptoceratoididae occurrences to the MBE on the basis of the stable isotope curve measured from belemnites of the Bersek Hill (PRICE et al. 2011). Moreover, we also outline and discuss the spatial and temporal abundance and diversity changes of this family with regards to paleoecologic and paleoenvironmental factors.

## Geological background

Levels with members of family Leptoceratoididae were found within Barremian sediments of the Bersek Hill and the Sümeg Süt-17 drill core, situated in the Transdanubian Range, Gerecse and Bakony mountains, respectively (Fig. 2A). Related to their previous paleogeographic position (Fig. 2B), both sections are within the ALCAPA (acronym from Alps, Carpathians and Pannonian Basin) terrain (CSONTOS & VÖRÖS 2004); however, these sections belonged to different segments of a foreland basin system (FODOR et al. 2013; FODOR & FŐZY 2013, 2022; FŐZY 2024).

### Sümeg Süt-17 (Süt-17) drill core

To better understand the Southern Bakony basin, the Hungarian Geological Survey drilled several boreholes in the area including the Sümeg Süt-17 core in 1983, which is situated within the town of Sümeg (Fig. 2A, B).

The extensively investigated core (HAAS et al. 1985) starts with a Jurassic pelagic limestone which grades into a Lower Cretaceous siliciclastic deposit called Sümeg Marl Formation (SMF). The depositional environment was interpreted (HAAS et al. 1985) as a calm deep neritic zone below the wave base. Upward increasing amount of terrigenous

material may be related to the southwestward movement of the forebulge towards the Southern Bakony basin of the Sümeg area (FODOR et al. 2013; FODOR & FŐZY 2013, 2022; FŐZY 2024). The SMF is rich in macro- and microfauna, which also point to an open neritic environment (HAAS et al. 1985, BENCE et al. 1990, KNAUER 1996). According to the most recent summary (Császár & HAAS 2023), this sedimentary unit was deposited in a shallow bathyal depth. Planispiral ammonites do not appear within the same interval together with Leptoceratoididae, but otherwise are relatively abundant in the Süt-17 core. Nevertheless, these are beyond the scope of this work.

### Bersek Hill quarry

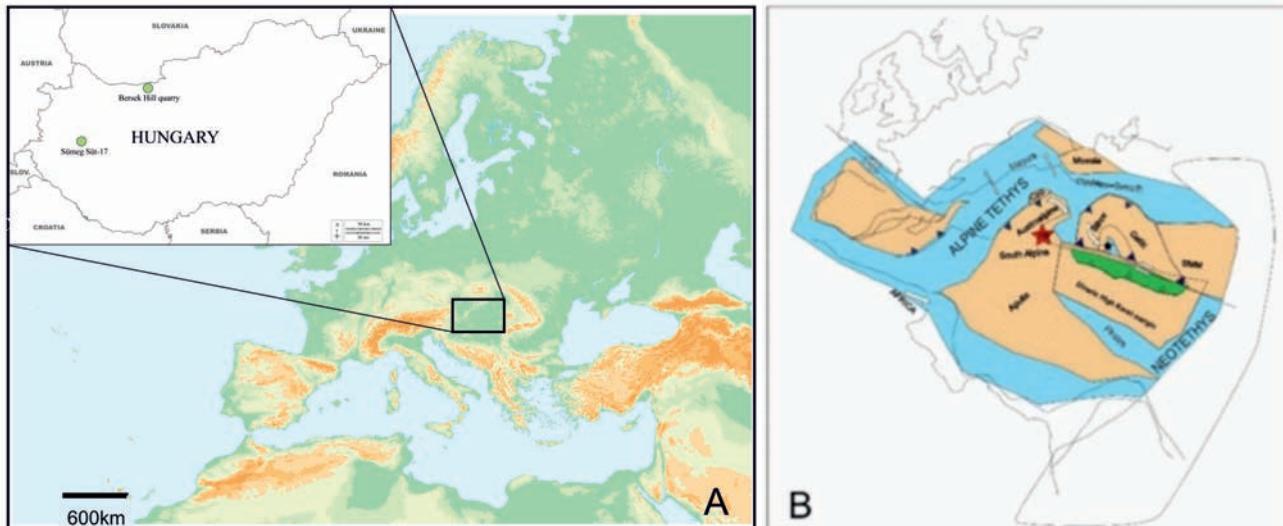
Another sedimentary unit where Barremian tiny heteromorphs were found is situated in the Gerecse Mountains, south from the small town of Lábatlan (Fig. 2A, B).

During the late Berriasian, in the Gerecse Basin a turbidite system connected to a foredeep basin was established, which caused the termination of carbonate sedimentation much earlier than in the Bakony Mountains. This resulted in the onset of a mixed siliciclastic–carbonate sedimentation in the late Berriasian (SASVÁRI 2009, CSÁSZÁR et al. 2012, FODOR et al. 2013, FODOR & FŐZY 2013, SZTANÓ et al. 2018, FŐZY 2024). The Lower Cretaceous “flysch” succession (KÁZMÉR 1987, FOGARASI 1995a, b) crops out in the northern wall of a huge open pit quarry at Bersek Hill (Fig. 3).

The so-called Bersek Marl Formation (BMF, FÜLÖP 1958), which represents the lower part of the clastic succession (Fig. 3), crops out in the lowest level of the quarry. Its age is early Valanginian to late Hauterivian based on its abundant ammonite findings (FŐZY 2017, 2024 and references within) and rich in apytychi. During the Barremian, input of coarse clastic material increased, and the marlstone deposition was replaced by the deposition of the Lábatlan Sandstone Formation (LSF, FÜLÖP 1958). Ammonites are less frequently found within this grey sandstone; however, its age was first established on the basis of ammonites (FŐZY 2017) as late Hauterivian/early Barremian to earliest Aptian (Lb-36 drill core, FŐZY et al. 2002).

The boundary between the Bersek and Lábatlan Formations (Fig. 3) is a greenish grey slump–fold unit (FOGARASI 1995a), which is a very important marker level observed continuously (FŐZY 1995, SZTANÓ et al. 2018). This greenish unit contains chaotically folded sandstone and marl layers, deformed in the frontal part of an extensive slump (FOGARASI 1995a, SZTANÓ et al. 2018).

The Lábatlan Sandstone Formation in the Bersek Hill is comprised of rhythmic alternation of sandy beds and marly intercalations (Fig. 3) interpreted as the margin of a turbidite system (FOGARASI 1995b, CSÁSZÁR et al. 2012, SZTANÓ et al. 2018). The upward coarsening and thickening sandstone series with thick, massive, amalgamated sandstones deposited on the progradational lobes and lobe complexes (SZTANÓ 1990, FODOR et al. 2013). The deposition of LSF was mostly controlled by gravity mass movements, mainly



**Figure 2.** Geographic position of the investigated sections. (A): present day (green circles mark the localities), (B): during the early Aptian after CSONTOS & VÖRÖS (2004). Red star marks the Transdanubian Range, blue areas are deep oceanic basins, brown areas are shallower neritic water masses. Thrust fronts marked with triangles, thrust zones with arrows. Continental areas are not coloured

**2. ábra.** A vizsgált területek földrajzi elhelyezkedése. (A): napjainkban (zöld körökkel jelölve), (B): valamint a kora apti során CSONTOS & VÖRÖS (2004) után. A vörös csillag a Dunántúlt-középhegységet, a kék területek az óceáni medencéket, a barna területek a sekélytengeri övezeteket jelölik. A takarófrontok háromszögekkel, mik a takaró zónák nyíllal vannak jelölve. A kontinentális területek fehérek

turbidity currents and rarely debris flows, where the two different paleocurrent directions were from east to west and northeast to southwest (in present direction) (FOGARASI 1995a, FODOR et al. 2013).

The depth of the basin is still debated, but on the basis of nannofossil studies and sedimentary features, FOGARASI (1995b) placed it between the aragonite (ACD) and calcite compensation (CCD) depths. Based on foraminifers, SZÜCS (2004) concluded that estimates of sea depth between ACD and CCD came from a probable misinterpretation and the

lack of aragonite ammonite shells is not a depositional feature but is due to diagenetic processes. The Barremian paleoposition of the Gerecse in a foredeep setting is in contrast to that of the Bakony Mts, since the Bakony Mts was probably located in the backbulge of the foreland basin system (TARI 1994, FODOR & FŐZY 2022).

The upper part of the Lower Cretaceous sedimentary cycle is missing from the early Aptian and upwards due to the tectonism related to the Alpine orogeny (TARI 1994, SASVÁRI 2009, FODOR & FŐZY 2013, SZIVES et al. 2018)



**Figure 3.** The north wall of the Bersek Hill quarry with the sequence of the Lábatlan Sandstone Formation (LSF) and the underlying Bersek Marl Formation (BMF). The boundary between the two sedimentary units (greenish grey slump-fold unit [base of LSF] and BMF) is marked with yellow line

**3. ábra.** A Bersek-hegy északi oldalában található szelvény feltárása a Lábatlani Homokkö Formációt (LSF), valamint a fekü Bersek Márta Formációt (BMF). A két képződmény határa (zöldesszürke, deformált homokkö réteg [LSF bázisa] és BMF között) sárga vonallal jelölve

## Material

### Sümeg Süt-17 drill core

The Leptoceratoididae from Sümeg Süt-17 borehole have been already depicted in the literature (HAAS et al. 1985). All of the relatively abundant ammonites revealed in the Süt-17 core are shelled, among them 28 specimens were determined to belong to Leptoceratoididae, which were investigated and photographed for taxonomic purposes. Our investigated heteromorph material is from between 257.5–297.4 meters, but in one level (263.6 m; core sample is archived as K.12649), mass occurrence of specimens is observed. Specimens were labelled with the exact depth of occurrence and a repository number with “K.” prefix. To our knowledge, further collecting work is not possible as no surface outcrop is present that reveals the Barremian part of the SLF.

Specimens are archived in the Cretaceous Collection of the Geological Survey Collection Department belongs to the Supervisory Authority of Regulatory Affairs (SARA) governmental institution.

### Bersek Hill quarry

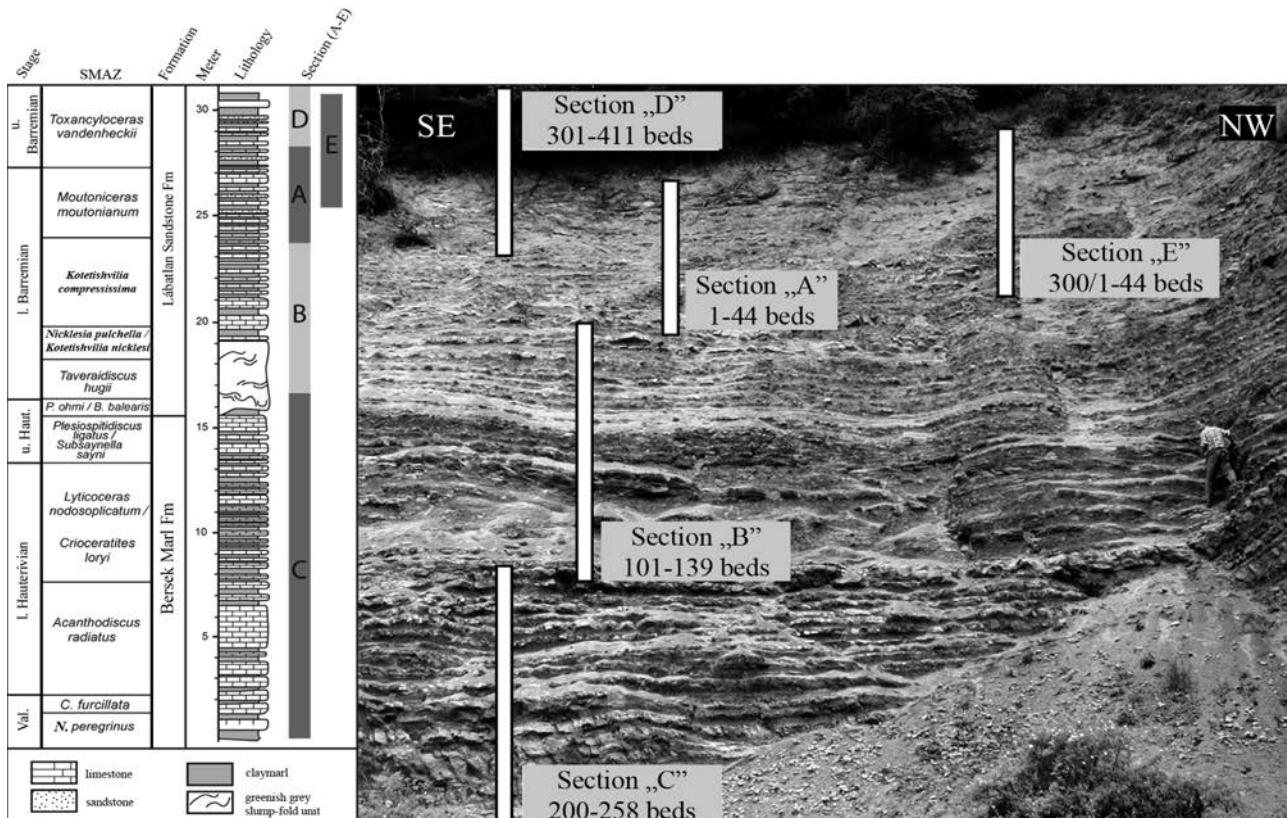
A huge collection of more than 11,000 ammonite internal moulds were collected by the FÜLÖP team and is informally called the “Fülop Collection”, which contains hetero-

morph ammonites in great numbers (FÓZY 2017), from which more than two dozens belong to the family Leptoceratoididae. These ammonites were collected in the early 1960’s from the A, B and E sections (Fig. 4). Accordingly, specimens from the Bersek Hill are labelled with a letter (A, B, E) and a number, where the letters refer to the exact section and the numbers mean bed numbers.

All specimens are internal moulds, no shelled specimens are found. The specimens are listed bed-by-bed in Appendix 1. During recent field work, five additional Leptoceratoididae remains (*M. moutonianum* Zone, *T. vandenheckii* Zone) and 78 rock samples were collected (A, B, E sections) in order to perform geochemical and microfossil investigations. Ammonites are housed in the Department of Paleontology and Geology of the Hungarian Natural History Museum and catalogued with “INV” prefix.

## Methods

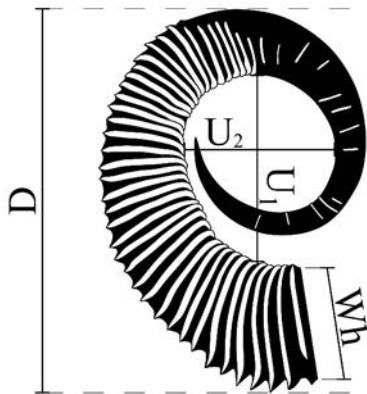
The investigated specimens underwent cleaning, preparation and photographing. Collected specimens were cleaned with soap water and prepared with Dremel vibrotool, all of them were measured with electronic scale, examined with lufe of 3x magnification. Ammonites were covered with NH<sub>4</sub>Cl vapor and photographed using NIKON camera and Xiaomi 12X cellphone with a Sony IMX766 camera.



**Figure 4.** Positions of different collecting sections of FÜLÖP named by FÓZY (2017 and references therein) as Sections A, B, C, D, E and this work (modified after FÓZY 2017) on the Bersek Hill succession. Abbreviations: Val.: Valanginian, l.: lower, u.: upper, Haut.: Hauterivian, SMAZ: Standard Mediterranean Ammonite Zonation is after SZIVES et al. (2023)

**4. ábra.** A FÜLÖP által létrehozott különböző szelvények elhelyezkedése a Bersek-hegyen. Ezeket FÓZY (2017) A, B, C, D, E szelvényeknek nevezte el (módosítva FÓZY 2017 után). Rövidítések: Val.: valangini, l.: alsó, u.: felső, Haut.: hauterivi, SMAZ: tethysi ammoniteszónák SZIVES et al. (2023) után

For purposes of stratigraphy, we used the latest Tethyan Standard Mediterranean Ammonite Zonation (SMAZ) recently updated by SZIVES et al. (2023). For measuring the small heteromorph specimens, we established metric parameters (Fig. 5).



**Figure 5.** Measurements of a leptoceratoid conch: D: diameter; Wh: whorl height; U1: height of the umbilical opening; U2: width of the umbilical opening

**5. ábra.** A vizsgált vázparaméterek egy leptoceratoid-maradványon: D: átmérő; Wh: kanyarulat magasság; U1: köldök magasság; U2: köldök szélesség

### Ammonite taxonomy

Our most important paleontologic result is the taxonomic revision of the Barremian small heteromorph fauna collected from Hungarian sections. During this work we confirmed that genera *Karsteniceras* and *Leptoceratoides* are different and should not be used as synonyms.

Taxonomic interpretation of the fauna is documented below; higher taxonomic ranks follow recent updates by HOFFMANN et al. (2022).

Phylum Mollusca LINNAEUS, 1758  
Class Cephalopoda CUVIER, 1797  
Order Ammonitida HAECKEL, 1866  
Superfamily Ancyloceratoidea GILL, 1871  
Family Leptoceratoididae THIEULOUY, 1966

Within the Leptoceratoididae, 12 genera (*Eoheteroceras*, *Hamulinites*, *Josticeras*, *Karsteniceras*, *Leptoceratoides*, *Manoloviceras*, *?Monsalveiceras*, *Orbignyceras*, *Sabaudiella*, *Vasicekites*, *Veveyiceras*, *?Veveyiella*) are separated (KLEIN et al. 2007). Separation of genera and species is very difficult because they share a similar biostratigraphic occurrence mostly in the Barremian.

