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András Galácz Jubilee Volume

Professor András GALÁCZ – a bibliography of his works from 1967 to 2014

Miklós KÁZMÉR[1]

This bibliography has been compiled upon the occasion of retirement of András Galácz, Professor of Palaeontology at Eötvös University, Budapest, at the age of seventy from... From what? He continues teaching, regularly publishes on his favourite topics of Jurassic ammonites, extinction, evolution and history of palaeontology, organizes postgraduate education and serves on university and academic committees. And there are many more fossils in how drawers and ideas in his mind waiting to be invited to light.

The bibliography reflects his manifold interests in various aspects of fossil life, his commitment to publish his results, commitment for careful documentation of fossils before using them for far-reaching conclusions in biostratigraphy, palaeoecology, evolution, palaeobiogeography, and plate tectonics.

His passion for teaching and for outreach to the wide general public yielded six textbooks and two popular science volumes. Ninety scientific publications: monographs and papers belong to his lasting legacy.

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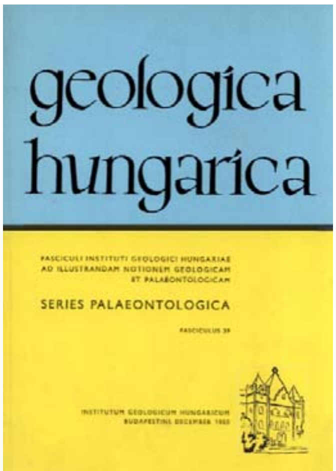

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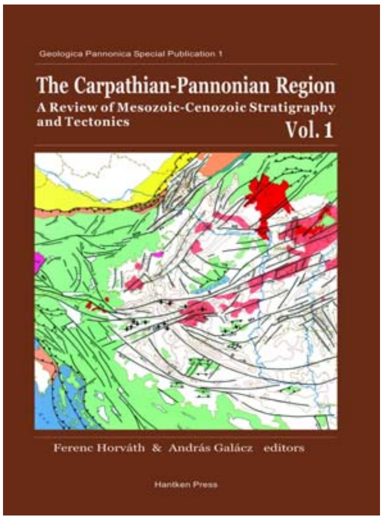

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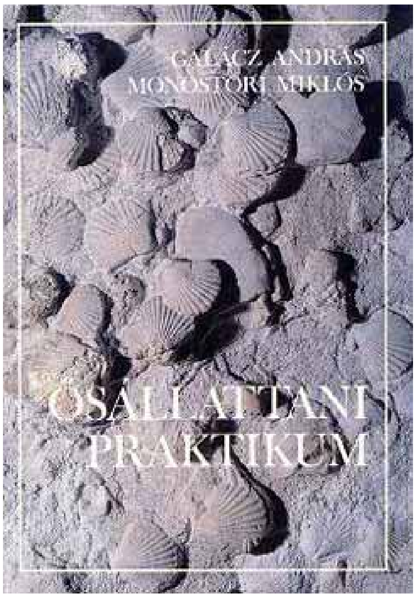

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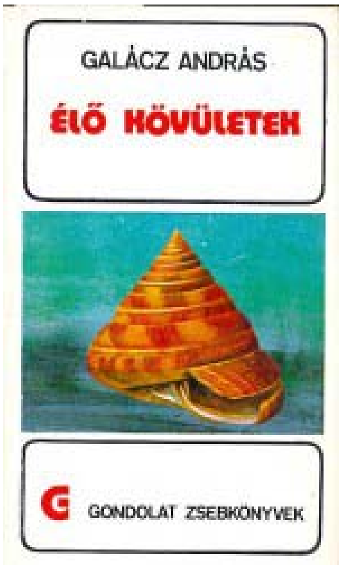

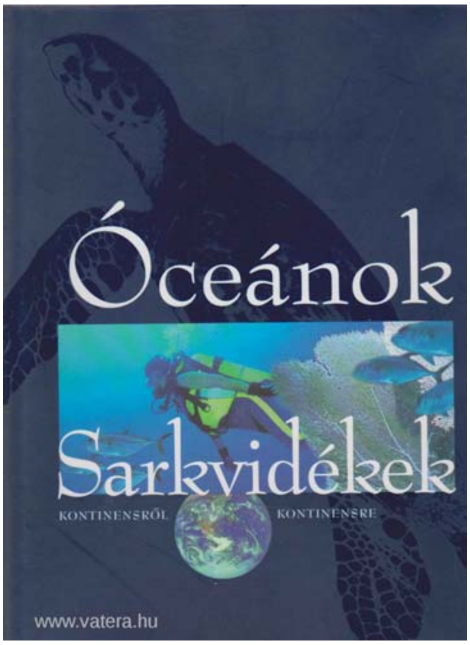

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András Galácz Jubilee Volume

András Galácz – 70
Joint episodes from two interconnected careers

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This volume, prepared as a tribute to the 70th birthday of András Galácz, should contain an essay of personal attitude dedicated to our celebrated colleague – so told me the Editor.

I felt immodest enough to believe myself appropriate to this mission, because, from the 70 years of András, I spent almost 50 in rather close connection with him. We have been class-mates, room-mates, friends, co-workers and good colleagues for long years until today. In the university years, others called us *twins*, and in fact, even at those times, our careers were strongly interconnected; we formed a *dyad*, as the jargon of the human behaviour science would say. Yet, I am not able to write a proper biography of András Galácz, instead, I want to pick up a few episodes from our interwoven careers, throwing some light to certain elements of the personality of my old friend.

In the summer of 1965, as undergraduate students of Eötvös University, we spent a few weeks in the field in the western Mecsek Mountains. Our field base was a vacant peasant house in the half-devastated village Gorica. Water and toilet outside; local food-supply restricted to milk from local cow; other food in the next village in a shop working twice a week. Our threesome group was led by Feri Székely, just graduated at a Soviet university, who reassured us that our situation was like heaven compared to the field circumstances what he experienced in Russia. We were still not fully satisfied but the cheerful character of Feri greatly amused us. Twenty years later we met him again quite surprisingly in a very far away place; but that’s another story. Our field task was to survey the ground-water table in the wider surrounding of Gorica. Measuring the water level in wells in the villages and estimating the output of springs at the headings of all side-valleys of the region of at least fifty square kilometres required dozens of kilometres daily walking. But, even after a so tiresome day, András forced me to go again to the field. “Just here, along the Gorica brook, they found a nice outcrop of Middle Triassic limestone bed surface full of bivalves – I heard from colleagues working for the Geological Survey” told me András. With some reluctance I joined him to visit the locality at the sunset twilight – and it was worth going there. That was the first strong sign of his obsession with fossils, and he started to infect me.

In the next year I got a new amount of infection from András. He convinced me to visit Barnabás Géczy, the senior lecturer at the Department of Palaeontology, and apply together for an independent research subject. Barna, our later master and mentor, was very happy and offered us the subject of Jurassic belemnoids[1]. From this time onwards we spent almost all our free time at the Department, continuously having our noses in the relevant palaeontological literature. András, better in English, translated the majority of the articles, while I undertook the German texts. At the same time, we took pleasure in the fascinating arrays of fossils at the collections of the Department: my infection went on and accomplished. Here we came across with the most curious belemnites from the Callovian of Villány; these rostra were heavily encrusted with fine grained but stiff calcareous sediment, as if they were in an extremely thick coat of breadcrumbs. Soon we became aware of the truth; András found the paper by Polish palaeontologists with the pioneering description of the stromatolites of Villány.[2]

Villány is the next point worth mentioning in our interconnected career. The Jurassic of Villány was the subject of my graduate thesis.[3] Quite naturally, András joined me for a few days to help in fieldwork (as I did the same in the case of his field work in the Bakony, in the Jurassic of Gyenespuszta[4]). In the summer of 1967 we, accompanied by Barnabás Géczy, travelled to Villány and found accommodation in a really poor peasant house near the vineyards. The conditions were similar to those we enjoyed few years earlier in Gorica but with two features to the worse: the landlady and her animals. The continuously flattering dog, the smell and grunting of pigs and the early morning crowing of the cock forced our master to leave Villány next day. We remained and tried to tolerate all this and the garrulous Aunt Janka. She was a widow, around sixty, with fleshy red nose, evoking the witch of tales. Living alone with her animals she was keen on talking with anyone. Putting aside our empathy we tried to spend as much time away from the house as we could. We took some longer field trips, for instance climbing up to the more than four hundred metres high Harsány Hill (Szársomlyó) without any strict scientific task or result. Another time András insisted on visiting the local swimming pool what he, as good swimmer, much enjoyed. After some hesitation I also preferred the cold water to Aunt Janka.

After graduation we both remained under the arms of Barnabás Géczy as junior scientists and room-mates at the Department of Palaeontology. András continued with the Middle Jurassic ammonoids[5] whereas I was charged with the Liassic brachiopods[6] of the Bakony. "Those were the days, my friend" – would I say with the contemporaneous pop song! Boundless enthusiasm and endless energy drove us to achieve more and more knowledge in our favourite fields. The fossils and the related literature were equally important to us and the work was hard, sometimes even painstaking in both fields.

In 1969, the world suddenly and unexpectedly opened for us. By good grace of fate (assisted by Barnabás Géczy and our British colleague Nicol Morton), in April we took part in a great symposium on the British Jurassic.[7] A glimpse of the "western life" in London! And the symposium and the field trips! The high level lectures, the personal contact with the leading Jurassic workers and the whole scientific atmosphere revealed the never seen perspectives of our research and determined our attitude for the future. Then, just in September of the same year, the high international society of the Jurassic arrived to Hungary for the Mediterranean Jurassic Colloquium.[8] We could meet again with Nicol Morton, John Callomon, Hugh Torrens, Derek Ager and many other celebrities. And, what is even more, on the field trip to the Bakony we were fortunate to hear the debates and opinions of Anthony Hallam, Daniel Bernoulli, Hugh Jenkyns and others on the most intriguing problems of the Jurassic sedimentary processes. We eagerly hung on every word....

The next months saw the most productive period of our joint career. Stimulated by the impressions, experiences and knowledge acquired at the international symposia, we decided to establish an up-to-date Jurassic sedimentary model of the Bakony. It was an attractive challenge to demolish the narrow-minded idea of the shallow marine Jurassic archipelago in the Bakony, so fashionable among many Hungarian geologists of that time[9]. We grasped a right moment, because the sedimentary evolution of the Mediterranean Jurassic was a hot topic in those years all over Europe. Seamounts, ferromanganese crusts, neptunian dykes, allodapic limestones, slumps and megabreccias swirled in our interconnected brains. That was a true intellectual joint venture. Sparkles of ideas and insights fluttered between us and slowly crystallized into revelations and formed promising elements of the new model. Walking to and fro in our room, I tried to formulate thoughts and sentences; András, sitting and smoking endlessly, pruned the thoughts or suggested better alternatives, corrected the sentences and wrote down the results. A model cannot stand without informative figures. András possessed the ability, what I always admired, to depict the idea what he had in mind. Finally the paper was born and, regrettably with two years delay, it appeared in the Földtani Közlöny[10]. It was written in Hungarian; still, it became one of our best cited, seminal papers. We often wondered, what impact this paper had if it would have been published in English in an international journal.

The first bifurcation of our joint careers commenced when I was offered a regular job in the Hungarian Natural History Museum, and András stayed at the Department of Palaeontology of Eötvös University, and further suffered the financial uncertainty: his job and salary depended on contracts month-by-month. But our connection, even if not so close than before, was continuous.

In the 1980's we took ample opportunity to visit the key localities of the Mediterranean Jurassic all across Italy. We took three or four study trips, one month each, mostly by András's big old Polski Fiat. Occasionally, Frank Horváth and Andrea Mindszenty were our companions in these voyages what we informally called geological entertainments. The story always started in Rome, where we had to spend some days to obtain our stipends in the very bureaucratic Foreign Ministry, what would not be possible without the help of our mentor, Bruno d'Argenio. The accommodation was in the marvellous Palazzo Falconieri, Via Giulia 1, in the inner city, where the Accademia Ungherese was housed.

When we first arrived at the Eternal City and, after a long and frustrating navigation, reached Via Giulia 1, and tried to enter our room, we bumped into the previous resident just leaving the compartment. Feri Székely was that person, who became a renowned hydrogeologist in the meantime and whom we did not see for twenty years after our adventures in Gorica.

Rome! Treasury of cultural heritage and miracles... and the timeless atmosphere with the scent of the Antiquity and the smell of rotten vegetables and fish of the morning market at the same time… András was fan of spending all the day and late evening in the squares and passages swarmed with tourists and the people of Rome, often without care of eating and drinking. I was desperate sometimes.

Then, after embarking the car in Naples, slowly we arrived at Sicily, at our much awaited place of geological wonders. Here, by courtesy of our colleagues Raimondo Catalano and Piero Di Stefano, we got comfortable accommodation and possibility to work ourselves in the field. But what a bizarre field! On a day we drove up to Bellolampo, a southward facing hillside near Palermo. After locating the outcrop where we wanted to measure the section and collect fossils, we looked around. A gentle but very broad valley dominated the landscape, with no trace of water or any life except the dried grass and some spiny bushes. No trees, no shadow. The single remarkable point of this half-deserted, barren scenery was a sizeable building, looking as a stable or cowshed, in a few hundred metres distance. We worked hard and with success. The sun rose to the zenith and the heatt became almost unbearable by lunch-time. András suggested going down and eating our poor field-lunch in the shadow of the curious building. With some anxiety and fear from potentially hiding dogs we proceeded there. The building seemed quite abandoned, with open windows but closed entrance. A shocking scene received us when we looked inside: several cadavers of cows lay on the floor, completely dried but still with swollen bellies. How and why this astonishing tragedy might happen?... No trace of fire… But before solving the riddle, the uneasy smell and a warning array of flies forced us to go quickly back to the sunny hillside for having the food. Other days of our Sicilian field-work were also harsh and physically proving. But even these adventures were not fruitless; they resulted in joint papers in Italian journals.[11]

On the next voyage of us we aimed at central Italy, at the Umbrian Jurassic localities. We were released by the Italian colleagues in the famous historical town of Gubbio, where they booked a very modest room for us in the outskirts. That place seemed a good field base for visiting many important Jurassic sections and localities of the Umbrian nappes. However, the weather crossed out the plans. The week we spent there was constantly rainy. The room was rather uncomfortable, with a matrimonial bed covered by a single large blanket. In the chilly nights we pulled our shared but indivisible blanket to and fro – but that wasn't matter, we were twins. The best quality of our house was its vicinity to the entry of the Bottaccione Gorge, renowned for its iridium-spotted K/T boundary layer. And what is more, at the entrance of the gorge, András discovered a small and cheap ristorante, in a rather shaky building. We regularly had our evening meal in this very familiar place, full with local people rather drinking than eating. In the absence of menu card, the corpulent but kind elderly landlady, whom András entitled as Mamma Bottaccione, nicely enumerated the daily dishes. The list was very short but included an unexpected item: roasted rabbit. That became the favourite of András, and I felt nostalgia for my childhood when rabbit was almost the only meat what we had rarely at home. For a few days we hoped to access the mountainous terrains but the weather kept on raining. Finally we decided to visit a few nearby historical towns as Urbino, Assisi, and eventually Firenze, on the way back to Rome. The atmosphere of the fascinating old cities was enjoyable even in rainfall, not to speak about the interiors of many churches with connected convents and museums full of masterpieces by Italian artists. I liked very much Raffaello and his followers, but András constantly tried to convince me that the trecento masters formed the summit of painting. Finally I accepted the greatness of Giotto and we arrived at a compromise around Fra Angelico Mantegna and Botticelli. For me it was a remaining impression to see András standing in front of a masterpiece, paralyzed by admiration.

I have to skip many further joint adventures of us and to mention sadly that our careers, though with frequent connecting links, started to deviate in the 1990's. It is true that our first great joint success in the topic of the Bakony Jurassic had a revival in the form of a highly cited international paper in 1998.[12] But then, different positions, different jobs, different scientific tasks and the decrease of our stamina by the obvious process of ageing, all worked against the formerly close connection and partnership. We met regularly on the occasions of the annual assemblies of the Hungarian palaeontologists where we were again room-mates; it reminded the good old days, but that was not the same, yet.

In the last decade I reached the highest degree of honour what a geologist in Hungary can, being elected to the members of the Hungarian Academy of Sciences. Success usually initiates jealousy in others. Although I never abused my position, in a somewhat paranoid way I started to be afraid that even my best colleagues and even my former “twin” slowly alienated from me. However, my suspicion and bad feeling incredibly vanished at once in this May. We were again room-mates with András at the annual meeting of palaeontologists in Győr. An unexpected, serious malady attacked me in the night. The first aid in the local hospital solved the acute crisis but I was obligated to visit my doctor in Budapest, next morning. Due to my physical state, the travel by mass transport posed a bitter problem to me. András, who continuously tried to soothe my shaken psyche, immediately offered to carry me to Budapest by his car although the next day was the excursion day of the meeting. My old friend was willing to miss the awaited field trip and spend a day with tiresome driving across half the country to help me.

This experience restored my weakening faith in human goodwill. But what is even more important, it proved that my old friend, András Galácz remained as good man as he was and that the ties connecting our lives remained as strong as before.

Notes (for the benefit of the younger scientist generation, born after the much of this story was over – by the editor)

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Some memories of András Galácz and of Hungary

Hugh TORRENS[1]

My first memories of András come from when I participated in the centenary celebrations for the Hungarian Geological Institute in 1969. An excursion went to Villány (FÜLÖP et al., 1969), where a famous, but anomalous, ammonite fauna had been recorded (TILL, 1910–11; LÓCZY, 1915), including the villainous genus *Villania,* which had had to have a whole new subfamily created for it by W.J. ARKELL in the Ammonite Treatise of 1957 (ARKELL et al., 1957). I will never forget how the various international groups, which included András, went to work at this famous locality. We, the English contingent, led by the much missed John Callomon (1928- 2010 - see obituary notice by Ian MILLS and Hugh TORRENS, 2010) soon realised that not all the ammonites could have come from the famous Cephalopod bed – nr. 5 – here, because, unconformably below it, lay beds which also yielded fossils, including ammonites, and these revealed different methods of geological diagnosis. The first to be found were nautiloids, which French experts said only confirmed the existing, but fallacious, date of these beds, as Middle Jurassic. Brachiopods were next found, which Derek Victor AGER (1923-1993), British brachiopodologist and Hungarophile, realised had to be Pliensbachian (Lower Jurassic). Then we found a single ammonite. This soon emerged as a specimen of *Apoderoceras*. It proved the presence of the Taylori Subzone, of the Jamesoni Zone, of the Pliensbachian (AGER and CALLOMON 1971, and TORRENS 2002b). This proved that *Villania* was a normal Pliensbachian ammonite, whose horizon has been misunderstood, Barna GÉCZY later produced a fine monograph of these and named new species as *Villania callomoni* and *Villania galaczi* (see GÉCZY, 1998) to triangulate this story.

My next involvements with András came after I had taken up another interest in the history of science. I had come across the strange silence surrounding the Austro-Hungarian naturalist and traveller Robert Townson (1762-1827) during the early years of the Napoleonic Was (see TORRENS, 1999) and I determined to try and uncover his complicated life and work. This culminated in a well remembered visit to Debrecen in 1997, when Peter Rózsa put on a fine conference to discuss Townson's life and work (RÓZSA, 2002). The extraordinary range of Townson's work then took a large and international team to evaluate it. Townson, a true polymath, was one of the 50 entries I did for the new Oxford Dictionary of Natural Biography (TORRENS, 2004). He had been one of the least well served in the original Victorian DNB (CARLYLE, 1899), where his origin and fate had remained quite unknown, and it could merely report that he had written a series of significant books in the 1790s, whilst based in Shropshire. My research on him had started in the 1970s, and led me on a fascinating trail, with which András helped. Townson proved to be the illegitimate London-born son of a merchant, who was soon orphaned. He then led a peripatetic life, which saw him first settling in Shropshire, and then studying in Edinburgh, Goettingen, and Vienna (whence he travelled to Hungary). He then applied, unsuccessfully, for naturalist's positions in Canada, Sierra Leone, and India, before deciding to emigrate to Australia in 1806. This work led me to accumulate a large research collection, of books in many languages, photos, slides, photocopies and copies of his several books. I offered all this to Shropshire Archives late in 2005, which accepted it, as a gift, early in 2006. Sadly, by April, they had decided it was all of mere „academic interest". So, in September 2006, I had to find a new home for it all, at Shrewsbury Museum (where what little of Townson's own natural history collections had survived). Then, in October 2012, following the loss of yet another natural history curator post there, I was warned that this museum had now put all this material „aside, prior to disposal", so it had to be rescued yet again. The results of this is that an even larger accumulation now resides in my most unsuitable garage. All this seems a sad way to treat the results of much dedicated research, and so I wonder if I might now find a Hungarian home for all my Townson archives. This would be a way of paying proper tribute to my friendship with, and gratitude to, András Galácz?

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Additional Middle to Upper Triassic ostracod faunas from the boreholes of Transdanubian Central Range (Hungary)

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(with 2 figures, 2 tables and 3 plates)

Relatively diverse ostracod faunas from Middle to Upper Triassic (Ladinian to Rhaetian) beds of the Transdanubian Central Range in Hungary are described and figured. The benthic faunas from five boreholes (Bat-2, Bút-2, Bht-6, Met-1 and Rzt-1) consist of 25 taxa belonging to 17 genera. Two species are new: *Ceratobairdia crassispinosa* n. sp. and *Dicerobairdia latispinosa* n. sp.. Based on ecological characteristics the studied benthic ostracod assemblages different normal marine deep to shallow sublittoral palaeoenvironments were recognized in this region of the Tethys Ocean. Moreover, the Carnian salinity crisis caused by a global lowstand could be proven.

Introduction

The knowledge about the Middle to Upper Triassic ostracod faunas from Hungary is sporadic and incomplete. First descriptions and illustrations of Triassic marine ostracods from Hungary were published by MÉHES (1911). From the Transdanubian Central Range, further studies have been made by BUNZA & KOZUR (1971), KOZUR (1970a; 1971abc; 1972b) and MONOSTORI (1991; 1995) about Anisian, by KOZUR (2004) and MONOSTORI & TÓTH (2013) about Ladinian, by SZÉLES (1965), BUNZA & KOZUR (1971), KOZUR (1971c; 1972a), KRISTAN-TOLLMANN et al. (1991) and MONOSTORI (1994) about Carnian and by KOZUR & ORAVECZ-SCHEFFER (1972) about Rhaetian ostracods. Moreover, from Upper Ladinian to Lower Carnian beds of the Mecsek Mts freshwater ostracods were described by MONOSTORI (1996). The main aim of the present work is to give a detailed modern systematic description of Middle to Late Triassic ostracods from five boreholes located in Transdanubian Central Range, W-Hungary. Moreover, a brief palaeoecological interpretation of the faunal composition is planned to complement the knowledge about the depositional environment of the studied Triassic formations. Documentation of this fauna can provide new data about the composition of ostracod assemblages in different environments of Triassic Tethys Ocean.

Geological setting and stratigraphy

The studied five boreholes (Barnag-2 (Bat-2), Balatonhenye-6 (Bht-6), Bakonykúti-2 (Bút-2), Mencshely-1 (Met-1) and Rezi (Rzt-1)) are situated in the Transdanubian Central Range, western Hungary (Fig. 1). The lithostratigraphical sections of the studied boreholes are shown in Fig. 2.

The studied sequence in the borehole Bút-2 consists of thick grey tuff beds alternating with thin crinoidal-brachiopodal marl and limestone layers, from where the samples were obtained, belonging to the Ladinian Buchenstein Formation. It is underlain by the Megyehegy Dolomite. The tuffaceous beds contain carbonized plant fragments in great abundance.

The borehole Met-1 penetrated Upper Ladinian to Carnian succession bearing the studied microfauna in thickness 440 m starting with pelagic thinly bedded grey cherty limestone of Füred Formation (HAAS & BUDAI 2004). This is overlain by thick grey marly-calcareous marly series of Veszprém Marl with rounded limestone intraclasts and mollusc fragments. This succession is strongly tectonized and its the upper part, there are nodular limestone beds of Nosztor Limestone Member in 20-25 m thickness with mollusc, Phyllopoda, brachiopod and crinoid fragments (CSILLAG & BUDAI 1987, unpublished report, Archives of Geological and Geophysical Institute of Hungary).

The studied Triassic sequences in boreholes Bat-2 and Bht-6 started with unbedded brownish grey crinoid, brachiopod and mollusc bearing calcareous marl and marly limestone layers of Csicsó Marl Member (Veszprém Marl Formation). Its upper part is strongly pyritized and dolomitized in borehole Bht-6. Moreover, under the overlaying Sándorhegy Formation there is a 1.5 m thick crinoidal limestone bed and a marl layer with bioclasts, oncoids and limestone intraclasts (BUDAI et al. 1999). The lower part of the Sándorhegy Formation, namely Pécsely Member is represented by bioturbated, intraclastic microcrystallized limestone, calcareous marl, dolomarl and dolomite series in the borehole Bht-6 and by thinly bedded grey marly limestone layers intercalated with laminited bituminous limestone beds with slumps and fish scales in the borehole Bat-2. In the upper part of the succession (Barnag Member) there are thin marl, calcareous marl and limestone beds with oncoids, ichnofossils, biogen fragments (brachipods and echinoderms) in lenticular bodies and mollusc bearing lumachella in different levels. The series of the Barnag Member in Bht-6 is very similar but thinner and underlaying with a dolomite body of Ederics Formation. The differences between the sequences of the studied boreholes can be explained by the palaeogeographical position. The layers of the borehole Bht-6 deposited proximal to the carbonate platform during the Carnian age. In both boreholes the Sándorhegy Formation is overlain by the Main Dolomite Formation (BUDAI et al. 1999).

Additional samples came from the Norian to Rhaetian Kössen Formation in Rzt-1. At Rezi the Kössen Formation consists of thinly bedded or laminited grey siltstone, marl, dolomarl, calcareous marl and clayey marl layers with mollusc lumachella in different levels. The Triassic succession is overlain by Pannonian strata (BUDAI 1987, unpublished report, Archives of Geological and Geophysical Institute of Hungary; BUDAI et al., 1999).

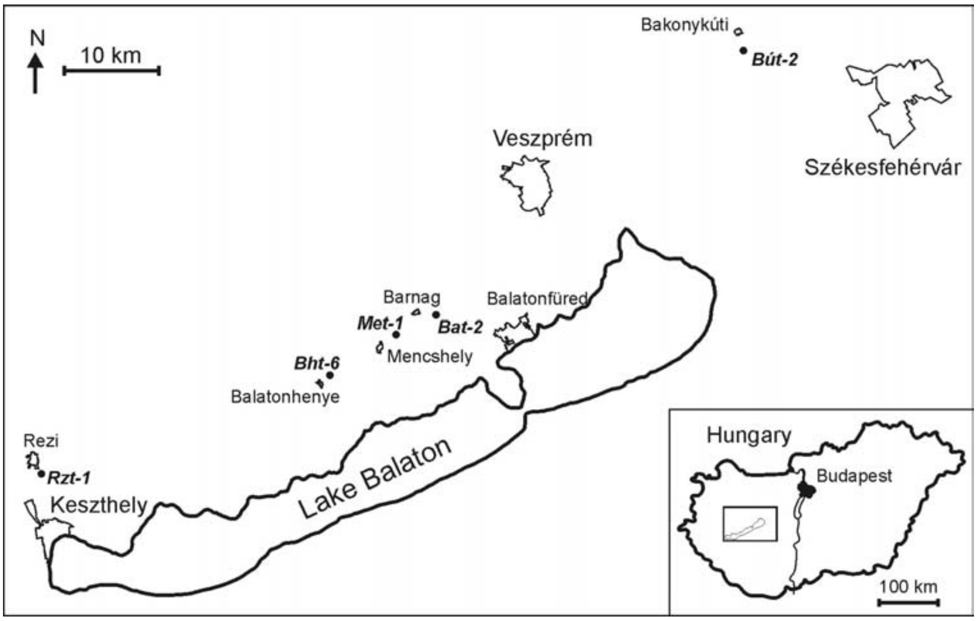

Fig. 1. Location of the studied boreholes in a simplified map of the Transdanubian Central Range, Hungary.

Material and methods

Seventy-six samples from five boreholes of the Transdanubian Central Range were studied for their ostracod content (Fig. 1). For each sample (n=8) from borehole Bút-2, about 200-300 g of air-dried silicified limestone was soaked in a dilute solution of chloridic and acetic acids to extract the silicified skeletal material.

For the microfaunal study of Triassic series in the boreholes Bat-2, Bht-6, Met-1 and Rzt-1, the samples were soaked in a dilute solution of hydrogen peroxide or treated by acetolysis following a protocol originally worked out by LETHIERS & CRASQUIN-SOLEAU (1988) with a slight modification to extract the carbonate skeletal microfauna. The palaeoecological interpretation is based on mainly the qualitative analyses and the semi-quantitative (percentage distribution) analyses of the specimens of the different taxa or groups. Unfortunately, in many samples there is very low, unrepresentative number of specimens.

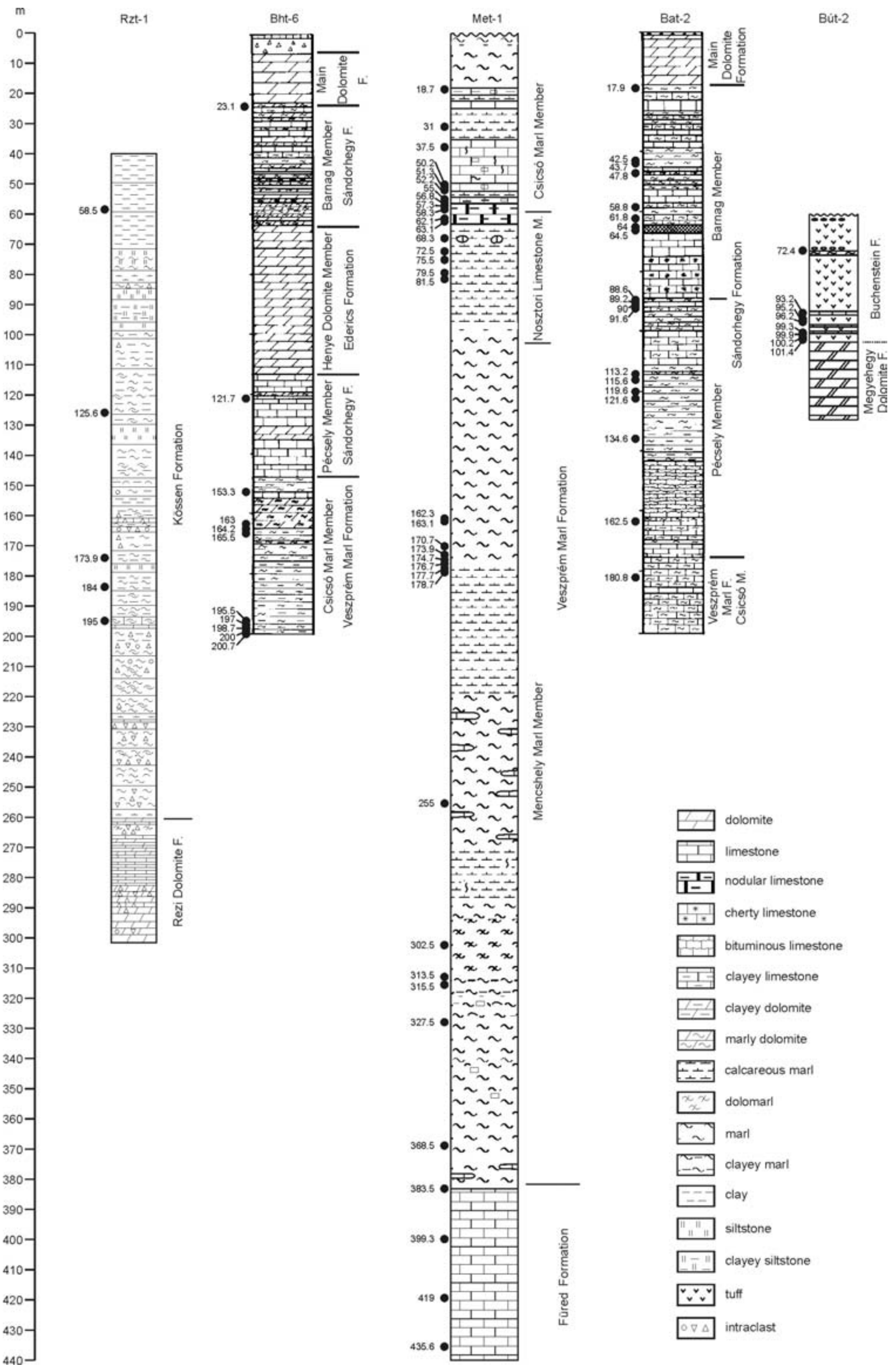

Fig. 2. Lithological logs of the studied boreholes representing Ladinian to Rhaetian sequences of the Transdanubian

Central Range (modified after BUDAI ET AL. 1999 and HAAS & BUDAI 2004).

Systematic palaeontology

Classification of the ostracods follows that of BECKER (2002), HORNE et al. (2002) and WHATLEY & BOOMER (2000). The specimens are deposited in the Department of Palaeontology of Eötvös University and in the Eötvös Museum of Natural History (Budapest, Hungary). Abbreviations: L=length, H=height and d=diameter. Number of specimens of the described taxa can be found in Appendix 1-2.

Class Ostracoda LATREILLE, 1802
Subclass Myodocopa SARS, 1866
Order Halocyprida DANA, 1853
Suborder Cladocopina SARS, 1866
Superfamily Cladocopoidea SARS, 1866
Family Polycopidae SARS, 1866
Subfamily Polycopinae SARS, 1866
Genus *Polycope* SARS, 1866
Type species: *Polycope orbicularis* SARS, 1866

Polycope aff. *aghdarbandensis* KRISTAN-TOLLMANN, 1991
Pl. 1, fig.1.

Remarks: The reticulation pattern is very similar to *Polycope aghdarbandensis* described by KRISTAN-TOLLMANN (1991, see pp. 197-198, pl. 1, figs 10-12) from Ladinian beds of NE-Iran but the cross-ribs are less developed than that of the holotype.
Dimensions: d=0.3 mm.
Occurrence: Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper).

Subclass Podocopa MÜLLER, 1894
Order Platycopida SARS, 1866
Suborder Platycopina SARS, 1866
Superfamily Cytherelloidea SARS, 1866
Family Cytherellidae SARS, 1866
Genus *Cytherella* JONES, 1849
Type-species: *Cytherina ovata* ROEMER, 1840

Cytherella cf. *persiensis* CRASQUIN-SOLEAU & TEHERANI, 1995
Pl. 1, figs 3-4.

Remarks: Similar to the *Cytherella persiensis* described by CRASQUIN-SOLEAU & TEHERANI (1995, see p. 32, pl. 1, figs 7-10) from Carnian beds of Zagros Mts. in Iran with valves flattening posterodorsally in ventral view, with slightly concave dorsal margin at the left valve in lateral view and with smooth valve surface. Dorsal and midventral overlap of the studied specimens is less distinct than that of the holotype.
Dimensions: L= 0.54-0.7 mm, H= 0.32-0.43 mm, L/H= 1.48-1.82
Occurrences: Balatonhenye, Barnag, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper).

Genus *Cytherelloidea* ALEXANDER, 1929
Type species: *Cythere (Cytherella) williamsoniana* JONES, 1849

Cytherelloidea unicostata BOLZ, 1970
Pl. 1, fig. 2.

1970 *Cytherelloidea unicostata* n. sp. – BOLZ, pp. 254-256, pl. 2, figs 31-33, text-fig. 6.
1973 *Cytherelloidea ? unicostata* BOLZ – KRISTAN-TOLLMANN, text-fig. 5/9.
?1992 *Cytherelloidea? unicostata* BOLZ, 1970 – DÉPÊCHE & CRASQUIN-SOLEAU, pl. 3, figs 1-2.

Remarks: Characteristic features are the valve surface ornamentation with a concentric ridge strongly developed anteriorly and posteriorly near the margins, a subcentral pit bounded by a longitudinal rib ventrally. The secondary ornamentation, the reticulation is indistinct because of the preservation potential of the carapace.
Dimensions: L=0.82 mm, H=0.44 mm, L/H=1.89.
Occurrences: Barnag, Rezi, Transdanubian Central Range (Hungary): Carnian to Rhaetian (Upper Triassic) (this paper); Northern Calcareous Alps, Zlambach beds (Austria): Norian to Raethian (Upper Triassic) (Bolz, 1970; KRISTAN-TOLLMANN, 1973).

Genus *Reubenella* SOHN, 1968
Type species: *Reubenella avnimelechi* SOHN, 1968

Reubenella picardi SOHN, 1968
Pl. 1, figs 5-6.

1968 *Reubenella picardi* n. sp. – SOHN, pp. 18-19, pl. 1, figs 27-32.
1983 *Reubenella picardi* Sohn – BASHA, pl. 2., figs 10-11.
1979 *Cytherelloidea picardi* (SOHN, 1968) – STYK, pp. 120-121, pl. 34, figs 5-7.
1982 *Cytherelloidea picardi* (SOHN, 1968) – STYK, pp. 18-19, pl. 1, figs 4-5.

Remarks: Characteristic features are the strong polygonal reticulation on the valve surface and the presence of the rounded subcentral pit. Stubby and more elongate forms co-occurred in the samples. This fact can be explained by sexual dimorphism.

Dimensions: L=0.5-1.68 mm, H=0.31-0.39mm, L/H=1.61-1.97.

Occurrences: Poland: Anisian (Middle Triassic) (STYK, 1979, 1982); Makhtesh Ramon (Israel): Anisian to Ladinian (Middle Triassic) (SOHN, 1968); Jordan Valley (Jordan): Ladinian (Middle Triassic) (BASHA, 1983); Bakonykúti, E-Bakony, Balatonhenye, Barnag, Balaton Highland (Hungary): Ladinian to Carnian (Middle Triassic) (this paper).

Order Podocopida MÜLLER, 1894
Suborder Metacopina SYLVESTER-BRADLEY, 1961
Superfamily Healdiacea HARLTON, 1933
Family Healdiidae HARLTON, 1933
Subfamily Hungarellinae KRISTAN-TOLLMANN, 1971
Genus *Hungarella* MÉHES, 1911
Type species: *Bairdia*? *problematica* MÉHES, 1911

Hungarella problematica (MÉHES, 1911)
Pl. 1, figs 7-10.

1911 *Bairdia*? *problematica* n. sp. – MÉHES, pp. 20-21, pl. 3, figs 14-18.
2013 *Hungarella problematica* (MÉHES, 1911) – MONOSTORI & TÓTH, p. 308, pl. 4, figs 14-17. cum. syn.

Remarks: Overlap of the left valve and the length/height of the carapace ratio very variable. The carapace is more or less laterally compressed posteriorly, the posterior spine absent.

Dimensions: L= 0.47-0.83 mm, H= 0.24-0.56 mm, L/H=1.33-1.5.

Occurrences: Dobrogea (Romania): Anisian (Middle Triassic) (CRASQUIN SOLEAU & GRADINARU 1996); Barnag, Balatonhenye, Felsőörs, Katrabóca II, Litér quarry, Mencshely, Nosztori Valley, Balaton Highland (Hungary): Anisian to Carnian (Middle to Upper Triassic) (MEHES 1911; KOZUR 1970A; MONOSTORI 1995; MONOSTORI & TOTH, 2013; SZELES 1965; this paper).

Suborder Bairdiocopina SARS, 1866
Superfamily Bairdiocypridoidea SHAVER, 1961
Family Bairdiocyprididae SHAVER, 1961
Genus *Bairdiacypris* BRADFIELD, 1935
Type species: *Bairdiacypris deloi* BRADFIELD, 1935

Bairdiacypris triassica KOZUR, 1971
Pl. 1, fig. 12.

1971c *Bairdiacypris triassica* n. sp. – KOZUR, pp. 5-6, fig. 2H-L.
2013 *Bairdiacypris triassica* KOZUR, 1971 – MONOSTORI & TÓTH, p. 313-314, pl. 3, figs 7-8, 10. cum. syn.

Dimensions: L=0.68 mm, H=0.38 mm, L/H=1.78.

Remarks: The specimen fit into the large variation (convexity of the dorsal margin) of the species detected by MONOSTORI & TÓTH (2013) from Ladinian beds of Litér quarry in Balaton Highland.

Occurrences: Katrabóca II, Felsőörs, Litér quarry, Mencshely, Nosztori Valley, Balaton Highland (Hungary): Ladinian to Carnian (Middle to Upper Triassic) (MÉHES 1911; KOZUR 1971c; MONOSTORI & TÓTH 2013; this paper).

Superfamily Bairdioidea SARS, 1887
Family Bairdiidae SARS, 1887
Genus *Acratia* DELO, 1930
Type species: *Acratia typica* DELO, 1930

Acratia goemoeryi KOZUR, 1970
Pl. 1, fig. 11.

1970a *Acratia goemoeryi* n. sp. – KOZUR, p. 391, pl. 3, figs 10-11.
2013 *Acratia goemoeryi* KOZUR, 1970 – MONOSTORI & TÓTH, pp. 308-309, pl. 4, figs 1-2. cum. syn.

Remarks: The specimens with stubby shape occur in the studied material which fit into the large variation of the species detected by CRASQUIN-SOLEAU & GRADINARU (1996) from Anisian beds of Romania.

Dimensions: L=0.57 mm, H=0.26 mm, L/H=2.24.

Occurrences: Greece, Austria, Slovakia, Hungary and Himalaya: Lower Triassic (KOZUR 1971c); South Tibet (China): Spathian to Anisian (Lower to Middle Triassic) (FOREL et al. 2011); Dobrogea (Romania): Anisian (Middle Triassic) (CRASQUIN-SOLEAU & GRADINARU 1996); Felsőörs, Litér quarry, Balaton Highland (Hungary): Anisian to Ladinian (Middle Triassic) (KOZUR 1970a; 1972b; MONOSTORI 1995; MONOSTORI & TOTH, 2013); Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper).

Genus *Bairdia* MCCOY, 1844
Type species: *Bairdia curta* MCCOY, 1844

Bairdia (Urobairdia) *angusta* (KOLLMANN, 1963)
Pl. 1, fig. 13.

1963 *Urobairdia angusta* n. sp. – KOLLMANN, p. 167, pl. 6, figs 1-4.

2013 *Bairdia (Urobairdia) angusta* KOLLMANN, 1963 – MONOSTORI & TOTH, p. 309, pl. 1, figs 10-12. cum. syn.

Remarks: The studied specimens have identical outline with the specimens illustrated on figs 1-2. by KOLLMANN (1963).

Dimensions: L= 0.68-0.88 mm, H= 0.38-0.51 mm, L/H= 1.75-1.76.

Occurrences: Felsőörs, Litér quarry, Mencshely, Nosztori Valley, Balaton Highland (Hungary): Anisian to Carnian (Middle to Upper Triassic) (MONOSTORI 1995; MONOSTORI & TOTH, 2013; SZELES 1965, this paper); Northern Calcareous Alps (Austria): Norian (Upper Triassic) (KOLLMANN 1963).

Bairdia cassiana (REUSS, 1868)

Pl. 1, fig. 14.

1868 *Cythere Cassiana* n. sp. – REUSS, p. 108.

2013 *Bairdia cassiana* (REUSS, 1868) – MONOSTORI & TÓTH, p. 310, pl. 2, figs 7-8. cum. syn.

Remarks: The studied specimens with more pointed posterior end fit into the large variation of the species recognized by MONOSTORI & TÓTH (2013).

Dimensions: L= 0.72-0.88 mm, H= 0.39-0.49 mm, L/H= 1.79-1.83.

Occurrences: Dobrogea (Romania): Anisian (Middle Triassic) (CRASQUIN-SOLEAU & GRADINARU 1996); Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper); Southern Alps, Cassian Beds (Italy): Carnian (Upper Triassic) (REUSS 1868; GÜMBEL 1869; URLICHS 1970; KRISTAN-TOLLMANN 1978); Barnag, Felsőörs, Katrabóca II, Litér quarry, Mencshely, Balaton Highland (Hungary): Anisian to Carnian (Middle to Upper Triassic) (MONOSTORI 1995; MONOSTORI & TOTH, 2013, this paper).

Bairdia jeancharlesi FOREL, 2011

Pl. 2, figs 1-2.

2011 *Bairdia jeancharlesi* FOREL n. sp. – FOREL & CRASQUIN, pp. 250-251, fig. 3I-L.

Remarks: The most characteristic features are the straight dorsal, posterodorsal and anterodorsal margin at the right valve. The small punctations cannot be detected on the valve surface probably due to the preservation potential.

Dimensions: L= 0.92-1.21 mm, H= 0.52-0.71 mm, L/H= 1.7-1.86.

Occurrences: S-Tibet: Smithian to Anisian (Lower to Middle Triassic) (FOREL & CRASQUIN, 2011); Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper); Mencshely, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper).

Bairdia ex gr. *margosulcata* BOLZ, 1971

Pl. 1, fig. 15.

Remarks: In the studied material one damaged carapace can be found with similar outline and anteriorly similar fine denticles projecting beyond the periphery to *Bairdia margosulcata* described by BOLZ (1971, see pl. 6, pp. 174-175, figs 77-81.) from Norian to Rhaetian beds of Northern Calcareous Alps.

Dimensions: L=1.15 mm, H=0.72 mm, L/H= 1.59.

Occurrence: Rezi, Balaton Highland (Hungary): Norian to Rhaetian (Upper Triassic) (this paper).

Genus *Ceratobairdia* SOHN, 1954

Type species: *Ceratobairdia dorsospinosa* SOHN, 1954

Ceratobairdia crassispinosa n. sp.

Pl. 2, fig. 3.

2013 *Ceratobairdia longispinosa* KOZUR, 1971 – MONOSTORI & TÓTH, p. 314, Pl. 3, fig. 1.

Derivatio nominis: After its two stout spines on the dorsal margin.

Holotype: Left valve, Eötvös Museum of Natural History, EMNH 2014.208.7.8, figured pl. 2, fig. 3.

Locus typicus: borehole Bút-2.

Stratum typicum: 72.4 m, Ladinian.

Material: 2 valves.

Diagnosis: A species of *Ceratobairdia* with two strong and symmetrically arranged anterodorsal and posterodorsal spines which are directed forwards and backwards with an angle of 45° and have a broad basis. The valves are lipped anteroventrally and posteroventrally.

Description: The shape of the left valve trapezoidal; anterior margin slightly pointed, dorsally slightly concave or straight and ventrally convex and lipped; dorsal margin slightly convex bearing two strong and symmetrically arranged anterodorsal and posterodorsal spines which are directed forwards and backwards with an angle of 45° and have a broad basis; posterior margin pointed, dorsally slightly concave or straight and ventrally convex and lipped; ventral margin slightly sinuous; valve surface smooth.

Dimensions: L= 0.65 mm, H= 0.34 mm, L/H= 1.9.

Comparison: Similar to *Ceratobairdia longispinosa* KOZUR, 1971, but at the type

specimen described by KOZUR (1971a, pp. 4-5, fig. 1e) the basal part of the spines is not broad. The shape of the valve and the spines at the specimen described by MONOSTORI & TÓTH (2013) as *Ceratobairdia longispinosa* coincides in all details with that of the holotype.
Occurrence: Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper).

Genus *Dicerobairdia* KOLLMANN, 1963
Type species: *Dicerobairdia bicornuta* KOLLMANN, 1963

Dicerobairdia latispinosa n. sp.
Pl. 2, fig. 6.

Derivatio nominis: After its short spines with broad basis on the dorsal margin.
Holotype: Carapace, Eötvös Museum of Natural History, EMNH 2014.207.1.4, figured pl. 2, fig. 6.
Locus typicus: borehole Bat-2.
Stratum typicum: 64 m, Carnian.
Material: 2 carapaces.
Diagnosis: A species of *Dicerobairdia* with a larger anterodorsal and a smaller posterodorsal spine which have very broad base. The valve is thickened at the margins. The valve surface is densely reticulated.
Description: The shape of the right valve trapezoidal; anterior margin dorsally slightly straight and passes with a break to its convex ventral part; dorsal margin slightly convex bearing a larger anterodorsal and a smaller posterodorsal spine which have very broad base; posterior margin pointed upward, its dorsal part slightly concave and its ventral part convex; ventral margin slightly sinuous; valve surface densely reticulated and the valve thickened at the margins.
Dimensions: L= 0.99 mm, H= 0.5 mm, L/H= 1.99.
Comparison: Similar to *Dicerobairdia bicornuta* KOLLMANN, 1963 (KOLLMANN, 1963, see pp. 182-183, pl. 1, figs 3-8; pl. 9, figs 1-2) from Rhaetian beds of Northern Calcareous Alps but Kollmann's specimen has more distinct spines situated less marginally than that of the holotype.
Occurrence: Barnag, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper).

Genus *Hiatobairdia* KRISTAN-TOLLMANN, 1970
Type species: *Hiatobairdia subsymmetrica* KRISTAN-TOLLMANN, 1970

Hiatobairdia subsymmetrica KRISTAN-TOLLMANN, 1970
Pl. 2, figs 4-5.

1970 *Hiatobairdia subsymmetrica* n. sp. – KRISTAN-TOLLMANN, pp. 286-287, pl. 35, figs 1-3.
1978 *Hiatobairdia subsymmetrica deformis* n. ssp. – KRISTAN-TOLLMANN, pp. 83-84, figs 1-7.
1980 *Hiatobairdia subsymmetrica* KRISTAN-TOLLMANN, 1970 – KRISTAN-TOLLMANN et. al., p. 179, pl. 9, figs 1-3.
1988 *Hiatobairdia subsymmetrica* KRISTAN-TOLLMANN – KRISTAN-TOLLMANN, text-fig. 6/2.

Remarks: Characteristic features are the subsymmetrical outline with slightly elongate angular ends and the valve surface ornamented with fine pits.
Dimensions: L= 0.85-1.05 mm, H= 0.42-0.58 mm, L/H= 1.8-2.1.
Occurrences: Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper); Barnag, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper); Dolomites, S-Tirol (Italy): Carnian (Upper Triassic) (Kristan-Tollmann, 1978); Zagros Mountains (Iran): Rhaetian (KRISTAN-TOLMANN et al. 1980; KRISTAN-TOLLMANN, 1988), Northern Calcareous Alps (Austria): Raethian (KRISTAN-TOLLMANN, 1970); Rezi, Balaton Highland (Hungary): Norian to Rhaetian (this paper).

Genus *Triebelina* BOLD, 1946
Type species: *Triebelina indopacifica* BOLD, 1946

Triebelina (*Mirabairdia*) *pernodosa* (KOLLMANN, 1963)
Pl. 2, figs 7-8.

1963 *Mirabairdia pernodosa* n. sp. – KOLLMANN, p. 177-178, pl. 1, figs 1-2, pl. 8, figs 1-6.
1971a *Triebelina* (*Mirabairdia*) *pernodosa illyrica* n. spp. – KOZUR, p. 17, fig. 1G.
1971a *Triebelina* (*Mirabairdia*) *balatonica* n. sp. – KOZUR, p. 15-16, figs 2I, 3C.
1971 *Mirabairdia pernodosa* KOLLM. – KRISTAN-TOLLMANN, text-fig 1/8.
1984 *Triebelina* (*Mirabairdia*) *pernodosa illyrica* KOZUR – SALAJ & JENDREJÁKOVÁ, pl. 2, figs 1-4.

Remarks: Characteristic features are the fine granular polygonal reticulation and the two or three nodes arranged in regular horizontal raw anterodorsally, anteroventrally, posterodorsally, and posteroventrally and in two vertical rows subcentrally on the valve surface. The nodes at the margins can be subdivided into smaller spines instead of the presence one distinct node. The position of the nodes can be changed on the valve surface. The posterior end bears denticles in most cases. Because of the large morphological variation of the ornamentation of *Triebelina*

(*Mirabairdia*) *pernodosa*, the justification of the subspecies *Triebelina* (*Mirabairdia*) *pernodosa illyrica* KOZUR, 1971 and of the species *Triebelina* (*Mirabairdia*) *balatonica* KOZUR, 1971 is questionable.
Dimensions: L= 0.84-1.13 mm, H= 0.43-0.69 mm, L/H= 1.56-2.13.
Occurrences: Western Carpathians (Slovakia): Anisian (Middle Triassic) (SALAJ & JENDREJAKOVA, 1983; KOZUR, 1971a); Balaton Highland (Hungary): Anisian (Middle Triassic) (KOZUR, 1971a); Dolomites, S-Tirol, Italy: Ladinian (Middle Triassic) (KRISTAN-TOLLMANN, 1971); Northern Calcareous Alps, Cassian beds (Austria): Ladinian (Middle Triassic) (KOLLMANN 1963); Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper).

Triebelina (*Nodobairdia*) *mammilata* (KOLLMANN, 1963)
Pl. 2, figs 9-10.

1963 *Nodobairdia mammilata* n. sp. – KOLLMANN, pp. 174-175, pl. 7, figs 6-15.
1973 ?*Nodobairdia mammilata* KOLLMANN – KRISTAN-TOLLMANN in KRISTAN-TOLLMANN & HAMEDANI, textfig. 12/9.
1994 *Nodobairdia mammilata* KOLLMANN, 1963 – MONOSTORI, pp. 316, 318, text-fig. 4/3. cum. syn.

Remarks: Characteristic features are the granular valve surface ornamentation and the presence of granular nodes at the anterodorsal, posterodorsal, anterior and posterior margins and the distinct ventral ridge which sometimes subdivided into nodes. There are additional small nodes on the valve surface.
Dimensions: L= 0.74-0.8 mm, H= 0.41-0.46 mm, L/H= 1.73-1.81.
Occurrences: Northern Calcareous Alps, Cassian beds (Austria): Ladinian (Middle Triassic) (KOLLMANN 1963); Dolomites, S-Tirol (Italy): Ladinian to Carnian (Middle to Upper Triassic) (KRISTAN-TOLLMANN 1971, 1978); Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper); Zsámbék, Gerecse (Hungary): Carnian (Upper Triassic) (KRISTAN-TOLLMANN et al. 1991); Barnag, Nosztori Valley, Rezi, Balaton Highland (Hungary): Carnian to Rhaetian (Upper Triassic) (MONOSTORI 1994, this paper); Zagros Mountains (Iran): Rhaetian (Upper Triassic) (KRISTAN-TOLLMANN et al. 1980; KRISTAN-TOLLMANN 1988).

Triebelina (*Ptychobairdia*) *kuepperi* (KOLLMANN, 1960)
Pl. 2, figs 12-13.

1960 *Ptychobairdia kuepperi* n. sp. – KOLLMANN, pp. 97-98, pl. 24, figs 1-5., pl. 25, figs 2-5, text-fig. 2ab.
1969 *Ptychobairdia kuepperi* KOLLMANN – KRISTAN-TOLLMANN, p. 84, pl. 1, figs 4-5.
1971 *Triebelina* (*Ptychobairdia*) *kuepperi* (KOLLMANN, 1960) – BOLZ, pp. 199-205, pl. 10, figs 141-154, pl. 11-14, figs 155-207, text-figs 27-29.
1971 *Ptychobairdia kuepperi* KOLLM. – KRISTAN-TOLLMANN, text-fig. 1/2.
1972b *Triebelina kuepperi* – KOZUR, pl. 2, fig. 1.

