

Crocodylian remains from the Miocene of the Fore-Carpathian Basin and its foreland—including the world’s northernmost Neogene crocodylian

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The geographic distribution of Crocodylia in Europe throughout the Cenozoic experienced fluctuations in the extension of its northern limit. Whereas crocodylians reached very high latitudes during the early Eocene (78°N), their northward extension was more moderate during almost the entire Paleogene and the Neogene. Here we reassess previous Early-to-Middle Miocene crocodylian records from the Fore-Carpathian Basin and its foreland, namely from marine limestones of Pińczów (Poland), and Židlochovice (Czechia) and from the new vertebrate site of Szczerców (Poland), currently interpreted as a freshwater paleoenvironment. All crocodylian material from these three sites represents Crocodylia indet. and its possible taxonomic attribution is discussed. The new Szczerców specimen, an osteoderm, represents the world’s northernmost record of a crocodylian from the entire Neogene.

Key words: Crocodylia, *Diplocynodon*, *Gavialosuchus*, *Tomistoma*, Miocene, Central Paratethys, Czechia, Poland.

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Introduction

During the Early and Middle Miocene, distinct climatic events occurred. First, a relatively warm period, known as the Miocene Climatic Optimum (MCO, the last significant warming event), extended throughout ca. 18 and 15 Ma. It was later followed by the Miocene Climatic Transition (MCT), a rapid cooling event between 15 and 13 Ma. Those climatic events inflicted dramatic changes in the distribution of faunal and floral assemblages (Zachos et al. 2001, 2008; Böhme 2003; Kováčová et al. 2011; Kopecká et al. 2022; Scheiner et al. 2023; Vernyhorova et al. 2023). This

applies to thermophilic ectothermic vertebrates in particular, crocodylians among them.

In the Early and Middle Miocene, central Europe was home to two different genera of Crocodylia: *Gavialosuchus* (often referred to as the extant genus *Tomistoma*) and *Diplocynodon*. *Gavialosuchus* was a marine long-snouted tomistomine gavialoid, with members of this group usually having a total body length over 6 m (Antunes 2017). The debate over which genus central European Middle Miocene tomistomines should belong to (either *Gavialosuchus* or *Tomistoma*) and their relationships are still unresolved and for the purpose of our study we prefer to use *Gavialosuchus*, following the original description by Toulou and Kail (1885). For more de-

tails about the *Gavialosuchus* or *Tomistoma* debate see e.g., Nicholl et al. (2020) or Burke et al. (2024). The other crocodylian present during the same time and region, *Diplocynodon*, was a basal endemic alligatoroid, predominantly freshwater, with a total body length between 1.5 and 3 m (Brochu 1999; Massonne and Böhme 2022; Venczel 2023).

The aim of this paper is a reappraisal of the crocodylian material from the Early-to-Middle Miocene of the Fore-Carpathian Basin and its foreland. The studied material includes crocodylian teeth from the lower Badenian limestones of Pińczów (Poland) and Židlochovice (Czechia). The latter represents an unpublished historical find from the Moravian part of Fore-Carpathian Basin. Additionally, we also describe a newly discovered crocodylian specimen from the Szczerców field of the Bełchatów mine (Poland), representing the world's northernmost record of crocodylians in the Neogene.

Institutional abbreviations.—KME, Krahuletz Museum, Eggenburg, Austria; LNEG, Museu Geológico, Lisbon, Portugal; MDLCA, Museo sardo di Geologia e Paleontologia “Domenico Lovisato”, University of Cagliari, Italy; MGGC, Collezione di Geologia “Museo Giovanni Capellini”, University of Bologna, Italy; MNHN, Muséum national d’Histoire naturelle, Paris, France; MWGUW, Museum of the Faculty of Geology, University of Warsaw, Poland (Stanisław Józef Thugutt Geological Museum); MZ, Polish Academy of Sciences, Museum of the Earth, Warsaw, Poland; NHMUK, Natural History Museum, London, UK; NMNH, National Museum of Natural History, Mdina, Malta; NMP, National Museum, Prague, Czechia; ÚGV, Department of Geological

Sciences, Faculty of Science, Masaryk University, Brno, Czechia.

Other abbreviations.—MCO, Miocene Climatic Optimum; MCT, Miocene Climatic Transition.

Palaeogeography of the Central Paratethys

The Paratethys was a widespread intercontinental bioprovince (Popov et al. 2004; Harzhauser and Piller 2007) situated along the northern margins of the vanishing Tethys Ocean, which eventually transformed into the Mediterranean realm in its western region. Comprising a system of connected basins, the Paratethys stretched for over 4000 kilometres from the North Alpine Foreland Basin to the Aral Sea.

The whole system developed during the Oligocene (Popov et al. 2004; Harzhauser and Piller 2007) and its palaeogeographic pattern profoundly and repeatedly transformed up until the Pliocene. Tectonic events that formed the Alpid orogenic belt caused significant changes in the local and regional palaeogeography. This led not only to the modelling of the individual basins but also to the opening and/or closing of interbasinal connections, shaping the temporary pattern of the Paratethyan system.

The general division of the Paratethys comprises three parts (Fig. 1): Western (Rhône Basin and North Alpine Foreland Basin), Central (Fore-Carpathian Basin with intramontane and back-arc basins: Pannonian, Vienna, etc.), and

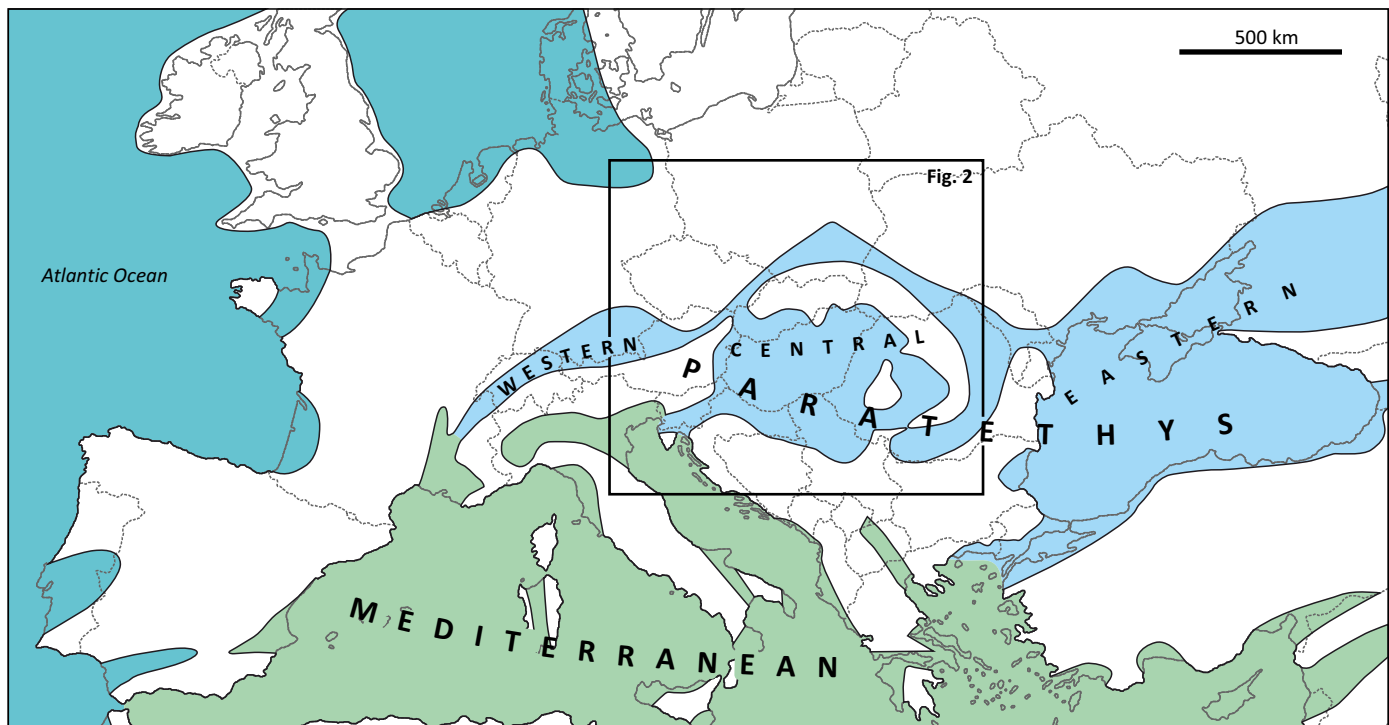


Fig. 1. Generalized palaeogeography of Europe during the Miocene epoch (after Rögl and Steininger 1983). The extent of Paratethyan and Mediterranean realms marked with light-blue and light-green, respectively.

Eastern, the largest, reaching from the Black Sea (temporally even from Eastern Carpathians) to the Aral Sea (e.g., Popov et al. 2004).

The complex palaeogeographic evolution and large dimensions of these Paratethyan realms resulted in separate regional stratigraphic divisions for each of them (Andreyeva-Grigorovich et al. 1997; Piller et al. 2007; Kováč et al. 2017). The correlation of these divisions with the standard stratigraphic division is locally uncertain but becomes more precise over time (Kováč et al. 2018). Moreover, the opening and closure of interbasin connections caused particular basins (e.g., Fore-Carpathian Basin) to be included into different realms of the Paratethys during its existence (Studencka et al. 1998; Studencka and Jasionowski 2011; Wysocka et al. 2016; Kováč et al. 2018).

During the Early Miocene and until the end of the Badenian (Middle Miocene, approximately mid-Serravalian) the Central Paratethys consisted of two main parts divided by the uplifted mountain range of the Carpathians, the northern fore-arc basin (Fore-Carpathian Basin) and the southern system of back-arc basins (see Figs. 1 and 2). The latter was dominated by the complex Pannonian Basin, which included some smaller sub-basins and was connected with some smaller neighbouring depressions such as the Transylvanian and Vienna basins (Kováč et al. 2007, 2017).

The end of the Early Miocene marked the beginning of a period of increased global temperature that lasted up almost until the end of the Middle Miocene, with its peak during the Langhian age (approx. early Badenian in regional Central Paratethys division), i.e., corresponding to global Miocene Climatic Optimum (Itoigawa 1989, Müller 1996; Piller and Harzhauser 2005; Harzhauser et al. 2007).

The rise of temperature generated by the widely open connections with the Indo-Pacific bioprovince resulted in the Central Paratethys developing a very rich and diverse fauna. In the Fore-Carpathian Basin, a marine fauna comprising taxa indicative of subtropical waters was documented within lower Badenian deposits (Bałuk and Radwański 1977; Radwański 1977, 1985, 2015; Doláková et al. 2008, 2014; Wysocka et al. 2016). Only rare findings of reptiles were reported from the Fore-Carpathian Basin (Roemer 1870; Radwański 1974, 1977, 1985, 2015). This warm period (MCO), interrupted by a relatively short cooling event (MCT; see Hohenegger et al. 2009; Wysocka et al. 2016), lasted almost until the end of the Badenian. After the MCT, warm-temperate invertebrate marine fauna re-appeared (Müller 1996; Riegl and Piller 2000; Radwański et al. 2006; Górka et al. 2012; Hyžný et al. 2012; Pivko et al. 2017; Górka 2018a, b).

The periods of warm and humid climate of the Miocene resulted not only in the development of specific faunules and deposits within the marine basins of Central Paratethys. It also facilitated the periodic development of rich vegetation in the foreland of the Fore-Carpathian Basin. That enabled the formation of coal (lignite) seams, the thickness of which increases significantly in local depressions, often of tectonic origin, along the Ohře/Eger Graben in Czechia, e.g., the Most

and Zittau Basins, extending into Poland (Rajchl et al. 2009; Brachaniec et al. 2022) or Bełchatów mines in Kleszczów Graben (Szynkiewicz 2000; Wagner and Matl 2007). Noteworthy, the northern foreland realm has been almost completely separated from the Fore-Carpathian Basin by the Bohemian Massif and the Central Polish Uplands. Between these highland areas a narrow ephemerical passage has occurred sporadically, connecting the northern foreland and the marine basin of the Fore-Carpathian Basin (see Fig. 2).

Intense mining of coal deposits gave way for unearthing vertebrate remains. They are quite common in coal basins in the Lusatia region of SE Germany (Leder 2012) and NW Bohemia (Czechia), mainly in the Most Basin (Dvořák et al. 2010; Ekrt et al. 2016; Chroust et al. 2021, 2023). To the contrary, vertebrate remains are very uncommon in the Miocene coal deposits of Poland, where just two sites yielding rather scarce vertebrate material have been discovered so far. One of them is the Bełchatów mine, where remains of fishes and small mammals (mainly rodents) were recorded (for details see Kowalski and Rzebiak-Kowalska 2002; Fostowicz-Frelik et al. 2012; Kovalchuk et al. 2020), accompanied by rare findings of proboscideans, artiodactyls, perissodactyls, and carnivores (Kowalski and Kubiak 1993; Van der Made and Kowalski 1996; Nadachowski 2001; Kowalski and Rzebiak-Kowalska 2002; Marciszak and Lipecki 2020). The second of the Polish sites, the Turów mine, yielded just one single shell fragment of Testudinoidea indet. (Brachaniec et al. 2022).

A review of Miocene crocodylians from Central Paratethys

Fossil remains of crocodylians of the Miocene age are numerous in Europe, but usually come from the Western Paratethys. This is the case of, for example, fossils from the North Alpine Foreland Basin in Bavaria that are attributed to *Diplocynodon* sp. and dated as Burdigalian (Böhme 2003, 2010). From the same basin, a partial maxilla originally described as *Gavialosuchus* cf. *gaudensis* (Rossmann et al. 1999), currently interpreted as Tomistominae indet. (Nicholl et al. 2020), is known from the Bodensee area with other putative mentions from southern Germany (Sach 2016). The same applies to the more northerly situated areas in Germany (e.g., Mainzer Becken or Hambach mine in North Rhine-Westphalia), where findings of *Diplocynodon* and/or other (often unidentified) crocodylians are abundant (Ludwig 1877; Schleich 1988; Mörs et al. 2000; Böhme and Ilg 2003; Macaluso et al. 2022).

