Vertebrate remains from the Upper Cretaceous (Santonian) Ajka Coal Formation, western Hungary

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Highlights:

Continental vertebrates from Upper Cretaceous swamp deposits are described.

These fossils reveal taxonomical overlapping with those from alluvial sediments.

Ankylosaurs preferred wetland habitats such as fluvial systems and coastal regions.

A B S T R A C T

Vertebrate remains from the Upper Cretaceous (Santonian) Ajka Coal Formation (Bakony Mountains, western Hungary) are described. Macro- and microfossils collected from two boreholes and from isolated chunks of sediment/matrix dumped on spoil heaps of the Jókai Mine represent pycnodontiform and lepisosteiform fishes, bothremydid turtles, the mosasauroid *Pannoniasaurus inexpectatus*, the crocodyliforms cf. *Theriosuchus*, *Iharkutosuchus makadii* and cf. *Allodaposuchus*, as well as ankylosaurian and theropod dinosaurs. This unit was deposited in a swampy lacustrine environment, in contrast with the neighbouring and contemporaneous floodplain deposit of the vertebrate-bearing Csehbánya Formation at Iharkút. Despite significant environmental differences, the faunal composition of the Ajka Coal Formation assemblage completely overlaps with that of the Csehbánya Formation, suggesting the occurrence of the same semi-aquatic and terrestrial species in both settings. The ankylosaurian remains further strengthen the previous view that ankylosaurs preferred wetland habitats such as fluvial systems and coastal regions.

Keywords:
Late Cretaceous
Continental vertebrates
Swampy environment
Dinosaurs
Hungary

1. Introduction

Vertebrate remains from the Mesozoic of Hungary are relatively rare and aside from a few isolated (occasionally articulated) remains only two localities are known to provide systematically collectable assemblages. In geochronological order, the first one is situated at Villány (Villány Hills, southwestern Hungary), and includes two outcrops of the Middle Triassic (Ladinian) Templomhegy Dolomite Member (Csukma Dolomite Formation) and the Upper Triassic (Carnian) Mészhegy Sandstone Formation. Recent systematic excavations and screen-washing of the fossiliferous beds have resulted in both macro- and microfossils of different groups of marine vertebrates (Ősi et al., 2014). The second locality is the Upper Cretaceous (Santonian) Iharkút (Bakony Mts, western Hungary) where excavations of the bone-bearing horizons of the Csehbánya Formation have yielded a diverse and rich continental-freshwater fauna during the past 14 years (Ősi et al., 2012).

Prior to the discovery of the Iharkút locality in 2000, some isolated bones and teeth were already known from the Upper Cretaceous Ajka Coal Formation (deposited roughly contemporaneously with the Csehbánya Formation), suggesting the potential for finding vertebrate-bearing horizons within the unit. Most of these specimens, however, were found by chance during the 140 years of underground coal mining activities (started in 1865) in the Ajka-Felső-Csinger-Gyepükaján Zone.

The first mention of a vertebrate fossil from the Ajka Coal Formation was made by Leopold Tausch (1886: 26), who presented merely a short note on a ‛small reptile or fish tooth fragment’ in his detailed review on the molluscan fauna of the Ajka coal beds. Unfortunately, most of the type specimens of the different molluscan species (Bandel and Riedel, 1994) or the precise location of this tooth cannot be identified.

The next discoveries of vertebrates in the Ajka coal beds was linked to extensive exploration drilling by the coal and bauxite mining industries in the area during the 1980s.

Various specimens were collected from cores and deposited in the collections of the Geological and Geophysical Institute of Hungary (MFGI, formerly Hungarian Geological Institute: MÁFI), but these have never been studied in detail. In 2013, due to rearrangement of the MFGI vertebrate collections, some specimens and pieces of bone-bearing cores were brought to the attention.

During the search for Cretaceous vertebrates in the Bakony Mountains in 1999 and 2000, the first specimens discovered were isolated fish and crocodilian teeth and a few bone fragments from the Upper Cretaceous (Santonian) Ajka Coal Formation. These specimens were recovered either by breaking up chunks of coal-bearing matrix dumped on spoil heaps of the Ajka collieries or collected by screen-washing these rocks. Recently, more screen-washing of approximately 60 kg of matrix collected in 2012 from these spoil heaps was conducted, yielding most of the microvertebrate remains described here.

In the present paper, we record these fragmentary but taxonomically important vertebrate fossils and discuss their palaeoecological implications in the light of vertebrate faunas of the contemporaneous Csehbánya Formation at Iharkút.

2. Localities and geological setting

2.1. Localities

Vertebrate remains from the Ajka Coal Formation have been collected from cores of the Káptalanfa-2 (from 803 m; final depth: 847.8 m) and Gyepükaján-12 (from 473 m; final depth: 606.3 m) boreholes, and from chunks of matrix dumped on spoil heaps of the Jókai Mine near Ajka-Alsó-Csinger (co-ordinates: N 47° 04´ 31´´, E 17° 33´ 55´´; see Fig. 1). Today, these spoil heaps have been excavated and overgrown, which means that extensive collecting of fossils has become much more difficult.

Although natural outcrops of the Ajka Coal Formation are extremely rare, a few sites (e.g., along the Bocskor Trench) and thin coal beds along the Csinger Valley between Ajka and Úrkút initiated a search for coal which led to the first mining activities in the area during the 1860s (Kozma, 1991).

2.2. Geological setting

As is typical in many parts of the Transdanubian Range, Upper Triassic rocks or, more rarely, Jurassic cherty limestone or Lower Cretaceous limestones, form the basement of Upper Cretaceous transgressive sequences (Figs. 1C, 2). During the early Late Cretaceous bauxites formed in the uneven karstic traps of the Triassic Dachstein Limestone and Hauptdolomit Formations (Haas and Jocha Edelényi, 1979). In some parts of the Bakony Mountains, bauxites and karstic palaeosurfaces were covered by the contemporaneous Csehbánya and Ajka Coal Formations during the Santonian. The two units are heterotopic facies being lateral equivalents with interfingered beds (Fig. 3) in the eastern part of the depositional environment. On the other hand, in the western part the Csehbánya Formation became a relatively thin unit superposed by the much thicker Ajka Formation (Fig. 2). The Csehbánya Formation is a floodplain unit that consists mainly of variegated clays, palaeosols and silt, with sand and sandstone layers (Jocha-Edelényi, 1988). Whereas this formation is typically thin or even absent in the western part of the basin, it does reach a thickness between 50 and 200 m more easterly (Pápa-Csehbánya Zone). At the Iharkút vertebrate locality, the Csehbánya Formation contains various fossiliferous layers, including a well-known continental vertebrate assemblage of over 10,000 specimens belonging to at least 35 taxa (see Ősi et al., 2012; Botfalvai et al., 2015).

The main depositional area of the Ajka Coal Formation was situated to the west-south-west of that of the Csehbánya Formation, and it was dominated by swampy and lacustrine environments in at least three different carbonate terrain subbasins (Ajka, Magyarpolány-Devecser and Gyepükaján) (see Császár and Góczán, 1988; Siegl-Farkas, 1988). In the area of Ajka and Gyepükaján, the relatively thin sequences of the Csehbánya Formation are overlain by the Ajka Coal Formation (Fig. 2). In contrast to the predominantly fluvial, alluvial lithofacies of the Csehbánya Formation, the Ajka Coal Formation comprises an alternation of lignite beds, marls, sands and sandstone beds, and grey to brownish carbonaceous to argillaceous pelitic sediments with interbedded molluscan lumachelles (Haas, 1983) and represents a lacustrine-palustrine sequence. Whereas the Ajka Coal Formation is over 110 m thick in the Gyepükaján area (e.g., Gyepükaján-10 and Káptalanfa-2 boreholes; see Fig. 2), it wedges out in the area of Magyarpolány and is absent at Iharkút. The Csehbánya Formation and most of the Ajka Coal Formation were laid down in freshwater environments and their age is Santonian on the basis of palynological and nannoplankton studies (Siegl-Farkas and Wagreich, 1996; Bodor and Baranyi, 2012; Bodrogi et al., 1998; see Fig. 3). Whereas the lacustrine, peat-fen environment of the Ajka Coal Formation generally grades into the marine Jákó Marl Formation (Haas et al., 1992), to the east, Upper Cretaceous rocks are mostly eroded in the Ajka Subbasin and the Ajka Coal Formation is overlain by Eocene shallow-marine limestones of the Szőc Limestone Formation.

3. Material and methods

Vertebrate remains from the boreholes Káptalanfa-2 and Gyepükaján-12 were discovered in the 1980s by Zoltán Partényi during examination of the cores (Fig. 4). These specimens are now housed in the collections of the Geological and Geophysical Institute of Hungary (MFGI). Whereas some specimens are still embedded in the cores and only one side can be studied, others have been freed completely from the matrix. These specimens usually are fragmentary, in part due the effects of drilling and in part because of the lack of preparation and conservation.