The earliest known stratigraphic distribution of the family reported by MATAMALES-ANDREU et al. (2019) is in the upper Hauterivian *Balearites krenkeli* Subzone of the *Balearites balearis* Zone where the genus *Hamulinites* appears. The appearance of several other genera is linked to the Faraoni Event during the late Hauterivian (*Pseudothurmannia ohmi* and *Pseudothurmannia mortilleti* subzonal bound-

ary), where *Karsteniceras* (*K. cf. beyrichoide*), *Sabaudiella* (*S. simplex* BUSNARDO, 2003) and *Leptoceratoides* (THIEULOUY, 1966) are first observed. Moreover, first reports of *Hamulinites munieri* (NICKLÈS, 1894) and *Hamulinites nicklesi* (AVRAM, 1999) were documented (COMPANY et al. 2005, LUKENEDER 2012, LUKENEDER & GRUNERT 2013, MATAMALES-ANDREU et al. 2019). Furthermore, VAŠÍČEK & WIEDMANN (1994) and MATAMALES-ANDREU et al. (2019) reported the first representatives of the genus *Veveyiceras* from the upper Hauterivian/lower Barremian *Pseudothurmannia picteti* Subzone.

The dispersal of Leptoceratoididae was rather rapid as the first *Sabaudiella* are also reported (AGUIRRE-URRETA & RAWSON 2012) from the uppermost Hauterivian *Sabaudiella riverorum* Zone (= upper part of the *Pseudothurmannia picteti* Subzone in the Mediterranean Province following SZIVES et al. 2023) of Neuquén Basin. In the lower Barremian deposits, various representatives of Leptoceratoididae are documented worldwide from the Central Atlantic (STAHLLECKER 1935, ROYO Y GOMEZ 1945, IMLAY 1954, ETAYO-SERNA 1968, MYCZYNSKI 1977, MYCZYNSKI & TIRF 1986, VAŠÍČEK & WIEDMANN 1994, KAKABADZE & HOEDEMAEKER 1997, VAŠÍČEK & HOEDEMAEKER 2003b, CASSON et al. 2020) and Japan (YABE et al. 1927; MATSUKAWA 1987, 1988, 2019, 2022; VAŠÍČEK & WIEDMANN 1994; OBATA & MATSUKAWA 2007).

Based on our material at disposal, we do not agree with VAŠÍČEK & WIEDMANN (1994) who used *Leptoceratoides* and *Karsteniceras* as synonyms. In our opinion, they show strong morphological differences that do not fall within intraspecific variation detailed below.

#### Genus *Leptoceratoides* THIEULOUY, 1966

Type species: *Crioceras* (*Leptoceras*) *pumilum* UHLIG, 1883

Genus *Leptoceratoides* is generally characterized by tiny, few centimetres in diameter criocone morphology (VAŠÍČEK & WIEDMANN 1994, WRIGHT et al. 1996), apart from *?Leptoceratoides heeri* (OOSTER, 1860), which is much bigger with different (cricone, ?baculicone, ?hamulicone) type of coiling. In our opinion, this species does not belong to *Leptoceratoides*, probably not even into the family Leptoceratoididae.

Ribbing pattern is simple; however, the direction of ribs may vary between species (VAŠÍČEK & WIEDMANN 1994, WRIGHT et al. 1996). Moreover, in certain species [*L. balaenaensis* (RIEBER, 1977)] rib direction, density and thickness may change during the ontogeny [*L. subtilis* (UHLIG, 1883), *L. pumilus* (UHLIG, 1883)] resulting in simple, but somewhat irregular ribbing pattern. The most important generic feature is that no ventrolateral tuberculation or spines are present, which clearly mark the difference from *Karsteniceras*. Likewise, the ribbing and suture are also simple with wide saddles and trifid lobes (SARASIN & SCHÖNDELMAYER 1902, VAŠÍČEK & WIEDMANN 1994, WRIGHT et al. 1996).

*Leptoceratoides balernaensis* (RIEBER, 1977)  
Plate I, Figures 1–4

- ?1967 *Leptoceras subtile* – DIMITROVA, p. 39, pl. 12, fig. 7  
\*1977 *Karsteniceras balernaense* – RIEBER, p. 779, pl. 1, figs 1–7, text-fig. 3.  
1994 *Karsteniceras balernaense* – VAŠÍČEK & WIEDMANN, p. 218, pl. 3, fig. 4.

Material – Three internal moulds in various state of preservation. The phragmocone of specimen from B/108 (INV.2023.12.) is a spire with several rounds. We collected a specimen from layer 300/40 of section E (INV.2023.32.) which has a similar character, while the remains from layer 16 of section A (INV.2023.21.) consist of a single phragmocone fragment.

Measurements

Bed numbers	Number	Wh (cm)	D (cm)	U <sub>1</sub> (cm)	U <sub>2</sub> (cm)
Bersek Hill, section B, bed 108	INV.2023.12.	0.415	1.98	1.08	—
Bersek Hill, section A, bed 16	INV.2023.21.	—	1.335	0.705	—
Bersek Hill, section E, bed 300/40	INV.2023.382.	0.455	1.365	0.685	—

Description – Criocone internal moulds with basically rectiradiate ribs (mainly on the body chamber), then towards the spire some ribs become rursiradiate. The ribs are simple, dense, high and there are no nodules on the ventrolateral side. No depression is visible on the ventral side. No lobeline is observed.

Discussion – The absence of nodules on the ventrolateral side rules out the possibility that the specimens belong to the genus *Karsteniceras*. Species of *L. brunneriformis* (AVRAM, 1999) or *L. svinitensis* (AVRAM, 1999) resemble the specimens, but the ribs are not as prominent as in these two species. The ribs of these two species are rectiradiate, whereas some reported transitional forms are characterised mainly by rectiradiate, and in some cases prorsiradiate ribs. The specimen depicted by DIMITROVA (1967) differs quite a bit from the holotype of the species as its ribbing is more rigid and the coiling is much more open.

Stratigraphic and geographic occurrence – The species occurs in the lower Barremian strata of the Bersek Hill section of the LSF Formation (B section 108, E section 300/40 and A section 16). The species is known from the Southern Alps (Breggia Gorge, Switzerland) and the Pre-Balkan (Krapchene, Bulgaria). The age of the remains is restricted to the Barremian (Switzerland), Bulgarian specimens are from lower Barremian strata. The specimens from Bersek Hill (Hungary) confirm the early Barremian age.

*Leptoceratoides pumilus* (UHLIG, 1883)  
Plate II, Figures 1–5; Plate III, Figures 1–5; Plate IV, Figures 1–3; Plate V, Figures 1, 2; Plate XI, Figure 4

- 1860 *Ancycloceras Escheri* – OOSTER, pl. 37, figs 3, 4.  
\*1883 *Crioceras (Leptoceras) pumilum* – UHLIG, p. 270, pl. 29, figs 4, 5, 6a, 6b.  
1927 *Leptoceras cfr. pumilum* – YABE et al., p. 73(41), pl. 15(4), fig. 30.  
1938 *Leptoceras parvulum* – ROMAN, pl. 35, figs 335–336 (= UHLIG 1883, pl. 29, figs 4, 5).

- ?1958 *Leptoceras parvulum* – FÜLÖP, pl. 7, fig. 3.  
1962 *Leptoceras pumilum* – MANOLOV, p. 532.  
1966 *Leptoceratoides pumilus* – THIEULOUY, p. 289.  
1969 *Leptoceras pumilum* – WIEDMANN, pl. 2, fig. 3 (= UHLIG 1883, pl. 29, fig. 6a).  
1972 *Leptoceratoides pumilus* – VAŠÍČEK, p. 54, pl. 4, fig. 5.  
1984 *Leptoceras pumilum* – AVRAM & KUSKO, p. 14, pl. 2, fig. 8.  
1985 *Leptoceras parvulum* – HAAS et al., p. 89, pl. 24, fig. 3.  
1987 *Leptoceratoides pumilus* – MATSUKAWA, p. 349.  
1994 *Karsteniceras pumilum* – VAŠÍČEK & WIEDMANN, p. 213, pl. 1, fig. 9 (= UHLIG, 1883, pl. 29, fig. 4). pl. 2, figs 3 (= UHLIG, 1883, pl. 29, fig. 6a), 4.  
2023 *Leptoceratoides pumilus* – VAŠÍČEK, p. 113.

Material – Several specimens in variable state of preservation. Most of them are fragments that accumulated in a single piece of rock, so the identification number does not indicate the specimen itself, but the hosting piece of rock. Among the Bersek sections, there are two specimens from layer 300/8 of section E (INV.2023.2.), seven remains from layer 300/11 (INV.2023.3., INV.2023.4., INV.2023.383., INV.2023.384., INV.2023.385.), and one fragment of a spire is from layer 16 of section A (INV.2023.30.). The specimens from Bersek Hill are internal moulds, while shelly specimens appear in the drill core of Süt-17.

Measurements

Bed / Depth (m)	Jele	Wh (cm)	D (cm)	U <sub>1</sub> (cm)	U <sub>2</sub> (cm)
Bersek Hill, section E, bed 300/8	INV.2023.2.	—	0.75	0.37	—
		—	0.61	0.32	—
Bersek Hill, section E, bed 300/11	INV.2023.3.	—	—	—	—
		3.7	1.05	3.7	—
		0.59	1.275	—	—
Bersek Hill, section E, bed 300/11	INV.2023.4.	0.535	1.37	0.575	—
Bersek Hill, section A, bed 16	INV.2023.30.	0.355	0.975	0.385	—
Bersek Hill, section E, bed 300/11	INV.2023.383.	—	—	—	—
Bersek Hill, section E, bed 300/11	INV.2023.384.	—	1.01	—	—
Bersek Hill, section E, bed 300/11	INV.2023.385.	0.41	—	—	—
Bersek Hill, section E, bed 300/11	INV.2023.401.	0.49	1.38	0.575	—
		—	—	—	—
Süt-17, 257.5 m	K.12639	0.265	1.145	0.785	—
Süt-17, 262.7 m	K.12646	0.44	1.26	0.545	0.52
Süt-17, 264.0 m	K.12647	0.34	1.19	0.54	0.47
		0.44	1.49	0.82	—
		0.475	1.56	0.83	0.655
		—	0.725	0.465	0.385
		0.245	0.92	0.54	0.365
		0.145	0.55	0.415	—
		0.29	0.99	0.57	0.47
		0.15	0.62	0.465	—
		0.165	0.795	0.525	—
		0.21	—	0.5	0.415
		0.365	1.22	0.69	—
		0.26	—	—	—
		0.235	0.86	0.48	0.395
		0.155	0.69	0.4	—
		0.26	0.85	0.52	0.475
		0.25	0.805	0.55	0.39
		0.23	0.62	0.39	0.35
		0.44	1.44	0.766	—
		0.28	1.065	0.61	—
		0.235	1.015	0.615	0.435
		0.145	0.67	0.425	—
		0.26	1.23	0.925	—
		0.24	0.96	0.595	—
Süt-17, 263.6 m	K.12649	0.565	—	1.085	—
		0.415	—	—	—
		0.555	—	—	—
Süt-17, 270.1 m	K.12655	—	—	—	—

**Description** – Finely ornamented criocone internal moulds are assigned to this species. The ribs are sharp, some on the body chamber becoming biconcave (INV.2023.3., INV.2023.4.) and rarely bifurcated (INV.2023.4., K.12649). Later they become rectiradiate as the ribs progress towards the spire. In some specimens, rursiradiate ribs are also observed in the body chamber (INV.2023.4.), and ribs may also be thickened on the phragmocone (INV.2023.2.). No ventral furrow is observed, no lobeline is visible.

**Discussion** – No nodules are visible on the ventrolateral part of the criocone phragmocone, so the remains belong to genus *Leptoceratoides*. Based on the irregular rib pattern (thickened ribs), *L. pumilus* and *L. subtilis* (UHLIG, 1883) are the most likely species that are similar to our fragments. Among them, only *L. pumilus* has biconcave, bifurcated ribs. A further difference is that the fragments do not show a thickening of the ribs in the ventrolateral part, nor a weakening of the ornamentation in the ventral part, which is characteristic of *L. subtilis*. Most of the specimens from Süt-17 do not show the biconcave ribs typical of the lectotype, except for a few specimens from samples K.12646 and K.12649 (pl. 4, fig 1a, 1b, 1c, 1d). Furthermore, the specimens show similarities with specimens illustrated by UHLIG (1883, pl. 29, fig. 6a) and VAŠÍČEK & WIEDMANN (1994, pl. 2, fig. 3), which also show rectiradiate ribs. Specimens with a similar appearance to the fauna of Sümeg (INV.2023.401., INV.2023.30.) are also known from Bersek Hill. The presence of morphological separation/variation within the species can be interpreted as intraspecific variation.

The difference between the genera *L. balernaensis* and *L. pumilus* is mainly reflected in the rib pattern. *L. balernaensis* has a smaller number of ribs, the distance between them does not vary, and the shape of the shell shows more variability compared to *L. pumilus*. This latter is more densely ornamented and the distance between the ribs and their thickness may vary. Furthermore, *L. pumilus* is characterized by lower ribs, which are often biconcave.

**Stratigraphic and geographic occurrence** – The species is present between 254.3 to 270.1 m of the Süt-17 borehole, as well as in the lower Barremian *M. moutonianum* Zone of the Bersek Hill quarry Lábatlan Sandstone (A section, bed 16) and in the upper Barremian *T. vandenheckii* Zone (E section, beds 300/11 and 300/8).

The species occurs at several localities in the Carpathians: Czechia (Tichá) and in the Silesian–Beskydy Mountains (Straconka and Górkí Wielkie) in Poland, as well as in the Romanian Carpathians. The species has also been documented from the Swiss Alps (Veveyse). Its presence in Japan (Shinano Province) is questionable. The species is typical of the Barremian period; specimens from Silesia (Tichá) are early Barremian. The Hungarian specimens are both early and late Barremian in age.

?*Leptoceratoides* sp.  
Plate V, Figure 3

**Material** – A single specimen in poor state of preservation from the Süt-17 drill core.

#### Measurements

Bed / Depth (m)	Jele	Wh (cm)	D (cm)	U <sub>1</sub> (cm)	U <sub>2</sub> (cm)
Süt-17, 297.4 m	K.12661	0.57	3.905	–	–

**Description** – Hamulicone phragmocone with prorsiradiate ribs on the body chamber, which towards the spire, become rectiradiate. The ventral part and the lobe line are not visible on the specimen.

**Discussion** – Due to the poor preservation of the specimen, the classification is questionable. The few morphological characters suggest the species may belong to ?*Leptoceratoides heeri*. We exclude this specimen from further interpretations, because this specimen is fundamentally different from leptoceratoid ammonites and probably belong to a different family.

**Stratigraphic and geographic occurrence** – The specimen is from Süt-17 297.4 m depth, its age is likely late Hauterivian–early Barremian inferred indirectly after HAAS et al. (1985).

#### Genus *Karsteniceras* ROYO Y GOMEZ, 1945

Type species: *Ancyloceras beyrichii* KARSTEN, 1858

Genus *Karsteniceras* is generally characterized by tiny, few centimetres in diameter criocone morphology (VAŠÍČEK & WIEDMANN 1994, WRIGHT et al. 1996), apart from *K. aequicostatum* VAŠÍČEK & HOEDEMAEKER 2003b and ?*K. filicostatum* (STAHLCKER, 1935), which are bigger. The ribbing pattern is similar to *Leptoceratoides*; the major difference is the presence of ventrolateral tuberculation, which is the generic feature of *Karsteniceras*. The suture is simple, very similar to *Leptoceratoides* (VAŠÍČEK & WIEDMANN 1994, WRIGHT et al. 1996).

#### *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994

Plate VI, Figures 1–3; Plate VII, Figures 1–3; Plate VIII, Figures 1–3; Plate IX, Figures 1–4; Plate X, Figures 1–5; Plate XI, Figures 1–3

1945 *Karsteniceras beyrichii* – ROYO Y GOMEZ, p. 461, pl. 71, fig. 1a, 1b, 1c.

1968 *Karsteniceras beyrichii* – ETAYO-SERNA, p. 54, pl. 1, figs 1–3, text-fig. 4: 8–9.

1978 *Karsteniceras beyrichii* – WIEDMANN, pl. 4, fig. 2a, 2b.

\*1994 *Karsteniceras ibericum* – VAŠÍČEK & WIEDMANN, p. 212, pl. 1, figs 4, 5.

**Material** – 19 fragments of specimens, which are mostly spire fragments, all are from the Bersek Hill.

#### Measurements

Bed	Rep. nr.	Wh (cm)	D (cm)	U <sub>1</sub> (cm)	U <sub>2</sub> (cm)
Bersek Hill, section A, bed 8	INV.2023.5.	0.66	–	–	–
Bersek Hill, section A, bed 8	INV.2023.6.	–	–	–	–
Bersek Hill, section A, bed 8	INV.2023.7.	0.51	1.82	0.93	0.655
Bersek Hill, section E, bed 300/35	INV.2023.8.	0.6	2.1	1.1	–
Bersek Hill, section A, bed 16	INV.2023.9.	–	–	–	–
Bersek Hill, section B, bed 108	INV.2023.11	–	1.97	0.97	–
Bersek Hill, section B, bed 114	INV.2023.13.	0.51	–	–	–
Bersek Hill, section B, bed 126	INV.2023.14.	–	1.72	0.635	–
Bersek Hill, section B, bed 116	INV.2023.15.	0.225	–	–	–
Bersek Hill, section A, bed 25	INV.2023.17.	0.29	–	–	–
Bersek Hill, section A, bed 25	INV.2023.18.	–	–	–	–
Bersek Hill, section A, bed 17	INV.2023.20.	0.35	1.4	0.72	–

Bersek Hill, section E, bed 300/40	INV.2023.22.	0.34	–	–	–
Bersek Hill, section A, bed 12	INV.2023.23.	–	–	–	–
Bersek Hill, section A, bed 7	INV.2023.24.	0.455	2.08	1.015	–
Bersek Hill, section E, bed 300/15	INV.2023.25.	0.26	–	0.615	–
Bersek Hill, section E, bed 300/15	INV.2023.28.	0.53	1.59	0.615	–
Bersek Hill, section B, bed 111	INV.2023.29.	–	1.2	0.44	–
Bersek Hill, section E, bed 300/11	INV.2023.381.	–	–	–	–
Bersek Hill, section E, bed 300/11	INV.2023.400.	–	–	–	–

Description – Criocone fragments of internal moulds, where dense rectiradiate ribs are present on the body chamber. In addition, few rursiradiate ribs also appear, which are not only present on the body chamber but also on the spire, and then, towards the spire, prorsiradiate ribs (INV.2023.6.) also appear. The spire itself is missing from the internal moulds. In the ventrolateral part, most of the ribs display small tuberculation, and a ventral furrow is visible. In some fragments, some ribs show thickening and a change in rib density (INV.2023.5.). In some specimens (INV.2023.20, INV.2023.25), the ribs pass the ventral part interrupting the course of the ventral depression. On two specimens (INV.2023.17, INV.2023.5), the ventral depression is not visible. In other specimens (INV.2023.25, INV.2023.381), the ventral depression is only visible on the ribs. No lobeline is visible on any specimens.