On the contrary, the crocodylian fossil record from the Central Paratethys is scarcer. In intramontane and back-arc basins of the Central Paratethys, crocodylian remains described as *Crocodylia* indet. (cf. *Diplocynodon* sp.) were found in the fossil site of Máriahalom (Mány-Zsambék Basin) in Hungary, the age of which, long considered as Chattian (late Oligocene), has been recently identified as

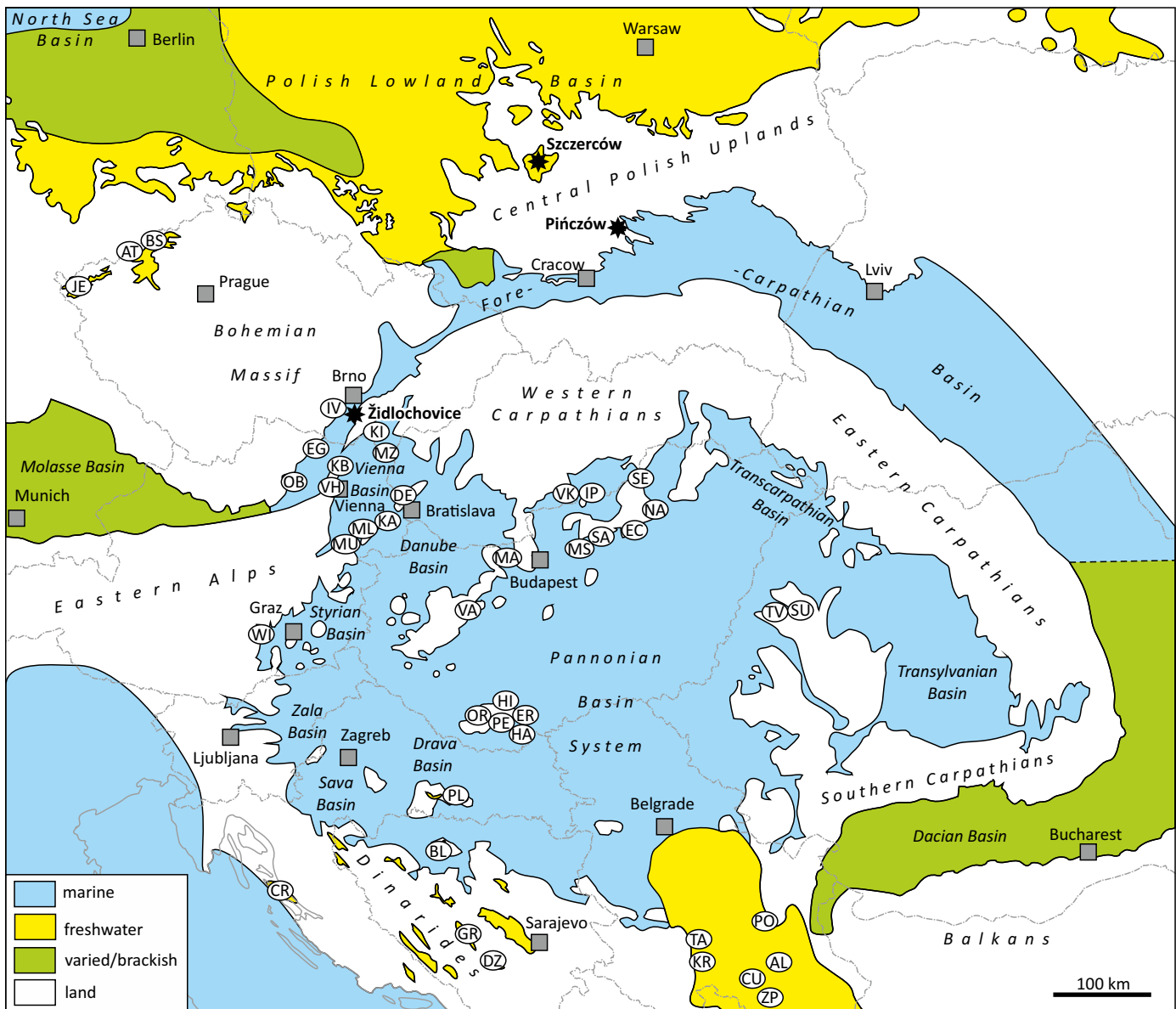


Fig. 2. Prevailing environments of the main palaeogeographic units of the Central Paratethys and adjoining areas in the Early–Middle Miocene time. Crocodylian-bearing sites marked with abbreviations, location of the discussed findings marked with asterisks. Abbreviations: AL, Aleksinac, Serbia; AT, Ahníkov and Tušimice, Czechia; BL, Banja Luka, Bosnia and Herzegovina; BS, Břešťany and Skyřice, Czechia; CR, Crmika beach, Croatia; CU, Čučale, Serbia; DE, Devínska Nová Ves, Slovakia; DZ, Džepi, Bosnia and Herzegovina; EC, Egercsehi, Hungary; EG, Eggenburg, Austria; ER, Erdősmecke, Hungary; GR, Gračanica, Bosnia and Herzegovina; HA, Himesháza, Hungary; HI, Hidas, Hungary; IP, Ipolytarnóc, Hungary; IV, Ivančice, Czechia; JE, Jehličná near Sokolov, Czechia; KA, Kaisersteinbruch, Austria; KB, Korneuburg Basin, Austria; KI, Kienberg, Czechia; KR, Kraljevo, Serbia; MA, Máriahalom, Hungary; ML, Mannersdorf am Leithagebirge, Austria; MS, Mátraszőlös, Hungary; MU, Müllendorf, Austria; MZ, Maustrenk, Austria; NA, Nagyvisnyó, Hungary; OB, Obritzberg, Austria; OR, Orfű-Bános, Hungary; PE, Pécs-Danitzpuszta and Pécsvárad, Hungary; PL, Poljanska, Croatia; PO, Popovac, Serbia; SA, Sámsonháza, Hungary; SE, Serényfalva, Hungary; SU, Subpiatră, Romania; TA, Tavnik, Serbia; TV, Vârciorog and Tășad, Romania; VA, Várpalota, Hungary; VH, Vienna, Austria; VK, Veľký Krtíš, Slovakia; WI, Wies, Austria; ZP, Žitni Potok, Serbia. Compiled after: Rzehak (1912); Kordos and Solt (1984); Młynarski (1984); Zapfe (1984, 1989); Kordos (1985); Böhme and Ilg (2003); Stefanović and Mijović (2004); Bulić and Jurišić-Poljšak (2009); Jipa and Olariu (2009); Alaburić and Marković (2010); Kováčová et al. (2011); Krstić et al. (2012); Gibbard and Lewin (2016); Hir et al. (2016, 2024); Neubauer et al. (2016); Wysocka et al. (2016); Sant et al. (2018); Luján et al. (2019); Vasilyan (2020); Chroust et al. (2021); Botfalvai et al. (2023); Hajek-Tadesse et al. (2023); Weydt et al. (2023); Březina et al. (2024); Sebe et al. (2024); and Harzhauser et al. (2025).

presumably Aquitanian (Kocsis et al. 2023). Slightly younger findings of Burdigalian age are known from the Ipolytarnóc area (remains identified as *Gavialis* sp. and crocodylian tracks) and Serényfalva (identified as *Crocodylus* indet.) in northern Hungary (Kordos and Solt 1984; Kordos et al.

2021). Younger remains (Ottungian; see Fig. 4) are known from Baňa Dolina Mine in Veľký Krtíš in Slovakia; teeth and an osteoderm from this locality were described by Čerňanský et al. (2012) as *Crocodyla* indet.; in the nearby site of Egercsehi in northern Hungary, remains described as

Crocodylus indet. of the same age were found (Kordos and Solt 1984). In the locality of Erdősmecke, near the Mecsek Mountains in southern Hungary, remains identified as belonging to the genus *Crocodylus* were recorded (Kordos and Solt 1984; Kordos 1985); however, their age is uncertain, ranging from Ottnangian to Karpatian (see Fig. 4).

Isolated teeth and one angular bone are described from the Korneuburg Basin in Austria and dated as Karpatian (Böhme 2002). Of Karpatian–Badenian age are findings of *Diplocynodon* sp. from Orfű-Bános near the Mecsek Mountains (Kordos and Solt 1984; Sebe et al. 2024). Zapfe (1984) reported teeth of *Crocodylus* sp. and *Diplocynodon* sp. from the upper lower Badenian of Kaisersteinbruch, Mannersdorf am Leithagebirge, and Müllendorf (Austria) in the southern part of the Vienna Basin. Of the same age is the tooth of *Crocodylus* sp. from Maustrenk near Zisterdorf, Austria, in the northern part of the Vienna Basin (Zapfe 1984). The tooth of *Crocodylia* indet. from Kienberg near Mikulov (Czechia) in the Moravian part of Vienna Basin (Březina et al. 2024) is of the latest early to earliest late Badenian age. *Diplocynodon ungeri* dated to the MN5 mammal unit (Badenian), is known from the Styrian Basin near Wies, Austria (Martin and Gross 2011). The sites of Nagyvisnyó (lower Badenian; Kordos and Solt 1984) and Sámsonháza (middle Badenian; Hír et al. 2016) are situated in northern Hungary, both of which yield crocodylian remains. Of late Badenian age are the localities of Mátraszőlős in northern Hungary (Kordos and Solt 1984), Várpalota near Székesfehérvár (Kordos and Solt 1984; Kordos 1985), and Hidas near the Mecsek Mountains, all of which yield *Diplocynodon* sp. (Kordos 1985; Hír et al. 2024). The western Romanian site of Subpiatră 2/1 yields *Diplocynodon* sp. of middle-to-late Badenian age (Venczel 2007; Hír et al. 2016). Isolated teeth tentatively ascribed to *Gavialosuchus* sp. are also known from the upper Badenian of Devínska Nová Ves in Slovakia (Schlögl and Holec 2004).

Along the southern margin of the Central Paratethys, crocodylian remains are known from the Lower and Middle Miocene of Serbia, predominantly from lacustrine deposits in the south of the country. Remains of *Crocodylia* indet. are known from the Lower Miocene of Aleksinac and Kraljevo (Jovanović et al. 2002; Vasilyan 2020), while *Crocodylus* sp. is known from the upper Lower Miocene of Čučale (Stefanović and Mijović 2004). Other crocodylian-bearing localities are the Middle Miocene site of Žitni Potok (Jovanović et al. 2002; Vasilyan 2020), the middle Badenian site of Tavnik (Krstić et al. 2012), and the famous lower Badenian site at Popovac yielding *Gavialosuchus eggenburgensis*, *Crocodylus moraviensis*, and *Alligatorinae* indet. (Jovanović et al. 2002; Alaburić and Marković 2010; Sant et al. 2018; Vasilyan 2020).

In the south-western margins of the Central Paratethys, the Early Miocene crocodylians are known from Crnika beach on the Croatian island of Pag (Bulić and Jurišić-Polšak 2009) and from Poljanska in the North Croatian Basin (Hajek-Tadesse et al. 2023). From Bosnia and Herzegovina three occurrences are known: Banja Luka of Early-

to-Middle Miocene age, the early Badenian Bugojno palaeolake in Gračanica with presumed *Diplocynodon* sp. (Vasilyan 2020), and the site of Džepi in the Prozor Basin also of early Badenian age (Neubauer et al. 2016).

The youngest certain occurrences of crocodylians in the coeval deposits of the intramontane and back-arc basins of the Central Paratethys are findings of *Diplocynodon* sp. are of the Sarmatian age. The findings of *Diplocynodon* sp. from the early Sarmatian are known from the Tășad, Vârciorog, and Subpiatră 2/2 sites in Romania (Venczel 2007; Hír et al. 2016) while the most recent report of the mid-Sarmatian osteoderm of *Crocodylia* indet. (? *Diplocynodon* sp.) from Hernals district of Vienna appears to be the latest known occurrence of the crocodylian in Central Paratethys (Harzhauser et al. 2025).

Even younger known crocodylian-bearing deposits in the Central Paratethys seem to be sands and gravels of the Pannonian Kálla Member exposed in the Pécs-Danitzpuszta, Pécsvárad, and Himesháza sand-pits in eastern Mecsek Mountains, but remains of *Diplocynodon* sp. in this site were most probably re-deposited from older Miocene deposits as a result of erosion following the Late Miocene uplift of the Mecsek Mountains (Botfalvai et al. 2023; Sebe et al. 2024). The putative younger occurrence of cf. *Diplocynodon* sp. from the lower Pontian of Götzendorf an der Leitha in Austria (Zapfe 1989) remains unconfirmed (Harzhauser et al. 2025).

Crocodylians are even scarcer in the Fore-Carpathian Basin, however, some particularly interesting findings have been recorded from this region. The Lower Miocene site of Eggenburg in Austria yielded the holotype skull of *Gavialosuchus eggenburgensis* Toulou & Kail, 1885. Another occurrence of a crocodylian is known from the Ottnangian, nearby Ivančice, in Czechia, where remains of the *Diplocynodon* sp., were found (Rzehak 1912). The Polish crocodylian fossil record in the Fore-Carpathian Basin has been so far limited only to a single tooth attributed to *Tomistoma* sp. from Pińczów (Radwański 1974, 1977, 1985, 2015; Antunes in Młynarski 1984).

The known record of crocodylian remains from the more distant foreland of Central Paratethys is limited practically to its western region, the NW part of the Bohemian Massif. In this area, *Diplocynodon ratelii* Pomel, 1847, is known from the Burdigalian (MN3 Mammal Zone) of Most Basin (Luján et al. 2019). The older records from this area come from the vicinity of Most—for example, from Břešťany (Liebus 1936) or Skyřice (Laube 1910; Luján et al. 2019), whereas modern findings were reported from Ahník (Chroust et al. 2021) near Kadaň. Further to the south, crocodylian remains were reported from Jehličná of the Sokolov Basin (Redlich 1902; Luján et al. 2019).