Remarks: The studied specimens with more or less developed dorsal and ventral ribs fit into the large variation of the species detected by BOLZ (1971) from Upper Triassic Zlambach beds of Northern Calcareous Alps.
Dimensions: L= 0.96-1.05 mm, H= 0.51-0.58 mm, L/H=1.8-1.86.
Occurrences: Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper); Barnag, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper); Northern Calcareous Alps (Austria): Norian to Raethian (KOLLMANN, 1960; BOLZ, 1971; KRISTAN-TOLLMANN, 1969, 1971).

Triebelina (*Ptychobairdia*) *circumvallata* (KRISTAN-TOLLMANN, 1969)
Pl. 2, fig. 11.

1969 *Ptychobairdia circumvallata* n. sp. – KRISTAN-TOLLMANN, pp. 85-86, pl. 2, figs 6-10.
1971 *Triebelina (Ptychobairdia) circumvallata* (KRISTAN-TOLLMANN, 1969) – BOLZ, pp. 205-207, pl. 14, figs 208-214, text-fig. 1f.
1972b *Triebelina circumvallata* – KOZUR, pl. 2, fig. 5.

Remarks: In the studied material one single poorly preserved carapace can be found with similar outline to the holotype and with the presence of the very characteristic concentrical peripheral distinct ridge.
Dimensions: L= 1.04 mm, H= 0.58, L/H= 1.79.
Occurrences: Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper); Northern Calcareous Alps, Zlambach beds (Austria): Norian to Raethian (BOLZ, 1971; KRISTAN-TOLLMANN, 1969).

Suborder Cypridocopina BAIRD, 1845
Superfamily Cypridoidea BAIRD, 1845
Family Paracyprididae SARS, 1923
Genus *Paracypris* SARS, 1866
Type species: *Paracypris polita* SARS, 1866

Paracypris sp.
Pl. 3, figs 1-2.

Remarks: Diagnostic features are the elongate subtriangular shape which tapers toward the very narrowly arched posterior end; the symmetrically rounded anterior margin; the straight or slightly concave posterodorsal margin; the slightly and symmetrically concave ventral margin and the smooth valve surface. The outline of the specimens is identical with that of *Paracypris* sp. 2. described by MONOSTORI (1994) from Carnian beds of Balaton Highland.
Dimensions: L= 0.59-0.65, H= 0.27-0.3 mm, L/H= 2.16-2.17.
Occurrence: Barnag, Nosztori Valley, Balaton Highland (Hungary): Carnian (Upper Triassic) (MONOSTORI 1994; this paper).

Suborder Cytherocopina BAIRD, 1850
Superfamily Cytheroidea BAIRD, 1850
Family Cytheruridae SARS, 1925
Subfamily Cytherurinae SARS, 1925
Genus *Judahella* SOHN, 1968
Type species: *Judahella tsorfatia* SOHN, 1968

Judahella fortenodosa (URLICHS, 1972)
Pl. 3, figs 3-4.

1972 *Monoceratina fortenodosa* n. sp. – URLICHS, p. 678, pl. 1, figs 6-8.
1980 *Monoceratina fortenodosa* URLICHS, 1973 – KRISTAN-TOLLMANN in KRISTAN-TOLLMANN et al., p. 187, pl. 8, fig. 10.
1988 *Triceratina fortenodosa* (URLICHS) – KRISTAN-TOLLMANN, text-fig. 6/10.
1991 *Triceratina fortenodosa* (URLICHS, 1972) – KRISTAN-TOLLMANN et al., pl. 8, figs 1-2.

Remarks: Diagnostic features are four dorsal, two anteroventral and one posteroventral nodes, a median furrow and a posteroventral spine. Because of the poor preservation potential the fine polygonal reticulation pattern cannot be recognized on the valve surface of the studied specimens.
Dimensions: L=0.52-0.54 mm, H= 0.21-0.22 mm, L/H= 2.31-2.5.
Occurrences: Bakonykúti, E-Bakony (Hungary): Ladinian (Middle Triassic) (this paper); Northern Calcareous Alps, Cassian beds (Austria): Norian (Upper Triassic) (URLICHS 1972; KRISTAN-TOLLMANN et al. 1991); Zagros Mountains (Iran): Rhaetian (Upper Triassic) (KRISTAN-TOLLMANN et al. 1980; KRISTAN-TOLLMANN 1988).

Genus *Kerocythere* KOZUR & NICKLAS, 1970
Type species: *Cythere raibliana* GÜMBEL, 1869

Kerocythere cf. *reticulata* KRISTAN-TOLLMANN, 1972
Pl. 3, figs 5-7.

Remarks: Similar to *Kerocythere reticulata* described by KRISTAN-TOLLMANN (1972, p. 46, pl. 2, figs 4-5.) from Carnian beds of Julian Alps (Italy).
Dimensions: L= 0.71-0.74 mm, H=0.36-0.42 mm, L/H= 1.75-2.
Occurrence: Barnag, Balatonhenye, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper).

Kerocythere veghae KOZUR, 1971
Pl. 3, figs 8-9.

1971 *Kerocythere veghae* n. sp. – KOZUR in BUNZA & KOZUR, pp. 49-51, pl. 4, figs 17-19.
1994 *Kerocythere veghae* KOZUR, 1971 – MONOSTORI, pp. 319-320. cum syn.

Remarks: The median ridge is weaker than that of the holotype. This phenomenon is linked to intraspecific variability.
Dimensions: L= 0.77-0.8 mm, H= 0.5-0.55 mm, L/H= 1.55-1.6.
Occurrences: Julian Alps (Italy): Carnian (Upper Triassic) (KRISTAN-TOLLMANN 1972; LIEBERMAN 1979); Veszprém Plateau (Hungary): Carnian (Upper Triassic) (BUNZA & KOZUR 1971); Northern Calcareous Alps (Austria): Carnian (Upper Triassic) (KRISTAN-TOLLMANN & HAMEDANI 1973), Balataonhenye, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper).

Family undetermined
Genus *Renngartenella* SCHNEIDER, 1957
Renngartenella sanctaecrucis KRISTAN-TOLLMANN, 1973
Pl. 3, figs 10-12.

1973 *Renngartenella sanctaecrucis* n. sp. – KRISTAN-TOLLMANN in KRISTAN-TOLLMANN & HAMEDANI, pp. 215-219, text-fig. 8/1-6, text-fig. 11.
1983 *Renngartenella sanctaecrucis* TOLLMANN & HAMEDANI – BASHA, pl. 1, fig. 15.
1994 *Renngartenella sanctaecrucis* KRISTAN-TOLLMANN, 1973 – MONOSTORI, pp. 320-321, text-fig. 5/5-7. cum. syn.

Remarks: Characteristic features are the polygonal reticulation pattern, the distinct median sulcus and the main swellings. The males are often more elongate than females.
Dimensions: L= 0.49-0.55 mm, H= 0.29-031 mm, L/H= 1.62-1.89.

Occurrences: Northern Calcareous Alps (Austria): Carnian (Upper Triassic) (KRISTAN-TOLLMANN & HAMEDANI 1973); Julian Alps (Italy): Carnian (Upper Triassic) (LIEBERMAN 1979); Jordan Valley (Jordan): Carnian (Upper Triassic) (BASHA 1983); Makhtesh Ramon (Israel): Carnian (Upper Triassic) (GERRY et al. 1990); Balatonhenye, Barnag, Nosztori Valley, Balaton Highland (Hungary): Carnian (Upper Triassic) (MONOSTORI 1994; this paper).

Genus *Simeonella* SOHN, 1968

Type species: *Simeonella brotzenorum* SOHN, 1968

Simeonella brotzenorum SOHN, 1968

Pl. 3, figs 13-15.

1968 *Simeonella brotzenorum* n. sp. – SOHN, pp. 23-24, pl. 2, figs 1-4, 6-8, 12-22.
1971 *Simeonella brotzenorum alpina* n. ssp. – BUNZA & KOZUR, pp. 4-5, pl. 1, figs 5-7, 13.
1971 *Simeonella brotzenorum norica* n. ssp. – BUNZA & KOZUR, pp. 5-6, pl. 1, fig. 3.
1973 *Simeonella brotzenorum* SOHN – KRISTAN-TOLLMANN in KRISTAN-TOLLMANN & HAMEDANI, text-fig. 13/2.
1974 *Simeonella brotzenorum* SOHN – HIRSCH & GERRY, pl. 2, figs 1-2.
1979 *Simeonella brotzenorum* SOHN, 1968 – LIEBERMAN, p. 103, pl. 5., figs 6-7.
1979 *Simeonella brotzenorum alpina* BUNZA et KOZUR – STYK, p. 119, pl. 28, figs 9-10.
1983 *Simeonella brotzenorum* SOHN – BASHA, pl. 1, fig. 11.
1990 *Simeonella brotzenorum* SOHN, 1968 – GERRY et al., p. 95, pl. 1, figs 3-5.
1994 *Simeonella brotzenorum nostorica* n. ssp. – MONOSTORI, pp. 324-325, text-fig. 6/1-6.

Remarks: Characteristic features are the small subquadrate shape, and the reticulation forming horizontally trending riblets. Because of the large morphological variation of *Simeonella brotzenorum*, the justification of the subspecies described by BUNZA & KOZUR (1971) and MONOSTORI (1994) is questionable.

Dimensions: L= 0.42-0.46 mm, H= 0.27-0.34 mm, L/H= 1.35-1.6.

Occurrences: Makhtesh Ramon (Israel): Ladinian to Carnian (Upper Triassic) (SOHN 1968; HIRSCH & GERRY 1974; GERRY et al. 1990); Northern Calcareous Alps (Austria): Carnian (Upper Triassic) (BUNZA & KOZUR 1971; KRISTAN-TOLLMANN & HAMEDANI 1973); Julian Alps (Italy): Carnian (Upper Triassic) (LIEBERMAN 1979); Jordan Valley (Jordan): Carnian (Upper Triassic) (BASHA 1983); Balatonhenye, Barnag, Nosztori Valley, Balaton Highland (Hungary): Carnian (Upper Triassic) (MONOSTORI 1994; this paper); Poland: Carnian (Upper Triassic) (STYK 1979).

Simeonella reissi SOHN, 1968

Pl. 3, fig. 16.

1968 *Simeonella reissi* n. sp. – SOHN, p. 24, pl 1, figs 1-5, 8-12.
1983 *Simeonella reissi* SOHN – BASHA, pl. 2, 3-5.

Remarks: Characteristic features are the fine reticulation pattern on the valve surface and the weak ribs dorsally and ventrally.

Dimensions: L= 3.25-4.34 mm, H= 0.21-0.32 mm, L/H= 1.4-1.44.

Occurrences: Makhtesh Ramon (Israel): Carnian (Upper Triassic) (SOHN 1968); Jordan Valley (Jordan): Carnian (Upper Triassic) (BASHA 1983); Balatonhenye, Balaton Highland (Hungary): Carnian (Upper Triassic) (this paper).

Characteristics and palaeoecological significance of Ladinian to Carnian ostracoda faunas from the Transdanubian Central Range

Middle to Upper Triassic deposits in the studied boreholes (Bat-2, Bht-6, Bút-2, Met-1, and Rzt-1) are characterized by poorly to moderately preserved podocopid ostracod faunas beside few reticulated polycopids in borehole Bút-2. Due to the poor to moderate preservation potential the specimens could be determined only on genus level in most cases. Two new species could be established namely *Ceratobairdia crassispinosa* n. sp. from the Ladinian beds of the borehole Bút-2 and *Dicerobairdia latispinosa* n. sp. from Carnian beds of the borehole Bat-2. The majority of the identified taxa were known only from the Middle to Upper Triassic. Only the species *Acratia goemoeryi* and *Bairdia jeancharlesi* occur in Lower Triassic section of South Tibet (FOREL & CRASQUIN 2011; FOREL et al. 2011). Relatively long ranges of the Triassic ostracod taxa and their distribution depending on the facies have made them not so good index fossils but they are very useful palaeoenvironmental indicators. The palaeoecological interpretation of the studied faunas is discussed in stratigraphical order.

In the studied Ladinian sections of the Buchenstein Formation in the borehole Bút-2 there are relatively diverse ostracod fauna with great abundance of the specimens. The distribution in faunal composition of ostracods in each bed is very similar; there is no significant trend in the changes of diversity and in the ratio of different taxa. The association of the studied benthic fauna, the dominance of ornamented bairdioids (*Ceratobairdia, Hiatobairdia* and *Triebelina*), the presence of *Reubenella* and the stubby *Acratia* suggests neritic, normal marine, middle sublittoral depositional environment with moderate water energy. The studied ostracod fauna from the E-Bakony is absolutely different from the Ladinian assemblages derived from pelagic limestone beds of the Buchenstein Formation in the Litér quarry of the Balaton Highland (MONOSTORI & TÓTH, 2013). The latter fauna characterized by the dominance of the smooth bairdioids, metacopids and Thuringian-type elements (sensu BECKER in BANDEL & BECKER, 1975) indicates open marine, more than 200 m deep, oligotrophic, low energy conditions. This phenomenon is explained by the different palaeogeographical position of the studied areas. During the Ladinian age the succession of the Litér quarry was formed in the so-called „Balaton Highland Basin", whereas the deposits of the borehole Bút-2 in a proximal position to the „Budaörs Platform" (HAAS & BUDAI, 1995).

In the boreholes Met-1 and Bat-2, the Upper Ladinian to Carnian ostracod assemblages in the series of the Füred Limestone and the Veszprém Marl are represented by poorly preserved specimens in very low abundance. The characteristic elements of the faunas are the smooth bairdioids including the subgenus *Urobairdia* with narrow pointed posterior end, the smooth metacopids (*Hungarella*), the cytherellid *Reubenella* and bairdicypridoids. The composition of the fauna with the absence of typical shallow water ostracods (e.g, cytheroids or ornamented bairdioids) suggests normal marine deep sublittoral low energy conditions.

The younger part of the Carnian series in the boreholes Bat-2 and Bht-6 belongs to the Sándorhegy Formation. The ostracod faunas derived from thin grey marly limestone beds in Bat-2 (162.5 to113.2 m) and from one sample (121.7 m) of the Bht-6 are represented by the predominance of the specimens belonging to three genera (*Renngartenella, Simeonella* and *Kerocythere*) as a signal of increasing variability of the salinity in marginal marine settings. Moreover, the sedimentological characteristics in borehole Bat-2, the bituminous laminated grey marly layers with fish scales supposed stratified water column with low oxygenated conditions in this shallow marine environment. Similar Carnian ostracod assemblages were described by MONOSTORI (1994) from the Nosztori Valley in Balaton Highland, by LIEBERMAN (1979) in Julian Alps of northern Italy, by SOHN (1968), HIRSCH & GERRY (1974), GERRY et al. (1990) from Israel. Thus this salinity crisis can be considered as widespread in the Western Tethys. The Upper Carnian ostracod faunas of the Sándorhegy Limestone in the borehole Bat-2 with the re-appearance and dominance of ornamented bairdioids (*Triebelina* and *Dicerobairdia*) and cytherellids indicate the stabilization of the well oxygenated, normal marine conditions with shallow sublittoral water depth. These palaeoenvironmental changes during the Carnian age detected by the ostracod faunas can be explained by sea-level fluctuations. The above-mentioned salinity crisis is caused by a regressive event which was well correlates to a global sea-level lowstand (GERRY et al. 1990).

Norian to Rhaetian beds of the Kössen Formation in Rzt-1 provided poorly preserved and few mostly undetermined ostracod specimens. The identified taxa belonging to the ornamented bairdioids (*Triebelina* and *Hiatobairdia*) which indicate probably shallow marine environment, however the poor fauna is not suitable for reliable palaeoecological interpretation.

Conclusions

Relatively diverse, moderately and poorly preserved Ladinian to Rhaetian ostracod faunas were described from five boreholes (Bat-2, Bht-6, Bút-2, Met-1 and Rzt-1) of the Transdanubian Central Range. Detailed systematic descriptions are given for 25 ostracod taxa (with 2 new species) belonging to 17 genera, 8 families, 6 suborders (Cladocopina, Platycopina, Metacopina, Bairdiocopina, Cypridocopina and, Cytherocopina) and three orders (Halocyprida, Platycopida and, Podocopida). Based on the palaeoecological interpretation of the ostracod faunas the following marine palaeoenvironments could be distinguished in this region of the Tethys:

– In the Ladinian deposits of the borehole Bút-2 the dominance of ornamented bairdioids beside *Reubenella* and stubby *Acratia* indicates shallower (middle sublittoral) normal marine depositional environment of the Buchenstein Formation in the E-Bakony than it was detected based on the ostracod studies derived from Ladinian series of Litér quarry in the Balaton Highland.

- The studied Upper Ladinian to Carnian ostracod assemblages with smooth bairdioids (e.g., *Urobairdia*), metacopids, bairdiocypridoids and cytherellids (*Reubenella*) in the boreholes Met-1 and Bat-2 suggest normal marine, deep sublittoral depositional environment of the Füred Limestone and the Veszprém Marl with low energy conditions.
- The Carnian salinity crisis caused by a regressive event could be recognized based on the predominance of the specimens of *Renngartenella, Simeonella* and *Kerocythere* in the faunal compositon of the boreholes Bat-2 and Bht-6. After this event, the re-appearance of the shallow sublittoral faunal elements (ornamented bairdioids) in the upper part of the Carnian series in the borehole Bat-2 proved the stabilization of normal marine conditions.
- The Norian to Rhaetian, poor faunas of the Kössen Formation in the borehole Rzt-1 supposed probably shallow marine environment based on the presence of the genera *Triebelina* and *Hiatobardia*.

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Locality	Bht-6						Bat-2															
Formation	S. Fm.	Veszprém Marl Fm.					Sándorhegy Fm.															V. M. Fm.
Member	P. M.	Csicsó Member					Barnag Member							Pécsely Member								Cs. M.
Sample	121.7 m	153.3 m	165.5 m	195.5 m	197 m	200 m	17.9 m	42.5 m	43.7 m	47.8 m	58.8 m	64 m	64.5 m	88.6 m	89.2 m	90 m	113.2 m	115.6 m	119.6 m	121.6 m	162.5 m	180.8 m
Cytherella cf. *persiensis*		2	6	~ 30	17	16	1	2	15	200<	6		14		5	50<						
Cytherelloidea unicostata													2									
Reubenella picardi	1	1	1		2							1		44								
Hungarella problematica				42	3	24				2												
Bairdia cassiana									2			1	15	1								
Dicerobairdia latispinosa												1	1									
Hiatobairdia subsymmetrica													1									
Triebelina (*Nodobairdia*) *mammilata*												7	11			1						
Triebelina (*Ptychobairdia*) *kuepperi*													1									
Paracypris sp.										15			1									2
Kerocythere cf. *reticulata*	250<															1						
Kerocythere veghae	150<																					
Renngartenella sanctaecrucis	8000<							1								1	50<	50<	18	17	2	
Simeonella brotzenorum	~ 400																				1	
Simeonella reissi	8000<																					

Appendix 1. - Quantitative data (number of specimens) of Carnian ostracod taxa from each sample from the studied boreholes Bat-2 and Bht-6. Abbreviations: S. Fm.= Sándorhegy Formation, P. M.= Pécsely

Locality	**Bút-2**							**Met-1**													**Rzt-1**		
Age	Ladinian							Carnian													Norian/ Rhaetian		
Formation	?	Buchenstein Fm.						Veszprém Marl Fm./Csicsó Member								Veszprém Marl Fm./Mencshely Marl M.				F. L.	K. Fm.		
Sample	72.4 m	93.2 m	95.2 m	96.6 m	99.3 m	99.9 m	100.2 m	31 m	51.3 m	52.2 m	56.8 m	57.8 m	58.3 m	60.2 m	62.1 m	170.7 m	173.9 m	177.7 m	178.7 m	435.6m	58.5 m	125.6 m	184 m
Polycope aff. *aghdarbandensis*			1																				
Cytherelloidea unicostata							3															1	
Reubenella picardi	2	15	5	1	14	2							1										
Hungarella problematica		30								1	11					1	7	1	1	7			
Bairdiacypris triassica								1	1	1	10				2			1		1			
Acratia goemoeryi	2	2	2																				
Bairdia (Urobairdia) angusta										4	10		3										
Bairdia cassiana		24	15	15	8		2			1									5				
Bairdia jeancharlesi		1	3	1										5									
Bairdia ex gr. margosulcata																						1	
Ceratobairdia crassispinosa	2																						
Hiatobairdia subsymmetrica		1	1																				1
Triebelina (Nodobairdia) mammilata	2	2	4			3	4														1		
Triebelina (Mirabairdia) pernodosa	11	26	33	19	13		8																
Triebelina (Ptychobairdia) circumvallata							1																
Triebelina (Ptychobairdia) kuepperi			11	13																			
Judahella fortenodosa	1	10																					

Member, V. M.= Veszprém Marl, Cs. M.= Csicsó Marl.

Appendix 2. - Quantitative data (number of specimens) of Ladinian to Rhaetian ostracod taxa from each sample from the studied boreholes Bút-2, Met-1 and Rzt-1. Abbreviations: F. L.= Füred Limestone, K. Fm.= Kössen Formation.

Plate 1

Fig. 1. *Polycope* aff. *aghdarbandensis* KRISTAN-TOLLMANN, 1991. RV in lateral view. Borehole Bút-2: 95.2 m

Fig. 2. *Cytherelloidea unicostata* BOLZ, 1970. RV in lateral view. Borehole Rzt-1: 125.6 m

Figs 3-4. *Cytherella* cf. *persiensis* CRASQUIN-SOLEAU & TEHERANI, 1995.
Fig. 3. RV in lateral view. Borehole Bat-2: 42.5 m
Fig. 4. C in left view. Borehole Bat-2: 89.2 m

Figs 5-6. *Reubenella picardi* SOHN, 1968.
Fig. 5. C in righ view. Borehole Bht-6: 121.7 m
Fig. 6. LV in lateral view. Borehole Bút-2: 96.6 m

Figs 7-10. *Hungarella problematica* (MÉHES, 1911).
Fig. 7. C in left view. Borehole Bht-6: 197.0 m
Fig. 8. C in dorsal view. Borehole Bht-6: 195.5 m
Fig. 9. C in left view. Borehole Bht-6: 200 m
Fig. 10. C in dorsal view. Borehole Bht-6: 195.5 m

Fig. 11. *Acratia goemoeryi* KOZUR, 1970. LV in lateral view. Borehole Bút-2: 72.4 m

Fig. 12. *Bairdiacypris triassica* KOZUR, 1971. C in right view. Borehole Met-1: 435.6 m

Fig. 13. *Bairdia (Urobairdia) angusta* (KOLLMANN, 1963). C in right view. Borehole Met-1: 56.8 m

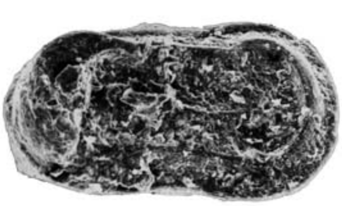
Fig. 14. *Bairdia cassiana* (REUSS, 1868). LV in lateral view. Borehole Bút-2: 93.2 m

Fig. 15. *Bairdia* ex gr. *margosulcata* BOLZ, 1971. C in right view. Borehole Rzt-1: 125.6 m

Scale bar = 100 μm. Abbreviations: C = Carapace, RV = Right valve, LV = Left valve.

Plate 1


1.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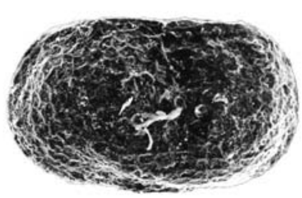
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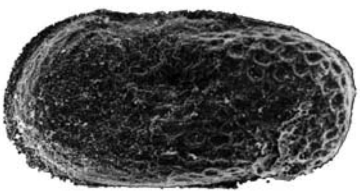
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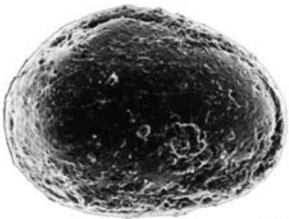
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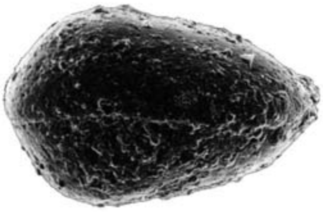
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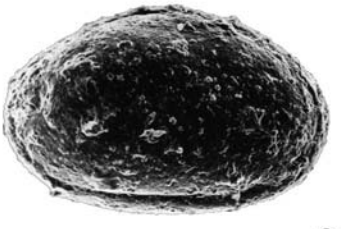
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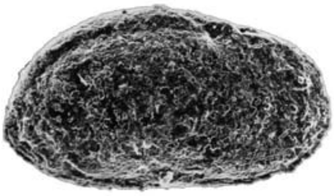
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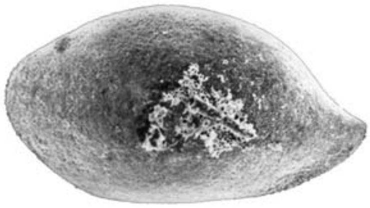
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Plate 2

Figs 1-2. *Bairdia jeancharlesi* FOREL, 2011.
  Fig. 1. LV in lateral view. Borehole Bút-2: 95.2 m
  Fig. 2. RV in lateral view. Borehole Bút-2: 96.6 m

Fig. 3. *Ceratobairdia crassispinosa* n. sp. LV in lateral view. Borehole Bút-2: 72.4 m. EMNH 2014.207.7.8.

Figs 4-5. *Hiatobairdia subsymmetrica* KRISTAN-TOLLMANN, 1970.
  Fig. 4. RV in lateral view. Borehole Rzt-1: 184 m
  Fig. 5. RV in lateral view. Borehole Bút-2: 96.6 m

Fig. 6. *Dicerobairdia latispinosa* n. sp. C in right view. Borehole Bat-2: 64.0 m EMNH 2014.208.1.4.

Figs 7-8. *Triebelina (Mirabairdia) pernodosa* (KOLLMANN, 1963).
  Fig. 7. RV in lateral view. Borehole Bút-2: 96.6 m
  Fig. 8. LV in lateral view. Borehole Bút-2: 95.2 m

Figs 9-10. *Triebelina (Nodobairdia) mammilata* (KOLLMANN, 1963).
  Fig. 9. RV in lateral view. Borehole Bat-2: 64.0 m
  Fig. 10. LV in lateral view. Borehole Bat-2: 64.0 m

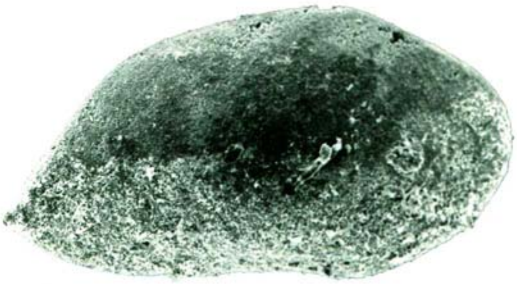
Fig. 11. *Triebelina (Ptychobairdia) circumvallata* (KRISTAN-TOLLMANN, 1969). RV in lateral view. Borehole Bút-2: 100.2 m

Figs 12-13. *Triebelina (Ptychobairdia) kuepperi* (KOLLMANN, 1960)
  Fig. 12. RV in lateral view. Borehole Bat-2: 64 m
  Fig. 13. RV in lateral view. Borehole Bút-2: 96.6 m

Scale bar = 100 µm. Abbreviations: C = Carapace, RV = Right valve, LV = Left valve.

Plate 3


1.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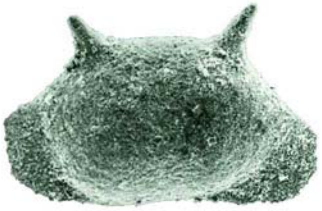
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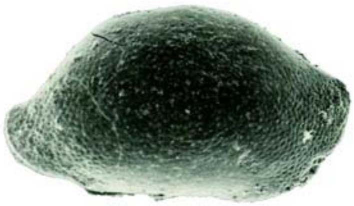
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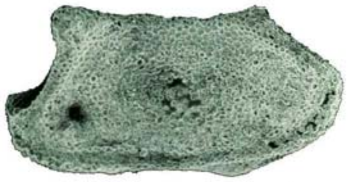
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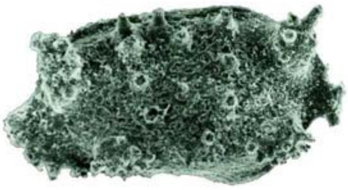
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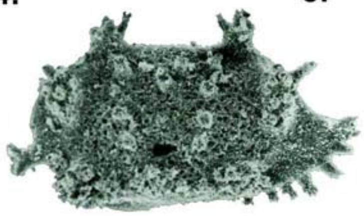
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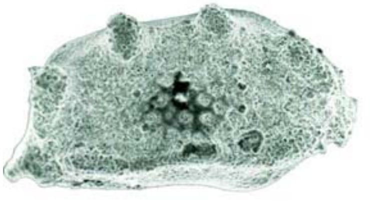
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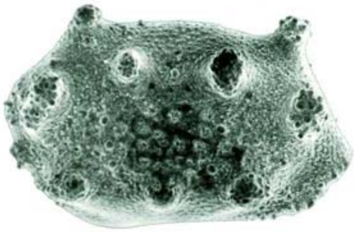
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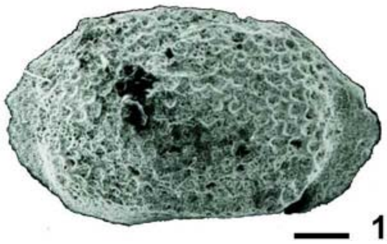
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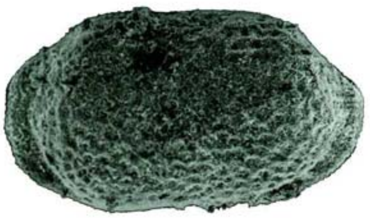
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Plate 3

Figs 1-2. *Paracypris* sp.
  Fig. 1. C in right view. Borehole Bat-2: 180.8 m
  Fig. 2. LV in lateral view. Borehole Bat-2: 180. 8 m

Figs 3-4. *Judahella fortenodosa* (URLICHS, 1972)
  Fig. 3. RV in lateral view. Borehole Bút-2: 93.2 m
  Fig. 4. LV. in lateral view. Borehole Bút-2: 93.2 m

Figs 5-7. *Kerocythere* cf. *reticulata* KRISTAN-TOLLMANN, 1972
  Fig. 5. C in right view. Borehole Bht-6: 121.7 m
  Fig. 6. C in left view. Borehole Bht-6: 121.7 m
  Fig. 7. C in dorsal view. Borehole Bht-6: 121.7 m

Figs 8-9. *Kerocythere veghae* KOZUR, 1971
  Fig. 8. C in left view. Borehole Bht-6: 121.7 m
  Fig. 9. C in dorsal view. Borehole Bht-6: 121.7 m

Figs 10-12. *Renngartenella sanctaecrucis* KRISTAN-TOLLMANN, 1973
  Fig. 10. C in right view. Borehole Bht-6: 121.7 m
  Fig. 11. C in right view. Borehole Bht-6: 121.7 m
  Fig. 12. C in left view. Borehole Bht-6: 121.7 m

Figs 13-15. *Simeonella brotzenorum* SOHN, 1968
  Fig. 13. C in right view. Borehole Bht-6: 121.7 m
  Fig. 14. C in left view. Borehole Bht-6: 121.7 m
  Fig. 15. C in dorsal view. Borehole Bht-6: 121.7 m
Fig. 16. *Simeonella reissi* SOHN, 1968. C in right view. Borehole Bht-6: 121.7 m

Scale bar = 100 µm. Abbreviations: C = Carapace, RV = Right valve, LV = Left valve.

Plate 3


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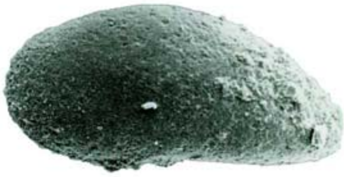
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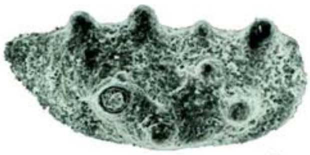
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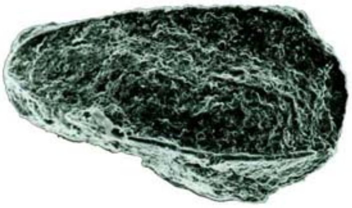
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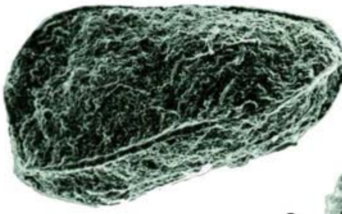
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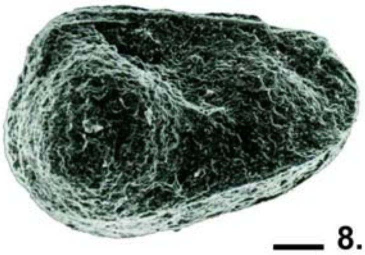
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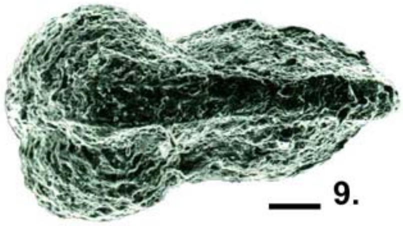
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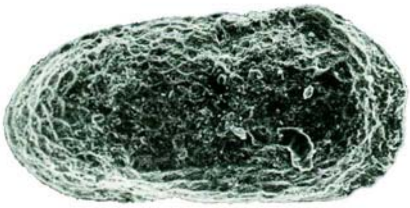
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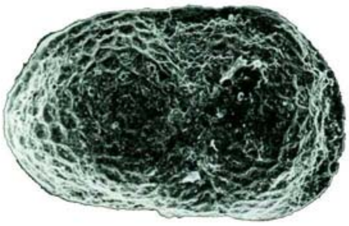
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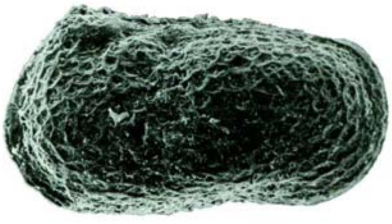
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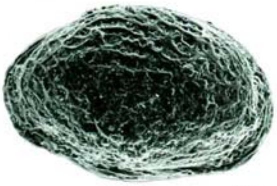
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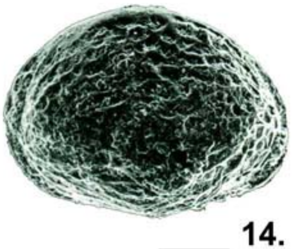
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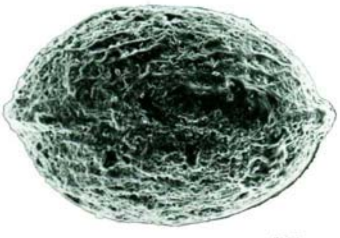
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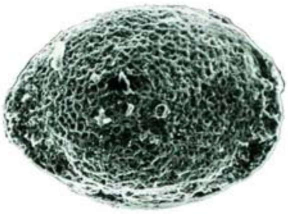
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Hantkeniana 9, 45—77, Budapest, 2014
András Galácz Jubilee Volume

Toarcian Dactylioceratidae (Ammonitina) from the Gerecse Mts (Hungary)

Zoltán KOVÁCS[1]

(with 2 figures and 7 plates)

Taxonomic and stratigraphic problems of the family Dactylioceratidae and genera *Dactylioceras*, *Microdactylites*, *Zugodactylites*, *Peronoceras*, *Porpoceras*, *Catacoeloceras*, *Mucrodactylites*, *Septimaniceras*, *Nodicoeloceras*, *Mesodactylites*, *Transicoeloceras*, *Telodactylites* and *Collina* included in it are briefly discussed. 31 species of Dactylioceratidae are described and illustrated from the Lower–Middle Toarcian ammonite assemblages of the Gerecse Mts (NE Transdanubian Range, Hungary). Four new species are introduced: *Microdactylites tardosensis* n. sp., *Nodicoeloceras dulaii* n. sp., *Mesodactylites pisznicensis* n. sp., *Telodactylites levisettii* n. sp. The fauna described here is closely allied to the Mediterranean Province of the Mediterranean-Caucasian Realm.

Introduction

This paper offers a detailed taxonomic treatment of species belonging to genera of the family Dactylioceratidae from the ammonite assemblages of the Gerecse Mts, as a contribution of the comprehensive treatment of the Toarcian ammonite material deposited in the Eötvös Museum of Natural History, Budapest. The material was collected from different localities of the Gerecse Mts (Figure 1) by the staff of the Geological Institute of Hungary between 1976 and 1982. The first taxonomic, quantitative and paleobiogeographic analyses were provided by GÉCZY (1984, 1985), the Middle Toarcian Ammonitina fauna and biostratigraphy were presented in detail by GÉCZY & SZENTE (2007), KOVÁCS (2010, 2013, 2014), whereas the taxonomy and biostratigraphy of Lower Toarcian assemblages were dealt with by KOVÁCS (2012). Ammonite materials of two other Toarcian sections from the Gerecse Mts (Kis-Teke Hill, Nagy-Pisznice Hill – Crocodile) were described by GÉCZY et al. (2008), and GALÁCZ et al. (2011), respectively. The constant dominance of suborders Phylloceratina and Lytoceratina, as well as the occurrences of several characteristic Ammonitina genera assigned these Toarcian assemblages to the Mediterranean Province, with close affinities to those known from Italy and Greece. Nevertheless, sporadic appearances of zonal indices enabled the application of the detailed NW European zonal stratigraphy for these basically Mediterranean ammonite faunal successions. The biostratigraphic subdivision of the Middle Toarcian in the Gerecse sections is shown on Figure 2.

The Lower–Middle Toarcian successions in the area are characterized by an "Ammonitico Rosso marl" subfacies, the Kisgerecse Marl Formation. It is a thin-bedded, red nodular marl of variable carbonate and clay content, that is rich in ammonites; however, the remains are mainly poorly to moderately preserved internal molds (KNAUER 2012).

Note: The following abbreviations are used in this paper for measurements (M): D – diameter, H – whorl-height, W – whorl-width, Uw – umbilical-width, PRLW – primary ribs of the last whorl. The description of suture-construction is based on VENTURI & FERRI (2001). Abbreviations: E – external lobe, L – lateral lobe, U – umbilical lobe, ES – external saddle, LS – lateral saddle.

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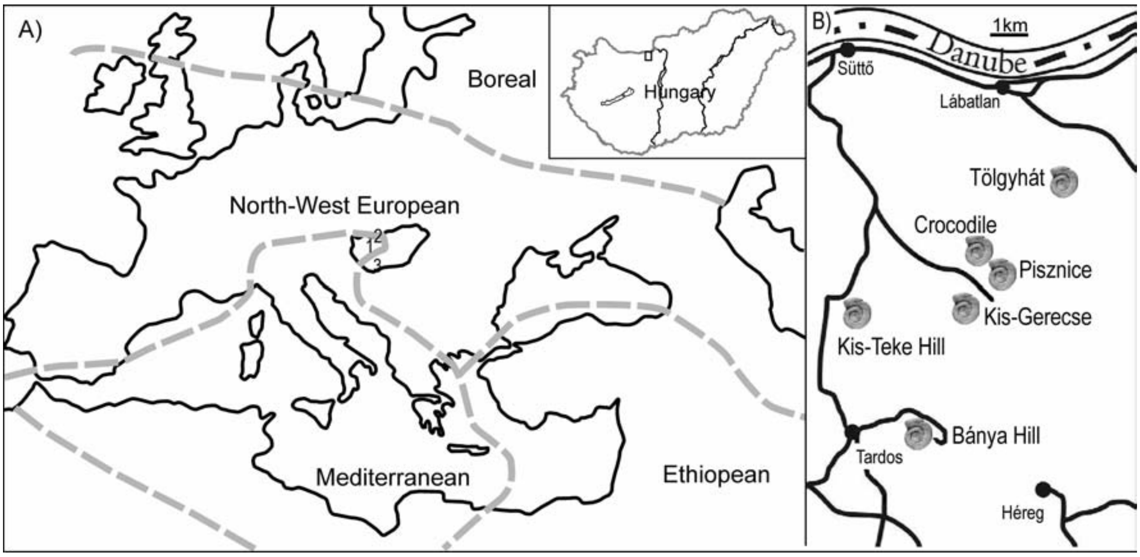

Figure 1. A) Middle Toarcian ammonite faunal provinces in Europe and W Asia: (Page 2008), 1 – Bakony Mts, 2 – Gerecse Mts, 3 – Mecsek Mts; B) Location of Toarcian sections examined in the Gerecse Mts.

Systematic paleontology

Classis Cephalopoda Cuvier, 1797
Subclassis Ammonoidea Zittel, 1884
Ordo Ammonitida Fischer, 1882
Subordo Ammonitina Fischer, 1882
Superfamilia Eoderoceratoidea Spath, 1929

Family Dactylioceratidae Hyatt, 1867

A comprehensive taxonomic, paleobiogeographic and phylogenic treatment of the family was recently presented by Rulleau et al. (2013) containing almost all publications issued on the Toarcian Dactylioceratidae. For the research of the family in the European faunal provinces during the Middle Toarcian, the following studies are of primary importance from the last 50 years: Géczy (1967a, 1990), Dagis (1968), Guex (1970, 1971, 1972, 1973), Pinna & Levi-Setti (1971), Schmidt-Effing (1972, 1975), Howarth (1978, 2013), Jiménez & Rivas (1991), Mouterde & Elmi (1991), Elmi et al. (1997), Kutygin & Knyazev (2000), Venturi & Ferri (2001), Fauré (2002), Metodiev (2003), Morard (2004), Rulleau (2007), and Venturi et al. (2010).

Based on marked differences concerning the morphology and paleobiogeographic range of genera, the family has been traditionally divided into *Dactylioceras*-group and *Nodicoeloceras*-group, however, without any consensus on subfamily- or genus-level classification. In this paper, both the two subfamilies proposed by Venturi & Ferri (2001) for Toarcian dactylioceratids, and the genus-level considerations by Rulleau et al. (2013) are accepted with some amendments. Accordingly, the following taxonomic scheme is used here to describe the examined ammonite assemblages:

- Family Dactylioceratidae Hyatt
  - Subfamily Dactylioceratinae Hyatt
    - Genera *Dactylioceras* Hyatt
      - *Microdactylites* Buckman
      - *Zugodactylites* Buckman
      - *Peronoceras* Hyatt
      - *Porpoceras* Buckman
      - *Catacoeloceras* Buckman
      - *Mucrodactylites* Buckman
      - *Septimaniceras* Fauré
  - Subfamily Nodicoeloceratinae Venturi et Ferri
    - Genera *Nodicoeloceras* Buckman
      - *Mesodactylites* Pinna et Levi-Setti
      - *Transicoeloceras* Pinna
      - *Telodactylites* Pinna et Levi-Setti
      - *Collina* Bonarelli

The stratigraphic range of Dactylioceratidae species known from the Gerecse sections is shown on Figure 2.

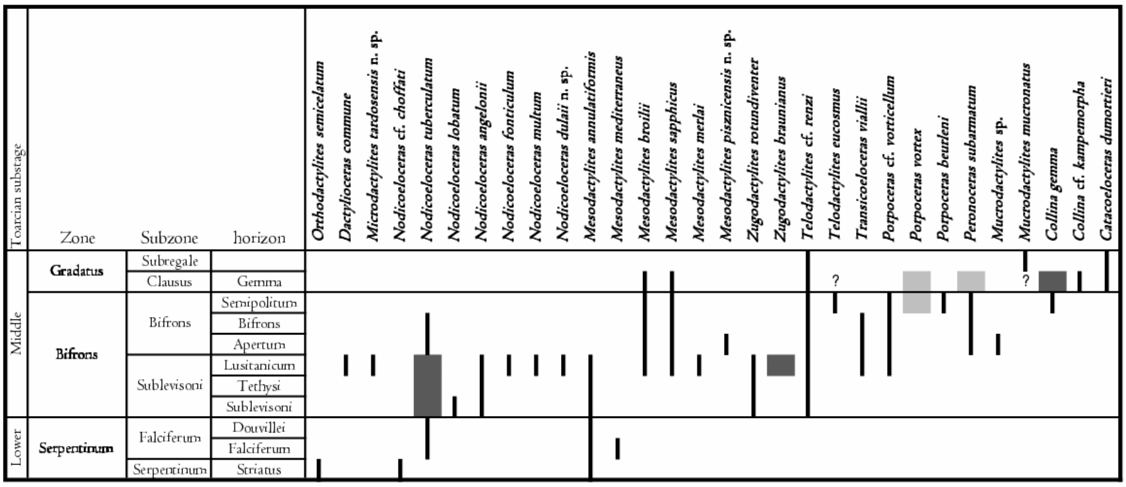

Figure 2. Chronostratigraphic distribution of dactylioceratid species in the Gerecse Mts (thin line: rare, light gray square: frequent, dark gray square: abundant)

Subfamily Dactylioceratinae HYATT, 1867

Genera placed within the taxon are connected by close phylogenetic lineage in the family, as well as are typical of the NW European faunal province.

Genus *Dactylioceras* HYATT, 1867

Type-species: *Ammonites communis* SOWERBY, 1815.

Remarks: The following subgenera are accepted in the literature: *D.* (*Dactylioceras*) HYATT, 1867, *D.* (*Eodactylites*) SCHMIDT-EFFING, 1972, *D.* (*Orthodactylites*) BUCKMAN, 1926, *D.* (*Iranodactylites*) REPIN, 2000. The second one that is thought to be the zonal index of the Toarcian Stage (ELMI 2007, COMAS-RENGIFO et al. 2010) probably derived from genus *Reynesoceras* SPATH in the uppermost Pliensbachien, and it was the ancestor of *Orthodactylites*.

From Toarcian localities of Hungary, *D.* (*Orthodactylites*) and *D.* (*Dactylioceras*) can be documented.

Subgenus *Dactylioceras* (*Orthodactylites*) BUCKMAN, 1926

Type-species: *Orthodactylites directum* BUCKMAN, 1926.

Diagnosis: Evolute coiling, slightly convex flanks, broad venter, subcircular section, dense to distant, annular, simple, bi- or trifurcating ribbing. Suture-line: wide, long E, shorter, trifid L, short, straight U lobes; wide ES, higher, narrower LS1.

Distribution: Tenuicostatum – lower Serpentinum Zones: Europe, North Africa, Iran, Tibet, NE Russia, North and South America. Hungary: Mecsek Mts (*D.* cfr. *anguinum* REINECKE, see VADÁSZ 1935), Gerecse Mts.

Dactylioceras (*Orthodactylites*) *semicelatum* (SIMPSON, 1843) (Plate 1, figs 1, 7)

1843 *Ammonites semicelatus* — SIMPSON, p. 20

1980 *Dactylioceras* (*Orthodactylites*) *semicelatum* (SIMPSON) — HOWARTH, p. 646, text-figs 2–3, pls 80–81, pl. 82, figs 11–12 (*cum syn.*)

2012 *Dactylioceras* (*Orthodactylites*) aff. *directum* (BUCKMAN) — KOVÁCS, p. 15, pl. 4, fig. 5

2013 *Dactylioceras* (*Orthodactylites*) *semicelatum* (SIMPSON) — RULLEAU et al., p. 72, pl. 4, figs 2–7 (*cum syn.*)

Material: Three fragmentary specimens (220.2011, 2014.55.1–2).

Measurements	D	H	H/D	W	W/H	Uw	Uw/D
220.2011	75	20	26.6%	18	90%	?	?
2014.55.1	75	20	26.6%	20	100%	38	50.6%
2014.55.2	72	20	27.7%	?	?	?	?

Description: Moderately evolute coiling, suboval whorl-section, slightly convex to flat flanks, rounded venter. The preserved part of the body chamber is one whorl in length. Dense, narrow, sharp, rectiradiate ribs crossing the venter. Almost all second ribs bifurcate at about mid-height without tubercles.

Remarks: The species *D.* (*Orthodactylites*) *directum* (BUCKMAN) recorded by KOVÁCS (2012) from the Gerecse Mts is regarded as a synonym of *D.* (*Orthodactylites*) *semicelatum*.

Distribution: Gerecse Mts: Serpentinum

Subzone: Kis-Gerecse and Bánya Hill B Sections.

Subgenus *Dactylioceras* (*Dactylioceras*) HYATT, 1867

Diagnosis: Evolute, compressed coiling, convex flanks, subrectangular to subcircular whorl-section, regular, furcating, dense to distant ribbing. Suture-line: wide, long E, shorter, trifid L, short, straight U lobes; wide ES, narrower LS1.

Remark: The genus probably was the descendant of *Orthodactylites*.

Distribution: Serpentinum – Bifrons Zones: Europe, North Africa, the Caucasus, Iran, Pakistan, Spitzbergen, Greenland, NE Russia, SE Asia, North and South America. Hungary: Mecsek Mts, Bakony Mts (Úrkút) [*D. commune* (SOWERBY), *D. toxophorum* BUCKMAN]), Gerecse Mts.

Dactylioceras (*Dactylioceras*) *commune* (SOWERBY, 1815)
(Plate 1, fig. 2)

1815 *Ammonites communis* — SOWERBY, p. 10, pl. 107, figs 2–3

1966 *Dactylioceras* sp. aff. *curvicosta* (BUCKMAN) — GÉCZY, p. 430, pl. 2, fig. 2

2013 *Dactylioceras* (*Dactylioceras*) *commune* (SOWERBY) — RULLEAU et al., p. 78, pl. 7, figs 2–4, pl. 8, figs 1–2, pl. 9, figs 1–2, 5–6, pl. 13, figs 1–2

Material: One wholly septate and one fragmentary specimens (2014.25.1–2).

Measurements	D	H	H/D	W	W/H	Uw
2014.25.1	52	13	25%	13	100%	?

Description: Evolute coiling, wide and shallow umbilicus, convex flanks, rounded venter, wide suboval section. Strong, distant, rectiradiate primary ribs bifurcate regularly at the shoulder without any tubercles. The paired secondaries bend slightly forward.

Remark: The species is typical of the NW European Province; however, it was recorded from Mediterranean localities (Austria, Italy, Greece, Southern Spain, Portugal) as well.

Distribution: Europe, the Caucasus, Iran, NE Russia, North and South America. Hungary: Bakony Mts (Úrkút). Gerecse Mts: Sublevisoni Subzone: Bánya Hill A and Pisznice Sections.

Genus *Microdactylites* BUCKMAN, 1926

Type-species: *Ammonites attenuatus* SIMPSON, 1855.

Diagnosis: Small size, evolute, compressed coiling, slightly convex to convex flanks, suboval to subcircular whorl-section, dense, single or bifurcating ribs. Simple suture-line: wide and short E and L, short U lobes, wide and low saddles.

Remarks: The validity of the taxon is debated in the literature (MORARD 2004, HOWARTH 2013, RULLEAU et al. 2013). The species placed within *Microdactylites* represent microconch forms of genus *Dactylioceras*.

Distribution: Serpentinum – lower Bifrons Zones: England, France, Germany, Italy.

Microdactylites tardosensis n. sp.
(Plate 1, fig. 3)

Holotype: 2014.26.1 (Eötvös Museum of Natural History)

Derivation of name: The name refers to the type locality.

Type locality and horizon: Sublevisoni Subzone, Bánya Hill A Section, Tardos, Gerecse Mts.

Material: 1 well-preserved internal mold of an adult specimen.

M	D	H	H/D	W	W/H	Uw	Uw/D	PRLW
2014.26.1	27	6	22.2 %	5	83.3 %	15	55.5 %	52

Diagnosis: Small size, evolute, compressed coiling, suboval whorl-section, sharp, rectiradiate, simple and bifurcating ribs, simple peristome.

Description: Evolute coiling, wide and shallow umbilicus, slightly convex flanks, rounded shoulder, arched venter, suboval whorl-section. The body chamber is about ¾ whorl in length. The peristome is simple and oblique, preceded by a wide and shallow contract. Sharp and rectiradiate ribs. One or two simple primaries alternate with ribs bifurcating at the ventrolateral shoulder, the secondaries pass the venter. The suture-line agrees with that of the genus.

Remarks: Based on size, suture-line and morphology, the new species is placed within genus *Microdactylites*. *M. tardosensis* n. sp. differs from *M. attenuatus* (SIMPSON) and *M. arcus* (BUCKMAN) in rectiradiate and more widely spaced ribs, from ?*M. gracilis* (SIMPSON) in compressed and more evolute coiling, and from ?*M. microdactyliformis* (MAUBEUGE) in more evolute shell.

Distribution: The specimen came from the condensed Bed 45 of the Bánya Hill A Section associated with *Hildoceras sublevisoni* FUCINI, *H. lusitanicum* MEISTER, *Harpoceras subexaratum* BONARELLI, *Dactylioceras commune*, and *Nodicoeloceras tuberculatum* (KOTTEK).

Genus *Zugodactylites* BUCKMAN, 1926

Type-species: *Ammonites braunianus* D'ORBIGNY, 1845.

Diagnosis: Small to medium-sized, evolute, compressed to somewhat depressed coiling; narrow, subcircular to suboval whorl-section; rounded venter. Keel appears on one species [*Z. pseudobranianus* (MONESTIER)]. Ribs fine, straight to slightly curved, moderately dense to dense. Primaries regularly bifurcate at small ventrolateral tubercles; secondaries are bent forward on the venter. Intricate suture-line: long and wide E, shorter, ramified L, straight, short U lobes, wide ES, low and asymmetrically divided LS1.

Remarks: *Zugodactylites* was treated in detail by e.g. FISCHER (1966), PINNA & LEVI-SETTI (1971), HOWARTH (1978), and RULLEAU et al. (2013). The genus probably derived from (*D.*) *Dactylioceras* in the lower Sublevisoni Subzone. It is characterized by sexual dimorphism, the microconch genus *Gabillytes* GUEX was described from France and England. Based on morphology and stratigraphic range, *Planicoeloceras* VENTURI et FERRI, 2001 is considered here as a synonym of *Zugodactylites*.

Distribution: Bifrons Zone: NW European Province (France, Northern Spain, England, Bulgaria, Romania, Russia), Mediterranean Province (Austria, Italy, Southern Spain, Portugal, ?Algeria). It was also recorded from the Spitsbergen, Iran, New Zealand, and North America. Hungary: Bakony Mts (Úrkút), Gerecse Mts. In the Gerecse sections, the acme of the genus coincides with that of *Frechiella* in the Lusitanicum horizon (KOVÁCS 2010).

Zugodactylites braunianus (D'ORBIGNY, 1845)
(Plate 1, figs 4–5, 9)

1845 *Ammonites braunianus* — D'ORBIGNY, p. 327, pl.104, figs 1–3
v 1966 *Zugodactylites sapunovi* n. sp. — GÉCZY, p. 440, pl. 1, fig. 3
v 2007 *Zugodactylites pseudobraunianum* (MONESTIER) — GÉCZY & SZENTE, pl. 1, figs 1–2
2008 *Zugodactylites braunianus* (D'ORBIGNY) — GÉCZY et al., pl. 1, fig. 9

Material: 35 specimens in different state of preservation (2014.38.1–34, and one specimen from the private collection of Mihály DUNAI).

