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Turonian marine amniotes from the Bohemian Cretaceous Basin, Czech Republic

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Abstract – Despite being known for over 155 years, the Late Cretaceous marine amniotes of the Bohemian Cretaceous Basin in the Czech Republic have received little recent attention. These fossils are however significant because they record a diverse range of taxa from an incompletely known geological interval: the Turonian. The presently identifiable remains include isolated bones and teeth, together with a few disarticulated skeletons. The most productive stratigraphical unit is the Lower–Middle Turonian Bílá Hora Formation, which has yielded small dermochelyoid sea turtles, a possible polycotylid plesiosaur and elements compatible with the giant predatory pliosauromorph *Polyptychodon*. A huge protostegid, together with an enigmatic cheloniid-like turtle, *Polyptychodon*-like dentigerous components, an elasmosaurid and a tethysaurine mosasauroid have also been found in strata corresponding to the Middle–Upper Turonian Jizera Formation and Upper Turonian – Coniacian Teplice Formation. The compositional character of the Bohemian Cretaceous Basin fauna is compatible with coeval assemblages from elsewhere along the peri-Tethyan shelf of Europe, and incorporates the globally terminal Middle–Upper Turonian occurrence of pliosauromorph megacarnivores, which were seemingly replaced by mosasauroids later in the Cretaceous.

Keywords: faunal turnover, Mosasauroidea, palaeobiogeography, Plesiosauria, Protostegidae.

1. Introduction

The Turonian (early Late Cretaceous, 93.9–89.8 Ma; Gradstein *et al.* 2012) represented a critical time of biodiversity turnover among Mesozoic marine amniotes. It chronicled the last appearances of macrophagous pliosauromorphs (Plesiosauri; Schumacher, 2011), the radiation of aquatic mosasauroid lizards (Mosasauroidea; Bardet *et al.* 2008) and the divergence of modern cheloniid sea turtles (Chelonioidea; Hirayama, 1997). Unfortunately, fossiliferous deposits of Cenomanian–Turonian age are generally poorly sampled (Benson *et al.* 2010). Nonetheless, the Late Cretaceous European Platform, which formed a shallow marine shelf adjacent to the Tethyan oceanic area, has a long history of discoveries from what are now the chalk-marl, limestone and glauconitic sandstone strata of the Czech Republic (see detailed summary below in Section 3), Croatia (e.g. Carroll & Debraga, 1992; Debraga & Carroll, 1993; Lee & Caldwell, 2000; Caldwell & Lee, 2004; Pierce & Caldwell, 2004; Dutchak & Caldwell, 2006), Poland (Bardet & Godefroit, 1995), Germany (e.g. Sachs, 2000; Diedrich & Hirayama, 2003; Karl *et al.* 2012), France (e.g. Rage, 1989; Bardet & Godefroit, 1995; Bardet *et al.* 1998, 2008; Houssaye, 2010) and England (e.g. Collins, 1970; Milner, 1987; Bardet & Godefroit, 1995). Important coeval records are also known from Russia (Welles, 1962; Storrs *et al.* 2000), Kazakhstan (Averianov, 2001), Japan (Sato *et al.* 2012), the Western Interior Seaway of North America (e.g. Welles, 1943, 1962; Welles & Slaughter, 1963; Carpenter, 1996, 1997; VonLoh & Bell, 1998; Bell & Polcyn, 2005; Polcyn & Bell, 2005; Schumacher & Everhart, 2005; Albright *et al.* 2007*a*, *b*; Schumacher, 2008, 2011; McKean, 2012; Schumacher *et al.* 2013), Mexico (Buchy *et al.* 2005*b*; Smith & Buchy, 2008) and the Gondwanan peripheries of Venezuela (Welles, 1962), Colombia (Páramo-Fonseca, 2000), Angola (Antunes, 1964; Lingham-Soliar, 1994; Jacobs *et al.* 2006; Mateus *et al.* 2009), Morrocco (Bardet *et al.* 2003*a*, *b*; Buchy *et al.* 2005*a*; Buchy, 2006) and possibly Australia (Kear *et al.* 2005).

Some of the earliest reports of Turonian marine amniotes derive from the Bohemian Cretaceous Basin (BCB) in the Czech Republic. Reuss (1855) figured the carapace of a small marine turtle found between Slavětín and Pátek in NW Bohemia that was similar to *Cimochelys* (‘*Chelone*’) *benstedi* (Mantell, 1841; synonymized with *Rhinochelys* Owen, 1851 by Collins, 1970) from the Middle Chalk of England, and additionally documented teeth of the giant plesiosaurian