Geological setting

Židlochovice.—This locality is situated in the southwestern part of Fore-Carpathian Basin (Figs. 2 and 3A) in close prox-

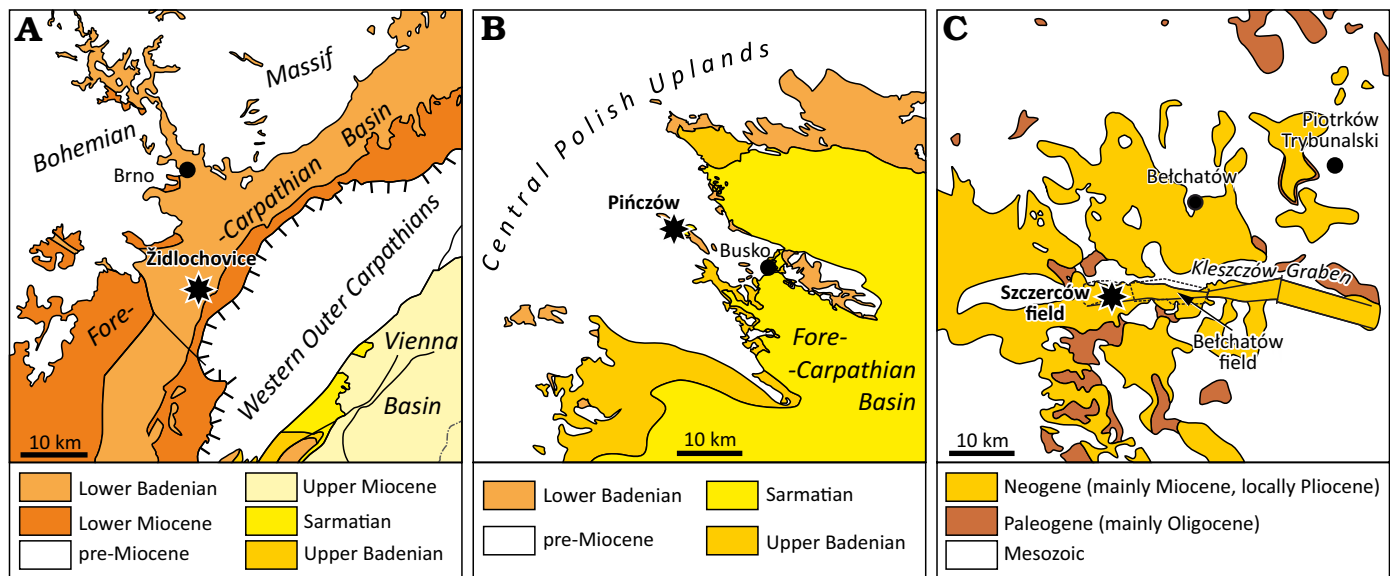


Fig. 3. Simplified geologic maps of the discussed localities. **A.** Židlochovice. **B.** Pińczów. **C.** Szczerców. Compiled after Buday (1963), Danel and Gałązka (2007), Haisig (2011), and Górka (2019).

imity to the Western Outer Carpathian nappe. This locality is represented by lower Badenian clays, sands and limestones, which build the northwestern slope of Výchon Hill. It is one of the richest palaeontological localities in Moravia and has consequently attracted palaeontologists and geologists since the 19th century (e.g., Hörnes and Reuss 1870; Rzehak 1880; Procházka 1893). An illustrative section (up to 30 m thick) was exposed by a large former brickyard and became the faciostratotype of the lower Badenian (i.e., Moravian, Upper Lagenidae Zone; see Cicha 1978). This fossil site was later comprehensively studied with the support of data from two boreholes (altogether 21 m thick section) and the section was biostratigraphically correlated with the NN5 Zone, 14.9 to 13.9 Ma (Doláková et al. 2014; see Fig. 4).

The lower Badenian sedimentary sequence of Židlochovice is characteristic by the dominance of pelitic sedimentation of unlaminated calcareous clays (“tegel”), which in the upper part alternate with calcareous sands to sandstones and limestones with dominance of red algae and bryozoans (Cicha 1978; Doláková et al. 2014). The rich flora of red algae and nanoplankton and the rich fauna of foraminifera, radiolarians, bryozoans, ostracods, mollusks, sea urchins, corals, bony fish, sharks and cetaceans indicate a marine, warm to subtropical palaeoenvironment shallowing-upwards from epibathyal/circalittoral (up to 250 m) to shallow (up to 20 m) infralittoral (Brzobohatý 1997; Seko et al. 2012; Doláková et al. 2014).

The original position of the tooth in the section is unknown, however residual algal limestone at the base of the crown of the studied crocodylian tooth suggests that it comes from the upper parts of the section, dominated by red-algal limestones. The limestones indicate shallow marine environment with seagrass meadows representing a shallowing and slight cooling event coeval with the regressive phase of

TB 2.4 cycle, dated at 14.2 to 13.6 Ma (Doláková et al. 2014; see also Fig. 4).

Pińczów.—The area is located in the northern marginal zone of the Fore-Carpathian Basin, and the fossiliferous site is situated in one of the quarries (Quarry no. 2; Młynarski 1984) located in the northernmost part of the town of Pińczów (Figs. 2 and 3B), formerly called Nowa Wieś. This quarry has been the source of stone since the Middle Ages but finally became abandoned in the early 2000s.

The whole section is dominated by red-algal (traditionally referred to as “lithothamnian”) organodetrital limestones, so-called “Pińczów limestones”, lithologically similar, e.g., to the Badenian “Leithakalk” in the Vienna Basin (Studencki 1979). The lower part of the section is composed of very-thick bedded, fine-grained limestones passing into coarser variety in the upper part. Frequent accumulations of rhodoliths and 1–2 local horizons of algal-bryozoan marls also occur. The thickness of the exposed section is approximately 15 m (Drewniak 1994; Studencki 1988a) but the total thickness of the Pińczów limestones in the area reaches up to 25 metres (Studencki 1988a).

The site has been known for years for its ubiquitous and rich fossils. The faunal assemblage comprises numerous invertebrate remains: corals, polychaetes, brachiopods, mollusks, crustaceans, and echinoderms (Kowalewski 1930, 1958; Radwański 1969, 1977, 2015; Förster 1979, Studencka and Studencki 1988; Studencki 1988b; Mączyńska 1993). Other remarkable findings from Pińczów limestones include vertebrate remains, such as those of chondrichthyans and teleost fish (Kowalewski 1930; Jerzmańska 1958; Pawłowska 1960; Radwański 1965), as well as marine mammals, whales (Czyżewska and Ryziewicz 1976; Czyżewska 1988; Czyżewska and Radwański 1991) and sirenians (Radwański 2015). The only reptile representative is a single crocodylian tooth reported by Radwański (1974, 1977, 1985,

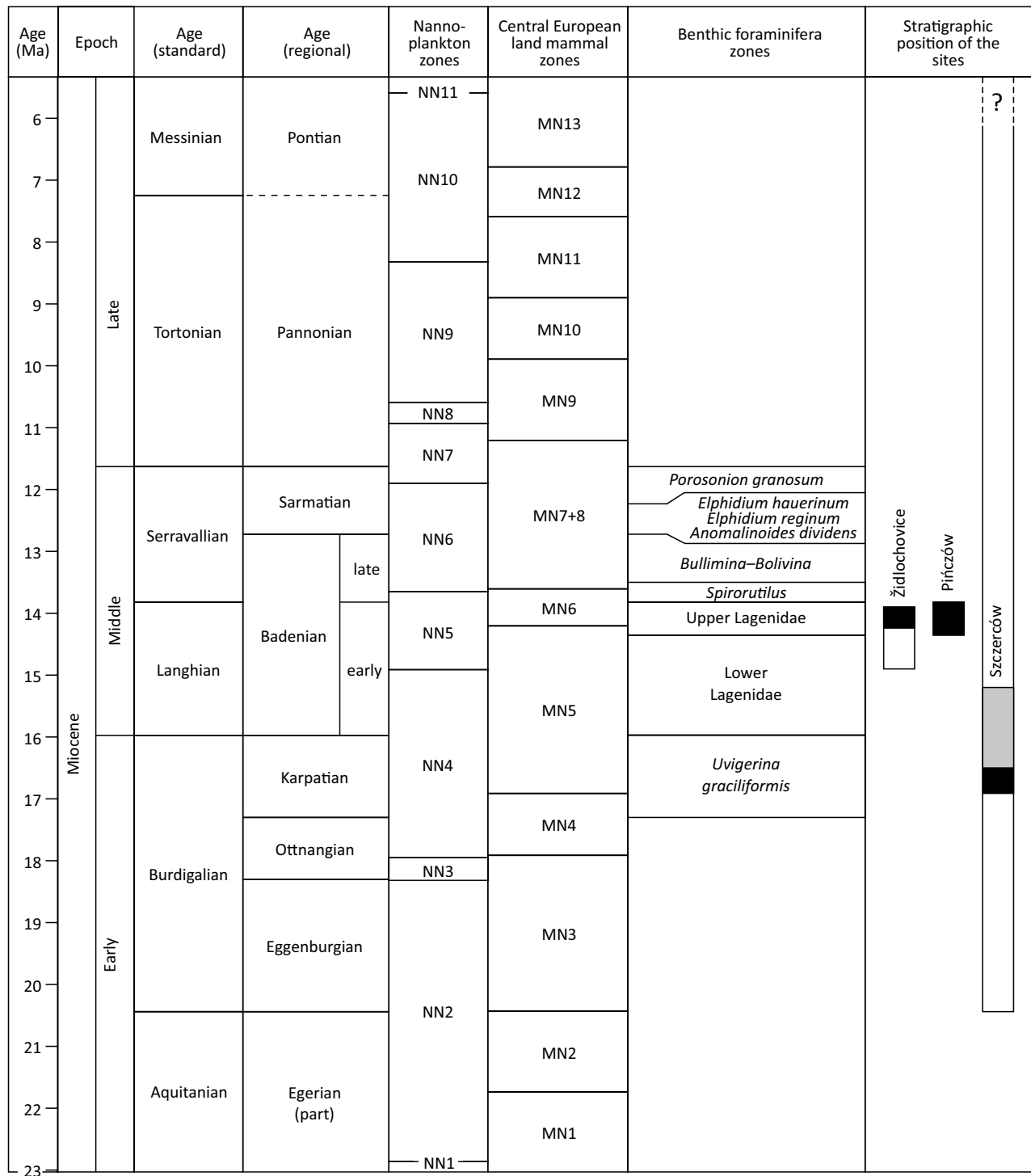


Fig. 4. Stratigraphic chart of the Miocene of the Central Paratethys. The stratigraphic position of the sites discussed in the text is indicated on the right-hand side. Black bands denote the most certain age of the material described in the present study; grey band denotes possible age; white bands correspond to the total stratigraphic range recorded in the sites. Compiled after: Harzhauser and Piller 2004; Kováč et al. 2005, 2007, 2018; Piller et al. 2007; Hohenegger et al. 2009, 2014; Pezelj et al. 2013; Doláková et al. 2014; Neubauer et al. 2015; Luján et al. 2019; Březina et al. 2021; and Ivanov 2022.

2015) and assigned to the genus *Tomistoma* (Antunes in Młynarski 1984). However, aside from a very basic description by Antunes in Młynarski (1984), this tooth has never been fully described in detail nor illustrated.

The composition of the marine fauna indicates a warm, subtropical shallow marine environment of oceanic salin-

ity (Pawłowska 1960; Radwański 1965, 1977, 1985, 2015; Bałuk and Radwański 1977; Czyżewska 1988). The age of the Pińczów limestones and coeval deposits in the Polish part of Fore-Carpathian Basin has been considered for decades as early Tortonian (e.g., Kowalewski 1930, 1958; Czarnocki 1933; Radwański 1969). In the early 1970s it was

confirmed that the exact age of the Pińczów limestones is early Badenian (see Fig. 4; Radwański 1973; Martini 1977; Studencki 1979; Górka 2019).

Further studies provided a more detailed stratigraphic position of the Pińczów limestones, they belong to the Upper Lagenidae Zone, i.e., the upper part of the lower Badenian (Studencki 1988a; Studencka 1999; Peryt 2013), and to the NN 5 nannoplankton zone (Martini 1977).

The long-lasting confusion regarding the determination of the age of the discussed deposits resulted in numerous inaccuracies. One of such examples is the case of the crocodylian tooth mentioned above, the age of which has been incorrectly attributed to as “Upper Miocene–Lower Tortonian” by Młynarski (1984). The latter author cited the outdated paper of Radwański (1965) literally, instead of applying the updated age affinity, i.e., early Badenian of the Middle Miocene.

Szczerców.—The site is located in the western mining field (i.e., Szczerców field) of the large lignite mine of Bełchatów, situated in central Poland (Figs. 2 and 3C). The Bełchatów mine opened in the 1970s and since then the thick succession of Miocene deposits including lignite seams has been intensively mined. The larger eastern field (Bełchatów field) is currently being filled with dump deposits, but through the last half of the century its deposits have been intensively palaeontologically studied (for a list of papers see Fostowicz-Freluk et al. 2012; Worobiec and Worobiec 2019; Kovalchuk et al. 2020). To the contrary, the Szczerców field has been operative for a shorter period of time (it has been operating since 1998 and the mining of lignite started in 2009), but its Miocene deposits have not been so intensively studied palaeontologically as the Bełchatów field. Because there is a large similarity in the depositional history between these two fields and the Szczerców field has not been studied as extensively, the geological features of the Bełchatów field could be treated as general benchmarks (see: Wagner and Matl 2007).

The lignite deposits of the Bełchatów mine belong to a thick Miocene succession reaching up to 600 m in thickness that was deposited in a ~30 km-long section of Kleszczów Graben, which in turn is ca. 80 km long and up to 3 km wide (Gotowała and Hałuszczak 2002). The Miocene succession lies on Upper Jurassic, Upper Cretaceous, and, locally, Paleogene rocks (Bielowicz and Morga 2021).

The Neogene succession, best recognised in the Bełchatów field, is traditionally divided in four complexes: (i) subcoal, (ii) coal, (iii) clayey-coal, and (iv) clayey-sandy.

The lowermost (i.e., subcoal) complex lies directly on an older substrate and comprises sands with clay and mud intercalations with thin layers of lignite. The overall thickness of the subcoal complex exceeds 100 m and its age is referred to as Eggenburgian (Szyrkiewicz 2000; Worobiec and Worobiec 2022).