M	D	H	H/D	W	W/H	Uw	Uw/D
MDPC2013.1	90	18	20%	?16	88.8%	57	63.3%
2014.38.1	61	14	23%	14	100%	33	54%
2014.38.2	53	11	20.7%	9	81.8%	32	60.3%
2014.38.3	48	10	20.8%	8	80%	30	62.5%
2014.38.4	43	10	23.2%	6	60%	25	58.1%
2014.38.5	40	11	27.5%	10	91%	20	50%

Description: Evolute, compressed coiling; shallow umbilicus, narrow, suboval whorl-section; high, rounded venter. Fine, straight to slightly curved, dense primaries bifurcate regularly at small ventrolateral tubercles, the secondaries are forwardly projected. The shell moderately varies in whorl width.

Remark: The specimen figured by GÉCZY & SZENTE (2007, pl. 1, figs 1–2, 2014.38.9) lacks the ventral keel, and is characterized by a narrow whorl that is not typical of *Z. pseudobraunianus*.

Distribution: Gerecse sections: Sublevisoni Subzone.

Zugodactylites rotundiventer BUCKMAN, 1927
(Plate 1, fig. 6)

1927 *Zugodactylites rotundiventer* — BUCKMAN, pl. 743
1978 *Zugodactylites rotundiventer* BUCKMAN — HOWARTH, p. 272, pl. 7, figs 5–6 *(cum syn.)*

Material: Eight poorly preserved specimens (2014.39.1–8).

Measurements	D	H	H/D	W	W/H	Uw	Uw/D
2014.39.1	45	11	24.4 %	14	127.2 %	24	53.3 %
2014.39.2	41	10	24.4 %	13	130%	18	44%

Description: Evolute coiling; wide, rounded venter, depressed suboval whorl-section. Ribbing similar to that of *Z. braunianus*.

Remark: *Z. rotundiventer* differs from *Z. braunianus* in wide whorls and low venter.

Distribution: Gerecse sections: Sublevisoni Subzone.

Genus *Peronoceras* HYATT, 1867

Type-species: *Ammonites fibulatus* J. DE C. SOWERBY, 1823.

Diagnosis: Evolute, compressed to depressed cadicone coiling, slightly convex flanks, low venter, subrectangular whorl-section. Ribs strong, prorsiradiate, fibulate on inner whorls, tuberculate to spined on ventrolateral shoulder. Suture-line: long, wide E, shorter, wide L, wide, ramified saddles.

Remarks: *Peronoceras* was treated in detail by e.g. HOWARTH (1978), and RULLEAU et al. (2013). The genus appeared in the upper Sublevisoni Subzone, it is the descendant of either (*D.*) *Dactylioceras* or *Zugodactylites*. It differs from

Porpoceras Buckman in regularly fibulate inner ribbing. The Mediterranean *Fibulocoeloceras* Venturi et Ferri differs in sculpture with alternating simple and fibulate ribs.

Distribution: Bifrons to lowermost Variabilis/Gradatus Zones: Europe, North Africa, the Caucasus, the Pamir, Iran, Vietnam, Japan, North and South America. Hungary: Mecsek Mts, Bakony Mts (Szentgál, Úrkút), Gerecse Mts.

Peronoceras subarmatum (Young et Bird, 1822)
(Plate 1, fig. 8, Plate 2, fig. 1, Plate 3, fig. 6)

1822 *Ammonites subarmatus* — Young & Bird, p. 250, pl. 13, fig. 3
v 2007 *Peronoceras subarmatum* (Young et Bird) — Géczy & Szente, pl. 8, fig. 1
v 2008 *Peronoceras subarmatum* (Young et Bird) — Géczy et al., pl. 1, fig. 12

Material: Ten specimens in different state of preservation (2014.44.1–10).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.44.1	95	18	18.9%	30	166.6%	56	59%
2014.44.4	87	20	23%	22.5	112.5%	50	57.4%
2014.44.2	77	17	22%	25	147%	45	58.4%
2014.44.3	57	14	24.5%	?20	142.8%	30	52.6%

Description: Evolute coiling, oblique flanks, broad, low, rounded venter, depressed, subrectangular section. The preserved body chamber more than one whorl in length. Primary ribs well-developed, regularly fibulate on inner whorls, trifurcate at ventrolateral spines. On the body chamber, trifurcating, spined ribs alternate with simple, or bifurcating, non-tuberculate ribs. Secondaries cross the venter in a zigzag pattern between spines that are not opposite each other.

Remarks: According to Rulleau et al. (2013), some records of *P. subarmatum* from the Mediterranean Province (Italy, Greece, Austria) might represent *Telodactylites* species. The Gerecse specimens are close to the type (refigured by Rulleau et al. 2013, pl. 34, fig. 4) in morphology.

Distribution: Gerecse sections: Bifrons Subzone to the lowermost Clausus Subzone.

Genus *Porpoceras* Buckman, 1911

Type-species: *Ammonites vortex* Simpson, 1855.

Diagnosis: Evolute coiling, subrectangular whorl-section. Fibulate, tuberculate to spined, bifurcating primary ribs alternate with nontuberculate, bifurcating ribs. The suture-line is similar to that of *Peronoceras*.

Remarks: The genus was dealt with by e.g. Howarth (1978), Jiménez & Rivas (1991), and Rulleau et al. (2013). *Porpoceras* probably derived from *Peronoceras* from that it differs in lack of regular fibulation.

Distribution: Bifrons to lower Variabilis/Gradatus Zones: Europe, the Caucasus, Iran, Pakistan, Russia, North and South America. Hungary: Bakony Mts (Csernye), Gerecse Mts.

Porpoceras vortex (Simpson, 1855)
(Plate 2, figs 2, 7, Plate 4, fig. 5)

1855 *Ammonites vortex* — Simpson, p. 60
v 2007 *Porpoceras vortex* (Simpson) — Géczy & Szente, pl. 8, fig. 4
2013 *Porpoceras* gr. *vortex* (Simpson)□*verticosum* Buckman — Rulleau et al., p. 101, pl. 29, fig. 2, pl. 30, figs 1–2, pl. 31, figs 1, 3, 5, pl. 32, figs 1, 3–6, pl. 33, figs 1–2, pl. 34, fig. 1

Material: 26 specimens in different state of preservation (2014.45.1–26).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.45.1	93	19	20.4%	21	110.5%	58	62.3%
2014.45.2	91	18	19.7%	17	94.4%	58	63.7%
2014.45.3	90	18	20%	20	111%	53	58.8%
2014.45.4	83	17	20.4%	16	94%	?	?
2014.45.5	78	15	19.2%	17	113.3%	48	61.5%
2014.45.6	63	14	22.2%	16	114.2%	35	55.5%

Description: Evolute coiling, shallow umbilicus, slightly convex flats, low venter, depressed, subrectangular whorl-section. The body chamber is about 10/8 whorl in length, the peristome is oblique. Irregularly fibulate, tuberculate ribs on the inner whorls, while trifurcating, spined ribs alternate with simple ribs on the external whorls. Ventrolateral spines alternate on the two sides of the venter. Secondaries show a zigzag pattern on the venter.

Distribution: Gerecse sections: Semipolitum to Gemma horizons.

Porpoceras cf. *vorticellum* (Simpson, 1855)
(Plate 2, figs 3–4)

1855 *Ammonites vorticellus* — Simpson, p. 61
1967a *Peronoceras* n. sp. aff. *vorticellum* (Simpson) — Geczy, p. 99, text-fig. 97, pl. 26, fig. 11
1991 *Porpoceras vorticellum* (Simpson) — Jimenez & Rivas, p. 176, pl. 7, figs 2–4 *(cum syn.)*

Material: Three poorly preserved specimens (2014.46.1–3).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.46.1	?58	15	25.8%	14	93.3%	36	62%
2014.46.2	35	7	20%	?	?	19	54.2%
2014.46.3	31	8	25.8%	9	112.5%	17	54.8%

Description: Evolute coiling, flat flanks, low venter, subquadrate whorl-section. Primary ribs sharp, prorsiradiate, irregularly fibulate. Almost each primary rib bifurcates at ventrolateral shoulder, tuberculate and simple furcating points alternate.

Remarks: The species differs from *P. vortex* in denser and weaker ribbing, and in weakly developed tubercles.

Distribution: Gerecse Mts: Lusitanicum to Semipolitum horizon: Pisznice, Bánya Hill A, and Kis-Gerecse Sections.

Porpoceras beurleni (Monestier, 1931)
(Plate 2, fig. 5)

1931 *Caeloceras* (*Porpoceras*) *Beurleni* n. sp. — Monestier, p. 48, pl. 1, figs 31, 35, pl. 9, fig. 11

1972 *Porpoceras beurleni* (Monestier) — Guex, p. 632, pl. 9, fig. 14, pl. 12, fig. 15

v 2007 *Peronoceras beurleni* (Monestier) — Géczy & Szente, pl. 1, fig. 3 (refigured here)

Material: One moderately preserved adult specimen (2014.47.1).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.47.1	57	12	21%	17	141.6%	33	57.8%

Description: Evolute coiling, convex flanks, flat venter, depressed, rounded subrectangular whorl-section. The preserved body chamber is a half whorl long. Primary ribs are strong, rectiradiate, distant, bifurcate, rarely trifurcate at ventrolateral tubercles. On the body chamber simple ribs appear irregularly crossing the venter and joining a tubercle on the opposite side. Fibulate ribs occur at the end of the last whorl. The sharp secondaries cross the venter in a zigzag pattern.

Remark: The specimen agrees with the neotype designated by Guex (1972).

Distribution: France. Gerecse Mts: Semipolitum horizon: Pisznice Section.

Genus *Catacoeloceras* Buckman, 1923

Type-species: *Catacoeloceras confectum* Buckman, 1923

Diagnosis: Moderately involute, depressed coiling, convex flanks, low, rounded venter, simple or bifurcating ribs, regular ventrolateral tubercles. Intricate suture-line: wide, developed E, somewhat shorter, trifid L, short U lobes, wide, ramified saddles.

Remarks: *Catacoeloceras* is the descendant of either *Peronoceras* or *Porpoceras*. It is characterized by sexual dimorphism, genus *Mucrodactylites* Buckman is considered as microconch. *Catacoeloceras* —mainly *C. crassum* (Young et Bird)— had been recorded many times from the lower Middle Toarcian of the Mediterranean Province (Pinna 1966). However, stratigraphical and paleobiogeographical revisions of the genus (Pinna & Levi-Setti 1971, Hengsbach 1985, Riegraf 1986, Rulleau et al. 2013) made it obvious that most figured specimens in the literature represent *Nodicoeloceras* taxa.

Distribution: Bifrons Subzone to middle Variabilis/Gradatus Zone: Europe, North Africa, Turkey, the Caucasus, Russia, Greenland, Indonesia, New Zealand, North and South America. Hungary: Bakony Mts (Csernye), Gerecse Mts. In the Gerecse sections it is known from the Gradatus Zone.

Catacoeloceras dumortieri (de Brun, 1932)
(Plate 2, fig. 6)

1932 *Coeloceras Dumortieri* n. sp. — de Brun, p. 106, pl. 5, fig. 3

v 2008 *Catacoeloceras dumortieri* (de Brun) — Géczy et al., p. 37, pl. 1, fig. 11 *(cum syn.)*

2013 *Catacoeloceras dumortieri* (de Brun) — Rulleau et al., p. 110, pl. 37, figs 2–3, 5–6, 8, pl. 38, figs 1–2

Material: One complete and one fragmentary specimens (2014.50.1–2).

Measurements	D	H	H/D	W	W/H	Uw	Uw/D
2014.50.1	48	10	20.8%	14	140%	23	48%

Description: Evolute coiling, slightly convex flanks, low, rounded venter, smooth on adult body chamber. The body chamber is somewhat shorter than one whorl in length, it becomes narrower on the last quarter whorl, the peristome is oblique, projected. Primary ribs straight, prorsiradiate, bifurcating at small ventrolateral tubercles, secondaries forwardly-curved.

Distribution: France, England, Germany, Italy, Austria, North Africa. Gerecse Mts: Gemma horizon: Kis-Teke Hill Section (2014.50.1), Subregale Subzone: Tölgyhát A Section (2014.50.2).

Catacoeloceras raquinianum (d'Orbigny, 1844)
(Plate 3, figs 1–2)

1844 *Ammonites Raquinianus* — d'Orbigny, p. 332, pl. 106, figs 1–5

2013 *Catacoeloceras raquinianum* (d'Orbigny) — Rulleau et al., p. 111, text-fig. 42, pl. 38, figs 3–7, pl. 39, figs 6, 8–11, pl. 42, fig. 7

Material: One adult specimen (2014.51.1), and one wholly septate specimen from the private collection of Zoltán EVANICS.

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.51.1	68	?15	22%	20	133.3%	?38	55.8%
EZPC.2013.2	43	12	28%	18	150%	21	48.8%

Description: Evolute coiling, convex flanks, broad, rounded venter, depressed, suboval whorl-section. The preserved body chamber is 3/4 whorl in length. Primary ribs strong, slightly prorsiradiate on the inner, rectiradiate on the last whorl, regularly bifurcating at small ventrolateral tubercles.

Remark: The species is typical of the NW European Province.

Distribution: France, Luxembourg, Germany, England, Spain, Bulgaria, ?Romania, Austria, ?Iran, ?Caucasus. Gerecse Mts: Tölgyhát Quarry and Bánya Hill Quarry Section without exact stratigraphic positions.

Genus *Mucrodactylites* BUCKMAN, 1927

Type-species: *Ammonites mucronatus* D'ORBIGNY, 1845

Diagnosis: Small shell, evolute, compressed coiling, rounded venter, suboval to subquadrate whorl-section, strong, simple and bifurcating primary ribs, projected secondaries. Suture-line: simple dactylioceratid with long, wide E, short, trifid L, short U lobes, high ES, wide, less ramified LS.

Remarks: Taxonomic treatments were presented by e.g. GUEX (1973), ATROPS & MOUTERDE (1994), METODIEV (2003), and RULLEAU et al (2013). Species assigned to the genus are thought to be microconch forms of *Catacoeloceras*. *Mucrodactylites* was considered as a synonym of *Collina* by HOWARTH (2013).

Distribution: Bifrons Subzone to Lower Variabilis Zone: NW European localities, Italy, Austria, ?Greece, North Africa, North and South America, Russia, Spitsbergen. Hungary: Mecsek Mts, Gerecse Mts.

Mucrodactylites mucronatus (D'ORBIGNY, 1845)
(Plate 3, figs 3–4)

1845 *Ammonites mucronatus* — D'ORBIGNY, p. 328, pl. 104, figs 4–8

1994 *Mucrodactylites mucronatus* (D'ORBIGNY) — ATROPS & MOUTERDE, p. 92, pl. 33, figs 4–6

2013 *Mucrodactylites mucronatus* (D'ORBIGNY) — RULLEAU et al., p. 116, pl. 43, figs 1–8

Material: Two fragmentary specimens (2014.52.1–2), and one adult, complete specimen from the private collection of Mihály DUNAI.

M	D	H	H/D	W	W/H	Uw	Uw/D
DMPC.2013.3	39	9	23%	12.5	138.8%	22	56.4%
2014.52.1	38	10	26.3%	12	120%	20	52.6%
2014.52.2	35	9	25.7%	?9	100%	18.5	52.8%

Description: Evolute coiling, convex flanks, low, rounded venter, subrectangular whorl-section. The body chamber is 3/4 whorl in length, the peristome is preceded by a constriction. Primary ribs distant, sharp, rectiradiate, straight, bifurcating at small ventrolateral tubercles. Secondaries strong, forwardly projected, crossing the venter in pairs or in irregular zigzag pattern.

Remark: The species is regarded as microconch form of *C. raquinianum* in the literature.

Distribution: Gerecse Mts: Specimen 2014.52.2 came from the lower Subregale Subzone of the Kis-Teke Hill Section, the others were collected in the Bánya Hill Quarry Section, their exact stratigraphic positions are unknown.

Mucrodactylites sp.
(Plate 7, fig. 5)

Material: One fragmentary, adult specimen (2014.53.1).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.53.1	30	8	26.6%	9	112.5%	17	56.6%

Description: Evolute coiling, rounded flanks and venter. The whorl-section is depressed subrectangular on the inner whorls, subcircular on the body-chamber. Ribs strong, rectiradiate, moderately dense, tuberculate at the furcation points on the inner whorls. Simple and bifurcating primaries alternate, secondaries are slightly forwardly bent. The ribbing becomes prorsiradiate at the peristome.

Remark: The density of ribs of the specimen differs from that of most *Mucrodactylites* species, it resembles the example figured by PINNA & LEVI-SETTI (1971, pl. 11, fig. 6).

Distribution: Gerecse Mts: Apertum horizon of the Pisznice Section, Bed 123.

Genus *Septimaniceras* FAURE, 2002

Type-species: *Ammonites zitteli* OPPEL, 1862

Diagnosis: Small shell, evolute coiling, cadicone inner whorls, subquadrate external whorls, distant to dense, tuberculate ribs with weak ribs between them on the inner whorls, alternating simple and looped ribs with ventrolateral tubercles on the last whorl. Suture-line: long, wide E, short, trifid L lobes, less ramified saddles.

Remarks: *Septimaniceras* was dealt with by FAURÉ (2002), HOWARTH (2013), and RULLEAU et al. (2013). It probably derived from *Peronoceras*. The genus is characterized by sexual dimorphism.

Distribution: Bifrons Subzone to Lower Variabilis Zone: France, ?Austria.

Septimaniceras cf. *nicklesi* (GUEX, 1971)

(Plate 3, fig. 5)

1971 *Collina nicklesi* n. sp. — GUEX, p. 238, pl. 2, fig. 3
2002 *Septimaniceras nicklesi* (GUEX) — FAURÉ, p. 712, pl. 9, fig. 24 (*cum syn.*)
2013 *Septimaniceras nicklesi* (GUEX) — RULLEAU et al., pl. 46, figs 6–11

Material: One adult macroconch specimen (2014.54.1).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.54.1	22.5	7	31%	8	114.2%	11	48.8%

Description: Evolute coiling, parallel flanks, low, slightly rounded venter, subquadrate whorl-section. The body-chamber is 3/4 whorl in length. Ribs slightly prorsiradiate, simple or fibulate and bifurcating at ventrolateral tubercles. The primaries become concave close to the peristome. Secondaries forwardly bent.

Remarks: The ornamentation with densely ribbed inner whorls is similar to that of *S. pseudoyoungi* (GUEX), but the almost flat ventral part, the whorl-section, and the sculpture of the last whorl are closer to that of the holotype of *S. nicklesi*, and to that of the examples represented in the literature. The state of preservation, however, does not allow the precise identification.

Distribution: Gerecse Mts: Bánya Hill Quarry Section, the exact stratigraphic position is unknown.

Subfamily Nodicoeloceratinae VENTURI et FERRI, 2001

The validity of the taxon is debated in the literature. Based on phylogenetic, morphological and paleobiogeographical considerations, it is accepted by authors who deal with the Mediterranean faunal province. The origin of the earliest representative (*Nodicoeloceras*) shows uncertainty. It derived from either (*D.*) *Orthodactylites* or *Kedonoceras* DAGIS in the uppermost Tenuicostatum Zone, and it was the ancestor of the characteristic Mediterranean dactylioceratid genus *Mesodactylites*.

Genus *Nodicoeloceras* BUCKMAN, 1926

Type-species: *Ammonites crassoides* SIMPSON, 1855.

Diagnosis: Moderately evolute to cadicone coiling, depressed whorls, convex flanks, low venter, ribs bifurcating at ventrolateral shoulder, ventrolateral tubercles or spines usually present. Intricate suture-line: wide, developed E and L, short U lobes, ramified saddles.

Remarks: Taxonomic treatments were presented by e.g. PINNA & LEVI-SETTI (1971), SCHMIDT-EFFING (1972), HOWARTH (1978), JIMÉNEZ & RIVAS (1991), and RULLEAU et al. (2013). A few taxa have been interpreted as morphotypes of the characteristic NW European species *Nodicoeloceras crassoides* (SIMPSON).

Distribution: Serpentinum to Bifrons Zones: Europe, Russia, North Africa, the Caucasus, Iran, Pakistan, Indonesia, North and South America. Hungary: Bakony Mts (Csernye, Szentgál, Úrkút), Gerecse Mts. In the Gerecse sections, the genus appears in the Serpentinum Subzone, it is abundant in the Sublevisoni Subzone, and disappears from the fauna in the upper Bifrons Subzone.

Nodicoeloceras cf. *choffati* (RENZ, 1912)

(Plate 3, fig. 7)

1912a: *Coeloceras Choffati* n. sp. — RENZ, p. 86, pl. 6, fig. 5.
1971: *Nodicoeloceras* choffati (RENZ) — PINNA & LEVI-SETTI, p. 100, p. 128, text-figs 14/M, 18/A, 21/26, pl. 4, figs 3–7, 10, 13 (*cum syn.*).
2012 *Nodicoeloceras* cf. *choffati* (RENZ) — KOVÁCS, p. 20, pl. 5, figs 1–2 *(cum syn.)*

Material: One poorly preserved specimen (222.2011).

Measurements	D	H	H/D	W	W/H	Uw	Uw/D
222.2011	46	12	26%	30	250%	19	41.3%

Description: Evolute coiling, deep umbilicus, oblique umbilical walls, slightly convex flanks, well-pronounced ventrolateral shoulder, low, broad and rounded venter, wide, rounded diamond-shaped whorl-section. No body chamber is preserved. Primary ribs rectiradiate, bi- or trifurcating at pronounced ventrolateral tubercles. Secondaries slightly forwardly bent, crossing the venter. Intricate suture-line.

Remarks: The specimen is similar to the type (RENZ 1912a, pl. 6, fig. 5) and to those figured in the literature, but the poor state of preservation does not allow the certain identification.

Distribution: Portugal, France, Italy, Greece, Austria, North Africa, South America. Gerecse Mts: Striatus horizon: Bánya Hill B Section.

Nodicoeloceras crassoides (SIMPSON, 1855) morphotype *multum* (BUCKMAN, 1928)
(Plate 3, fig. 8)

1926 *Multicoeloceras multum* — BUCKMAN, p. 42, pl. 785
v 1966 *Nodicoeloceras* n. sp. aff. *multum* (BUCKMAN) — GÉCZY, p. 433, pl. 2, fig. 6

Material: Four fragmentary specimens (2014.29.1–4).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.29.1	53	14	26.4%	22	157%	23	43.4%

Description: Moderately evolute coiling, convex flank, rounded venter, wide, depressed, rounded subrectangular section. The length of the body chamber cannot be searched, the peristome is preceded by a wide constriction. Primary ribs sharp, straight, slightly prorsiradiate, simple or bi-trifurcating at the shoulder. Several furcation points bear small tubercles, secondaries straight. The suture-line is richly ornate with long, ramified lobes and saddles.

Remark: *N. tuberculatum* differs in subrectangular section, and in ornamentation with stronger tubercles and fibulate ribs on adult body chamber.

Distribution: Bifrons Zone: England. Hungary: Bakony Mts (Úrkút). Gerecse Mts: Lusitanicum to Apertum horizons: Pisznice and Kis-Gerecse Sections.

Nodicoeloceras crassoides (SIMPSON, 1855) morphotype *fonticulum* (SIMPSON, 1855)
(Plate 4, fig. 1)

1855 *Ammonites fonticulus* — SIMPSON, p. 57
1912 *Coeloceras fonticulum* (SIMPSON) — BUCKMAN, pl. 59
1967a *Peronoceras* cf. *fonticulum* (SIMPSON) — GÉCZY, p. 98, text-fig. 95, pl. 26, fig. 2
2012 *Catacoeloceras crassum* (YOUNG et BIRD) — KOVÁCS, p. 18, pl. 5, figs 3–4

Material: 3 wholly septate specimens (2014.28.1–3).

Measurements	D	H	H/D	W	W/H	Uw	Uw/D
215.2011	50	14	28%	24	170%	24	48%

Description: Moderately evolute coiling, convex flank, rounded venter, depressed subrectangular section. Primary ribs strong, rectiradiate, bifurcating at the shoulder. Tuberculate and non-tuberculate ribs alternate.

Remarks: *N. fonticulum* resembles *N. tuberculatum* in morphology, but differs in more depressed whorls and regular ornamentation.

Distribution: Serpentinum to Bifrons Zones: England, France, Luxembourg, Germany, Bulgaria, Italy, Greece, Spain, the Caucasus. Hungary: Bakony Mts (Csernye). Gerecse Mts: Lusitanicum horizon: Cocodile and Bánya Hill B Sections, Bifrons horizon: Kis-Teke Hill Section.

Nodicoeloceras tuberculatum (KOTTEK, 1966)
(Plate 4, figs 2–4, 6–7, Pl. 5, figs 6–7)

1966 *Catacoeloceras tuberculatum* n. sp. — KOTTEK, p. 135, text-fig. 65, pl. 17, figs 1–3
v 1966 *Peronoceras baconicum* n. sp. — GÉCZY, p. 438, pl. 1, fig. 2
2012 *Nodicoeloceras tuberculatum* (KOTTEK) — KOVÁCS, p. 18, pl. 6, figs 3–4 *(cum syn.)*

Material: 83 specimens in different state of preservation (Middle Toarcian: 2014.30.1–72, and one specimen from the private collection of Zoltán EVANICS).

M	D	H	H/D	W	W/H	Uw	Uw/D
221.2011	92	21	22.8%	23	109.5%	50	54.3%
EZPC7536	75	16	21.3%	21	131.2%	42	56%
2014.30.1	67	15	22.3%	20	133.3%	40	59.7%
2014.30.2	51	13	25.5%	18	138.4%	27	53%
2014.30.3	50	12.5	25%	18	144%	27	54%
2014.30.4	47	13	27.6%	20	153.8%	23	49%
2014.30.5	45	11	24.4%	20	181.8%	23	51%
2014.30.6	33	9	27.2%	16	177.7%	16.5	50%

Description: Evolute coiling, convex flanks, broad and low venter, depressed, rounded subrectangular whorl-section. The body chamber is 5/4 whorl in length. Primary ribs strong, rectiradiate, bifurcating at ventrolateral tubercles on the phragmocone. On the body chamber one or two simple ribs alternate with bifurcating ribs, as well as fibulate bifurcating primaries occur irregularly that resemble the sculpture of *Peronoceras desplacei* (D'ORBIGNY).

Remarks: *N. tuberculatum* specimens show moderate variability in whorl-section and in style of ribbing. The species is close to *N. crassoides* (Simpson) in morphology, but differs in depressed subrectangular section, and tuberculate–fibulate sculpture. *N. angelonii* (Ramaccioni) is similar in size and morphology, but differs in subcircular section, and in lack of fibulate ribs. The genus level classification of the species is discussed in the literature. It is placed within *Nodicoeloceras* here because the phragmocone bear tuberculate but non-fibulate ribbing, therefore the ornamentation differs from that of genera *Mesodactylites* and *Peronoceras*. The taxon can be recognized as the Mediterranean counterpart of *N. crassoides*.

Distribution: Greece, Italy, North Africa, the Caucasus. Hungary: Bakony Mts, Gerecse Mts. In the Gerecse sections *N. tuberculatum* is the most frequent species of the genus, it ranges in the Falciferum Subzone (13 specimens) to the Bifrons Zone (lowermost Semipolitum horizon) (70 specimens).

Nodicoeloceras crassoides (Simpson, 1855)
morphotype cf. *lobatum* (Buckman, 1927)
(Plate 5, fig. 4)

1927 *Lobodactylites lobatum* — Buckman, pl. 730
1967a *Catacoeloceras* cf. *lobatum* (Buckman) — Géczy, p. 95, text-fig. 92, pl. 26, fig. 5
1971 *Nodicoeloceras lobatum* (Buckman) — Pinna & Levi-Setti, p. 103, text-figs 14/S, U, 21/18, pl. 4, fig. 8, pl. 5, figs 1–2, 7
2002 *Nodicoeloceras lobatum* (Buckman) — Fauré, p. 709, pl. 9, fig. 5

Material: Four wholly septate specimens (2014.27.1–4).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.27.1	38	10.5	27.6%	13	123.8%	18.5	48.6%

Description: Evolute coiling, convex flanks, almost flat venter, rounded subrectangular whorl-section. Rectiradiate, simple and bifurcating primary ribs alternate. Ventrolateral furcating points bear weakly developed tubercles, the secondaries cross the venter. The suture-line is richly ornate with ramified lobes and saddles.

Remarks: The species differs from both the nominate species and *N. tuberculatum* in narrower whorls, and in finer and denser ribbing without fibulation.

Distribution: England, France, Italy. Hungary: Bakony Mts (Csernye). Gerecse Mts: Sublevisoni horizon: Kis-Gerecse Section, Lusitanicum horizon: Tölgyhát Section, Semipolitum horizon: Pisznice Section.

Nodicoeloceras angelonii (Ramaccioni, 1939)
(Plate 5, figs 1, 3)

1939 *Deroceras Angelonii* (Mgh.) — Ramaccioni, p. 182, pl. 12, fig. 13
1971 *Nodicoeloceras angelonii* (Ramaccioni) — Pinna & Levi-Setti, p. 104, text-figs 12/G, 14/T, 15/G, 18/B, 21/24, pl. 5, figs 9–10, pl. 6, figs 2–4
1991 *Nodicoeloceras* gr. *angelonii* (Ramaccioni) — Jiménez & Rivas, p. 167, pl. 7, fig. 5
2013 *Nodicoeloceras angelonii* (Ramaccioni) — Metodiev et al., p. 71 (partim), fig. 3/j–k

Material: Five specimens in different state of preservation (2014.31.1–5).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.31.1	65	15	23%	?20	133%	36	55.3%
2014.31.2	50	12	24%	14	116.6%	27	54%

Description: Evolute coiling, convex flanks, rounded venter, subcircular whorl-section. Ribs sharp, rectiradiate, simple or bifurcating at small ventrolateral tubercles, dense on the phragmocone, somewhat distant on the body chamber. Fibulation absent.

Distribution: Italy, Greece, Southern Spain, Montenegro, Morocco. Hungary: Bakony Mts (Szentgál). Gerecse Mts: Sublevisoni Subzone: Pisznice, Bánya Hill A and Tölgyhát Sections.

Nodicoeloceras dulaii n. sp.
(Plate 5, fig. 5)

Holotype: 2014.32.1 (Eötvös Museum of Natural History)

Derivation of name: In honour of Alfréd Dulai, Hungarian paleontologist.

Type locality and horizon: Sublevisoni Subzone, Bánya Hill A Section, Tardos, Gerecse Mts.

Material: 1 well-preserved internal mold of an adult specimen.

Measurements:

M	D	H	H/D	W	W/H	Uw	Uw/D	PRL W
2014.32.1	44	11	25%	13.5	122%	24	54%	65

Diagnosis: Evolute coiling, subquadrate whorl-section, sharp, rectiradiate, simple and bifurcating, tuberculate ribbing.

Description: Evolute coiling, moderately deep umbilicus, low umbilical wall, rounded margin, slightly convex, parallel flanks, rounded shoulder, flat venter, subquadrate whorl-section. The last whorl is slightly eccentric. The preserved part of the body chamber is 9/8 whorl in length. The ribs are sharp and rectiradiate. Simple and bifurcating primaries alternate, furcating points bear well-developed ventrolateral tubercles. A few fibulate ribs appear irregularly on the phragmocone. The ribbing changes in style on the last half whorl, bifurcating fibulate pairs of primaries alternate with simple ribs. The secondaries are straight. Suture-line is dactylioceratid.

Remarks: Based on style of coiling, on irregular fibulation, on regularly tuberculate ribbing, and on lack of zigzag pattern of secondary ribs the new species is placed within genus *Nodicoeloceras*. Considering the size, and the appearance among abundant *N. tuberculatum*, the new species possibly represents a microconch form of the genus. *N. dulaii* n. sp. is similar to *N. tuberculatum* in ornamentation with fibulate ribs on the body chamber, however, it differs in size, and in subquadrate section. Two specimens figured by PINNA & LEVI-SETTI (1971) resemble the new species: *Peronoceras andrei* (SIMPSON) on plate 11, fig. 10, and *P. fibulatum* (SOWERBY) on fig. 16 bear similar fibulate sculpture, but both have more involute coiling with higher whorls.

Distribution: The specimen came from Bed 44 of the Bánya Hill A Section associated with *Hildoceras lusitanicum*, *Nodicoeloceras tuberculatum* (34 specimens), *N. angelonii*, *Mesodactylites annulatiformis* (BONARELLI), *Polyplectus pluricostatus* HAAS, *Phymatoceras elegans* (MERLA).

Genus *Mesodactylites* PINNA et LEVI-SETTI, 1971

Type-species: *Coeloceras annulatiforme* BONARELLI, 1899, designated by PINNA & LEVI-SETTI (1971).

Diagnosis: Small to medium-sized, cadicone to moderately evolute coiling, convex flanks, rounded venter, subcircular section, ribs simple or bifurcating, ventrolateral tubercles mainly on the phragmocone. Suture-line: wide, long E, shorter, trifid L, short U lobes, wide, divided saddles.

Remarks: Detailed treatments of *Mesodactylites* were presented by e.g. PINNA & LEVI-SETTI (1971), DEZI & RIDOLFI (1975), VENTURI & FERRI (2001), VENTURI et al. (2010), and RULLEAU et al. (2013). The genus was recently recognized as a synonym of *Nodicoeloceras* by HOWARTH (2013). *Mesodactylites* is typical of the Mediterranean Province, as the descendant of *Nodicoeloceras*.

Distribution: Serpentinum to Bifrons Zones: Italy, Greece, Southern Spain, Portugal, Austria, Southern France, North Africa. Hungary: Bakony Mts (Úrkút), Gerecse Mts: Lower—Middle Toarcian.

Mesodactylites annulatiformis (BONARELLI, 1899)
(Plate 5, fig. 2, Plate 6, fig. 1)

1867–1881 *Ammonites* (*Stephanoceras*) *Desplacei* D'ORBIGNY — MENEGHINI, p. 76, pl. 16, figs 7–8.
1899 *Coeloceras annulatiforme* — BONARELLI, p. 212
2012 *Mesodactylites* aff. *annulatiformis* (BONARELLI) — KOVÁCS, p. 20, pl. 4, figs 6–7 *(cum syn.)*

Material: Five poorly preserved specimen (217.2011, 2014.33.1–4).

M	D	H	H/D	W	W/H	Uw	Uw/D
217.2011	78	18	23%	18	100%	?	?
2014.33.1	60	14	23.3%	18	128.5%	31	51.6%

Description: Moderately evolute coiling, shallow umbilicus, convex flanks, low, rounded venter, and subcircular whorl-section. The body chamber 5/4 whorl long. Ribs moderately dense, sharp, rectiradiate, passing the venter. Some primaries bifurcate above the mid-height at small tubercles, others bifurcate without any tubercles. 1–2 simple ribs occur between bifurcating ribs.

Distribution: Italy, Portugal, Greece, North Africa, (?)Austria, (?)northern Spain. Gerecse Mts: Four specimens from the Serpentinum Subzone. The specimen figured here came from the Sublevisoni Subzone in the Bánya Hill A Section.

Mesodactylites mediterraneus (RENZ, 1912)
(Plate 6, fig. 2)

1912a: *Coeloceras Desplacei* D'ORB. n. var. *mediterranea* — RENZ, p. 68
1971: *Mesodactylites mediterraneus* (MEISTER) — PINNA & LEVI-SETTI, p. 93, p. 127, text-fig. 21/1, pl. 2, figs 9, 13, 14, pl. 3, fig. 9 (*cum syn.*)
2012: *Mesodactylites mediterraneus* (RENZ) — KOVÁCS, p. 20, pl. 6, figs 1–2 (*cum syn.*)

Material: One moderately preserved specimen (225.2011).

M	D	H	H/D	W	W/H	Uw	Uw/D
225.2011	76	21	27.6%	26	123%	40	52.6%

Description: Evolute coiling, shallow umbilicus, rounded umbilical margin and ventrolateral shoulder, convex flanks, broad and low venter, depressed wide oval whorl-section. The preserved body chamber is one whorl in length. Moderately developed, radial, simple and bifurcating ribs alternate almost regularly, and cross the venter.

Remarks: *M. annulatiformis* is similar in morphology, but differs in more pronounced ribbing. *Nodicoeloceras crassoides* differs in wider whorls.

Distribution: Portugal, Spain, Italy, Greece, Algeria. Gerecse Mts: uppermost Pseudoserpentinum horizon: Bánya Hill B Section.

Mesodactylites broilii (MITZOPOULOS, 1930)
(Plate 6, figs 3–4)

1930 *Coeloceras* (*Dactylioceras*) *Broilii* (nov. spec.) — MITZOPOULOS, p. 89, pl. 8, fig. 5a–c
1985 *Catacoeloceras broilii* (MITZOPOULOS) — HENGSBACH, p. 390, text-fig. 23, pl. 9, figs 28–29

Material: 11 moderately preserved specimens (2014.34.1–11).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.34.1	33	10	30.3%	14	140%	15	45.4%
2014.34.2	31	10	32.2%	14	140%	13	42%
2014.34.3	30	9	30%	13	144.4%	13	43.3%
2014.34.4	27	8	29.6%	12	150%	11	40.7%

Description: Moderately evolute coiling, convex flanks, and broad, rounded venter. Whorl-section depressed suboval on the inner, while slightly higher, subcircular on the last half whorl. The body chamber is 5/4 whorl in length. Ribs dense, sharp, rectiradiate, alternating simple and bifurcating. Furcation point tuberculate on the inner whorls. Ribs more distant and prorsiradiate at the peristome.

Distribution: Italy, Austria, Spain, southern France, Romania. Gerecse sections: Lusitanicum to Gemma horizons.

Mesodactylites sapphicus (RENZ, 1912)
(Plate 6, fig. 5)

1912b *Coeloceras Sapphicum* RENZ (nov. spec.) — RENZ, p. 613, text-fig. 26
1966 *Dactylioceras annulatiforme sapphicum* (RENZ) — KOTTEK, p. 129
1971 *Mesodactylites sapphicus* (RENZ) — PINNA & LEVI-SETTI, p. 94, text-fig. 21/3, pl. 2, fig. 12, pl. 3, figs 1–3
v 2008 *Mesodactylites sapphicus* (RENZ) — GÉCZY et al., pl. 1, fig. 10

Material: Three specimens in different state of preservation (2014.35.1–3).

Measurements	D	H	H/D	W	W/H	Uw	Uw/D
2014.35.1	40	10	25%	15	150%	21	52.5%

Description: Moderately evolute, depressed coiling, convex flanks, broad venter, and rounded subrectangular whorl-section. The body chamber is 5/4 whorl in length. Ribs concave, bifurcating at the shoulder. Primaries fine on the phragmocone, ventrolateral tubercles at all fourth furcation point. Ribs simple, distant and strong on the last half whorl.

Distribution: Greece, Italy. Gerecse Mts: Lusitanicum horizon of the Bánya Hill A Section, and Gemma horizon of the Kis-Teke Hill Section.

Mesodactylites merlai (PINNA, 1969)
(Plate 6, figs 6–7)

1969 *Peronoceras merlai* n. sp. — PINNA, p. 16, pl. 4, fig. 9
1991 *Nodicoeloceras merlai* (PINNA) — JIMÉNEZ & RIVAS, p. 166, pl. 4, figs 9–14

Material: One wholly septate, and one fragmentary specimens (2014.36.1–2).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.36.1	63	16	25.3%	18	112.5%	34	54%
2014.36.2	45	10	22.2%	?	?	22	48.8%

Description: Moderately evolute coiling, convex flanks, rounded venter, depressed suboval to subcircular whorl-section. The preserved body chamber is more than one whorl in length. Primary ribs dense, rectiradiate to slightly prorsiradiate, simple or fibulate and tuberculate on the inner whorls, mostly simple on the second half of the last whorl.

Distribution: Italy, southern Spain. Gerecse Mts: Lusitanicum horizon: Pisznice Section.

Mesodactylites pisznicensis n. sp.
(Plate 6, fig. 8)

Holotype: 2014.37.1 (Eötvös Museum of Natural History)

Derivation of name: The name refers to the type locality.

Type locality and horizon: *Hildoceras apertum* horizon, Pisznice Section of Nagy-Pisznice Hill, Süttő region, Gerecse Mts.

Material: 1 well-preserved internal mold.

Measurements:

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.37.1	54	12	22.2%	20	166%	31	57.4%

Diagnosis: Medium-sized, evolute, depressed coiling, suboval whorl-section, sharp, simple or spined, bifurcating ribs.

Description: Evolute shell, wide, deep umbilicus, rounded umbilical margin and ventrolateral shoulder, convex flanks, broad, rounded venter, depressed, suboval section. The preserved body chamber is one whorl long, peristome absent. Primary ribs are sharp, slightly prorsiradiate, irregularly bifurcating at well-developed ventrolateral spines. 2–4 simple ribs occur between each bifurcating rib. There is a single fibulate–bifurcating pair of ribs on the body chamber. Suture-line is dactylioceratid.

Remarks: Based on suture-line and morphology, the new species is placed within genus *Mesodactylites*. It is closely allied to *M. merlai* in size and coiling, but differs in spined ribbing, and in lack of specific fibulate ribs on the inner whorls. Both *M. annulatiformis* and *Nodicoeloceras angelonii* differ in lack of spines, *N. tuberculatum* differs in higher whorls with tuberculate and fibulate ribbing, and *N. crassoides* (SIMPSON) differs in ornamentation and stratigraphic range. *N. spicatum* (BUCKMAN) bears similar spined ribbing on the inner whorls, but it is characterized by more involute coiling, higher whorls, and radial ribs.

Distribution: The specimen came from Bed 123 of the Pisznice Section associated with *Mucrodactylites* sp., *Hildoceras apertum* GABILLY, *Frechiella kammerkarensis* (STOLLEY), *Phymatoceras narbonense* (BUCKMAN), *Furloceras pulcher* (MERLA), and *F. speciosum* (MERLA).

Genus *Transicoeloceras* PINNA, 1966

Type-species: *Transicoeloceras angustum* PINNA, 1966.

Diagnosis: Small, involute to sphaerocone coiling, deep umbilicus, broad, convex venter, rounded subtrapezoid whorl-section with maximum thickness at the shoulder. Ribs fine, simple or furcating, tuberculate. Suture-line: wide, long E and L, short U lobes, wide, less intricate saddles.

Remarks: The genus was dealt with by PINNA (1966), PINNA & LEVI-SETTI (1971), JIMÉNEZ & RIVAS (1991), VENTURI & FERRI (2001), RULLEAU et al. (2013). It appeared in the Bifrons Subzone, and probably derived from *Mesodactylites*. The genus was recognized as *Catacoeloceras* by HOWARTH (2013), but the validity is sustainable for morphological, stratigraphical and geographical reasons.

Distribution: Bifrons to lower Gradatus Zones: Italy, Southern Spain, France, South America. Hungary: Bakony Mts (Úrkút), Gerecse Mts.

Transicoeloceras viallii PINNA, 1966
(Plate 7, figs 1–2, 7)

1966 *Transicoeloceras viallii* n. sp. — PINNA, p. 126, text-fig. 2/b, pl. 7, figs 16–17
1967b *Catacoeloceras tethysi* n. sp. — GÉCZY, p. 294, text-figs 1–7
1991 *Transicoeloceras viallii* (PINNA) — JIMÉNEZ & RIVAS, p. 176, pl. 7, figs 2–4 *(cum syn.)*

Material: Eight poorly preserved specimens (2014.40.1–8).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.40.1	23	10	43.4%	18	180%	6	26%
2014.40.2	20	7	35%	14	200%	?	?
2014.40.3	18	?	?	15	?	?	?

Description: Cadicone coiling, narrow, deep umbilicus, low, oblique flanks, and broad, rounded venter. Primary ribs fine, rectiradiate, often fibulate to strong ventrolateral tubercles, irregularly bi-, tri- or quadfurcating. Secondaries fine and dense.

Remarks: *T. viallii* moderately varies in ornamentation. The specimen presented by GÉCZY (1967b) as *tethysi* n. sp. bears a non-tuberculate body chamber with bifurcating ribs.

Distribution: Gerecse sections: Lusitanicum to Bifrons horizons.

Genus *Telodactylites* PINNA et LEVI-SETTI, 1971

Type-species: *Peronoceras eucosmus* LIPPI-BONCAMBI, 1947, designated by VENTURI & FERRI (2001).

Diagnosis: Small to medium-sized shell, evolute, depressed coiling, wide and deep umbilicus. Oblique flanks, broad and low venter. Wide subtrapezoidal whorl-section with maximum thickness at the shoulder. Sharp, dense, tuberculate, fibulate and spined ribbing. Suture-line: wide, ramified E, shorter, trifid L, short U lobes, well-developed, divided ES, narrower, divided LS1.

Remark: The genus was regarded as a synonym of genus *Porpoceras* by HOWARTH (2013), however, the validity was acknowledged by VENTURI & FERRI (2001), VENTURI et al. (2010), and RULLEAU et al. (2013). *Telodactylites* is typical of the Mediterranean Province, and is considered as the Mediterranean counterpart of *Porpoceras*. The origin of the genus is uncertain, it is probably the descendant of *Mesodactylites* in the upper Bifrons Subzone.

Distribution: Gradatus Zone: Italy, Greece, Southern Spain, Austria, Portugal, North Africa, Chile. Hungary: Bakony Mts (Csernye), Gerecse Mts.

Telodactylites eucosmus (LIPPI-BONCAMBI, 1947)
(Plate 7, figs 3–4)

1947 *Peronoceras eucosmus* MERLA in schedis — LIPPI-BONCAMBI, p. 145, pl. 2, fig. 21
v 1967a *Peronoceras zeissi* n. sp. — GÉCZY, p. 98, text-fig. 96, pl. 26, fig. 1, pl. 44, fig. 39
2011 *Telodactylites eucosmus* (LIPPI-BONCAMBI) — GALÁCZ et al., p. 325, pl. 2, figs 2–3

2013 *Telodactylites eucosmus* (Lippi-Boncambi) — Rulleau et al., p. 105, pl. 36, figs 1, 4–5, 7, 10

Material: Three moderately preserved specimens: 2014.41.1–2, and SzO.2012.41 from the private collection of Orsolya Székelyhidi).

Measurement	D	H	H/D	W	W/H	Uw	Uw/D
2014.41.1	67	15	22.3%	17	113.3%	40	59.7%
SPC.2012.41	62	13	21%	19	146%	39	63%
2014.41.2	50	11	22%	14	127.2%	29	58%

Description: Evolute, depressed coiling, oblique and slightly convex flanks, edged shoulder, broad and low venter, and subtrapezoidal whorl-section. Three–four sharp, prorsiradiate or rectiradiate ribs are looped to long ventrolateral spines, separating irregularly by simple ribs rising from the umbilicus and crossing the venter. Three forwardly projected secondaries issue from each spine.

Remark: Recently a specimen of this rare species was represented from Tardos by Rulleau et al. (2013, pl. 36, fig. 10).

Distribution: Gerecse Mts: Semipolitum horizon: Pisznice Section (2014.41.1), Gradatus Zone: Bánya Hill Quarry Section (SzO.2012.41), Crocodile Section without exact stratigraphic position (2014.41.2).

Telodactylites cf. *renzi* Pinna et Levi-Setti, 1971
(Plate 7, figs 6, 9)

1971 *Telodactylites renzi* n. sp. — Pinna & Levi-Setti, p. 117, text-figs 14/B, 21/7, pl. 10, figs 1–5

1975 *Telodactylites* cfr. *renzi* (Pinna et Levi-Setti) — Dezi & Ridolfi, p. 41, text-figs 113–115

1981 *Peronoceras* cf. *renzi* (Pinna et Levi-Setti) — Hillebrandt & Schmidt-Effing, p. 49, text-fig. 18/c–e, pl. 4, fig. 8

Material: 11 poorly preserved specimens (2014.42.1–11).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.42.1	41	12	29.2%	24	200%	19	46.3%
2014.42.2	29	13	44.8%	20	153.8%	14	48.2%

Description: Moderately evolute, depressed coiling, low, oblique flanks, broad, low, rounded venter, and subrectangular section. Primary ribs strong, rectiradiate, simple or bi- or trifurcating at ventrolateral nodes or spines.

Remarks: Due to the poor state of preservation, the specific fibulate ribs on the inner whorls cannot be traced, nevertheless, the overall morphology of the specimens is close to that of the types. *T. renzi* differs from *N. fonticulum* in wider and more depressed whorls.

Distribution: Italy, Chile. Gerecse sections: Sublevisoni to Subregale Subzones.

Telodactylites levisettii n. sp.
(Plate 7, fig. 8)

Holotype: 2014.43.1 (Eötvös Museum of Natural History)

Derivation of name: In honour of Franco Levi-Setti, Italian paleontologist.

Type locality and horizon: Bánya Hill A Section, Tardos, Gerecse Mts, the exact stratigraphic position is unknown.

Material: 1 well-preserved internal mold of an adult specimen.

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.43.1	51	13	25.5%	12	92.3%	28	55%

Diagnosis: Evolute, compressed coiling, subquadrate whorl-section, simple or fibulate, tuberculate, bi- or trifurcating ribbing.

Description: Medium-sized, evolute, compressed coiling, shallow umbilicus, slightly convex flanks, low, almost flat, slightly rounded venter, subquadrate section. The body chamber is one whorl in length, the peristome is preceded by a constriction. Simple, bifurcating and fibulate ribs alternate irregularly on the innermost whorls, while ribs are regularly fibulate from the last quarter of the phragmocone. Furcating points tuberculate on the inner whorls, spined on the body chamber. Fibulate ribs regularly trifurcate on the first half of the body chamber, while the forwardly bent secondaries show a zigzag pattern on the last half.

Remarks: Based on the morphology, the species is placed within genus *Telodactylites*. *T. eucosmus* differs in wider whorls, subtrapezoid whorl-section, and looped, spined primary ribs, *T. renzi* differs in much wider, depressed whorls, *T. achermanni* Pinna et Levi-Setti differs in wider whorls with distant fibulate ribs. The morphology of the specimen resembles that of *Peronoceras fibulatum* (J. de C. Sowerby), but differs in more convex flanks, almost flat venter, not regularly fibulate inner whorls, and denser fibulation on the last whorl.

Genus *Collina* Bonarelli, 1893

Type-species: *Collina gemma* Bonarelli, 1893.

Diagnosis: Medium-sized, evolute, compressed coiling; subquadrate to suboval whorl-section;

rounded venter. Primary ribs widely spaced, straight, rectiradiate, single or fibulate, bi- or trifurcating at ventrolateral tubercles, secondaries arched forward, raised in the middle of the venter. Intricate suture-line: long and wide E, shorter, ramified L, straight U lobes, wide ES and LS1.

Remarks: Taxonomic treatments were presented by e.g. Pinna & Levi-Setti (1971), Schmidt-Effing (1972), Jiménez & Rivas (1991), Venturi & Ferri (2001), Venturi et al. (2010), and Rulleau et al. (2013). The genus is one of the late descendant of *Mesodactylites*, it is typical of the Mediterranean Province.

Distribution: upper Bifrons to Gemma/Clausus Subzones: Italy, Southern Spain, Portugal, Greece, Austria, Morocco, Algeria, North and South America. Hungary: Bakony Mts (Csernye, Úrkút), Gerecse Mts. In the Gerecse sections, the genus ranges in the upper Bifrons to Clausus Subzones, and *C. gemma* Bonarelli forms a biohorizon in the latter subzone.

Collina gemma Bonarelli, 1893
(Plate 7, figs 10–11)

1893 *Collina Gemma* n. f. — Bonarelli, p. 205, text-fig.
v 1966 *Collina noszkyi* n. sp. — Géczy, p. 441, pl. 2, fig. 5
v 1967a *Peronoceras umbra* (Ramaccioni, 1939) — Géczy, p. 100, text-fig. 98, pl. 26, fig. 4, pl. 64, fig. 40
v 1967a *Collina meneghinii* Bonarelli — Géczy, p. 102, text-fig. 99, pl. 25, fig. 5, pl. 64, fig. 41
v 2011 *Collina gemma* Bonarelli — Galácz et al., pl. 6, fig. 4

Material: 87 specimens in different state of preservation (2014.48.1–87).

M	D	H	H/D	W	W/H	Uw	Uw/D
2014.48.1	62	15	24.2%	10,5	70%	35	56.4%
2014.48.2	60	13	21.6%	10	77%	37	61.6%
2014.48.3	57	12	21%	9	75%	35	61.4%
2014.48.4	54	13	24%	10	77%	32	59.2%
2014.48.5	50	11	22%	10	91%	31	62%
2014.48.6	50	12	24%	9	75%	30	60%

Description: Evolute coiling, shallow umbilicus, slightly convex flanks, subquadrate to suboval whorl-section. Low and rounded venter on the inner whorls. Primary ribs rectiradiate, single or paired, furcating at well-developed ventrolateral tubercles, distant on the inner, while dense on the last whorl. The forwardly projected secondaries form a pseudo-keel on the body chamber.

Remarks: As types of *C. gemma* (refigured by Gallitelli Wendt 1969, pl. 6, fig. 3) and of *C. meneghinii* Bonarelli, 1899 (*A. subarmatus* in Meneghini 1867–81, pl. 14, fig. 6, refigured by Pinna 1969, pl. 4, fig. 7) are remarkably similar, the validity of the latter taxon was rejected by Pinna & Levi-Setti 1971. Although both species were accepted by Venturi et al. (2010), based on morphological considerations, the arrangement by Pinna & Levi-Setti (1971) is acknowledged here.

Distribution: Gerecse sections: Semipolitum to Gemma horizons.

Collina cf. *kampemorpha* Kottek, 1966
(Plate 7, fig. 12)

1966 *Collina kampemorpha* nov. sp. — Kottek, p. 138, text-fig. 66, pl. 17, fig. 6
1971 *Collina kampemorpha* Kottek — Pinna & Levi-Setti, p. 113, fig. 21/22, pl. 9, figs 12, 14

Material: One fragmentary specimen (2014.49.1).

Measurements	D	H	H/D	W	W/H	Uw
2014.49.1	80	20	25%	17	85%	?

Description: a with evolute coiling, convex flanks, rounded venter, subquadrate section on the inner, suboval section on the last whorl. Ribs strong, tuberculate on the inner, looped to spines on the last whorl.

Remark: The overall morphology of the specimen is close to that of the type, but the poor state of preservation does not allow the certain arrangement.

Distribution: Greece, Italy. Gerecse Mts: Gemma horizon: Pisznice Section.

Conclusion

The taxonomic survey of the Dactylioceratidae completes the general picture of the Toarcian ammonite faunal composition of the Gerecse Mts. The family is represented by 13 genera with 31 species. Some species, whose Hungarian occurrence has been known only from the Mecsek Mts (*M. mucronatus*) or from the Bakony Mts (*N. multum*, *N. lobatum*), are described now from the Gerecse Mts as well. A few species are first recorded from Hungary (*C. raquinianum*, *S.* cf. *nicklesi*, *N. angelonii*, *M. merlai*), and the rich material made possible to introduce four new species. Based on the diversity of the examined material, the taxonomic validity of the subfamily

Nodicoeloceratinae, and genera *Mesodactylites*, *Transicoeloceras*, and *Telodactylites* typical of the Mediterranean Province is confirmed here.