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Aptychodon cretaceus Reuss, 1855 (considered invalid by Welles, 1962) from Bílá Hora in the western suburbs of Prague. These specimens were later discussed by Fritsch (1878), who also reported teeth attributed to the English Cretaceous pliosauromorph *Polyptychodon interruptus* Owen, 1841 in his landmark monograph on the Cretaceous reptiles and fish of Bohemia. Using the Czech spelling of his name, Frič (1877*a*) produced popular reconstructions, and conducted systematic investigations on fossils from what are now known as the Turonian–Coniacian Bílá Hora, Jizera and Teplice formations (Frič, 1877*b*, 1879, 1889*a*, *b*). Zahálka (1895, 1896) described possible lizard remains found close to the village of Nebužely in N Bohemia; these have since been shown to be a teleost fish (Ekrt, 2012), however. Bayer (1896, 1897, 1898) gave an account of tooth-bearing bones referred to *P. interruptus*, and taxonomically re-evaluated finds from quarries in the Bílá Hora Formation around Prague. Laube (1896) established *Pygmaeochelys michelobana* Laube, 1896 based on a partial turtle carapace from Lower Turonian rocks (Zahálka, 1897; Čech *et al.* 1980) at Měcholupy in NW Bohemia. Sadly, this specimen has since been lost. Jahn (1904) noted the discovery of a possible mandible of *P. interruptus* in Cenomanian strata near Hájek in E Bohemia. Fritsch (1905*a*, *b*) introduced a number of novel taxonomic designations that were later detailed by Fritsch & Bayer (1905) and catalogued by Bayer (1905). These included the plesiosaurians *Cimoliasaurus bernardi* Owen, 1850 (Pliosauridae indet. *sensu* Welles, 1962; Kear, 2002) and *C. lissaensis* Fritsch, 1905*a* (indeterminate Plesiosauria; Bardet & Godefroit, 1995; Kear, 2002), the turtle *Chelone? regularis* Fritsch, 1905*a* and supposed mosasauroids *Iserosaurus litoralis* Fritsch, 1905*a* and *Hunosaurus fasseli* Fritsch, 1905*a* (both reassigned to Plesiosauria indet.; Welles, 1962; Persson, 1963). Fritsch (1906) subsequently named *Cimoliasaurus vicinus* Fritsch, 1906 (the type material of which could not be relocated for this study) and *C. teplicensis* Fritsch, 1906 (both *nomina dubia* following Bardet & Godefroit, 1995; Kear, 2002), and documented new specimens of *I. litoralis* (Fritsch, 1910). Shortly after Antonín Jan Frič died in 1913, Bayer (1914) published a short review of the Bohemian Cretaceous reptiles, in which he concluded that none of Frič's fossils could be recognized as mosasauroids. Furthermore, Edinger (1934) reidentified a purported endocranial cast of *P. interruptus* (*sensu* Fritsch, 1905*b*) excavated at Bílá Hora as a natural sediment infill derived from the skull of a large turtle. Later assessments by Augusta & Soukup (1939) also described plesiosaurian remains, and Zázvorka (1965) announced the discovery of a jaw representing the first definitive Czech mosasauroid; this was found buried in a garden near Dolní Újezd in E Bohemia. Most recently, Ekrt *et al.* (2001) and Wiese *et al.* (2004) figured plesiosaurian bone fragments and a mosasauroid tooth (held in a private collection) from the Teplice Formation at Úpohlavy in NW Bohemia. Ekrt *et al.* (2012) also re-evaluated some key historical specimens. As a complement to these studies, this paper provides a contemporary character state synopsis of Bohemian Cretaceous Basin marine amniote fossils from the Czech Republic and discusses both their palaeobiogeographical and biostratigraphical implications.

2. Depositional and lithostratigraphical settings

The Bohemian Cretaceous Basin is an intracontinental depositional depression that formed via basement faulting of the Bohemian Massif during the Middle Cretaceous (Uličný, 2001). Its extremities today extend from Brno in E Moravia, across Bohemia to the N and W of Prague and over the German border into S Saxony around Dresden (Fig. 1). Sedimentation within the Bohemian Cretaceous Basin began during the Late Albian or earliest Cenomanian (Valečka & Skoček, 1991) with displaced fault zones creating topographical lows adjacent to erosional source areas in the Cretaceous archipelago of the West and East Suedetic Islands and the Central European Island (Čech, 2011). Depositional settings were initially continental, as indicated by the sandstone, conglomerate and bioturbated mudstone-siltstone sequences of the Peruc-Korycany Formation (Uličný *et al.* 1997; Čech *et al.* 2005). These record a transition from fluvial to estuarine and finally shallow littoral conditions (corresponding to the Peruc, Korycany and Pecinov members, respectively) generated by a NW-trending marine transgression through the Early–Late Cenomanian (Valečka & Skoček, 1991; Uličný *et al.* 2009; Čech, 2011). A subsequent shift towards open shelf conditions is signified by a profound basin-wide sandstone–glauconitic siltstone facies change across the Cenomanian–Turonian boundary (Valečka & Skoček, 1991). This coincides with establishment of a shallow seaway between the Boreal North Sea Basin and the Tethys Ocean (Čech, 2011). Transgressive conditions continued through the Early–Middle Turonian as represented by the marlstones and micritic limestones of the Bílá Hora Formation (Uličný *et al.* 1997; Čech *et al.* 2005). Successive upwardly coarsening, progradational cycles of marlstones through fine-gravelly siliclastic sandstones occur through the sequentially overlying Jizera Formation, and reflect sea-level fluctuations during the Middle–Late Turonian (Valečka & Skoček, 1991). These are also distinguished by prominent sedimentological (e.g. Uličný, 2001; Laurin & Uličný, 2004; Wiese *et al.* 2004) and biostratigraphical markers (ammonites, belemnites, inoceramid bivalves, calcareous nannoplankton (e.g. Švábenická, 1999; Svobodová *et al.* 2002; Košťák *et al.* 2004; Wiese *et al.* 2004; Vodrážka *et al.* 2009), which terminate in a marked sandstone–marlstone contact (with condensed phosphatic coprolite-rich horizons) between the Jizera and Upper Turonian – Coniacian Teplice formations. Offshore muds continued to accumulate through the Coniacian and Santonian (yielding