The coal complex, with a total thickness exceeding 100 m, is divided into two subcomplexes: non-productive and productive (Pawelec and Bielowicz 2016). The former comprises sands with thin lignite seams. The productive subcom-

plex is dominated by thick lignite seams, where the thickest (the main seam, D) reaches 40–60 m (Szyrkiewicz 2000). In the upper part of the main seam a thick layer of lacustrine chalk (lacustrine limestone) occurs. The rich vertebrate faunal assemblage (referred to as the Beł-C; Stuchlik et al. 1990; Szyrkiewicz 2000) was collected there and determined to belong to the MN 4 Mammal Zone (Kowalski 1993b, 1994; Kovalchuk et al. 2020). Above the main seam there are thinner seams, C (the older) and B (the younger, divided into B1 and B2). Below the seam C a thin tuffite layer (so called paratonstein) of FT (i.e., fissure track) age 18.1 ± 1.7 Ma occurs (Burchart et al. 1988). The age of the coal complex is defined as Ottnangian to Karpatian (Worobiec and Worobiec 2022).

Above the seam B, in the topmost part of the coal complex, there is a thick layer of lacustrine chalk where vertebrate fauna was recorded. This faunal assemblage (Beł-B) represents the MN 5 Mammal Zone (Kowalski 1993b; Kovalchuk et al. 2020).

The coal complex is separated from the clayey-coal complex by the distinct erosional surface (Stuchlik et al. 1990; Szyrkiewicz 2000). The clayey-coal complex comprises grey-to-greenish clays with thin lignite intercalations, and layers of muds, sand and even gravels. In its lower part a relatively thick lignite seam (seam A) occurs, with tuffite (paratonstein) layer in its top. The fission-track age of paratonstein is 16.5 ± 1.3 Ma (Burchart et al. 1988). In the upper part of the complex some thin lignite seams and layers of lacustrine chalk were recorded. The occurring vertebrates (Beł-A) indicate an MN 9 Mammal Zone (Kowalski 1993a). The age of the clayey-coal complex ranges from late Karpatian to Sarmatian, presumably even Pannonian (Szyrkiewicz 2000; Worobiec et al. 2012).

The youngest complex, i.e., clayey-sandy, contains whitish and grey gravels, sands and greenish clays with a total thickness reaching up to a few dozens of metres and with its erosional boundary at the top (Szyrkiewicz 2000). The age of that complex is referred to as Pannonian to ?Pliocene (Worobiec et al. 2012).

The succession in the Szczerców field shows a high level of similarity to the Bełchatów field, however there are some significant differences, as presented below.

The characteristics of the subcoal complex corresponds to those of the Bełchatów field—it is composed of sands with two thin layers of lignite and reaches up to 100 m. The age of the complex, by analogy to the Bełchatów field, is presumably Eggenburgian (Wagner and Matl 2007; Pawelec and Bielowicz 2016).

The coal complex is composed of two subcomplexes. The lower, non-productive subcomplex reaches up to 100 m and is composed of fine-grained carbonaceous sands and thin lignite seams. The productive subcomplex is built of one to two thick lignite seams and its thickness ranges from a few metres in the western part up to 140 m in the east (Wagner and Matl 2007; Pawelec and Bielowicz 2016). This subcomplex is more compact when compared to the Bełchatów field and seams B and C known from the Bełchatów field do not

appear to have comparable seams in the Szczerców field (see Wagner and Matl 2007: fig. 1). However, the age of the Szczerców coal complex is Otnagian to Karpatian similarly to Bełchatów field (Wagner and Matl 2007).

Clayey-coal complex is built of clays (locally carbonaceous) with sandy intercalations and layers of xylite coals correlated with lignite seam A known from the Bełchatów field (Wagner and Matl 2007). The thickness of that complex reaches up to 90 m (Pawelec and Bielowicz 2016) and its age by lithostratigraphic analogy to the Bełchatów field should be referred to as Karpatian to Sarmatian, presumably even Pannonian (Wagner and Matl 2007).

The Szczerców clay-sand complex is represented by greenish clays, silts and its maximum thickness reaches 80 m (Pawelec and Bielowicz 2016). The supposed age of the complex is Pannonian to ?Pliocene.

The main difference between the two mining fields is the high percentage of lacustrine chalk deposits in the Szczerców field compared to Bełchatów. The thickness of lacustrine chalk lithosomes in Szczerców reaches up to 90 m and two main levels were recognised there (Wagner and Matl 2007). The older level (II) occurs in the western part of the field in the upper part of the subcoal complex and lower part of the coal complex. It represents MN 4 Mammal Zone (ca. late Otnagian to early Karpatian). The younger level (I) occupies the upper part of the coal complex and the lower part of the clayey-coal complex. Its age is determined as MN 5–6 mammal zones (late Karpatian to early Badenian). Locally, an additional level (Ia) occurs, belonging to MN 7–8 mammal zones, mainly of Sarmatian age (Wagner and Matl 2007).

The particular lacustrine chalk bed, bearing a crocodylian osteoderm, occurred in the uppermost part of the coal complex, thus it represents the younger level of lacustrine chalk (I). We found there only scarce plant material of *Magnolia* cf. *burseracea* (Menzel, 1913) Mai, 1975, *Umbelliferopsis molassicus* Gregor, 1982, and unidentifiable wood fragments that are not sufficiently informative for environmental reconstruction. However, more information was obtained from the lacustrine chalk from the lower part of the clayey-coal complex, which is slightly younger than the investigated crocodylian specimen. Aside from small fragments of wood and leaves (presumably of Cyperaceae), a relatively rich assemblage of carpological remains was found (ca. 300 specimens representing 14 taxa stored at the Polish Academy of Sciences, Museum of the Earth in Warsaw, Poland). All identified taxa are representatives of different types of wetlands vegetation. The only tree typical of the Cenozoic swamp forests that was recorded is *Nyssa disseminata* (Ludwig, 1857) Kirchheimer, 1937 (Mai 2000). Remaining woody taxa can be assigned to swamp forests understory or shrub bogs including *Frangula solitaria* Gregor, 1977, *Lyonia danica* Friis, 1985, *Myrica ceriferiformoides* Bůžek & Holý, 1964, and *M. burseracea* (Mai 2000; Kowalski 2017). A few herbaceous plants typical of reeds have also been identified, including *Cladium oligovasculare* Mai in Knobloch, 1978, *Dulichium vespiforme* C. Reid & E.M. Reid, 1908, *Carex* sp.,

Umbelliferopsis molassicus (see Gregor 1982; Mai 2000). Another herbaceous plant from Szczerców, *Decodon gibbosus* (E.M. Reid, 1920) Nikitin, 1929, could occur in a wide range of non-arborescent types of wetlands (Kvaček and Sakala 1999). Macrophytes are represented only by *Potamogeton* sp.; this floating leaved genus occurs today in various aquatic habitats (Cook et al. 1974), but in the clayey-coal complex in Szczerców it most likely indicates the presence of open (full-sun), stagnant water (pond or lake) or a slow flowing river. The striking feature of this sample is the apparent lack of *Taxodium* and *Glyptostrobus*, two of the most characteristic European Cenozoic swamp forest trees (LePage 2007; Kunzmann et al. 2009), documented also from the neighbouring Bełchatów field (Stuchlik et al. 1990). This indicates that swamp forests may not have been fully developed in Szczerców in the studied time and area. Considering the lithological characteristics of the deposits, the presumed structure and height of vegetation may result from specific water chemistry. Comparable conditions can be observed in modern minerotrophic peatlands (Bedford and Godwin 2003; Mitsch and Gosselink 2015) often populated by narrowly adapted ecological specialists, calciphilic species in particular. However, most species identified are ecological generalists, typical of Neogene coal-producing plant communities. On the other hand, we cannot exclude that some (edaphic) specialists can hide among the few unidentified disseminules (e.g., *Potamogeton* sp.). Climatic conditions cannot be precisely estimated based on the few fossil taxa found in the samples, because of the very broad preferences of their closest living relatives.

According to Wagner and Matl (2007), who dated the different stratigraphic levels in Szczerców using freshwater malacofauna assemblages as the biostratigraphic indicators, the level that yields the crocodylian osteoderm belongs to MN 5–6 Mammal Zone (upper Karpatian–lower Badenian, i.e., upper Burdigalian–Langhian standard stages). However, because the fission-track age of paratonstein above the lignite seam A in the Bełchatów field is 16.5 ± 1.3 Ma, the age of the discussed lacustrine chalk should be also considered as Karpatian. It is younger than ca. 16.8 Ma (i.e. MN 4/MN 5 transition, see Fig. 4) but likely not younger than 16.5 Ma (black band in Fig. 4). Nevertheless, considering the confidence interval (± 1.3 Myr), it cannot be definitely excluded that the described crocodylian osteoderm may be significantly younger, even as young as 15.2 Ma, and therefore of early Badenian age (marked with a grey band in Fig. 4).

Material and methods

Palaeozoological material.—The studied material comprises two isolated teeth and one dorsal osteoderm.

The studied tooth from Židlochovice comes from the collection of Anthon Rzehak (1855–1923), but he never mentioned it in any of his works, despite correctly recognizing it as a crocodile tooth in his handwritten label. The specimen is

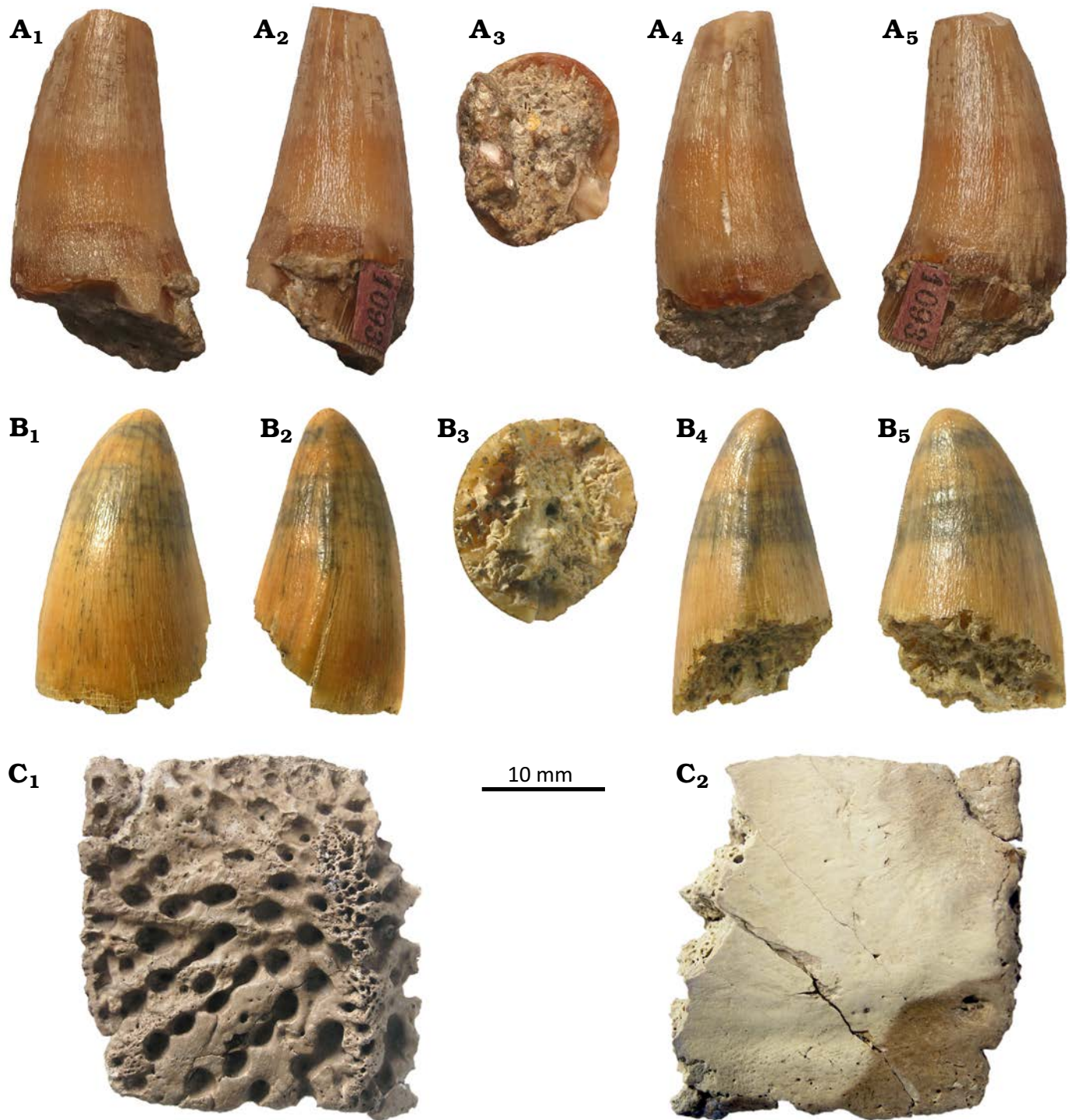


Fig. 5. The discussed remains of *Crocodylia* indet. from the Miocene of Fore-Carpathian Basin and its foreland. **A.** ÚGV E1093, an isolated tooth from the lower Badenian (Langhian) of Židlochovice, Czechia; lingual (A₁), mesial/distal (A₂), basal (A₃), distal/mesial (A₄), and labial (A₅) views. **B.** MWGUW/ZI/113/067, an isolated tooth from the lower Badenian (Langhian) of Pińczów, Poland (previously referred to as *Tomistoma* sp.); labial (B₁), mesial/distal (B₂), basal (B₃), distal/mesial (B₄), and lingual (B₅) views. **C.** MWGUW/ZI/113/064, a dorsal osteoderm from Karpatian-?lower Badenian (Burdigalian-?Langhian) of Szczerców mining field, Poland, the world's northernmost recorded Neogene crocodylian; dorsal (C₁) and ventral (C₂) views.

housed in the Paleontological collection of the Department of Geological Sciences, Faculty of Science, Masaryk University, Brno under inventory number ÚGV E1093.