Discussion – Based on the generic features – criocone phragmocone and small tubercles on the ventrolateral part – the specimens are assigned to genus *Karsteniceras*. On the basis of its irregular rib pattern, the specimens resemble *K. beyrichii*, but there is no ventral depression displayed at any *Karsteniceras* species but *K. ibericum*. A further difference is that *K. beyrichii* has been described only from the Central Atlanticum, in contrast to *K. ibericum*, which has been detected from the Alpine Tethys and Neotethys basins.

Stratigraphic and geographic occurrence – The species has been described from the Western Tethyan region, mainly from the Iberian Peninsula (Sierra Mediana, Spain) and the Alps (Ranzenberg, Vorarlberg, Austria; WIEDMANN 1978). In the Central Atlantic it occurs in Colombia, where it was reported from Barremian strata, in Austria it was discovered around the lower/upper Barremian boundary, while in Spain it occurs only in the upper Barremian strata. The Hungarian findings confirm the early Barremian occurrence of the species.

#### *Karsteniceras* sp. 1 Plate XII, Figures 1–3

Material – Four badly preserved internal moulds from the Bersek Hill.

##### Measurements

Bed	Rep. nr.	Wh (cm)	D (cm)	U <sub>1</sub> (cm)	U <sub>2</sub> (cm)
Bersek Hill, section A, bed 16	INV.2023.10.	0.47	–	–	–
Bersek Hill, section A, bed 35	INV.2023.16.	–	–	–	–
Bersek Hill, section E, bed 300/15	INV.2023.27.	–	–	–	–

Description – The specimens have simple rectiradiate ribs. The width of the ribs is greater than the distance between them and there is no abrupt change in the spacing

(density) of the ribs. Nodules are visible in the ventrolateral part. In the ventral part, no depression and no lobeline are visible.

Discussion – Species level identification is not possible on the basis of the morphological features observed on the internal moulds, most likely due to the poor preservation.

Differences between *Karsteniceras* sp. 1 and *K. ibericum* are manifested in the ornamentation. In *Karsteniceras* sp. 1, rectiradiate ribs are observed, equally spaced apart, whereas in *K. ibericum* specimens, the ribbing pattern is rather irregular as rectiradiate and prorsiradiate ribs both appear, as well as rursiradiate ones. In addition, on *K. ibericum*, a thickening of the ribs and a change in the density of the ornamentation are also observed. Furthermore, no ventral depression is visible on the specimens, which is present on the majority of *K. ibericum* specimens.

Stratigraphic and geographic occurrence – The specimens occur in different strata of the LSF of the Bersek Hill. The lowest occurrence is in the *M. moutonianum* Zone (in beds 16 and 35 of section A), followed by the *T. vandenheckii* Zone (in bed 300/15 of section E).

#### *Karsteniceras* sp. 2 Plate XII, Figure 4

Material – A single internal mould of a specimen from the Bersek Hill.

##### Measurements

Bed	Rep. nr.	Wh (cm)	D (cm)	U <sub>1</sub> (cm)	U <sub>2</sub> (cm)
Bersek Hill, section E, bed 300/15	INV.2023.26.	0.26	1.12	0.615	–

Description – Criocone phragmocone with rectiradiate ribs on the body chamber. Towards the spire, rursiradiate ribs also appear on the remains. There is no visible thickening between the ribs and no abrupt change in rib spacing (density). Tuberculation is visible on the ventrolateral part. No ventral depression and lobe are visible.

Discussion – The morphological features of the phragmocone and the poor preservation do not allow species level specification. Both rectiradiate and rursiradiate ribs appear on *Karsteniceras* sp. 2, which shows similarity with *K. ibericum*, but no variation in the density of ornamentation and thickness of ribs is observed. Furthermore, the ventral depression, which is characteristic of *K. ibericum*, is not visible on the specimen.

Stratigraphic and geographic occurrence – The internal moulds are from the *T. vandenheckii* Zone of Bersek Hill (E section, bed 300/15).

#### Stratigraphy

##### Bersek Hill quarry

Compilation of an integrated section log is the main stratigraphic achievement of this work, which allows comparing different bed numberings of FÜLÖP, FŐZY and FOGARASI

available in the literature (FÜLÖP 1958; FÓZY 1995, 2017; FOGARASI 1995a, b, 2001; FÓZY & FOGARASI 2002; FÓZY & JANSEN 2009; PRICE et al. 2011).

Originally, all the specimens collected by the FÜLÖP team were assigned a letter (A, B, C, D, E) and a number. Some of them were published by FÜLÖP (1958). After FÜLÖP passed away, for many years it was not clear what these letters meant. This problem was solved in the late 1990's by István FÓZY with the help of the late Tibor STEINER, the last living member of the original collecting team by then, who showed the positions of collected sections, which likely corresponded to the letters (A, B, C, D, E). Their approximate position on the quarry wall was also shown by Tibor STEINER, depicted on Fig. 4. However, the lack of the original field notes was still a problem that inhibited the precise identification of ammonite bearing beds in the field (FÓZY 1995, 2017). FOGARASI (1995a, b, 2001), who worked on the nannofossils and sedimentary features of Bersek Hill, gave his own, new bed numberings and documented an extremely detailed sedimentologic log based on his field observations. His results were documented in his PhD (FOGARASI 2001) and later published (FÓZY & FOGARASI 2002). In 2015, FÓZY & SZENTE also prepared a new section log with new bed numbers based on their field observations. This log is not published but was used on the field during our sampling.

Our objective was to reconcile the various bed numbering systems. We examined the bed thicknesses in the field and the fauna given by the various authors. Based on these observations, we created a synthesis of bed numbers (Appendix 2) and made a composite section.

The integrated stratigraphic column (Appendix 2) includes the bed numbers of

(i) FÜLÖP's sections (A, B, C, D, E) and bed numbers displayed on the ammonites. FÓZY published his works with these numberings;

(ii) FOGARASI (2001) (115 beds) based on his very precisely measured lithology;

(iii) this work, where we collected 78 samples to nannofossil and geochemical analysis.

As a first step, on the basis of lithology observed in the field, we identified marker beds and used *i–iii* numberings. Two beds fit the requirement: the greenish grey slump bed at the base of LSF (Fig. 3) with an approximate 3-metres-thickness, which decreases with distance, and a massive sand bed of uniform, 20 cm thickness numbered as "Bed 20". After fixing these two marker levels as *i–iii* numberings, we correlated the pack of 113 beds of FOGARASI and the 43 beds with our numbers based on observations of bed thicknesses and lithology. Matching of these *i–iii* beds is completed. The greatest inconsistency was around the top 1–8 beds of ours because were measured these thicker than the top few beds of FOGARASI.

The next step was the most problematic: to fit the original bed and section (A, B, E) numbers of FÜLÖP displayed on the ammonites to the integrated stratigraphic column. In order to proceed with this, ammonite biozones given by

FÓZY (2017) were fit to the integrated stratigraphy on the basis of lithology, number of collected specimens and even based on the non-ammonitiferous beds. We double-checked our correlations in the field by short collecting campaigns. These resulted in several new specimens with only five of them suitable for specific identification. Our correlation was the least precise for section B where only the biozones and the base of the LSF were possible to be determined, and not the exact beds.

### *Sümeg Süt-17 drill core*

The ammonite fauna of Süt-17 drill core was published by HAAS et al. (1985) focussing on biostratigraphical points. The tiny heteromorph mass occurrence was also displayed on a plate. However, the lack of modern biostratigraphic framework of microfossil groups, age indicative ammonites and chemostratigraphy makes it difficult to assign a precise stratigraphic position of Leptoceratoididae occurrences within the *M. moutonianum* Zone approximate; the comparisons to Bersek Hill section are somewhat hypothetical.

## Occurrences of Leptoceratoididae

### *Bersek Hill quarry*

Leptoceratoididae from the Bersek Hill are diverse (Plates I–IV, VI–XII) with co-occurrences of *Leptoceratoides* and *Karsteniceras* species. Specimens from this locality are internal moulds with variable but mostly medium to poor state of preservation. Their abundance is given bed-by-bed (Fig 6).

### *Sümeg Süt-17 drill core*

Our findings related to Leptoceratoididae are the following:

(i) five accumulation levels (270.1 m; 264.0 m; 263.6 m; 262.7 m; 257.5 m) of Leptoceratoididae were observed;

(ii) from 297.4 m depth, a ?*Leptoceratoides* sp. was found, which is excluded from this investigation due to its uncertain taxonomic position discussed above;

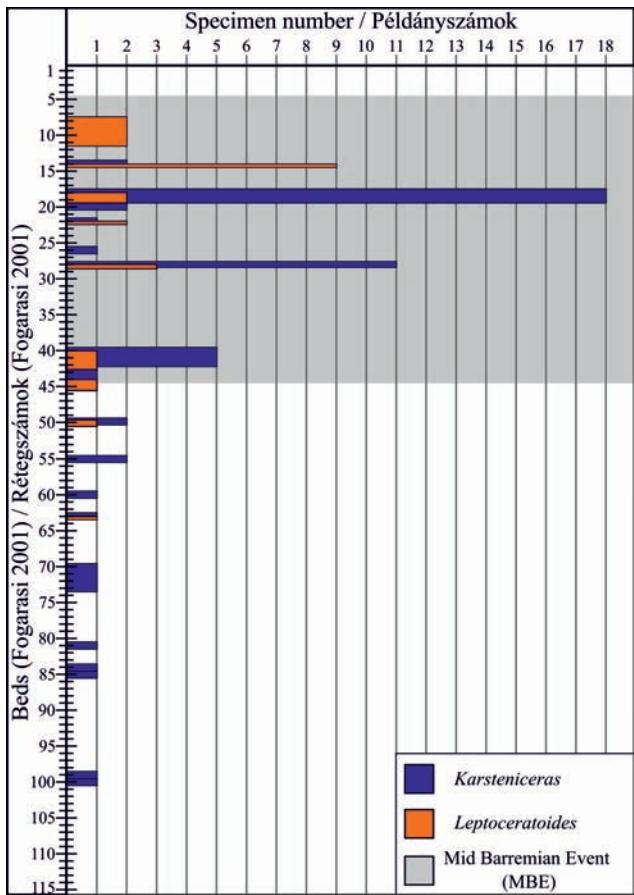
(iii) all are shelled specimens;

(iv) 28 specimens were eligible for species level determination, among them 27 is *L. pumilus*;

(v) a mass occurrence level (263.6 m) is found with more than 20 specimens in a 10 cm of diameter drill core – and 100% of them is *L. pumilus*;

(vi) no planispiral ammonites or accompanying macrofauna is present between 264.0 m and 262.7 meters, also at 257.5 m;

(vii) Leptoceratoididae in Süt-17 (Plates II, IV, V) are less diverse compared to the Bersek Hill fauna.



**Figure 6.** Specimen numbers of *Karsteniceras* spp. and *Leptoceratoides* spp. at the Bersek Hill. Grey band represents the inferred MBE interval (detailed below). Data is visualized from the Appendix I. data matrix

**6. ábra.** *Karsteniceras* spp. és *Leptoceratoides* spp. példányai a Bersek-hegyen. Szürke sáv jelöli a Középső Barremi Eseményt (részletesen lejjebb). Adatok megjelenítése az 1. számú melléklet mátrixából származik

## Discussion

### Paleoenvironmental perturbations during the Mid Barremian Event

During the mid Barremian time interval, an environmental change took place and caused a positive 0.5‰ shift of the  $\delta^{13}\text{C}$  that is documented by SPROVIERI et al. (2006) and named as Mid Barremian Event, along with the radiation of planctonic foraminifers and the sudden change of the radiolarian faunas (COCCIONI et al. 2003). MAHANIPOUR & EFTEKHARI (2017) observed an increasing trend in the number of warm water taxa in NC5D [nannozone] that they linked to a warming event that occurred during the mid Barremian. Moreover, reported from southern Spain (AGUADO et al. 2014), an increasing trend in the number of eutrophic nannofossil taxa is also recorded from the middle part of NC5D nannozone which may indicate intermittent episodes of relative eutrophication of surface waters throughout the latest Hauterivian to earliest late Barremian interval. This also suggests warm and humid climatic conditions in the adjacent hinterlands with increased freshwater, nutrient rich runoff into the basin. Under these climatic conditions, the less saline sur-

face waters facilitated the stratification of the water column including the development of dysoxic/anoxic bottom environments. In summary, both authors link bottom anoxia to increased pelagic primary production. Fertile pelagic water-masses might be unfavorable for most of the ammonites but provided an interval of opportunity for tiny Leptoceratoidea. The very recent summary of MARTÍNEZ et al. (2023) based on cyclostratigraphic observations, is that 1‰ PDB increase of bulk carbonate  $\delta^{13}\text{C}$  values and a reduced pelagic sedimentation rate is observed during the MBE, which, in their interpretation could be a consequence of basin starvation at a time of fastest rise in sea level.

## Characterization of the Mid Barremian Event in Hungary

### Bersek Hill quarry

The precise stratigraphic position of the *M. moutonianum* Zone can be depicted on the basis of previously published data (FŐZY & JANSEN 2009; PRICE et al. 2011). The separate 5-point running mean stable  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  isotope excursions measured from different belemnite taxa were previously published by PRICE et al. (2011) where mean values are plotted against the lithologic log and stratigraphic and percentile Leptoceratoididae occurrences (Figure 7).

The latter displays the characteristics of the Mid Barremian Event as a slight positive +0.5‰ shift in  $\delta^{13}\text{C}$  values. Moreover, a slow but continuous increase the  $\delta^{18}\text{O}$  values from the early Hauterivian towards the mid Barremian is observed which was interpreted by PRICE et al. (2011) as a gradual warming. They concluded that the Mg/Ca data run parallel the  $\delta^{18}\text{O}$  data suggest that the overriding control on the oxygen isotope trends is indeed temperature and not evaporation or/and freshwater input. This fits to the concept of MBE by AGUADO et al. (2014) and MARTÍNEZ et al. (2023) who both assume a warm and humid pulse during the MBE.

Moreover, stratigraphic occurrences of the documented Leptoceratoididae specimens can be separated as *L. balernaensis* occurs in the *M. moutonianum*, while *L. pumilus* mainly in the *T. vandenheckii* Zone. Their stratigraphic occurrence displays only few beds that overlap at the top *M. moutonianum* Zone. *K. ibericum* is the most common species found from basal *K. compressissima* to basal *T. vandenheckii* Zones. Leptoceratoididae diversity peak observed in section A, bed 16 and a mass occurrence level at section E, bed 300/11 are both within the *M. moutonianum* Zone and, based on the above mentioned observations, might have been deposited during the MBE.

### Sümeg Süt-17 drill core

Biodiversity loss of the macrofauna is observed between 264.0 and 262.7 meters (HAAS et al. 1985, table 4) where the otherwise abundant planispiral ammonites and associated macrofauna is absent, only monospecific Leptoceratoididae

were found and named here as the “Leptoceratoididae interval”. Compiling published data (HAAS et al. 1985) with our findings, we assume this 1.3-meter-thick “Leptoceratoididae interval” might have been deposited during the Mid Barremian Event, but the exact stratigraphic position of *M. moutonianum* Zone (including the MBE) needs further confirmation. Taking the lithology in consideration, between 270–273 metres a double terrigenous input peak was observed on the CaCO<sub>3</sub> curve by HAAS et al. (1985, fig. 27a–b). In our opinion this reflects two sudden increases in terrigenous material. These might be linked to two rapid pulses of a warmer and more humid climatic conditions and/or intensification of orogenic (uplift) movements. However, biostratigraphic uncertainties and the lack of chemostratigraphy make these assumptions and possible comparisons to the Bersek Hill section hypothetical to a degree.

### Paleoecology and lifestyle of Leptoceratoididae

Paleoecology and lifestyle of heteromorph ammonites, including tiny Leptoceratoididae are still poorly understood (LUKENEDER 2003, 2005). However, all authors agree in the specialized nature of heteromorphs. Here we summarize the limited information available in the literature on this family.

RIEBER (1977) was the first who suspected a nectic mode of life for *Leptoceratoides balernaensis* (RIEBER, 1977) grazing above the anoxic seafloor. VAŠÍČEK & WIEDMANN (1994) connected the presence of small Leptoceratoididae with dark grey or black, organic matter rich pyritic muddy laminated sediments which are indicative of anoxia. They concluded that their habitat might be related to seafloor algal mats where they were grazing similar to those of Middle Jurassic heteromorphs (DIETL 1978). Due to the excellent state of preservation, all mentioned authors believe that these tiny forms did not suffer post-mortem transportation. Later, WESTERMANN (1996) interpreted a stable vertical position in the water column for criocones (= gyrocones see LUKENEDER 2015) based on the strong resistance of the forms against water currents thus indicating a pseudoplanktonic lifestyle within the epipelagic zone. LUKENEDER (2015) also shared this opinion.