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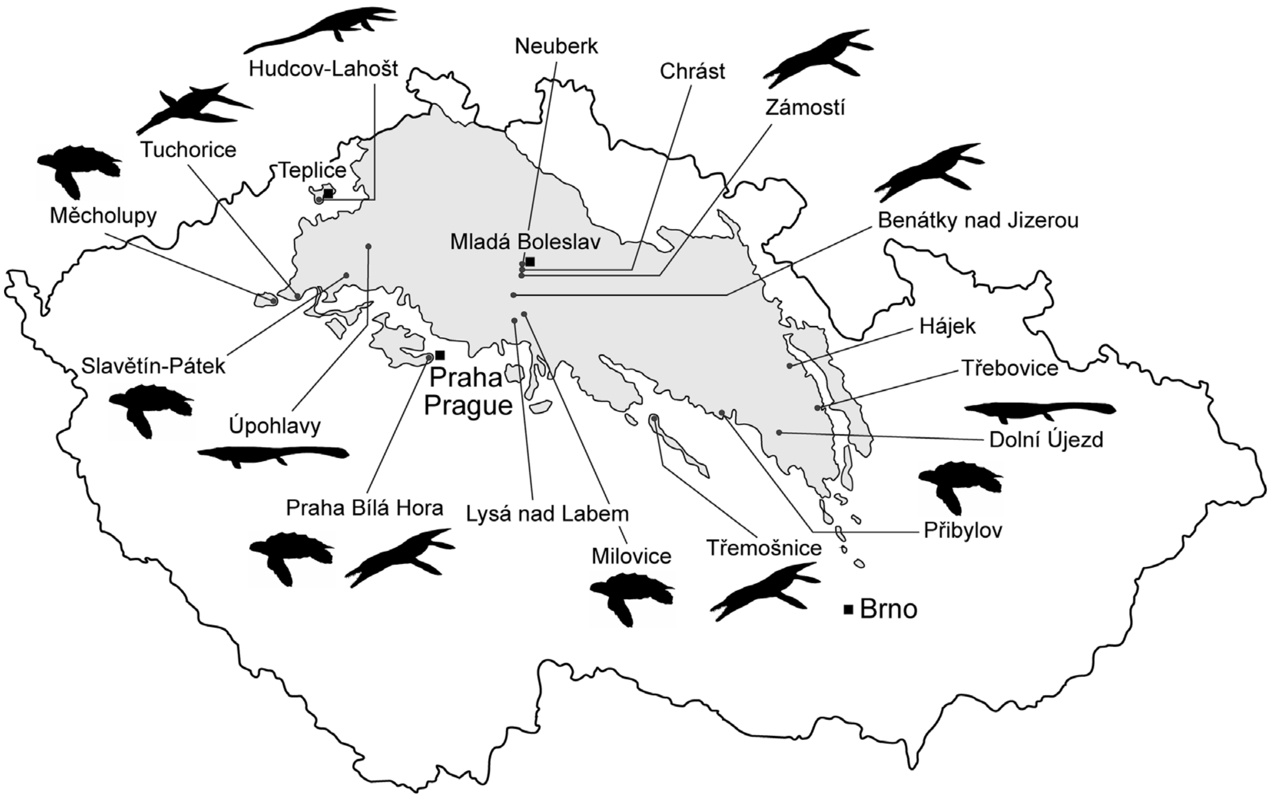

Figure 1. Diagrammatic map showing the boundaries of the Bohemian Cretaceous Basin within the Czech Republic and the distribution of identifiable marine amniote fossil occurrences (developed from Ekrt *et al.* 2001).

a maximum succession thickness of > 1000 m; Valečka & Skoček, 1991), but subsequent strata have been lost to basinal inversion and erosion during the Cenozoic (Čech, 2011).

3. Survey of the marine amniote fossils

Marine amniote remains have been found at numerous localities throughout the Bohemian Cretaceous Basin (see Fig. 1; Table 1). However, historical accounts indicate that discoveries were rare (Frič, 1877*b*; 1889*a*), even when quarrying was at its most intensive during the late nineteenth and early twentieth centuries. The majority of specimens now housed in public collections therefore date from this timeframe, and typically comprise either isolated or occasionally associated elements (e.g. Reuss, 1855; Frič, 1889*a*; Fritsch, 1906). The taphonomic disposition of the material is consistent with post-mortem carcass dismemberment under aerobic conditions, such as those that predominated in the Bohemian Cretaceous Basin during the Turonian (Uličný *et al.* 2009). Individual bones and teeth also usually display extensive surface damage (e.g. fragmentation, corrosion, edge rounding, carbonate dissolution of mineralized tissue remnants) coherent with transport via wave action and currents prior to burial, together with subsequent diagenetic alteration. Although little detailed stratigraphical information exists for many of the museum specimens, more recent excavations at the active Úpohlavy quarry site in NW Bohemia have shown that vertebrate remains, including shark and fish teeth, occur within condensed horizons (e.g. the Upper Coprolite Bed of the Teplice Formation; Ekrt *et al.* 2001; Wiese *et al.* 2004). Conversely, the serendipitous recovery of many historical marine amniote fossils implies a random distribution, but admittedly this is extrapolated from very poor site data.