The tooth from Pińczów was collected by Prof. Andrzej Radwański (1934–2016) in the 1960s–1970s and is housed

at the Museum of the Faculty of Geology, University of Warsaw (Stanisław Józef Thugutt Geological Museum) under inventory number MWGUW/ZI/113/067. The specimen was reported by Radwański (1974, 1977, 1985, 2015), and by Antunes in Młynarski (1984).

Table 1. The fossil material of crocodylians used for comparisons.

Species	Number	Material	Age	Locality	Reference
<i>Diplocynodon ratelii</i>	MNHN Ar888	teeth	Early Miocene	Artenay, France	unpublished
<i>Diplocynodon hantoniensis</i>	NHMUK OR 25166	teeth	late Eocene	Hordwell Cliff, UK	Rio et al. 2020: fig. 13A–C
<i>Diplocynodon hantoniensis</i>	NHMUK OR 30317	tooth	late Eocene	Hordwell Cliff, UK	Rio et al. 2020: fig. 13D
<i>Diplocynodon hantoniensis</i>	NHMUK OR 46434	osteoderm	late Eocene	Hordwell Cliff, UK	Rio et al. 2020: fig. 20B
<i>Diplocynodon hantoniensis</i>	NHMUK R.5214	osteoderm	late Eocene	Hordwell Cliff, UK	Rio et al. 2020: fig. 20C
<i>Diplocynodon cf. ratelii</i>	NMP Pv 11650–62	teeth	Early Miocene	Ahnikov, Czechia	Chroust et al. 2021: fig. 6
<i>Diplocynodon cf. ratelii</i>	NMP Pv 11663–11668	osteoderms	Early Miocene	Ahnikov, Czechia	Chroust et al. 2021: fig. 7
<i>Gavialosuchus eggenburgensis</i>	KME F/2368	tooth	Early Miocene	Eggenburg, Austria	unpublished
<i>Gavialosuchus eggenburgensis</i>	KME F/3707	tooth	Early Miocene	Eggenburg, Austria	unpublished
<i>Tomistoma calaritanum</i>	MDLCA 148	teeth	Late Miocene	Mirrionis (Cagliari), Sardinia, Italy	Nicholl et al. 2020: fig. 5C
<i>Tomistoma lusitanica</i>	LNEG 4783	teeth	Early Miocene	Lisbon, Portugal	unpublished
<i>Tomistoma lusitanica</i>	LNEG 4794	teeth	Early Miocene	Lisbon, Portugal	unpublished
<i>Tomistoma lusitanica</i>	LNEG 8709.19	teeth	Early Miocene	Lisbon, Portugal	unpublished
<i>Melitosaurus champsoides</i>	NHMUK PV OR41151	snout with teeth	Early Miocene	Gozo Island, Malta	Nicholl et al. 2020: fig. 3
<i>Tomistoma gaudense</i>	NMNH-T11228	teeth	Early Miocene	Gozo Island, Malta	Nicholl et al. 2020: fig. 5B
<i>Tomistoma calaritanum</i>	MDLCA 14401	osteoderms	Late Miocene	Piazza d'Armi (Cagliari), Sardinia, Italy	Zoboli et al. 2019: fig. 8

The single dorsal osteoderm from the Szczerców mining field was collected by our prospecting team (MG, RK, SL-T) in June 2023 during fieldwork in the Bełchatów lignite mine and is kept at the Museum of the Faculty of Geology, University of Warsaw under inventory number MWGUW/ZI/113/064. The coordinates for the point where the osteoderm was collected are 51°14'00.0"N, 19°10'07.6"E, 61.14 m a.s.l.

The specimens from Pińczów and Židlochovice were supposedly embedded in a limestone matrix, but the exact method of their extraction is unknown (they were most probably extracted mechanically). The specimen from Szczerców was embedded in a lacustrine chalk sample that was picked up from the surface. The osteoderm was partially broken because of the deformation of the surrounding soft matrix. After the sample was softened with water, the osteoderm was manually extracted and glued back.

The fossil material of crocodylians that was used for comparisons is presented in Table 1.

Palaeobotanical material.—For further examination two samples of lacustrine chalk were taken from Szczerców: (i) sample 1b-2023 from the topmost part of the coal complex where the crocodylian remains were found; (ii) sample 1b-2022 from lower part of the clayey-coal complex. The matrix of the samples was dissolved using 8% acetic acid. The residuum was washed on a sieve of a mesh 0.5 mm, then dried, and examined with the use of a stereomicroscope to extract fossil plant remains. The collection of fossil plants is stored at the Polish Academy of Sciences, Museum of the Earth in Warsaw, Poland, under inventory numbers MZ VII/160/5–7, 10, 12–22.

Systematic palaeontology

Order Crocodylia Gmelin, 1789

Crocodylia indet.

Fig. 5.

Material.—ÚGV E1093, tooth from Židlochovice, Czechia, lower Badenian. MWGUW/ZI/113/067, tooth from Pińczów, Poland, lower Badenian. MWGUW/ZI/113/064, osteoderm from Szczerców, Poland, Karpatian–?lower Badenian.

Description.—**Teeth:** ÚGV E1093 is conical, more slender and more lingually curved when compared to the specimen from Pińczów (MWGUW/ZI/113/067). It displays the crown portion, and the apicobasal length of the tooth is approximately 30 mm (Fig. 5A). However, the apical tip and the root are missing. The tooth is partially infilled by a matrix composed of bioclasts and sand grains. The enamel is generally smooth, containing several cracks, and similar in thickness to the Pińczów specimen. Both mesial and distal carinae are present, one of them is more distinct along the edge but disappears in the proximal part. The surface has faint and diffused longitudinal striations. Incremental bands are not as significant as in the Pińczów specimen. The tooth displays the general pattern of slender curved conical teeth, but it is impossible to determine its precise position in the jaw.

MWGUW/ZI/113/067 (Fig. 5B) is quite robust and displays only the crown portion. The apicobasal length of the tooth is approximately 25 mm. The base is partially covered with calcareous sediment. The enamel is smooth and quite thin. The tooth is conical, stout and slightly blunt. A small

lingual curvature and both mesial and distal carinae are present. The tooth itself has faint longitudinal striations and is crossed by incremental bands of grey colour. The tooth does not display the general pattern of premaxillary teeth, which are slender, more conical, and curved. Also, the globular morphotype typical for the posterior dentition of alligatoroids is not displayed either.

Osteoderm: MWG UW/ZI/113/064, a single isolated dorsal osteoderm (Fig. 5C) is partially preserved and lacks the anterior articular facet, as well as the right part of the bone, located laterally to the medial keel. The external surface is covered by subcircular pits and holes, with some degree of merging between them. The pits extend right up to the left lateral and posterior edges. The medial longitudinal keel is present, but its sagittal apex is broken. From an internal view, the surface is smooth, with small foramina, which are accumulated in the posterior edge, where the posterior articular facet is present. In the left posterolateral aspect of the interior surface, close to the edge a pit is present caused by damage of unknown origin.

Remarks.—Due to the scarcity of the preserved material (i.e., a single osteoderm and two isolated teeth), the possibility of identifying the material with precision is somewhat hindered. Detailed comparisons with remains of *Diplocynodon*, *Gavialosuchus/Tomistoma*, and *Melitosaurus* did not allow us to form a definitive opinion on the generic affiliation. Therefore, we deem the attribution to *Crocodylia* indet. as sufficient. During the Miocene, the Central Paratethys was home to only two crocodylian genera: *Diplocynodon* and *Gavialosuchus*. Whereas the dentition is generally very similar among *Crocodylia*, a few important differences have been observed. Adult *Diplocynodon* has much smaller teeth in overall size when compared to adult *Gavialosuchus*. However, the 4th and 5th maxillary and 3rd and 4th dentary teeth are enlarged in *Diplocynodon*, and the posterior 9th, 10th or 11th maxillary and 11th or 12th dentary teeth are large as well. In some specimens, teeth are quite large and robust and the crown itself can reach more than 30 mm in apico-basal length (Chroust et al. 2021; Massonne and Böhme 2022). The dental enamel in basal view seems to be generally thicker in *Gavialosuchus* or *Tomistoma* compared to *Diplocynodon*. However, in a closer look, enamel thickness is variable among the teeth. The smoothness of the enamel is typical for *Diplocynodon*, whereas teeth of *Gavialosuchus* or *Tomistoma* contain apicobasal ridges and therefore the surface is rough. When the enamel is worn, gavialoid teeth can resemble those of *Diplocynodon* (morphotype D in Venzel et al. 2023). Nevertheless, this character could be more tied to taphonomic conditions rather than phylogenetic relations (Christopher A. Brochu, personal communication 2024). The presence of longitudinal striation is more frequent in *Diplocynodon* than in *Gavialosuchus* or *Tomistoma* but this character can also be misleading. The described teeth follow the pattern observed in *Diplocynodon*; however, the sample does not include any globular teeth, which

are present in *Diplocynodon* and absent in *Gavialosuchus*, and therefore of higher diagnostic value.

A puzzling issue is the former generic assignment of the tooth MWG UW/ZI/113/067 (Fig. 5B) to *Tomistoma*. The specimen was identified by Miguel Telles Antunes (see Antunes in Młynarski 1984), after a putative mail correspondence with Andrzej Radwański. In fact, his description was not supported by any image of the specimen and the main argument for its identification as *Tomistoma* was the size of the specimen (“very big [...] but not yet a gigantic one”; Antunes in Młynarski 1984: 134). Furthermore, Antunes in Młynarski (1984: 135) noted that the tooth was “more delicate [...] than those found so far among [...] this group of reptiles” and suggested that the Pińczów specimen may represent a distinct genus from *Tomistoma* or *Gavialis*. Herein, we suggest a series of potential reasons that can explain this confusion.

Firstly, the tooth was found in marine deposits and therefore its affinity to the *Tomistoma*, which inhabited marine environments, seemed reasonable. Secondly, the Pińczów fossil site was in the past referred to as Tortonian, i.e., Late Miocene in standard (“Mediterranean”) stratigraphy. In the Late Miocene only Tomistominae and true crocodyles (*Crocodylidae*) were present in Europe (Delfino and Rossi 2013; Nicholl et al. 2020; Delfino et al. 2021; Rio and Mannion 2021). Moreover, in 1984, the presence of the genus *Crocodylus* in Late Miocene deposits of Europe was still unconfirmed. Thirdly, and we assume this as the strongest argument, Antunes had most probably no opportunity to see the original specimen, only its photographs. Unfortunately, the photographs that were most presumably presented by Andrzej Radwański to Marian Młynarski and/or Miguel Telles Antunes displayed the specimen twice of its natural size and lacked a scale bar (we have recently gained access to the relevant photographs in Andrzej Radwański’s archives). Miguel Telles Antunes most probably assumed the scale of photographs to be 1:1 and thus estimated the length of the tooth at 50 mm. This would be consistent with the phrase “very big” and Antunes’ belief that the tooth belonged to *Tomistoma*, considering the fact that adult tomistomine teeth are much larger when compared to other crocodylians of similar age and geographic origin.

There are differences also in osteoderms between gavialoids and diplocynodontines. Firstly, osteoderms are much bigger and thicker in adult *Gavialosuchus* or *Tomistoma* when compared to adult *Diplocynodon*. Dorsal osteoderms of *Diplocynodon* always have a medial keel and in gavialoids is generally absent. A similar pattern was observed in the study of *Tomistoma lusitanica* (Vianna & Moraes, 1942) (Milan Chroust, personal observation 2024). However, this is not the case of *Tomistoma calaritanum* osteoderms, in which the keel is partially present (Zoboli et al. 2019). In *Gavialosuchus* or *Tomistoma*, dorsal osteoderms are wider than longer, whereas in *Diplocynodon* are mostly wider or subquadrate, however, this requires further study. Lastly, after comparisons with *Tomistoma calaritanum* mate-

rial published in Zoboli et al. (2019), the external surface of dorsal osteoderms in *Tomistoma* generally has smooth edges without subcircular pits (see Zoboli et al. 2019: fig. 8), whereas in *Diplocynodon* subcircular pits are more present in the entire external surface, including even the edges of the osteoderm. Therefore, the described dorsal osteoderm is more consistent with the pattern observed in *Diplocynodon*. However, our sample does not include any ventral bipartite osteoderms, which occur in *Diplocynodon* but not in *Gavialosuchus*, and are of higher diagnostic value.

Therefore, all these discussed observations guardedly point to the generic assignment of the presented remains to the genus *Diplocynodon*. However, due to the scarcity of the material and lack of more diagnostic elements, we attribute the teeth and osteoderm to *Crocodylia* indet.

Discussion

The northernmost occurrence of crocodylians in the Cenozoic.—In the northern hemisphere, crocodylians currently inhabit tropical and sub-tropical zones ranging from 0–35° latitudes (Stevenson 2019). However, the northern limit of this range is reached only by alligatoroids (American and Asian alligators) and is a result of co-occurring natural conditions together with anthropogenic pressure (see below).

But how was the northernmost record changing throughout the Cenozoic era, especially during the warming periods? According to their physiology, with rising global temperatures, we can assume an expansion of the crocodylian biogeographic range to higher latitudes (Markwick 1998; Rio and Mannion 2021).

In the beginning of the Paleogene, the global distribution of crocodylians was generally similar to that of the Late Cretaceous (Markwick 1998; Puértolas-Pascual et al. 2015; Rio and Mannion 2021). The Danian (early Paleocene) records of *Borealosuchus* from Ravenscrag Formation in southern Canada occur at almost 52°N (Wu et al. 2001; Lindblad et al. 2022). Danian crocodylomorphs in Europe occurred even more northerly (see Fig. 6A and Table 2)—the range of *Thoracosaurus* in Denmark and southern Sweden exceeds 55°N (Puértolas-Pascual et al. 2015). In the Selandian (middle Paleocene), the range of North American crocodylians decreased to ca. 49°N (Wu et al. 2001; Lindblad et al. 2022) while European occurrences still exceeded 55°N in Denmark (Puértolas-Pascual et al. 2015). This changed in the Thanetian (late Paleocene) when the northern limit of crocodylians shifted to the south—the northernmost occurrence is known from Jeumont in NE France at 50°18'N (Puértolas-Pascual et al. 2015).