Some authors (RIEBER 1977; VAŠÍČEK & WIEDMANN 1994; LUKENEDER & TANABE 2002; LUKENEDER 2003, 2005, 2007) have documented mass occurrence of Leptoceratoididae. The abundance of *Karsteniceras ternbergense* is above 90% in low oxygenated facies as LUKENEDER & TANABE (2002) and LUKENEDER (2003, 2005, 2007) reported. These authors interpreted its mass occurrence to indicate *r*-lifestyle (opportunistic) strategy. They assumed these forms were adapted to low oxygen levels that likely dominated the dysoxic sea bottom. They placed this environment to the epipelagic zone with approximate water depth of 70–80 m (LUKENEDER 2003), where the lack of bottom currents likely allowed the in-situ fossilization of finely detailed shells together with their aptichi (LUKENEDER & TANABE 2002).

Nutricline depths were measured in the eastern Pacific where the number and diversity of planktonic organisms is concentrated in the 35–80 m depth zone (LONGHURST 1985). When comparing this observation with those of LUKENEDER & TANABE (2002), it becomes apparent that these tiny forms were possibly quasi-planktonic and preferred the most nutrient rich interval of the epipelagic zone which could have easily been dysoxic.

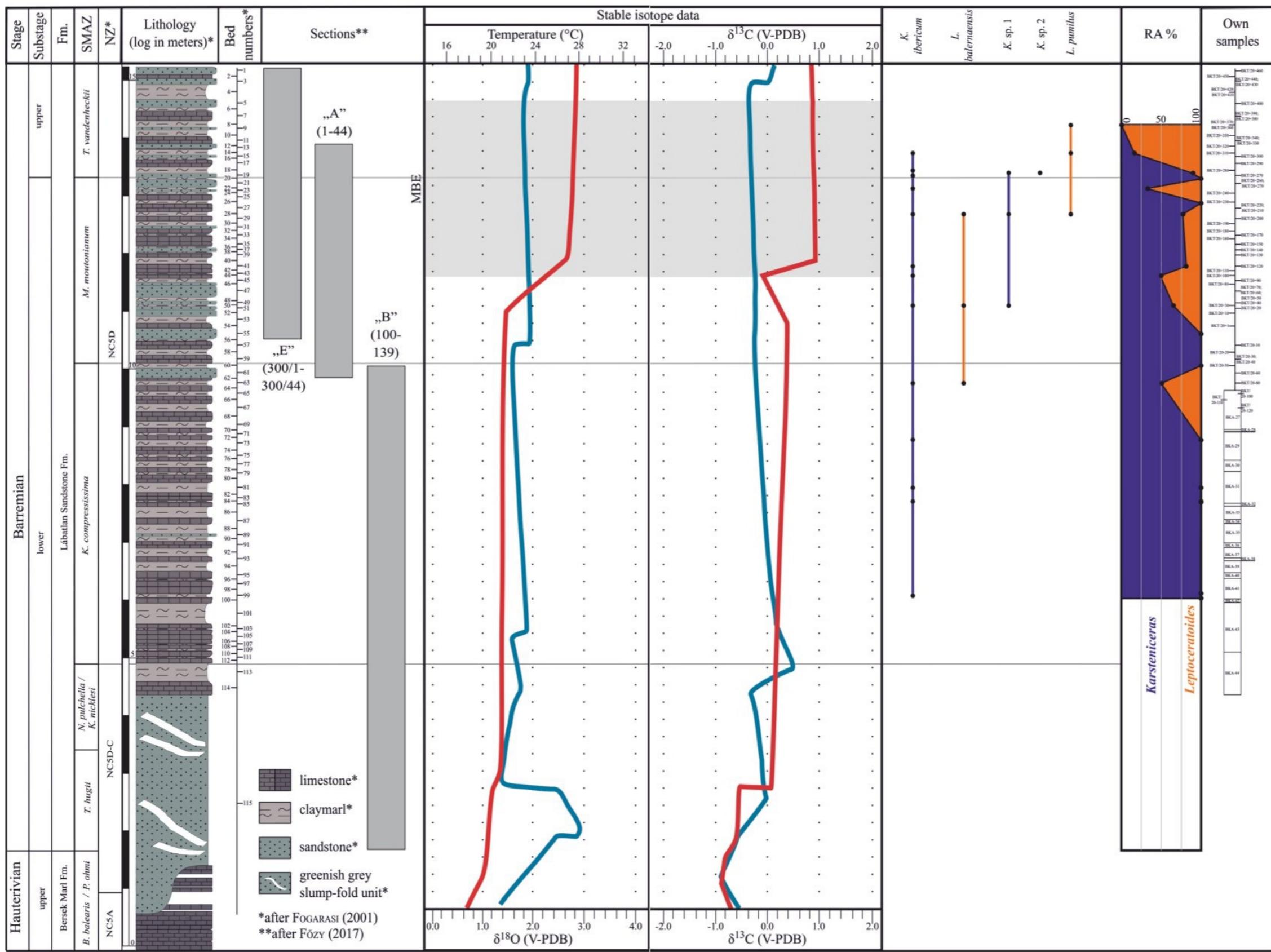
COMPANY et al. (2005) and LUKENEDER & GRUNERT (2013) believe that small Leptoceratoididae as *Karsteniceras*, *Sabaudiella* and *Hamulinites* might have lived planktonic “drifter” lifestyle. COMPANY et al. (2005) inferred that they might have lived in the epipelagic area and, therefore, anoxic events did not affect their population negatively. Nevertheless, nutrient increase during dysoxic/anoxic periods is directly linked to their increase in diversity according to these authors. Based on data reported by WESTERMANN (1996), LUKENEDER & TANABE (2002), COMPANY et al. (2005) and LUKENEDER & GRUNERT (2013), it can be assumed that the planktonic, plankton-feeding criocone shell Leptoceratoididae lived in the most nutrient-rich (nutricline) depth range of the epipelagic zone. Their fragile shell (with high interfacial resistance) might have made it difficult for Leptoceratoididae – which might have been passive drifters – to move out of this zone, thus their chances of survival would have significantly declined due to the reduced nutrient supply within this zone.

The main food source of Cretaceous heteromorphs was likely zooplankton, as confirmed by the morphology of the jaws and radula and the remains of prey animals (gastropoda, crustacea, crinoidea) (WIPPICH & LEHMANN 2004, KRUTA et al. 2011, HOFFMANN et al. 2021).

Tiny heteromorphs were more diverse in the proximal Gerecse basin, while *L. pumilus* was exclusively present in the distal Bakony basin (if we accept that the two Leptoceratoididae findings are the same age). This may give the idea that they might have lived in the epipelagic area but even tiny heteromorph ammonites could have had different ecological preferences and might have tolerated certain stress factors like lack of food, water clarity or dysoxia differently. We do not believe that with such a fragile shell these tiny forms were grazing among the sea grass and risk injuries. Combining our results with WESTERMANN (1996), it seems logical that these tiny criocone Leptoceratoididae were attracted to certain vertical levels (close to, or even within the nutricline) and movement out vertically from this level was at the minimum challenging – or almost impossible – due to the shape of the conch.

### Local response of Leptoceratoididae to the Mid Barremian Event

Appearance of family Leptoceratoididae is linked to the upper Hauterivian (COMPANY et al. 2005, LUKENEDER 2012, LUKENEDER & GRUNERT 2013, MATAMALES-ANDREU et al. 2019) where their first representatives are observed in sedi-



**Figure 7.** Biostratigraphy, lithology, sections, bed numbers and stratigraphic occurrences of identified *Karsteniceras* (*K.*) spp. and *Leptoceratooides* (*L.*) spp. of Bersek Hill quarry. Relative abundances (RA%) of these two genera (on the right) are plotted against the lithologic log. Inferred stratigraphic position of the Mid Barremian Event (MBE) is shaded grey. Chemostratigraphy data lines are simplified, measured from *Duvalia/Pseudobelus* is coloured blue, *Vaunagites pistilliformis/Belemnites pistilliformis/Hibolithes* is coloured with red line (after PRICE et al. 2011).

Abbreviations: Fm.: Formation, NZ.: Calcareous nannofossil zonation

**7. ábra.** A Bersek-hegy integrált biosztratigráfiája, litológiája, szelvények és rétegszámok elhelyezkedése, valamint a *Karsteniceras* (*K.*) spp. és *Leptoceratooides* (*L.*) spp. rétegtani elterjedése. Belemnitesz-taxonokból kinyert kemosztratigráfiai adatok felhasználásával készült trendvonalak mutatják a Középső Barremi Eseményt (szürke mezővel jelölve), ahol a kék vonal a *Duvalia/Pseudobelus* taxonokat, míg a vörös vonal jelöli a *Vaunagites pistilliformis/Belemnites pistilliformis/Hibolithes* taxonokat (PRICE et al. 2011).

Rövidítések: Fm.: Formáció, NZ.: mészházú nannofosszil zónák, RA: Relatív abundancia (%)

mentary sequences. Their dispersal was rather rapid towards the Central Atlantic and Japan during the early Barremian, but the members of this family were only present as suppressed elements in ammonite assemblages. In contrast, their mass occurrences are observed in middle Barremian deposits.

If we accept the hypothesis that the “Leptoceratoididae interval” of Süt-17 and the Leptoceratoididae from the Bersek Hill are coeval, the diversity of the family shows spatial and temporal changes. The greatest diversity of tiny heteromorphs is within *M. moutonianum* Zone of Bersek Hill (Fig. 6), with co-occurrence of *Karsteniceras ibericum*, *Leptoceratoides balernaensis* and *L. pumilus* (Fig. 7). In contrast, a monospecific mass occurrence of *L. pumilus* is visible (263.6 m) at Süt-17.

In our opinion, diversity differences may be related to the different paleogeographic positions and likely reflect different paleoceanographic features of the two basins: sediments of Süt-17 were deposited in a shallow bathyal depth of a back-bulge of the foredeep (Bakony Basin) (TARI 1994, FODOR & FÓZY 2022) where increasing terrigenous input upward in the section reflects a regression according to HAAS et al. (1985); while the Bersek Hill succession (Gerecse basin) was deposited in a forebulge side of a foredeep basin (FODOR et al. 2013). If we assume the Leptoceratoididae occurrences of Bersek Hill and Süt-17 are coeval, there could be a starvation of detrital (but not carbonate) sediments in the distal Bakony basin because siliciclastic sediments are trapped on the platform at times of rapid rise in sea level. Meantime, there would be a greater influx of nutrients on the continental shelves (or in basins closer to them, like in the Gerecse basin), so primary productivity would be higher there compared to pelagic settings. This is in apparent contrast with HAAS et al. (1985), which warrants further investigations.

This observed temporal and spatial shift in diversity is linked to phenomena which might be closely related to the environmental perturbations during the Mid Barremian Event, in particular, coincident with the orogenic movements of the Alpine system:

(i) *Expanding dysoxia*: the vertical expansion of the oxygen minimum zone forced the less tolerable forms to leave and provided opportunity to various tiny heteromorphs to take over the more nutrient rich, proximal (however deeper) basin of the Gerecse (Bersek Hill). In the meantime, within the more distal Bakony basin (Süt-17) only one species, *L. pumilus* was able to handle the expanding dysoxic environment, which is supported by the complete lack of the accompanying fauna. Although many ammonites with different conch types could migrate vertically to higher, therefore, more oxygenated parts of the water column, criocone shell type allow only limited vertical migration (WESTERMANN 1996, LUKENEDER 2015). Vertical (and horizontal) migration necessarily occurs if the food sources leave the area or die due to expanding dysoxic conditions of the water column or the seafloor. Moreover, dwelling in the bottom might be important for hatching and was impos-

sible for those groups that did not tolerate dysoxic conditions;

(ii) *Different food supply*: tiny heteromorphs moved to the proximal (but deeper) Gerecse basin, but not due to the expanding anoxia but in search of more easily available nutrients. The Gerecse basin was closer to the thrust front; therefore, higher detrital input and nutrients supported greater diversity of planctic and nektic groups than in the more distal Bakony basin;

(iii) *Increased riverine input* of fresh water can intensify during humid periods – like the Mid Barremian Event – or during periods of more intense uplift of the hinterland. Freshwater input may also play an important role as it facilitates both the stratification of the water column and changes in diversity of fitoplankton living on the sea surface. Runoff is more expressed in the proximal Gerecse basin; therefore, the greater diversity is directly related to the increased nutrient supply there. We do not agree with PRICE et al. (2011) who linked the lower oxygen isotope values from the Barremian part of the Bersek Hill section to episodes of increased freshwater input due to arid climatic conditions. In contrast, we believe their data are consistent with the scenario of AGUADO et al. (2014) and MARTÍNEZ et al. (2023) who interpreted the onset of more humid and warm climatic conditions that characterize the MBE.

## Conclusions

1) A precise integration of independent stratigraphic columns of different authors is presented here on the Barremian strata of the Lábatlan Sandstone Formation of the Bersek Hill from the *K. compressissima*, *M. moutonianum* and *T. vandenheckii* Zones. Reliability of the integrated column is the lowest in the lower *K. compressissima* Zone.

2) Tiny heteromorph ammonites can be observed in certain levels in both the Bersek Hill quarry and Süt-17 drill core, also mass occurrence levels of them are reported. These are taxonomically revised to belong to family Leptoceratoididae apart from one specimen from Süt-17 (297.4 m).

3) Our taxonomic analysis confirmed that the genera *Karsteniceras* and *Leptoceratoides* should be kept as different genera and not be used as synonyms.

4) There is a stratigraphic shift between species that can be observed at the Bersek Hill: *L. balernaensis* occurs in the *M. moutonianum*, while *L. pumilus* mainly in the *T. vandenheckii* Zone. Their stratigraphic occurrence displays only a few beds that overlap at the top *M. moutonianum* Zone. *K. ibericum* is the most common species found from basal *K. compressissima* to basal *T. vandenheckii* Zones.

5) There are major differences in the assemblage composition of Leptoceratoididae between the two sections: assemblage of Süt-17 dominated by *L. pumilus*, while assemblage of Bersek Hill is comprised by *K. ibericum*, *L. balernaensis* and *L. pumilus*. The synchronicity of Leptoceratoididae occurrences from Süt-17 drill core and Bersek Hill is not fully established and thus remain hypothetic.

6) Discussion on the lifestyle and paleoecology of criocone Leptoceratoididae ammonites is presented.

7) Based on already published stable isotope and biostratigraphic data, we suggest the presence of the Mid Barremian Event within the *M. moutonianum* Zone of the Bersek Hill at sections E and A. Position of the MBE in Süt-17 core can only be inferred indirectly.

### Acknowledgements

With this contribution we would like to tribute to the scientific works and outstanding personality of our beloved professors, András GALÁCZ and Attila VÖRÖS, on their 80th birthday. Both authors are lucky to know them, grateful for the supervision, the help, the kind guidance and the possibility of joint work with them. We wish them a lot more healthy and active years with our warmest regards and deepest honour.

The authors are extremely grateful for Miguel COMPANY

and István FÓZY for their constructive comments and critical arguments, which improved the quality of the manuscript greatly. We also thank Alex LUKENEDER for his review. The authors are also grateful for the help of Attila FOGARASI, Tamás MÜLLER, Viktor KARÁDI, Emma VADLER, Emőke MOHR and István SZENTE for their support during the fieldwork, for the information they provided on the sections and for reviewing the geological setting section. Zdenek VAŠÍČEK is warmly thanked for providing access to missing literature. We acknowledge the comments and corrections on the geological settings made by László FODOR and Orsolya SZTANÓ. Klára PALOTÁS, together with the SARA Geological Survey Collection Department and colleagues of the Department of Paleontology and Geology of the Hungarian Natural History Museum, are deeply thanked for providing the available specimens and technical support. We thank Zsolt TILK and the HOLCIM Company for providing access to the Bersek Hill quarry sections.

This research was supported by the OTKA NKFIH K135309 grant.

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Manuscript received: 21/12/2023

### Plate I – I. tábla

**Figure 1.** *Leptoceratoides balernaensis* (RIEBER, 1977) – INV.2023.12. BHQ; section B; bed 108; Compressissima Zone.

**Figure 2.** *Leptoceratoides balernaensis* (RIEBER, 1977) – INV.2023.382. BHQ; section E; bed 300/40; Moutonianum Zone.

**Figure 3.** *Leptoceratoides balernaensis* (RIEBER, 1977) Holotype (RIEBER 1977, Pl. 1, Fig. 1)

**Figure 4.** *Leptoceratoides balernaensis* (RIEBER, 1977) – INV.2023.21. BHQ; section A; bed 21; Moutonianum Zone.

1. ábra. *Leptoceratoides balernaensis* (RIEBER, 1977) – INV.2023.12. Bersek-hegy; B szelvény; 108. réteg; Compressissima zóna.

2. ábra. *Leptoceratoides balernaensis* (RIEBER, 1977) – INV.2023.382. Bersek-hegy; E szelvény; 300/40. réteg; Moutonianum zóna.

3. ábra. *Leptoceratoides balernaensis* (RIEBER, 1977) Holotípus (RIEBER 1977, pl. 1, fig. 1)

4. ábra. *Leptoceratoides balernaensis* (RIEBER, 1977) – INV.2023.21. Bersek-hegy; A szelvény; 21. réteg; Moutonianum zóna.

### Plate II – II. tábla

**Figure 1.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.384. BHQ; section E; bed 300/11; Vandenheckii Zone.

**Figure 2.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.385. BHQ; section E; bed 300/11; Vandenheckii Zone.

**Figure 3.** *Leptoceratoides pumilus* (UHLIG, 1883) Lectotype (VAŠÍČEK & WIEDMANN 1994, pl. 1, fig. 9)

**Figure 4.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12647. Sümeg Süt-17; 264.0 m; Barremian?

**Figure 5.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12646. Sümeg Süt-17; 262.7 m; Barremian?

- 1. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – INV.2023.384. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.
- 2. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – INV.2023.385. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.
- 3. ábra.** Leptoceratoides pumilus (UHLIG, 1883) Lektotípus (VAŠÍČEK & WIEDMANN 1994, pl. I, fig. 9)
- 4. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – K.12647. Sümeg Süt-17; 264,0 m; Barremi?
- 5. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – K.12646. Sümeg Süt-17; 262,7 m; Barremi?