The Ammonitina assemblages studied here contain 335 dactylioceratid specimens. The taxonomic composition of this fauna is somewhat different from that of other Mediterranean localities. It is characterized by the abundance of *Collina* and the above mentioned characteristic Mediterranean genera; the most frequent species are *C. gemma* (26.2%) and *N. tuberculatum* (25%). Besides these Mediterranean taxa, however, the relatively frequent occurrence of the characteristic NW European genera *Zugodactylites* (13.1%) and *Porpoceras* (9%) with sporadic appearance of *Catacoeloceras* (4 spp.), *Mucrodactylites* (4 spp.) and *Septimaniceras* (1 sp.) are remarkable. The results show a mixed palaeobiogeographic feature. The dominance of Phylloceratina and Lytoceratina is a clear Mediterranean feature, but the co-existence of Mediterranean and NW European Ammonitina genera indicates a presumed Submediterranean transitional area between the two faunal provinces.

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Plate 1

The specimens have been coated with ammonium chloride before photography, and are shown in their natural size.

Fig. 1. *Dactylioceras* (*Orthodactylites*) *semicelatum* (SIMPSON, 1843) – 2014.55.2, Bánya Hill B, Bed 12 (Serpentinum Subzone)

Fig. 2. *Dactylioceras* (*Dactylioceras*) *commune* (SOWERBY, 1815) – 2014.25.1, Bánya Hill A, Bed 45 (Sublevisoni Subzone)

Fig. 3. *Microdactylites tardosensis* n. sp. – 2014.26.1, 1x (3a–b), 1.5x (3c–d), Bánya Hill A, Bed 45 (Sublevisoni Subzone)

Fig. 4. *Zugodactylites braunianus* (D'ORBIGNY, 1845) – 2014.38.5, Bánya Hill A, Bed 42 (Sublevisoni Subzone)

Fig. 5. *Zugodactylites braunianus* (D'ORBIGNY, 1845) – 2014.38.2, Bánya Hill A, Bed 42 (Sublevisoni Subzone)

Fig. 6. *Zugodactylites rotundiventer* BUCKMAN, 1926 – 2014.39.2, Bánya Hill A, Bed 41 (Sublevisoni Subzone)

Fig. 7. *Dactylioceras* (*Orthodactylites*) *semicelatum* (SIMPSON, 1843) – 220.2011, Kis-Gerecse, Bed 113 (Serpentinum Subzone)

Fig. 8. *Peronoceras subarmatum* (YOUNG et BIRD, 1822) – 2014.44.3, Bánya Hill A, Bed 40 (Bifrons Subzone)

Fig. 9. *Zugodactylites braunianus* (D'ORBIGNY, 1845) – 2014.38.1, Pisznice, Bed 124 (Bifrons Subzone)

Plate 1

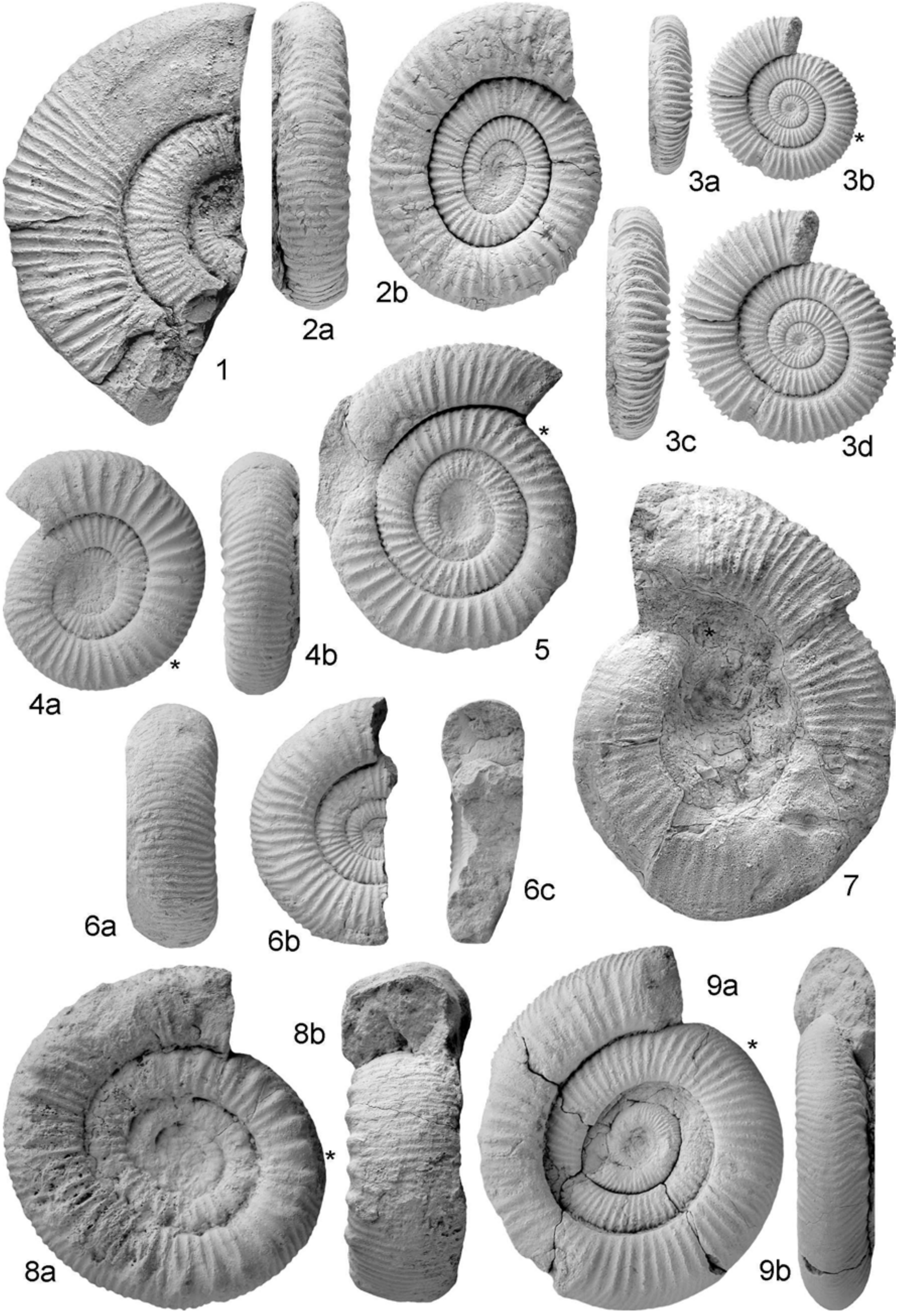


Plate 2

Fig. 1. *Peronoceras subarmatum* (YOUNG et BIRD, 1822) – 2014.44.2, Pisznice, Bed 120 (Bifrons Subzone)

Fig. 2. *Porpoceras vortex* (SIMPSON, 1855) – 2014.45.6, Kis-Gerecse, Bed 81 (Bifrons Subzone)

Fig. 3. *Porpoceras* cf. *vorticellum* (SIMPSON, 1855) – 2014.46.2, Bánya Hill A, Bed 41 (Sublevisoni Subzone)

Fig. 4. *Porpoceras* cf. *vorticellum* (SIMPSON, 1855) – 2014.46.1, Kis-Gerecse, Bed 83 (Bifrons Subzone)

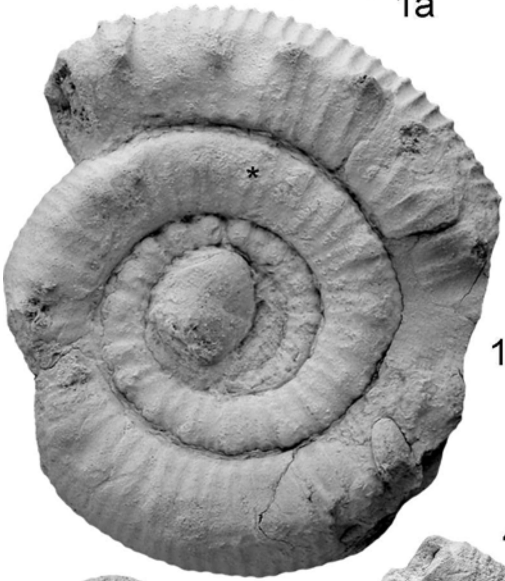
Fig. 5. *Porpoceras beurleni* (MONESTIER, 1931) – 2014.47.1, Pisznice, Bed 118 (Bifrons Subzone)

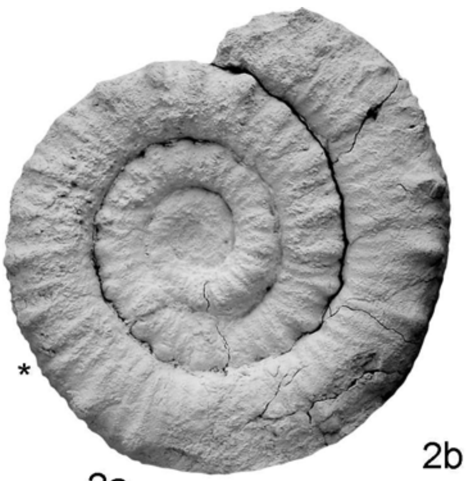
Fig. 6. *Catacoeloceras dumortieri* (DE BRUN, 1932) – 2014.50.1, Kis Teke Hill, Bed K13 (Clausus Subzone), (6a – ventral view at D 44)

Fig. 7. *Porpoceras vortex* (SIMPSON, 1855) – 2014.45.1, Kis-Gerecse, Bed 81 (Bifrons Subzone)

Plate 2


1a


1b


2a


2b


6a

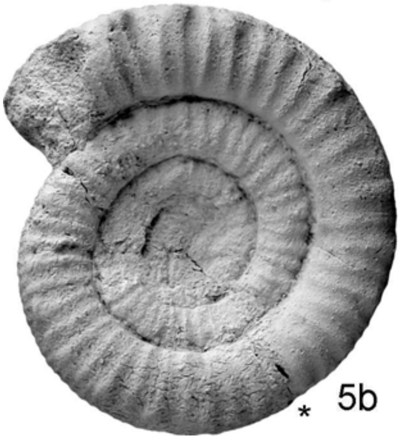

6b


6c


3


4a


5a


5b


4b


7

Plate 3

Fig. 1. *Catacoeloceras raquinianum* (D'ORBIGNY, 1844) – 2014.51.1, Tölgyhát Quarry, from debris

Fig. 2. *Catacoeloceras raquinianum* (D'ORBIGNY, 1844) – EZPC.2013.2, Bánya Hill Quarry, from debris, Collection Evanics, Z.

Fig. 3. *Mucrodactylites mucronatus* (D'ORBIGNY, 1845) – DMPC.2013.3, Bánya Hill Quarry, from debris, Collection Dunai, M.

Fig. 4. *Mucrodactylites mucronatus* (D'ORBIGNY, 1845) – 2014.52.1, Bánya Hill Quarry, from debris

Fig. 5. *Septimaniceras* cf. *nicklesi* (GUEX, 1971) – 2014.54.1, Bánya Hill Quarry, from debris

Fig. 6. *Peronoceras subarmatum* (YOUNG et BIRD, 1822) – 2014.44.1, Kis-Gerecse, Bed 81 (Bifrons Subzone)

Fig. 7. *Nodicoeloceras* cf. *choffati* (RENZ, 1912) – 222.2011, Bánya Hill B, Bed 12 (Serpentinum Subzone)

Fig. 8. *Nodicoeloceras crassoides* (SIMPSON, 1855) morphotype *multum* (BUCKMAN, 1928) – 2014.29.1, Kis-Gerecse, Bed 90 (Bifrons Subzone)

Plate 3

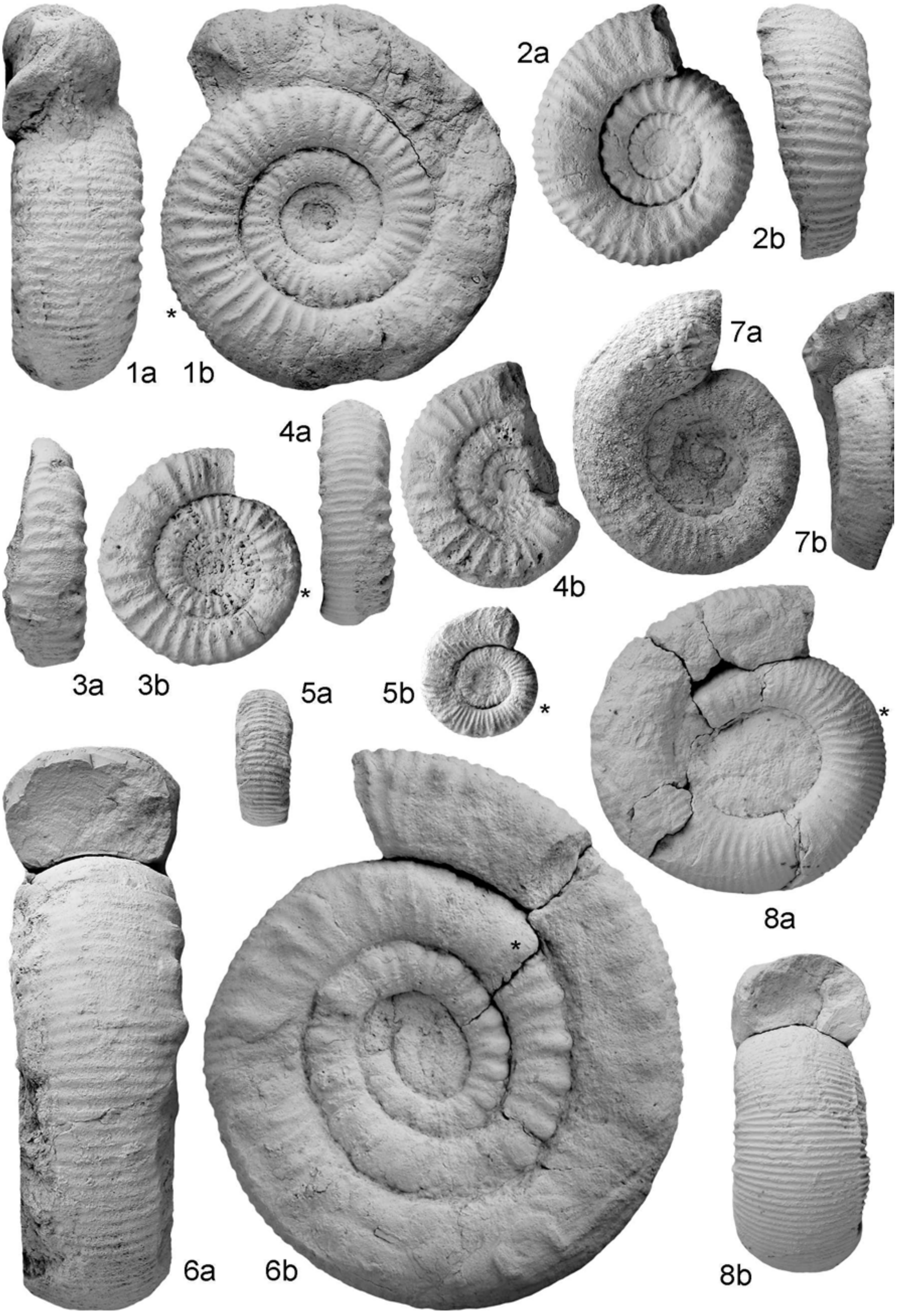


Plate 4

Fig. 1. *Nodicoeloceras crassoides* (SIMPSON, 1855) morphotype *fonticulum* (SIMPSON, 1855) – 215.2011, Bánya Hill B, Bed 1 (Sublevisoni Subzone)

Fig. 2. *Nodicoeloceras tuberculatum* (KOTTEK, 1966) – 2014.30.1, Bánya Hill A, Bed 44 (Sublevisoni Subzone)

Fig. 3. *Nodicoeloceras tuberculatum* (KOTTEK, 1966) – EZPC7536, Bánya Hill Quarry, from debris, Collection Evanics, Z.

Fig. 4. *Nodicoeloceras tuberculatum* (KOTTEK, 1966) – 2014.30.3, Bánya Hill A, Bed 43 (Sublevisoni Subzone)

Fig. 5. *Porpoceras vortex* (SIMPSON, 1855) – 2014.45.2, Kis-Gerecse, Bed 79 (Clausus Subzone)

Fig. 6. *Nodicoeloceras tuberculatum* (KOTTEK, 1966) – 2014.30.4, Bánya Hill A, Bed 44 (Sublevisoni Subzone)

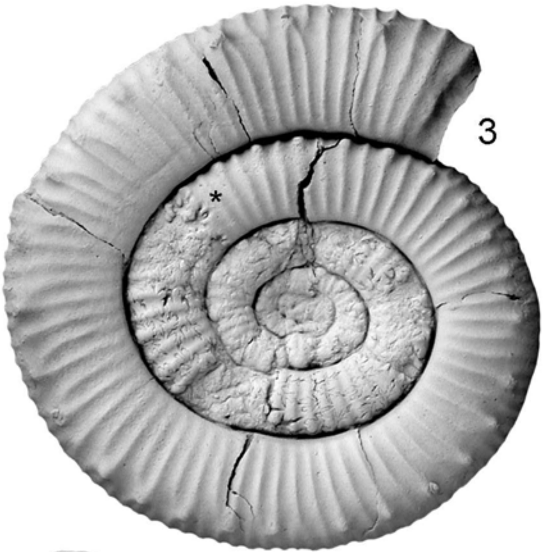
Fig. 7. *Nodicoeloceras tuberculatum* (KOTTEK, 1966) – 2014.30.6, Bánya Hill B, Bed 8 (Falciferum Subzone)

Plate 4


1a


1b

2

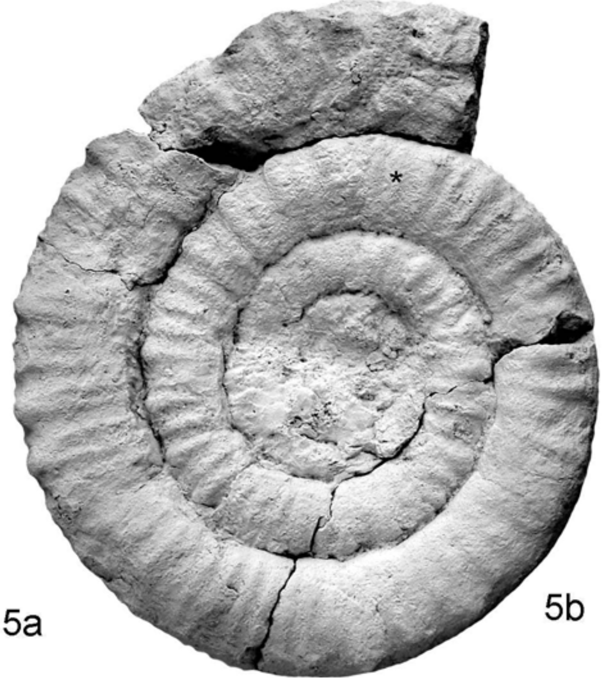


3

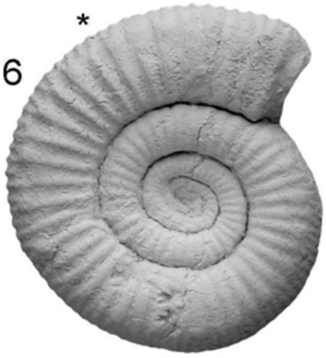
4a


4b


5a



5b



6


7

Plate 5

Fig. 1. *Nodicoeloceras angelonii* (RAMACCIONI, 1939) – 2014.31.2, Tölgyhát A, Bed 113 (Sublevisoni Subzone)

Fig. 2. *Mesodactylites annulatiformis* (BONARELLI, 1899) – 2014.33.1, Bánya Hill A, Bed 44 (Sublevisoni Subzone)

Fig. 3. *Nodicoeloceras angelonii* (RAMACCIONI, 1939) – 2014.31.1, Tölgyhát A, Bed 113 (Sublevisoni Subzone)

Fig. 4. *Nodicoeloceras crassoides* (SIMPSON, 1855) morphotype cf. *lobatum* (BUCKMAN, 1927) – 2014.27.1, Kis-Gerecse, Bed 97 (Sublevisoni Subzone)

Fig. 5. *Nodicoeloceras dulaii* n. sp. – 2014.32.1, Bánya Hill A, Bed 44 (Sublevisoni Subzone)

Fig. 6. *Nodicoeloceras tuberculatum* (KOTTEK, 1966) – 221.2011, Pisznice, Bed 133 (Falciferum Subzone)

Fig. 7. *Nodicoeloceras tuberculatum* (KOTTEK, 1966) – 2014.30.2, Bánya Hill A, Bed 43 (Sublevisoni Subzone)

Plate 5


1

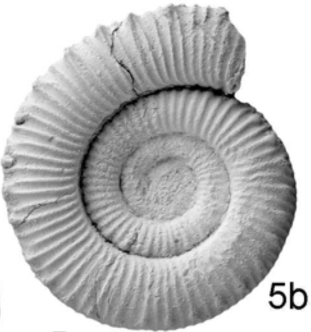

2a


3


4a

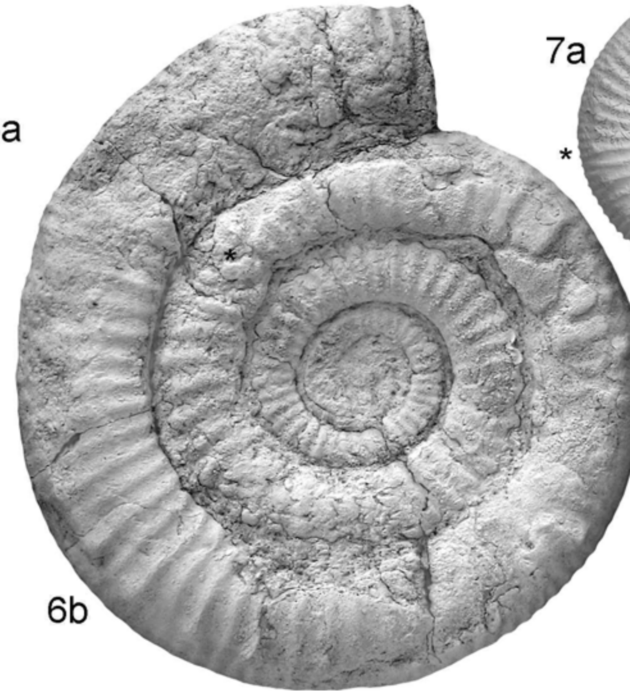

2b


4b


5a


5b


6a


6b


7a


7b

Plate 6

Fig. 1. *Mesodactylites annulatiformis* (BONARELLI, 1899) – 217.2011, Kis-Gerecse, Bed 112 (Serpentinum Subzone)

Fig. 2. *Mesodactylites mediterraneus* (RENZ, 1912) – 225.2011, Bánya Hill B, Bed 4 (Falciferum Subzone)

Fig. 3. *Mesodactylites broilii* (MITZOPOULOS, 1930) – 2014.34.1, Bánya Hill A, Bed 36 (Bifrons Subzone)

Fig. 4. *Mesodactylites broilii* (MITZOPOULOS, 1930) – 2014.34.4, Pisznice, Bed 128 (Sublevisoni Subzone)

Fig. 5. *Mesodactylites sapphicus* (RENZ, 1912) – 2014.35.1, Bánya Hill A, Bed 41 (Sublevisoni Subzone)

Fig. 6. *Mesodactylites merlai* (PINNA, 1969) – 2014.36.1, Pisznice, Bed 124 (Bifrons Subzone)

Fig. 7. *Mesodactylites merlai* (PINNA, 1969) – 2014.36.2, Pisznice, Bed 124 (Bifrons Subzone)

Fig. 8. *Mesodactylites pisznicensis* n. sp. – 2014.37.1, Pisznice, Bed 123 (Bifrons Subzone)

Plate 6

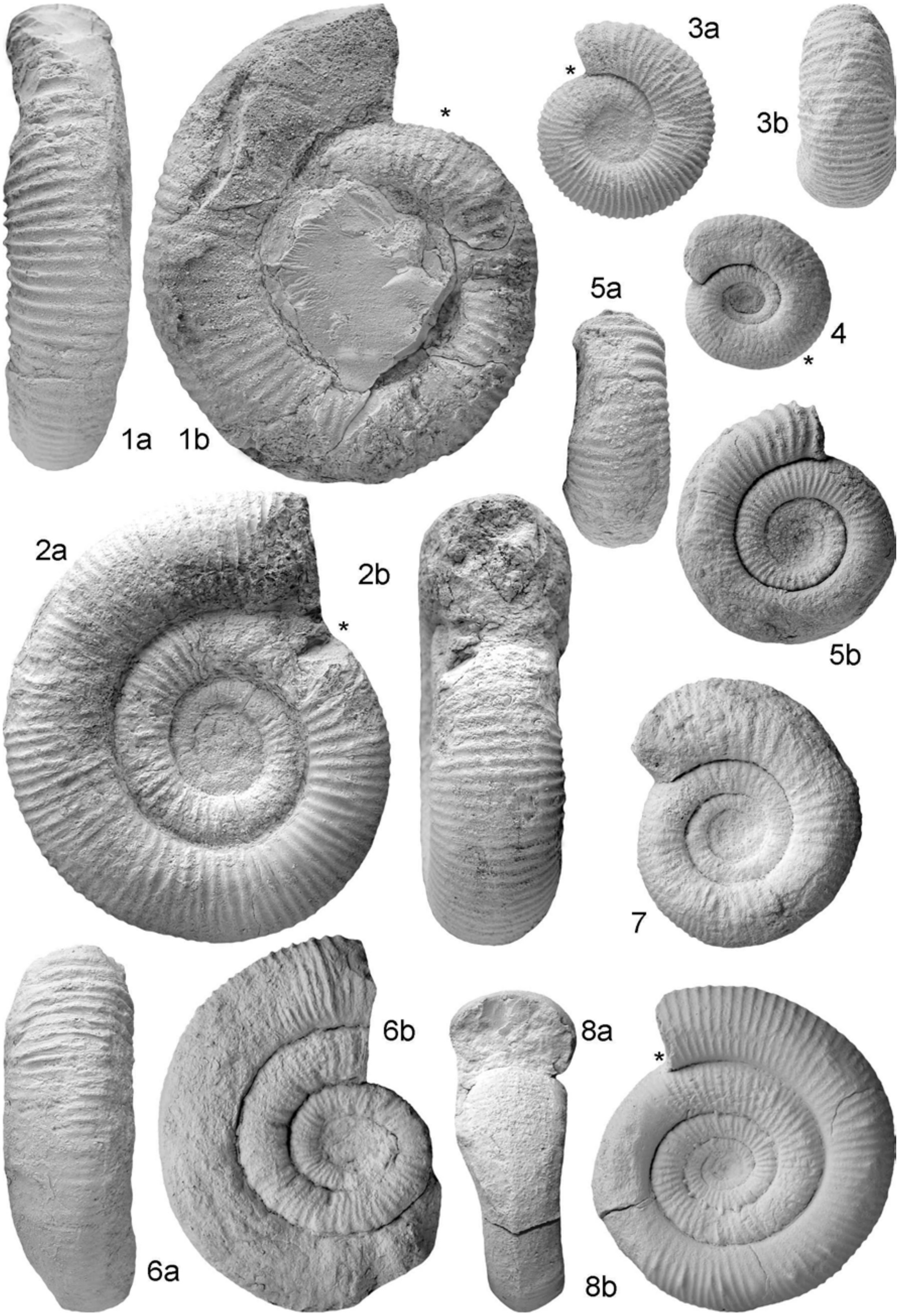


Plate 7

Fig. 1. *Transicoeloceras viallii* PINNA, 1966 – 2014.40.2, Kis Teke Hill, Bifrons Zone, not bed by bed collection

Fig. 2. *Transicoeloceras viallii* PINNA, 1966 – 2014.40.3, Kis-Gerecse, Bed 89 (Bifrons Subzone)

Fig. 3. *Telodactylites eucosmus* (LIPPI-BONCAMBI, 1947) – 2014.41.2, Pisznice–Crocodile, from debris

Fig. 4. *Telodactylites eucosmus* (LIPPI-BONCAMBI, 1947) – SPC.2012.41, Bánya Hill Quarry, Gradatus Zone, not bed by bed collection, Collection Székelyhidi, O.

Fig. 5. *Mucrodactylites* sp. – 2014.53.1, Pisznice, Bed 123 (Bifrons Subzone)

Fig. 6. *Telodactylites* cf. *renzi* PINNA et LEVI-SETTI, 1971 – 2014.42.1, Kis-Gerecse, Bed 92 (Sublevisoni Subzone)

Fig. 7. *Transicoeloceras viallii* PINNA, 1966 – 2014.40.1, Kis Teke Hill, Bifrons Zone, not bed by bed collection

Fig. 8. *Telodactylites levisettii* n. sp. – 2014.43.1, Bánya Hill A, from debris

Fig. 9. *Telodactylites* cf. *renzi* PINNA et LEVI-SETTI, 1971 – 2014.42.2, Kis-Gerecse, Bed 87 (Bifrons Subzone)

Fig. 10. *Collina gemma* BONARELLI, 1893 – 2014.48.4, Kis-Gerecse, Bed 79 (Clausus Subzone)

Fig. 11. *Collina gemma* BONARELLI, 1893 – 2014.48.6, Kis Teke Hill, Bed K11 (Clausus Subzone)

Fig. 12. *Collina* cf. *kampemorpha* KOTTEK, 1966 – 2014.49.1, Pisznice, Bed 117 (Clausus Subzone)

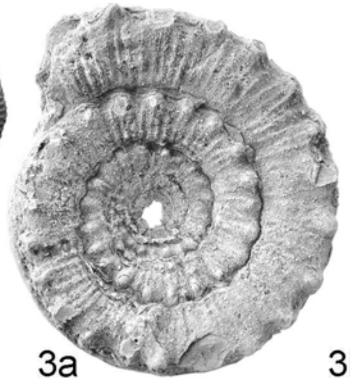
Plate 7

1a


1b

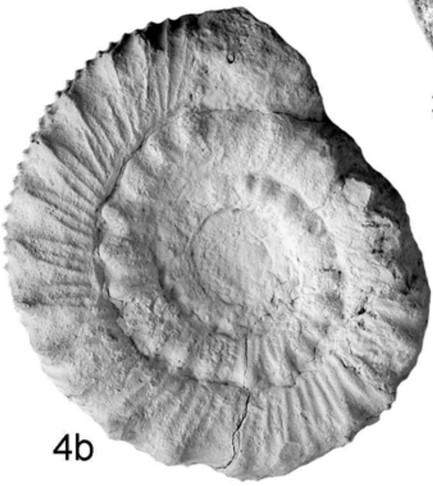

2a

2b


3a


3b


4a


4b

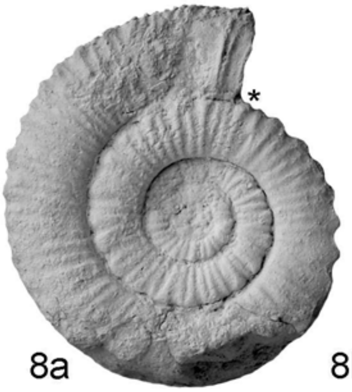

5a


5b


6a


6b

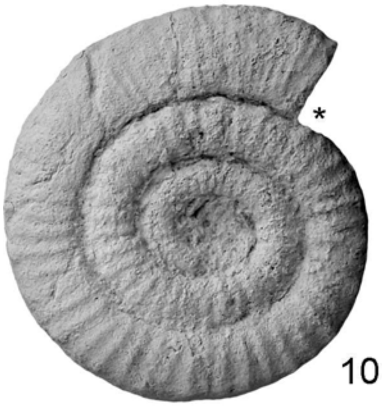
7



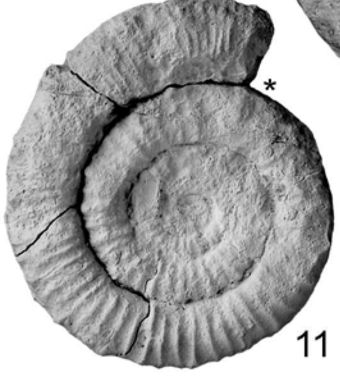
8a


8b


9



10



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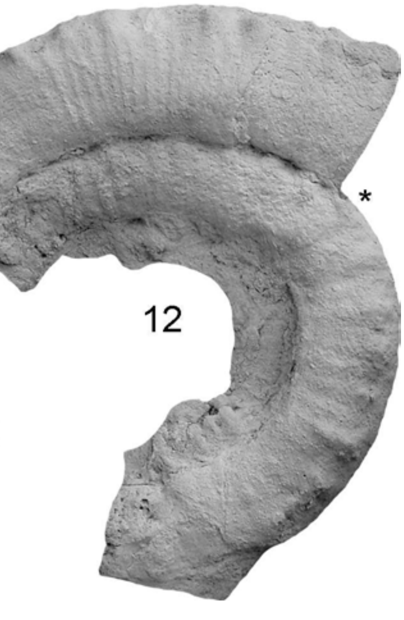

12

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Albian benthic ostracods from the boreholes Vst-8 and Agt-2 (Vértes Foreland, NW-Hungary)

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(with 3 figures, 1 table and 2 plates)

The benthic ostracod faunas from the Albian succession of the Vértessomló Siltstone in the boreholes Vst-8 and Agt-2 were examined and compared. In the present study 10 species belonging to 8 genera were identified. The aim of the study was to give a picture of the palaeoenvironment during the Albian age in this region of the Tethys using the ostracods. The dominance of platycopids in benthic assemblages of both boreholes indicates low-oxygenated bottom water conditions. Moreover, the low diversity, the presence of mainly deeper marine environment favouring podocopid forms and the absence or weakly developed eye spot bearing ostracods indicate a normal marine, shallow bathyal depositional environment. However, differences in the faunal composition of the two boreholes could be observed which can be explained with the different palaeogeographical position of the studied sequences during the Albian.

Introduction

Only a few studies have been made on ostracods from the Cretaceous sections of Hungary. These include the taxonomy and the palaeoecological interpretations of the Albian (ZALÁNYI 1959) and Cenomanian (MONOSTORI 2000) faunas from the Transdanubian Central Range. The Albian ostracod assemblages from the Vértessomló Siltstone have not been published yet. The goal of this work is the detailed systematical descriptions of the Albian benthic faunas from the boreholes Vértessomló Vst-8 and Agostyán Agt-2. The planktonic ostracod fauna of these boreholes was published in 2013 by CSÉFÁN & TÓTH. Further aim is to detect the depositional environment of these sequences because ostracods, living in every aquatic environment, are very useful in the palaeoenvironmental reconstructions. Different assemblages occur in marine settings characterized by different water depth, substrate, temperature, salinity, water energy and oxygen content.

Geological setting

The studied boreholes are located in the Vértes Foreland, in the eastern zone of the Transdanubian Central Range, north-western Hungary (Fig. 1). The studied Vértessomló Siltstone Formation was deposited during the Early Cretaceous in a semi-enclosed basin. This grey silty and marly sequence interfingers with a platform carbonate, called Környe Limestone Formation to the southwest and with the Lábatlan Sandstone Formation to the northeast (CSÁSZÁR 2002). The succession reaches its maximum thickness (410 m) in the borehole Agt-2 (JÁMBOR et al. 1973) (Fig. 2). The age of the Vértessomló Siltstone Formation is Lower to Middle Albian based on mainly foraminiferal studies (BODROGI 1992; CSÁSZÁR 1998, 2002; FÜLÖP 1975; GÖRÖG 1993, 1996). In the borehole Vst-8 only the lower Albian part is represented (GÖRÖG 1996).

Material and methods

There were 114 samples examined: 23 from the borehole Vst-8 and 91 from the borehole Agt-2, respectively. The Vértessomló Siltstone mainly consists of silty marls, argillaceous marls and marly limestone layers. The ostracods were extracted with hydrogen-peroxide from the silty samples, and with cold acetolysis, modified after LETHIERS & CRASQUIN-SOLEAU (1988) from the more calcareous samples. For the identification and the illustration of the ostracods the photos were made by scanning electron microscope. For the palaeoecological interpretations semi-quantitative analyses of the faunas were used.

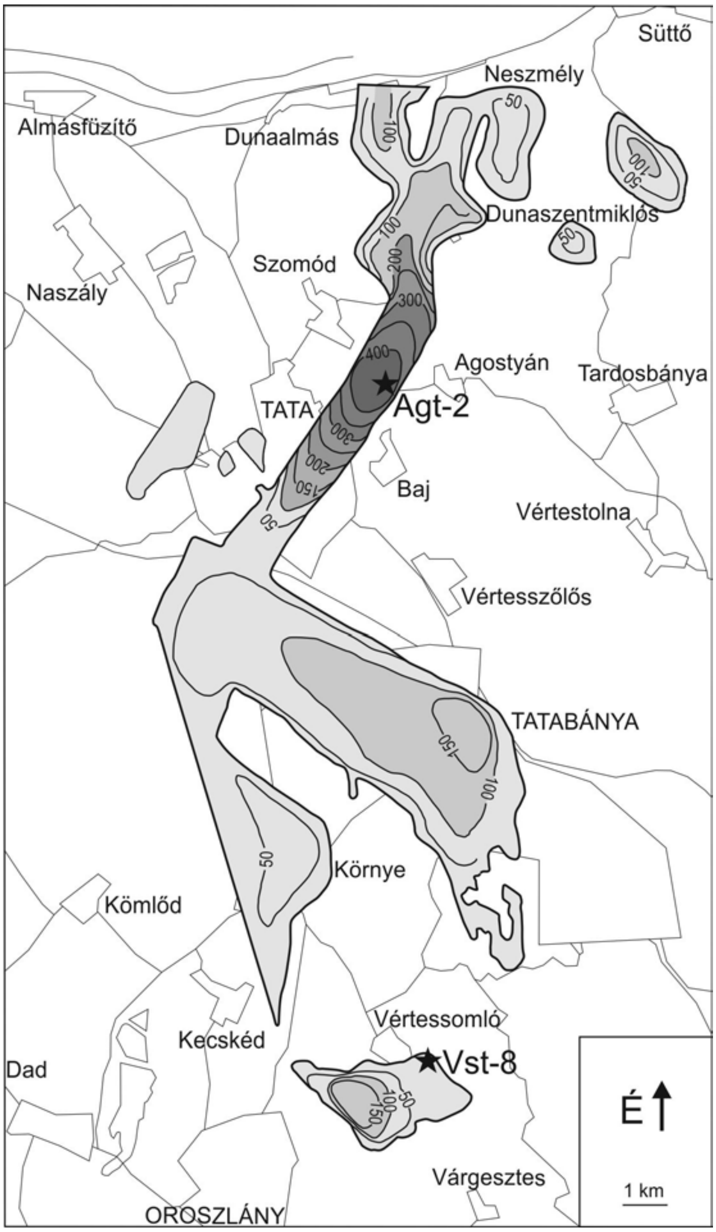

Fig. 1. Geographical locations of the boreholes Vst-8 and Agt-2 and recent extent and thickness distribution of the Vértessomló Siltstone Formation (after CSÁSZÁR, 2002).

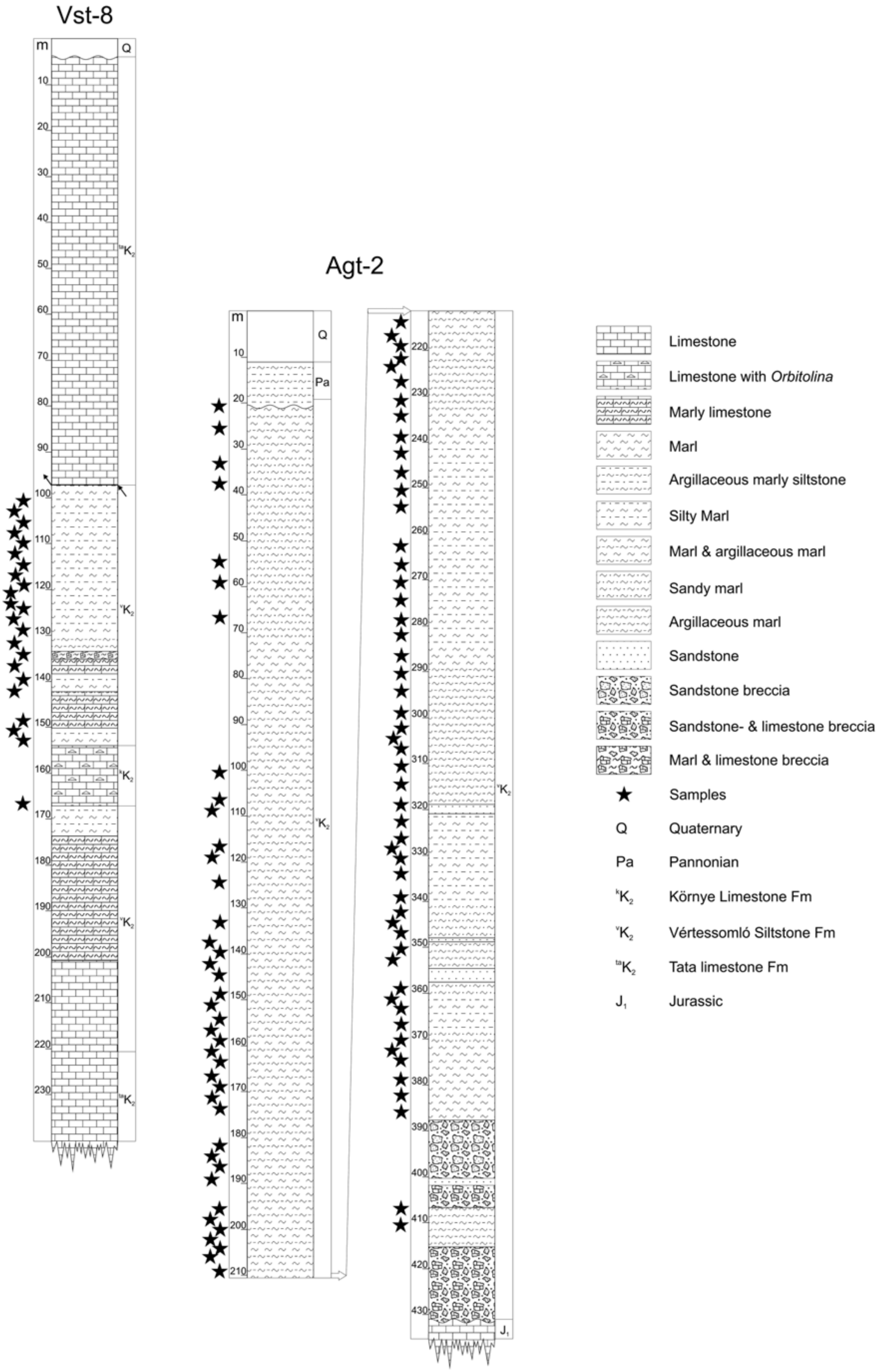

Fig. 2. Lithostratigraphical sections of the boreholes Vst-8 and Agt-2.

Systematic part

Classification of the ostracods follows that of HORNE et al. (2002). The specimens are deposited in the Department of Palaeontology of Eötvös University (Budapest, Hungary).
The number of specimens per sample can be found in Table 1. (right valve/left valve, carapace).
Abbreviations: L=length and H=height.

Phylum Arthropoda SIEBOLD & STANNIUS, 1845
Subphylum Crustacea PENNANT, 1777
Class Ostracoda LATREILLE, 1806
Subclass Podocopa MÜLLER, 1894
Order Platycopida SARS, 1866
Superfamily Cytherelloidea SARS, 1866
Family Cytherellidae SARS, 1866
Genus *Cytherella* JONES, 1849
Type species: *Cytherina ovata* ROEMER, 1841

Cytherella gr. *ovata* (ROEMER, 1841)
Pl. 1. Figs 1—4.

1841. *Cytherina ovata* n. sp. – ROEMER, p. 104, pl. 16. figs 21. a-b.
1845. *Cytherina ovata* – REUSS, p. 16, pl. 5. fig. 35.
1854. *Cytherella ovata* ROEMER – BOSQUET, pp. 45-48, pl. 8, fig 1.
1956. *Cytherella ovata* (ROEMER) – DEROO, p. 1508, pl. 1, figs 4—6.
1958. *Cytherella ovata* (ROEMER 1841) – OERTLI, p. 1502, pl. 1, figs 10—29.
1959. *Cytherella ovata* (ROEMER) – ZALÁNYI, pp. 522—524, pl. 4, fig. 4., text-fig. 63.
1964. *Cytherella ovata* (ROEMER, 1841) – BAYNOVA & TALEV, p. 20. pl. 1. figs 4—6.
1965. *Cytherella ovata* (ROEMER, 1840) – KAYE, pp. 385—386, pl. 50, fig. 10.
1965. *Cytherella ovata* (ROEMER, 1840) – KAYE & Barker, pp. 385—386, pl. 50, fig. 10.
1966. *Cytherella ovata* (ROEMER, 1841) – GRÜNDEL, p. 12, pl. 1, fig. 2.
1966. *Cytherella ovata* (ROEMER, 1841) – HERRIG, pp. 718—728, text-figs 11—19, pl. 2, figs 1—7, pl. 44. figs 6—8.
1971. *Cytherella ovata* (ROEMER, 1841) – DAMOTTE, pp. 55—56, pl. 1, figs 2—7.
1971. *Cytherella* cf. *ovata* (ROEMER) – KEEN & SIDDIQUI, p. 61, pl. 1, figs 1, 9.
1974. *Cytherella ovata* (ROEMER, 1840) – DAMOTTE & FREYTEt, pp. 202—203, pl. 1, fig. 1.
1974. *Cytherella* gr. *C. ovata* (ROEMER, 1841) – ROSENFELD & RAAB, pp. 3—4, pl. 1, figs 3—5.
1976. *Cytherella* „*ovata*" (ROEMER, 1840) – BREMAN, pp. 82—83, pl. 1, fig. 1, pl. 2, fig. 1e.
1976. *Cytherella ovata* (ROEMER) – JAIN, pp. 202—203, figs 3. C—D.
1977. *Cytherella* gr. *ovata* (ROEMER, 1841) – CHAROLLAIS et al., pl. 1, fig. 1.
1978. *Cytherella ovata* (ROEMER, 1841) – NEALE, pl. 1, figs 1—2.
1978. *Cytherella ovata* (ROEMER) – SWAIN, pp. 251—252, pl. 1, figs 2—5.
1979. *Cytherella ovata* (ROEMER, 1840) – DAMOTTE, p. 276, pl. 6/1, fig. 1.
1982. *Cytherella* ex gr. *ovata* (ROEMER, 1840) – WEAVER, pp. 12—14, pl. 1, figs 1—5, pl. 2, fig. 20; figs 7—8.
1985. *Cytherella* gr. *C. ovata* (ROEMER, 1840) – AINSWORTH, p. 27, fig. 9/16.
1985. *Cytherella ovata* (Roemer, 1841) – BABINOT et al., pl. 48, fig. 1, pl. 55, figs 1—2.
1985. *Cytherella* gr. *ovata* (ROEMER, 1841) – VIVIERE, p. 135, pl. 1, fig. 1.
1988. *Cytherella ovata* (ROEMER) – JARVIS et al., fig. 15/a.
1990. *Cytherella* cf. *ovata* (ROEMER, 1841) – MAJORAN, pl. 1, figs 1—12.
1991. *Cytherella* gr. *ovata* (ROEMER, 1840) – SHAHIN, p. 133, pl. 1, fig 5.
1992. *Cytherella ovata* (ROEMER, 1841) – WITTE et al., pp. 46—47, pl. 1, figs 8—10.
1993. *Cytherella ovata* (ROEMER, 1841) – BABINOT & GROSHENY, p. 101, pl. 1, figs 1—4.
2000. *Cytherella ovata* (ROEMER, 1841) – MONOSTORI, pp. 6—7, pl. 1, figs 1—6.
2000. *Cytherella* cf. *ovata* (ROEMER, 1840) – MORSI, p. 50, pl. 1, figs 1—2.
2002. *Cytherella* cf. *ovata* (ROEMER, 1841) – EL-NADY, p. 597, pl. 1, figs 10—11.
2006. *Cytherella* aff. *ovata* (ROEMER, 1841) – ANDREU & BILOTTE, p. 58, pl. 1, figs 1—5.
2007. *Cytherella* ex gr. *ovata* (ROEMER, 1841) – BABINOT et al., p. 41, pl. 1, figs 1—3.
2008. *Cytherella ovata* (ROEMER, 1841) – EL NADY et al., p. 542, pl. 1, fig. 6.
2009. *Cytherella* cf. *ovata* (ROEMER, 1841) – SCHUDACK & Schudack, fig. 10/15.
2010. *Cytherella ovata* (ROEMER, 1841) – ALLAMEH et al., pl. 1, fig. 6.

Dimensions: L: 0.57—0.89 mm
H: 0.37—0.59 mm
L/H: 1.4—1.8

Remarks. Characteristic features are the following: carapace oval in lateral view; anterior margin evenly rounded; dorsal margin arched and gently sloping from mid-length; posterior margin asymmetrically rounded; ventral margin straight to convex and right valve overlaps the left one. According to DAMOTTE (1971) the holotype of this variable species is unfortunately lost and does not have a detailed description and illustration. Furthermore, the carapace is characterless because the valve surface smooth, the intra-specific variability of the shape and the size is great. Due to these facts, the species level classification of the extinct species belonging to the genus *Cytherella* is difficult.

Occurrences and stratigraphic ranges. England: Aptian-Turonian (KAYE & BARKER 1965; NEALE 1978, JARVIS et al. 1988), Ireland: Aptian-Maastrichtian (KEEN & SIDDIQUI 1971; AINSWORTH 1985), France: Aptian-Campanian (DEROO 1956; OERTLI 1958; DAMOTTE 1971; DAMOTTE & FREYTET 1974; DAMOTTE 1979; BABINOT et al. 1985; BABINOT & GROSHENY 1993; ANDREU & BILOTTE 2006; BABINOT et al. 2007), Netherlands: Cenomanian (WITTE et al. 1992), Switzerland: Albian (CHAROLLAIS et al. 1977), Hungary: Albian-Cenomanian (ZALÁNYI 1959; MONOSTORI 2000; this paper), Spain: Albian-Turonian (BREMAN 1976; SWAIN 1978; SCHUDACK & SCHUDACK 2009), Algeria: Cenomanian (Majoran 1990), Egypt: Cenomanian-Maastrichtian (MORSI 2000; EL-NADY 2002; EL-NADY et al. 2008.), Israel: Cenomanian-Turonian (ROSENFELD & RAAB 1974), Iran: Turonian-Santonian (ALLAMEH et al. 2010), India: Albian (JAIN 1976).

Cytherella parallela (REUSS, 1846)
Pl. 1. Figs 5—6.

1845. *Cytherina parallela* – REUSS, p. 16, pl. 5, fig. 33.
1958. *Cytherella* cf. *parallela* (REUSS, 1846) – OERTLI, pp. 1501—1502, pl. 1, figs 1—9.
1966. *Cytherella parallela* (REUSS, 1846) – GRUENDEL, p. 12, pl. 1, fig. 4.
1966. *Cytherella parallela* (REUSS, 1845) – HERRIG, pp. 728—736, text-fig. 20—24, pl. 3, figs 1, 2, 4.
1971. *Cytherella* cf. *parallela* (REUSS, 1846) – DAMOTTE, p. 56, pl. 1, fig. 8.
1974. *Cytherella* cf. *C. parallela* (REUSS) – ROSENFELD & RAAB, p. 3, pl. 1, figs 1—2.
1976. *Cytherella* cf. *C. parallela* (REUSS, 1845) – BREMAN, pp. 84—85, pl. 2, fig. 2a.
1976. *Cytherella* cf. *parallela* (REUSS) – JAIN, p. 203, figs 3. E—F.
1977. *Cytherella* gr. *parallela* (REUSS, 1846) – CHAROLLAIS et al., pl. a, fig 2.
1978. *Cytherella parallela* (REUSS) – SWAIN, p. 251, pl. 1, fig. 1.
1979. *Cytherella* cf. *parallela* (REUSS, 1845) – DAMOTTE, pp. 276—277, pl. 6/1, fig. 2.
1985. *Cytherella parallela* (REUSS, 1846) – BABINOT et al., pl. 48, fig. 2, pl. 55, fig. 10.
1991. *Cytherella* cf. *parallela* (REUSS, 1845) – SHAHIN, p. 134, pl. 1, figs 6—7.
1993. *Cytherella* cf. *parallela* (REUSS, 1845) – BABINOT & Grosheny, p. 101, pl. 1, figs 5—7.
1997. *Cytherella parallela* (REUSS) – ISMAIL & SOLIMAN, pl. 2, figs 4—5.
2000. *Cytherella parallela* (REUSS, 1845) – MONOSTORI, pp. 7—8, pl. 1, figs 7—8, pl. 2, figs 1—2.
2002. *Cytherella parallela* (REUSS, 1846) – EL-NADY, p. 597, pl. 1, fig. 12.
2006. *Cytherella* aff. *parallela* (REUSS, 1846) – ANDREU & Bilotte, p. 60, pl. 1, figs 6—8.
2007. *Cytherella* cf. *parallela* (REUSS, 1846) – BABINOT et al., p. 41, pl. 1, fig. 4.

Dimensions: L: 0.61—0.88 mm
H: 0.31—0.51 mm
L/H: 1.6—2.1

Remarks. Characteristic features are the following: Carapace sub-rectangular in lateral view. Right valve overlaps left. Surface smooth. The studied specimens are the most similar in details to those described by OERTLI (1958), BREMAN (1976), BABINOT et al. (1985, 2007), BABINOT & GROSHENY (1993), MONOSTORI (2000) and ANDREU & BILOTTE (2006).

Occurrences and stratigraphic ranges. England: Albian (DAMOTTE 1971), France: Aptian-Turonian (OERTLI 1958; DAMOTTE 1971; DAMOTTE 1979; BABINOT et al. 1985; BABINOT & GROSHENY 1993; ANDREU & BILOTTE 2006), Switzerland: Albian (CHAROLLAIS et al. 1977), Germany: Cenomanian (DAMOTTE 1971), Hungary: Albian-Cenomanian (MONOSTORI 2000; this paper), Egyipt: Cenomanian-Coniacianan (ISMAIL & SOLIMAN 1997; EL-NADY 2002), Israel: Cenomanian-Turonian (ROSENFELD & RAAB 1974), India: Albian (JAIN 1976).

Order Podocopida SARS, 1866
Superfamily Bairdioidea SARS, 1866
Family Bairdiidae SARS, 1888
Genus *Bairdia* MCCOY, 1844
Type species: *Bairdia curta* MCCOY, 1844

Bairdia sp.
Pl. 1. Fig. 7.

Dimensions: L: 1.17 mm
H: 0.77 mm
L/H: 1.5

Remarks. Dorsal margin trapezoidal. Posterior end pointed. Ventral margin convex. The single specimen is poorly preserved.

Occurrences and stratigraphic ranges. Lower Albian (this paper).

Superfamily Cytheroidea BAIRD, 1850
Family Cytheridae BAIRD, 1850
Subfamily Protocytherinae LIUBIMOVA, 1955
Genus *Protocythere* TRIEBEL, 1938
Type species: *Cytherina triplicata* ROEMER, 1841

Protocythere albae DAMOTTE & GROSDIDIER, 1963
Pl. 1. Figs. 11—12.