It is striking that from the late Paleocene to the Middle Miocene, i.e., for over 40 Myr, the northern limit of crocodylian distribution in Europe was located at approx. the present-day 51°N parallel (see Figs. 6 and 7 and Table 2). Obviously, the true value of palaeolatitude of this limit was a bit different during the Cenozoic. From ca. 60 Ma to 20 Ma,

due to the northward continental drift of central Europe, the true value of palaeolatitude was slowly increasing from ca. 42°N to 46°N and this rate markedly doubled in the Neogene (paleolatitude.org; also see van Hinsbergen et al. 2015). It can thus be estimated that the true palaeolatitude value for the Szczerców site (present-day 51°14'N) in the late Burdigalian (i.e., ca. 16.5 Ma) was approx. 47°N. Similar values can be obtained based on palaeogeographic reconstructions of the Tethyan (Mediterranean) realm and its surroundings (Ricou 1994; Perrin et al. 1998). From this point forward, the present-day coordinates are used unless clearly stated otherwise, with the understanding that the true palaeolatitude values were lower during the early stages of the Cenozoic.

This broad distribution of crocodylians was possible due to the Paleocene greenhouse climate following the Cretaceous climatic optimum with a slowly increasing mean annual temperature. This trend peaked and ended with the Paleocene–Eocene Thermal Maximum, without a significant impact on crocodylian distribution (Zachos et al. 2001, 2008; Mannion et al. 2015; Westerhold et al. 2020).

The warm climate during the early Eocene caused favourable conditions for crocodylians (Markwick 1998; Zachos et al. 2008; Mannion et al. 2015; Westerhold et al. 2020). The Ypresian (early Eocene) is the age of the northernmost recorded range limit of crocodylian distribution, remains of *Allognathosuchus* sp. were found in the Canadian Arctic, at over 78°N in Ellesmere Island, Nunavut (Dawson et al. 1976; Estes and Hutchison 1980) and at over 74°N in Banks Island, Northwest Territories (Eberle et al. 2014). The Asian record of crocodylians is known from almost 50°N, in Mongolia (Iijima et al. 2019). The northernmost Ypresian occurrence in Europe is at 51°26'N in Sheppey Island, United Kingdom (Benton and Spencer 1995).

From the Lutetian (early middle Eocene) to the Zanclean (Early Pliocene), i.e., during almost 45 Myr, Europe took the lead as the most favourable area for the northernmost distribution of crocodylians (see Figs. 6, 7 and Table 2). The northernmost record of Lutetian crocodylians is known from Geiseltal in Germany, over 51°N (Hastings and Hellmund 2017). Bartonian and Priabonian (late middle Eocene to late Eocene) occurrences of *Diplocynodon* sp. exceeding 50°N are known from Czechia (Böhme 2007; Chroust et al. 2019; see Fig. 6A and Table 2), but they are slightly surpassed by findings from southern England (Benton and Spencer 1995).

The cooling event at the transition to the Oligocene caused a decline in crocodylian diversity and distributional range, with only the genus *Diplocynodon* persisting in central Europe (Martin 2010; Mannion et al. 2015; Chroust et al. 2019; Macaluso et al. 2019; Celis et al. 2020). Other genera like *Asiatosuchus*, *Allognathosuchus*, *Hassiacosuchus*, *Boverisuchus* or sebecosuchians like *Bergisuchus* do not appear to survive the Eocene–Oligocene transition (Macaluso et al. 2019).

After this cooling event, the genus *Diplocynodon* did not change its range significantly. The 51°N parallel again served as a general northern boundary of crocodylian dis-

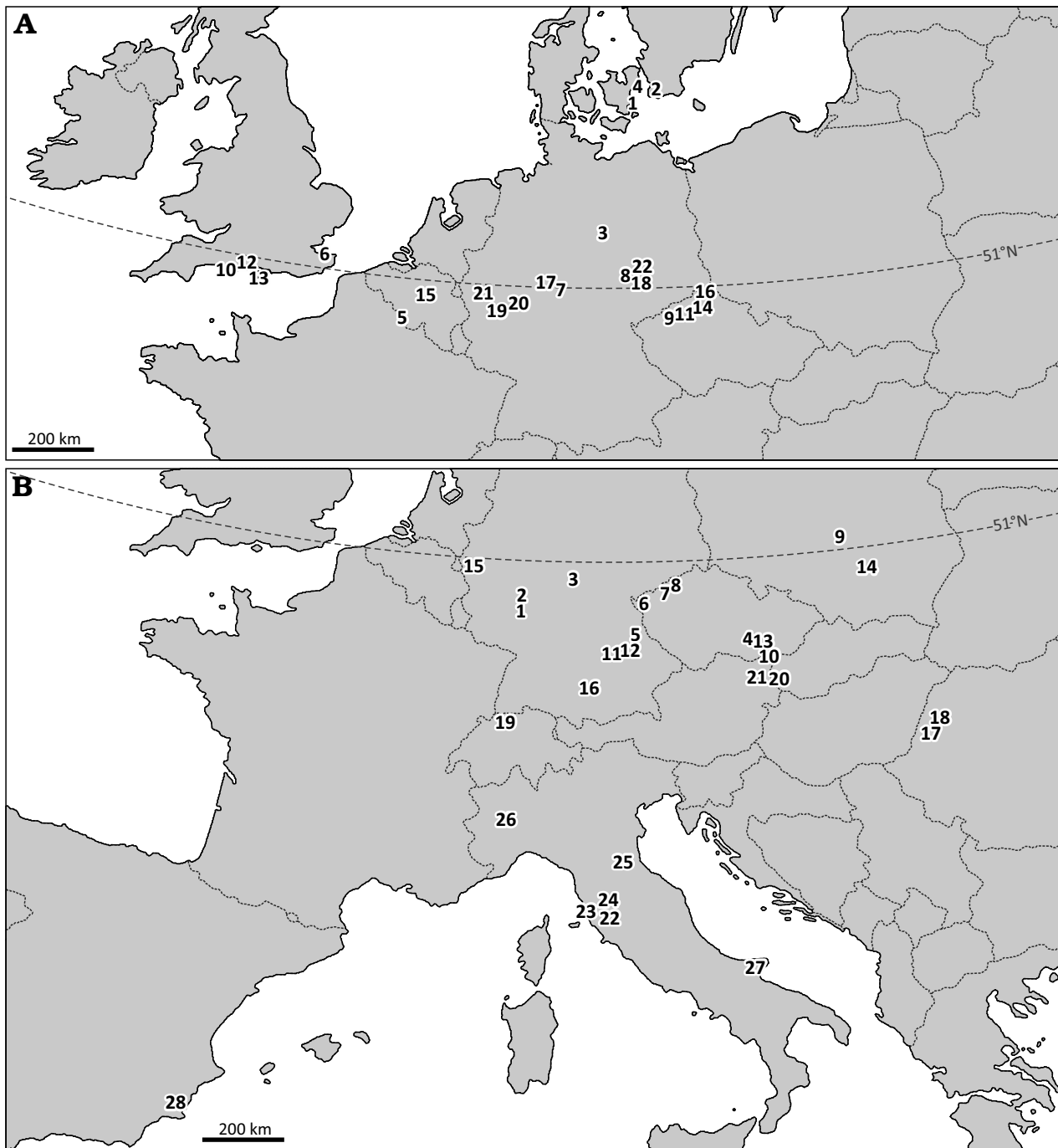


Fig. 6. Northernmost occurrences of crocodylians in Europe in succeeding stages of Paleogene and Neogene. **A.** Paleogene occurrences. Paleocene: Danian: 1, Faxe Quarry, Denmark; 2, Limhamn quarry near Malmö, Sweden; Selandian: 3, Walbeck near Weferlingen, Germany; 4, Gemmas Allé, Denmark; Thanetian: 5, Jeumont, France. Eocene: Ypresian: 6, Warden Point, Sheppey Island, England; Lutetian: 7, Stolzenbach near Borken, Germany; 8, Geiseltal, Germany; Bartonian: 9, Kučlín, Trupelník Hill, Czechia; 10, Creech Barrow Hill, England, UK; Priabonian: 11, Roudniky, Czechia; 12, Hordle Cliff near Milford on Sea, England, UK. Oligocene: Rupelian: 13, Bouldnor Cliff, Isle of Wight, England, UK; 14, Bechlejovice near Děčín, Czechia; 15, Hoogbutsel near Leuven, Belgium; 16, Seifhennersdorf, Germany; 17, Altenburg III and IV pit-mines, Borken, Germany; 18, Böhlen and Espenheim near Leipzig, Germany; Chattian: 19, Enspel near Marienberg, Germany; 20, Gusternhain, Germany; 21, Rott near Hennef, Germany; 22, Breitenfeld near Leipzig, Germany. **B.** Neogene occurrences. Miocene: Aquitanian: 1, Mombach and Weisenau, Mainz, Germany; 2, Biebrich and Mainz-Kastel, Wiesbaden, Germany; Aquitanian–Burdigalian: 3, Kaltennordheim, Germany; Burdigalian: 4, Ivančice, South Moravian Region, Czechia; 5, Wackersdorf near Schwandorf, Germany; 6, Jehličná near Sokolov, Czechia; 7, Ahníkov and Tušimice, Czechia; 8, Břešťany and Skyřice, Czechia; Burdigalian–?Langhian: 9, Szczerców, Poland; Langhian: 10, Kienberg near Mikulov, Czechia; 11, Appertshofen and Denkendorf near Ingolstadt, Germany; 12, Undorf near Regensburg, Germany; 13, Židlochovice, Czechia; 14, Pińczów, Poland; 15, Hambach, Germany; ?Langhian–Serravallian: 16, Kirrberg near Balzhausen, Germany; Serravallian: 17, Tășad and Vârciorog, Romania; 18, Subpiatră, Romania; 19, Anwil, Switzerland; 20, Devinská Nová Ves, Slovakia; 21, Vienna, Austria; Tortonian: 22, Casteani and Ribolla, Italy; Messinian: 23, Montebamboli, Italy; 24, Radicondoli, Italy; 25, Cava di Monticino, Italy; 26, Moncucco Torinese, Italy. Miocene–Pliocene transition: latest Messinian–earliest Zanclean: 27, Gargano, Italy. Pliocene: Zanclean: 28, Puerto de la Cadena, Spain. For references see Table 2.

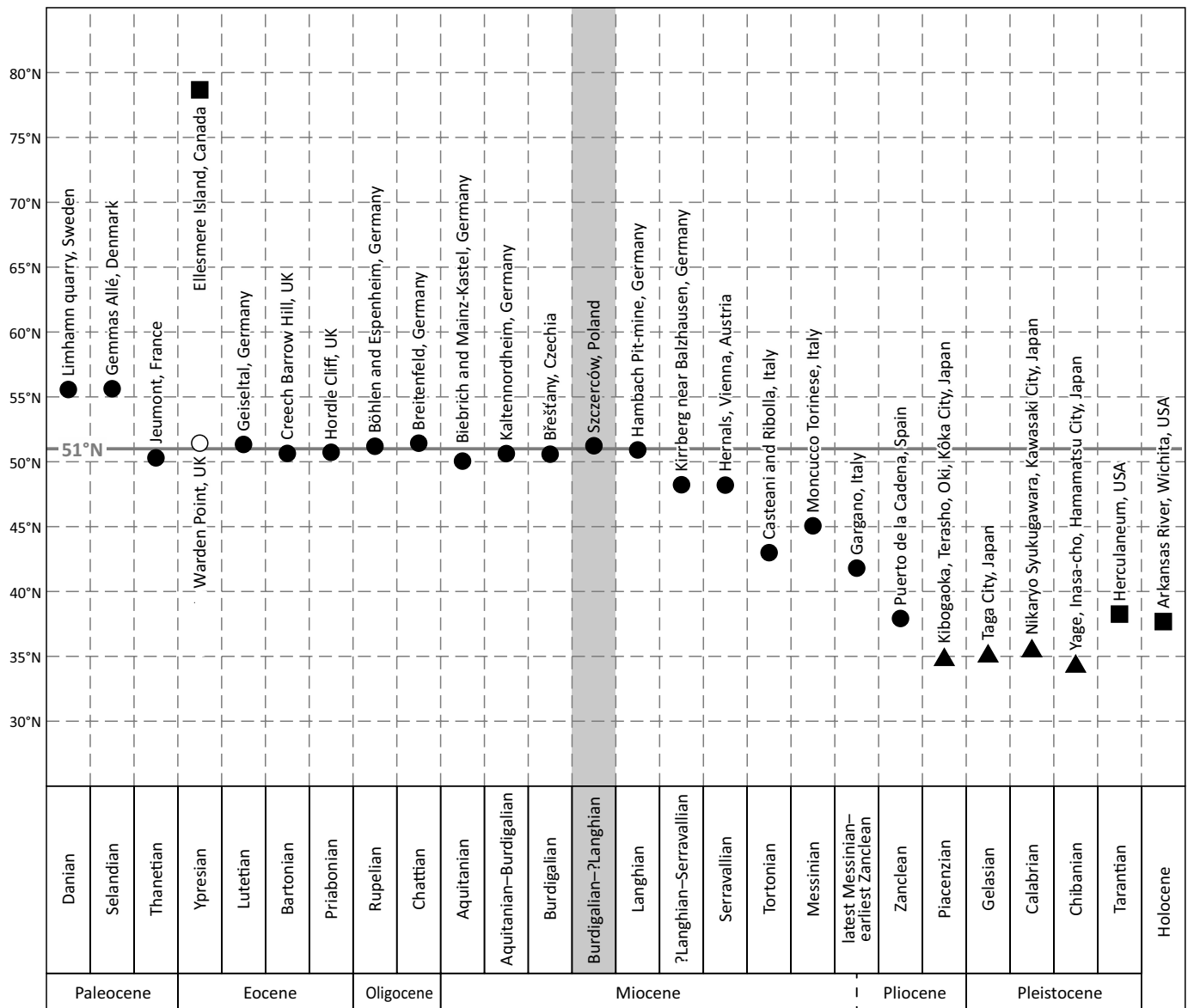


Fig. 7. The northernmost occurrences of crocodylians throughout the Cenozoic. Records with black symbols indicate the world’s northernmost occurrences. Occurrences in Europe marked with circles, in North America with squares, in eastern Asia with triangles. Note the relatively stable location of the northern limit of crocodylian distribution in Europe at approx. the present-day 51°N parallel throughout the Thanetian to Langhian timespan. For references see Table 2.

tribution (see Fig. 7). This is not only confirmed by the northernmost records from the Rupelian (lower Oligocene) of Böhlen and Espenheim near Leipzig (Karl 1990, 2007) and of Borken (Karl 2007; Karl and Müller 2008; Rio et al. 2020) in Germany (all slightly exceeding 51°N) but this is even further supported by a series of other Rupelian records approaching 51.0°N from Czechia, Belgium, England, and Germany (Smith 2003; Böhme 2007; Wolff et al. 2007; Chroust et al. 2019; see Fig. 6A and Table 2). This distribution pattern was generally similar in the Chattian (upper Oligocene) although the northernmost occurrences were solely reported from Germany, with the most northerly located site of Breitenfeld (51°25'50"N) near Leipzig (Karl 1991, 2007). Other German occurrences (see Fig. 6A and Table 2), almost reaching 50°N, are in the western part of

the country (Ludwig 1877; Böhme and Lang 1991; Mörs 2002; Mayr and Poschmann 2009).