Most documented marine amniote fossils from the Bohemian Cretaceous Basin are accessioned into the Department of Paleontology at the National Museum (NMP) in Prague. Some disruption and damage to these collections took place during WWII; however, almost all of the specimens have since been relocated and were made available for this study (see full specimen list in Table 2). Additional material described in published assessments by Ekrt *et al.* (2001) and Wiese *et al.* (2004) is housed in the Institute of Geology and Palaeontology at Charles University Prague (PG). Original finds reported by Fritsch & Bayer (1905) have also been 'rediscovered' in the Oblastní Museum in Most, NW Bohemia (OMM) and the Regional Museum in Teplice (RMT), NW Bohemia (Ekrt *et al.* 2012); these were also reassessed in this study.

3.a. Marine turtles

Marine turtle fossils from the Bohemian Cretaceous Basin comprise several incomplete postcranial skeletons as well as a few isolated elements. Karl (2002) and Karl *et al.* (2012) ascribed (without explicit character justifications) the small carapaces of *Cimochelys* ('*Chelone*') *benstedi* (Reuss, 1855; NMP Ob-00006

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Table 1. Documented marine amniote fossil localities in the Bohemian Cretaceous Basin, Czech Republic.

Locality	Stratigraphic unit/stratigraphic age	Lithology/marine amniote fossils
Hájek: abandoned quarry near Sudslava, E Bohemia	Korycany Member, Peruc-Korycany Formation/Upper Cenomanian	Coarse- to fine-grained glauconitic sandstones/mandible attributed to *Polyptychodon* (Jahn, 1904)
Praha-Bílá Hora: abandoned quarries extending from Strahov to Ladronka, central Bohemia	Bílá Hora Formation/Lower Turonian	Sandy or silty marlstones and spongolite marlstones/*Chelone regularis* limb bone (Fritsch, 1905*a*), *Aptychodon cretaceus* teeth (Reuss, 1855), *Polyptychodon* cranial/postcranial remains (e.g. Fritsch, 1878; Fritsch & Bayer, 1905)
Slavětín-Pátek: abandoned quarry between Slavětín and Pátek, N Bohemia	Bílá Hora Formation/Lower Turonian	Spongilitic sandy marlstones/carapace of '*Chelone*' *benstedi*
Tuchořice: abandoned quarry near Tuchořice, N Bohemia	Bílá Hora Formation/Lower Turonian	Marlstones/plesiosaurian tooth (Bayer, 1905)
Přibylov: abandoned quarry in Přibylov near Skuteč, E Bohemia	Bílá Hora Formation/Lower–Middle Turonian	Sandy marlstones/plesiosaurian postcranial fragments referred to *Cimoliasaurus lissaensis* (Fritsch & Bayer, 1905)
Třemošnice: abandoned quarry near Třemošnice, E Bohemia	Bílá Hora Formation/Lower Turonian	Spongilitic sandy marlstones/partial skull attributed to *Iserosaurus* sp. (Bayer, 1905)
Měcholupy: uncertain location near Měcholupy (Michelob), N Bohemia	Bílá Hora Formation?/Lower or Middle Turonian	Spongilitic sandy marlstones/carapace of *Pygmaeochelys michelobana* (Laube, 1896)
Dolní Újezd: garden excavation in Dolní Újezd part of Přibyňoves, E Bohemia	Jizera Formation?/Middle–Upper Turonian	Siliceous limestones/mosasauroid maxilla (Zázvorka, 1965)
Milovice: abandoned quarry close to church in Milovice, central Bohemia	Jizera Formation/Middle Turonian	Calcareous siltstones with limestone horizons/partial skeleton referred to *Iserosaurus literalis*; reptile vertebra (Fritsch, 1910)
Lysá nad Labem: abandoned quarry 4 km from Milovice, central Bohemia	Jizera Formation/Middle Turonian	Calcareous siltstones with limestone horizons/bone fragments (Fritsch & Bayer, 1905)
Benátky nad Jizerou (Nové Benátky): uncertain location NE of Benátky castle, central Bohemia	Jizera Formation/Middle–Upper Turonian	Marlstone/*Polyptychodon* teeth (Bayer, 1905)
Chrást: railway cutting close to Mladá Boleslav, central Bohemia	Jizera Formation/Middle–Upper Turonian	Silty marlstones/plesiosaurian postcranial fragments referred to *Cimoliasaurus vicinus* (Fritsch, 1906)
Zámostí: abandoned quarries N of Zámostí castle near Mladá Boleslav, central Bohemia	Jizera Formation/Upper Turonian	Alternating glauconitic and calcareous sandstones/teeth and jaw fragment of *Polyptychodon* (Bayer, 1897; Fritsch & Bayer, 1905)
Neuberk: abandoned quarries close to Neuberk castle in Mladá Boleslav, central Bohemia.	Jizera Formation/Upper Turonian	Calcareous sandstones/plesiosaurian vertebra (Bayer, 1905)
Úpohlavy: active quarry near Lovosice in N Bohemia	Teplice Formation/Upper Turonian	Bioturbated sandy and silty marlstones (upper Coprolitic Bed)/plesiosaurian bone fragments and mosasauroid tooth (Ekrt *et al.* 2001; Wiese *et al.* 2004)
Hudcov-Lahošt: abandoned quarries between villages near Teplice, N Bohemia	Teplice Formation/Upper Turonian	Limestones ('Hudcov Limestone')/plesiosaurian postcranial elements referred to cf. *Plesiosaurs bernardi*, *Cimoliasaurus teplicensis*, and *Hunosaurus fasseli* (Frič, 1889; Fritsch & Bayer, 1905)
Třebovice: recovered during rail station rennovation near Česká Třebová, E Bohemia	Teplice Formation/Upper Turonian	Glauconitic marlstones/bone fragments attributed to plesiosaurians (Augusta & Soukup, 1939)