1963. *Protocythere albae* n. sp. – DAMOTTE & GROSDIDIER, pp. 54—55, pl. 1, fig. 3.
1966. *Protocythere albae* DAMOTTE & GROSDIDIER,

1963 – GRÜNDEL, pp. 25—26, pl. 4, figs 9—10, text-fig. b/a-b.
1971. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – BERTRAM & KEMPER, pl. 2, figs 3—4.
1971. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – DAMOTTE, p. 89, pl. 5, fig. 15.
1971. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – KEEN & SIDDIQUI, p. 64, pl. 2, figs 4, 8.
? 1971. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – RISCH, pp 59—60, pl. 8, figs 1—4.
1977. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – CHAROLLAIS et al., pl. 2, figs 8—9.
1978. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – WIEL, pl. 2, fig. 7.
1979. *Protocythere (Protocythere) albae* DAMOTTE & GROSDIDIER, 1963 – DAMOTTE, p. 285, pl. 6/2, fig. 21.
1985. *Protocythere (Protocythere) albae* DAMOTTE & GROSDIDIER, 1963 – BABINOT et al., pl. 53. figs 15—16, pl. 54, fig. 1.
1989. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – ELSTNER & KEMPER, pl. 2, figs 7—8.
1991. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963 – KEMPER, pl. 3, figs 4—5.

Dimensions: L: 0.94—1.00 mm
H: 0.50—0.55 mm
L/H: 1.8

Remarks. *Protocythere* with three subparallel ridges. Dorsal ridge arched and extends over the dorsal margin. Anterior side of the median and ventral ridges are weakly connected, which is more characteristic on the right valve. Left valve overlaps right on the anterodorsal, anteroventral and posterodorsal sides. The specimens resemble the most to those described by GRÜNDEL (1966), BERTRAM & KEMPER (1971), ELSTNER & KEMPER (1989) and apart from the posterior spines to the specimen of WIEL (1978). Differs from the otherwise similar form *Protocythere derooi* OERTLI in the morphology of the ribs and in carapace size (sensu OERTLI, 1958, p. 1509-1510 pl. 6, figs 129-143).

Occurrences and stratigraphic ranges. England: Albian (DAMOTTE 1971), Ireland: Cenomanian (KEEN & SIDDIQUI 1971), France: Albian (DAMOTTE & GROSDIDIER 1963; GRÜNDEL 1966; BABINOT et al. 1985; DAMOTTE 1971, 1979; WIEL 1978), Switzerland: Albian (CHAROLLAIS et al. 1977), Germany: Albian (GRÜNDEL 1966; BERTRAM & KEMPER 1971; ELSTNER & KEMPER 1989; KEMPER 1991), Hungary: Lower Albian (this paper).

Protocythere galileensis ROSENFELD & RAAB, 1984
Pl. 1. Fig. 13.

1984. *Protocythere galileensis* n. sp. – ROSENFELD & RAAB, pp. 101–102, pl. 4, figs 4—6.
1996. *Protocythere galileensis* ROSENFELD & RAAB, 1984 – ZGHAL et al. , p. 79, pl. 1, figs 27—28.

Dimensions: L: 0.86 mm
H: 0.44 mm
L/H: 2

Remarks. *Protocythere* with straight dorsal and ventral margin and three straight ridges. Median and ventral ridges joined together on the anterior side, forming a rotated U shape. Differs from the holotype in the less prominent dorsal ridge.

Occurrences and stratigraphic ranges. Tunisia: Albian (ZGHAL et al. 1996), Israel: Aptian-Albian (ROSENFELD & RAAB 1984). Hungary: Lower Albian (this paper).

Family Cytherideidae SARS, 1925
Subfamily Schulerideinae MANDELSTAM, 1959
Genus *Schuleridea* SWARTZ & SWAIN, 1946
Type species: *Schuleridea acuminata* SWARTZ & SWAIN, 1946

Schuleridea rhomboidalis NEALE, 1960
Pl. 1. Figs 8—10.

1960. *Schuleridea rhomboidalis* n. sp. – NEALE, p. 210, pl. 2, figs 1, 2, 5, 7, 8.
1978. *Schuleridea rhomboidalis* NEALE, 1960 – NEALE, pl. 7, fig. 14, pl. 8, figs 1—2.
1980. *Schuleridea rhomboidalis* NEALE, 1960 – DAMOTTE & Rey, p. 23, pl. 1, figs 25—26.
1985. *Schuleridea rhomboidalis* NEALE, 1960 – BABINOT et al., pl. 46, fig. 7.
1991. *Schuleridea* cf. *S. rhomboidalis* NEALE, 1960 – SWAIN & CHUANLI, p. 75—76, pl. 2, figs 18—19.

Dimensions: L: 0.65—1.02 mm
H: 0.31—0.61 mm
L/H: 1.3—1.9

Remarks. Right valve trapezoidal in lateral view. Left valve is more rounded and entirely overlaps the right one. Eye tubercle almost always visible. Differs from the holotype in the less rounded left valve with more prominent posterodorsal angle. The specimens resemble the most to those described by NEALE (1978) and BABINOT et al. (1985). Strong sexual dimorphism with more elongated males can be recognized.

Occurrences and stratigraphic ranges. England: Hauterivian-Barremian (NEALE 1960, 1978), France: Barremian (BABINOT et al. 1985), Portugal: Hauterivian (DAMOTTE & REY 1980), western North Atlantic Ocean: Albian or Cenomanian (SWAIN & CHUANLI 1991). Hungary: Lower Albian-Middle Albian (this paper).

Family Trachyleberididae SYLVESTER-BRADLEY, 1948
Subfamily Trachyleberidinae SYLVESTER-

BRADLEY, 1948

Genus *Rehacythereis* GRUENDEL, 1973
Type species: *Cythereis luermannae* TRIEBEL, 1940

Rehacythereis bartensteini (OERTLI, 1958)
Pl. 2. Figs 1—3.

1958. *Cythereis bartensteini* n. sp. – OERTLI, pp. 1513—1514, pl. 8, figs 171—179, pl. 9, figs 197—198.
1971. *Cythereis bartensteini* OERTLI, 1958 – RISCH, p. 60, pl. 8, figs 11—14.
1985. *Rehacythereis bartensteini* (OERTLI, 1958) – BABINOT et al., pl. 49, fig. 5.
1993. *Rehacythereis bartensteini* (OERTLI, 1958) – ANDREU et al., p. 110, pl. 5, fig. 8.
2007. *Rehacythereis bartensteini* (OERTLI) – BABINOT et al., pl. 6, figs 16-17.
2007. *Rehacythereis* aff. *bartensteini* (OERTLI) – BABINOT et al., pl. 6, fig. 15
2007. *Rehacythereis* cf. *bartensteini* (OERTLI, 1958) – BABINOT et at. p. 56.

Dimensions: L: 0.66—0.84 mm
H: 0.39—0.46 mm
L/H: 1.5—2.0

Remarks. *Rehacythereis* with well-developed and small tubercles on the anteromarginal ridge and with a distinct sub-central tubercle. Secondary ornamentation is punctation and weak reticulation. Sexual dimorphism is present with more elongated males. Differs from the holotype and from the very similar specimens described by BABINOT et al. (1985) in the less developed reticulation. The eye tubercle is less pronounced as well. The weaker ornamentation could be caused by the preservation of the carapaces and/or the poorer environmental conditions that persisted in the deeper parts of the ocean.

Occurrences and stratigraphic ranges. France: Aptian-Albian (OERTLI 1958; BABINOT et al. 1985; BABINOT et al. 2007), Northern Limestone Alps: Albian (RISCH 1971), Morocco: Albian (ANDREU et al. 1993), Hungary: Lower Albian-Middle Albian (this paper).

Rehacythereis luermannae (TRIEBEL, 1940)
Pl. 2. Figs 4—6.

1940. *Cythereis lürmannae* n. sp. – TRIEBEL, pp. 201—204, pl. 6, figs 63—66.
1964. *Cythereis lurmannae* TRIEBEL, 1940 – KAYE, pp. 66—67, pl. 8, figs 11—15.
1966. *Cythereis luermannae* TRIEBEL, 1940 – GRÜNDEL, p. 36, pl. 6, fig. 23.
1971. *Cythereis luermannae* TRIEBEL, 1940 – BERTRAM & Kemper, p. 38, pl. 1, figs 1, 2, 5, 6.
1971. *Cythereis luermannae* TRIEBEL, 1940 – DAMOTTE, p. 66, pl. 2, fig. 13.
1972. *Cythereis* aff. *lürmannae* TRIEBEL, 1940 – DONZE & PORTHAULT, pp. 364—367, pl. 3, figs 8—10.
1977. *Cythereis (Rehacythereis?) luermannae* TRIEBEL, 1940 – DAMOTTE, pl. 1, fig. 4.
1978. *Cythereis luermannae* TRIEBEL, 1940 – WIEL, pl. 1, figs 7—8.
1979. *Cythereis luermannae* TRIEBEL, 1940 – DAMOTTE, pp. 281-282, pl. 6/2, fig. 12.
1982. *Rehacythereis luermannae bemerodensis* (KEMPER, 1971) – WEAVER, p. 80, pl. 12, figs 1—2.
1982. *Rehacythereis luermannae luermannae* (TRIEBEL, 1940) – WEAVER, p. 79, pl. 11, figs 20—21.
1985. *Cythereis (Rehacythereis) luermannae* TRIEBEL, 1940 – BABINOT et al., pl. 52, figs 1—3.
1989. *Cythereis luermannae* TRIEBEL, 1940 – FRIEG & KEMPER, pl. 18, figs 1—9.
1992. *Rehacythereis luermannae* (TRIEBEL, 1940) – WITTE et al., pp. 74—75, pl. 7, figs 2, 4, 5.
1996. *Rehacythereis luermannae* (TRIEBEL, 1940) – HERNGREEN et al., pl. 9, fig. 17.
2011. *Cythereis (Rehacythereis)* cf. *luermannae hannoverana* BERTRAM & KEMPER, 1981 – SAUVAGNAT & WEIDMANN, p. 171, pl. 1, figs 7—8.

Dimensions: L: 0.68—0.90 mm
H: 0.38—0.45 mm
L/H: 1.8—2.0

Remarks. *Rehacythereis* with weaker ornamentation than that of the holotype. Sub-central tubercle and marginal ridges are visible on most specimens. Secondary ornamentation is punctation and weak reticulation. The presence of reduced and varied ornamentation on this form may be due to the life style in a stress environment and therefore may be an ecophenotypic variation.

Occurrences and stratigraphic ranges. England: Albian-Cenomanian (GRÜNDEL 1966; DAMOTTE 1971, 1979; WEAVER 1982), France: Albian-Cenomanian (GRÜNDEL 1966; DAMOTTE 1971, 1977, 1979; BABINOT et al. 1985), Netherlands: Albian-Cenomanian (WITTE et al. 1992; HERNGREEN et al. 1996), Switzerland: Cenomanian (SAUVAGNAT & WEIDMANN 2011), Germany: Albian-Cenomanian (GRÜNDEL 1966; BERTRAM & KEMPER 1971; DAMOTTE 1971, 1979; WEAVER 1982; FRIEG & KEMPER 1989), Poland: Albian-Cenomanian (GRÜNDEL 1966), Canada: Albian (WITTE et al. 1992). Hungary: Lower Albian (this paper).

Genus Cythereis JONES, 1849
Type species: *Cytherina ciliata* REUSS, 1846

Cythereis ex gr. *fahrioni* (BISCHOFF, 1963)
Pl. 2. Fig. 7.

Dimensions: L: 1.17 mm
H: 0.57 mm
L/H: 2.0

Remarks. Large *Cythereis* with distinct reticulated valve surface. The carapace strongly resembles *C. fahrioni* (Bischoff, 1963, pp. 31—33, pl. 12, figs 90—93, pl. 13, fig. 94) from the Middle Albian of Lebanon but the median ridge and sub-central tubercle are virtually missing. Only one moderately preserved specimen occurs in the material so it can be classified only to the group *C. fahrioni* with certainty.

Occurrences and stratigraphic ranges. Lower Albian (this paper).

Superfamily Pontocypridoidea Müller, 1894
Family Pontocyprididae Müller, 1894
Genus *Pontocyprella* Mandelstam in Liubimova, 1955
Type species: *Bairdia harrisiana* Jones, 1849

Pontocyprella harrisiana (Jones, 1849)
Pl. 2. Fig. 8.

1849. *Bairdia harrisiana* n. sp. – Jones, p. 25—26, pl. 6, fig. 17a—f.
1962. *Pontocyprella harrisiana* (Jones) – Neale, pl. 6, figs 12—13.
1964. *Pontocyprella harrisiana* (Jones, 1849) – Baynova & Talev, p. 24, pl. 2, figs 6—7.
1965. *Pontocyprella harrisiana* (Jones, 1849) – Baynova, pl. 1, figs 10—11.
1966. *Pontocyprella harrisiana* (Jones, 1849) – Gründel, p. 17, pl. 2, fig. 9.
1966. *Pontocyprella harrisiana* (Jones, 1849) – Herrig, pp. 788—789, text-fig. 58, pl. 14, figs 2a, b.
1982. *Pontocyprella harrisiana* (Jones, 1849) – Weaver, pp. 29—30, pl. 4, figs 17—20.
1992. *Pontocyprella harrisiana* (Jones, 1849) – Witte et al., p. 52, pl. 2, fig. 14.
1997. *Pontocyprella harrisiana* (Jones, 1849) – Slipper, pl. 6, figs 4—5.
2000. *Pontocyprella* n. sp. aff. *P. harrisiana* (Jones, 1849) – Monostori, pp. 15—16, pl. 8, fig. 7, pl. 9, figs 1—3.
2007. *Pontocyprella harrisiana* (Jones, 1849) – Babinot et al., p. 47, pl. 3, figs 11—12.
2007. *Pontocyprella harrisiana* (Jones, 1849) – Vaziri et al., p. 133, pl. 3, fig. k.
2009. *Pontocyprella harrisiana* (Jones) – Vaziri, pl. 6, figs e—f.
2011. *Pontocyprella* cf. *harrisiana* (Jones, 1849) – Babinot & Colin, p. 753, pl. 8, fig. 9.

Dimensions: L: 0.59—1.17 mm
H: 0.27—0.77 mm
L/H: 1.7—2.4

Remarks. *Pontocyprella* with elongated, smooth carapace. Anterior margin asymmetrically rounded. Anterodorsal margin straight and slopes from middle length. Posterodorsal margin convex. Posterior margin pointed. Ventral margin concave. The specimens resemble the most to those described by Baynova & Talev (1964), Witte et al. (1992), Slipper (1997), Monostori (2000) and Babinot et al. (2007).

Occurrences and stratigraphic ranges. England: Albian-Turonian (Jones 1849; Gründel 1966; Neale 1973; Weaver 1982; Slipper 1997; Vaziri 2009), France: Barremian-Aptian (Babinot et al. 2007; Babinot & Colin 2011) Netherlands: Cenomanian (Witte et al. 1992), Germany: Albian-Cenomanian (Gründel 1966; Weaver 1982), Poland: Albian-Cenomanian (Gründel 1966), Hungary: Albian-Cenomanian (Monostori 2000, this paper), Morocco: Valanginian (Babinot & Colin 2011), Iran: Albian-Cenomanian (Vaziri et al. 2007).

Superfamily Cypridoidea Baird, 1845
Family Candonidae Kaufmann, 1900
Subfamily Paracypridinae Sars, 1923
Genus *Paracypris* Sars, 1866
Type species: *Paracypris polita* Sars, 1866

Paracypris jonesi Bonnema, 1941
Pl. 2. Fig. 9.

1941. *Paracypris jonesi* n. sp. – Bonnema, p. 115, pl. 3, figs 24—28.
1958. *Paracypris jonesi* Bonnema, 1940 – Oertli, p. 1503, pl. 2, figs 30—38.
1965. *Paracypris jonesi* Bonnema – Liubimova, p. 26—27, pl. 2, figs 8—9.
1975. *Paracypris jonesi* Bonnema – Jain, p. 207, figs 1. U—V.
1985. *Paracypris* cf. *jonesi* Bonnema, 1941 – Babinot et al., pl. 48, fig. 3.
2005. *Paracypris jonesi* Bonnema, 1941 – Shahin, p. 756, pl. 1, fig. 20.
2008. *Paracypris* aff. *jonesi* Bonnema, 1941 – Morsi et al., pp. 165—166, pl. 1, fig. 17.

Dimensions: L: 0.76—0.91 mm
H: 0.31—0.36 mm
L/H: 2.5—2.7

Remarks. The specimens are identical in shape with the holotype figured and described by Bonnema (1941).

Occurrences and stratigraphic ranges. France: Aptian-Albian (Oertli 1958; Babinot et al. 1985), Netherlands: Maastrichtian (Bonnema 1941), Hungary: Lower Albian (this paper), Egypt: Maastrichtian-Eocene (Shahin 2005; Morsi et al. 2008), India: Coniacian-Maastrichtian (Jain 1975a, 1975b).

Results

As a result of the studies 11 ostracod taxa were identified which includes 10 species and 8 genera. The most common ostracod genus was the platycopid *Cytherella* in both boreholes (Fig. 3). In the borehole Vst-8, the percentage of platycopids fluctuates around 50% between depths 135 m and 119 m. The percentage at depth 117 m is greatly reduced, then it reaches high values again from 115 m depth. In the borehole Agt-2, the percentage of platycopids from the bottom to 125 m depth is greater than 80%. In the samples above the values drop to 40-60 %. The second most frequent genus was the *Schuleridea* that is more common in the borehole Vst-8 than in the borehole Agt-2. The *Pontocyprella* appears in great abundance mainly in the lower parts of both boreholes. The ornamented trachyleberid ostracods, namely *Rehacythereis* and *Cythereis*, are few in numbers in the borehole Agt-2, but they occur in large amounts in the middle part, between depths 140 m and 123 m, of the borehole Vst-8. The ornamentation of the trachyleberids as well shows differences comparing the specimens of the two boreholes. The more ornamented forms occur in the borehole Vst-8. The genera *Bairdia*, and *Protocythere* and *Paracypris* are represented by only a few carapaces.

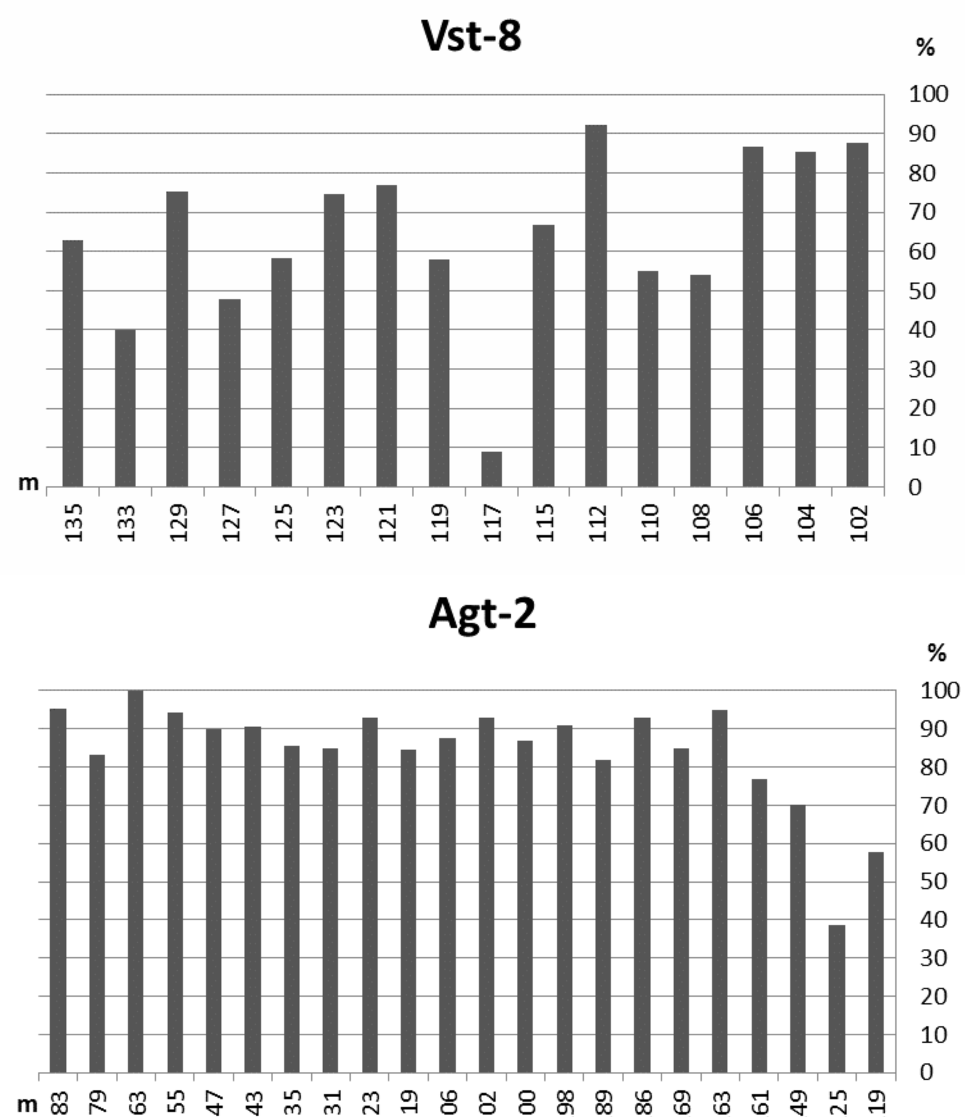

Fig. 3. Percentage of platycopids in the two boreholes.

Discussion

The palaeoecological interpretation of the benthic ostracod faunas from the boreholes Vst-8 and Agt-2 is to provide new data about the depositional environment of the Vértessomló Siltstone.

High proportion of platycopid *Cytherella*s in each sample of both boreholes likely indicates low oxygenated bottom water conditions in this subbasin of the Tethys according to previous studies of BOOMER & WHATLEY (1992) and WHATLEY et al. (1994) on Early Jurassic ostracod faunas. Following the calculations of WHATLEY et al. (2003) it was possible to estimate the oxygen content in the sea water using the "Platycopid signal", the percentage distribution of the platycopids. The samples containing more than 10 specimens were used in the analysis. The palaeo-oxygen level values in the borehole Vst-8 varied between 1.4 ml/l and 6.0 ml/l with an average of 3.1 ml/l, and were constant low in the borehole Agt-2 (between 1.0 ml/l and 2.0 ml/l).

The ratio of platycopids indicate higher oxygen levels than the estimation of SZINGER (2008) based on foraminifers, who could distinguish three intervals in the borehole Vst-8, that cannot be detected with the ostracods. However, some authors argue the usability of platycopids in the palaeo-oxygen level reconstruction, considering studies on recent ostracods living in the oxygen minimum zone (e.g. BRANDÃO & HORNE 2009). Nonetheless, it provided an opportunity to compare the results of this paper with the results of SZINGER (2008).

The genera *Cytherella* and *Pontocyprella* with smooth carapaces indicate normal marine environment with bathyal water depth, because they were dominant in open marine, terrigenous facies during the Cretaceous (e.g., BABINOT 1995). The trachyleberids and *Schuleridea* favoured the more calcareous platform environment in this periode, although they could have occurred in the shallow parts of the bathyal zone as well (BABINOT & COLIN 1983). *Bairdia*, *Protocythere* and *Paracypris* were all widespread considering their habitat. Whereas *Protocythere* was most common in the littoral zone, *Paracypris* was typical of deeper waters. The low diversity in the samples of both boreholes is also a supporting evidence of deeper water environment.

The amount of light is reduced toward the basin floor caused mainly by the sediment particles suspended in the water. The lower intensity of light may result in weaker or absent eye spots on the carapaces. Therefore the specimens living closer to the platform have distinct eye spots, while the forms occupying the basin have weaker or missing eye spots. This differences can be recognized on the trachyleberids and *Schuleridea*s of the studied ostracod faunas.

In conclusion, the depositional environment of the Vértessomló Siltstone was a shallow bathyal basin with normal marine and low oxygenated bottom water conditions during the Albian based on the ostracod assemblages of both boreholes.

Comparing the ostracod faunas of the two boreholes, the amount of specimens per samples are lower in the borehole Agt-2 due to the higher sediment input and to the stable low oxygenated bottom water conditions inside the basin. Whereas, the succession of the borehole Vst-8 was formed closer to the carbonate platform, the oxygen content fluctuated in this environment based on the composition changes of the fauna.

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Table 1. Distribution of ostracod taxa in the borehole Vst-8 and Agt-2.

m	*C. ovata*		*C. parallela*		*Bairdia*		*Protocythere*		*Schuleridea*		*R. bartensteini*		*R. luermannae*		*Cythereis*		*Pontocyprella*		*Paracypris*	
Agt2	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d
21																				
26	1/1		0/1							1										
34	1/0																	1		
38		1		1																
55	2/0	3		1																
59				1																
67		3																		
101										1										
107			1/0							2										
109		1								1		1								
117	1/1	2	1/0							2										
119	1/0	8		2						5										
125		1	0/1	3						4								4		
134										2										
138		1								2										
140	0/1	1		1						1		1								
143		1																		
145				1																
149	2/4	1								3										
151		1																		
155		1								1										
157	1/1	1								2								1		
159	2/2	1		1						1										
161	2/1	5		2						3										
163	2/3	9	1/0	4						1										
167	1/0	1		1						1										
169	6/6	1	1/2	1						3										
171		2								1										
173				1						1										
182	3/0		1/0							1										
184		1	1/0																	
186	6/3	2	1/1							1										
189	3/2	2	0/1	1						1										
196	2/0			2																
198	5/1	1		1						1										
200	5/3	8		4						3										
202	4/2	3	1/1	2					0/1											
204	2/4	1	1/0																	
206	7/7	1	2/2	2						2								1		
209	4/2			2						1										
213	1/0		3/1							2										
217		1		1																
219	2/3		2/3	1						1				1						
222																				
223	6/2	2	2/0	1						1										
227	1/1	1	0/1	1																
231	7/5	2	1/0	2						3										
235	6/3	1	1/0	1						1								1		
239	2/0	2	1/0	1				1												
243	5/3	3	2/2	4					1/0	1										
247	8/9	5	2/2	1					0/1	2										
251			1/0						0/1											
255	5/5	2	1/0	3																
263	8/6	11	1/0	1					1/0											
267	1/1	2		3						1										
271		1																		
275	3/0	1		1																
279	5/1		4/3	2					0/1	1				1						

m	*C. ovata*		*C. parallela*		*Bairdia*		*Protocythere*		*Schuleridea*		*R. bartensteini*		*R. luermannae*		*Cythereis*		*Pontocyprella*		*Paracypris*	
Agt2	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d	r/l	d
283	2/4	4	2/5	3										1						
287	2/1	1		1																
291														1			1/0			
295		1		1																
299	1/0	3	0/1	1										1				1		
303	0/1	2	0/1	3																
305		1																4		
307	0/1	1		1													0/1	1		
311	1/0	3	1/1											1				3		
315	1/0	2		1														1		
319	0/1	1		1														1		
323	1/0	3						1												
327		2	0/1	2						1										
329	0/1	2		1						2										1
331		3																1		
335		1																		
339	0/1			1										1						
343		2																		
345		1																		
347	1/1	2							1/0	1										
351	1/1	1																		
353	1/1	1		2																
359				1						1								1		
361				1					0/1											
363			0/1							1										
367	0/1		1/1																	
371	1/0	1		1																
373	2/0			1						1										1
375		2								2										
379	1/1	1	0/1															1		
383	1/0		0/1											1						
387	1/0																			
407		1						1												
Vst-8																				
102	0/1	8		10					0/2	1										
104	9/9	26	7/2	12					0/1	10										
106	12/6	18	2/5	9					1/0	8										
108	2/1	4	1/1	4					4/2	1								2		2
110			1/0	15					1/0	7								3		2
112	6/4	6	3/5	6					0/1	3										
115		8								3										1
117				1		1				4		2					1/0	3		
119	23/16	27	7/6	30					2/5	38		2						26		4
121	2/1	26	0/3	12						8								4		1
123	24/17	5	18/15	12						7		21						1		2
125		15		11						7		3						9		1
127		11		11						11		7						17		1
129	32/27	13	3/4	24						8		11						14		
133		3		1						5		2				1				
135	8/6	5	3/3	7					1/0	8		10								
137		2										1								2
140	24/18	18	11/10	20					0/1	6		29								2
142	1/0	2																		
149				1						2										
151	1/0	1	0/1	1						4								3		
153		1		1						5								1		
168	1/0	3		3						1										

Plate 1

Figs 1—4. *Cytherella* gr. *ovata* (ROEMER, 1841)
- Fig. 1. Carapace in left view. Borehole Agt-2: 267 m
- Fig. 2. Carapace in right view. Borehole Agt-2: 247 m
- Fig. 3. Carapace in left view. Borehole Vst-8: 142 m
- Fig. 4. Carapace in left view. Borehole Vst-8: 125 m

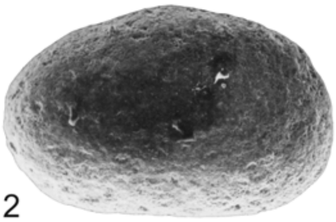
Figs 5—6. *Cytherella parallela* (REUSS, 1845)
- Fig. 5. Carapace in left view. Borehole Agt-2: 169 m
- Fig. 6. Carapace in left view. Borehole Agt-2: 243 m
- Fig. 7. *Bairdia* sp. Right valve. Borehole Vst-8: 117 m

Figs 8—10. *Schuleridea rhomboidalis* NEALE, 1960
- Fig. 8. Carapace in right view. Female. Borehole Vst-8: 110 m
- Fig. 9. Carapace in right view. Male. Borehole Vst-8: 140 m
- Fig. 10. Carapace in right view. Female. Borehole Agt-2: 235 m

Figs 11—12. *Protocythere albae* DAMOTTE & GROSDIDIER, 1963
- Fig. 11. Carapace in right view. Borehole Agt-2: 407 m
- Fig. 12. Carapace in left view. Borehole Agt-2: 323 m
- Fig. 13. *Protocythere galileensis* ROSENFELD & RAAB, 1984. Carapace in right view. Borehole Agt-2: 239 m

Plate 1


1


2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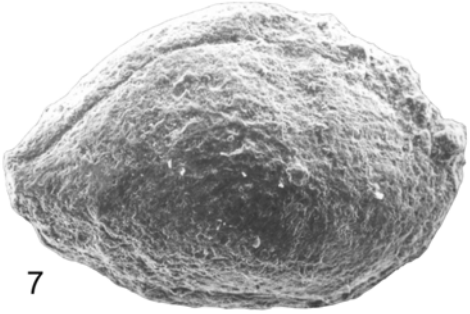
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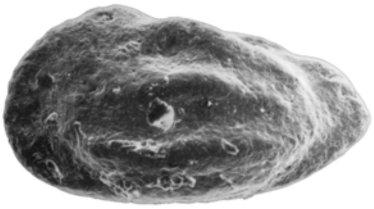
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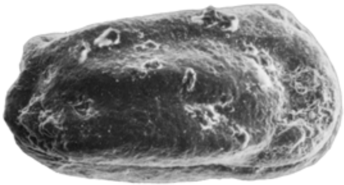

13

100µm

Plate 2

Figs 1—3. *Rehacythereis bartensteini* (OERTLI, 1958)
    Fig. 1. Carapace in right view. Borehole Vst-8: 125 m
    Fig. 2. Carapace in right view. Borehole Vst-8: 140 m
    Fig. 3. Carapace in left view. Borehole Vst-8: 123 m

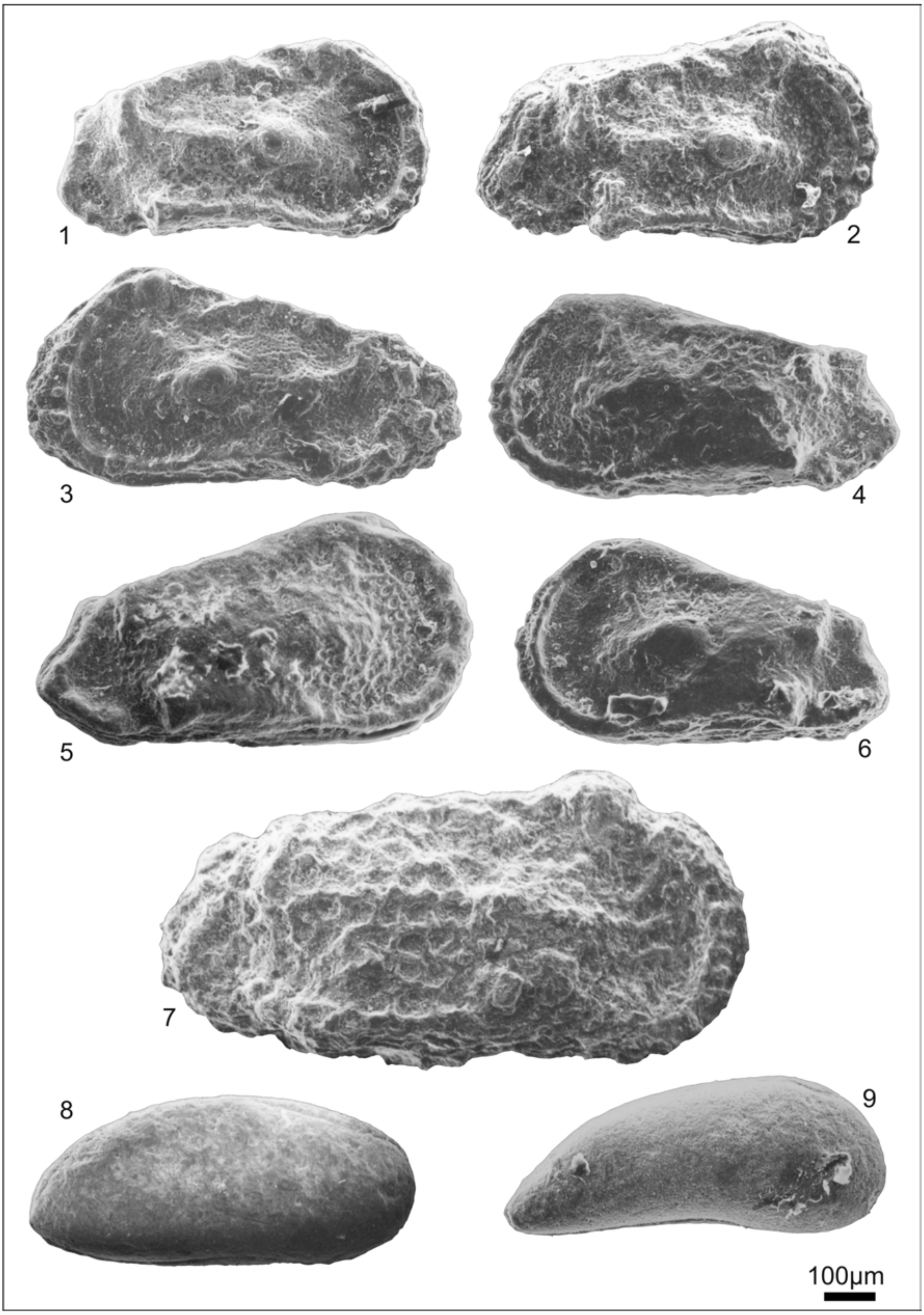
Figs 4—6. *Rehacythereis luermannae* (TRIEBEL, 1940)
    Fig. 4. Carapace in left view. Borehole Agt-2: 311 m
    Fig. 5. Carapace in right view. Borehole Agt-2: 291 m
    Fig. 6. Carapace in left view. Borehole Agt-2: 339 m

Fig. 7. *Cythereis* ex gr. *fahrioni* (BISCHOFF, 1963). Carapace in right view. Borehole Vst-8 133 m

Fig. 8: *Pontocyprella harrisiana* (JONES, 1849). Carapace in right view. Borehole Agt-2: 319 m

Fig. 9. *Paracypris jonesi* BONNEMA, 1941. Carapace in right view. Borehole Vst-8: 110 m

Plate 2



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New frog (Lissamphibia: Anura) remains from the Upper Cretaceous (Santonian) Csehbánya Formation (Iharkút, Bakony Mountains) with a new method: large-scale extraction of microvertebrate fossils

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(with 3 figures)

Intensive screen-washing carried out at the Upper Cretaceous Iharkút paleovertebrate locality (Hungary) has produced several tons of screened substance. In this work an improved method is described for the extraction of microfossils from sediments based on wax-lard flotation. Besides previously described taxa, many fragmentary lissamphibian bones were unearthed from this paleovertebrate locality among some partially identified bone fragments. This suggests the Iharkút lissamphibian fauna was more diverse than suggested by the taxa described so far.

Introduction

Microvertebrate assemblages are a very important source of paleontological and paleoecological information. A large number of microvertebrate fossils are recovered by screen washing technology, which can provide much more information on rare taxa than a complete skeleton (e.g. BASZIO 2008). This is especially important regarding lissamphibians because the size of their bones is mostly only some millimeters (up to 1-2 cm), so their recovery in fossiliferous deposits is very difficult with macroscopic methods.

The Iharkút Upper Cretaceous (Santonian) palaeovertebrate locality is very rich in vertebrate and microvertebrate fossils (e.g. fishes, lizards, crocodile and dinosaur teeth etc.), where a varied lissamphibian fauna has also become known (e.g. ŐSI et al. 2012). From the Iharkutian screen-washed sediments the family Albanerpetontidae (Allocaudata) was unearthed, two new frog genera were described, and species such as *Bakonybatrachus fedori* (Anura: Archaeobatrachia, Discoglossidae), *Hungarobatrachus szukacsi* (Neobatrachia) and some fragmentary remains of pelobatid frogs were also detected (e.g. SZENTESI and VENCZEL 2010, 2012; SZENTESI 2012; SZENTESI et al. 2013). This rich lissamphibian fauna is unique among the Upper Cretaceous European localities. It is a special virtue that this assemblage contains a Gondwanan element (*Hungarobatrachus*) next to the usual Euramerican fauna. The screen-washed lissamphibian remains from the Iharkút sediments are mostly very fragmentary, but some interesting frog remains were found among them. This suggests that many remains of other species are hidden in this paleovertebrate locality. The most interesting specimens of these have been described herein with taphonomical, paleoecological and paleo-biogeographical implications.

Material and methods

Since 2001, more than 250 tons of deposits have been screen-washed on the annual excavations at Iharkút. All deposit types were examined for microvertebrate records that can be found at the paleovertebrate locality, such as clays, breccias, sand, red and variously colored paleosols, dark green silts full of amber and plant fossil-containing light-colored clay). All studied deposits contained mainly microvertebrate fossils, except the plant fossil-containing light-colored clay. More than half of the screen-washed sediments (about 100 kg) have been examined so far. Fossil seeds, fruits, snail shells and Ostracoda have been unearthed from these deposits, besides the numerous microvertebrate fossils. About 560 of these bone fragments were classified as lissamphibians, but only 15% of these are suitable for taxonomic studies.

Picking of microfossils under a light microscope is very exhausting and lengthy work, hence it is very useful to reduce the volume of screened substance as much as possible without damage or elimination of irrecoverable fossil material. FREEMAN (2010) developed a new method for field and laboratory use that solves this problem. The method uses a mixture of paraffin wax and lard to obtain teeth and small bones from deposits. This is a useful technology, but the paraffin–lard mixture is recovered using petroleum, which material is harmful for human health and the environment as well. Moreover, the mixture is dissolved and lost during the process. Its other disadvantages are that it requires expensive and large equipment (e.g. a concrete mixer), and their transportation to the field is very difficult and costly. Therefore, except for the recipe of the basic mixture (ratio of paraffin wax to lard) all phases have been revised (Fig. 1).

The method consists of the following steps:

1. The paraffin-lard mixture (in a proportion of 3 to 1) is prepared in a pot, with the mixture occupying approximately ¼ of the pot. Then the same amount of water is added to the mixture while stirring slowly and then heating to boiling point. During the process the paraffin and the lard are melted and mixed.
2. While stirring continuously, cold water is poured into the pot. Because of the cold water the wax mixture precipitates and granulates.
3. The wax-lard granules are filtered with a metal sieve while the water drips out. Granules are relatively soft, which property is retained at room temperature too.
4. ¼ of a bucket is filled with the dry deposit. Then the wax-lard mixture is added in a 3 to 1 ratio. More granules cannot be mixed with the sediment.
5. The mixture is rubbed to the wall of the bucket by hand, while the wax mixes with the bone-bearing sediment. The wax-lard mixture sticks to teeth and bones while it forms granules again. While this stuck material cools down during rubbing it becomes harder and thicker so it saves the vulnerable microfossils from mechanical damage.
6. The bucket is filled with cold water while stirring. The fossil bearing granules float on the surface of the water.
7. Filtration of bone-bearing wax-lard granules are filtered through a metal sieve. This step is repeated 2 to 4 times so all the granules are obtained.
8. The recovered fossil-bearing granules are poured into the pot, which is then filled completely with water.
9. During boiling the wax-lard mixture melts off fossils which settle to the bottom of the vessel in about five minutes.
10. Pour the wax-lard containing hot water carefully to another vessel. From this material granules can be made again (based on steps 1 to 3), which can be immediately re-used.

Even larger clasts fall into pieces during such manipulation, so the resulting silt and clay can be washed out, thus the amount of residue is reduced. After drying, this material can be stored and any remaining fossils can be picked out with the usual methods (e.g. under a light microscope).

Advantages of the method

Application of a wax mixture besides the traditional method of picking out bones can also be used to obtain other fossils, such as oogonia of Chara, seeds and fruits, snail shells, Ostracoda and eggshell fragments, etc.

The residue is significantly enriched in microfossils, so they can be picked out more rapidly.

Approx. 70% of fossil seeds and fruits can be separated from the examined deposits using a wax-lard mixture, and the ratio is similarly large in the case of bones and teeth.

The paraffin wax mixture saves the bones and other microfossils from mechanical damages in the treated sediment.

The sediment adhering to the wax-lard mixture is a small fragment (about 10-20%) of the original material, the exact amount depending on the quantity of wood char in the treated deposit. In contrast, the amount of microfossils in the used wax-lard mixture reaches 80-90%. Meanwhile, only few plant fragments or sediment grains remain in this residue.

The quantity of treated sediment is reduced by 20% on average from the original amount. This decrease is due to the fact that the less cemented clasts fall into pieces so they can be screen-washed more easily from the sediment.

Almost 100% of the wax-lard mixture is retrievable and reusable several times.

This method does not require any special or large, unwieldy equipment. Therefore, it is also practical on field trips for identification of fossiliferous deposits.

Any lard or paraffin wax that might be spilled is decomposed easily, so this method does not cause pollution in the field.

Shortcomings of the method

It is impossible to pick up all fossils from the sediment, as non-adherent fossils always remain in the treated material.

The wax-lard mixture also sticks to cracked wood char or fusinite. Although it is still suitable for obtaining seeds, in such rich sediments the wax-lard mixture may not be able to pick out more than 40% of bone and tooth fossils. Another drawback is that in these sediments the color of bones is also black, so it is more difficult to separate these elements.

* * *

A Polaron SC7620 Mini Sputter Coater/Glow Discharge System machine and a Hitachi S-2600N scanning electron microscope have been used for the preparation of SEM photos.

Anatomical and taxonomical conventions

This work follows the common English terms for anatomical structures and the anatomical orientation system. The classification of frogs is based on the work of Sanchíz (1998) and also takes into account results described by Frost et al. (2006). The size of the frogs described here was estimated using the method developed by Esteban et al. (1995).

Institutional abbreviations: **MTM**: Hungarian Natural History Museum, Budapest; **MTM VER**: Geological Collection of Hungarian Natural History Museum, vertebrates.

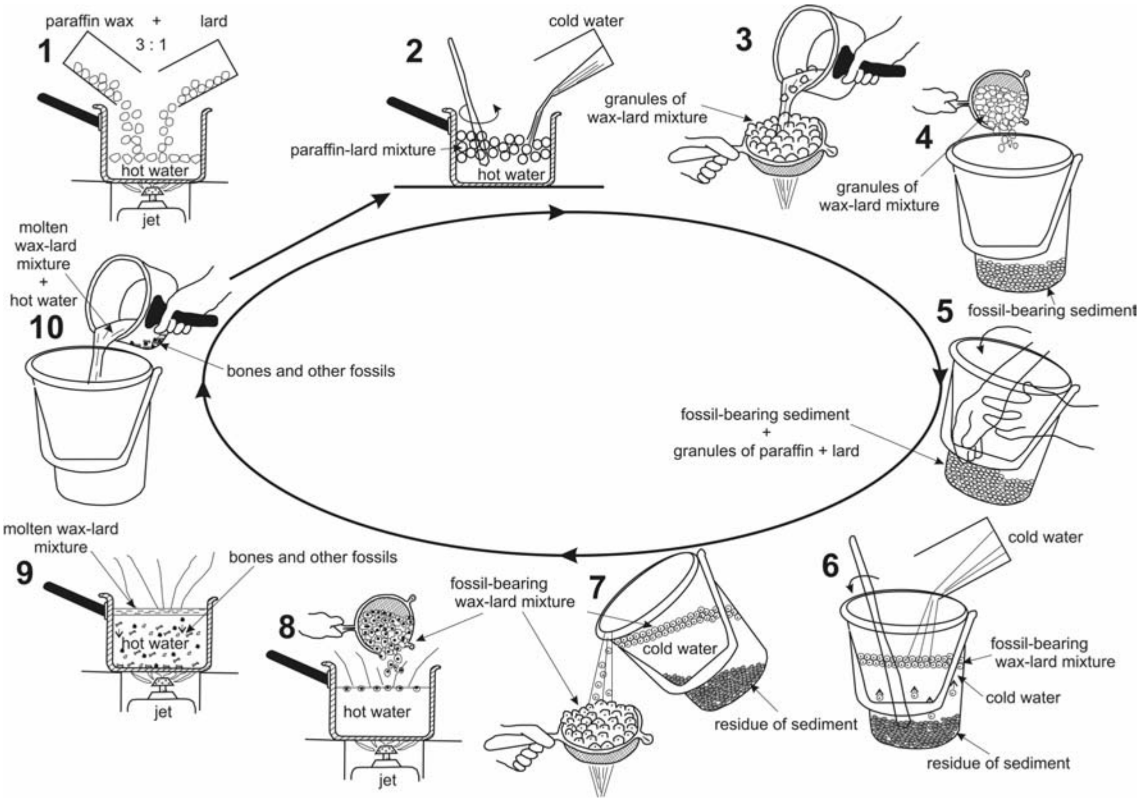

Fig. 1. Steps of the improved extraction method of microvertebrate fossils from sediments using a paraffin-lard mixture

Description of lissamphibian material with remarks

Class Amphibia LINNAEUS, 1758
Superorder Salientia LAURENTI, 1768
Order Anura FISCHER VON WALDHEIM, 1813
Suborder Archaeobatrachia REIG, 1961
Family Discoglossidae GRAY, 1825

Discoglossidae indet. 1
Fig. 2/1

Material – Fragmentary left ilium (MTM V2010.291.1.) from the Upper Cretaceous (Santonian) paleovertebrate locality of Iharkút.

Description – The small, very fragmentary bone is the posterior part of the ilium. The acetabulum is relatively deep and large. The ventral acetabular expansion (= pars ascendens) is very small, while the acetabular rim strongly extends over a wide and deep groove. In ventral view, the anterior projection of the ilium (= vexillum) is wide, it is narrow and wedge-shaped anteriorly, and leans ventrolaterally. The dorsal protuberance (= tuber superius), pars ascendens and pars descendens are lacking. The dorsal crista (= crista iliaca) is not intact but it is wide on its base and relatively low. In cross section the dorsal crista forms a drop shape with the vexillum. From this feature it follows that the dorsal crista may be slightly higher and probably only a thin crest is missing from it. Between the dorsal crista and the anterior projection of the ilium there is a deep, lengthy groove on the anterior part of the bone. Laterally, the surface of the bone is smooth. In posterior view, the acetabular rim projects strongly laterally, the ventral part is flared while the dorsal crista is slightly curved medially.

Remarks – This left ilium belongs to the family Discoglossidae due to the following characters: (1) a ventrally wide ilioischiadic junction with a relatively low dorsal crista; (2) and a relatively large acetabulum with a laterally strongly projected acetabular rim in association with a very small supraacetabular expansion (e.g. SANCHÍZ 1998). This specimen belongs to a small (probably juvenile) frog with an estimated snout length of about 20-25 mm.

This left ilium differs from *Bakonybatrachus fedori* in the significantly wider ilioischiadic junction and the more prominent acetabular rim (SZENTESI and VENCZEL 2012). The stout and low dorsal crest is typical for Discoglossidae. However, the crista iliaca is not only characteristic of this group, it can also be found in all members of Pipidae, leptodactylids, hemyphractin hylids and ranids (e.g. PRASAD and RAGE 2004). Pipids bear strong ridges on the medial surface of the dorsal crest (e.g. TRUEB and HANKEN 1992, KOVALENKO 1999), while in leptodactylids there is a long and high ridge on the dorsal crista which projects from the dorsal protuberance (e.g. TYLER 1989, PONSSA 2008). In hemyphractin hylids the dorsal crest is very low, thin and plate-like with a straight dorsal margin (e.g. SANCHÍZ 1998). The dorsal crest of ranid frogs is significantly higher relative to the vexillum (e.g. FROST et al. 2006). The relatively deep and large acetabulum of this specimen is similar to that of *Eodiscoglossus* (e.g. EVANS et al. 1990, FOLIE and CODREA 2005) but the acetabular rim is more prominent. The vexillum is rounded in cross section and the crista iliaca is thick and wedge-like. The acetabulum is also large in *Paralatonia transylvanica* and *Discoglossus sardus* but the acetabular rim of *Paralatonia* protrudes above the margin of the bone, while the ventral supraacetabular expansion of *Discoglossus* is significantly wider. In posterior view, the ilioischiadic junction of this specimen is similar in width to that of *Latonia* (e.g. ROČEK 1994, VENCZEL 2004) but the acetabular rim projects more and at a larger angle. The angle of this projection is significantly smaller than in *Paradsicoglossus americanus* (BLAIN et al. 2010).

Discoglossidae indet. 2
Fig. 2/2ab

Material – Fragmentary right ilium (MTM VER 2014.10.) from the Upper Cretaceous (Santonian) paleovertebrate locality of Iharkút.

Description – Small sized, fragmentary right ilium where the posterior region of the vexillum is preserved, as well as parts of the supraacetabular and preacetabular regions. A low dorsal crest is present, on which the dorsal protuberance is not prominent. In contrast with this, the supraacetabular fossa is deep and projects anterodorsally. The preacetabular part strongly bulges laterally while in posterior view, the ventral part of the ilium is broad and it is tapered dorsally. A relatively deep preacetabular fossa is present, but its size and dimension are not visible. In medial view, the iliac shaft (= vexillum) is distinct from the dorsal crista. The interiliac tubercle was probably robust because it is strongly projected mediodorsally.

Remarks – The low dorsal crest combined with a prominent interiliac tubercle is a discoglossid character (e.g. Sanchíz 1998). This ilium differs from *Bakonybatrachus*, *Eodiscoglossus, Wealdenbatrachus* and *Latonia* in the featureless dorsal protuberance and the deep supraacetabular fossa (e.g. Fey 1988, Evans et al. 1990, Venczel 2001, Szentesi and Venczel 2012). It differs from *Paradiscoglossus* in its robust interiliac tubercle (Estes and Sanchíz 1982).

Anura indet. 1

Fig 3/1a-c

Material – Fragmentary left pterygoid (MTM V2008.20.1.) from the Upper Cretaceous (Santonian) paleovertebrate locality of Iharkút.

Description – This fragmentary left pterygoid is very robust. The largest part of the ramus interior and posterior is lacking. The ramus maxillaris is prolonged and thick, the margo orbitalis is dominant and curved dorsomedially, while it is concave posteromedially. The sulcus pterygoideus is wide and deep but it is filled with sediment. In posterior view, the ramus posterior is nearly elliptical in cross section, while the r. interior is nearly circular. The dorsomedial edge of the margo orbitalis is almost on the same level as the ramus posterior. The ventral surface of this bone is smooth but in its longitudinal axis there is a shallow groove which widens and it is deeper posteriorly.

Remarks – This shape is general in many frogs (see Sanchíz 1998) but this very robust feature suggests that this bone probably belongs to *Hungarobatrachus*. As it is an isolated bone and so are all bones of *Hungarobatrachus*, it cannot be classified as such, even if this bone were intact.

Anura indet. 2

Fig. 3/2

Material – Fragmentary presacral vertebra (MTM VER 2014.11.) from the Upper Cretaceous (Santonian) paleovertebrate locality of Iharkút.

Description – Only the ventrally sandglass-like centrum is preserved from this vertebra, and even that is fragmentary. The vertebra is procoelous, its body is flattened dorsoventrally, the cotyle is relatively deep and rounded.

Remarks – This basic feature can be found in many frogs, including discoglossids and ranids (e.g. Bailon 1999).

Anura indet. 3

Fig. 3/3ab

Material – Fragmentary urostyl (MTM VER 2014.12.) from the Upper Cretaceous (Santonian) paleovertebrate locality of Iharkút.

Description – Anteriorly, on this fragmentary urostyl the condyloid fossae are slightly elliptical and deep with a well developed rim, and they are close to each other. The fragmentary canalis coccygeus was possibly wide and rounded while the dorsal crista is not preserved.

Remarks – A similar feature equally appears in several archaeobatrachians and neobatrachians (e.g. Sanchíz 1998) but more precise identification of this fragmentary bone is impossible.

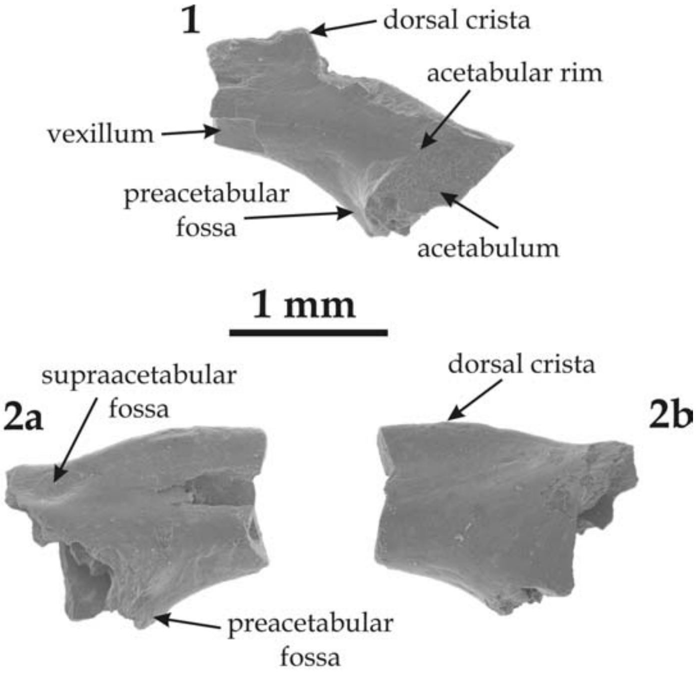

Fig. 2. Frog ilia from the Upper Cretaceous (Santonian) paleovertebrate locality of Iharkút, Bakony Mountains, Hungary. 1, Discoglossidae indet. 1 left ilium (MTM V2010.291.1.) in lateral view; 2ab, Discoglossidae indet. 2, right ilium (MTM VER 2014.10.), (2a) in lateral and (2b) medial views.