The Miocene recorded the highest peak of crocodylian radiation, particularly in the southern hemisphere (Celis et al. 2020). In the northern hemisphere, while North American and Asian alligatoroids did not reach 50°N during the Miocene (Li and Wang 1987; Brochu 1999; Rio and Mannion 2021), crocodylians did so in Europe, even exceeding 51°N (Szczerców).

In the beginning of the Miocene, tomistomines and diplocynodontines were present in central Europe (Böhme 2003; Luján et al. 2019; Chroust et al. 2021). During the Miocene Climatic Optimum, temperatures were more favourable again for crocodylians, which allowed them to expand their distribution northward. Indeed, diplocynodontines spread across western and central Europe, while tomistomines were located mostly in the Mediterranean area

Table 2. The northernmost occurrences of crocodylians throughout the Cenozoic. Records in bold indicate the world's northernmost occurrences, underlined records denote northernmost occurrences in Europe, in grey are the records described in this paper.

Epoch	Age (species for the Holocene)	Locality	Latitude	Reference	
Holocene/ Recent	<i>Alligator mississippiensis</i>	extant, exceptional: Arkansas River, Wichita, Kansas, USA	37°40'45.0"N	Cragin 1885	
		extant, constant: Merchants Millpond, North Carolina, USA	36°26'10.0"N	Gardner et al. 2016; Whiting et al. 2016	
	<i>Alligator sinensis</i>	fossil: Wangyin site, Yanzhou District, Jining City, Shandong Province, China	35°27'41.0"N	Iijima et al. 2016	
		historic: Hongze Lake, Jiangsu Province, China	33°40'00.0"N	Thorbjarnarson and Wang 1999	
		extant: Yangtze River Valley, Anhui Province, China	31°00'00.0"N	Thorbjarnarson et al. 2002	
Pleistocene	Late Pleistocene	Herculaneum, Missouri, USA	38°15'26.0"N	Olson 1940; Mehl 1962; Preston 1979	
		Jones Spring, Missouri, USA	38°03'58.5"N	Haynes 1985	
	Chibanian	Yage, Inasa-cho, Hamamatsu City, Shizuoka Prefecture, Honshu, Japan	34°50'16.0"N	Nojima and Itoigawa 2017; Iijima et al. 2018	
		Machikane-yama, Toyonaka City, Osaka Prefecture, Honshu, Japan	34°48'25.0"N	Aoki 1983; Iijima et al. 2018	
	Calabrian	Nikaryo Syukugawara, Kawasaki City, Kanagawa Prefecture, Honshu, Japan	35°37'12.6"N	Iijima et al. 2018	
		Kaminokuchi, Takatsuki City, Osaka Prefecture, Japan	34°53'10.0"N	Iijima et al. 2018	
	Gelasian	Taga City, Shiga Prefecture, Honshu, Japan	35°13'33.4"N	Iijima et al. 2018	
Hino Town, Kōka City, and Konan City, Shiga Prefecture, Honshu, Japan		35°01'34.0"N	Iijima et al. 2018		
Pliocene	Piacenzian	Kibogaoka, Terasho, and Oki, Kōka City, Shiga Prefecture, Honshu, Japan	34°57'01.5"N	Iijima et al. 2018	
		Nomura-cho, Kameyama City, Mie Prefecture, Honshu, Japan	34°51'01.0"N	Iijima et al. 2018	
		Hatamura, Iga City, Mie Prefecture, Honshu, Japan	34°46'09.0"N	Iijima et al. 2018	
	Zanclean	<u>Puerto de la Cadena, Murcia, Spain</u>	<u>37°55'09.0"N</u>	<u>Piñero et al. 2017</u>	
		Gray Fossil Site, Washington County, Tennessee, USA	36°23'10.0"N	Keenan and Engel 2017	
Miocene–Pliocene transition	latest Messinian–earliest Zanclean	<u>Gargano, Apulia, Italy</u>	<u>41°48'00.0"N</u>	<u>Kotsakis et al. 2004; Delfino et al. 2007</u>	
Miocene	Messinian	<u>Moncuco Torinese, Piedmont, Italy</u>	<u>45°03'36.5"N</u>	<u>Colombero et al. 2017</u>	
		Cava di Monticino, Brisighella, Emilia-Romagna, Italy	44°13'29.1"N	Kotsakis et al. 2004; Villa et al. 2021	
		Radicondoli, Tuscany, Italy	43°15'34.0"N	Kotsakis et al. 2004	
		Montebamboli, Tuscany, Italy	43°04'37.0"N	Kotsakis et al. 2004; Delfino and Rook 2008	
	Tortonian	<u>Casteani and Ribolla, Tuscany, Italy</u>	<u>42°59'32.0"N</u>	<u>Kotsakis et al. 2004; Delfino and Rook 2008</u>	
		UNSM locality Sh-107, Sheridan County, Nebraska, USA	42°48'00.0"N	Whiting and Head 2020	
		George Sawyer Ranch, Cherry County, Nebraska, USA	42°41'24.0"N	Mook 1946; Whiting and Head 2020	
	Serravallian	<u>Hernals, Vienna, Austria</u>	<u>48°13'25.0"N</u>	<u>Harzhauser et al. 2025</u>	
		Devinská Nová Ves – Sandberg, Bratislava, Slovakia	48°12'00.0"N	Schlögl and Holec 2004; Pivko et al. 2017	
		Anwil, Basel-Country, Switzerland	47°27'00.0"N	Böhme 2003	
		Subpiatră, Bihor District, Romania	47°01'13.0"N	Hír et al. 2016	
		Tășad and Vărciorog, Bihor District, Romania	46°59'00.0"N	Hír et al. 2016	
	?Langhian–Serravallian		<u>Kirrburg near Balzhausen, Bavaria, Germany</u>	<u>48°13'37.4"N</u>	<u>Böhme 2003</u>
	Langhian	<u>Hambach Pit-mine, North Rhine-Westphalia, Germany</u>	<u>50°54'34.6"N</u>	<u>Mörs et al. 2000; Macaluso et al. 2022</u>	
		Pińczów, Świętokrzyskie Voivodeship, Poland	50°31'56.0"N	Radwański 1974, 1977, 1985, 2015; this paper	
		Židlochovice, South Moravian Region, Czechia	49°02'31.6"N	this paper	
		Undorf near Regensburg, Bavaria, Germany	49°01'38.0"N	Böhme and Ilg 2003	
		Denkendorf near Ingolstadt, Bavaria, Germany	48°55'57.0"N	Böhme and Ilg 2003	
		Appertshofen near Ingolstadt, Bavaria, Germany	48°52'21.3"N	Böhme 2003	
Kienberg near Mikulov, South Moravian Region, Czechia		48°48'13.5"N	Brezina et al. 2024		
Burdigalian–?Langhian		<u>Szczerców field of Belchatów pit-mine, Łódź Voivodeship, Poland</u>	<u>51°14'00.0"N</u>	<u>this paper</u>	

Epoch	Age	Locality	Latitude	Reference
Miocene	Burdigalian	<u>Břešňany near Bílina, Ústí nad Labem Region, Czechia</u>	<u>50°35'00.0"N</u>	<u>Liebus 1936;</u> <u>Chroust et al. 2021</u>
		Marianna Pit-mine, Skyřice near Most, Ústí nad Labem Region, Czechia	50°29'00.0"N	Laube 1910; Chroust et al. 2021
		Tušimice near Chomutov, Ústí nad Labem Region, Czechia	50°26'00.0"N	Laube 1901, 1910; Luján et al. 2019
		Ahníkov I/II-Merkur North Pit-mine, Ústí nad Labem Region, Czechia	50°26'00.0"N	Chroust et al. 2021
		Friedrich-Anna mine, Jehličná near Sokolov, Karlovy Vary Region, Czechia	50°12'09.0"N	Redlich 1902; Luján et al. 2019
		Wackersdorf near Schwandorf, Bavaria, Germany	49°18'00.0"N	Gregor et al. 1989
	Ivančice, South Moravian Region, Czechia	49°07'01.2"N	Rzehak 1912	
	Aquitanian–Burdigalian	<u>Kaltennordheim, Thuringia, Germany</u>	<u>50°37'40.0"N</u>	<u>Herbst 1857</u>
	Aquitanian	<u>Biebrich and Mainz-Kastel, Wiesbaden, Hesse, Germany</u>	<u>50°03'00.0"N</u>	<u>Berg 1966; Schleich 1988</u>
		Mombach and Weisenau, Mainz, Rhineland-Palatinate, Germany	50°01'00.0"N	Ludwig 1877; Berg 1966; Schleich 1988
Oligocene	Chattian	<u>Breitenfeld near Leipzig, Saxony, Germany</u>	<u>51°25'50.0"N</u>	<u>Karl 1991, 2007</u>
		Rott near Hennef, North Rhine-Westphalia, Germany	50°45'15.0"N	Böhme and Lang 1991; Mörs 2002
		Gusternhain, Hesse, Germany	50°40'10.0"N	Ludwig 1877; Laube 1901
	Enspel near Marienberg in Westerwald, Rhineland-Palatinate, Germany	50°37'15.0"N	Mayr and Poschmann 2009	
	Rupelian	<u>Böhlen and Espenheim near Leipzig, Saxony, Germany</u>	<u>51°11'35.0"N</u>	<u>Karl 1990, 2007</u>
		Altenburg III and IV pit-mines, Borken, Hesse, Germany	51°02'07.0"N	Karl 2007; Karl and Müller 2008
		Seifhennersdorf, Saxony, Germany	50°56'03.5"N	Böhme 2007
		Hoogbutsel near Leuven, Brabant, Belgium	50°50'46.0"N	Smith 2003
		Bechlejovice near Děčín, Ústí nad Labem Region, Czechia	50°45'38.0"N	Böhme 2007
		Bouldnor Cliff, Isle of Wight, England, UK	50°42'30.0"N	Wolff et al. 2007
Eocene	Priabonian	<u>Hordle Cliff near Milford on Sea, Hampshire, England, UK</u>	<u>50°43'43.0"N</u>	<u>Benton and Spencer 1995</u>
		drilling Ru 60, Roudníky, Ústí nad Labem Region, Czechia	50°39'30.0"N	Böhme 2007
		Calf Creek near Eastend, Saskatchewan, Canada	49°38'00.0"N	Holman 1972
	Bartonian	<u>Crech Barrow Hill, Dorset, England, UK</u>	<u>50°38'29.5"N</u>	<u>Benton and Spencer 1995</u>
		Kučlín-Trupelník Hill near Bílina, Ústí nad Labem Region, Czechia	50°32'17.0"N	Böhme 2007; Chroust et al. 2019
	Lutetian	<u>Geiseltal, Sachsen-Anhalt, Germany</u>	<u>51°20'02.0"N</u>	<u>Hastings and Hellmund 2017</u>
		Stolzenbach near Borken, Hesse, Germany	51°00'36.0"N	Schleich 1994
	Ypresian	<u>Ellesmere Island, Nunavut, Canada</u>	<u>78°40'10.0"N</u>	<u>Dawson et al. 1976;</u> <u>Estes and Hutchison 1980</u>
		Eames River, Aulavik National Park, Banks Island, Canada	74°10'00.0"N	Eberle et al. 2014
		Warden Point, Sheppey Island, Kent, England, UK	51°26'00.0"N	Benton and Spencer 1995
Paleocene	Thanetian	<u>Jeumont, Maubeuge, Nord Department, France</u>	<u>50°18'00.0"N</u>	<u>Puértolas-Pascual et al. 2015</u>
	Selandian	<u>Gemmas Allé, Amager, Copenhagen, Denmark</u>	<u>55°37'41.9"N</u>	<u>Puértolas-Pascual et al. 2015</u>
		Walbeck near Weferlingen, Saxony-Anhalt, Germany	52°17'39.0"N	Puértolas-Pascual et al. 2015
	Danian	<u>Limhamn quarry near Malmö, Sweden</u>	<u>55°34'03.1"N</u>	<u>Puértolas-Pascual et al. 2015</u>
	Faxe Quarry, Sjælland, Denmark	55°15'29.8"N	Puértolas-Pascual et al. 2015	

(Böhme 2003; Martin and Gross 2011; Nicholl et al. 2020). However, *Gavialosuchus eggenburgensis* from Eggenburg (Austria) dated to the Burdigalian, is an exception and reached 48°64'N and therefore represents the northernmost Neogene record of tomistomines (Toula and Kail 1885). The northernmost record of diplocynodontines during the Aquitanian comes from the Mainz/Wiesbaden area at ca. 50°N (Ludwig 1877; Schleich 1988). Younger, Burdigalian northernmost findings are relatively common in the Most Basin, NW Czechia, at ca. 50°30'N (Laube 1901, 1910; Liebus 1936; Luján et al. 2019; Chroust et al. 2021). However, these occurrences are slightly surpassed by an old record attributed to the Early Miocene age from Kaltennordheim,

central Germany (Herbst 1857). Another Lower Miocene occurrence of supposed Burdigalian age is the present record of the osteoderm from Szczerców (51°14'00"N), the world's northernmost record of a Neogene crocodylian (see Fig. 6B and Table 2). The northern range limit of crocodylians in Europe then reached the 51°N parallel and persisted through the Langhian, with the northernmost records from the coal deposits of Hambach, western Germany (Mörs et al. 2000; Macaluso et al. 2022) and from the littoral facies of Pińczów, Poland (Radwański 1974, 1977, 1985, 2015; Antunes in Młynarski 1984; see Figs. 3B, 5B, 6B, and Table 2). The area of distribution of crocodylians in Europe during the Early Miocene and the Langhian (i.e., MCO)

was comparable to that of the late Paleocene through the Oligocene (Figs. 6, 7, and Table 2).