Specimens collected by our research team in 1999 and 2000, as well as material obtained by screenwashing in 2014, are housed in the collections of the Hungarian Natural History Museum (MTM). Microvertebrate remains (Fig. 5) form a significant part of the vertebrate collection from the Ajka Coal Formation; these were obtained in 2014 by screenwashing *c.* 60 kg of coal-bearing sediments, collected in 2012. In order to dissolve this matrix 20 per cent acetic acid was used. Due to the large amount of residue, consisting mainly of coalified plant debris and molluscan shell fragments, saturated $ZnCl_2$ solution was used as a heavy liquid (density around 1.9 g/cm^3) to separate the dominant (approximately 80 per cent) coalified plant fragments from the remainder of the residue. Approximately 200 cm^3 of residue was put in a 1.000 cm^3 beaker, and zinc-chloride solution was poured on top of it. While the carbonized wood floated to the surface of the solution, bones, teeth, as well as molluscan shells, accumulated on the bottom of the beaker. The floating waste was removed with a small kitchen sieve, after which the solution was decanted, and the residue was washed and decanted repeatedly with water to remove the weakly acidic solution left in the pores of the vertebrate remains. Consequently, the black or dark brown vertebrate specimens (small bone fragments and teeth) could be more easily separated from the white molluscan shells under a light microscope. However, this method has several drawbacks and is far from ideal. First, although fortunately not as expensive as other alternatives such as polytungstate, the usage of zinc-chloride is quite costly when used for large-scale separation: the total amount of $ZnCl_2$ used for separation of the residue of the 60 kg sediment was about 20 kg. Second, its solution is acidic, which means that it can cause damage to vertebrate remains if not used rapidly enough and not washed out properly. Third, it reacts with the calcareous components of the residue, so that it cannot be re-used (also hindered by black colouration caused by tiny carbonized wood particles). Fourth, careful safety measures have to be taken to avoid skin contact and inhalation. In short, the use of $ZnCl_2$ as a heavy liquid for the separation of microvertebrate remains in screenwashing residues is an operable method, but a more practical substitute still needs to be found for large-scale (>1.000 kg) screenwashing and separation.

4. Description and comparisons

Osteichthyes Huxley, 1880

Actinopterygii Klein, 1885

Pycnodontiformes Lehman, 1966

Pycnodontiformes indet.

Fig. 5A, C–E.

Material. Fifteen isolated teeth (MTM V.2000.32; MTM VER 2015.18; MTM VER 2015.20; MTM VER 2015.22).

Description. The two largest teeth (overall length 4.5 and 3.9 mm, respectively) are oval in shape, have a worn and smooth occlusal surface and are identical to those described from Iharkút (Gulyás, 2009; Ősi et al., 2012; see Fig. 5C). Four teeth are oval to slightly triangular, unabraded, or only slightly worn, showing complex occlusal crown morphology. They have a central groove that is shallow and wide on some of the teeth or deeper and elongate on others, and its margins are ornamented occlusally by shallow bumps and short radial grooves (Fig. 5D–E).

Five hooked and labio-lingually strongly flattened teeth (MTM VER 2015.20; 1 mm < overall length <2 mm) may represent pharyngeal teeth of pycnodontiforms. These have a slightly transparent crown with a pointed apex (Fig. 5A).

Holostei Müller, 1845

Lepisosteiformes Hay, 1930

Lepisosteidae Cuvier, 1825

Lepisosteidae indet.

Figs. 4A–B, 5B.

Material. Ten isolated teeth (MTM VER 2015.19; MTM VER 2015.23) and a single vertebra (MFGI V.18761).

Description. As typically seen in lepisosteiform teeth, they are pointed, conical in shape and have lanceolate, smooth crowns with circular cross sections. Closer to the base, they bear fine longitudinal grooves (Fig. 5B). Their size ranges from one to three millimetres. These teeth are virtually identical to lepisoteid teeth described from the Csehbánya Formation (Ősi et al., 2012). They markedly differ from the pointed, non-lanceolate fang teeth of the main tooth row of *Lepisosteus* and more similar to those of the lanceolate teeth seen *Atractosteus* (Grande, 2010). The teeth from the Ajka Coal Formation, however, have an apically more rounded crown.

The vertebra (Fig. 4A–B) is laterally wider than high (maximum width 7 mm; greatest length 4.5 mm), slightly opisthocoel and the centrum has oval articulation surfaces. Short transverse processes are present laterally.

Sauropsida Goodrich, 1916

Testudines Linnaeus, 1758

Eupleurodira Gaffney and Meylan, 1988 (*sensu* Gaffney, Tong and Meylan, 2006)

Pelomedusoides Cope, 1868

Bothremydidae Baur, 1891

Bothremydidae indet.

Fig. 4C–E.

Material. A few shell fragments (MFGI V.18763; MFGI V.18764).

Description. MFGI V.18763 most likely represents an anterior or posterior element of the peripheral ring, judging from the presence of a free lateral margin and a scale sulcus that is perpendicular to this margin (Fig. 4E). MFGI V.18764 is interpreted as being exposed in visceral view. The specimen is an indeterminate shell fragment (Fig. 4C–D). Faint decoration is present in this specimen; this is reminiscent of the ‘pelomedusoid’ pattern consisting of weakly granulated polygons (Gaffney et al., 2006) or scattered capillary furrows, also visible in *Foxemys trabanti* from the Csehbánya Formation (Rabi et al., 2012). Based on the shell surface texture, the size of the specimens and on the fact that *Foxemys* is very common in the nearby and contemporaneous Csehbánya Formation, the turtle shell fragments from the Ajka Coal Formation are assigned to indeterminate bothremydids. Late Cretaceous bothremydids in Europe are found predominantly in freshwater deposits, whereas most other members of the group led a nearshore, marine lifestyle (Gaffney et al., 2006; Rabi et al., 2012). The shell fragments from the Ajka Coal all originate from freshwater horizons.

Squamata Oppel, 1811

Mosasauroidea Camp, 1923

Tethysaurinae Makádi, Caldwell and Ősi, 2012

Pannoniasaurus Makádi, Caldwell and Ősi, 2012

Pannoniasaurus inexpectatus Makádi, Caldwell and Ősi, 2012

Fig. 4F–G.

Material. A single dorsal vertebra (MTM V.2000.21).

Description. This specimen was collected in 2000 from the Ajka Coal Formation on spoil heaps of the collieries (Makádi et al., 2012), and it actually represents the first specimen of *Pannoniasaurus* ever found, although not recognised as such until subsequent finds at Iharkút were made. This vertebra was tentatively referred to as *Pannoniasaurus* in the original description of the genus, on the basis of general morphological similarity to hundreds of *Pannoniasaurus* vertebrae found at Iharkút (Makádi et al., 2012).

The dorsal vertebra measures 36 mm in length, suggesting a total body length of around 3.5 metres for this individual, as compared to relative sizes of mosasaurs (Russell, 1967) and modern varanoids (LM, pers. obs. on a juvenile *Varanus niloticus*). It is heavily distorted by lateral compression and dorsal structures are incomplete. The neural canal is visible only at the posterior end and the left postzygapophysis is more or less intact with the left zygantrum, while the left prezygapophysis and neural spine are broken, having only their bases preserved. The structures on the right side are either crushed or missing, and have an elongated 3-cm-long bone fragment pressed in between them, which may correspond to a rib fragment. Despite its condition, the vertebra is similar in its observable morphological characteristics to those described for *Pannoniasaurus* (Makádi et al., 2012) and, albeit to a lesser extent, to those of *Tethysaurus* (Bardet et al., 2003). These similarities are as follows: the centrum is V-shaped in ventral view, the condyle and cotyle are oval and oblique, the vertebral condyle was most probably flared (= precondylar constriction) as indicated by the worn edge of the condylar flange (the spongeous bony tissue is visible), and zygosphenes/zygantra were probably large and functional.

Although the specimen is compressed, it clearly has not suffered long transport, as suggested by limited signs abrasion; as such, it is indicative of the presence of the genus also in the Ajka area. The presence of *Pannoniasaurus* in the Ajka Coal Formation demonstrates that these freshwater mosasaurs were abundant not only in the floodplain area, but also in the lacustrine environment and most probably in the coastal swamps as well.

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Mesoeucrocodylia indet.

cf. *Theriosuchus* sp.

Fig. 5I–K..

Material. Seven isolated teeth (MTM VER 2000.32; MTM VER 2015.25).