### Plate III – III. tábla

- Figure 1.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.2. BHQ; section E; bed 300/8; Vandenheckii Zone.
- Figure 2.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.3. BHQ; section E; bed 300/11; Vandenheckii Zone.
- Figure 3.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.4. BHQ; section E; bed 300/11; Vandenheckii Zone.
- Figure 4.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.383. BHQ; section E; bed 300/11; Vandenheckii Zone.
- Figure 5.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.30. BHQ; section A; bed 16; Moutonianum Zone.

- 1. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – INV.2023.2. Bersek-hegy; E szelvény; 300/8. réteg; Vandenheckii zóna.
- 2. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – INV.2023.3. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.
- 3. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – INV.2023.4. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.
- 4. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – INV.2023.383. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.
- 5. ábra.** Leptoceratoides pumilus (UHLIG, 1883) – INV.2023.30. Bersek-hegy; A szelvény; 16. réteg; Moutonianum zóna.

### Plate IV – IV. tábla

- Figure 1.** Mass-occurrence of *Leptoceratoides pumilus* (UHLIG, 1883) from drilling core (Süt-17) – K.12649. 263,6 m; Barremian?
- Figure 2.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.401. BHQ; section E; bed 300/11; Vandenheckii Zone.
- Figure 3.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12649. Sümeg Süt-17; 263,6 m; Barremian?
- 1. ábra.** *Leptoceratoides pumilus* (UHLIG, 1883) tömeges megjelenése a Süt-17 fúrásban – K.12649. 263,6 m; Barremi?
  - 2. ábra.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.401. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.
  - 3. ábra.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12649. Sümeg Süt-17; 263,6 m; Barremi?

### Plate V – V. tábla

- Figure 1.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12655. Sümeg Süt-17; 263,6 m; Barremian?
- Figure 2.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12639. Sümeg Süt-17; 257,5 m; Barremian?
- Figure 3.** *Leptoceratoides?* sp. – K.12661. Sümeg Süt-17; 297,4 m; Barremian?
- 1. ábra.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12655. Sümeg Süt-17; 263,6 m; Barremi?
  - 2. ábra.** *Leptoceratoides pumilus* (UHLIG, 1883) – K.12639. Sümeg Süt-17; 257,5 m; Barremi?
  - 3. ábra.** *Leptoceratoides?* sp. – K.12661. Sümeg Süt-17; 297,4 m; Barremi?

### Plate VI – VI. tábla

- Figure 1.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.22. BHQ; section E; bed 300/40; Moutonianum Zone.
- Figure 2.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 (ETAYO-SERNA 1968, pl. 1, figs 1, 2, 3)
- Figure 3.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.6. BHQ; section A; bed 8; Vandenheckii Zone.
- 1. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.22. Bersek-hegy; E szelvény; 300/40. réteg; Moutonianum zóna.
  - 2. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 (ETAYO-SERNA 1968, pl. 1, figs 1, 2, 3)
  - 3. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.6. Bersek-hegy; A szelvény; 8. réteg; Vandenheckii zóna.

### Plate VII – VII. tábla

- Figure 1.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.7. BHQ; section A; bed 8; Vandenheckii Zone.
- Figure 2.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.24. BHQ; section A; bed 7; Vandenheckii Zone.
- Figure 3.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.28. BHQ; section E; bed 300/15; Vandenheckii Zone.
- 1. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.7. Bersek-hegy; A szelvény; 8. réteg; Vandenheckii zóna.
  - 2. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.24. Bersek-hegy; A szelvény; 7. réteg; Vandenheckii zóna.
  - 3. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.28. Bersek-hegy; E szelvény; 300/15. réteg; Vandenheckii zóna.

### Plate VIII – VIII. tábla

**Figure 1.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.5. BHQ; section A; bed 8; Vandenheckii Zone.

**Figure 2.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.17. BHQ; section A; bed 25; Moutonianum Zone.

**Figure 3.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.25. BHQ; section E; bed 300/15; Vandenheckii Zone.

**1. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.5. Bersek-hegy; A szelvény; 8. réteg; Vandenheckii zóna.

**2. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.17. Bersek-hegy; A szelvény; 25. réteg; Moutonianum zóna.

**3. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.25. Bersek-hegy; E szelvény; 300/15. réteg; Vandenheckii zóna.

### Plate IX – IX. tábla

**Figure 1.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.8. BHQ; section E; bed 300/35; Moutonianum Zone.

**Figure 2.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.9. BHQ; section A; bed 16; Moutonianum Zone.

**Figure 3.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.11. BHQ; section B; bed 108; Compressissima Zone.

**Figure 4.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.13. BHQ; section B; bed 114; Compressissima Zone.

**1. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.8. Bersek-hegy; E szelvény; 300/35. réteg; Moutonianum zóna.

**2. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.9. Bersek-hegy; A szelvény; 16. réteg; Moutonianum zóna.

**3. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.11. Bersek-hegy; B szelvény; 108. réteg; Compressissima zóna.

**4. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.13. Bersek-hegy; B szelvény; 114. réteg; Compressissima zóna.

### Plate X – X. tábla

**Figure 1.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.14. BHQ; section B; bed 126; Compressissima Zone.

**Figure 2.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.15. BHQ; section B; bed 116; Vandenheckii Zone.

**Figure 3.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.20. BHQ; section A; bed 17; Moutonianum Zone.

**Figure 4.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.18. BHQ; section A; bed 25; Moutonianum Zone.

**Figure 5.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.400. BHQ; section A; bed 16; Moutonianum Zone.

**1. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.14. Bersek-hegy; B szelvény; 126. réteg; Compressissima zóna.

**2. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.15. Bersek-hegy; B szelvény; 116. réteg; Vandenheckii zóna.

**3. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.20. Bersek-hegy; A szelvény; 17. réteg; Moutonianum zóna.

**4. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.18. Bersek-hegy; A szelvény; 25. réteg; Moutonianum zóna.

**5. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.400. Bersek-hegy; A szelvény; 16. réteg; Moutonianum zóna.

### Plate XI – XI. tábla

**Figure 1.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.29. BHQ; section B; bed 111; Compressissima Zone.

**Figure 2.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.381. BHQ; section E; bed 300/11; Vandenheckii Zone.

**Figure 3.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.23. BHQ; section A; bed 12; Moutonianum Zone.

**Figure 4.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.401. BHQ; section E; bed 300/11; Vandenheckii Zone.

**1. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.29. Bersek-hegy; B szelvény; 111. réteg; Compressissima zóna.

**2. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.381. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.

**3. ábra.** *Karsteniceras ibericum* VAŠÍČEK & WIEDMANN, 1994 – INV.2023.23. Bersek-hegy; A szelvény; 12. réteg; Moutonianum zóna.

**4. ábra.** *Leptoceratoides pumilus* (UHLIG, 1883) – INV.2023.401. Bersek-hegy; E szelvény; 300/11. réteg; Vandenheckii zóna.

### Plate XII – XII. tábla

**Figure 1.** *Karsteniceras sp. 1* – INV.2023.10. BHQ; section A; bed 16; Moutonianum Zone.

**Figure 2.** *Karsteniceras sp. 1* – INV.2023.16. BHQ; section A; bed 35; Moutonianum Zone.

**Figure 3.** *Karsteniceras sp. 1* – INV.2023.27. BHQ; section E; bed 300/15; Vandenheckii Zone.

**Figure 4.** *Karsteniceras sp. 2* – INV.2023.26. BHQ; section E; bed 300/15; Vandenheckii Zone.

**1. ábra.** *Karsteniceras sp. 1* – INV.2023.10. Bersek-hegy; A szelvény; 16. réteg; Moutonianum zóna.

**2. ábra.** *Karsteniceras sp. 1* – INV.2023.16. Bersek-hegy; A szelvény; 35. réteg; Moutonianum zóna.

**3. ábra.** *Karsteniceras sp. 1* – INV.2023.27. Bersek-hegy; E szelvény; 300/15. réteg; Vandenheckii zóna.

**4. ábra.** *Karsteniceras sp. 2* – INV.2023.26. Bersek-hegy; E szelvény; 300/15. réteg; Vandenheckii zóna.

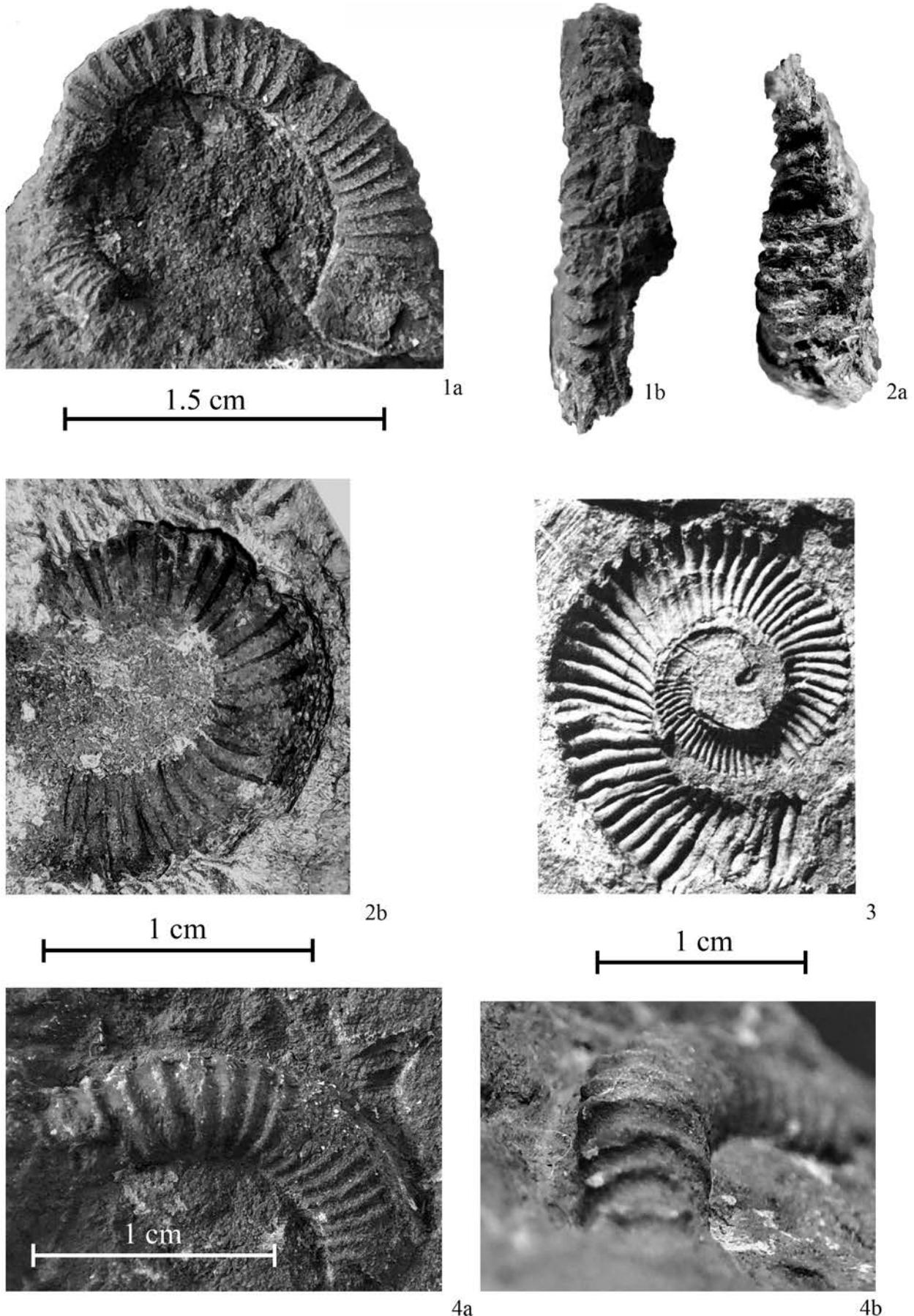
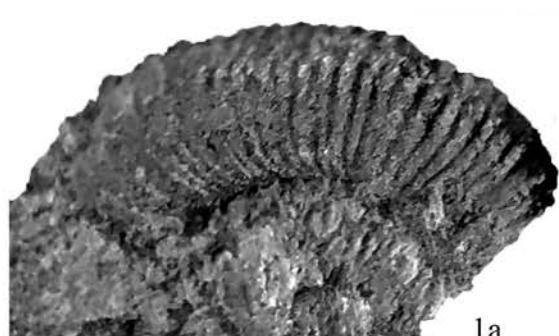
**Plate I – I. tábla**

Plate II – II. tábla



1a



1b



2a

1 cm

1 cm



2b



3

2 cm



4

1 cm



1 cm

5

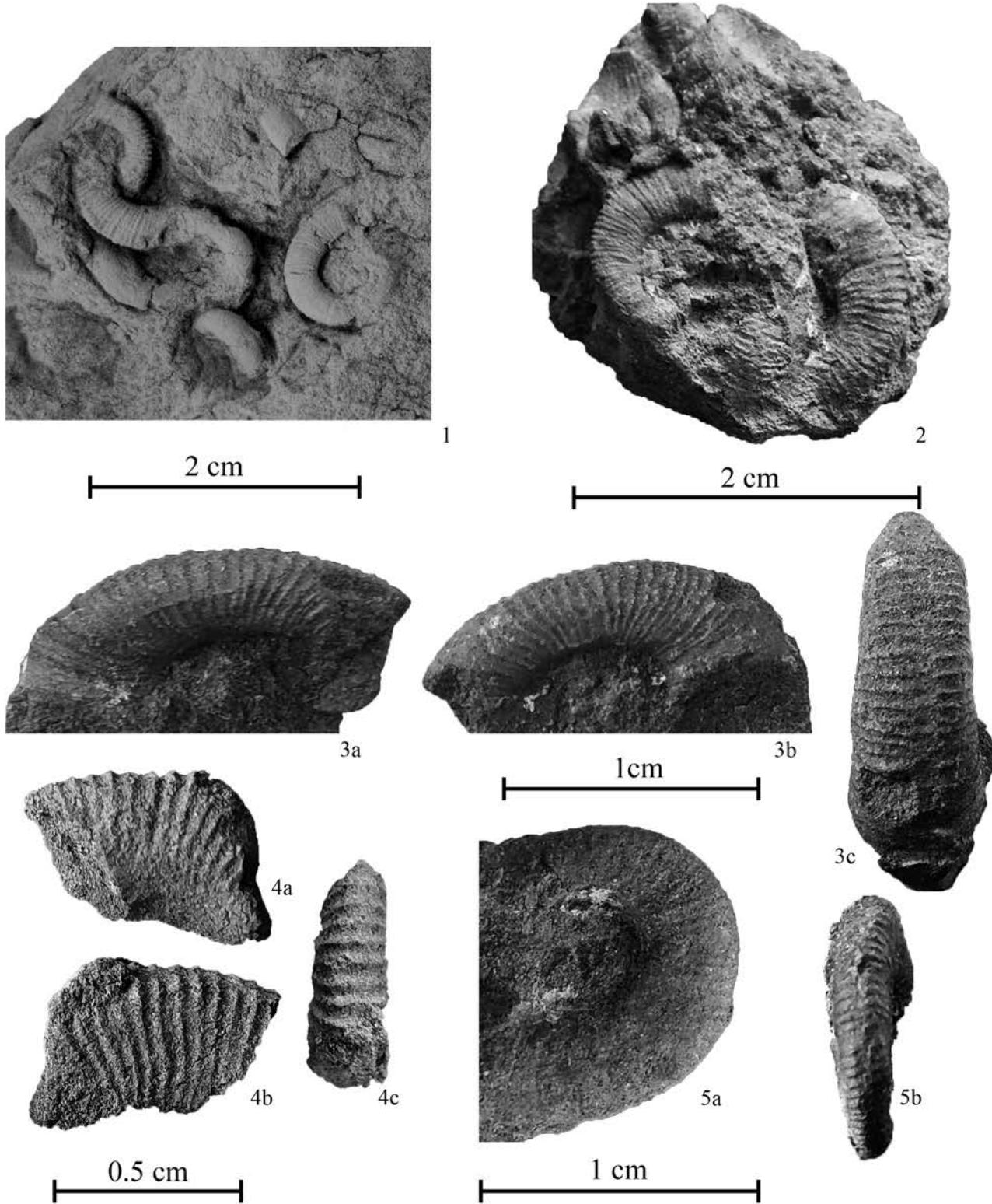
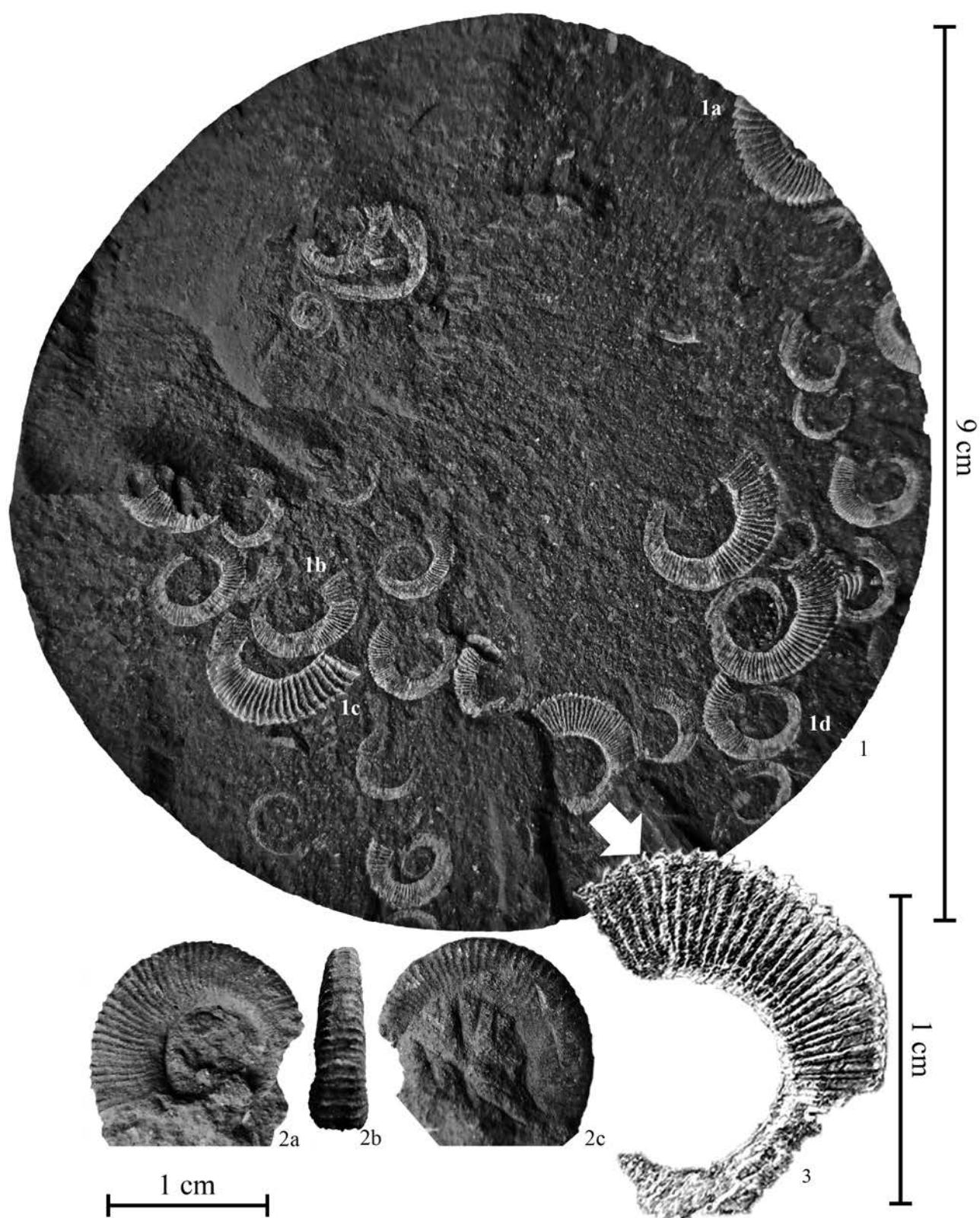
**Plate III – III. tábla**