is 72.8 mm long) and *Pygmaeochelys michelobana* (Laube, 1896), found in the Lower Turonian Bílá Hora Formation at Slavětín-Pátek and Měcholupy, respectively (stratigraphical correlations established by Zahálka, 1897; Čech *et al.* 1980), to *Rhinochelys cantabridgiensis* Lydekker, 1889*a*, a taxon known primarily from the Cenomanian of England (Collins, 1970). This classification followed Collins (1970), who assigned shell material previously designated as *Cimochelys benstedi* (*sensu* Zangerl, 1960) to *Rhinochelys* (otherwise represented by skull remains) because of phylogenetic and stratigraphical compatability. Moody (1993), Hirayama (1994, 1997) and Hooks (1998) likewise adopted this assumption, but recognized only the monotypic species, *R. pulchriceps* (Owen, 1851), which they placed (using *R. pulchriceps* + *Cimochelys benstedi* as a generic hypodigm) within Chelonioidea (true sea turtles) as either a basal representative (Hirayama, 1994, 1997) or immediate sister taxon to Protostegidae (Hooks, 1998).

Our reassessment of the Bílá Hora Formation marine turtle fossils confirms referral to Dermochelyoidea (Protostegidae + Dermochelyidae; *sensu* Hirayama, 1998; Kear & Lee, 2006), since the partially disarticulated carapace from Slavětín-Pátek (NMP Ob-00006) displays reduced distal portions of the costals and narrow, rectangular neurals (Fig. 2a). Exposure of NMP Ob-00006 in internal view additionally reveals insertion of the ribs into distinct groves on the posterior peripherals, a trait shared with derived protostegids (Protostegina; Hooks, 1998) and apparently also the lost holotype of *Pygmaeochelys michelobana* (Laube,

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Table 2. Inventory of diagnostic Late Cretaceous (Turonian) marine amniote fossils re-assessed for this study.

Taxon	Description	Specimen number	Locality/ stratigraphic age
cf. *Polyptychodon* sp. (‘*Aptychodon cretaceus*’)	Isolated teeth	NMP Ob-00007 (internal cast of NMP Ob-00044), NMP Ob-00044, NMP Ob-00053, NMP Ob-00055–NMP Ob-00068, NMP Ob-00082–NMP Ob-00087, NMP Ob-00094–NMP Ob-00096, NMP Ob-00122 (internal cast of NMP Ob-00211), NMP Ob-00123–NMP Ob-00124 (internal casts of NMP Ob-00044), NMP Ob-00211	Praha-Bílá Hora/Lower Turonian
cf. *Polyptychodon* sp.	Partial mandible	NMP Ob-00045/NMP Ob-00073	Praha-Bílá Hora/Lower Turonian
cf. Pliosauridae indet.	Vertebral centrum	NMP Ob-00020	Praha-Bílá Hora/Lower Turonian
Plesiosauria indet.	Bone fragments, vertebral centrum	NMP Ob-00202	Praha-Bílá Hora/Lower Turonian
Dermochelyoidea indet. (‘*Chelone regularis*’)	Isolated femur	NMP Ob-00002/NMP Ob-00050 (part/counterpart), NMP Ob-00051 (internal cast of NMP Ob-00002/NMP Ob-00050)	Praha-Bílá Hora/Lower Turonian
Chelonioidea indet.	Skull endocast	NMP Ob-00080	Praha-Bílá Hora/Lower Turonian
Dermochelyoidea indet. (‘*Chelone*’ *benstedi*)	Partial carapace	NMP Ob-00006	Pátek/Lower Turonian
cf. Polycotylidae indet.	Isolated tooth	NMP Ob-00214	Tuchorice/Lower Turonian
Indeterminate pliosauromorph (‘*Iserosaurus* sp.’)	Skull roof	NMP Ob-00043, NMP Ob-00074– NMP Ob-00076, NMP Ob-00097	Třemošnice/Lower–Middle Turonian?
Chelonoidea indet.	Isolated coracoid	NMP Ob-00003	Přibylov/Lower–Middle Turonian
Protostegidae indet. (‘*Iserosaurus literalis*’)	Disarticulated carapace, plastron, coracoid, humerus, other elements	NMP Ob-00021, NMP Ob-00054, NMP Ob-00072, NMP Ob-00078, NMP Ob-00093, NMP Ob-00162–NMP Ob-00169, NMP Ob-00170, NMP Ob-00201, NMP Ob-00212, NMP Ob-00213	Milovice/Middle Turonian
Chelonoidea indet.	Isolated cervical vertebra	NMP Ob-00081	Milovice/Middle Turonian
Tethysaurinae indet.	Isolated maxilla	NMP Ob-00052, NMP Ob-00069, NMP Ob-00071, NMP Ob-00088	Dolní Újezd/Middle–Upper Turonian?
cf. *Polyptychodon* sp.	Isolated tooth	NMP Ob-00105	Benátky nad Jizerou/Middle–Upper Turonian
Plesiosauria indet. (‘*Cimoliasaurus lissaensis*’)	Propodial and possible rib fragments	NMP Ob-00004, NMP Ob-00005, NMP Ob-00021	Chrást/Middle–Upper Turonian
cf. *Polyptychodon* sp.	Premaxillary section of snout	NMP Ob-00019	Zámostí/Middle–Upper Turonian
Plesiosauria indet.	Isolated vertebral centrum	NMP Ob-00077	Neuberk/Upper Turonian
Plesiosauria indet.	Vertebral centra, other fragments	PG Uy 2000/1–PG Uy 2000/11	Úpohlavy/Upper Turonian
Plesiosauria indet. (‘*Hunosaurus fasseli*’)	Associated phalanges	OMM G/pal1028, NMP Ob-00047–NMP Ob-00049 (casts of OMM G/pal1028)	Lahošt/Upper Turonian
Elasmosauridae indet. (‘*Cimoliasaurus teplicensis*’)	Vertebral centra, associated rib fragments, scapula, possible propodial	NMP Ob-00046, NMP Ob-00098–NMP Ob-00100, NMP Ob00106–NMP Ob-00117, RMT PA 1477	Hudcov/Upper Turonian