Description. Crocodyliform teeth are the commonest elements in the screenwashed material of the Ajka Coal Formation. Some of them are labiolingually flattened and pointed with slightly constricted crown and pseudoziphodont carinae (Fig. 5I–K). In some specimens the pseudoziphodont carina is barely recognised due to the poor preservation. The labiolingual surfaces of the crown are ornamented with fine longitudinal wrinkles that curve slightly mesially or distally to terminate at the carinae. The carina is not only a narrow, sharp keel, but a mesiodistally wider, flattened margin of the crown. The crowns of two additional teeth (MTM VER 2015.25) are strongly eroded, so neither the carinae nor the apical region can be observed. Only the basal half of the crown is preserved in these specimens, bearing longitudinal enamel wrinkles and a slightly constricted base.

The features seen in these teeth are most closely similar to those of the mesoeucrocodylian genus *Theriosuchus* from Upper Jurassic–Maastrichtian deposits (Martin et al., 2010, 2014, references therein), including the Santonian Csehbánya Formation (Ősi et al., 2012), and thus allow a tentative assignment as cf. *Theriosuchus* sp.

Eusuchia Huxley, 1875

Hylaeochampsidae Andrews, 1913

Iharkutosuchus makadii Ősi, Clark and Weishampel, 2007

Fig. 5L–N.

Material. Two isolated teeth (MTM VER 2015.24).

Description. One of the specimens (Fig. 5L–M) referred to *Iharkutosuchus* is an anteriorly positioned, spatulate tooth identical to those described from Iharkút (Ősi, 2008). It has rounded, strongly constricted crown without cingulum or secondary rows of lingual cusps. The crown surface is not completely smooth, but has a fine rugose texture. Labially the crown is spatulate with a slightly worn apical region. The spatulate part is divided by fine grooves into three parts both labially and lingually. There is a massive central portion bordered mesiodistally by flatter regions. The mesiodistal margins do not bear carinae.

The other tooth (Fig. 5N) has a slightly mesiodistally elongate, rectangular crown. Based on its shape, it could have been a multicusped tooth, but its occlusal surface is strongly eroded making the enamel–dentine junction well exposed. Though the outer outline of the main row of cusps can be observed, the extent of wear makes the number of cusps or rows of cusps parallel to the main row of cusps uncertain. The margin of the crown along the secondary cusps is damaged making it slightly concave. The main row is composed of a large central cusp, and a pair of smaller cusps mesially and distally. Compared to the teeth of *Iharkutosuchus* from Iharkút, this specimen is from the median portion (11th–14th) of the tooth row (Ősi, 2008).

Eusuchia indet.

cf. *Allodaposuchus* sp.

Fig. 5F–H.

Material. Ten isolated teeth (MTM VER 2015.21; MTM V.2000.22; MTM VER 2015.26).

Description. Some of the teeth are tall, pointed and labiolingually slightly flattened. Their surface is ornamented by fine longitudinal enamel wrinkles, but in contrast to teeth of *Theriosuchus*, the wrinkles do not terminate on the carinae (Fig. 5F–H). The carinae are sharp and smooth, the crown being slightly constricted. A few other teeth are bulbous representing a more posterior tooth position (Fig. 5F). Most of the teeth have slightly worn apical regions (Fig. 5F). The morphology of these teeth occurs frequently among various eusuchian forms such as the Late Cretaceous basal eusuchian *Allodaposuchus* which is known from several European localities (Puértolas-Pascual et al., 2013, references therein), including the Santonian-aged locality of Iharkút (Rabi and Delfino, 2012; Ősi et al., 2012). Here we tentatively refer these teeth to cf. *Allodaposuchus* sp.

Ornithischia Seeley, 1888

Ankylosauria Osborn, 1923

Nodosauridae Marsh, 1890

Nodosauridae indet.

Figs. 4H–I, 5O.

Material. A single tooth (MTM VER 2015.28) and an osteoderm (MFGI V.18762).

Description. A single tooth (Fig. 5O) and a fragmentary osteoderm can be referred to ankylosaurian dinosaurs. The tooth preserves the central portion of the crown and is strongly worn. Neither the cuspidate carinae nor any of the cingula are preserved. In basal view the circular pulp cavity is visible. The labiolingually flattened, low and triangular crown is of proportions typical of ankylosaurian teeth.

The osteoderm (Fig. 4H–I) preserves approximately the central one quarter of the complete element. Its greatest preserved dimensions are 33 mm anteroposteriorly and 45 mm lateromedially (the complete osteoderm could have been approximately 70–80 mm in length). Of the original lateromedial margins it preserves a 21-mm-long part on one side and a 22-mm-long part on the other. These margins are irregular and markedly crenulate as seen in ankylosaurian osteoderms. Most of the dorsal keel of the osteoderm was damaged during collecting, but it is clear that the keel is asymmetrically positioned being much closer to one of the margins of the element, a feature typically seen in marginal, oval-shaped ankylosaurian osteoderms. Based on this feature, the dorsal surface of the bone is slightly inclined on one side, yet steeply inclined on the other side of the keel. The inner structure of the bone is spongious as usual in ankylosaurian osteoderms.

Based on the features outlined above, the specimen can be clearly referred to ankylosaurs and it shows an identical morphology to the oval-shaped, medium-sized, low-keeled osteoderms of *Hungarosaurus tormai* which is known from the stratigraphically equivalent alluvial Csehbánya Formation (Ősi, 2005; Ősi and Makádi, 2009). The lack of diagnostic features, however, prevents a more precise taxonomical assignment, especially given that a second nodosaurid taxon, *Struthiosaurus*, has also been recorded from Iharkút (Ősi and Prondvai, 2013).

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Theropoda indet.

Fig. 5P–Q.

Material. A single tooth (MTM VER 2015.27).

Description. A single, small (apicobasal height 1.3 mm, crown base length 0.9 mm, crown base width 0.4 mm) pointed tooth (Fig. 5P–Q) can be referred to theropod dinosaurs. The crown base is not constricted and it has a mesiodistally elongated, oval to flattened cross section with a low (0.44) crown base/crown height ratio. The crown curves distally under a crown angle of 57º. Bands of growth or enamel wrinkles are absent. Basally the labial and lingual sufaces of the crown are slightly concave. Neither of the carinae is serrated (Fig. 5Q). Whereas the mesial carina is present in the sagittal plane of the crown, the distal carina extends slightly obliquely basally. Although unpublished, an almost identical isolated tooth has been found at Iharkút.

Teeth lacking serrations appear in several clades of theropods including unenlagiine dromaeosaurs (*Buitreraptor* Makovicky et al., 2005), ornithomimosaurs (*Pelecanimimus* Pérez-Moreno et al., 1994) and enantiornithine birds (Chiappe and Walker, 2002). In addition, the tooth-based taxa *Paronychodon* and *Euronychodon* are also characterised by the lack of serrated carinae. The smooth-edged theropod tooth from Ajka differs from those of enantiornithines and *Pelecanimimus* in the lack of a constricted crown base (Chiappe and Walker, 2002). *Buitreraptor* has roughly similar tooth crowns, but these are more distally curved (Makovicky et al., 2005) than the Ajka specimen. *Paronychodon* teeth are characterised by longitudinal grooves on at least one side of the crown (Zinke and Rauhut, 1994), and longitudinal ridges are present on the high, recurved teeth of *Euronychodon* described from the Upper Cretaceous of Portugal (Antunes and Russell, 1991). These features are not present on the tooth from Ajka. Although hesperornithid teeth also lack serrated carinae and have a generally similar outline of the crown in labiolingual view, they do show nearly planar lingual and strongly convex labial sides (Martin and Stewart, 1977; Martin et al., 1980) not present in the present specimen. Teeth of *Ichthyornis* are triangular and convex labiolingually (Martin and Stewart, 1977), but not as curved distally as the tooth from Ajka. Some bird teeth with no serrations from the Upper Cretaceous of Alberta are similar in size and cross section (Sankey et al., 2002, fig. 5/39-42), but they are proportionally taller and not as curved distally as the Ajka tooth is.

In conclusion, the theropod tooth with smooth carinae from Ajka has a crown morphology similar to those of some dromaeosaurid and enantiornithine theropods. Post-cranial remains of enantiornithines and dromaeosaurid-like Paravians are both present in Iharkút, suggesting that this tooth might belong to one of these groups. The question whether it is from a bird (e.g., the buzzard-sized *Bauxitornis*) or from a dromaeosaurid, or perhaps an ornithomimid theropod, still remains open until more complete cranial material has been unearthed.

Sauropsida indet.

Fig. 4J–K.

Material. A single bone fragment (MFGI V.18765).

Description. A complex fragmentary bone (Fig. 4J–K) was recovered from the core of borehole Gy-12 (at a depth of 473 m). The specimen is rather flat with one (probably outer) side being slightly ornamented by some shallow pits and grooves. The other (probably inner) side is concave with a smoother surface, and at least three nutritive foramina can be observed on its left side (Fig. 4H). This surface appears to be divided by two thin bone septa, the right one being at the cut end of the specimen. Due to core drilling the specimen was cut at two ends showing a relatively uniform, spongious inner texture.