Plate IV – IV. tábla



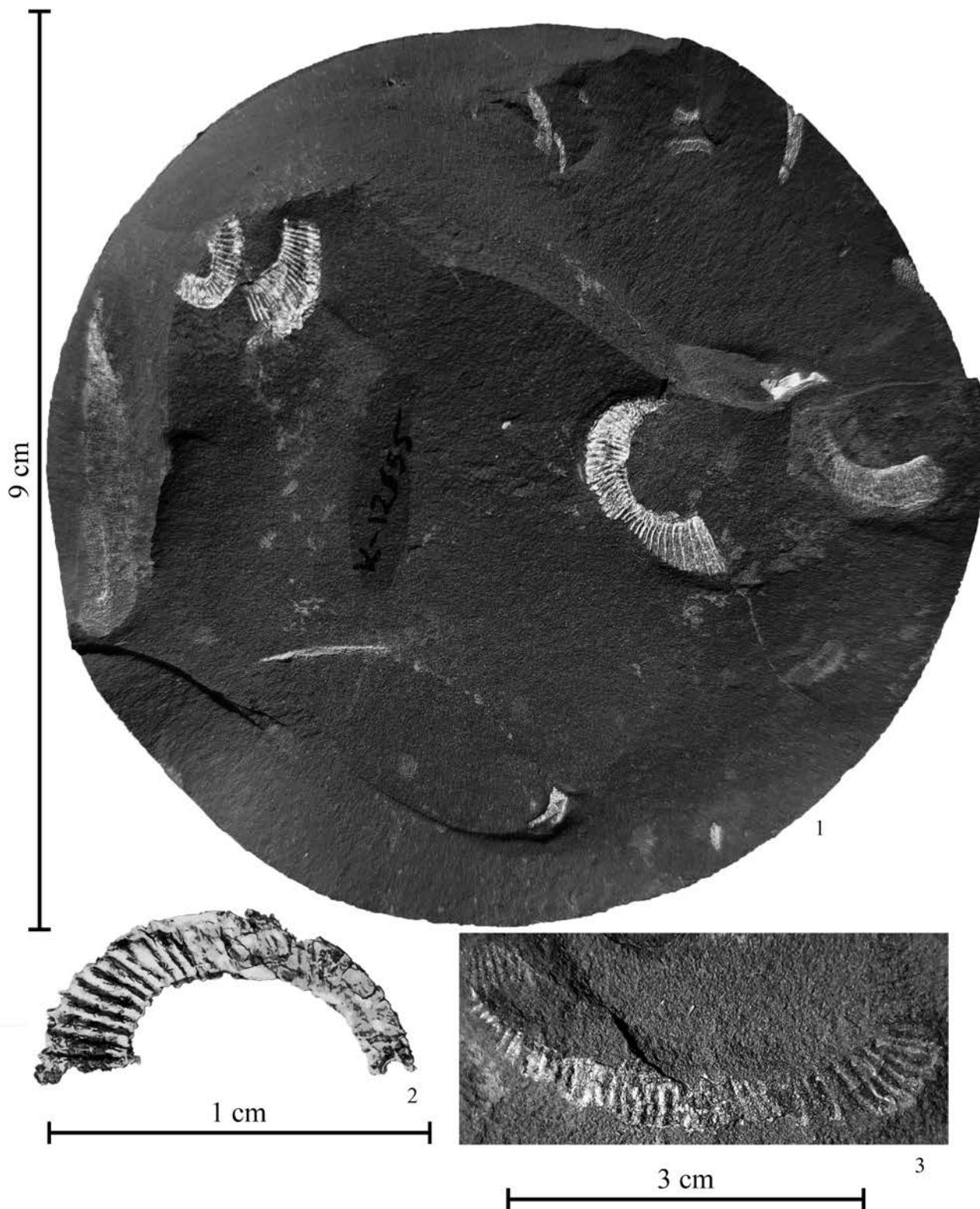
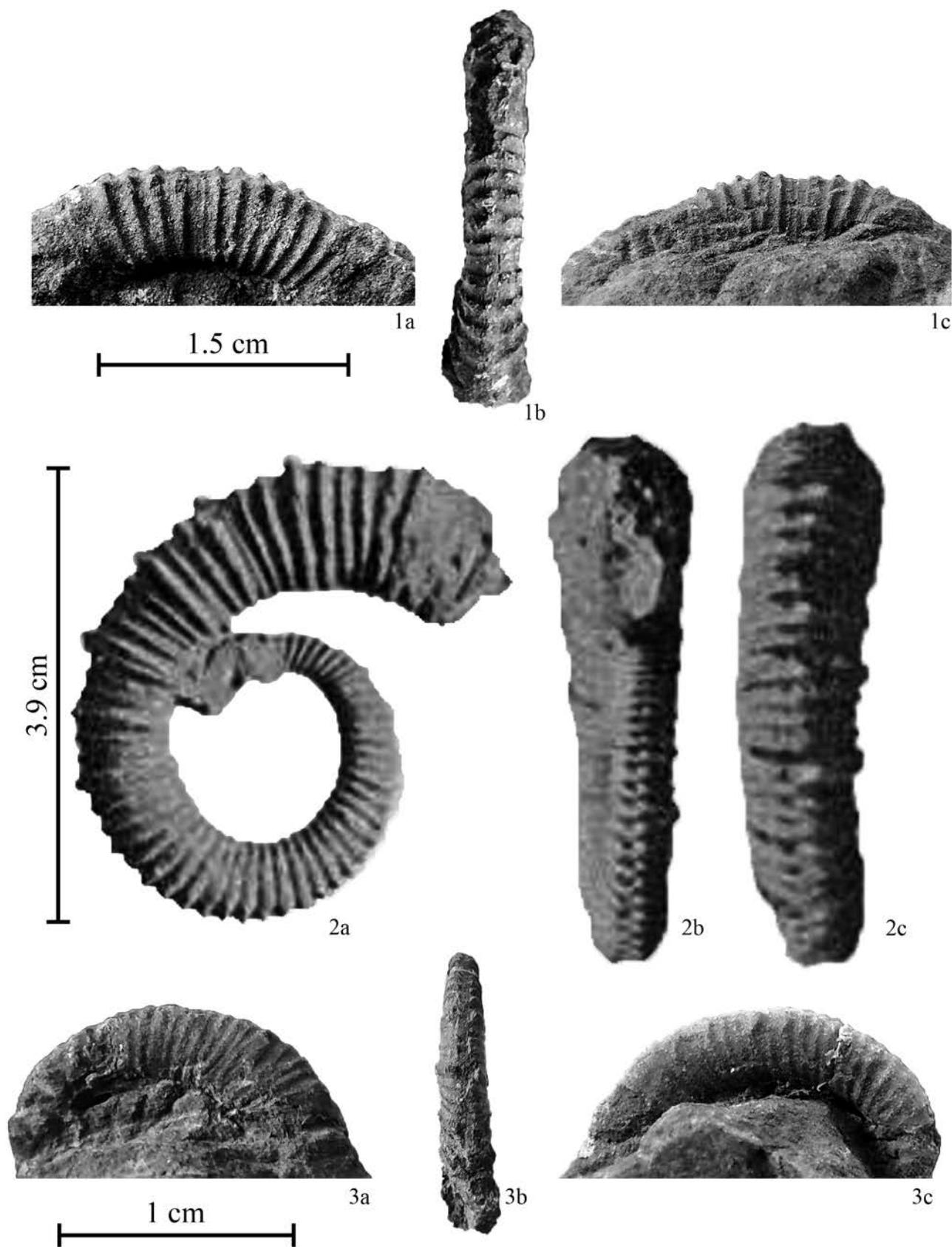
**Plate V – V. tábla**

Plate VI – VI. tábla



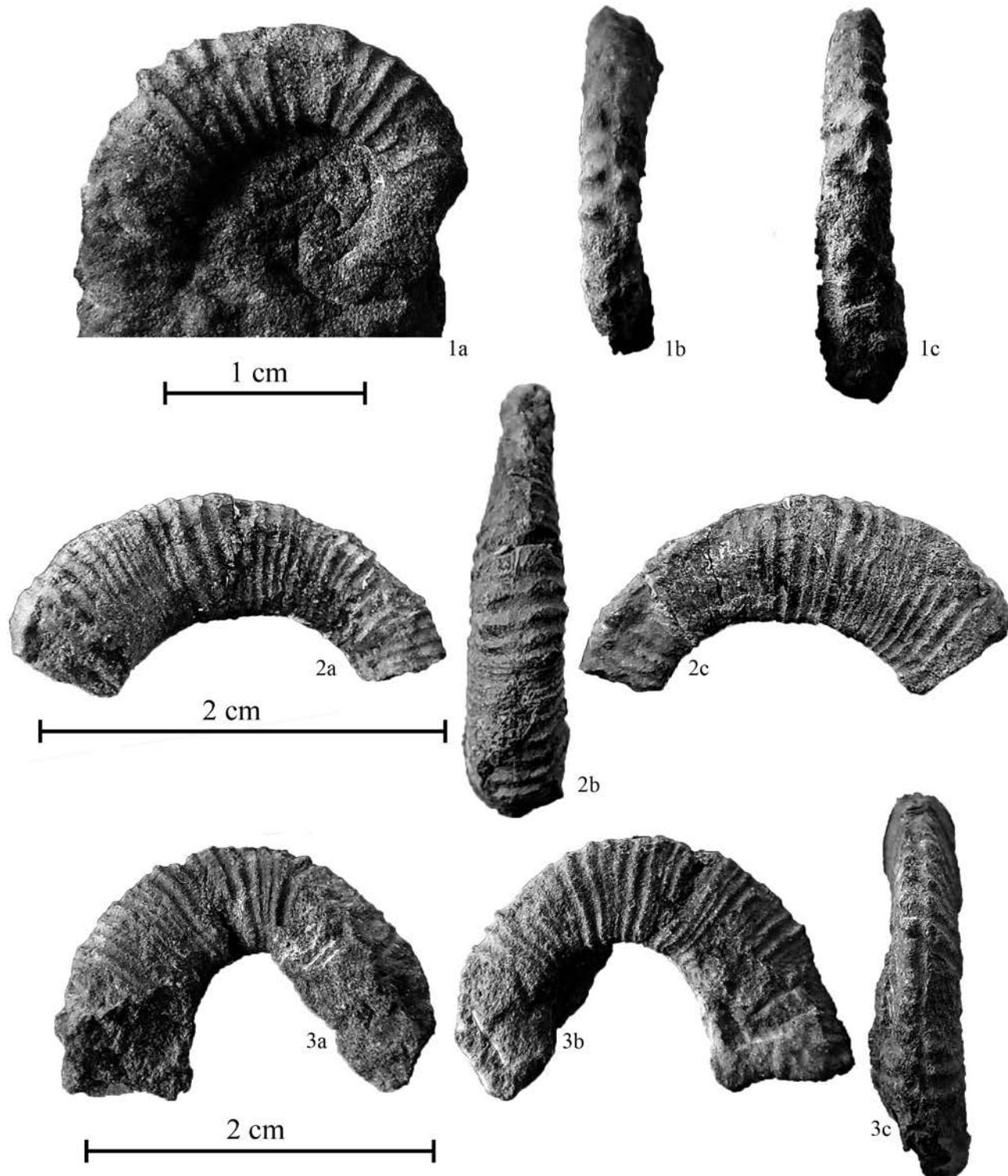
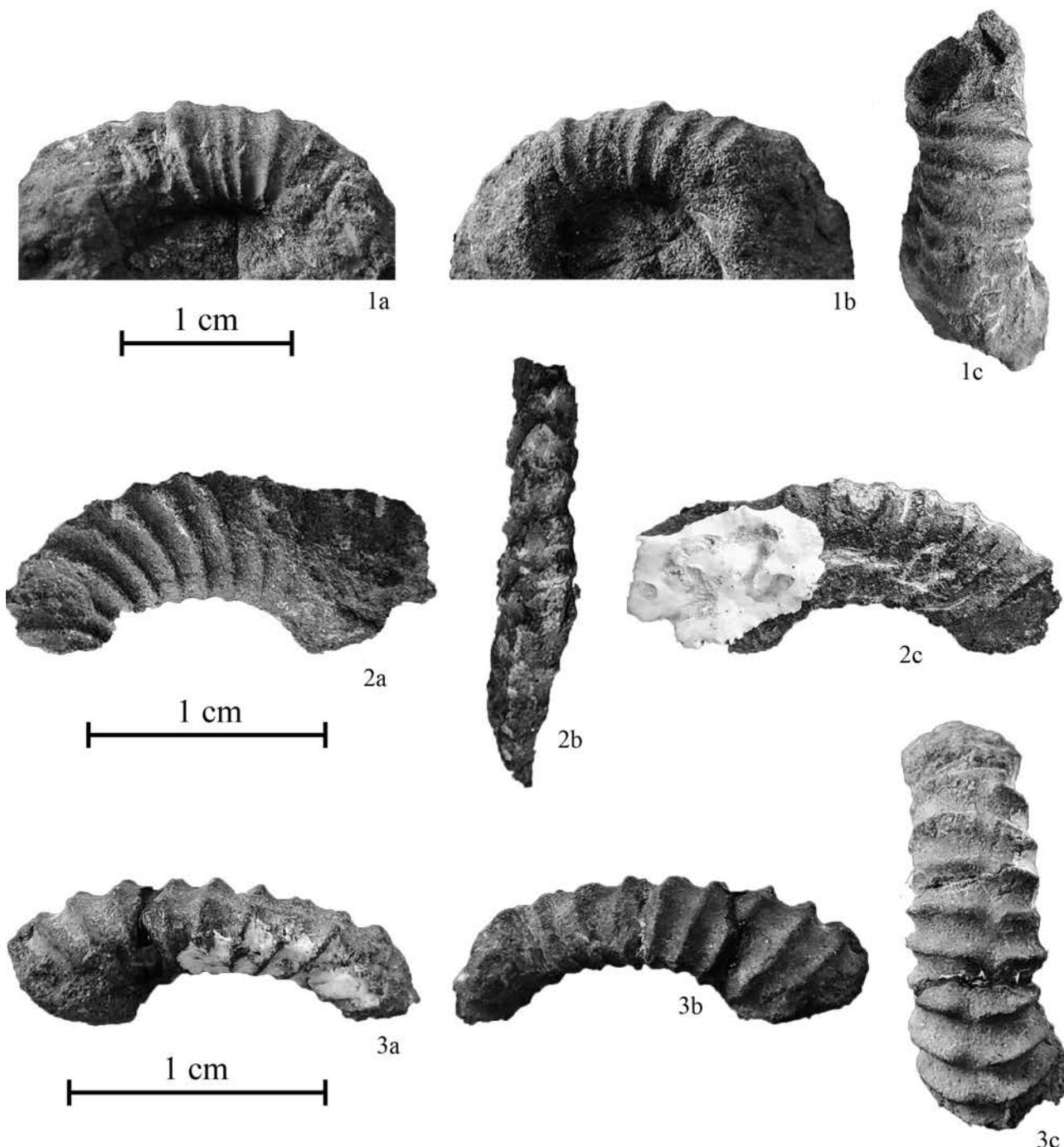
**Plate VII – VII. tábla**