1896, p. 33, figs 1, 4). However, beyond this stratigraphical contemporaneity we find no convincing evidence for specific attribution of the Bohemian Cretaceous Basin turtle material to *Rhinochelys*.

Other turtle remains from the Bílá Hora Formation similarly manifest dermochelyoid affinities. NMP Ob-00002 and NMP Ob-00050 (Fig. 2b, c) from Bílá Hora, named as ‘*Chelone regularis*’ by Fritsch (1905*a*), comprise part and counterpart impressions of an isolated femur (not a tibia as suggested by Fritsch 1905*a*), whose proximal articular head is eroded but the distal trochanters (visible in the cast NMP Ob-00051; Fig. 2d) are connected by a bony ridge; this is an unequivocal synapomorphy of dermochelyoids (Hirayama, 1998). Fritsch (1905*b*, p. 3) additionally reported a neural (‘neuralreihe’; NMP Ob-00001) of ‘*Chelone regularis*’, but this is probably a fragment from a nautiloid shell. An isolated coracoid (NMP Ob-00003; Fig. 2e) is also known from the Bílá Hora Formation at Přibylov, and cannot be placed beyond Chelonioidea indet.

The partial endocast of a turtle skull (NMP Ob-00080) identified by Edinger (1934) and listed as *Rhinochelys* by Karl (2002) and Karl *et al.* (2012) incoporates impressions from the underside of the supraoccipital, the *crista supraoccipitalis*, and the inner surfaces of the posterior dermocranial elements together with part of the quadrate (Fig. 2f, g).

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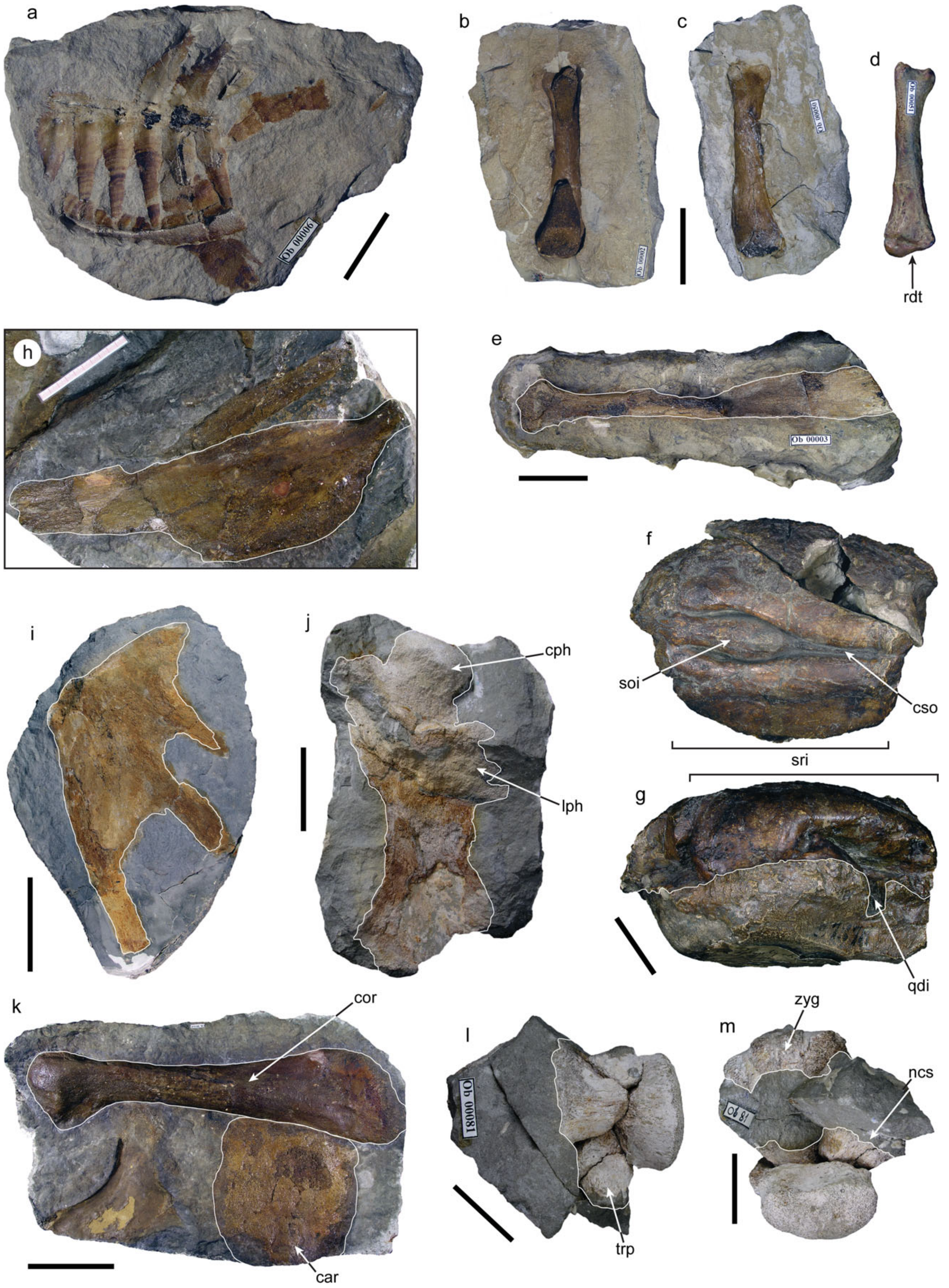