5. Discussion

5.1. Comparison of the vertebrate faunas of the Ajka Coal and Csehbánya Formations

Vertebrate remains from the Ajka Coal Formation are extremely scanty compared to the diverse and rich assemblages collected from the Csehbánya Formation, but most of the specimens can still be referred to lower taxonomic levels. Although the two formations represent two different environments (see 5.2. chapter below), the composition of the Ajka vertebrate fauna greatly overlaps with that of Iharkút. Pycnodontiform and lepisosteiform fishes, bothremydid turtles, crocodilians including cf. *Theriosuchus*, *Iharkutosuchus* and cf. *Allodaposuchus*, the freshwater mosasaur *Pannoniasaurus* and ankylosaurian and theropod dinosaurs identified from the Ajka Coal Formation have all been recorded from the Csehbánya Formation as well. Remains of these taxa frequently occur in the Iharkút assemblage. It should be noted, however, that *I. makadii* and *P. inexpectatus* are the only taxa recognised at species level in both formations, and otherwise the taxonomic overlap is currently only confirmed at higher taxonomic levels. The only taxon represented by a single tooth from both formations is a theropod dinosaur (Fig. 5P–Q). In 2014, a similarly small, distally curved tooth with no serrations was discovered from the Csehbánya Formation by sorting the screenwashed residue of several tonnes of sediment, indicating that this theropod was quite uncommon in the Iharkút setting. Although there is no evidence yet of enantiornithine birds from the Ajka Coal Formation, the Ajka theropod tooth might belong to this group, which is also poorly known from skeletal elements (i.e, a few limb bones) from the Csehbánya Formation (Dyke and Ősi, 2010).

Based on the few, mainly microvertebrate, remains described here, the Ajka fauna is dominated by aquatic or semi-aquatic forms, truly terrestrial elements being solely ankylosaurian and theropod dinosaurs. This composition probably correlates with the lesser degree of sediment transport into the swampy environment of the Ajka Basin during the deposition of coal-bearing beds as compared to that of the floodplain environment of a very low-gradient river in the Iharkút area (Botfalvai et al., 2015). The low amount of allochthonous sediment particles (i.e., sand, silt) in the fossiliferous coal-bearing beds is suggestive of autochthonous deposition of the specimens found by screenwashing. The taxa in common between the Ajka and Iharkút faunas suggest that these forms probably inhabited at least two different, yet contemporaneous freshwater environments. In the case of *Iharkutosuchus makadii*, freshwater molluscs present in both the Ajka Coal and Csehbánya formations could constitute to a potential food resource judged from its inferred omnivorous diet including hard-shelled prey on the basis of tooth wear analysis (Ősi and Weishampel, 2009).

Of the ankylosaurian remains from the Ajka Coal Formation the highly eroded preservation of the tooth may reflect an extended period of transport. The partially intact margins of the osteoderm (MFGI V.18762), however, are suggestive of an autochthonous origin. A taphonomic analysis of the very abundant ankylosaur material from Iharkút (Botfalvai et al., 2015) has strengthened the theory that ankylosaurs preferred wetland habitats such as fluvial systems and coastal regions (Horner, 1979; Lee, 1996; McCrea et al., 2001) and the ankylosaurs from the Ajka Coal Formation are therefore consistent with this pattern. The abundance of teeth referred to the crocodilian cf. *Allodaposuchus* in the Ajka Coal Formation may suggest that these small- to medium-sized freshwater predators were common elements in both the swampy environment of Ajka and the floodplains of Iharkút.

5.2. Palaeoenvironment

The present distribution of the Ajka Coal Formation indicates that it was laid down at least in three different subbasins near Ajka, Magyarpolány-Devecser and Gyepükaján (Császár and Góczán, 1988). The Ajka and Magyarpolány-Devecser subbasins went through similar sedimentary events, with sequences starting with freshwater, shallow-swamp strata deposited during the palynological zones A or B. In the macrospore flora forms related to Isoetaceae are common. By the time of zone C, the environment had turned into a lacustrine, nutrient-rich marsh in the Ajka Subbasin, while at Magyarpolány the fluvial influence became more dominant, and the area was filled with fluvial sediments (Siegl-Farkas, 1988). Frequent remains of seeds and fruits from the Magyarpolány Subbasin suggest an arboraceous environment (Rákosi and Barbacka, 2000).

During the time of palynological zones A and B the third subbasin, Gyepükaján, was permanently covered by freshwater and the environment was lacustrine based on algal flora (Rákosi and Barbacka, 2000). It has been suggested that a sequence of Dachstein Limestone partly closed the Gyepükaján Subbasin towards the east-north-east of the other subbasins (Császár and Góczán, 1988). By the time of zone C a freshwater marsh environment became dominant in this area as well.

The environment changed during the time interval of zone D, when marine influence became more characteristic. The coal formation became lagoonal paralic in nature, the flora and invertebrate fauna being unified. Based on ostracod (Monostori, 1988) and molluscan studies (Czabalay, 1988) the water became brachyhaline to mesohaline.

The palynological data suggest *Normapolles*-related forests with fern-dominated underwood in a tropical or subtropical climate during the deposition of the Ajka Coal and Csehbánya Formations (Siegl-Farkas and Wagreich, 1996; Bodor and Baranyi, 2012). Seasonality of precipitation can be presumed, as based on the tree rings in fossil wood related to *Araucaria* (L. Rákosi, pers. comm., 08. 2003).

Coal deposition in the Ajka region was characteristic during the time interval of the palynozones B–D. Plant mesofossils were very common in the area of the Jókai Mine, being suggestive of their autochthonous nature. For example, *Padragkutia haasi* is one of the most abundant species representing a wetland forest (Rákosi, 1991). *Podocarpoxylon ajkaense* has also been described from this subbasin and might have been the dominant coal-forming conifer in the area (Greguss, 1949).

Vertebrate remains from the Ajka Subbasin (lepisosteiform and pycnodontiform fishes, bothremydid turtles, *Pannoniasaurus*, *Theriosuchus*, *Iharkutosuchus*, *Allodaposuchus*, ankylosaurian and theropod dinosaurs) were found in chunks of the coal-bearing strata as dumped on the spoil heaps of the Jókai Mine, which means that their exact stratigraphic provenance cannot be determined. Vertebrate remains (lepisosteiform fishes, bothremydid turtles, ankylosaurian dinosaurs) brought up by drilling are from boreholes Gy-12 and Kf-2, representing the Gyepükaján Subbasin, and their exact stratigraphic position could be determined. A single unidentified bone fragment (MFGI V.18765) originates from a depth of 473 m in borehole Gy-12, from which level also spores of *Cyathidites australis*, *Leiotriletes* sp. and *Lobasporites lobatus* have been described (Rákosi and Barbacka, 2000). Thus, this level corresponds to the boundary of palynozones C and D, as based on correlations with palynoflora of wells Gy-9 and Kf-6. Marine influence cannot be ruled out in the bone-bearing section of borehole Gy-12.

In the case of borehole Kf-2, the vertebrate remains (bothremydid turtles, ankylosaurian dinosaurs) were recovered from a depth of 803 and 804 metres. Here, *Horstisporites harrisii* and *Erlanisporites spinosus* macrospores were found together with the planktonic *Schizosporites reticulatus*. In addition, *Munieria*-related green algae and *Azollopsis pusilla* were found (Rákosi and Barbacka, 2000). These imply a lacustrine, freshwater environment and the *Operculispermum* seeds suggest that the wetland forest was relatively close to the depositional environment. *Costatheca* and *Spermatites* are also common at this level, but their precise taxonomic affinity remains uncertain.

6. Conclusions

Although the fossiliferous, coal-bearing beds of the Upper Cretaceous Ajka Coal Formation have been known for 150 years, the first informative vertebrate remains were discovered only during the last three decades. These remains include macroscopic specimens from boreholes Kf-2 and Gy-12, as well as macro- and microscopic remains collected by manual breakup and/or screenwashing of chunks of matrix dumped on the spoil heaps of the Jókai Mine. They represent lepisosteiform and pycnodontiform fishes, bothremydid turtles, mosasaurs (*Pannoniasaurus inexpectatus*), crocodilians referred to cf. *Allodaposuchus*, cf. *Theriosuchus* and *Iharkutosuchus makadii*, and ankylosaurian and theropod dinosaurs. Microvertebrate remains indicate that, similar to the Iharkút fauna, semi-aquatic forms of crocodilians were the predominant inhabitants of the swampy lacustrine habitats of the Ajka Subbasin. The fauna of the Ajka Coal Formation strongly overlaps with that of the contemporaneous Csehbánya Formation, suggesting the occurrence of these taxa in the swampy environments as well as along the floodplains of a very low-gradient river.