Plate VIII – VIII. tábla



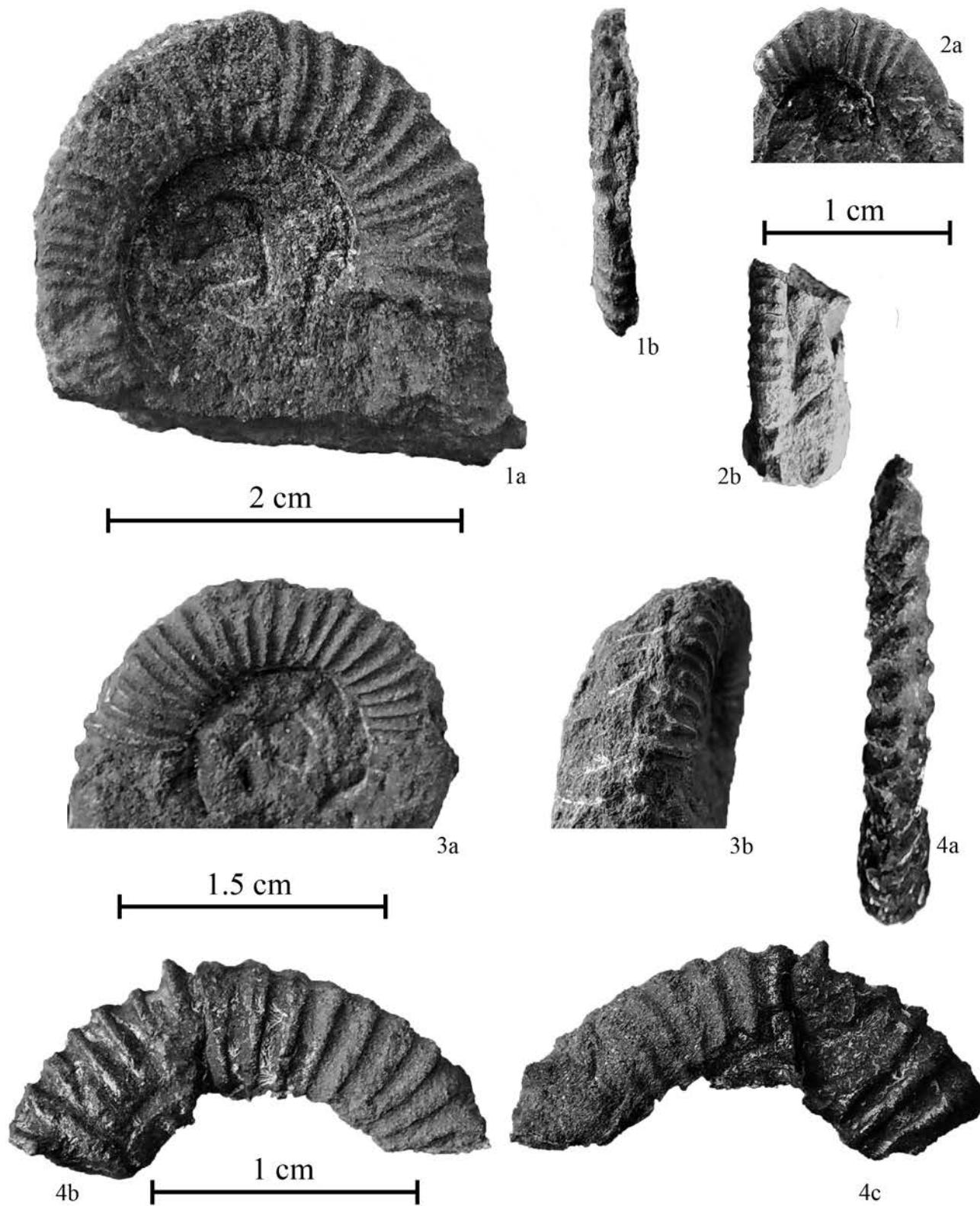
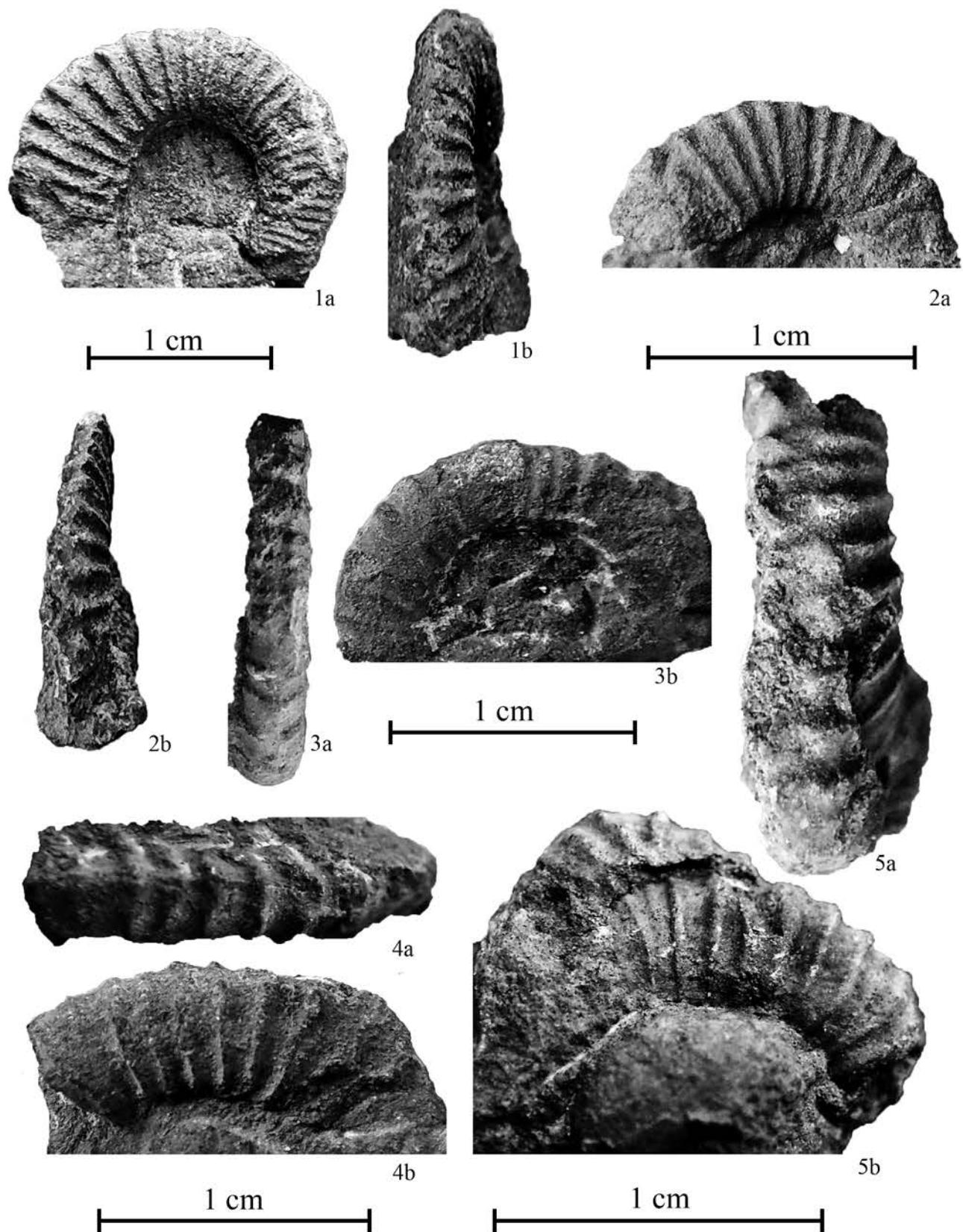
**Plate IX – IX. tábla**

Plate X – X. tábla



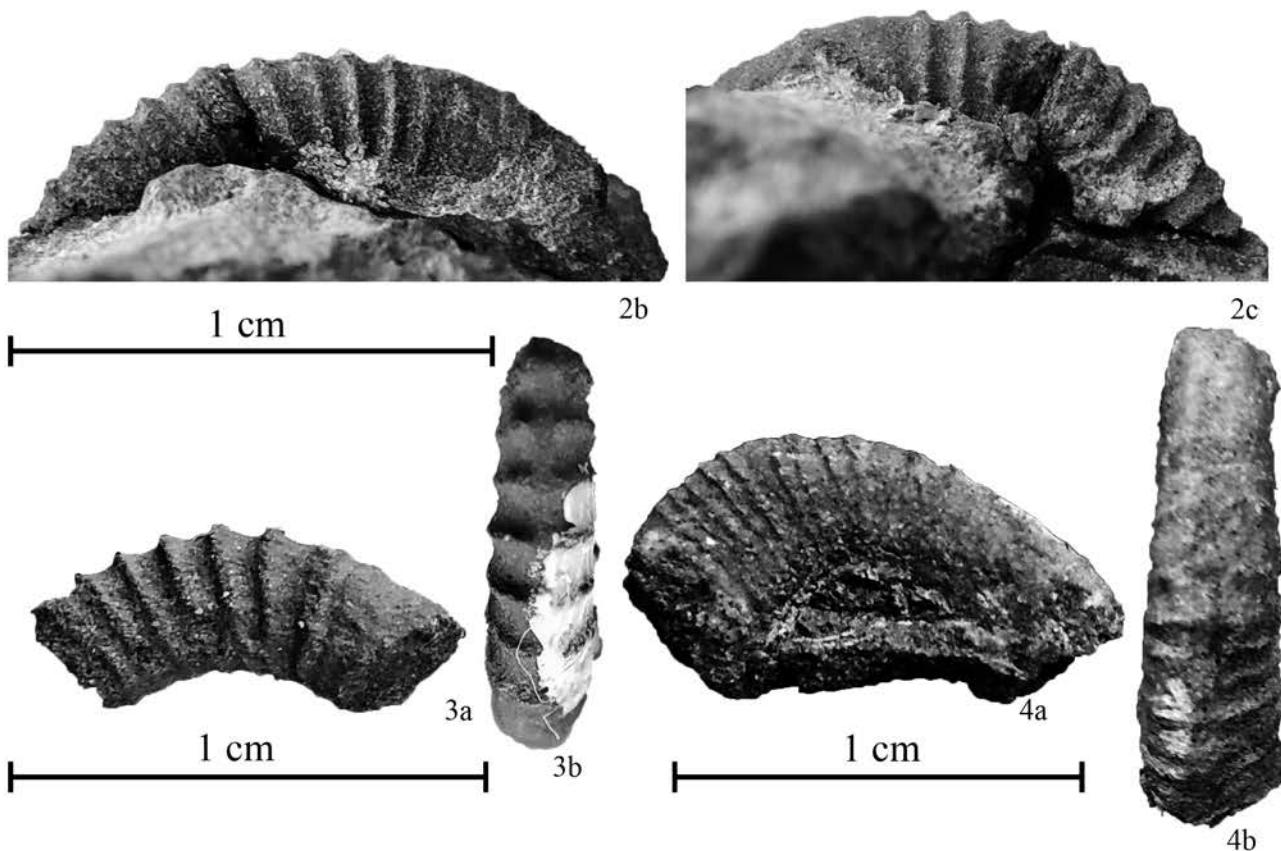
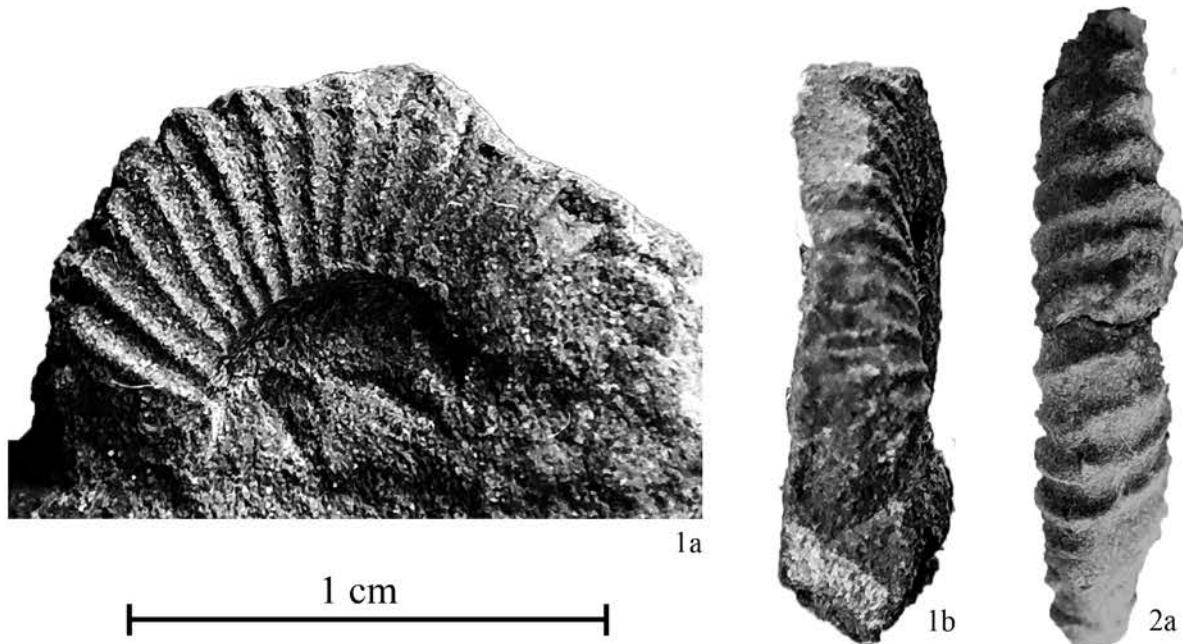
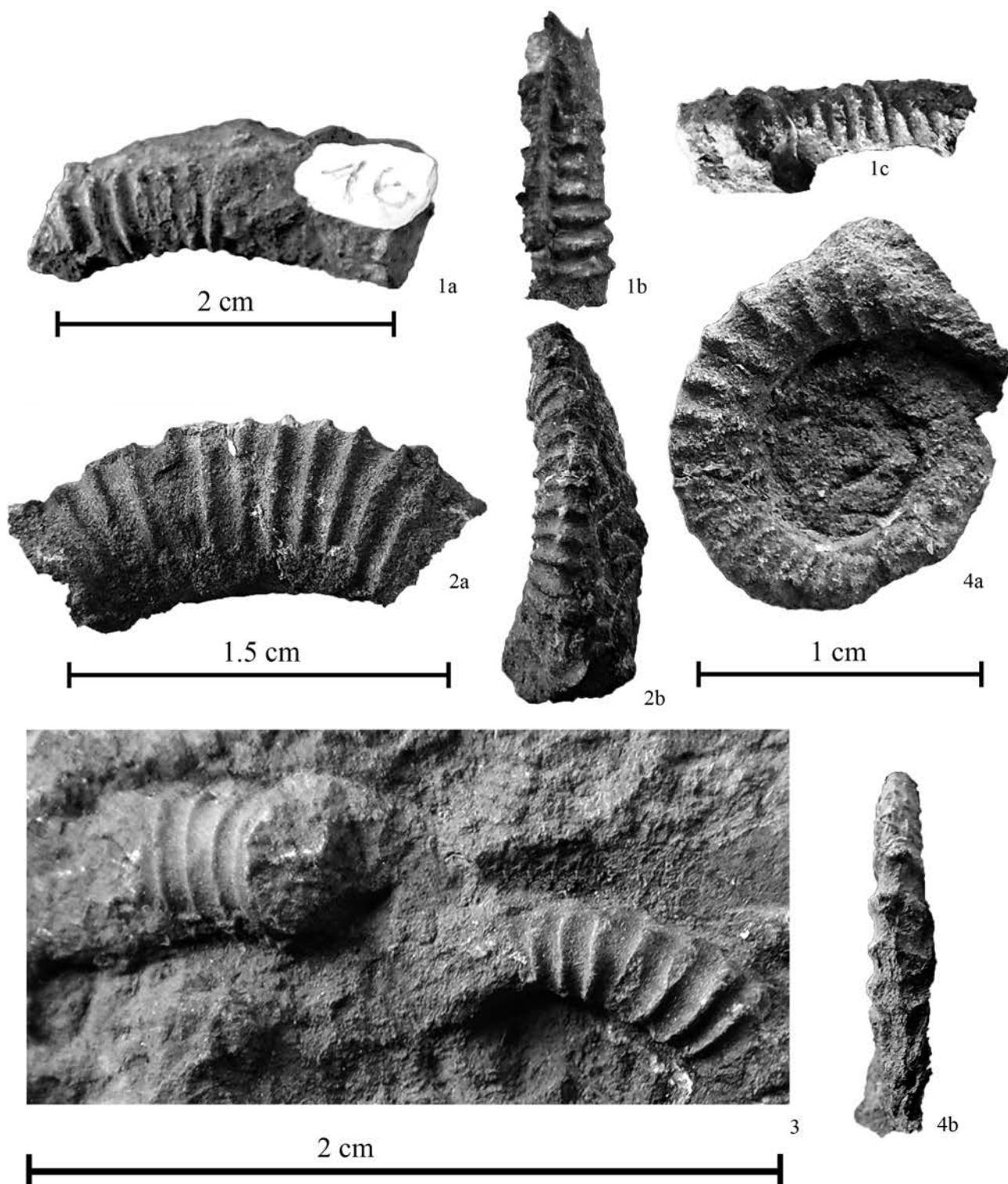
**Plate XI – XI. tábla**

Plate XII – XII. tábla



## Galácz András és Vörös Attila tisztelete a rendszertanban

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### Tribute to András Galácz and Attila Vörös in taxonomy

#### Abstract

In this short paper I list the species names that were named in honour of András GALÁCZ and Attila VÖRÖS, Hungarian geologists and paleontologists by their colleagues, friends and students. In addition to the sources of taxa, a few type specimens are re-illustrated.

I thank Alfréd DULAI, Vasily MITTA, Attila ŐSI, János SZABÓ and István SZENTE for their professional help.

#### Összefoglalás

Jelen közlemény célja, hogy közreadja azoknak a fajneveknek a listáját, melyekkel őslénytani tanulmányok szerzői – kollégák, barátok, tanítványok, tisztelők – elismerésüket fejezték ki a két idén jubiláló geológus és paleontológus, GALÁCZ András és VÖRÖS Attila tudományos munkássága iránt. A taxonok forrásai mellett néhány típuspéldány is újrafelkészítésre kerül.

Az adatgyűjtéshez és az illusztrációkhoz nyújtott segítségért a következő kutatókat illeti köszönet: DULAI Alfréd, Vaszilij MITTA, ŐSI Attila, SZABÓ János, SZENTE István.