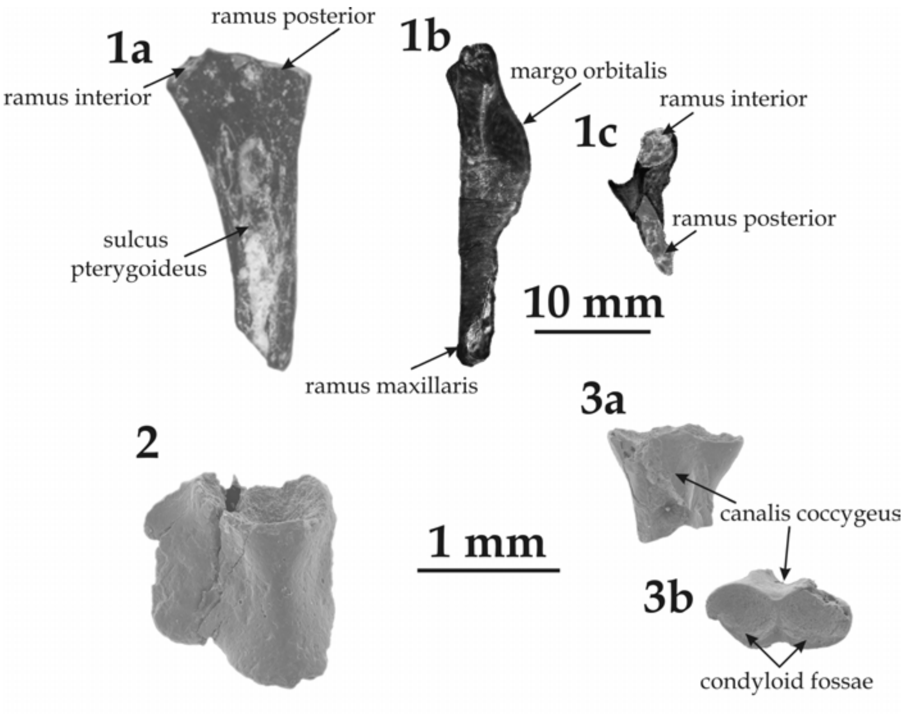

Fig. 3. Frog fossils from the Upper Cretaceous (Santonian) paleovertebrate locality of Iharkút, Bakony Mountains, Hungary. 1a-c, Anura indet. 1, left pterygoid (MTM V2008.20.1.), (1a) in laterodorsal (macro photo with Cannon 600), (1b) lateral and (1c) posterior views (1b-1c graphics by macrophoto); 2, Anura indet. 2, presacral vertebra (MTM VER 2014.11.) in ventral view; 3ab, Anura indet. 3, urostyl (MTM VER 2014.12.) (3a) in dorsal and (3b) anterior views.

Taphonomical remarks

The frog remains originate from different layers of the Csehbánya Formation at Iharkút paleovertebrate locality. These layers are formed by various deposits as basic breccia, dark green silt full of amber, clay etc., which indicates a multiform deposition environment (SZENTESI 2012). It follows that these bones are preserved to very different extent. In the high energy medium only those bones can remain relatively intact which are not transported too long. The bones of the frogs living farther from the former river or backwater were transported much longer, so these are more fragmentary than for example the bones of *Hungarobatrachus* (e.g. SZENTESI and VENCZEL 2010).

Paleobiological, paleoecological and paleo-biogeographical implications

Based on their anatomical characters, taphonomical condition and recent analogies in literature, it appears that the Upper Cretaceous lissamphibians of the Iharkút paleovertebrate locality adopted different lifestyles. *Bakonybatrachus fedori* and the above mentioned Discoglossidae indet. frogs probably adopted a periaquatic lifestyle while the *Hungarobatrachus* was an aquatic form. Albanerpetontids and pelobatids probably lived farther from the open water surfaces, due to their burrowing lifestyle (SZENTESI 2012). The taphonomical studies of this paleo lissamphibian fauna suggest the same. In the European Upper Cretaceous paleovertebrate localities discoglossid remains are the most common fossils next to albanerpetontids (e.g. SANCHÍZ 1998, MCGOWAN 2002, BÁEZ et al. 2009, SZENTESI et al. 2013). Compared with the paleo-biogeographical data in the literature the Iharkutian lissamphibian fauna consists of Laurasian (albanerpetontids, discoglossids) and Gondwanan (*Hungarobatrachus*, a representative of Neobatrachia) elements, which means that this paleo-environment was a zone where two faunas were mixed, at least in the Santonian (e.g. SZENTESI and VENCZEL 2012).

Conclusions

In this work an improved method has been described for the large-scale extraction of microfossils from original soft deposits and from screen-washed sediments. It is useful for picking up various microvertebrate as well as other microfossils (e.g. seeds, fruits, invertebrate shells and eggshell fragments etc.). This technique can also be effectively used during field work.

The above described frog remains suggest that the Iharkút lissamphibian fauna is more diverse than previously thought and the appearance of further amphibian groups is expected from this paleovertebrate locality.

Based on taphonomical and paleobiological studies it appears that the Iharkutian lissamphibians lived in different paleo-environments.

Compared with other European lissamphibian paleo-faunas the one described above is relatively diverse and its special feature is the mixing of Laurasian and Gondwanan faunas.

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I am indebted to Attila Ősi (MTA-ELTE Lendület Dinosaur Research Group) who generously made the fossils available which are described herein. I am grateful to Krisztina Buczkó (Department of Botany, Hungarian Natural History Museum) for her assistance in the production of the SEM photos and to Márton Venczel (Ţării Crişurilor Museum, Oradea, Romania) who assisted in producing the macro photos. I am grateful to Eszter Veszelinov (Department of Foreign Languages, Szent István University), who helped to improve the English in this paper. This project was supported by the Hungarian Natural History Museum, the Hungarian Scientific Research Fund (OTKA NF 84193) and the Hantken Foundation.

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A possible taphonomical evidence for the palaeoecological role of the giant shrews (Mammalia, Soricidae) in the Carpathian Basin

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(with 11 figures, and 1 table)

The study on some toothmarks on the medial surface of the right ulna of a middle sized carnivore mammal are present in this paper. It is shown here as a possible taphonomical evidence of carrion-eating diet of the Late Miocene *Crusafontina endemica* GIBERT, 1974 shrew (Mammalia, Soricidae) from Sümeg locality (Western Hungary). Also other palaeoecological relations (nutrition and ecotype preference) of the giant shrews (the members of Anourosoricini and Beremendiini tribes of family Soricidae) from the Late Miocene to Middle Pleistocene age of the Carpathian Basin are overviewed in the present article.

Introduction

Shrews are relatively small animals, but we can find quite large sized fossil species in several groups of them. Some of these taxa have recent representatives as well, like the Asian "mole shrew" (*Anourosorex squamipes*) in tribe Anourosoricini.

We can find "giant shrews" among the fossil Soricidae species of the Carpathian Basin from the Late Miocene to the Middle Pleistocene ages. These "giants" could have been more than duplicated dimensions than the average sized shrews of Hungary in the present (Figures 1-2). These forms belong to two different phylogenetic lines (tribes Anourosoricini and Beremendiini, Figure 3), but they could play similar ecological roles in the different ages of the Carpathian Basin in consequence of their convergent adaptive development.

We can suppose them to have special diets in comparison with the most of the recent shrews on the basis of their extraordinary largeness and increased claim to the nutritive material.

Some tooth-marks on a fragmentary bone of a middle sized mammal from the Late Miocene Sümeg locality could give a new evidence to the carrion-eating diet of the large sized Anourosoricini shrew, *Crusafontina endemica*.

This taphonomical evidence is shown in the present paper and also an overview on the ecological role of the giant shrews (the members of tribe Anourosoricini and Beremendiini) is given here.

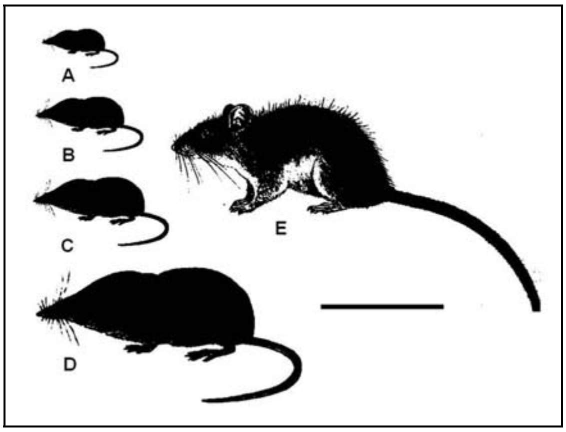

Figure 1. Comparison of the measurements of the giant shrews with that of the most common recent ones in Hungary and a big sized rodent. A = *Sorex minutus* (ca. 5 cm), B = *Sorex araneus* (ca. 7 cm), C = *Neomys fodiens* (ca. 9 cm), D = *Kordosia topali* (ca. 18 cm), E = *Rattus rattus* (Scale bar = 10 cm).

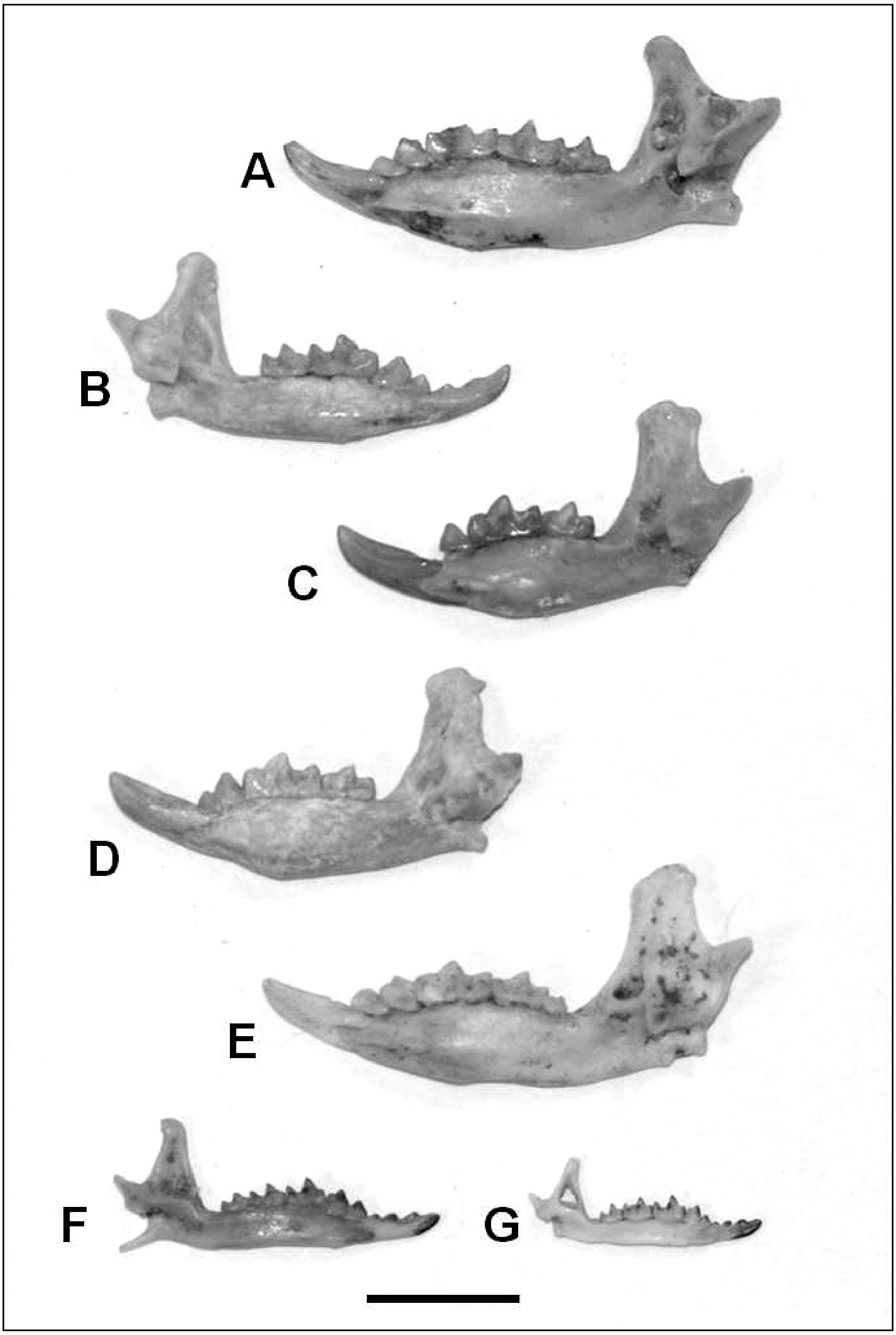

Figure 2. The jaws of the giant shrews of the Carpathian Basin (A-D) and for comparison the recent Anourosoricini form (E), an average and a small sized living *Sorex* species (F-G). All the photos were taken in lingual view and in the same magnitude (scale bar = 5 mm). A: *Beremendia fissidens* (PETÉNYI, 1864), right mandible, Villány 3. B: *Crusafontina kormosi* (BACHMAYER & WILSON, 1970) left mandible, Polgárdi 4. C: *Amblycoptus oligodon* KORMOS, 1926, right mandible, Polgárdi 4. D: *Kordosia topali* (JÁNOSSY, 1972), right mandible, Polgárdi 5. E: *Anourosorex squamipes* MILNE-EDWARDS, 1872, right mandible, Vietnam. F: *Sorex araneus* LINNAEUS 1758, left mandible, Vaskapu 2. G: *Sorex minutus* LINNAEUS 1766, left mandible, Vaskapu 2.

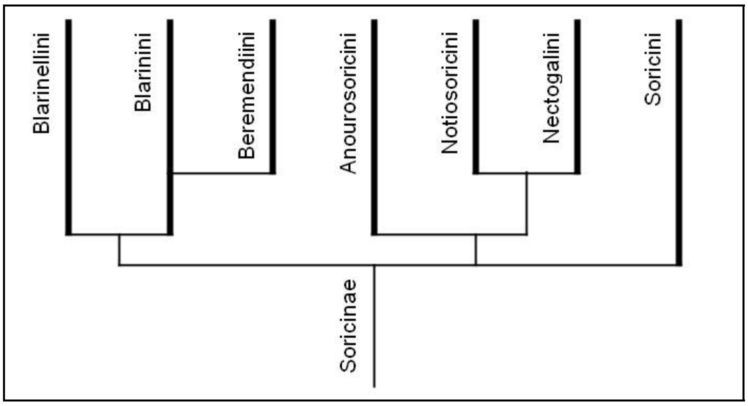

Figure 3. Phylogenetic relations between Anourosoricini and Beremendiini tribes, the two giant shrew groups of the Carpathian Basin (after van Dam 2010).

Localities and stratigraphy

Tribe Anourosoricini is represented in Hungary by three genera: *Crusafontina*, *Amblycoptus* and *Kordosia*. The tribe appears with Genus *Crusafontina* in the Carpathian Basin in the Late Miocene Alsótelekes and Rudabánya localities (MN 9 Zone) (Mészáros 2000a).

Crusafontina occurs with two species in the Carpathian Basin: *C. endemica* is present from MN 9 Zone to the first part of MN 10 Zone, in Alsótelekes (Mészáros 1999b), and Sümeg (Mészáros 1996) localities and perhaps in Rudabánya (Ziegler & Mészáros 2004), while *C. kormosi* appears in the end of MN 11 Zone and disappears in the middle of MN 13 Zone. It was found in Kohfidisch (Bachmayer & Wilson 1970), Tihany (Mészáros, 2008), Csákvár (Mészáros 1996), Tardosbánya (Mészáros 1998a) and Polgárdi 4 (Mészáros 1999a) sites. The taxonomical status of the Rudabánya form is not clear, it could have been ranged to an other species.

Genus *Amblycoptus* contains only one species: *A. oligodon*. It is reported from MN 12-13 Zones, Tardosbánya (Mészáros 1998a), Egyházasdengeleg (Hír & Mészáros 1995), Széchenyi Hill (Mészáros 1996), Polgárdi 2 and 4 (Mészáros 1999a) localities.

Only *Kordosia topali* occurs among the *Kordosia* species in Hungary, in Polgárdi 5 (Mészáros 1999a) and Osztramos 1 (Mészáros 1997b) sites. It appears in the middle of MN 13 Zone and disappears in the Lower Pliocene MN 14 Zone.

Tribe Beremendiini is a monogeneric group which contains only genus *Beremendia*. Two forms, *B. fissidens* and *B. minor* were found in Hungary from its four species. Both of them appear here in the Lower Pliocene Osztramos 1 locality (MN 14 Zone, Reumer 1984, Jánossy 1986). *Beremendia fissidens* disappears in the middle Pleistocene. It is reported also from Csarnóta (Reumer 1984), Beremend (Jánossy 1986), Villány (Reumer 1984), Dunaalmás (Jánossy 1986), Nagyharsányhegy (Jánossy 1986), Újlak Hill (Jánossy 1986), Süttő 19 (Pazonyi et al. 2014), Somssich Hill 2 (Botka & Mészáros 2014 a, b) and Tarkő (Jánossy 1986). *Beremendia minor* is known to the late Early Pleistocene (Somssich Hill 2, Botka & Mészáros 2014b). For the stratigraphical ranges see Figure 4.

The ages, and the Anourosoricini or Beremendiini occurrences with the reporting references are summarized in Table 1. The ages of the Late Miocene localities were pointed out in Mészáros 2000a. The stratigraphical position of the Pliocene and the Pleistocene sites are used here as it was stated in Botka & Mészáros (2014b).

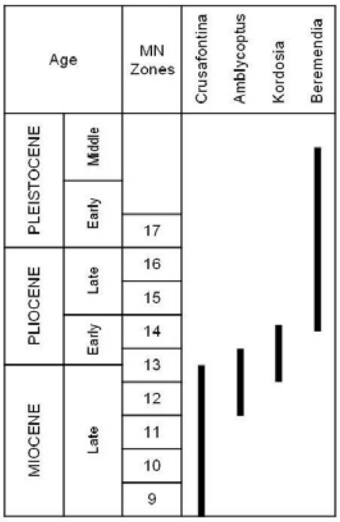

Figure 4. Stratigraphical occurrence of the studied genera in the Carpathian Basin.

Table 1. The age of the studied localities with the Anourosoricini or Beremendiini occurrences and the reporting references.

Locality	Age	Species	Reference
Alsótelekes	MN 9	*Crusafontina endemica*	MÉSZÁROS 1999b
Rudabánya	MN 9	*Crusafontina endemica*	ZIEGLER & MÉSZÁROS 2004
Sümeg	MN 10	*Crusafontina endemica*	MÉSZÁROS 1996
Kohfidisch	MN 10	*Crusafontina kormosi*	BACHMAYER & WILSON 1970
Tihany	MN 11	*Crusafontina kormosi*	MÉSZÁROS 2008
Csákvár	MN 11	*Crusafontina kormosi*	MÉSZÁROS 1996
Tardosbánya	MN 12	*Crusafontina kormosi* *Amblycoptus oligodon*	MÉSZÁROS 1998a
Egyházasdengeleg	MN 12	*Amblycoptus oligodon*	HÍR & MÉSZÁROS 1995
Széchenyi Hill	MN 12	*Amblycoptus oligodon*	MÉSZÁROS 1996
Polgárdi 2,4,5	MN 13	*Crusafontina kormosi* *Amblycoptus oligodon* *Kordosia topali*	MÉSZÁROS 1999a
Osztramos 1,2,3,4,7,8,14	MN 14, MN 16 – Middle Pleistocene	*Kordosia topali Beremendia fissidens Beremendia minor*	REUMER 1984, JÁNOSSY 1986, MÉSZÁROS 1997b
Csarnóta 1,2,4	MN 15, MN 17	*Beremendia fissidens*	REUMER 1984
Beremend 1,2,3,4,5,8,9,11,15	MN 16 – Early Pleistocene	*Beremendia fissidens*	JÁNOSSY 1986
Villány 1,2,3,5,6,7,8,11	MN 17 – Middle Pleistocene	*Beremendia fissidens*	REUMER 1984, JÁNOSSY 1986
Dunaalmás 4	MN 17 – Early Pleistocene	*Beremendia fissidens*	JÁNOSSY 1986
Nagyharsányhegy 2,3,4,5	MN 17 – Early Pleistocene	*Beremendia fissidens*	JÁNOSSY 1986
Újlak Hill	Early Pleistocene	*Beremendia fissidens*	JÁNOSSY 1986
Süttő 19	Early Pleistocene	*Beremendia fissidens*	PAZONYI et al. 2014
Somssich Hill 2	Early Pleistocene	*Beremendia fissidens* *Beremendia minor*	BOTKA & MÉSZÁROS 2014a, b
Tarkő	Middle Pleistocene	*Beremendia fissidens*	JÁNOSSY 1986

Taxonomy

Nomenclature for the morphological descriptions are used after REUMER (1984) and MÉSZÁROS (1997) in the taxonomical part.

Phylum Vertebrata LINNAEUS, 1758
Classis Mammalia LINNAEUS, 1758
Order Eulipotyphla WADDELL et al., 1999
Family Soricidae FISCHER VON WALDHEIM, 1817
Subfamily Soricinae FISCHER VON WALDHEIM, 1817

Tribe Anourosoricini ANDERSON, 1879

The common characters of Anourosoricini species are as follows: Large dimensions, upwardly widening coronoid process, tight internal temporal fossa, trigonal upper condyloid facet, oblong-shaped lower one, very narrow interarticular area. They have two or three upper antemolars, their lower incisor is acuspulate or bicuspulate. Dental formula may be 142/123, 133/123, 142/122 and 132/122 (MÉSZÁROS 1997b).

By this time six valid genera is ranged in the tribe Anourosoricini (VAN DAM 2010), but three of them (*Darocasorex*, *Paranourosorex*, and the only recent *Anourosorex*) were not reported from the Carpathian Basin (Figure 5).

Genus *Crusafontina* GIBERT, 1974

This genus has the most complete dentition in the tribe Anourosoricini. Dental formula is 143/123. M^3, and M_3 are reduced, but always are present. Upper condylar facet is triangular or oval, lower one is oblong, interarticular area is very narrow. Internal temporal fossa is subtriangular to round or oval. I^1 is with buccal cingulum. A^1 is without parastyle. P^4 is pentagonal because of the projecting parastyle. P^4 and M^1 are with distinct posterior emargination. M^1 parastyle is projecting less or equally far buccally compared to metastyle. M^2 with complete talon. I_1 is mono-, bi-, or tricuspulate. P_4 is with posterolingual depression. M_1 and M_2 are with entocristid.

Two of the *Crusafontina* species are definitely reported from the Carpathian Basin (VAN DAM 2004).

Crusafontina endemica GIBERT, 1974.

The I^1 apex is long, with L/H not smaller than about 1.40. Metastyle of M^1 is extending more buccally than parastyle, and hypoconal flange is not protruding lingually. The I_1 is bi- to tricuspulate. The M_3 talonid contains a small basin. M_3–M_1 length ratio is not smaller than about 0.40 (VAN DAM 2004).

Crusafontina kormosi (BACHMAYER & WILSON, 1970)

Medium-sized *Crusafontina* species. The I^1 apex is long, with L/H ratio smaller than about 1.40. M^1 metastyle and parastyle is extending buccally about equally far and hypoconal flange not protruding lingually. I_1 is bicuspulate. M_3 talonid is either with closed basin, with terminal heel or missing. M_3–M_1 length ratio is smaller than about 0.40 (VAN DAM 2004).

Genus *Amblycoptus* KORMOS, 1926

Large sized Anourosoricini, but somewhat smaller than Kordosia. The third lower and upper antemolars are missing, but A^3 is present. I_1 is acuspulate, the parastyle of A^1 is missing. P^4 is pentagonal in occlusal view. Dental formula is 142/122 (MÉSZÁROS 1997b).

Amblycoptus oligodon KORMOS, 1926

For *A. oligodon* is the only known species of the genus, the morphological characters are the same as there.

Genus *Kordosia* MÉSZÁROS 1997

Kordosia has the most reduced dental formula in the tribe Anourosoricini: 132/122. A^3, M^3 and M_3 is always missing, ventral profile of P^4 is much like an oblong. PW of M^1 is far less than AW, I_1 is acuspulate. On the mandible the internal temporal fossa is extremely tight. Dental formula is 132/122. (MÉSZÁROS 1997b)

Two species, *Kordosia jessiae* (DOUKAS 1995) and *Kordosia topali is* ranged here. By this time only *K. topali* is found in the Carpatian Basin.

Kordosia topali (JÁNOSSY, 1972)

Larger sized *Kordosia* species, than *K. jessiae*. I^1 may be without cingulum and with convex margin (MÉSZÁROS 1997b).

Tribe Beremendiini REUMER, 1984

This is the only monogeneric tribe among the Soricinae, comprising only the extinct genus *Beremendia.* Separation of this tribe from the other tribes is based on the intermediate position of its morphology between Soriculini (bifid I^1 and presence of entoconid crests) and Blarinini (structure of the condyle and intense dark red pigmentation) (REUMER 1984).

Genus *Beremendia* KORMOS, 1934

Upper incisor is strongly fissident, teeth are heavily pigmented, it has Blarinini-like condyle with broad interarticular area and anteriorly placed lower facet, the lower incisor is acuspulate, the entoconid crests are present (REUMER 1984).

The genus contains four valid species (*B. fissidens, B. minor, B. pohaiensis* and *B. jiangnanensis*) but the two latter do not occur in Europe.

Beremendia fissidens (PETÉNYI, 1864)

Teeth are intensively stained a dark red. The I^1 is strongly fissident with a bifid apex. Four upper antemolars are present. A^1 and A^2 are of about equal size, A^3 is smaller and A^4 is smaller again. The A^4 is reduced, hidden and not visible in buccal view or is lacking. The posterior emargination is moderate on the P^4, M^1 and M^2. The parastyle of the M^1 is moderately developed. The M^3 is relatively small. The I_1 is grooved, acuspulate, the apex curves upwards. The A_2 is bicuspid and has a posterolingual basin. The M_3 is reduced. The ramus is strong and robust. The coronoid process is stout, anterolaterally curved, the angle of the curve may vary. The angular process is short and flat. The external pterygoid fossa is definitely or less deeply pocketed. The upper facet is narrow, its shape may vary from elliptic to oval. The interarticular area is broad with a lingual margin. The lower facet leans strongly anteriorly and it is not visible in buccal view. The internal temporal fossa is small, deep and pocketed (REUMER 1984).

Beremendia minor RZEBIK-KOWALSKA, 1976

The dimensions of the species are significantly smaller than that of *B. fissidens* (not only the dental elements but also the size of the mental foramen, its anterior basin and the parameters of the symphysis fossa). The angle of the I^1 is smaller between the ventral part of the apex and the anterior margin of the talon. The I_1 has a more pointed apex and a more curved lower incisor. The M_3 has a high entoconid, a rounded hypolophid and its posterior margin of the talonid is round (BOTKA & MÉSZÁROS 2014b).

Remarks

We know further large sized shrews (for example *Dinosorex*) from the Miocene of the Carpathian Basin (MÉSZÁROS 2000a). As these species today is not ranged in family Soricidae, and their ecological role in this area is less clear, they are not discussed here.

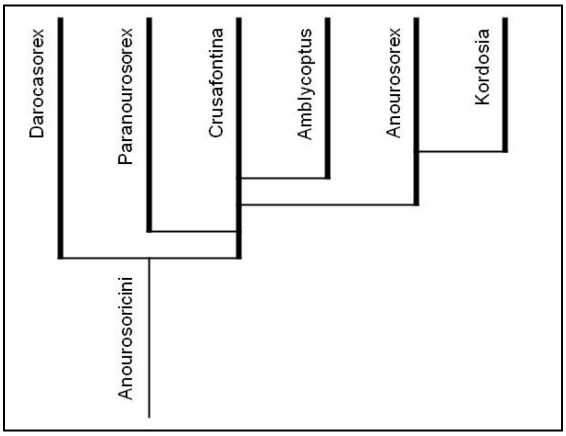

Figure 5. Phylogenetic relations between the genera of the Anourosoricini tribe. This sketch was made after the data of VAN DAM (2010, fig. 3), but in the case of *Ablycoptus* and *Kordosia* it was modified on the basis of the phylogenetic analysis of MÉSZÁROS (1997a, fig. 12-13) and the occurrences of the Anourosorici species in the Carpathian Basin (MÉSZÁROS 1997b and 1998b).

Taphonomical results

László Kordos and Ray Bernor lead an excavation in the Late Miocene Sümeg palaeontological locality in the summer of the 2001st year. Miranda Armour-Chelu and the present author were the members of the researcher team. She discovered some tooth-marks on a fragmentary bone and called the author's attention to this taphonomical remain. She raised, that these bites could have been caused by a large sized soricid.

Figure 6. Proximal fragment of the right ulna of a middle sized carnivore mammal, from medial view, Sümeg, working number in the excavation: R2, 1974/131, C.482. (Scale bar = 10 mm).

The bites were seen from medial view on a proximal fragment of the right ulna of a middle sized carnivore mammal (Figure 6), of which working number in the Sümeg excavation was R2, 1974/131, C.482. There are some thin tooth-marks and many extensive, shallow nibble-marks on this surface. Moreover, we can see two deep, parallel grooves, which are the only well-identifiable tooth-marks on it (Figure 7).

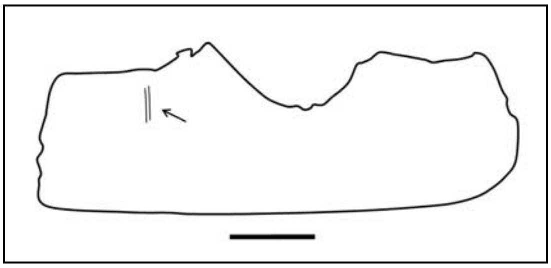

Figure 7. The position of the parallel tooth-marks on the medial surface of the ulna fragment from Sümeg locality. The distance between them is 0.3 mm, which is corresponding to the gap between the upper incisors' apexes of *Crusafontina*. (Scale bar = 10 mm).

Merely the insectivorous mammals are so little sized as they were able to make the studied marks. Otherwise, the smaller shrew species of the Sümeg fossil assemblage were evidently too small to bite those (MÉSZÁROS 1996).

However the upper incisor's apexes of giant shrews, represented in the age of the Sümeg site by *Crusafontina*, perfectly fit into the grooves. The distance between the tooth-marks is 0.3 mm, which is corresponding to the gap between the in-site upper incisors' apexes in the complete *Crusafontina* maxillae (Figure 8).

In spite of the fact that shrews can kill little vertebrates (HABERL 2002), the middle sized mammal species, whose bone fragment is studied here, was surely too big as to be a prey of *Crusafontina*. The big shrew probably fed on its carcass, eating the soft tissues and scratching the surface of the bone under it. Therefore we can take into consideration this taphonomical finding as an evidence to the carrion-eating diet of the giant shrews of the Carpathian Basin.

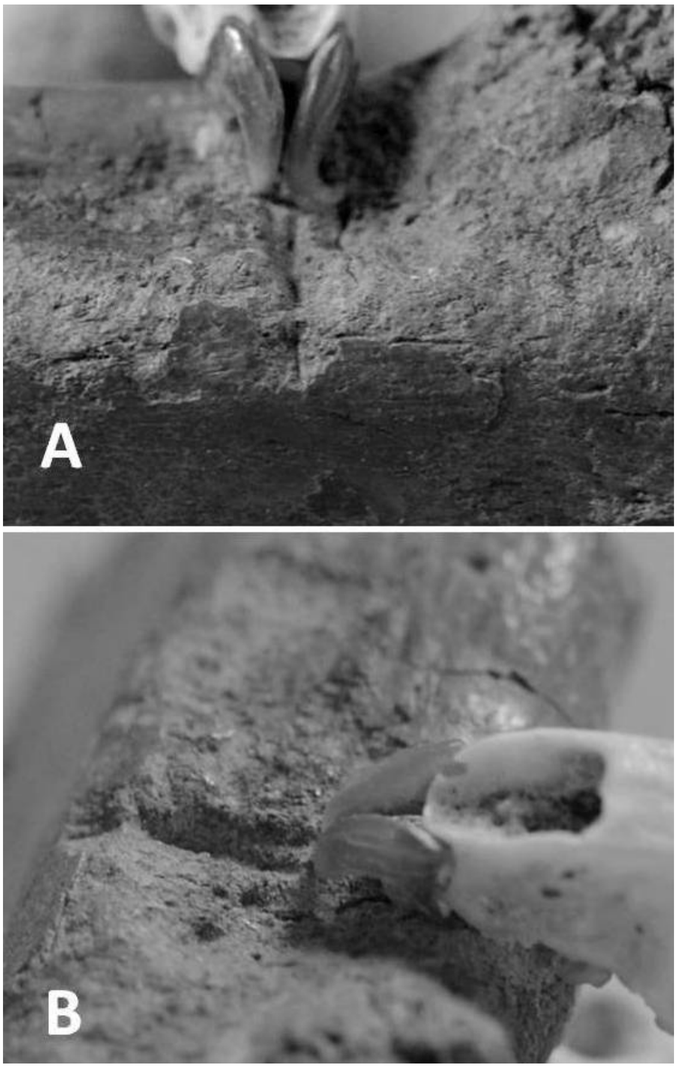

Figure 8. Parallel tooth-marks on the medial surface of the ulna fragment, with the upper incisors of a *Crusafontina* skull remain.

Palaeoecological overview

Nutrition

In its dental formula and structure *Crusafontina* is the less specialized species of tribe Anourosoricini in the Hungarian fossil record. In spite of this, its P^4 shows the signs of characteristic adaptation. There is a strong edge on its buccal margin, formed by the paracone and its posterior prolongation. (Figure 9). This structure is very similar to the cutting edge of the carnivore molars. We suppose, that *Crusafontina* adapted to diversified died, eating not only insects, worms and snails, but often vertebrate carcasses. Among the recent shrews we can also find examples for such nourishment (*Neomys*, in HABERL 2002).

However, on the basis of its dental structure we suppose *Crusafontina* to be more adapted to carrion eating than *Neomys*. This hypothesis is supported by the taphonomical finding shown in the present article.

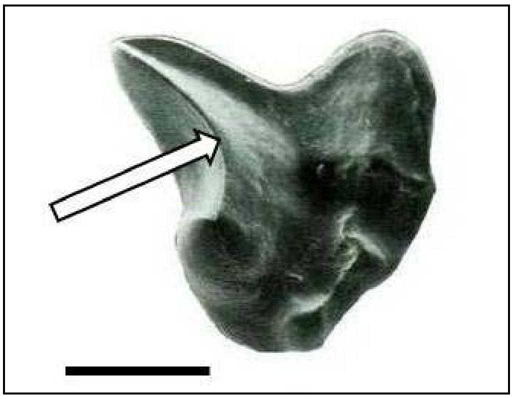

Figure 9. *Crusafontina kormosi* (BACHMAYER & WILSON, 1970), left P^4 in occlusal view from Tardosbánya (after MÉSZÁROS 1998b). The cutting edge is marked by the white arrow. Scale bar = 1 mm.

The climate of the Carpathian Basin turned drier and more extreme after MN 13 Zone (MÉSZÁROS 2000b). The climatic changes yielded decreasing in the insect fauna in some of the ecotypes of the area. This ecological crisis caused significant evolutionary changes in tribe Anourosoricini (MÉSZÁROS 2014).

In the line of *Amblycoptus*, the missing insects were supplied with the vertebrate carcasses, while *Kordosia* adapted to snail-eating. The evolution of the latter genus could have been in progress outside of the Carpathian Basin, in the philogenetic line of the ancient *Anourosorex* forms (Figure 5), if so they immigrated here later.

The nutrition changes yielded transformations in the dental morphology. The cutting edge became stronger on the pentagonal *Amlycoptus* P^4 but disappeared on the oblong and plate *Kordosia* one (Figure 10).

From the MN 14 Zone the Anourosoricini genera disappeared from the Carpathian Basin, but the empty ecological niche (the role of the giant shrew with diversified nourishment) was filled by the anew raising Beremendiini (JÁNOSSY & KORDOS 1997).

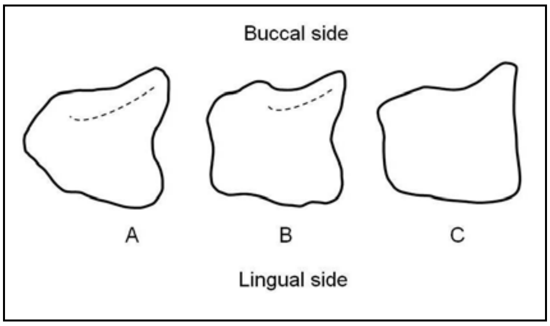

Figure 10. The outline of the occlusal surface of P^4. A – The "pentagonal" form of *Crusafontina* and *Amblycoptus* with strong cutting edge marked by the dotted line (this edge becomes more stronger at *Amblycoptus*). B – The "square" outline of recent genus *Anourosorex* with shorter edge which is ranged to the ectoloph of M^1. C – The "square" form becomes "oblong" but without distinct cutting surface at *Kordosia*. (After MÉSZÁROS 1994, figs 7, 10, 16 and 19.)

Today *B. fissidens* is said to be venomous. This hypothesis is induced by its specially adapted lower incisor on which there is a well-marked "venom groove" running along the medial side of its crown (Figure 11).

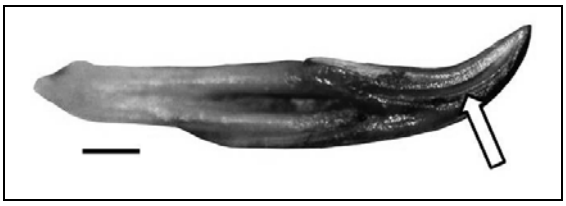

Figure 11. *Beremendia fissidens* (PETÉNYI, 1864), left I_1 in lingual view from Somssich Hill 2 (after BOTKA & MÉSZÁROS 2014a). The venom grove is marked by the white arrow. Scale bar = 1 mm.

FURIÓ et al. (2010) analyzed the anatomical characters of *Beremendia*. According to them the diet of this form was highly specialized in coleopterans and gastropods.

However its nutrition could have been more complete, because BENNÁSAR *et al.* (2014) have found taphonomical evidences of that *B. fissidens* may have had the capacity to bite prey larger than itself (small mammals e.g. moles). The addition of small vertebrates to complement a diet based on insects and snails could have been a way of responding to the needs of the high metabolic rate characteristic of the giant shrews.

Ecotype preference

After the climatic changes in the Carpathian Basin, beside the large grasslands, there were gallery forests and bushy areas along the larger water-courses and on the coasts of the Pannonian Lake (KÁZMÉR, 1990 MÉSZÁROS 2000b). On the basis of their very close relation to the extant *Anourosorex squamipes,* living in the mountain forests of SE Asia, the Anourosoricini genera may be indicate these well-watered, forested environments.

They are described from wooded or at least partly wooded areas. (MÉSZÁROS 1998c). Further, the morphometrical analyses, made by KERNER (2003) on the limb-bones of *Crusafontina*, *Amblycoptus* and *Kordosia*, showed that these animals can move equally well in the water and on the land.

B. fissidens is reported as well from ecotypes nearby open water bodies (lakes or rivers) by several authors (for example AGUSTÍ et al. 2011, CUENCA-BESCÓS et al. 2005, FURIÓ et al. 2010, GARCIA et al. 2014, PAZONYI et al. 2013, SZENTESI 2014). That is why we suppose, that it lived in similar ecotypes in the Carpathian Basin as the earlier Anourosoricini shrews.

Acknowledgements

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Dental remains of *Elephas antiquus* FALCONER & CAUTLEY, 1847 (Mammalia, Proboscidea, Elephantidae) in Hungary

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(with 1 figure and 4 plates)

Despite the fact that hundreds of fossil proboscidean remains are known from Lower Miocene to Upper Pleistocene sediments in Hungary, only five specimens (four molars and a tusk fragment) from three different localities (Győrszabadhegy, Bükkábrány and the Castle Hill of Buda) can be referred securely as *Elephas antiquus*. The scant record and the lack of high-resolution stratigraphic information do not allow extensive conclusions. However it seems that forest elephants inhabited the territory in at least two periods (namely 800-700 ka and 500-400 ka).

Introduction

Fossil proboscideans are known from Lower Miocene to Upper Pleistocene sediments in Hungary. GASPARIK (1993, 2001, 2004, and 2007) made a comprehensive synthesis on the taxonomy, chronology and ecology of the deinotheres, gomphotheres and mastodons formerly inhabiting the region, whereas VÖRÖS (1979, 1981, 1983, 1985, and 2004) dealt with the elephantid remains. During the last few years several new finds came to light, and our knowledge on proboscideans greatly expanded, and so VIRÁG (2009) and VIRÁG & GASPARIK (2012) have begun the re-interpretation of some older material. As a continuation of this intention, this paper focuses on the revision of dental remains (molars and tusks) referable or previously referred as *Elephas antiquus* and some accompanying elephantid finds recovered from the territory of Hungary.

Elephas antiquus was a large sized proboscidean characterized by straight tusks and often associated with woody vegetation of warmer interglacial periods during the Middle and Late Pleistocene of Europe, hence its common name is forest or straight-tusked elephant. The taxon was introduced by FALCONER & CAUTLEY (1847) based on the description of an incomplete mandible (with a second left lower molar) from England. The exact locality of the type specimen is unknown, however, based on its preservation, it is likely retrieved from the Middle Pleistocene terrace deposits of the Thames River at Grays (see PALOMBO & FERRETTI 2005 for details). The skeletal and dental variability of this species is well-known, since abundant material was found from the continental Europe (especially from Germany and Italy) to date. Despite this fact, different opinions can still be found in the literature on the nomenclature and interpretation of this taxon. AGUIRRE (1968-1969) and ALBAYRAK & LISTER (2012) attributed the species to the genus *Palaeoloxodon* MATSUMOTO, 1924, whereas MAGLIO (1973), MOL et al. (2007), and TSOUKALA et al. (2011) placed it in the genus *Elephas* LINNAEUS, 1758. BEDEN (1983) and PALOMBO & FERRETTI (2005) considered *Palaeoloxodon* as a subgenus of *Elephas*. MAGLIO (1973) considered the Asiatic *Elephas namadicus* FALCONER & CAUTLEY, 1845 as a senior synonym of the European *E. antiquus*, whereas Adrian LISTER (see note E2 of appendix C1 in SHOSHANY & TASSY 1996) provisionally suggested a geographic separation for the two species until additional evidence becomes available. Since this problematic issue is beyond the scope of the present study, *E. antiquus* is used here for European material with only one exception.

Material and methods

The tusk and the molars (9) used in the present paper are stored in the Hungarian Natural History Museum (HNHM) and the Geological and Geophysical Institute of Hungary (GIH). An additional molar fragment from Bükkábrány (collected by Márton PALOTAI on October 24, 2007) was provided for analysis by the courtesy of Miklós KÁZMÉR. The examined specimens were recovered from 4 different Hungarian localities (Fig. 1). Standard morphometric parameters (such as the number of plates, the so called laminar frequency, the thickness of enamel, as well as the length, width, and height of teeth) were recorded following the methodology of VIRÁG (2009) and VIRÁG & GASPARIK (2012) with a digital caliper with a precision of 0.003 mm. Letter "m" followed by a number in subscript was used for indicating the exact positions of the lower molars. Letter "M" with a superscript number concerns to upper molars.

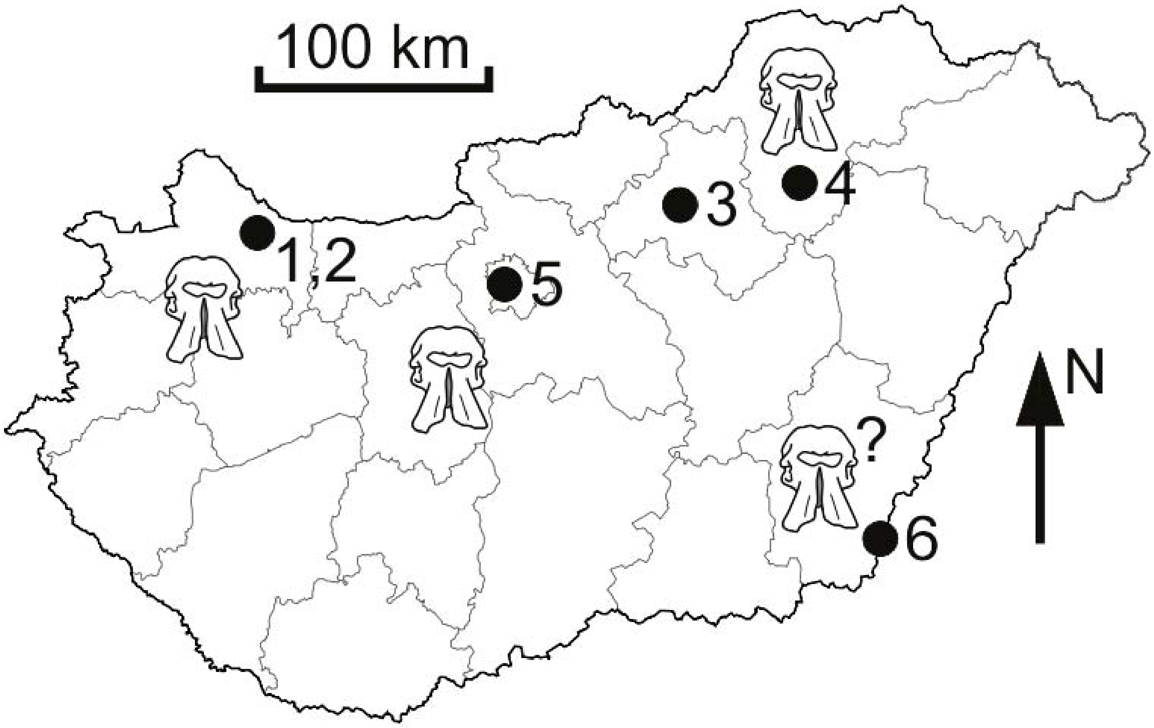

Fig. 1. Map of the Hungarian localities mentioned in the text. Skulls are indicating *E. antiquus* finds.
Legend: 1: Győrújfalu, 2: Győrszabadhegy, 3: Visonta, 4: Bükkábrány, 5: Castle Hill of Buda, 6: Lökösháza.

Localities

Győrújfalu and Győrszabadhegy

More than 35 m thick fluvial sediments were transected during the gravel mining activity near Győrújfalu, which is situated in Northwestern Hungary, 5 km northwest from the centre of Győr, south from the river Danube. Numerous plant, mollusc and vertebrate remains were found since 1983 from the sandy gravel layers located at a depth of 20-31 m from the surface (see the details in JÁNOSSY & KROLOPP 1994 and PONGRÁCZ 1993, 1996). The microvertebrate fauna, especially the co-occurrence of *Mimomys savini* and voles belonging to the *Microtus* (*Pitymys*) *hintoni-gregaloides* group suggests a late Early or an early Middle Pleistocene age (approximately 1.0-0.6 Ma) for the locality. The mammalian assemblage can be correlated with the *Mimomys savini* Rodent Zone and the Nagyharsányhegyian or Templomhegyian Substage of the local biochronological system (see in KRETZOI & PÉCSI 1979). Considering the aforementioned age estimation, the only incongruous faunal element is

Mimomys reidi, the last occurrence of which in the Central European region can be dated back to 1.8-1.7 Ma according to MAUL & MARKOVA (2007). The identification of the latter species is however most likely erroneous, since it is based on only one first lower molar, that is more hypsodont than the typical representatives of the taxon and shows no signs of cement in the re-entrant angles of the tooth.

Győrszabadhegy is located close to the above mentioned site, 3 km south from the centre of Győr. A few elephantid molars have been recovered from the gravels in the vicinity of this municipality, but unfortunately neither detailed stratigraphic information, nor the exact localities are available.

Bükkábrány and Visonta

A large open-cast lignite mine is situated on the southern foothills of the Bükk Mountains (Northeastern Hungary) in the vicinity of Bükkábrány. The Upper Miocene lignite is covered by Pliocene, fluvial, yellow or gray coloured clays and clayey or sometimes pebbly sands. The overlying sediments for the latter sequence are Pleistocene gravels. A few large mammal remains came to light from the gravels during the extensive mining activity, but unfortunately, detailed stratigraphic data are not available.

Another open-cast lignite mine with a similar section is located on the southern foothills of the Mátra Mountains near Visonta, 50 km west from Bükkábrány. Numerous vertebrate remains (including mammoths) were recovered so far from the Pleistocene gravels covering the rest of the sequence.

Castle Hill, Budapest

The top of the Castle Hill (or Várhegy) at the Buda side of Budapest is covered with a 7 to 10 m thick travertine layer. The underlying sediments are weakly cemented, calcareous, and clayey silts as well as fluvial, cross-bedded, sandy gravels, which provided numerous vertebrate remains (including proboscideans) since the middle of the 20th century. Several sections were opened or sealed behind masonry to date due to construction works in the cave and cellar system located under the Castle District. According to the faunal revision made by KORDOS (2004), the age of the fluvial gravels can be correlated with Marine Isotope Stage (MIS) 14 or 12, whereas the overlying calcareous, clayey silt deposited during MIS 11. The latter can be correlated with the *Lagurus transiens–Arvicola cantiana* Rodent Zone (see the details of the zonation in KORDOS 1994) which can be dated to 500-400 ka. According to the U/Th dating of KELE (2009) the age of the covering travertine is 400-350 ka. Microvertebrate remains were recovered from the reddish brown clay infilling of the karstic cavities in the freshwater limestone during the construction works of the Hilton Hotel. Based on the latter fauna, JÁNOSSY (1976) introduced the so called Castellum Phase to the local biochronological system. KORDOS (2004) correlated the age of the infilling sediments with MIS 7 or 6 (which means approximately 200 ka).

Characteristics of *E. antiquus*

The skull of *E. antiquus* has a flat dorsal profile and a characteristic double-domed vertex. The premaxillaries are fan shaped and extremely wide distally. The mandible is short with a weakly developed symphyseal rostrum. Tusks are large, and weakly curved. The molars are usually narrow and extremely high compared to a mammoth. The relative crown height or hypsodonty index (i.e. the ratio of the height and the width of the tooth) of the last molars varies from 1.8 to 2.0, or exceeds 2.0 in some cases. The number of plates (excluding talons and platelets) on the aforementioned teeth is usually 16 or 17 but can reach up to 20 according to PALOMBO & FERRETTI (2005) or varies between 15 and 21 according to ALBAYRAK & LISTER (2012). The plates have an S-shaped curvature from lateral view. Laminar frequency (which represents the number of plates that occur within 10 cm along the longitudinal plane of the molar) varies between 5 and 6. The enamel is 2.0-3.0 mm thick, usually heavily wrinkled and one to three acute folds (or sinuses) are frequently present on both the anterior and posterior sides of each loop. The incipient wear figures on the occlusal surface are often formed by a large oval central loop and two small circular lateral loops. This is the so called dot-dash-dot or ring-loop-ring pattern which usually appears on several consecutive plates in the case of *E. antiquus*, whereas not typical in the case of mammoths.

Reappraisal of dental remains

Győrújfalu

The HNHM V.84.105 specimen (Plate I/A-B), which is a right m_3, was referred by JÁNOSSY & KROLOPP (1994) to the "archaic form of *Palaeoloxodon antiquus*" based on the opinion of István VÖRÖS. The tooth is built up from 13 plates and a posterior platelet. The occlusal wear reached the base of the crown at the anterior part of the molar, however the base of the first root is still visible and its position suggests that only one anterior plate is missing. The plates are more or less straight in lateral view. The laminar frequency is approximately 4. The thickness of enamel varies between 2.9 and 3.6 with an average of 3.4 mm. The tooth crown is relatively wide (91 mm) and low (92 mm). The unworn height can be estimated up to maximum 130 mm, which results in a maximum 1.4 hypsodonty index. Based on the low plate count and laminar frequency, the thick enamel, and the relatively low tooth crown, the specimen most likely belongs to *Mammuthus meridionalis* (NESTI, 1825). The only characteristics that could support *E. antiquus* are the acute posterior enamel folds appearing on the medial part of the occlusal surface and the wear figures of the 5th an 6th plates (counted from posterior to anterior direction) which are broadly similar to the typical dot-dash-dot pattern but the lateral loops are more elongated.

The m_3 depicted Plate I/C-D shows remarkably similar, maybe a bit more advanced morphology compared to the HNHM V.84.105 specimen, but its measurements still remain in the range of *M. meridionalis* (the data and the photographs were made available for me by the courtesy of Hans van ESSEN in the case of this molar). The exact locality of the specimen is unknown, but it was recovered from sandy gravel in the vicinity of Győr. The tooth has 15 plates, an anterior talonid, and a posterior platelet. The first root is visible and the occlusal wear has never reached the base of the crown, although it is close to the latter in the most anterior part of the molar. The plates are more or less straight in lateral view in this case too. The laminar frequency is approximately 4.5, which is somewhat higher than in the case of the HNHM V.84.105 specimen. The enamel thickness ranges from 3.0 to 3.7 with an average of 3.1 mm. The tooth crown is wide (97 mm) and low (126 mm) compared to an advanced mammoth or a typical *E. antiquus*. The hypsodonty index is approximately 1.3. The incipient wear resulted in three equally wide loops (i.e. dash-dash-dash pattern) on the 3rd plate (counted from anterior to posterior direction) and the enamel is only moderately folded.

The other specimen from Győrújfalu stored in the paleontological collection of the HNHM is the V.84.106 molar fragment. It has now 7 plates and a posterior talon, but the anterior part is missing. The anterior sides of the enamel loops are convex, whereas the posterior sides are concave, which occurs more often in the case of the upper dentition. The tooth is tapering towards the posterior end, which suggests that it is a third molar. The maximal width of the specimen is now 80 mm, but the missing anterior plates may have been wider. The laminar frequency is 6.8. The enamel is 2.2-2.8 mm thick with an average of 2.5 mm and heavily wrinkled. The incipient occlusal wear resulted in dot-dash-dot pattern on the 1st and 2nd, dash-dash-dash pattern on the 3rd and 4th, and dash-dot-dash pattern on the 5th and 6th plates (counted from posterior to anterior direction). The latter two configurations rarely occur on *E. antiquus* molars. Despite the fragmentary preservation of the molar, based on the aforementioned data, it is most plausibly referable to *M. trogontherii* (POHLIG, 1885).