After the cooling event of the Miocene Climatic Transition the diversity and spatial distribution of crocodylians in the northern hemisphere started to decline gradually and never exceeded the former latitudinal values (Mannion et al. 2015). Although in the Serravallian the northernmost occurrences were still located in central Europe, the northern limit of the range barely exceeded 48°N, known localities (see Figs. 6B, 7 and Table 2) are Kirrberg near Balzhausen, Germany (latest Langhian?–early Serravallian age; Böhme 2003), Devinská Nová Ves—Sandberg, Slovakia (Schlögl and Holec 2004; Pivko et al. 2017), and Hernals district of Vienna (Harzhauser et al. 2025)—the latter two of confirmed Serravallian age. In the Late Miocene the northern range limit of crocodylians shifted to the south, and the Tortonian northernmost records are known from the Italian localities of Casteani and Ribolla (ca. 43°N; Kotsakis et al. 2004; Delfino and Rook 2008), but they are closely followed by North American occurrences from Nebraska (Mook 1946; Markwick 1994; Whiting and Head 2020). In the Messinian, a short-lasting northward shift can be observed when crocodylians returned to northern Italy (Moncucco Torinese, ca. 45°N; Colombero et al. 2017). Generally, European tomistomines and diplocynodontines probably went extinct during the Late Miocene (Böhme 2003; Luján et al. 2019; Nicholl et al. 2020) and in southern Europe they were gradually replaced by the extant genus *Crocodylus* (Delfino et al. 2007; Delfino and Rook 2008; Delfino and Rossi 2013; Delfino et al. 2021). The latter is reported from the uppermost Miocene and Pliocene of southern Europe; however, it never reached higher latitudes than its predecessors and was apparently confined to the coastal areas or areas somehow linked to the coast. From the Miocene–Pliocene transition (Messinian–Zanclean) a crocodylian record is known from Gargano, Italy (almost 41°N; Kotsakis et al. 2004; Delfino et al. 2007, 2021). Unidentified teeth from Puerto de la Cadena, Spain (Piñero et al. 2017) located at almost 38°N (Fig. 6B and Table 2) are the world's northernmost crocodylian record of Zanclean age and represent the last known occurrence of crocodylians in Europe.

For the late Pliocene and almost the entire Pleistocene the centre of northernmost crocodylian occurrences shifted to Japan (Aoki 1983; Nojima and Itoigawa 2017; Iijima et al. 2018) and reached ca. 35°N for almost 3.5 Myr (see Fig. 7 and Table 2). This limit was exceeded by *Alligator mississippiensis* in Missouri, USA (ca. 38°N) only in the latest Pleistocene (Olson 1940; Mehl 1962; Preston 1979; Haynes 1985).

In the Holocene, the northernmost limit of crocodylians, represented by alligators *A. mississippiensis* and *A. sinensis* moved southward, to a large extent due to human activity (Thorbjarnarson et al. 2002; Gardner et al. 2016; Pan et al. 2019).

The current northernmost limit of the natural range of crocodylians belongs to *Alligator mississippiensis*, which reaches the north-eastern coastal area of North Carolina,

up to Albemarle Sound (Kellogg 1929; Whiting et al. 2016), locally even reaching ca. 36°25'N (Merchants Millpond; Gardner et al. 2016: 545, fig. 1). However, there are exceptional historical reports of individuals reaching as far as 38°N, e.g., Arkansas River in Wichita, Kansas (Cragin 1885).

The range of *A. sinensis* decreased gradually. Fossil remains from the Neolithic of the Wangyin site, Shandong Province in China were located at ca. 35°42'N, i.e., similar to the Pleistocene range of crocodylians in Japan (Iijima et al. 2016). In historic times the northern limit of this range retracted to 33°40'N (Hongze Lake, Jiangsu Province in China; Thorbjarnarson and Wang 1999; Iijima et al. 2016). The species was recently at the verge of extinction and its range shrunk to just a few water bodies in Yangtze River Valley, Anhui Province in China at ca. 31°N (Thorbjarnarson et al. 2002; Iijima et al. 2016).

Like most of the ectothermic fauna, crocodylians are sensitive to climatic changes and therefore serve as a climatic indicator (Markwick 1998; Böhme 2003). The crucial limiting factor for their distribution, aside from the humidity, is the minimal mean annual temperature. Most of the extant taxa live in temperatures above the freezing point, however, alligators are better adapted to cold, and the short-time freezing is not limiting for them. *Alligator mississippiensis* lives in an environment with a mean annual temperature of 16.4 °C and a minimal mean annual temperature of 1.7 °C, whereas *Alligator sinensis* lives in even colder conditions, with a mean annual temperature of 15.7 °C and a minimal mean annual temperature of -1.7 °C (Haller-Probst 1997). *Alligator mississippiensis* is often spotted in frozen waters, where only the distal snout is kept above the frozen water surface level for breathing (Brisbin et al. 1982). The occurrence of a crocodylian in Szczerców may suggest subtropical or warm-temperate conditions, with minimal mean annual temperature not falling below freezing point at ca. 47° northern latitude in the late Burdigalian of Europe (present-day 51°N). For more precise palaeoclimatic reconstruction, a more diversified fossil sample is needed.

Environmental requirements of *Diplocynodon* and possible dispersal routes.—Despite the presented material not being able to be classified at a lower taxonomic level, it brings new information about crocodylian biogeography and potential environmental requirements. Only two crocodylian genera are known from the Central Parathetys area in the Middle Miocene, with these two taxa being traditionally split between two environmental settings: *Diplocynodon* from freshwater environments and *Gavialosuchus* inhabiting marine settings. The *Crocodylia* indet. material described here (teeth and osteoderm) is more reminiscent of *Diplocynodon* than *Gavialosuchus*, and therefore the possibility of *Diplocynodon* inhabiting a marine setting is worth discussing. In fact, *Diplocynodon* occurrences in other marine deposits of the Parathetys Sea have been a topic of discussion in the context of its saltwater tolerance (Sabău et al. 2021; Venczel and Codrea 2022; Kocsis et al. 2023; Venczel

2023). Extant true crocodiles (Crocodylidae) have lingual glands to help them exclude the salt and therefore persist in hyperosmotic conditions across the seas. Alligators and caimans (Alligatoridae) lack lingual glands and therefore their presence in saltwater conditions is limited (Taplin et al. 1982; Taplin and Grigg 1989; Brochu 1999; Stout 2024). However, *Alligator mississippiensis* or *Caiman latirostris* could temporarily survive in a hyperosmotic environment (Taplin and Grigg 1993) and surprisingly, *A. mississippiensis* has been observed offshore in the Gulf of Mexico, 63 km distance from the mainland (Else 2005). Several examples of fossil alligatoroids (including the genus *Diplocynodon*) have been found in coastal deposits, and alligatoroids have also been suggested to disperse between continents throughout the Cenozoic (Stout 2024). Here, the described material is identified as *Crocodylia* indet. and comes from both freshwater and marine deposits. Based on traditional interpretations, the freshwater material (the osteoderm from Szczerców) could be arguably attributed to *Diplocynodon*, while the marine material (teeth from Pińczów and Židlochovice) could be linked to *Gavialosuchus*. After our examination of the material, all three specimens tentatively resemble *Diplocynodon* and therefore, the environmental requirements of the genus *Diplocynodon* are further discussed here. The Pińczów and Židlochovice sites represent shallow marine ecosystems rich in faunal assemblages typical of sub-tropical shallow waters of oceanic salinity. The preserved crocodylian material is fragmentary (teeth only), and therefore, transport from land and later re-deposition into marine deposits is possible. In both of these sites the mentioned remains are the only documented possible terrestrial elements among otherwise a very rich marine fauna. Although the terrestrial fauna at these sites is minor, at least an occasional marine lifestyle cannot be excluded for *Diplocynodon* as the hypothetical representative of both teeth from the discussed localities. Such an assumption is supported by the presence of *Diplocynodon kochi* in marine deposits from Romania (Venczel and Codrea 2022). A similar case has been described from the Máriahalom fossil site in Hungary, where dozens of teeth were tentatively assigned to the genus *Diplocynodon*. The isotopic composition of the dental enamel of the Máriahalom teeth is consistent with a brackish water environment (Kocsis et al. 2023). As such, if our hypothetical attribution to the genus *Diplocynodon* is correct, the herein presented material is consistent with the presence of this genus in a definite freshwater environment (Szczerców) but also supports its putative presence in marine environments (Pińczów and Židlochovice).

Therefore, the described findings: (i) contemplate the possibility of an at least partial marine lifestyle of *Diplocynodon*, (ii) throw into question the simplified division (and often diagnosis) of two discussed genera in relation to the environment, i.e., *Gavialosuchus* as saltwater and *Diplocynodon* as freshwater dwellers. This also assumes the potential coexistence of these two genera in particular environmental niches. Both extant *A. mississippiensis*

and *Crocodylus acutus* also inhabit the coastal area of the southern tip of the Florida peninsula (Mazzotti et al. 2007, 2009). A similar sympatric coexistence was found in northern Australia, where *Crocodylus porosus* and *Crocodylus johnstoni* share the tidal rivers (Webb et al. 1983). In northern India, *Gavialis gangeticus* and *Crocodylus palustris* also cohabit in the same areas (Choudhary et al. 2018). Also, the current distributions of *Tomistoma schlegelii* and *Crocodylus siamensis* overlap in Mesangat Lake on Kalimantan Island, Indonesia (Staniewicz et al. 2018). The same fit for the fossil forms, for example, the coexistence of Late Miocene alligatoroid and gavialoid taxa is highlighted by the unique degree of crocodylian sympatry observed in the Urumaco Formation in Venezuela (Scheyer et al. 2013), similar to that at La Venta in Colombia (Wilson and Parker 2023). And of course, the European Eocene sites like Messel and Geisetal are also famous for the high niche partitioning of crocodylians (Morlo et al. 2004; Hastings and Hellmund 2017; Brochu and Miller-Camp 2018).

For the fossil forms here discussed, a different diet is presumed, where *Gavialosuchus* is a specialized ichthyophagous taxon (Antunes 2017), and *Diplocynodon* has a more generalized diet, comprising small mammals and herpetofauna like amphibians, snakes or turtles (Hastings and Hellmund 2017). A few findings of the coexistence of those two taxa exist in the literature but have never been solidly demonstrated; for instance, the material from German Molasse Basin in Ulm (Heizmann et al. 1989) or Portuguese Tagus Basin near Lisbon (Antunes 1994). In the case of the German and Austrian material, the coexistence has not been confirmed (Böhme 2003: supplement 1). However, to reveal these trophic relations, more fossil evidence is required.

The possible presence of *Diplocynodon* in the Szczerców field was undoubtedly allowed due to the freshwater environment in the Kleszczów Graben. The site was located in the southern part of the Polish Lowland Basin and was included in the catchment area of the North Sea Basin during the considered timespan of Early-to-Middle Miocene. The whole area was then most probably included within the fluvial system of the hypothetical Eridanos river flowing from Scandinavia, through the region of the modern Baltic Sea, northern Poland, northern Germany, and Denmark to the North Sea Basin (see Gibbard and Lewin 2016). Noteworthy, similar was the situation in the Most Basin in Czechia, drained by a river flowing NW, i.e., to the North Sea Basin (“Central River”; Mach et al. 2014: fig. 6). Both of these areas where *Diplocynodon* presence was recorded were thus included within the large system of fluvial/lacustrine/swamp environments reaching as far as NW Germany and including also the site of Hambach. As such, this vast freshwater domain was the most probable route of dispersal of *Diplocynodon* across inland central Europe, situated away from marine basins of the Paratethys.

In the context of various findings of *Diplocynodon* in central Europe, the dispersal routes of this genus cannot be restricted to freshwater basins only and seashore pathways

should also be taken into consideration. This possibly applies to the specimens from Pińczów and Židlochovice, if they are indeed *Diplocynodon*. While the presence of rivers along the shores of the Fore-Carpathian Basin is obvious, they could not provide significant connections (i.e., dispersal routes) with the predominantly freshwater Polish Lowland Basin (or North Sea Basin in general) due to morphological barriers such as the Bohemian Massif and Central Polish Uplands. This means that putative saltwater tolerance of *Diplocynodon* is potentially an important factor that should be taken into consideration when reconstructing possible routes of dispersal of the representatives of this genus.

Conclusions

The current study presents records of Crocodylia indet. from the Karpatian (upper Lower Miocene) and lower Badenian (lower Middle Miocene) of the Fore-Carpathian Basin and its foreland, as the described material is either new or has been previously assigned to the gavialoid genus *Tomistoma*. A new specimen is described from the site of Szczerców, Poland, which was previously not known for yielding any vertebrate remains. A thorough compilation of the northernmost occurrences of these reptiles during the Cenozoic shows that the material from Szczerców is also the world's northernmost record of a crocodylian from the entire Neogene. The palaeoenvironment reconstruction of Szczerców points towards this locality being a freshwater swamp, but other sites are reconstructed as being shallow marine. The taxonomic attribution of crocodylian remains together with their plausible ecology is discussed.

The description of a crocodylian from Szczerców opens the possibility to explore new vertebrate findings in the Middle Miocene of central Poland, and it specifically helps better understand the composition of the inland fauna in the north of the Central Paratethyan coast. The study of this region could help us establish biogeographical links between southwestern and eastern localities and draw the bigger picture of Eurasian faunal exchanges.

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