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CAPTIONS

Fig. 1. Localities yielding Late Cretaceous vertebrate fossils, distribution and geology of the Ajka Coal Formation; (A) location of the Ajka Coal area in western Hungary; (B) distributional map of the Ajka Coal Formation (light grey) with position (green triangles) of boreholes Káptalanfa-2 (Kf-2) and Gyepükaján-12 (Gy-12) (after Császár and Góczán, 1988), the spoil heaps of the Jókai Mine in the Ajka Subbasin (green asterisk), and the locality of Iharkút (green circle). The red dashed line shows the position of the section in C; (C) simplified geological section of the Ajka Subbasin (after Kozma, 1991).

Fig. 2. Stratigraphy of well Káptalanfa-2 (after Haas et al., 1992); B–D are palynozones (after Siegl-Farkas, 1988). The ankylosaur skeleton marks the position of the ankylosaurian osteoderm (MFGI V.18762) and bothremydid turtle shell fragments (MFGI V.18763; MFGI V.18764) discovered in this core.

Fig. 3. Age of vertebrate remains calibrated with palynological zones (after Siegl-Farkas, 1988; Siegl-Farkas and Wagreich, 1996; Bodrogi et al., 1998).

Fig. 4. Macrovertebrate remains from the Ajka Coal Formation; (A–B) Lepisosteidae indet., vertebra (MFGI V.18761) in dorsal and posterior views, respectively; (C–D) Bothremydidae indet., shell fragment in core (MFGI V.18764) in inner and outer views, respectively; (E) Bothremydidae indet., shell fragment in core (MFGI V.18763); (F–G) *Pannoniasaurus inexpectatus* (MTM V.2000.21), dorsal vertebra in right and left lateral views, respectively; (H–I) Ankylosauria indet., osteoderm in core (MFGI V.18762) in dorsal view and line

drawing of the same, respectively; (J–K) unidentified sauropsid bone (MFGI V.18765) in inner and outer views, respectively.

Fig. 5. Microvertebrate remains from the Ajka Coal Formation discovered by manual breakup and screenwashing of matrix from spoil heaps of the Jókai Mine in the Ajka Subbasin; (A) Pycnodontiformes indet., pharyngeal tooth (MTM VER 2015.20); (B) Lepisosteidae indet., tooth crown (MTM VER 2015.19); (C) Pycnodontiformes indet., tooth (MTM VER 2015.18) in occlusal view; (D) Pycnodontiformes indet., tooth (MTM VER 2015.22) in occlusal view; (E) Pycnodontiformes indet., tooth (MTM VER 2015.18) in occlusal view; (F) cf. *Allodaposuchus* sp., posterior tooth (MTM VER 2015.21) in ?labial view; (G) cf. *Allodaposuchus* sp., tooth (MTM V.2000.22) in labial view; (H) cf. *Allodaposuchus* sp., tooth (MTM VER 2015.26) in lingual view; (I) cf. *Theriosuchus* sp., tooth (MTM V 2000.32) in lingual view; (J–K) cf. *Theriosuchus* sp., tooth (MTM VER 2015.25) in occlusal and lingual views, respectively; (L–M) *Iharkutosuchus makadii*, incisiviform tooth (MTM VER 2015.24) in lingual and ?mesial views, respectively; (N) *Iharkutosuchus makadii*, strongly worn multicusped tooth (MTM VER 2015.24) in occusal view; (O) Ankylosauria indet., strongly worn and broken tooth (MTM VER 2015.28) in ?lingual view; (P–Q) Theropoda indet., tooth (MTM VER 2015.27) in ?lingual and distal views, respectively.

Figure 1 color

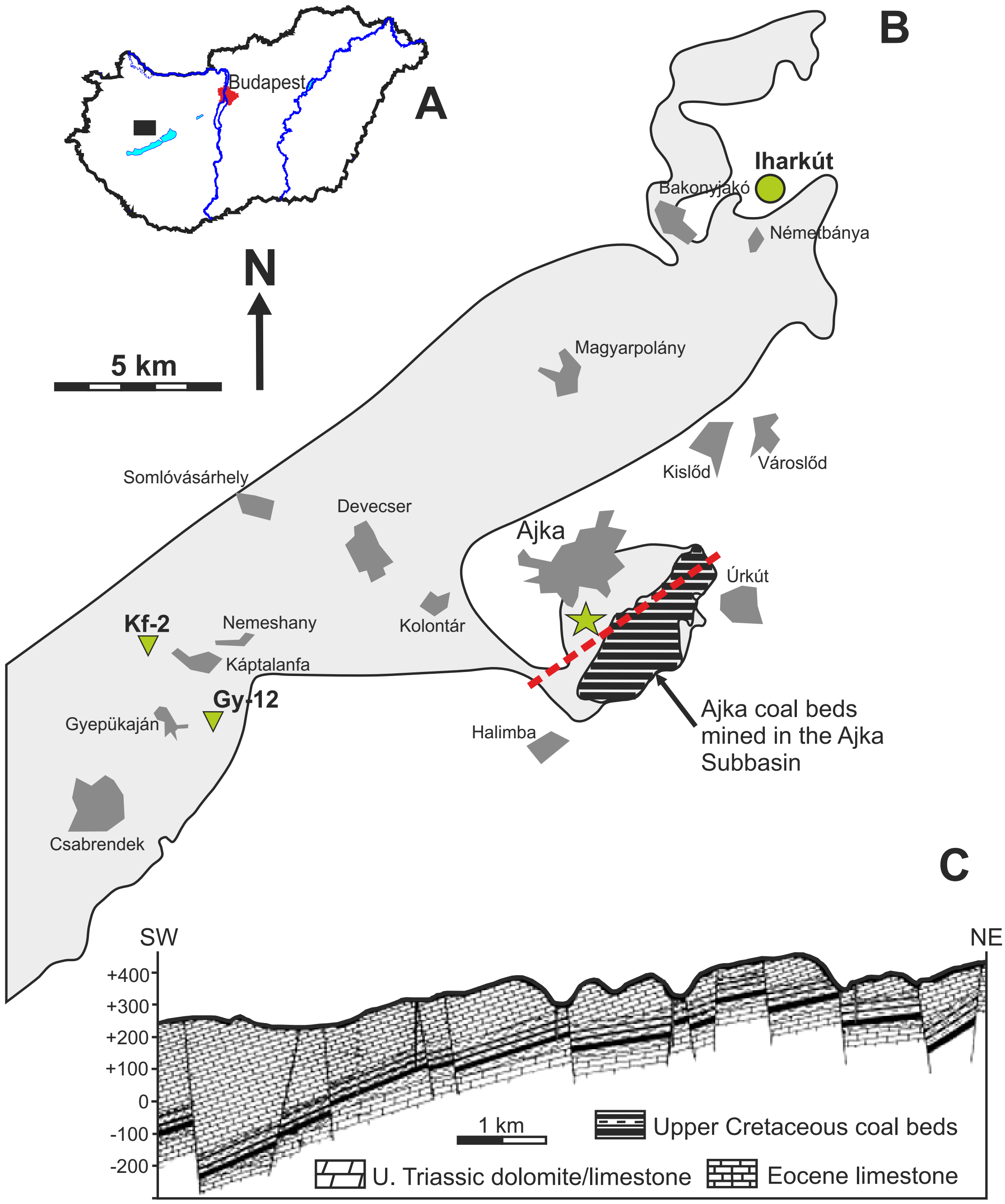
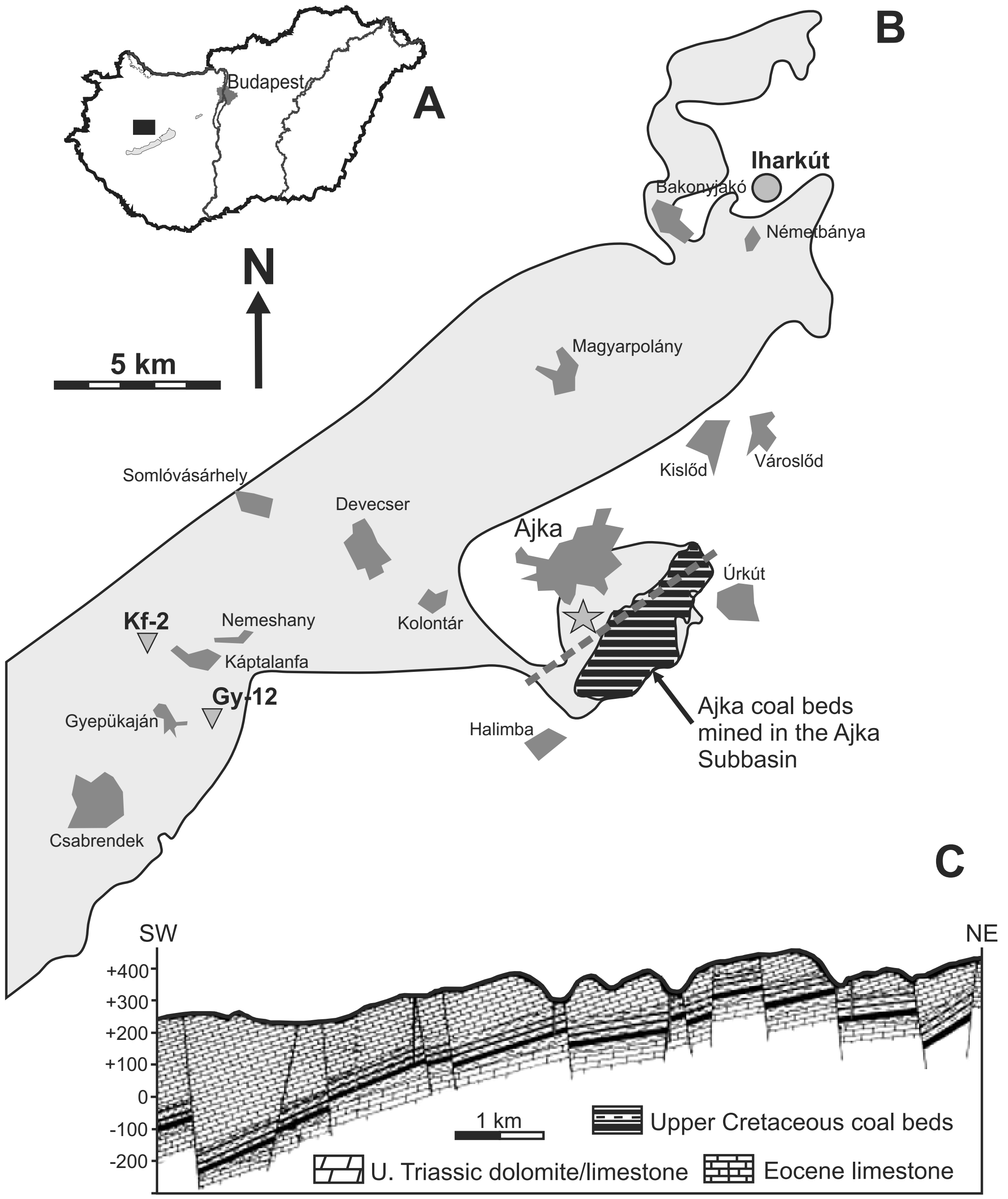