#### Galácz Andrásról elnevezett fosszilis fajok

*Eucycloidea galaczi* SZABÓ, 1983  
bajoci (középső jura) csiga (Magyarország) (SZABÓ 1983)

*Limea (Pseudolimea) galaczi* SZENTE, 1995 (*I. tábla, 2. ábra*)  
bath (középső jura) kagyló (Magyarország) (SZENTE 1995)

*Metophioceras galaczi* GÉCZY & MEISTER, 2007  
sinemuri (kora jura) ammonitesz (Magyarország) (GÉCZY & MEISTER 2007)

*Villania galaczi* GÉCZY, 1998  
pliensbachi (kora jura) ammonitesz (Magyarország) (GÉCZY 1998)

*Geczcyceras galaczi* KOVÁCS, 2009 (*I. tábla, 5–6. ábra*)  
toarci (kora jura) ammonitesz (Magyarország) (KOVÁCS 2009)

*Cadomites galaczi* PAVIA, 2002  
késő bajoci – kora bath (középső jura) ammonitesz (Olaszország) (PAVIA 2002)

*Sokurella galaczi* MITTA, 2004 (*I. tábla, 3–4. ábra*)  
bath (középső jura) ammonitesz (Oroszország) (MITTA 2004)  
*Dichotomosella galaczi* VÖRÖS, 1995  
bath (középső jura) brachiopoda (Magyarország) (VÖRÖS 1995)

*Bakonydraco galaczi* ŐSI, WEISHAMPEL & JIANU, 2005  
santoni (késő kréta) azhdarchid repülő hüllő (Magyarország) (ŐSI et al. 2005)

Megjegyzés: GÉCZY Barnabás és Christian MEISTER baki sinemuri–pliensbachi ammoniteszmonografiájában (GÉCZY & MEISTER 2007) a 9–10. ábrán szerepel egy „*Catriceras galaczi*” fajnév (Horizon à Catriceras galaczi) – ez

azonban elírás. A név az ugyanebben a tanulmányban bevezetett, kora pliensbachi *Catriceras pannonicum* nov. sp. MEISTER & GÉCZY faj- és horizontnév helyett áll tévesen (lásd GÉCZY & MEISTER 2007: 195, 214, figs 27–29; MEISTER 2010).

*Pyrgotrochus vorosi* SZABÓ, CONTI, MONARI & WENDT, 2019  
(*I. tábla, 1. ábra*)  
oxfordi (késő jura) csiga (Olaszország) (SZABÓ et al. 2019)

*Alebusirynchia vorosi* BAEZA-CARRATALÁ, DULAI & SANDOVAL, 2018 (*I. tábla, 7. ábra*)  
sinemuri (kora jura) brachiopoda (Spanyolország) (BAEZA-CARRATALÁ et al. 2018)

### Vörös Attiláról elnevezett fosszilis fajok

*Tetracapnuchosphaera ? voeroesi* KOZUR, MOIX & OZSVÁRT, 2009  
karni (késő triász) radiolaria (Törökország) (KOZUR et al. 2009)

*Mochlodon vorosi* ŐSI, PRONDVAI, BUTLER & WEISHAMPEL, 2012 (*I. tábla, 8. ábra*)  
santoni (késő kréta) rhabdodontida dinosaurusz (Magyarország) (ŐSI et al. 2012)

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## I. tábla – Plate I

**Fig. 1.** *Pyrgotrochus vorosi* SZABÓ, CONTI, MONARI & WENDT, 2019. Holotype/holotípus, length/hossz: 24,2 mm (2×). SZABÓ et al. (2019, fig. 9/H)

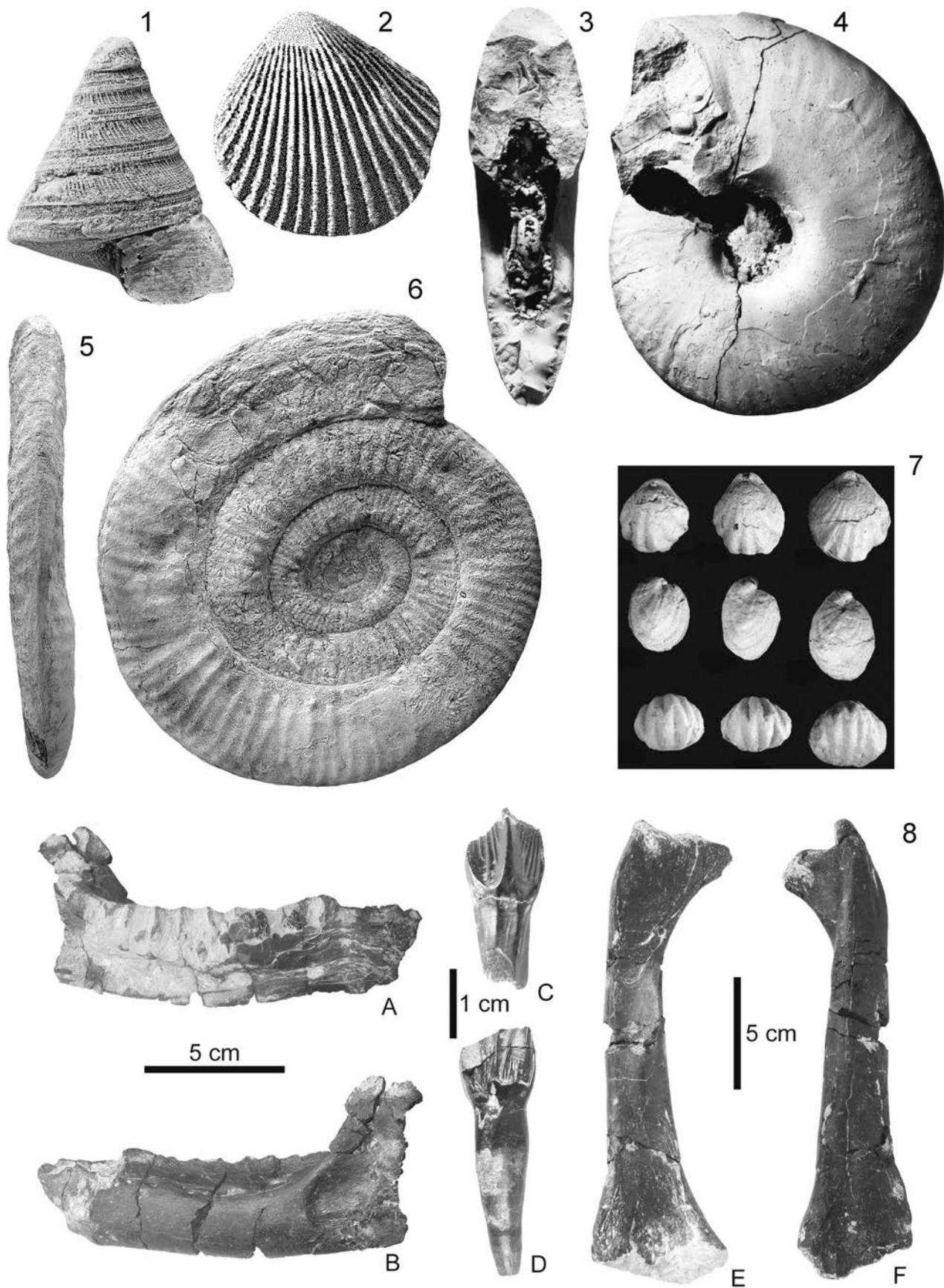
**Fig. 2.** *Limea (Pseudolimea) galaczi* SZENTE, 1995. Holotype/holotípus, length/hossz: 20,5 mm (2×). SZENTE (1995, pl. 3, fig. 8).

**Figs 3–4.** *Sokurella galaczi* MITTA, 2004. Holotype/holotípus, D 72 mm (1×). MITTA (2004, pl. 3, fig. 1)

**Figs 5–6.** *Geczyceras galaczi* KOVÁCS, 2009. Holotype/holotípus, D 194 mm (0,5×). Kovács (2009, fig. 8)

**Fig. 7.** *Alebusirhynchia vorosi* BAEZA-CARRATALÁ, DULAI & SANDOVAL, 2018. Length of specimens/példányok hossza: 7–9 mm (1,6×). KORSÓS & BARINA (2018, fig. 20)

**Fig. 8.** *Mochlodon vorosi* ŐSI, PRONDVAI, BUTLER & WEISHAMPEL, 2012. Holotype/holotípus. ŐSI (2012, fig. 61)

**I. tábla – Plate I**

## Hírek, ismertetések

Összeállította: PIROS Olga

### Események, rendezvények

#### Beszámoló a 27. Magyar Őslénytani Vándorgyűlésről

A Magyarhoni Földtani Társulat Őslénytani és Rétegtani Szakosztállyának legfontosabb éves rendezvénye a Magyar Őslénytani Vándorgyűlés, melyet idén 2024. május 31. és június 1. között, immár 27. alkalommal rendeztünk meg. A terepbejárással egybekötött konferenciának ezúttal az Eger határában álló Mátyus Udvarház adott otthont.

Az idei találkozónkra 60 fő regisztrált, a bejelentett és megtartott előadások száma 29, a bemutatott poszterek száma négy volt. A jelenlévők között köszöntöttük az idén 80. születésnapjukat ünneplő GALÁCZ András és VÖRÖS Attila professzor urakat, sokunk kedves kollégáit, sőt mestereit.

Számos korábbi alkalmazásban hasonlóan most is volt vendégelőadónk Peter ALSEN, a Dániai és Grönlandi Geológiai Szolgálat munkatársa személyében. Vendégünk *The limestones in the Cretaceous of Greenland – and their associated fossils* címmel tartott előadást, és egyúttal a grönlandi terepi tapasztalatairól is beszámolt.

A csütörtöki és a szombati délelőtti szekciókban elhangzott előadások – a szokásnak megfelelően – a legkülönbözőbb korok és ősmaradványcsoportok kapcsán született legújabb tudományos eredményekről számoltak be. Az olykor nagyon speciális témaikkal foglalkozó előadások között volt két általános érdeklődésre is számot tartó, a szokásos 15 percnél hosszabb prezentáció is: MAGYAR Imre *Százéves a Paratethys, Európa neogén beltengere* címmel, míg GALÁCZ András *Mi (vagy ki) a Homo sapiens típusa?* címmel tartott előadást.

A program feszített volt, a jó hangulatú, demokratikus léggörben egymást követték az előadások. Az előadók között professzorok és hallgatók egyaránt voltak.

A szakosztály vezetősége az idén is díjazta a fiatal kollégák által bemutatott legjobb előadásokat és posztereiket. Az immár hagyományos versenyben az alábbi kollégák kapták a Földtani Társulat és a Magyar Dinoszaurusz Alapítvány által felajánlott könyvdíjakat:

GÓGÖS Gergő (hallgatói kategória), SEGESDI Martin (PhD kategória), Koczó Levente (poszter kategória).

A vándorgyűlés második napja ez alkalommal is egy terepbejárás volt, melynek során a szervezők jelentős mértékben támaszkodtak DÁVID Árpád kollégának helyismeretére. A bérelt autóbuszszal megtett út megállói a következők voltak: Nagyvisnyó, Lukács-hegy (alsó miocén); Nagyvisnyó, I. sz. vasúti bevágás (felső karbon); Nagyvisnyó, Mihalovits-kőfejtő (felső perm); Eger-Felnémet, mészkőbánya (középső triász). Az utóbbi helyen szakmai vita alakult ki, mert az újonnan előkerült, nagy méretű megalodontid kagylók alapján a kőzet korát többen késő triásznak vélték. Az utolsónak tervezett megállót – az egri volt Wind-féle téglagyár agyaggödrének meglátogatását – elmosta a közelgő zivatar. A kirándulás résztvevői a heves esőt a Szépasszony-völgyében, SIKE Tamás pincészetében vészelték át a szakavatott borász és kitűnő borai társaságában; senki nem ázott el.

Idén, a társulat valamennyi szakosztállyának vezetőségéhez hasonlóan, az Őslénytani és Földtani Szakosztály vezetősége is meg-

újult. A jelenlévők titkos szavazás útján a következő három évre megválasztották elnöknek PIROS Olgát, titkárnak MOHR Emőkét, vezetőségi tagoknak FŐZY Istvánt, BOSNAKOFF Mariannt, BOTFALVAI Gábort, ÖSI Attilát és SZIVES Ottilit, póttagnak pedig KARÁDI-KAPILLER Viktort és GALÁCZ Andrásrát.

A rendezvény programját, az előadások kivonatát és a kirándlásvezető tartalmazó társulati kiadványunk az idén is megjelent, miként az elmúlt 26 évben minden alkalommal. Az ISBN számmal ellátott, 2024-es „sárga füzet” 56 oldal terjedelmű.

FŐZY István

#### Geoprogram kisiskolásoknak

(Balatonfüredi, 2024. június 19.)

A Magyarhoni Földtani Társulat Észak- és Közép-dunántúli Területi Szervezete balatonfüredi általános iskolásoknak nyújtott ismeretterjesztő programot a város külterületén található Száka-hegyi Geológiai Bemutatóhelyen. Az egykor kőfejtőben feltárolt a középső triász Füredi Mészkő Formáció körülbelül 237 millió éve, sekélytengeri lagúnakörnyezetben lerakódott, látványos rétegsora. A BUDAI Tamás exelnök által szerkesztett ismertető táblákkal és a térség talán legszebb térráncképződményével rendelkező bemutató ösvényen a Radnóti Miklós Általános Iskola négy osztálya – mintegy 120 harmadikos és negyedikes tanuló – interaktív geosétán és foglalkozáson ismerkedett testközelből a földtani alapfogalmakkal.

A program napján 36 fokos hőség tombolt, ami nem ideális egy ilyen rendezvényhez, ám ezzel a helyzettel is megbirkóztunk. Bár szakmai körökben nem kedvelik a feltárasban terpeszkedő bokrokat – mi ez esetben nagyon megbecsültük őket. A kőfejtő rövid bejárását követően a „delelő bokrok” tenyérnyi árnyékába leültetett gyerekserg meghallgatott egy kifejezetten erre a térségre adaptált „geomesét”, amely egy kis gyík és Kamon, a mesélő kő barátságáról szól. A kisdiákoknak mesébe ágyazott, de valódi helyszínen (Lóczy-barlang és környéke) játszódó, az ő szintjükön megfogalmazott földtani folyamatokat (pl. diogenезis, karsztosodás, borsókő képződése stb.) kellett felismerniük. Ezt követően kis csoportokban a geosétához és a meséhez kapcsolódó geotötök töltötték ki a gyerekek. Mind a szervezőknek, mind a tanároknak és a diákoknak közös sikerelmény volt, hogy szinte az összes csoport maximális pontszámot ért el!





(Fotó: CSERNY Tibor)

A rendezvény kiváló lehetőséget teremtett a szakmai és földtani értekekre nyitott jövő generáció nevelésére, amit társulatunk a színvonalas tudományos kutatómunka mellett szintén küldetésének tekint.

*CSERNY Tibor, SÁRDY Julianna*

## Könyvismertetés

### Vörös Attila: The Middle Jurassic brachiopods of the Transdanubian Range, Hungary. – *Geologica Hungarica, series Palaeontologica* 61, 1–116.

VÖRÖS Attila akadémikus a hazai őslénytan kiemelkedő személyisége és a mezozoos (elsősorban jura) brachiopodák nemzetközileg elismert kutatója. Munkája során már eddig is számos monografiával örvendeztette meg az őslénytan iránt érdeklődőket, részben a triász ammoniteszek, részben a jura brachiopodák feldolgozásának eredményeképpen. Ez utóbbi területen a hazai jura fauna általános áttekintése (1997), a pliensbachi fauna részletes feldolgozása (2009), majd a Pygopidae-monográfia (2022) után

most a Dunántúli-középhegység középső jura faunája került sorra. Bár ez az anyag mind példányszámban, mind fajszámban jelentősen elmarad a liász faunáktól (1282 példány, 16 nemzetseg, 28 faj), a maga nemében így is kiemelkedő, hiszen ez a Mediterrán térség leggazdagabb ismert középső jura együttese. A vizsgált anyag nagy része a Földtani Intézet rendszeres és részletes földtani térképezései során került elő a Bakonyban az 1960-as és 1970-es években. Az ezekhez kapcsolódó árkolasok és részletes, réteg szerinti gyűjtések nagy mennyiségű brachiopoda-példányt tártak fel. Noszky Jenő, VIGH Gusztáv és a szerző kiegészítő gyűjtései is jelentősen hozzájárultak a vizsgált fauna megismeréséhez.

Korábban csak előzetes faunalisták és dokumentációk jelentek meg a hazai középső jura brachiopoda-faunáról (VÖRÖS 1993, 1997, 2001; VÖRÖS & DULAI 2007), a részletes rendszertani feldolgozást a most publikált *Geologica Hungarica*-kötet tartalmazza. A monográfia bevezető része a Dunántúli-középhegység középső jura rétegtanát, majd a brachiopodákat tartalmazó szelvényeket és a gyűjtési pontokat mutatja be az egyes fajok előfordulási adataival. A fauna általános ismertetését, idő- és térbeli változását, a vázlatos őskörnyezeti és részletes ősföldrajzi elemzéseket számos informatív ábra illusztrálja. A monográfia legnagyobb terjedelmű része a brachiopoda-fauna részletes rendszertani leírását adja, a bemutatott fajok közül egy, a nemzetek közül négy taxon új a tudományra nézve. A leírásokat 57 ábra kíséri, amelyek főleg a brachiopodák belső morfológiáját ábrázolják a sorozatsziszolatos vizsgálatok alapján. A kötet végén öt fotótábla mutatja be a leírt brachiopoda-fajok különböző morfológiáját.

Az angol nyelvű monográfia szakmailag magas színvonallú, nagyon sok lényeges új eredményt tartalmaz, így a kötet szakmai lektoraként jó szívvé ajánlom az őslénytan és a jura időszak iránt érdeklődő szakemberek, egyetemi hallgatók és ősmaradványgyűjtők számára.

A kötet kereskedelmi forgalomba nem kerül. Aki szeretne hozzájutni, forduljon PALOTÁS Klárához ([klara.palotas@sztfh.hu](mailto:klara.palotas@sztfh.hu)).

*DULAI Alfréd  
Magyar Természettudományi Múzeum*

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