Figure 2. (Colour online) Diagnostic marine turtle fossils from the Bohemian Cretaceous Basin, Czech Republic. (a) Partial dermochelyoid carapace (NMP Ob-00006) in internal view. Indeterminate dermochelyoid femur preserved as impressions in (b) part (NMP Ob-00002) and (c) counterpart blocks (NMP Ob-00050), with a (d) plaster cast shown in posterior view (NMP Ob-00051). (e) Chelonioid coracoid in lateral view (NMP Ob-00003). Indeterminate chelonioid endocranial cast (NMP Ob-00080) in (f) dorsal and (g) lateral views. Components of a large protostegid skeleton including: (h) a costal (NMP Ob-00165) in internal view; (i) stellate hyo/hypoplastron fragment (NMP Ob-00212); (j) humerus (NMP Ob-00021) in dorsal view; and (k) coracoid and flattened carpal element

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Posterior expansion of the skull roof suggests poor development of the upper temporal emargination, which is a plesiomorphic feature of chelonioids (Joyce, 2007).

A dissarticulated skeleton (individually numbered NMP Ob-00021, NMP Ob-00054, NMP Ob-00072, NMP Ob-00078, NMP Ob-00093, NMP Ob-00162–NMP Ob-00170, NMP Ob-00201, NMP Ob-00212, NMP Ob-00213) from the Middle Turonian (Havlíček *et al.* 2001) Jizera Formation strata at Milovice represents a huge protostegid (humeral length = 298.8 mm). This specimen was originally described as a marine squamate ('*Iserosaurus litoralis*') by Fritsch (1905*a*, *b*, 1910) but subsequently referred to '*Archelon*' cf. *copei* (Wieland, 1909) by Karl (2002). It displays a number of diagnostic states coherent with referral to Protostegidae: reduced costals (NMP Ob-00165; Fig. 2h); stellate hyo-hypoplastral elements (NMP Ob-00212; Fig. 2i); humerus with lateral process located distal to the caput humeri and enlarged within the anterior portion of the shaft (NMP Ob-00021; Fig. 2j); widely divergent (>110°) scapular processes (evident from the plaster cast 'femur' photographed by Fritsch, 1910, plate 8, fig. 2); an elongate coracoid; and flattened carpal elements (NMP Ob-00164; Fig. 2k; see character distributions in Zangerl, 1953*a*; Hirayama, 1994, 1997, 1998; Hooks, 1998; Lehman & Tomlinson, 2004; Kear & Lee, 2006). Hooks (1998) variously reassigned the remains of '*Archelon*' *copei* to *Microstega* Hooks, 1998 or *Archelon ischyros* Wieland, 1896 based on differing degrees of costal reduction – not discernible in the Milovice fossils. The humerus (NMP Ob-00021) from Milovice also lacks reduction of the lateral process to a low ridge, which is a trait otherwise indicative of *Archelon* Wieland, 1896 (Hooks, 1998); we therefore reject assignment of the Bohemian Cretaceous Basin protostegid to this genus (*sensu* Karl, 2002).

An isolated cervical vertebra (NMP Ob-00081), figured by Fritsch (1910, plate 9, figs 1, 2), has also been recovered from Milovice. This latter specimen has a noticably short centrum (36.6/43.3 mm long/wide; Fig. 2l), which resembles those of protostegids (e.g. Zangerl, 1953*a*, p. 116, fig. 53; Elliott, 1997, p. 251, fig. 4). Conversely, its posterior condyle (Fig. 2m) is dorsoventrally compressed (23.4/36.54 mm high/wide) like those of both cheloniids (Hirayama, 1994, 1998) and basal chelonioids such as *Toxochelys* Cope, 1873 (see Zangerl, 1953*b*, plate 20B). The ventral surface of the centrum is badly damaged but what might be the broken base of a ventral keel is evident (Fig. 2l). The neurapophysis is disarticulated but preserves remnants of the zygopophyses and the neurocentral suture, which apparently bisected the transverse process as in modern cheloniids (Zangerl, 1960).