Figure 1 BW



Budapest
A
N
5 km
B
Iharkút
Bakonyjákó
Németbánya
Magyarpolány
Kislőd
Városlőd
Somlóvásárhely
Devecser
Ajka
Úrkút
Kf-2
Nemeshany
Kolontár
Káptalanfa
Gy-12
Gyepükaján
Halimba
Ajka coal beds mined in the Ajka Subbasin
Csabrendek
C
SW
NE
+400
+300
+200
+100
0
-100
-200
1 km
Upper Cretaceous coal beds
U. Triassic dolomite/limestone
Eocene limestone

Figure 2 color

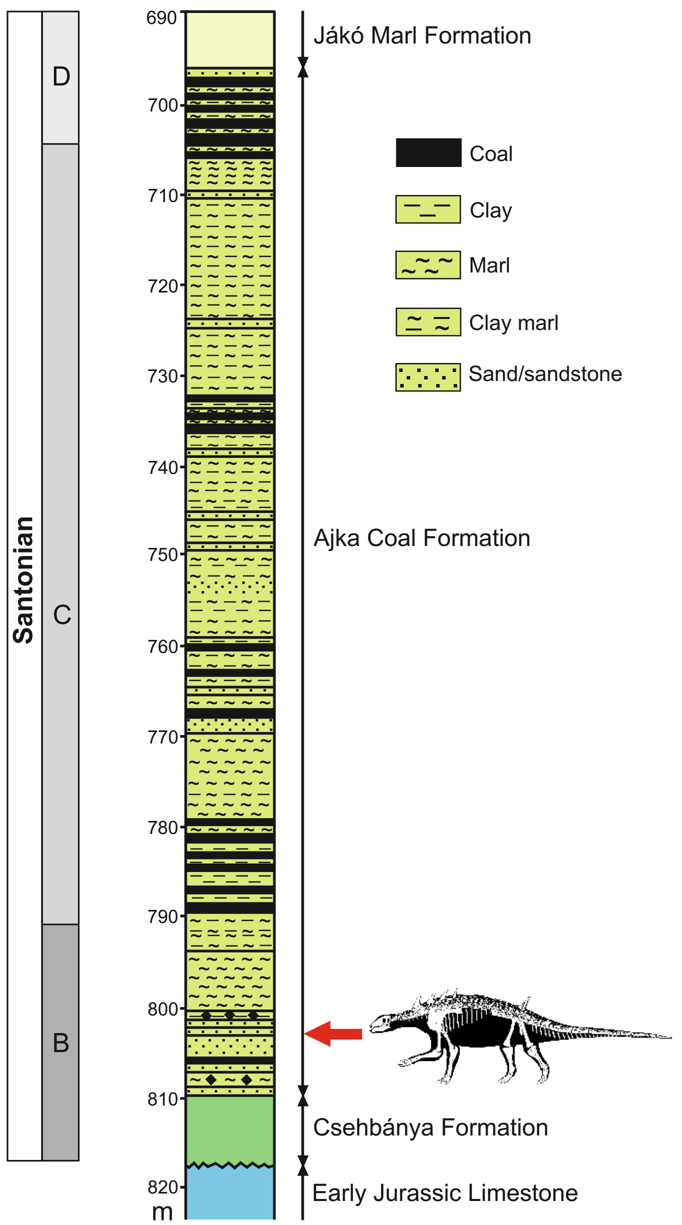
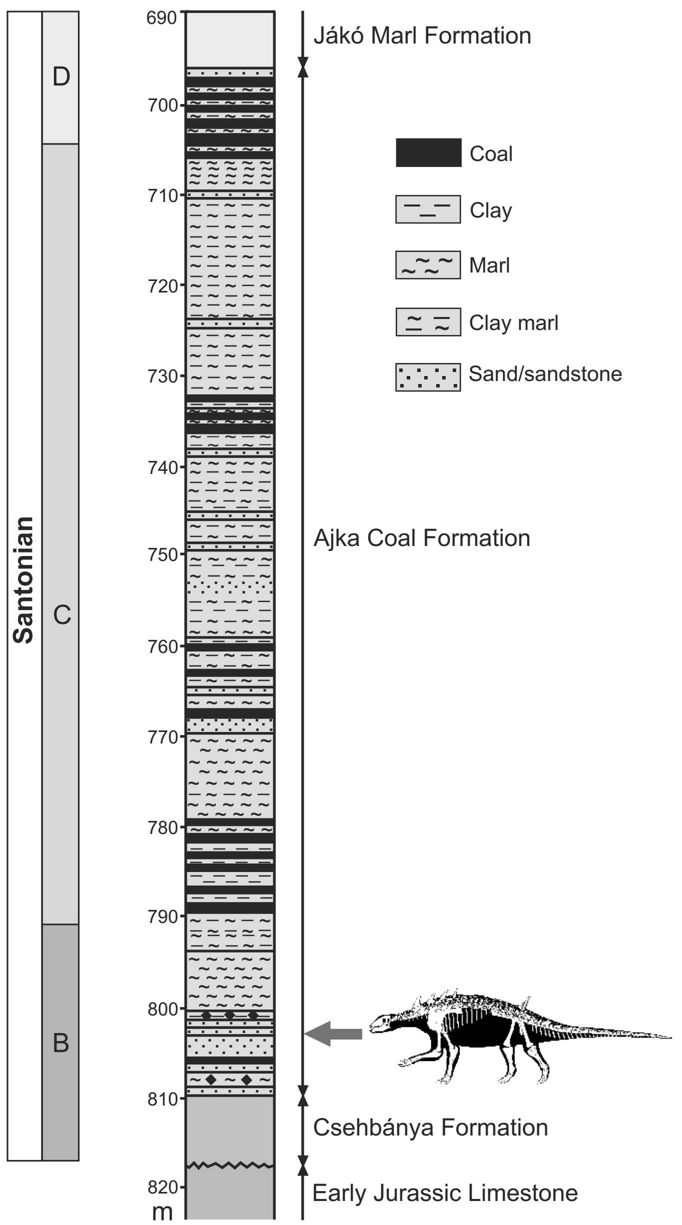


Figure 2 BW



Santonian
D
C
B
690
700
710
720
730
740
750
760
770
780
790
800
810
820
m
Jákó Marl Formation
Ajka Coal Formation
Csehbánya Formation
Early Jurassic Limestone
Coal
Clay
Marl
Clay marl
Sand/sandstone