In addition to the above mentioned material, PONGRÁCZ (1996) depicted a molar fragment on his Fig. 5/B with 8 remaining plates under the name of "ancient form of forest elephant". The laminar frequency seems low and the enamel is remarkably thick. The tooth is heavily worn and fragmented even from the lateral sides. The apical region of an elephantid molar is usually subdivided into three so called pillars by two clefts (van ESSEN 2011). The widths of these pillars determine the characteristics of the incipient wear pattern. Since the occlusal wear proceeded beyond the lowest level of the clefts in this specimen, the loops are completely fused from side to side of the crown. However, two infolding of the loops are visible close to the medial part of the occlusal surface, and it could be a clue for a dash-dot-dash pattern, which makes the original determination unlikely. The specimen is most plausibly referable to *M. meridionalis.*

In summary, the presence of *E. antiquus* at Győrújfalu can not be verified based on the available data, although there are several other finds from the site in the private collection of László PONGRÁCZ, which have not been studied by the present author to date. It seems that specimens formerly referred to this taxon from this locality are representatives of the genus *Mammuthus* BROOKES, 1828.

Győrszabadhegy

The most complete molar from this site is a left m_3 without inventory number (Plate II/A-B). It is built up from 17 plates, and a platelet is missing on the posterior end of the tooth based on the remaining cement interval. It is possible, that the original tooth had one more lamella on the anterior end as well, therefore the original number of plates was most plausibly 18. The plates have an S-shaped curvature from lateral view. The laminar frequency is 5.1. The enamel thickness varies between 1.9 and 2.6 with an average of 2.3 mm. Acute folds are visible on both the anterior and posterior sides of several loops. The incipient wear resulted in dot-dash-dot pattern on the 7th, 8th, 9th, and 10th plates (counting from posterior to anterior direction). The tooth crown is narrow (74 mm) and high (138 mm), resulting in a hypsodonty index around 1.85.

There is an other tooth from the locality without inventory number stored in the paleontological collection of the HNHM (Plate II/B-C). The molar has 11 plates and a posterior talonid. Two anterior plates are missing based on the position of the first root, therefore the original number of the plates can be estimated up to 14. The occlusal surface is slightly concave in lateral view and curved when viewed from the top, which occurs usually in lower dentition. The tooth is not tapering towards the posterior end and the posterior wall of the last plate is approximately perpendicular to the occlusal surface. In addition the posterior root is triangular and widens towards the end of the tooth. These features suggest that it is a second molar (a left one based on its curvature). The plates have an S-shaped curvature from lateral view. The laminar frequency is 5.6. The thickness of enamel ranges from 1.9 to 2.9 with an average of 2.4 mm. A well-developed median sinus and some additional acute folds are visible on the anterior and posterior sides of almost all loops. Dot-dash-dot pattern is visible in the case of the 2nd, 3rd, 4th, 5th, and 6th plates (counting from posterior to anterior direction). The crown of the tooth is narrow (62 mm) and high (138 mm but the unworn height can be estimated up to 140 mm), resulting in a hypsodonty index around 2.2. Greater estimates are also possible, since the bases of the so called cement islets are 40-45 mm lower at the medial part of the molar compared to the lateral basal enamel extremes which were the starting points for height measurements in the present study.

The HNHM V.79.32 specimen is a fragment built up from the remains of 6 plates, the anterior and posterior ends of the molar are both missing. The plates have an S-shaped curvature from lateral view, similarly to the above discussed teeth. A transversal fracture in the case of the most anterior lamella reveals 25-30 mm deep medial clefts which are dividing the apical region into three pillars. The lateral pillars are significantly narrower than the medial one, consequently, the incipient occlusal wear would have resulted in dot-dash-dot pattern on the plate. The laminar frequency is 5.6. The enamel is 2.8-2.9 mm thick. The tooth crown is narrow (65 mm) and high (155 mm), resulting in a hypsodonty index around 2.3.

Considering all evidence, the above discussed specimens can be referred as typical representatives of *E. antiquus*.

Castle Hill, Budapest

The GIH V.21665 specimen (Plate III/G-H) depicted by both JÁNOSSY (1986 on his Fig. 1 of Plate III) and VÖRÖS (2004 on his Fig. 4/3) was the first forest elephant find recognised in the Hungarian material. According to MOTTL (1943) the tooth was recovered from the weakly cemented, calcareous, and clayey silt layers sectioned by a cellar system lying under 14, Országház Street and 7, Szentháromság Street. The specimen is only a molar fragment which can be referred to *E. antiquus* based on the occlusal wear pattern, although it is important to note, that similar pattern can be seen in some cases on heavily worn teeth belonging to the genus *Mammuthus*. The enamel is heavily and regularly wrinkled and 2.5 mm thick in average. An acute fold is visible on both the anterior and posterior sides of the lozenge-shaped loops.

In addition, MOTTL (1942, 1943) described and depicted several mammoth teeth which were found in the fluvial gravels under 72, Úri Street. Some of these remains (GIH V.21619, GIH V.21620 and GIH V.21621, Plate III/A-F) were available for the present author as well. The teeth can be identified as second lower and upper molars with a reconstructed number of 11-13 plates, a laminar frequency between 5.5 and 6.5, and an enamel thickness between 2.0 and 3.0 mm. The width of the molars varied between 80 and 90 mm, whereas the unworn height most plausibly ranged from 140-150 mm. These estimates result in hypsodonty indices around 1.6-1.8. According to MAGLIO (1973), plate number on second molars of *M. meridionalis* hardly ever reached 11. Referring these specimens to *M. trogontherii* is therefore more plausible. As MOTTL (1943) noticed, the remains are morphologically indeed very similar to the material recovered from Mosbach (Germany), a site which can be dated to approximately 500 ka (see e.g. LISTER et al. 2005). This observation, on the on hand, is in agreement with the stratigraphical interpretation of KORDOS (2004) and, on the other hand, gives a maximum age for the overlying calcareous and clayey silt layer from which the above mentioned *E. antiquus* molar was recovered.

Bükkábrány

VIRÁG (2012) reported a tusk fragment (HNHM PAL 2012.13.1) from Bükkábrány (Plate IV/A-B) which can be referred to *E. antiquus* based on the so called Schreger pattern visible on the cross section of a tusk. Angles, formed by the intersecting and curved Schreger lines, open towards the pulp cavity, and not farther than 10 mm from the cement dentine junction, varied between 96° and 136° with an average of 115°, which is much larger than the typical values for a mammoth according to the comparative data of PALOMBO & VILLA (2001).

In addition, a molar fragment with only the remains of 4 plates came to light from the locality on October 24, 2007. All of the plates are broken into half along the sagittal plane. The remaining loops (the medial and one of the laterals) are elongated and approximately equally wide which suggest a dash-dash-dash occlusal wear pattern. Based on this assumption, the original width of the tooth can be estimated up to 80-90 mm. The elevated laminar frequency (7-8) and the thin enamel (1.1-1.7) suggest a form more advanced than *M. meridionalis*, and so the molar is tentatively referred here as *M. trogontherii*.

Lökösháza

In addition to the above discussed material, VÖRÖS (2004 on his Fig. 4/2) depicted a narrow molar fragment with 9 remaining plates, relatively thin and more or less regularly wrinkled enamel. Based on the available data, it can not be ruled out that the molar belonged to an *E. antiquus* as he stated, however it should be noted that the incipient wear result in dash-dash-dash wear pattern which is more typical for mammoths in the case of two lamella and the remaining plates have a bipartite structure which is an anomalous and possibly atavistic condition in the case of elephantids. The molar was recovered from the gravel quarry at Lökösháza (Southeastern Hungary) and was unfortunately not available for the present author.

Discussion and conclusions

According to ALBAYRAK & LISTER (2012), representatives of the lineage that gave rise to *E. antiquus* migrated outside Africa through the Levant approximately 900 ka. One of the earliest records of the group in Eurasia could be Dursunlu in Turkey which is close to the presumed migration route. According to their opinion, forest elephants became widespread in the continent by the time *M. meridionalis* went extinct and more advanced *M. trogontherii* migrated into the region (at around 800-700 ka).

Due to the lack of high-resolution stratigraphic information, the exact date of the arrival of *E. antiquus* to Hungary is not clear at the present state of knowledge, however it is plausible that the specimens from Bükkábrány and Győrszabadhegy represent an early immigration of the taxon. At Győrszabadhegy, only the presence of *E. antiquus* was detected, but at Győrújfalu, a geographically close site with a similar gravel sequence, both *M. meridionalis* and *M. trogontherii* were recognized. The situation is somewhat similar in the case of Bükkábrány, from where *E. antiquus* and *M. trogontherii* were described in the present article. In a similar section at Visonta, *M. meridionalis* and *M. trogontherii* were recovered from stratigraphically close horizons (see FODOR & VÖRÖS, 1990 and VIRÁG 2009 for details). Unfortunately *E. antiquus* fossils have not been found at the locality to date. It is probable, that similarly to the Ponte Galeria Formation in Italy (see PALOMBO & FERRETTI 2005 for details), the aforementioned sections contain the period of the faunal turnover discussed above.

It was accepted for a long time that *E. antiquus* went extinct in Europe at the end of the Eemian interglacial (MIS 5e), approximately 115 ka, although STUART (2005) and MOL et al. (2007) presented some reasonable but not conclusive evidence for the survival of some isolated populations to approximately 50 ka or as late as 34-33 ka. Nevertheless, the last known occurrence of the species in Hungary at the Castle Hill of Buda can be dated between 500 and 400 ka which is significantly older compared to data from the rest of Europe. It seems that several gaps are exist in the Hungarian forest elephant record, which suggests that *E. antiquus* was not a permanent element of the fauna but migrated into the region only for geologically short periods of time as stated by István VÖRÖS (see in JÁNOSSY & KROLOPP 1994).

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Plate I

M. meridionalis molars from Győr and Győrújfalu.

A. *M. meridionalis* right m_3 (HNHM V.84.105) in occlusal view from Győrújfalu.

B. *M. meridionalis* right m_3 (HNHM V.84.105) in lingual view from Győrújfalu.

C. *M. meridionalis* left m_3 in occlusal view from the vicinity of Győr (photo by courtesy of Hans van ESSEN).

D. *M. meridionalis* left m_3 in buccal view from the vicinity of Győr (photo by courtesy of Hans van ESSEN).

Plate 1

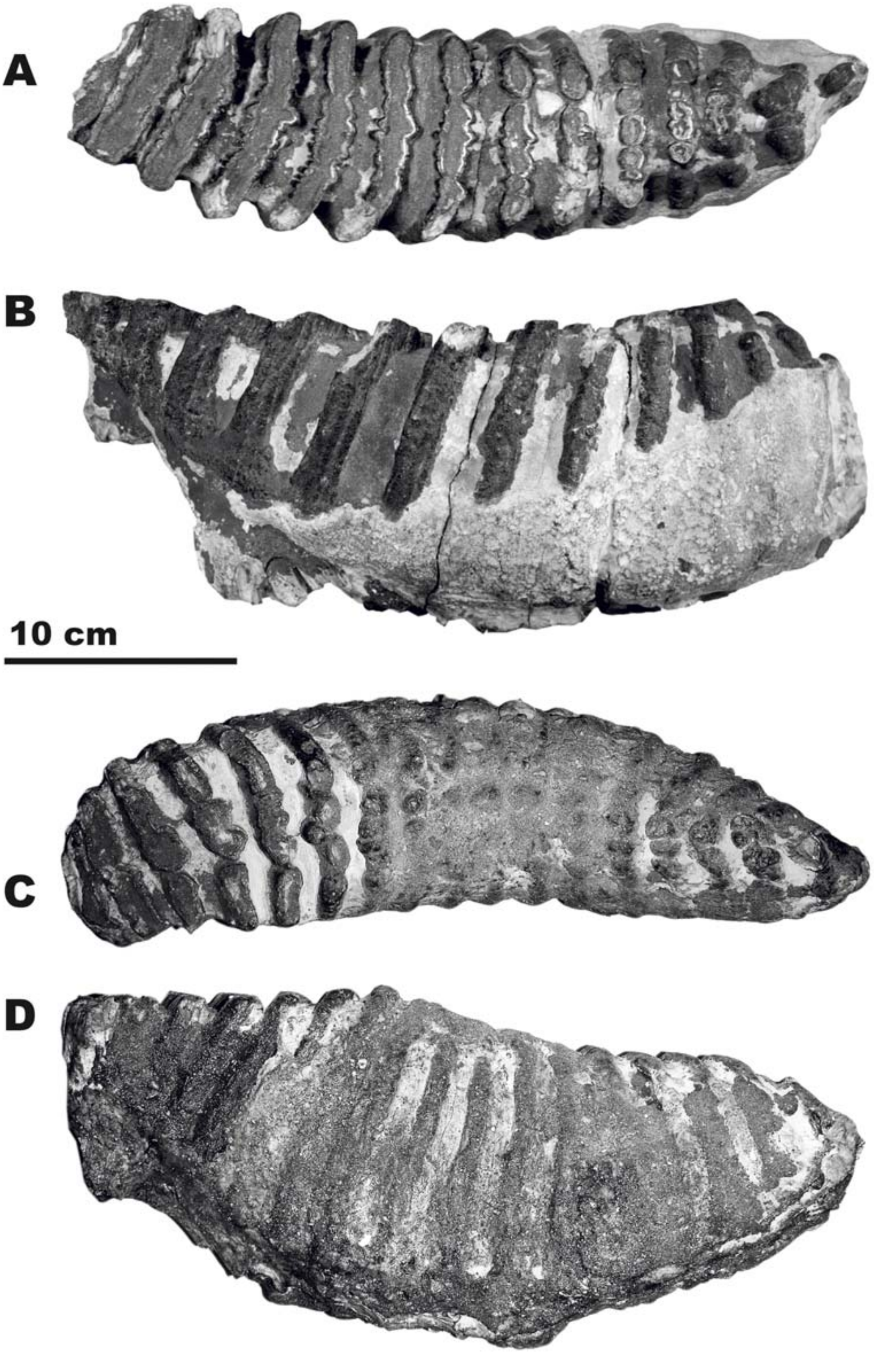


Plate II

E. antiquus molars from Győrszabadhegy

A. *E. antiquus* left m_3 in occlusal view from Győrszabadhegy.
B. *E. antiquus* left m_3 in buccal view from Győrszabadhegy.
C. *E. antiquus* left m_2 in occlusal view from Győrszabadhegy.
D. *E. antiquus* left m_2 in lingual view from Győrszabadhegy.

Arrows are indicating plates with dot-dash-dot wear pattern.

Plate II

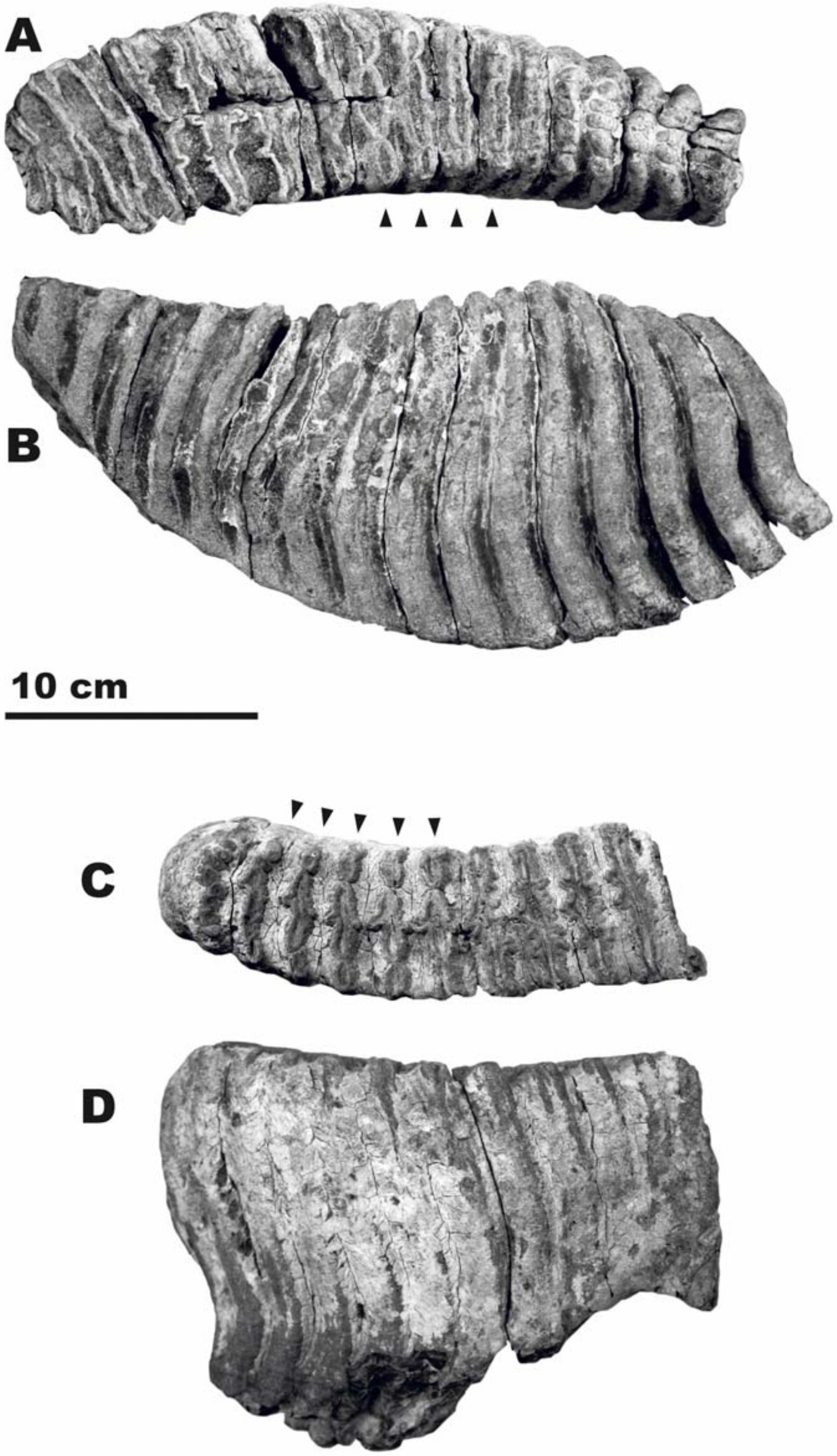


Plate III

M. trogontherii and *E. antiquus* molars from the Castle Hill of Buda.

A. *M. trogontherii* left M^2 (GIH V.21621) in lingual view from the Castle Hill of Buda.
B. *M. trogontherii* left M^2 (GIH V.21621) in occlusal view from Castle Hill of Buda.
C. *M. trogontherii* M^2 (GIH V.21620) in lateral view from Castle Hill of Buda.
D. *M. trogontherii* M^2 (GIH V.21620) in occlusal view from Castle Hill of Buda.
E. *M. trogontherii* left m_2 (GIH V.21619) in occlusal view from the Castle Hill of Buda.
F. *M. trogontherii* left m_2 (GIH V.21619) in lingual view from Castle Hill of Buda.
G. *E. antiquus* molar (m?) in occlusal view from Castle Hill of Buda.
H. *E. antiquus* molar (m?) in lateral view from Castle Hill of Buda.

Plate III

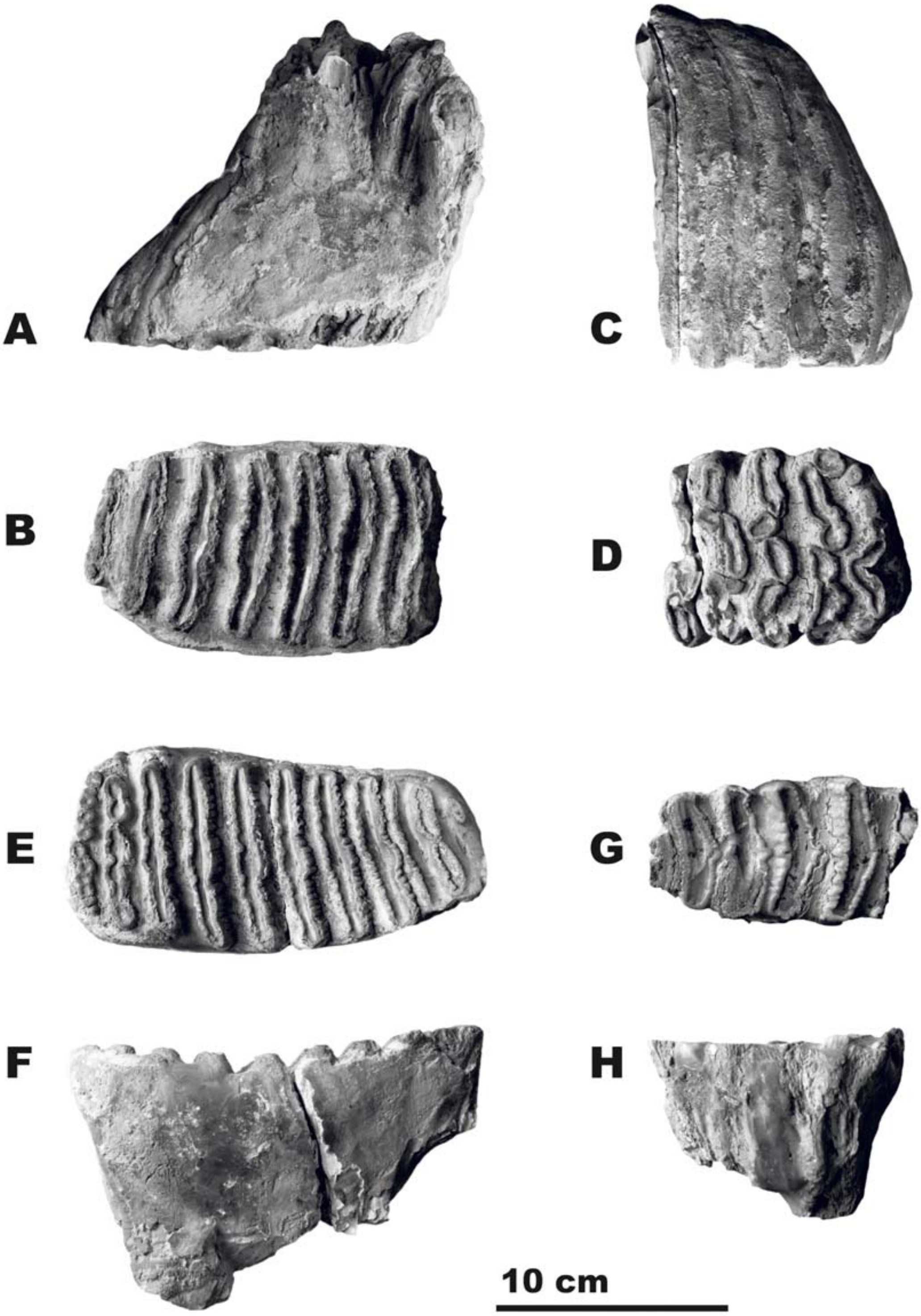


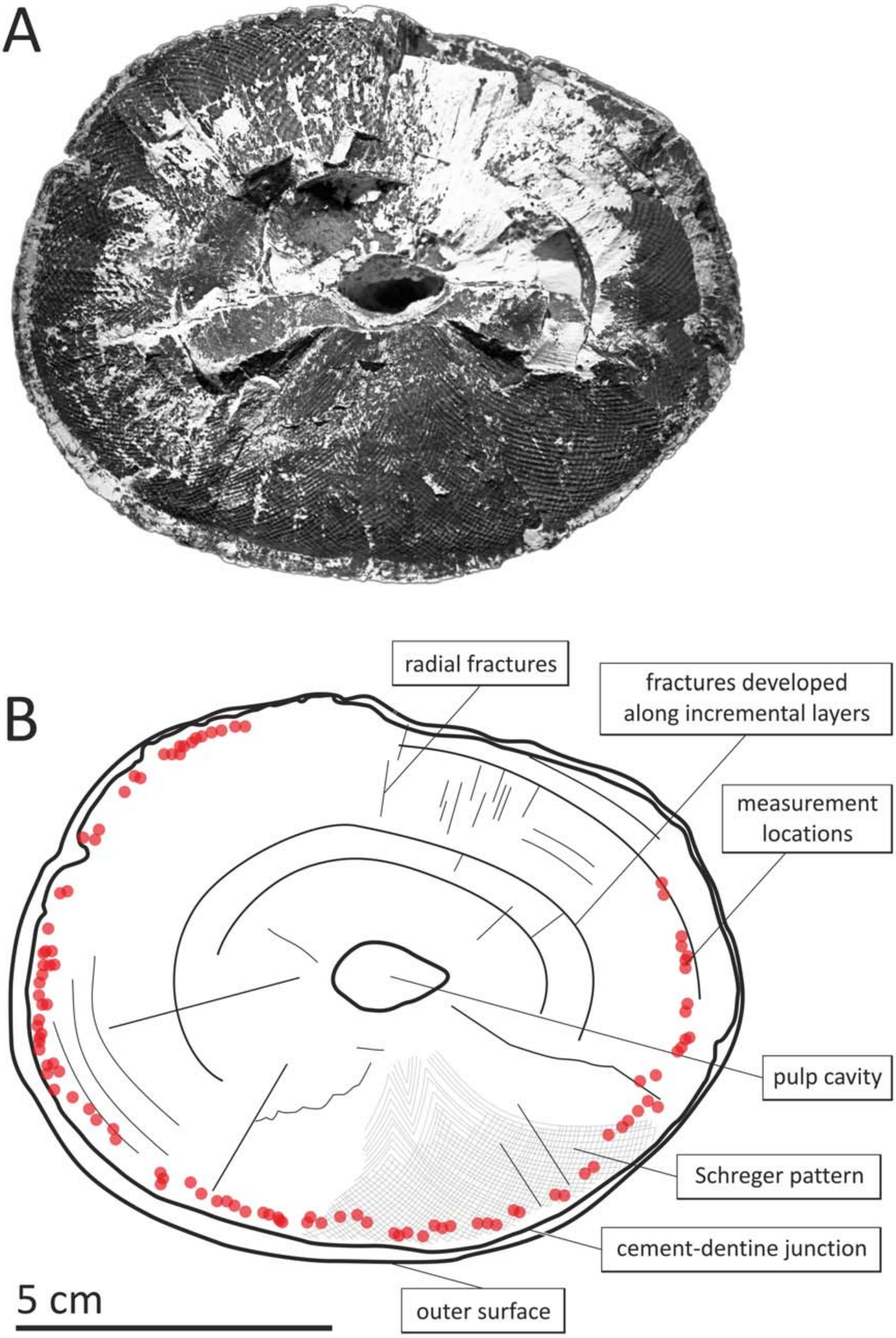
Plate IV

E. antiquus tusk from Bükkábrány

A. *E. antiquus* tusk fragment (HNHM PAL 2012.13.1) in transverse profile from Bükkábrány.

B. Schematic drawing of an *E. antiquus* tusk fragment (HNHM PAL 2012.13.1) in transverse profile from Bükkábrány.

Plate IV


A
B
radial fractures
fractures developed along incremental layers
measurement locations
pulp cavity
Schreger pattern
cement-dentine junction
outer surface
5 cm

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Tree ring pattern of roots exhumed by soil erosion

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(with 31 figures and 1 table)

Mountains are subject to uplift and erosion. Human interference with the landscape by intensive agriculture, construction works, and tourism contributes to the removal of soil. We measured erosion rate by root exposure dating. Results of a pilot study of Shen Men Mt. at Tianshui and Kong Tong Mt. at Pingliang, Gansu province of China are reported here. New exhumation markers are introduced, separating aboveground features from mechanical stress-induced features. Change from root texture to stem texture, as defined by ring width and latewood width changes, reaction wood, distorted symmetry, simple and repeated wounds, open and closed wounds, abraded wound, onlap and offlap pattern of wound-affected growth increments, and simple and multiple discolouration by phenolic staining are illustrated and described here.

Introduction

Soil erosion is a primary driver of land degradation worldwide (VERHEIJEN et al., 2009). New, pristine areas are brought into cultivation to replace degraded lands, especially in developing countries. However, clearing natural vegetation cover makes land increasingly prone to erosion. Removal of the uppermost layer of land not only affects fertility, but, among others, increases downstream sedimentation, blocks irrigation channels and reduces the design life of reservoirs (ROMERO-DÍAZ et al., 2012). Construction of transport lines and urban development changes relief. Even increasing tourism takes its toll, by over-using existing paths. Extreme weather events, especially heavy rainfall, remove an increasing amount of soil from unprotected surfaces.

There is a multitude of studies describing and measuring the pattern and rate of soil erosion, ranging from the simple pin method up to high-resolution terrestrial laser scanning (e.g. GODFREY et al., 2008; LUCÍA et al., 2011). However, time series longer than a couple of years are rare, and decadal-scale measurements – mostly represented by radionuclide dating – lack annual temporal resolution (MABIT et al., 2008).

Tree roots are suitable for dendrochronological dating, i.e. can be cross-dated with each other and with tree trunks (KRAUSE & ECKSTEIN, 1994). This make them suitable for dating purposes. Dendrogeomorphological analysis of exposed tree roots is a method capable of dating soil erosion on a decadal to centennial temporal scale at annual (occasionally even at seasonal) resolution (for a recent review see STOFFEL et al., 2013). Both sheet erosion of slopes and linear erosion of gullies can be quantified.

Most soil erosion studies are related to arable soils (e.g. ZHENG, 2006), while forested regions are neglected in this respect (ZHOU et al., 2013).

Most studies have been done in the USA, the Mediterranean area and in the Alps (see STOFFEL et al., 2013, for an exhaustive list). Additionally, a gully erosion story was pubished by KÓRÓDY et al. (2009) in Hungary. There were only two studies in China, one on hillslopes in the temperate north (ZHOU et al., 2013) and another on karst in the subtropical south (LUO et al., 2011).

SCHULMAN'S (1945) seminal paper started the 'career' of root-based soil erosion studies. First the age of exposed roots (e.g. HUECK, 1951), then dating the starting asymmetry of buttress roots (LAMARCHE, 1961), and dating cambium damage were the methods used. When cambium is damaged, it dies back, and growth is discontinued along various sectors of the root circumference. However, segments diametrically opposed, usually in lower parts, continue growing. It was a 'revolutionary' new method in assessing erosion rates over millennia (LAMARCHE, 1963). A further step on methodological development was recognizing that growth rings, which are mostly concentric in underground settings, tend to change to elliptical cross-section of various eccentricity (MCCORD, 1987). Dating the initiation of reaction wood in exposed roots, in combination with scar-induced cambium dieback became a further indicator of initial root exposure (CARRARA and CARROLL, 1979). In the present paper we provide detailed description of select root cross sections from Gansu Province, People's Republic of China, applying these features to describe and quantify root exhumation caused by erosion and lowering of soil surface.

Root growth

Where do roots grow?

LAMARCHE'S method (1961) of root exhumation dating is based on the assumption that roots start to grow at the soil surface. This opinion is maintained in the reviews of GÄRTNER (2007) and STOFFEL et al. (2013) without further comment. We challenge this assumption.

The depth distribution of tree roots is controlled by a multitude of factors, e.g. species and age, climate (esp. temperature), soil properties, nutrient availability, etc. (ZIEMER, 1981; ZIEMER et al., 1991; SCHMIDT et al., 2001; ROERING et al., 2003; SCHWARZ et al., 2010). The major factor influencing rooting depth is water supply or lack of it (desiccation) (EAPEN et al., 2005). Negative factors affecting root distribution close to the surface are frost (REPO et al., 2014) and desiccation, both affecting mainly young roots (TRON et al., 2014).

Considering these factors we suggest that roots in temperate climate start growing not on the soil-air surface, but beneath at least a few cm of soil cover (Figs 1-2). Roots growing near the surface will suffer dieback soon. Unfortunately, root depth below soil has not been studied systematically in natural settings; assessment of this factor will be considered elsewhere.

While in temperate environments at least 10 cm of soil and/or abundant leaf litter provides protection from most of the above factors (ROERING et al., 2010), in subtropical and tropical environments young roots can grow without the protective layer of soil or leaf litter (Figs 5-8). Roots – under a certain soil cover and precipitation/temperature conditions – grow at a more or less constant depth. This depth is shallow, if compared to the tens of metres high trees these roots support. Majority of roots grow in the 15-25 cm depth interval on steep slopes of the Oregon Coast Range, US (ROERING et al., 2010).

We suppose the root andt its axis (the pith) is not displaced while in the soil. This is true only if free growth is allowed on all sides. If there is anything hard the root cannot push aside by its growth, either the root cross-section will be distorted or the root axis will be removed or both. Other roots and stones are the most frequent agents in displacing root axis . One should be careful to avoid sampling these roots.

Roots can be found above ground even in lack of any erosion. Increase of root diameter by growth causes the top of the root appear above the soil. This is not considered erosion, but even this root is suitable for erosion measurement. To avoid this pitfall we measure the location of the root's axis (the pith) and calculate any change of ground level relative to it.

Material and methods

The sites

Shi Men Mountain near Tianshu in eastern Gansu province (34° 26' 27" N, 106° 02' 29", 2085 m above sea level) is a sacred mountain with several Taoist shrines. Rock is coarse granite bearing thin soil. The mountain has steep ridges, where many roots are conveniently exposed. Still, there is a thin, brown forest soil cover on granite. Forest trees are Chinese pine (*Pinus tabulaeformis*). Thirty root disk samples were taken (SMM101–SMM130). Six of them are related to a living tree, which was also sampled (Table 1) (FANG et al., in prep.).

Kong Tong Mountain (Fragrance Hill) is west of Pingliang town in eastern Gansu. There is a monastery on terraces and on the hilltop between 1900-2000 m elevation above sea level. Kongtong Mountain is a national geopark (ZHANG, 2008). Annual precipitation is 500-600 mm, annual mean temperature is 8.9 °C. Soil is mountain brown earth, occasionally skeletal soil. A young, broadleaved forest is growing on 30-40° steep slopes. The soil is covered by 10-15 cm thick, halfway degraded, loose leaf litter, penetrated by young rootlets. There are no roots visible on the surface. Larger trees are 50-150 years old. There is no forest management. The sampled trees are Chinese pine (*Pinus tabulaeformis*). Five root disk samples were taken (KTM101–KTM105) (Table 1).

Sampling and measurements

For quantification of the erosion rate two parameters are needed: the number of rings grown since exposure and the thickness of the eroded soil layer since exposure. We suppose – in absence of contrary data – that the root axis was stable during growth.

Results and discussion

Microscopic versus *macroscopic analysis*

Recently there has been a shift in studies of root-based erosion measurement from ring width variations and textural changes towards microscopic analysis and dating of exposure (GÄRTNER et al., 2001; STOFFEL et al., 2013). While the latter method is certainly more sensitive to oncoming exhumation, and can sense the approach of soil surface even a few years before it reaches the root (CORONA et al., 2011), it needs special wood anatomical equipment and is time-consuming. Therefore we stick to the 'old-fashioned' identification of tree-ring pattern features to promote further studies in this field by those who has no access to specialized laboratory. Large number of data, gathered from a rich variety of sites is necessary to provide meaningful information for geomorphological and geological studies.

Exhumation markers in conifers

Exhumation is the process when roots growing underground appear at the soil surface due to natural or man-made causes. Exhumation can be rapid or slow, yielding sudden or gradual change of root texture, respectively. We discuss those markers below which can be recognized without any special equipment (no microtome and anatomical thin sections are needed). Features visible on the sanded and polished surface of a root disk by a simple microscope, even by a hand lens, or on magnified digital photographs, are described below.

PATEL (1965) recognized long time ago that roots – having their own texture while underground – produce tissue similar to stem wood in the year or season of exhumation. FAYLE (1968) described wider tree rings, occurrence of compression wood, and smaller cell diameter (associated with thicker cell walls) in those portions of root which grew above ground.

1) *Change from root texture to stem texture* around the circumference (Figs 13-31). Cell lumina in earlywood of stems reflect temperature and moisture at the start of the growing season (ANTONOVA & STASOVA, 1993). The same applies to roots (CORONA et al., 2011). Soil cover protects roots from oscillating extremes (esp. of frost and drought) to a considerable degree. The reduced environmental signal mostly yields uniformly sized cell lumina and thin walls in the earlywood of conifer roots. Latewood is often a single row of cells only. Exposure to aboveground conditions usually yields smaller cell lumina and thicker cell walls, both in the earlywood and in the latewood. In macroscopic view this change is displayed as lighter below-ground and darker above-ground rings. Latewood is particularly affected by aboveground conditions: it is significantly thicker than the underground latewood. In short: roots produce xylem similar to that of stems after exposure to aboveground conditions (Patel, 1965). Appearance of stem texture in roots usually occurs all around the circumference. This is an easy way to distinguish it from reaction wood, which is mostly reduced to a sector of the disk only.
2) *Reaction wood* is formed in the wood under mechanical stress (Figs 14-16, 20-26).

Conifers' reaction wood has wider rings than normal and latewood is accentuated, thicker, and much darker than usual, containing an extra amount of lignin. The difference in color results from much thicker and rounded cell walls of earlywood and latewood tracheids. It is always below an inclined stem, branch or root, supporting it against gravity. Reaction wood starts to grow in stems upon tilting for any reason. In roots its growth starts probably when the root loses the support of soil during exhumation, and mechanical stress – extension – is generated below the axis. The first ring with reaction wood dates the exhumation of the root (compression wood is always missing in the underground portion of roots: WESTING, 1965). Reaction wood extends to partial circumference of the root only; mostly to the lower part but not exclusively (Figs 28-31), depending on the direction of stress. Multiple tilting events in the same stem may be recognized by changes in – among others – orientation of compression wood (STOFFEL & CORONA, 2014). Similar features in roots are unexplained yet. Reaction wood can be overprinted by factors affecting the growth of the whole plant. Formation of reaction wood has not been studied experimentally in roots and we are not aware of many details of growth. The most obvious feature of the appearance of reaction wood is the distortion of the circular symmetry of the cross section into an elliptical one; however, asymmetry can appear without any reaction wood present. Dark, lignin-rich, thick latewood might appear simultaneously in the first reaction wood ring, or later, or not at all.

3) *Distorted symmetry* (Fig. 31). The change from circular to elliptical to variable-axis elliptical rings (of twisted symmetry) (LAMARCHE, 1961, 1963; MCCORD, 1987) is also a marker of root exhumation. The growth of rings with eccentric symmetry and of reaction wood goes hand-in-hand (CARRARA & CARROLL, 1979). For a detailed study lately see BODOQUE et al. (2011, with references).
4) *Wounds* (Figs 18-19, 21, 24-31) are caused by injury to the root by mechanical means, mostly above ground, rarely below ground. If the cambium is damaged and suffers dieback, growth is stopped at that place, bark falls off, and an open wound is formed. Wounds do not date exhumation precisely to the year: injury can be later than the year of exhumation (**i** – reaction wood precedes wound by one year). There are various geometries of wound cross-sections, discussed below.

- *Onlap* (Fig. 15). Onlap is the geological phenomenon of successively younger rock strata extending progressively further across an erosion surface cut in older rocks (CHRISTIE-BLICK, 1991). In turn, we use this notion for successively younger rings overgrowing an erosion surface or a wound in tree stems and roots. Undamaged cambium around the wound allows growth to continue in adjacent areas, and the wound is slowly covered by new tissue, called callus (KRAUSE & ECKSTEIN, 1994; SCHWEINGRUBER, 1996). As the newly formed rings prograde over the dead surface of the wound, the geometry produced is called onlap, a term borrowed from geology (CHRISTIE-BLICK, 1991).
- *Offlap* (Fig. 31). If under adverse conditions the wound cannot be overgrown, and the cambium dieback continues, an offlap geometry of rings is produced. (The term is borrowed from geology: CHRISTIE-BLICK, 1991). In extreme cases it leads to unidirectional growth, usually on the underside of the root. Often it indicates repeated wounding, e.g. on animal or tourist path. This feature is analogous to strip bark formation on stems . Growth of offlapping rings leaves wounds open, exposed to abrasion. Offlap is not to be confused with eroded ring terminations. Offlapping rings grow under a bark cover, under reduced cambium activity.
- *Open* versus *closed wound*. A closed – completely overgrown – wound (Fig. 18) indicates mechanical injury at least several years ago. It is important to discover these closed wounds, as they indicate an exhumation event previous to those ones identified from seeing the surface of the root.
- *Repeated injury* (Fig. 17) indicates that the wound is still open to mechanical effects. The first one marks the first exhumation, while others indicate sustained influence of harmful effects. It can include repeated closure of the wound.
- *Abraded wound* (Figs 26, 29, 31). Abrasion of the wounded surface can lead to loss of information). Even in this case a detailed story of erosion is preserved along the flanks of the eroded wound. Erosion can be pre-exhumation (if done by undeground rodents, for example), but mostly it is a post-exhumation process.

Roots bearing abraded wounds still maintain growth on the underside (LAMARCHE, 1963).

5) *Phenolic staining* (by dark, reddish brown compounds) adjacent to the wound (Figs 17-18, 23). These precipitates isolate the open wound from infection by bacteria and fungi. Spreading beyond the actual margin of wounded tissue phenolic stains indicate the presence of a wound even if the transverse section we study does not display the injured portion itself. Identifying phenolic staining is crucial to find hidden, overgrown wounds. External surface of the stain is parallel with a ring – this is the year when the injury occurred.

Features of roots were first discussed extensively by KRAUSE & ECKSTEIN (1994). All the trees they studies were windthrown trees, therefore no exhumation markers have been found.

Relative dating of exhumation features

Wound – in the year of exhumation or later (almost never in a preceding year) in case of rapid exhumation.

Stem texture – up to 3 years before exhumation in case of slow process (CORONA et al., 2011); same year as exhumation in case of rapid process.

Reaction wood – wider rings plus enhanced latewood: can be earlier or later than exposure or missing completely. Practically simultaneous with rapid exhumation in most cases.

Phenolic substances – extends externally as far as the wound, internally as far as the pith. Develops in unspecified time, in months to years.

Conclusions

Roots, when exhumed above ground, display various features in their altered tissue. Features are grouped as (1) change from root texture to stem texture (gradual or sudden), (2) formation of reaction wood of increased ring width and lignin content, (3) injuries causing wounds and their overgrowth ring patterns, and (4) phenolic staining. Recognition of these features allows us to date the exhumation and decide whether it was slow or fast.

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Fig. 1. Mango tree roots in road cut. Photo: Aaron Escobar. Roots extend into the soil (rather into bare rock about the diameter of the trunk. http://commons.wikimedia.org/wiki/File:Exposed_mango_tree_roots.jpg. Accessed 2 November 2014.

Fig. 2. Temperate climate with arid summer and freezing winter (Mecsek Hills, Hungary). Beech roots grow along the interface between a 10-15 cm thick humic level and a felspar-rich sand derived from strongly weathered Carboniferous granite (Bátaapáti, Mecsek Hill, Hungary). Soil cover protects young roots from winter frost and from summer desiccation.

Fig. 3. Tropical climate of year-round humid air and no frost. Root system of teak (*Tectona grandis*), on sale in a woodworking specialty shop in Yogyakarta, Indonesia. Major roots do not extend deeper than 40-60 cm into the soil, while extending extensively laterally. Photo #6317.

Fig. 4. Thick roots arranged parallel with the slope. Exhumation was due to construction of the path. Warm temperate climate at medium high elevation; frost occurs in winter. Kong Tong Mt., Gansu, China. Photo #3070.

Fig. 5. Subtropical climate with year-round humid air and rare winter frost. Roots of cliffside trees grow downwards on the cliff surface, seeking water. Subtropical climate - no frost, closed canopy – no desiccation. On this vertical wall certainly there was no leaf littter cover ever protect the young roots. Guibei Hill National Scenic Area, Guizhou province, China. Photo #5849.

Fig. 6. Tree with broken branch. A seedling is growing in the wound: stem upward, roots downward, hanging in the air. There is neither winter frost nor summer drought in this subtropical region: roots can grow practically anywhere without soil or litter cover. Southern Guizhou, China Photo #5878

Fig. 7. Roots of streetside tree overgrow pavement blocks. Subtropical climate with year-round humid air and rare winter frost. Luodian, southern Guizhou, China. Photo #2040

Fig. 8. Roots of streetside tree overgrowing iron grill in Hong Kong (subtropical climate of year-round humidity and no winter frost.). Photo A. Boc.

Fig. 9. Moderately exposed and wounded roots before sampling; leaf litter carefully removed. Xingren, Guizhou, China. Photo #6121.

Fig. 10. Exhumed root, marked with a cross at the highest point above ground. Kong Tong Mountains, Gansu, China. Photo #3023

Fig. 11. The thick root, marked with black cross, parallel with the slope is an excellent erosion marker. The thin root across the thick one is unsuitable for erosion studies: although grown under soil cover, its axis has been uplifted above the thick root. Uplift is caused both by thickening of the thin root and by thickening of the underlying, thick root. Shi Men Mountain, Tianshu, Gansu, China. Photo #2710.

Fig. 12. A small hole dug around the root, ready for sampling.. It is important to clear the underside of the root from soil and stones, so the saw won’t hit anything. Shi Men Mountain, Tianshu, Gansu, China. Photo #2699.

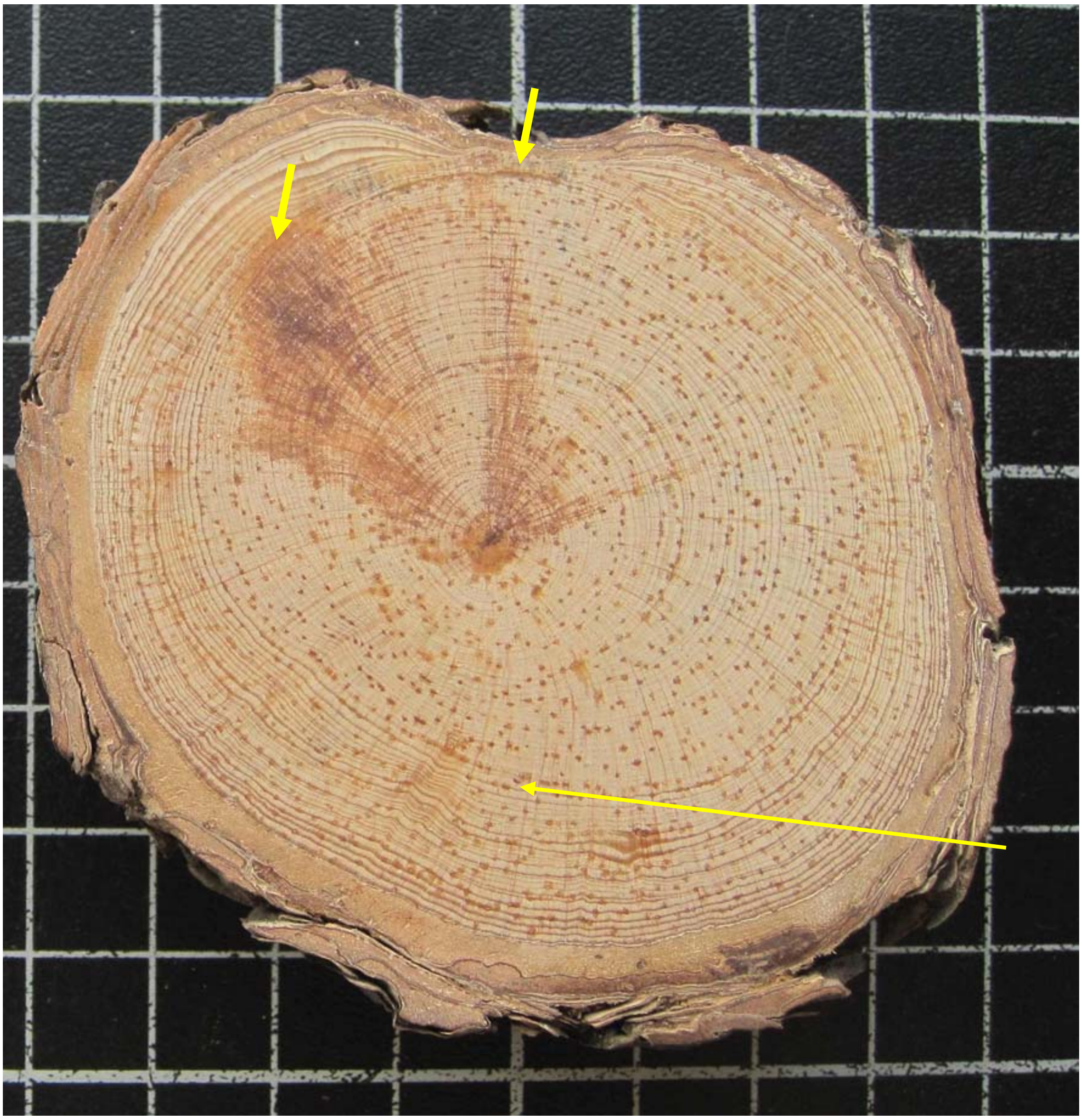

Fig. 13. Gradual change from root texture to stem texture. Centre: root texture, margins: stem texture. Root texture consists of wide, light-coloured earlywood and very narrow, barely visible, dark-coloured latewood. Latewood of central rings gradually changes into slightly wider, better visible latewood (thin arrow); it is the period when the root was gradually exhumed. Wounds (wide arrows) on top and in the upper left sector were formed at least three years apart. The top wound caused narrower rings to grow with slightly thicker latewood on top. The same rings are less distinguished at the bottom sector, indicating that the root was partially exposed to the elements, partially buried below the soil. Both wounds are marked by brownish phenolic compounds deposited towards the pith. The top wound was fully overgrown by onlapping rings and covered by bark. Resin ducts visible throughout. Exhumation 22 and 80 mm on both sides, respectively. Photo #2251. Tianshui, Gansu, China. Sample SMM129. Scale: 10 × 10 mm grid pattern in background.

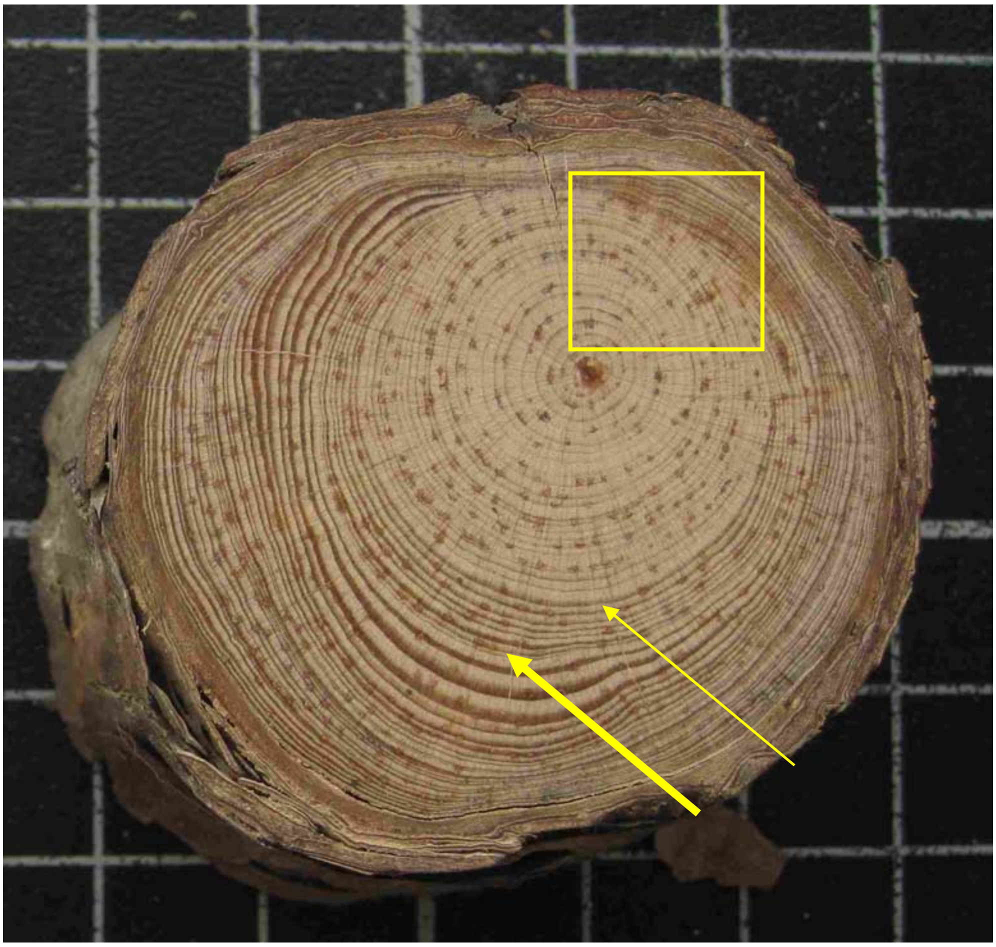

Fig. 14. Stepwise change from root texture to stem texture. Root texture consists of wide, light-coloured earlywood and narrow, dark-coloured latewood. Where narrow latewood of central rings suddenly changes to highly visible (dark and wide) latewood (thin arrow), it is the year when the root was rapidly exhumed. This exhumation preceded the appearance of reaction wood (thicker rings with thick latewood) (thick arrow), a marker of mechanical stress. Barely visible latewood portion displays circular symmetry. Visible latewood portion lost well-defined circular symmetry: rings are extremely narrow on top. Reaction wood portion with wide rings and wide latewood lost all symmetry and displays growth in variable directions. Resin ducts visble throughout. Rectangle: see Fig. 15. Exhumation 22 and 80 mm on both sides, respectively. Photo #2255. Tianshui, Gansu, China. Sample SMM118. Scale: 10 × 10 mm grid pattern in background.

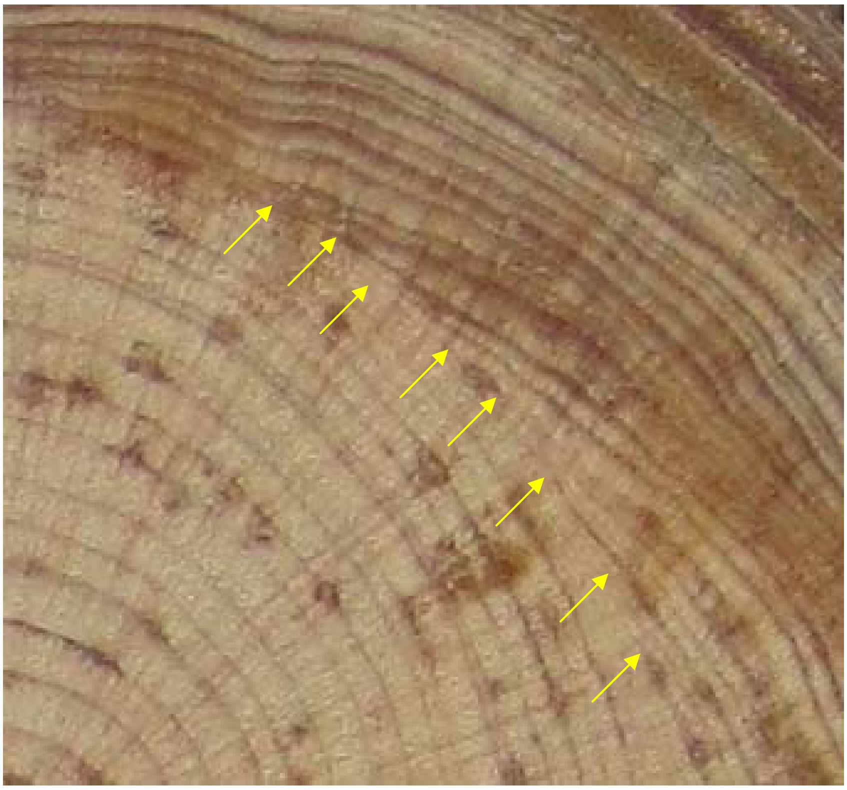

Fig. 15. Enlarged portion of Fig. 14. Onlapping rings formed during the healing of a wound. Arrow marks the terminations of the wedged rings on the surface of the last undamaged ring, i.e. the year of injury. Photo #2255. Tianshui, Gansu, China. Sample SMM118. Scale: see rectangle and 10 × 10 mm grid pattern in background on Fig. 14.