Figure 3 color

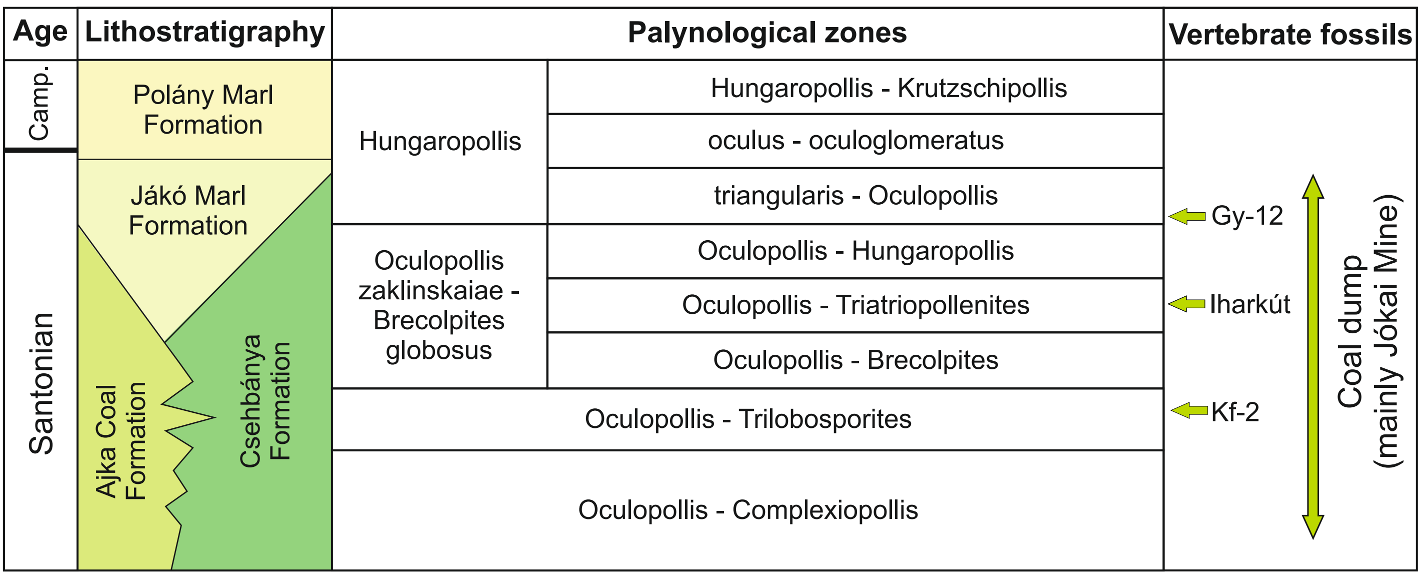


Figure 3 BW

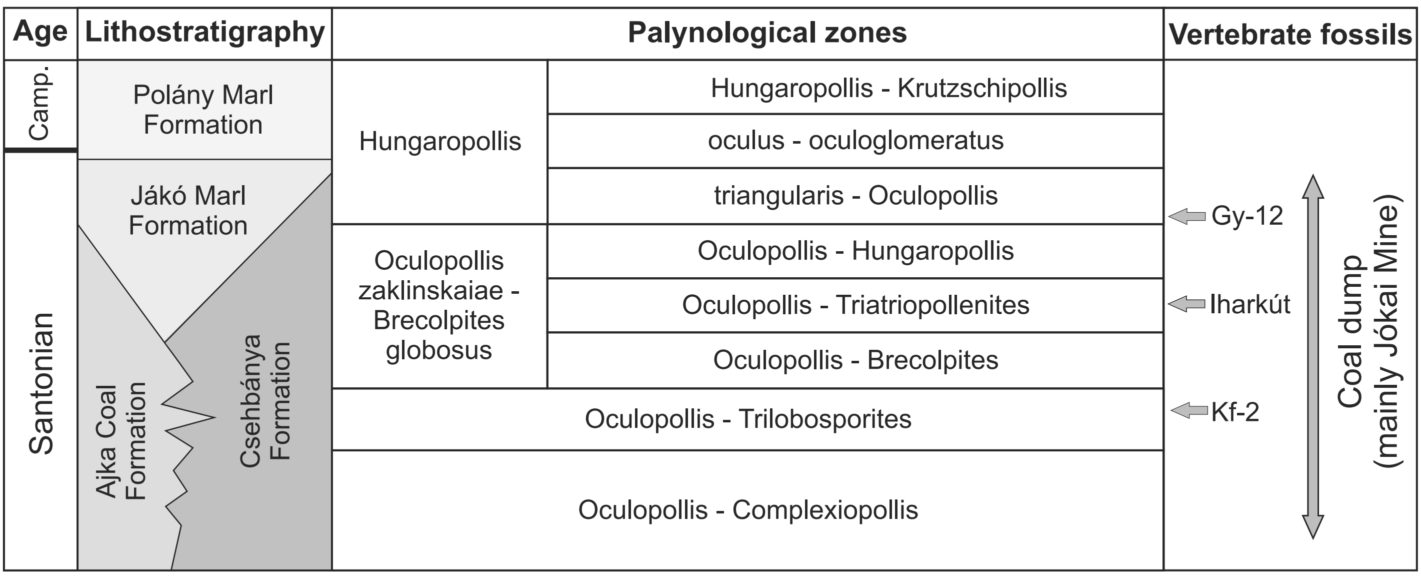

Age
Lithostratigraphy
Palynological zones
Vertebrate fossils
Camp.
Santonian
Polány Marl Formation
Jákó Marl Formation
Ajka Coal Formation
Csehbánya Formation
Hungaropollis
Oculopollis zaklinskaiae - Brecolpites globosus
Hungaropollis - Krutzschipollis
oculus - oculoglomeratus
triangularis - Oculopollis
Oculopollis - Hungaropollis
Oculopollis - Triatriopollenites
Oculopollis - Brecolpites
Oculopollis - Trilobosporites
Oculopollis - Complexiopollis
Gy-12
Iharkút
Kf-2
Coal dump (mainly Jókai Mine)

Figure 4 color
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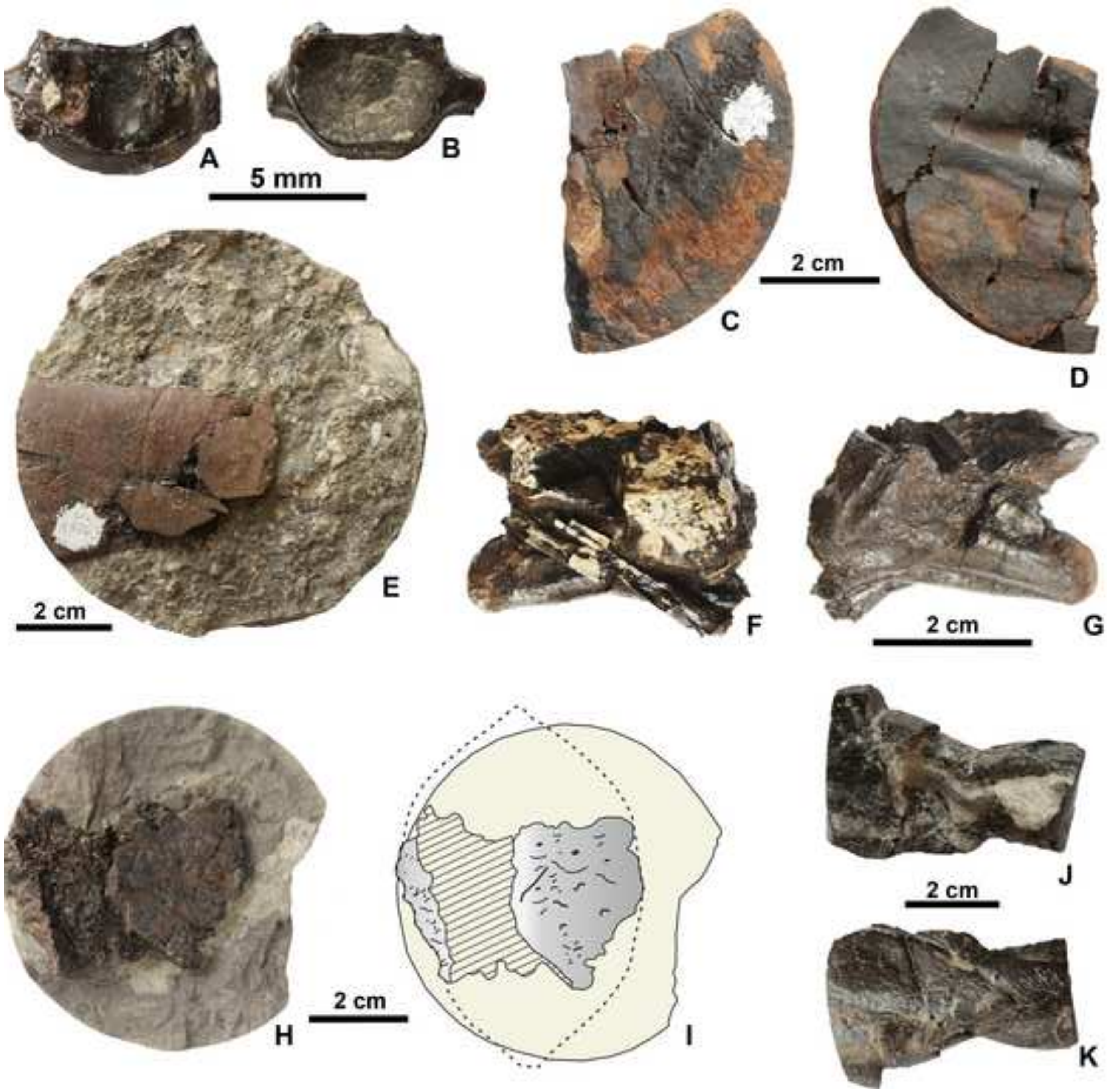