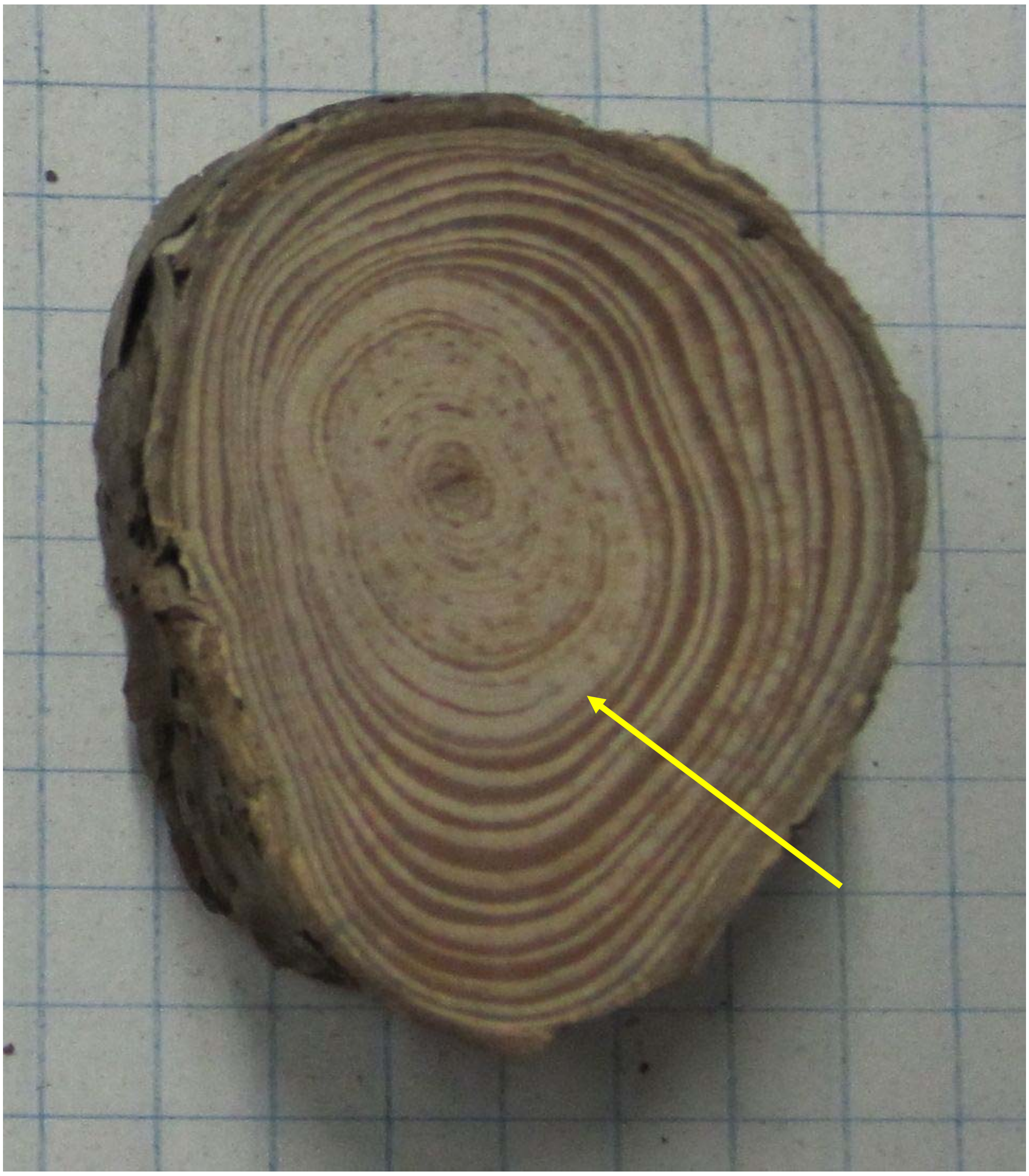

Fig. 16. Central root texture of narrow rings and inconspicuous latewood suddenly changes to 3 white rings of uncertain affiliation (probably initial reaction wood). Sudden appearance of reaction wood (wide rings and wide, dark latewood simultaneously) marks rapid exhumation of the root (__arrow__). There was no particular symmetry either before or after exhumation. Tianshui, Gansu, China. Sample SMM110. Photo #3078. Scale: 5 × 5 mm grid pattern in background.

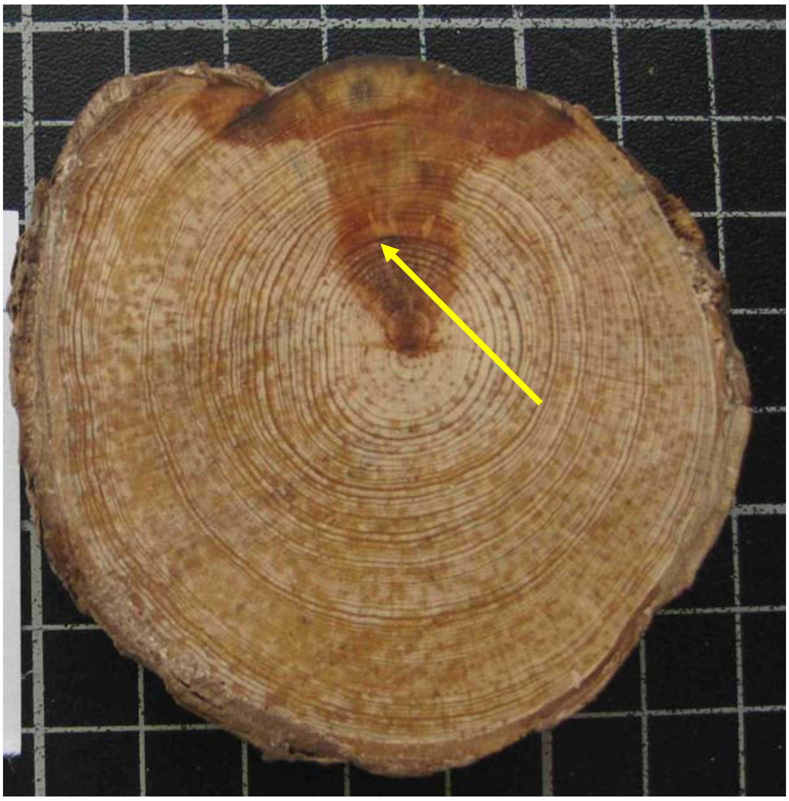

Fig. 17. Gradual change from root texture to stem texture (mostly stem texture). Root section displaying almost circular symmetry. (The oval shape is caused by the plane of section across a division of the young root.) Initial, narrow rings with barely visible latewood grew underground. These are surrounded by wider rings with well-defined latewood grown above ground. Change is gradual, indicating progressive exhumation of the root (see details on Fig. 18.). Four years after expressed latewood growth started, an injury external to this section (arrow) caused increased ring width in part of the circumference. There was no cambium dieback in this section. Brown spots caused by repetitive deposition of phenolic substances due to repated injuries (dark colouration) protect the damaged portion from infections. A second, major damage on top caused cambium dieback and loss of phloem and bark. Onlapping rings left of the wound started to overgrow the wound. Eight years later another event damaged the rings overgrowing the big wound. During the next five years this wound has been overgrown by another set of onlapping rings. This root does not display reaction wood despite repeated injury above ground.All latewod is of even thickness around the circumference. Kong Tong Mts., Gansu, China. Sample KTM105.. Photo #2252. Scale: 10 × 10 mm grid pattern in background.

Fig. 18. Magnified image of the central portion of Fig. 17. Change is gradual from central root texture towards stem texture indicating progressive exhumation of the root. An injury external to this section (arrow) caused increased ring width in part of the circumference. There was no cambium dieback in this section. Brown spots were caused by deposition of phenolic substances due to the injury (dark colouration) to protect the damaged portion from infections. Kong Tong Mts., Gansu, China. Sample KTM105.. Photo #2252. Scale: 10 × 10 mm grid pattern in background.

Fig. 19. Initial wide rings were gradually replaced by narrower rings, following the usual age-related decrease of groth of stems. Initial rings bear reasonable amount of latewood, while later, narrow rings have only very thin latewood. Exhumation date can be approached by the first injury only: a black wound, a dark deposit of phenolic substances below, and a single ring of the same year with accentuated latewood gives evidence. There are further two minor injuries, accentuated by phenolic compounds. The root is surrounded by thick bark, i.e. it is now fully above ground in the whole cross-section. Despite this, there is no obvious reaction wood. Tianshui, Gansu, China. Sample SMM119. Photo #3068. Scale: 5 × 5 mm grid pattern in background.

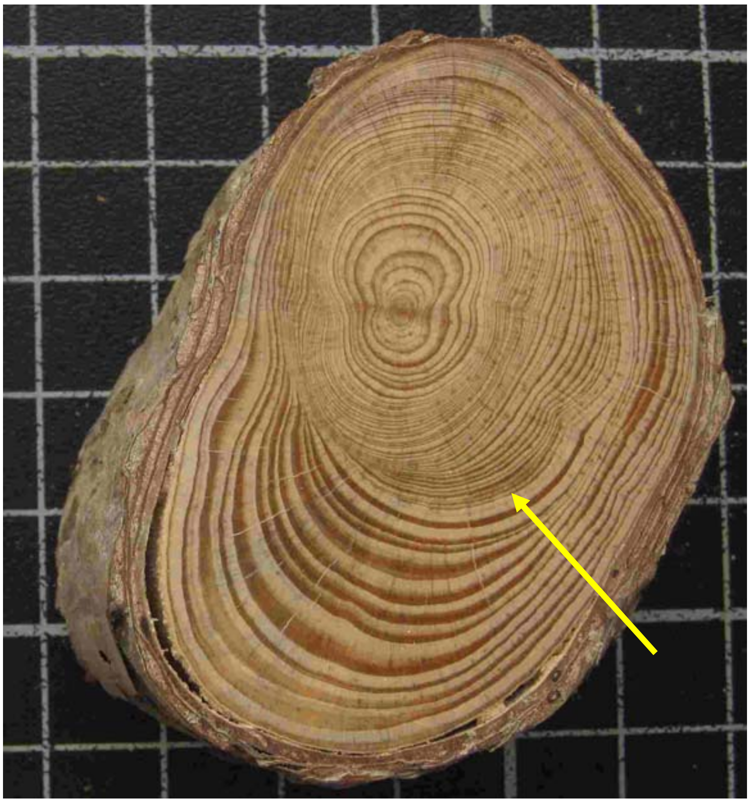

Fig. 20. Root section displays narrow rings with thin latewood grown underground. Rapid exhumation yielded reaction wood of wide rings and thick latewood (arrow). Symmetry deteriorated from an inner oval shape to an outer, highly asymmetric one. Direction of fastest growth changed repeatedly, showing a twisted pattern. Tianshui, Gansu, China. Sample SMM109. Photo #2254. Scale: 10 × 10 mm grid pattern in background.

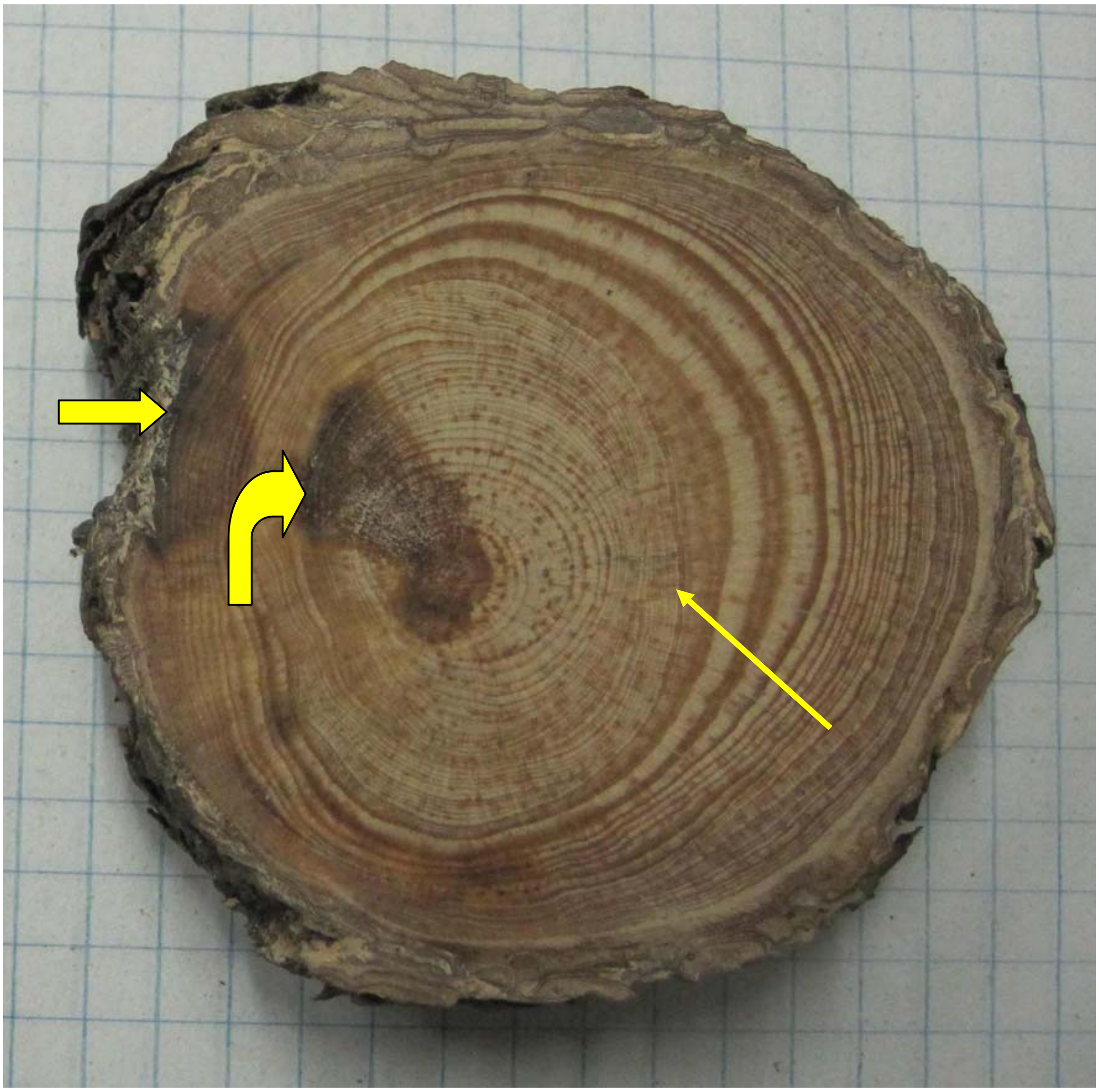

Fig. 21. The central, oval-shaped portion of the root displaying underground texturesuffered injury laterally (thick, curved arrow). Phenolic compounds protect the root here. Although yielding 1-2 thicker rings, the general appearance did not change markedly, it remained similar to the undeground pattern of narrow rings with very thin latewood. Later there was a sudden change to 4-5 very thick rings with marked latewood, i.e. reaction wood (thin arrow). Later rings are somewhat wider than the rings of the underground portion, having latewood of several cell rows. This is stem texture. The stem-textured portion has different symmetry, than the root-textured portion, indicating different stress affecting the root. A second damage on the left (thick, straight arrow) is protected by the brown spot of phenolic compounds. Attempts to overgrow and heal this wound are visible, but unsuccessful. Site of the wound was damaged repeatedly, eroding about ten external rings. Tianshui, Gansu, China. Sample SMM127. Photo #3058. Scale: 5 × 5 mm grid pattern in background.

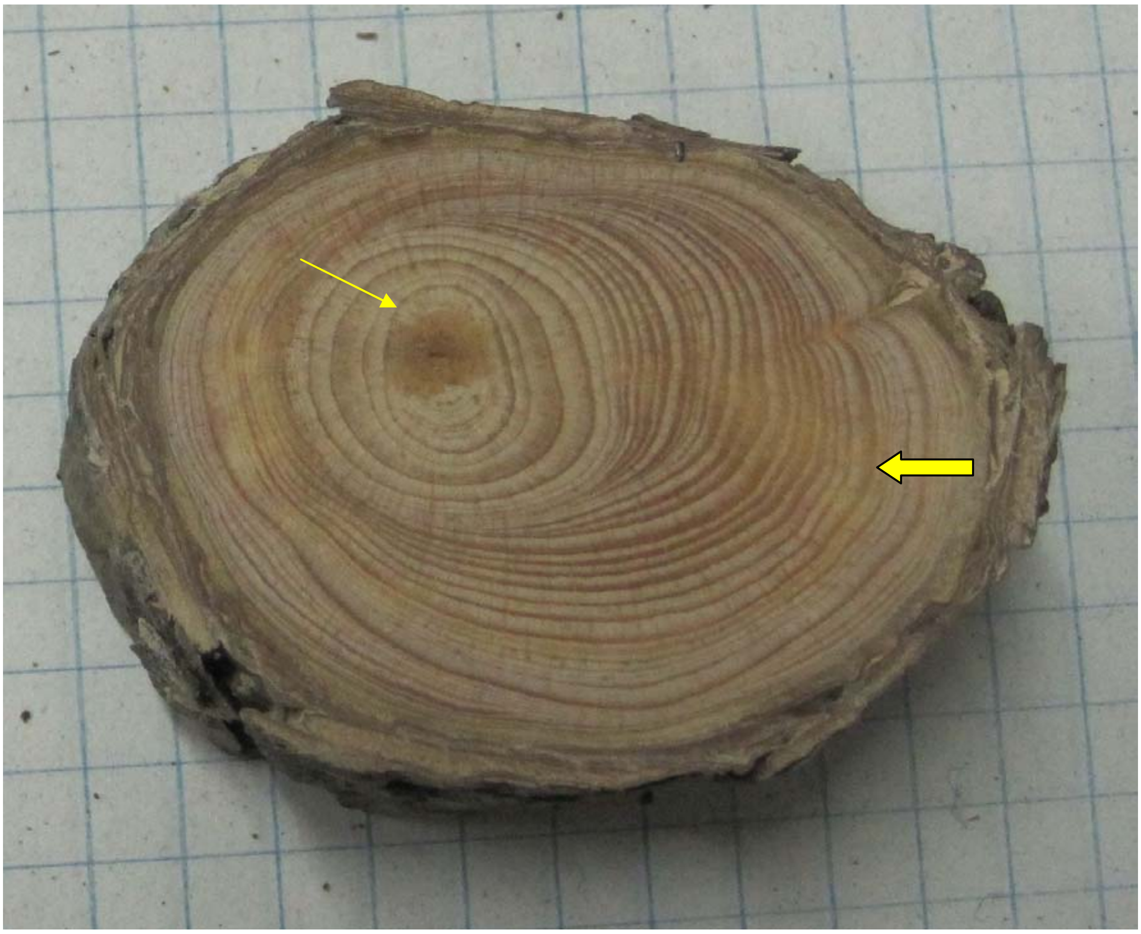

Fig. 22. A vertically elongated oval of root texture with narrow rings suddenly changes to wide rings with marked latewood (reaction wood) (thin arrow). Reaction wood indicates also a change of stress: the root started to grow laterally rather. Rings are wider on the left than on the right, and latewood is thicker here: the right side is the compression wood. Subsequently anomalous stresses cease: rings are narrow and latewood is less marked (with the exception of a single ring). Tianshui, Gansu, China. Sample SMM116. Photo #3066. Scale: 5 × 5 mm grid pattern in background.

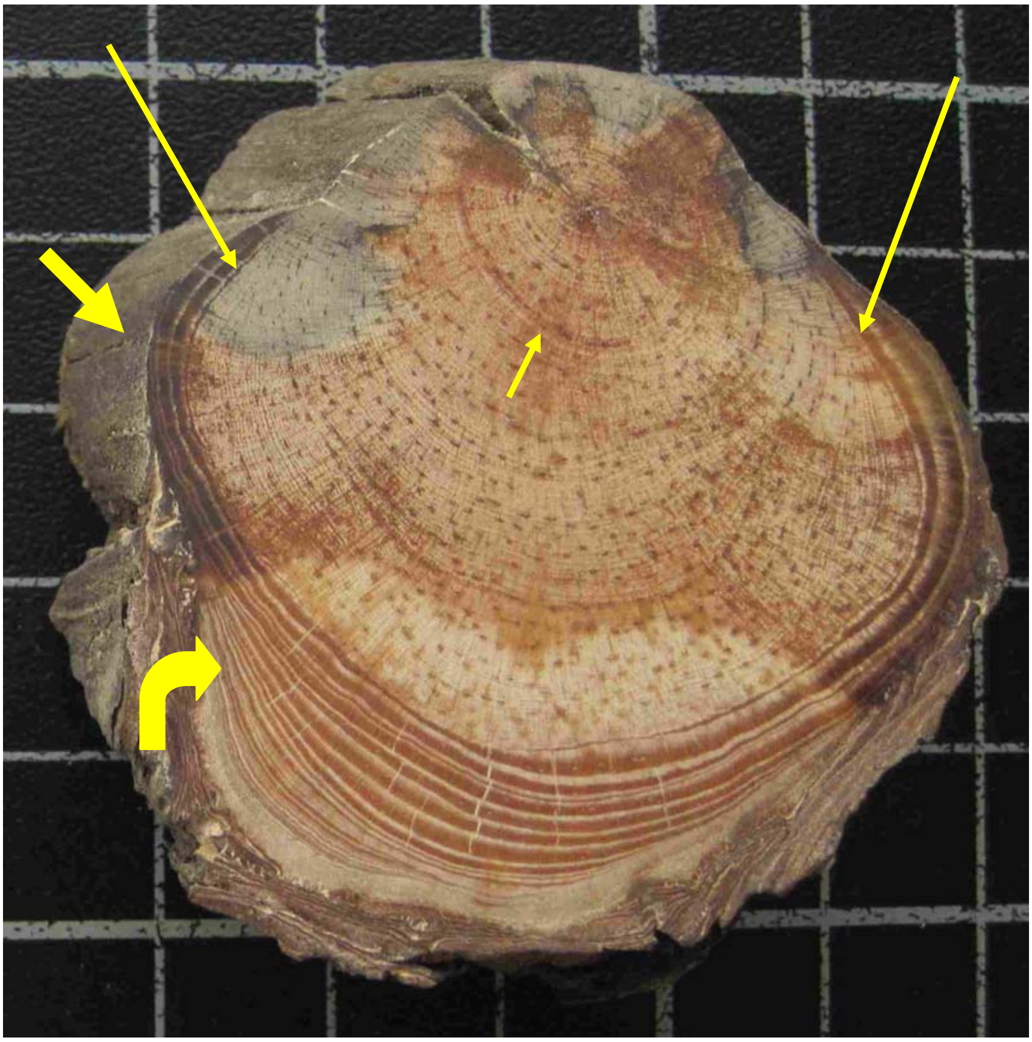

Fig. 23. This heavily asymmetric, eroded root disk describes a complex history of growth and exposure. Initial rings of almost perfect circular symmetry change to elliptical rings (short arrow), where a narrow, dark feature intertwines. Neither ring width nor latewood width changes here. Marked asymmetry is produced by growth having been concentrated at the bottom: rings of even thickness and very narrow latewood follow each other. Along the left and right flanks rings narrow upwards until they are impossible to be distinguished from each other near the top. A probable exhumation event and subsequent injury caused cambium dieback. Sudden increase in ring width and latewood width (reaction wood) marks reaction wood: onlapping rings (long arrows) progress along the wounded surface towards the top of the root. Probably a second injury caused cambium dieback, stopping growth of reaction wood rings on both sides (thick arrow). An offlapping sequence of retreating rings (curved arrow) certainly indicates something else than erosion of root: the retreating ring boundaries are uniformly covered by bark. All of the bark-free, dead surface of the disk (more than half of the circumference) is protected by phenolic substances. Note that many of the narrow rings at the top have been eroded. Tianshui, Gansu, China. Sample SM124. Photo #2257. Scale: 10 × 10 mm grid pattern in background.

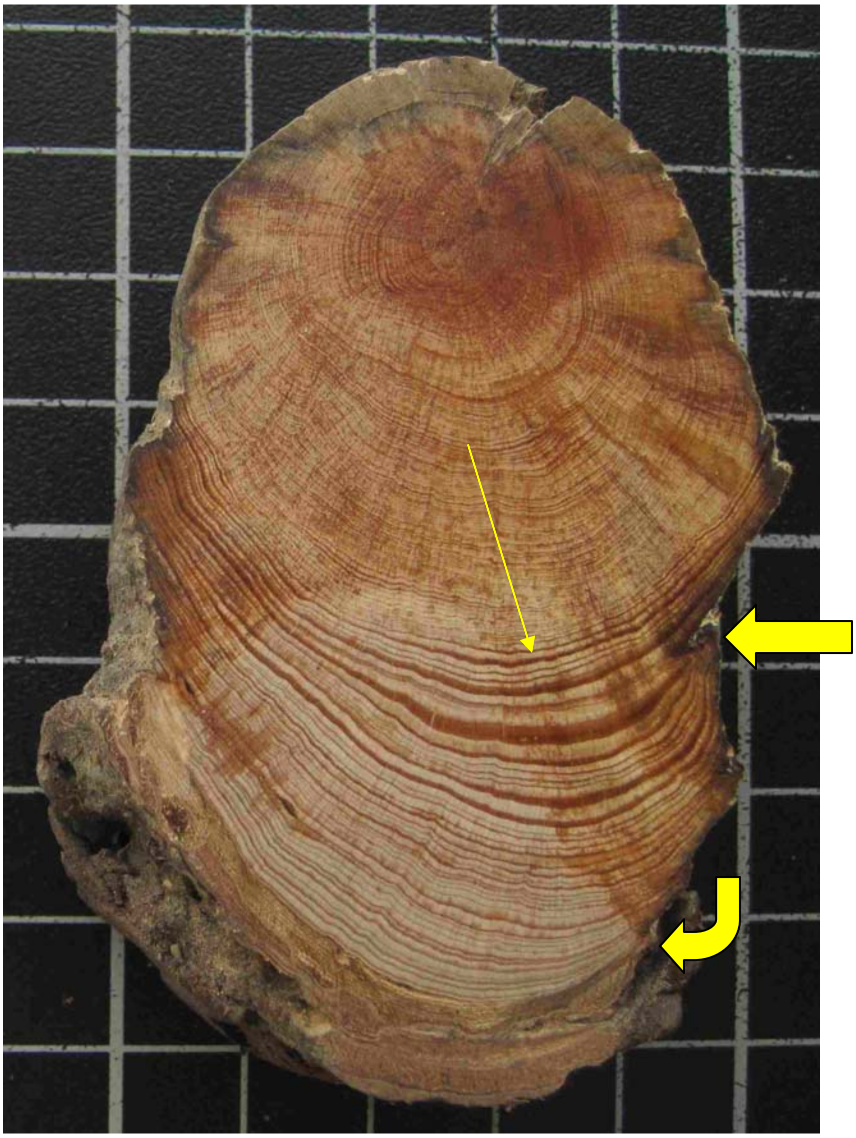

Fig. 24. Root section heavily eroded both on top and sides – the only meaningful information about exhumation history is coded in ring width and latewood width changes. Narrow rings with no remarkable latewood suddenly give place to reaction wood of wide rings and wide latewood (thin arrow). This was certainly a major erosion event caused by exhumation. Exact dimensions of the wound cannot be assessed, since all relevant parts on top and both sides have been eroded since. Asymmetry of the thin-ringed portion can be assumed only due to heavy erosion. The reaction wood portion has grown mostly downward, constrained be repeated lateral erosion. A major wound started to be covered by onlapping rings (wide arrow), while later rings display offlap (retreating growth) (curved arrow). Tianshui, Gansu, China. Sample SMM101. Photo #2258. Scale: 10 × 10 mm grid pattern in background.

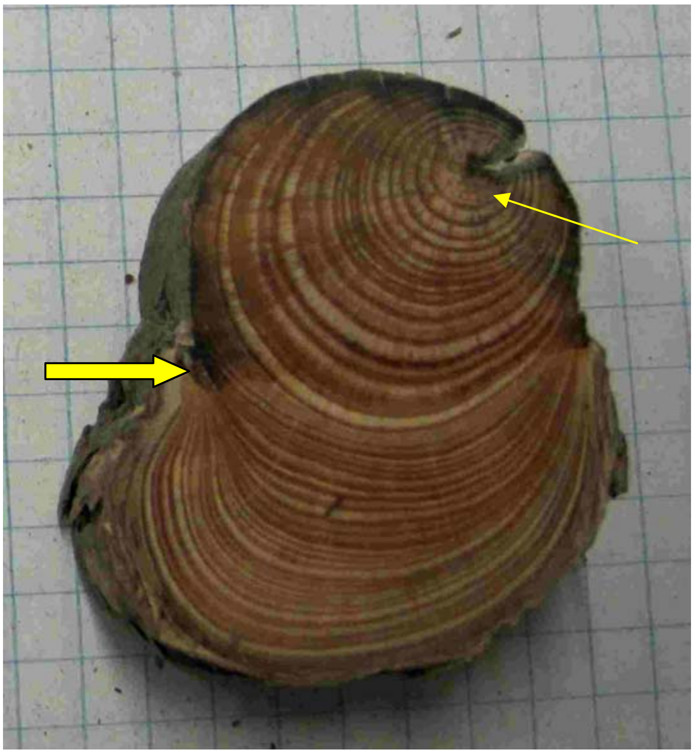

Fig. 25. This heavily eroded root (both on top and on sides) display a particular ring succession. Following the first 4-5 rings – which clearly grew underground indicated by the insignificant amount of latewood – the root has only reaction wood rings: wide rings and wide, dark latewood. Change is abrupt (thin arrow) due to rapid exhumation. Due to mechanical stress the root grew asymmetrically, first laterally, then downwards. A major injury killed the cambium along 60% of the circumference, opening the bark-less root sectors to erosion (thick arrow). The remaining sector with cambium on the lower part of the root kept growing the reaction-wood rings, slightly overlapping the wound. Post-injury latewood is thinner than pre-injury latewood! Minor discolouration by phenolic compounds above the line connecting the two wounds protects the upper part of the root from infections. Tianshui, Gansu, China. Sample SMM125. Photo #3072. Scale: 5 × 5 mm grid pattern in background.

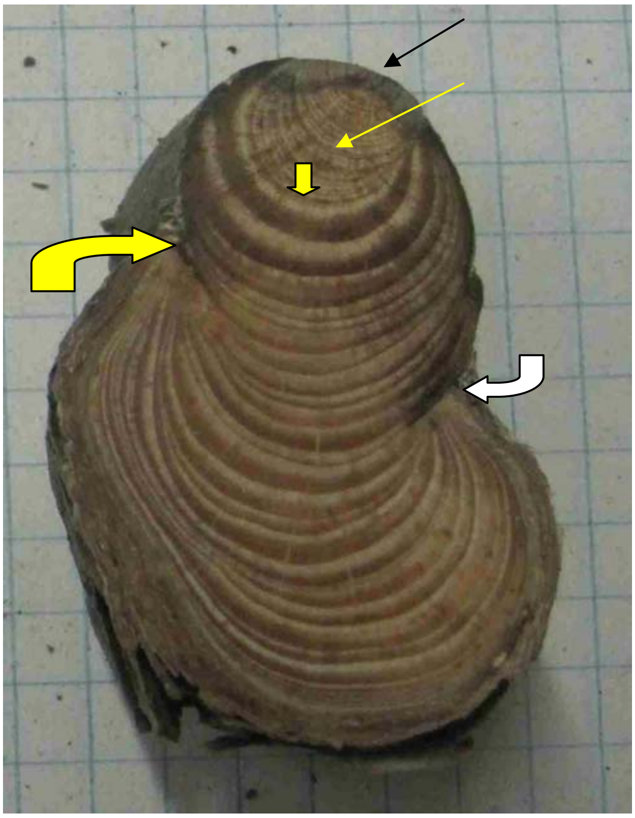

Fig. 26. Initial rings have been heavily eroded, down to the pith (pith marked by thin, black arrow). Following a decade of underground growth with narrow rings and narrow latewood, rapid exhumation and injury yielded damage to about the top half of the perimeter. The remaining lower half kept growing. Boundary between the two parts is marked by a narrow, yellow arrow. After two years a 60% cambium dieback occurred, yielding asymmetric growth. Both events allowed sustained growth of narrow rings and slightly thickened latewood, possibly undeground. A rapid, major change in mechanical stresses initiated the growth of reaction wood (wide arrow) (two extra wide rings with extra wide latewood). Sustained, asymmetric growth of reaction wood downwards formed the mass of the root. Later two wounds (curved arrows) caused cambium dieback, subsequently overgrown by onlapping rings. Each injury caused change of growth direction, ultimately producing a a twisted root. Slight discoloration in the upper right quadrant due to deposition of phenolic substances protects the root from biological damages. Tianshui, Gansu, China. Sample SMM117. Photo #3067. Scale: 5 × 5 mm grid pattern in background.

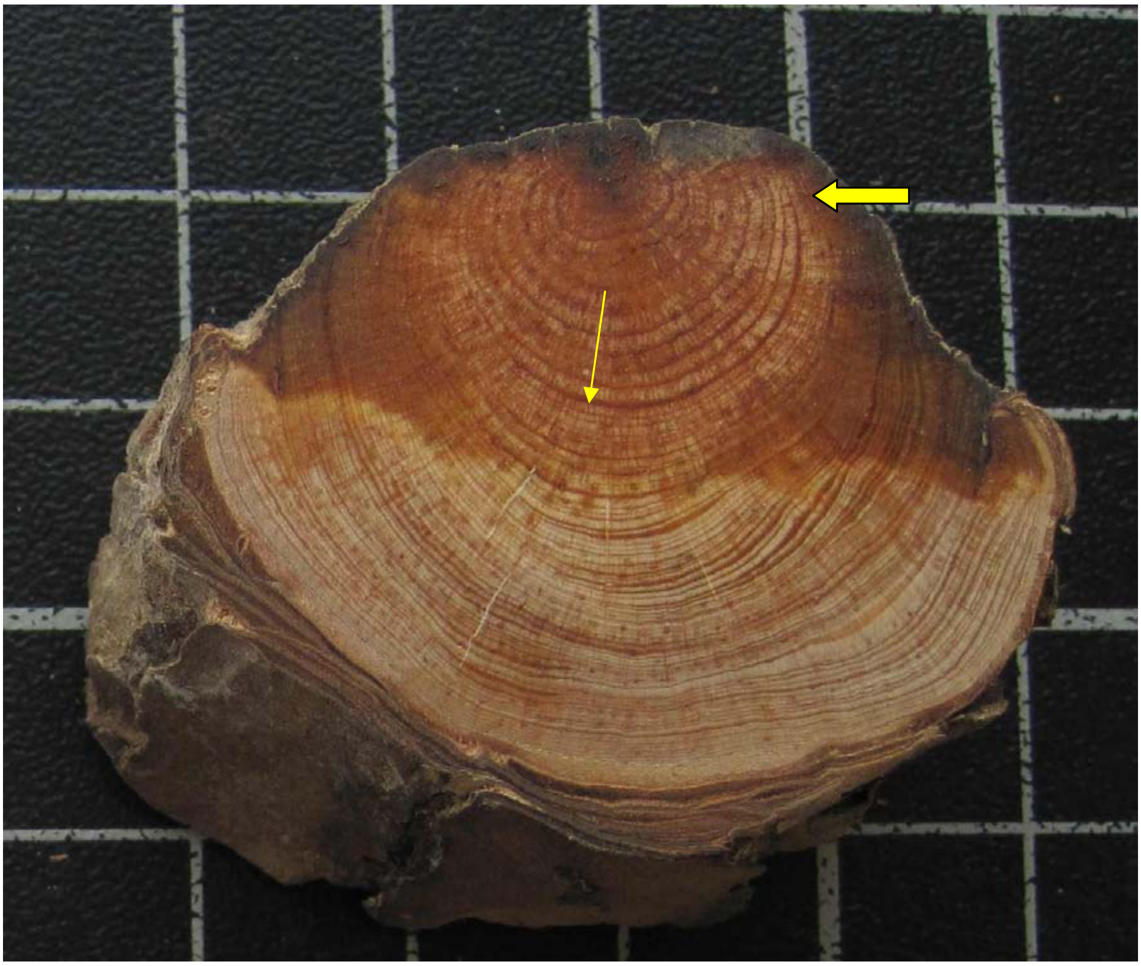

Fig. 27. This root suffered lot of erosion both on top and laterally, which removed much evidence of its exhumation history. This can be reconstructed only from changes in ring and latewood width. Wide rings with visible latewood form the centre. These suddenly give place to narrow rings with barely visible latewood (thin arrow). Termination of the latter rings (rather growth increments only) is on top of the section, indicated by significant narrowing (wide arrow). Unfortunately, this portion is camouflaged by dark brown phenolic compunds, which protect the barkless, bare root from biological degradation. Below the phenol-dyed portion, which is still protected by the bark, allowing sustained growth, bundles of rings displaying variable thickness of ring width and latewood width follow. These mark localized stress of uncertain origin. Ring width gradually decreases downward, reflecting the aging of the wood. Most of this root section is made of stem-like texture, except a few rings in the centre. Kong Tong Mts., Gansu, China. Sample KTM104. Photo #2259. Scale: 10 × 10 mm grid pattern in background.

Fig. 28. This root section is almost fully covered by intact bark, except on the top. Here, dark phenolic compounds protect the exposed wood from biological degradation. The wound exposed inner rings: about twenty, narrow rings have been eroded, possibly by repeated injuries. The central, symmetrical rings are narrow, bearing barely visible latewood: this is root texture, grown underground. However, this portion bears numerous resin ducts (scattered, small, brown spots), which indicate injury, not visible in this section. The resin duct-containing section is eclosed in a light-coloured spot of phenolic compounds. The root texture suddenly gives place to thicker rings with visible latewood (thin arrow), which are reaction wood formed due to exposure-induced stress. Tianshui, Gansu, China. Sample SMM106. Photo 3060. Scale: 5 × 5 mm grid pattern in background.

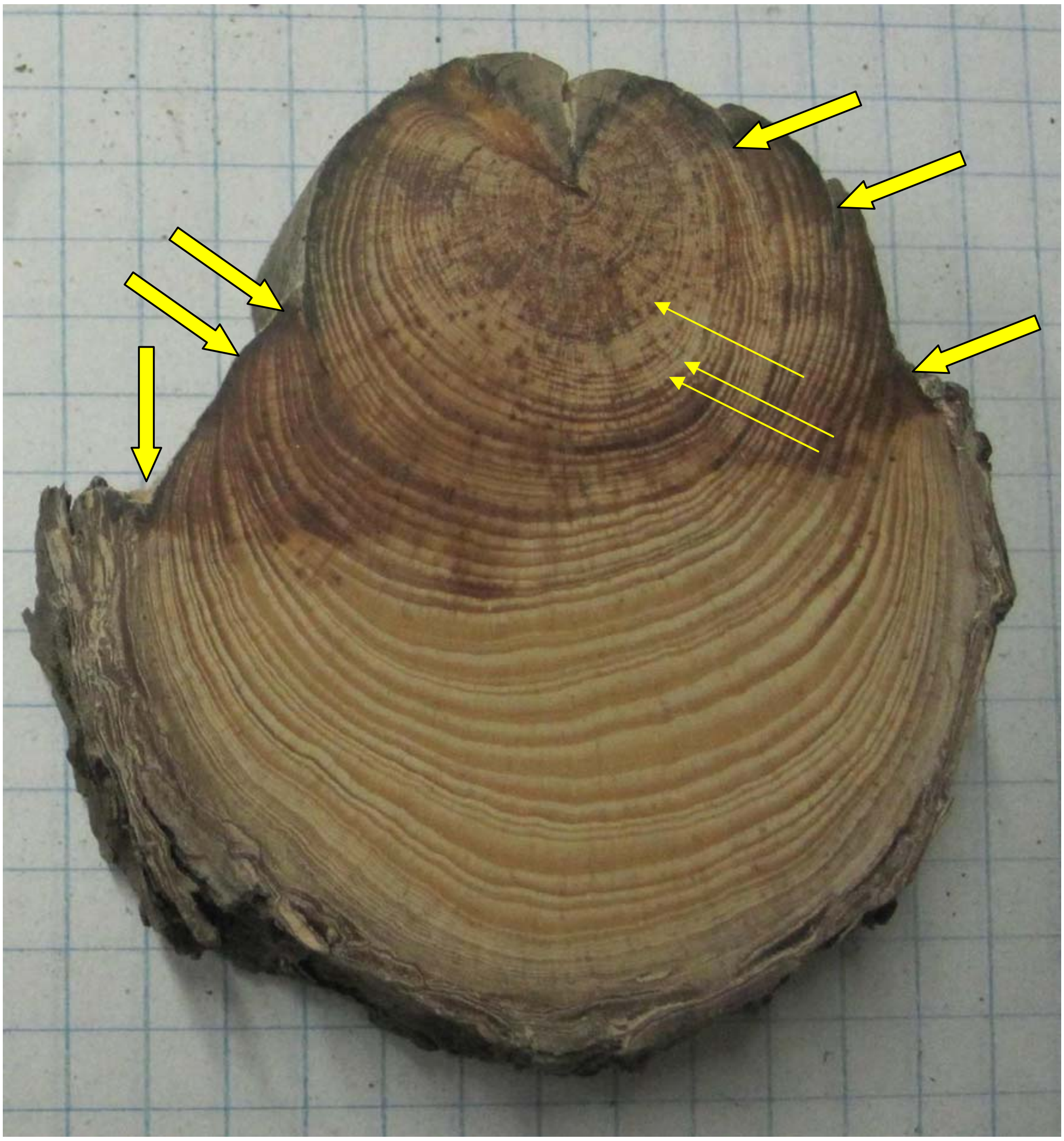

Fig. 29. Severely eroded root, which suffered multiple injuries. An almost circular innermost portion of very narrow rings and barely visible latewood is surrounded by a similar bundle of rings, with slightly thicker latewood. Their boundary is sharp, indicating rapid exhumation process (thin arrow). The root did not reach the surface while these rings grew. The next sharp boundary (double thin arrow) where reaction wood of moderately wide rings and moderately thick latewood starts, is the first result of exhumation , probably out of this section, in the vicinity. From here onwarda all rings belong to reaction wood of variable, but considerable ring width and latewood width. Repeated wounds are partially repeatedly overgrown by onlapping rings (wide arrows). Wounds extend far below the onlapping rings along the circumference, allowing exact dating of the injury. Tianshui, Gansu, China. Sample SMM126. Photo #3063. Scale: 5 × 5 mm grid pattern in background.

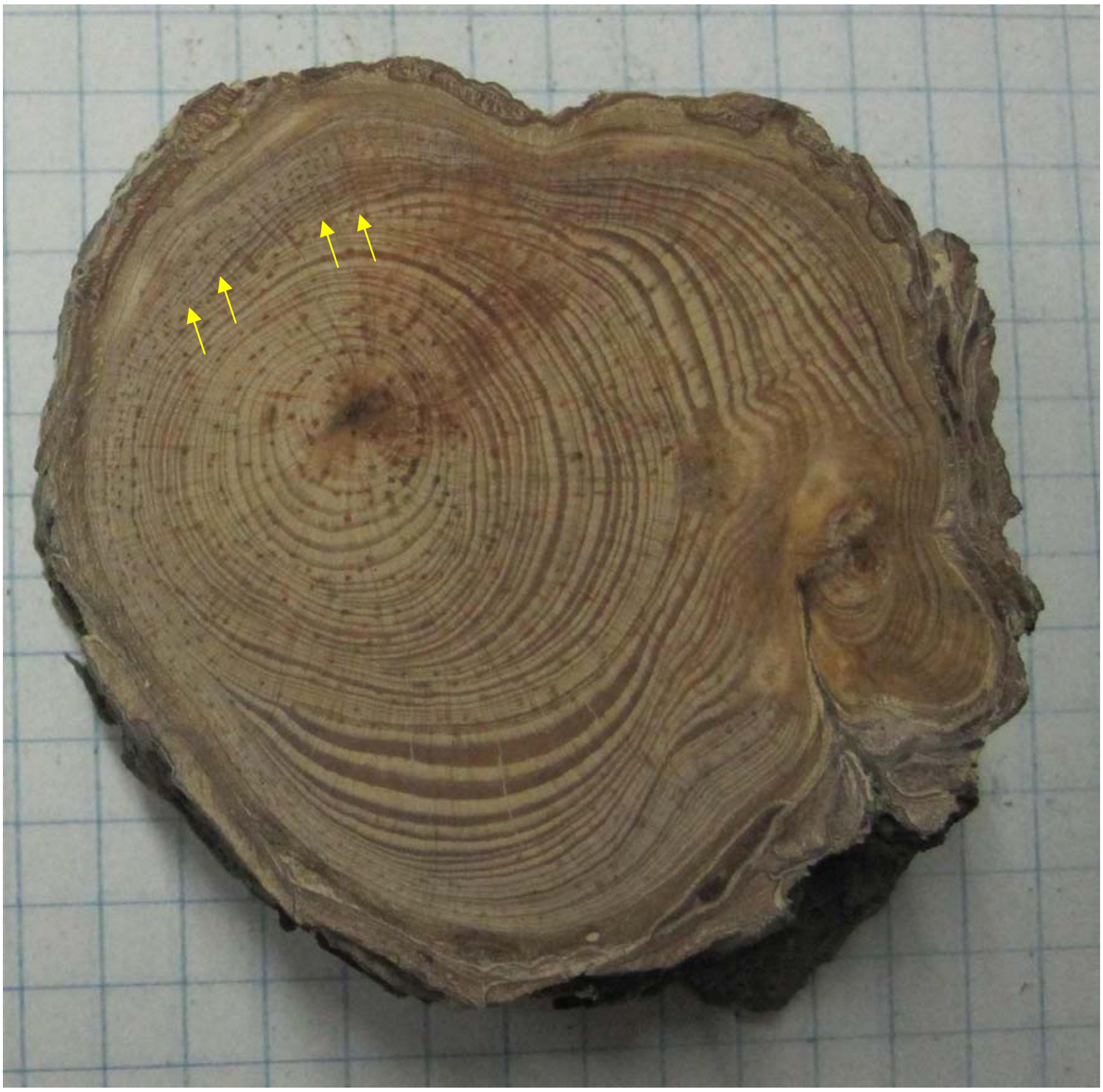

Fig. 30. Initial root texture gradually changes to stem texture, indicating gradual exhumation. More than six rings in the centre are typical root rings: narrow ones with barely visible latewood. All are almost perfectly circular. With slowly increasing latewood width the perfect circular symmetry deteriorates: thicker rings of various ellipticity follow, with a few, partial reaction wood rings (thick latewood). Onlapping rings without any trace of injury indicate cessation of cambial activity in this section without expressed physical damage to the root. A set of thin arrows indicate terminations. Strongly curved rings on the right belong to an enclosed branching root. Tianshui, Gansu, China. Sample SMM115. Photo #3064. Scale: 5 × 5 mm grid pattern in background.

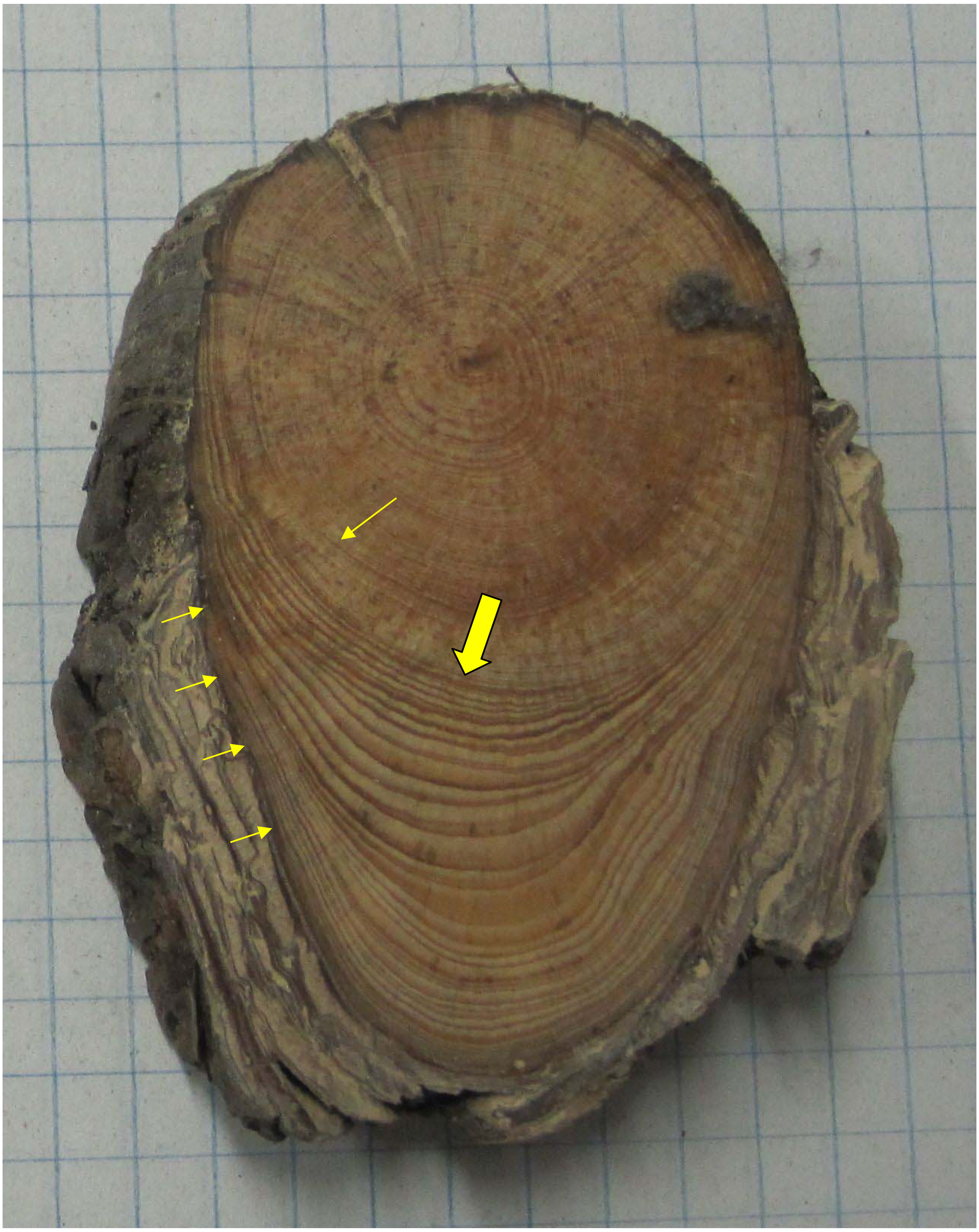

Fig. 31. Strongly eroded root with marked downward asymmetry. Perfectly circular central part of root texture: thin rings and barely visible latewood. Rings starting from thin arrow lose circular symmetry, although both rings and latewood remain thin. The cause of this change is not obvious from this section: probably increased stresses under less soil cover acting on the root are responsible for the change – start of exhumation(?) Sudden appearance of reaction wood (wide arrow) is a marker of rapid exhumation. Certainly an injury occurred at this time, although the wound has disappeared due to erosion of the upper part of the wood. Whether the injury was repeated or not, we cannot tell – all evidence were lost to abrasion. Offlapping rings terminations (set of four thin arrows) are markers of gradual cambium dieback. This retreat of cambium is responsible for the lack of onlapping rings which normally overgrow open wounds. Tianshui, Gansu, China. Sample SMM130. Photo #3076. Scale: 5 × 5 mm grid pattern in background.

Table 1. Date of anatomical changes in root texture due to exhumation.

Sample number	Root above soil		Wound								Symmetry	Reaction wood							Disk photo
	in part	fully	no-ne	near-by	open	partly overgrown	fully healed / overgrown	repeated wounding	abrasion / partial loss of rings	phenolic compounds	initially cricular / changed to elliptical	none	wide rings	thick latewood	asymmetric growth			external thin rings	
															downwards	laterally	changing axis		
Tianshui 1																			
SMM101		+											1972-	1972-					#2258
SMM102	+																		
SMM103	+																		#3083
SMM104	+					2001, 2005		+		--	1998		1998-	1998-	+	+		--	#3059
SMM105	+												1993-	1993-	1993-			2003-	#3061
SMM106	+				+					+			1990-		1990-			--	#3060
SMM107	+												1993-	1993-		1993-			#3070
SMM108	+																		#3084
SMM109	+		+							--	--		1983-, 1998-	1983-, 1998-	1998-	1983-	+	--	#2254
SMM110	+												1995	1995-	1995-	1995-			#3078
SMM111		+											1976-	1976-				1991-	#3086
SMM112	+									+			2000-	2000-					#3079
SMM113	+												1989-	1989-			2000-		#3085
SMM114	+								+				1987-1996	1987-1996				1997- pith 1983	#3081
SMM115	+	No clear buried / exposed boundary – exposure signals everywhere																	#306

Sample number	Root above soil		Wound								Symmetry	Reaction wood							Disk photo
	in part	fully	no-ne	near-by	open	partly overgrown	fully healed / overgrown	repeated wounding	abrasion / partial loss of rings	phenolic compounds	initially cricular / changed to elliptical	none	wide rings	thick latewood	asymmetric growth			external thin rings	
															downwards	laterally	changing axis		
																			4
SMM116	+																		#3066
SMM117		+							+				1983-2005	1983-2005			1973-	2006-pith 1956	#3067
SMM118	+		+								1978		1978-	1978-	1978-				#2255
SMM119	+						1973, 1986, 1988	+		+									#3068
SMM120	+	BRL																	#3077
Tianshui 2																			
SMM121	+	BRL																	#3087
SMM122	+	BRL																	#3065
SMM123	BRL	+																	#2256
SMM124		+											1987-	1987-					#2257
SMM125		+							+				1967-	1967-	1984-	1967-	1984-		#3072
SMM126		+			1972					+			1960-	1960-	1960-	--	--	1998-	#3063
SMM127		+					+	1967, 1982		+			1982-	1982-		1982-		1994	#3058
SMM128	+									+			1990-2000	1990-2000				2001-	#3082
SMM129							+	1989, 1999		+	--		--	1985-	--	--	--	--	#2251
SMM130		+							+				1982-	1982-	1982-				#307

Sample number	Root above soil		Wound								Symmetry	Reaction wood							Disk photo
	in part	fully	no-ne	near-by	open	partly overgrown	fully healed / overgrown	repeated wounding	abrasion / partial loss of rings	phenolic compounds	initially cricular / changed to elliptical	none	wide rings	thick latewood	asymmetric growth			external thin rings	
															downwards	laterally	changing axis		
																			4
Kong Tong Mts																			
KTM101	+																		
KTM102	+																		
KTM103	+																		
KTM104	+													1952-					#2259
KTM105	+					1998				+					--	--	--	--	#2252

All disks were cut between 25 and 29 May 2010. The growth year barely started. Almost all samples bear a thin earlywood of 2010.
BRL – broadleaved tree.