Figure 4 BW

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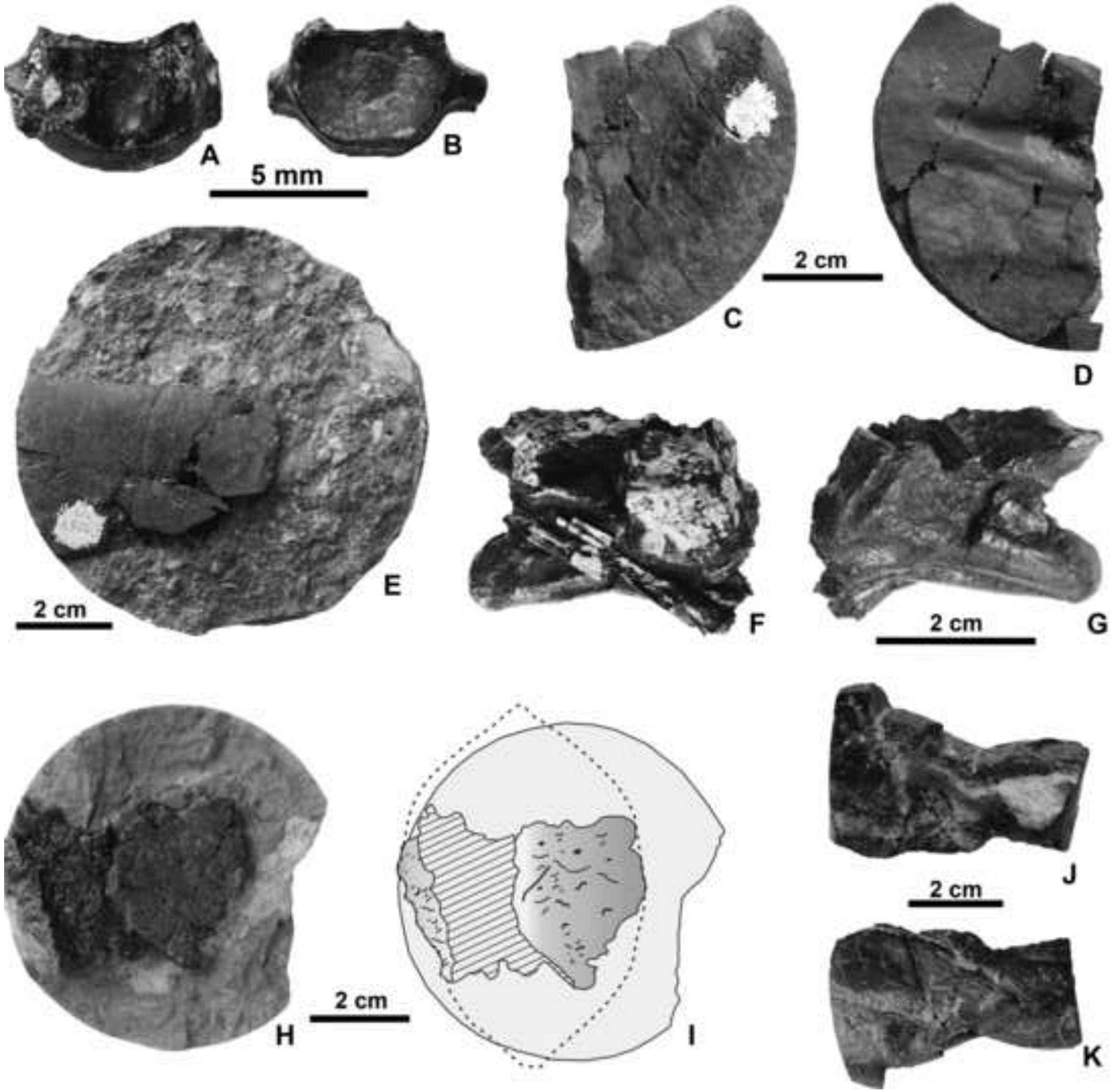

Figure 5 color

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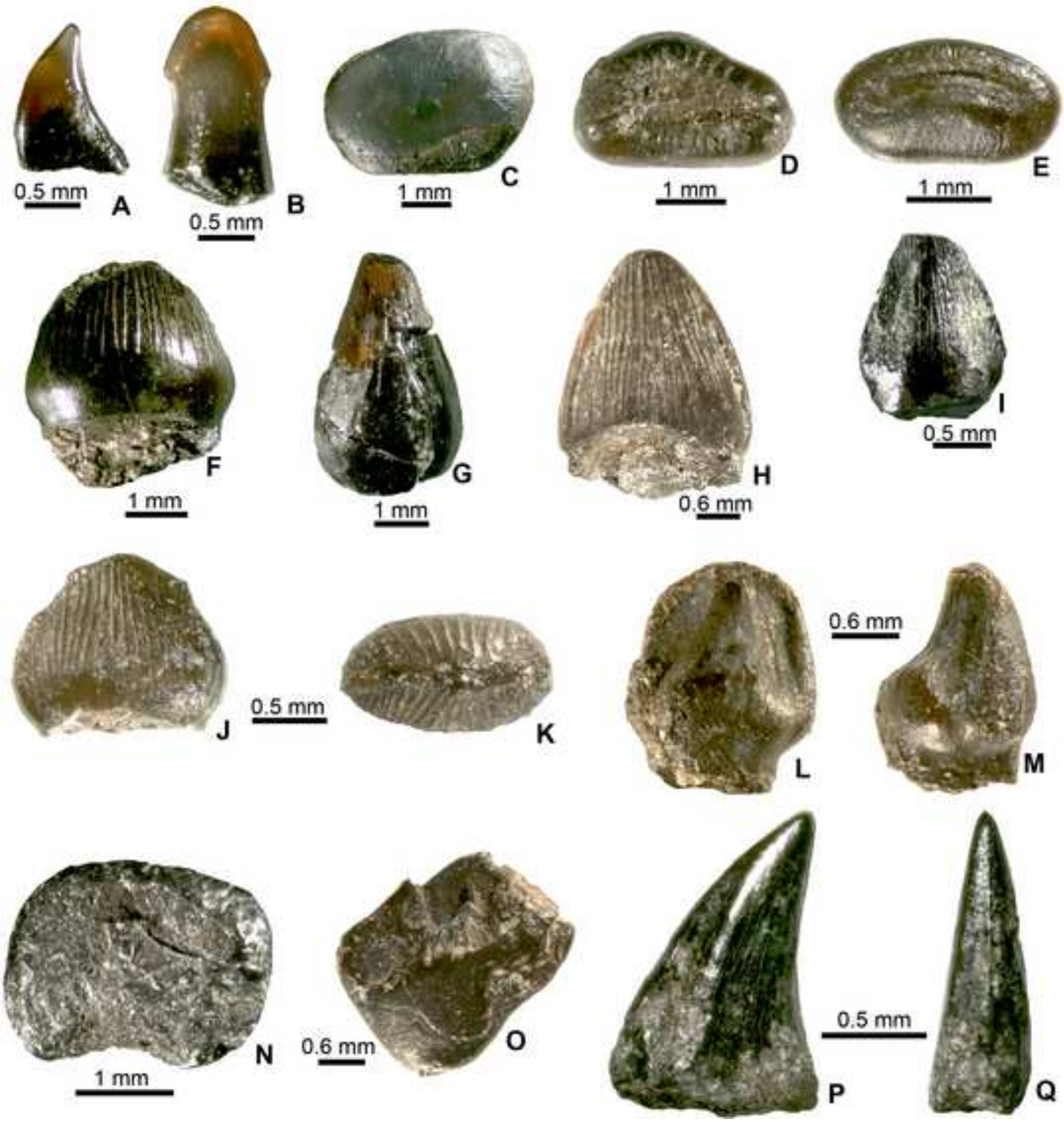

Figure 5 BW

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