3.b. Plesiosaurians

Plesiosaurians represent the most numerically common and stratigraphically ubiquitous component of the Bohemian Cretaceous Basin fossil marine amniote fauna. Despite this, diagnostic remains are only known from sediments of Turonian age. The purported mandible of *Polyptychodon* (NMP Ob-5583) reported by Jahn (1904) from the Upper Cenomanian Peruc–Korycany Formation appears to be a phosphatic concretionary mass with amorphous internal structure.

Early Turonian plesiosaurian material from the Bílá Hora Formation at Bílá Hora (age correlated by Čech *et al.* 1980) incorporates both isolated teeth and associated skeletal elements. Of particular note is a short curved tooth (NMP Ob-00214; Fig. 3a), preserved partly as an impression (maximum height = 17.1 mm), which displays a circular cross-section and closely spaced (<1 mm apart) enamel ridges restricted to the lingual side of the crown. Similar 'gracile' (*sensu* O'Keefe, 2001) tooth morphologies with 'asymmetrically' distributed (= present on one face of the tooth, *sensu* O'Keefe, 2001; Großmann, 2007), fine enamel ridges are observable in many plesiosauroid taxa (Sato, 2003; Druckenmiller & Russell, 2008). The dentitions of Cretaceous polycotylids (e.g. *Thililua* Bardet, Pereda Suberbiola & Jalil, 2003*a*; *Dolichorhynchops tropicensis* McKean, 2012) and some elasmosaurids (e.g. *Eromangasaurus* Kear, 2005*a*) being especially compatible. On the other hand, the majority of elasmosaurids exhibit labio-lingually compressed teeth (e.g *Hydrotherosaurus* Welles, 1943, *Callawayasaurus* Carpenter, 1999, *Terminonatator* Sato, 2003, *Futabasaurus* Sato, Hasegawa & Manabe, 2006; see also character discussion in Druckenmiller & Russell, 2008) and their overall crown height is usually much larger (up to 40 mm; see Buchy, 2006, p. 9, table 3).

Both the Bílá Hora Formation and Middle–Upper Turonian Jizera Formation have yielded remains traditionally attributed to the enigmatic large pliosauromorph (*sensu* O'Keefe, 2002) *Polyptychodon interruptus* (e.g. Fritsch, 1878, 1905*a*; Bayer, 1896, 1897, 1898; Fritsch & Bayer, 1905). Fritsch (1878), additionally referred the isolated teeth of *Aptychodon cretaceus* (e.g. the natural impression NMP Ob-00082 described by Reuss, 1855; Fig. 3b) to *P. interruptus*; however, Welles (1962) considered both these taxa to be non-diagnostic. Irrespectively though, their large

(NMP Ob-00164). Indeterminate chelonioid cervical vertebra (NMP Ob-00081) in (k) ventral and (l) posterior views. Scale bars represent 30 mm in (a–e, l, m); 50 mm in (f, g, j); 100 mm in (h, i, k). Abbreviations: car – carpal; cor – coracoid; cph – caput humeri; cso – *crista supraoccipitalis* impression; lph – lateral process distal to humeral head; ncs – neuro-central suture; qdi – quadrate impression; rdt – ridge between distal trochanters; soi – supraoccipital impression; sri – skull roof impression; trp – transverse process; zyg – zygopophysis base.

Figure 3. (Colour online) Diagnostic plesiosaurian fossils from the Bohemian Cretaceous Basin, Czech Republic. (a) Possible polycotylid tooth (NMP Ob-00214) in labial (top) and lingual (bottom) views. Remains compatible with the large pliosauromorph *Polytychodon*. (b) Tooth impression referred to '*Aptychodon cretaceus*' (NMP Ob-00082). (c) Natural mould (NMP Ob-00211) and (d) plaster

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size (NMP Ob-00082; maximum height of preserved impression = 114 mm), coupled with distinctive crown ornamentation comprising prominent, closely spaced ridges that extend to the apex but bifurcate and become densely packed towards the crown-base, is consistent with dental remnants typically attributed to *Polyptychodon* from the Cenomanian–Turonian of Europe (Bardet & Godefroit, 1995) and North America (Welles & Slaughter, 1963; VonLoh & Bell, 1998). Note that Schumacher (2008) and Schumacher *et al*. (2013) distinguished the North American Late Cretaceous *P. hudsoni* Welles & Slaughter, 1963, *Brachauchenius lucasi* Williston, 1903 and *Megacephalosaurus eulerti* Schumacher, Carpenter, & Everhart, 2013 from *P. interruptus* because they display branching enamel ridges; we likewise employ this convention for the Bohemian Cretaceous Basin specimens since they manifest the same trait.

Polyptychodon-like teeth from the Bílá Hora Formation (see Table 2 for specimen list) are often preserved as impressions with the original mineralized tissues dissolved during diagenesis (e.g. NMP Ob-00211; shown together with a plaster cast NMP Ob-00122; Fig. 3c, d). Regardless, these specimens provide further states that are coherent with published definitions of *Polyptychodon* (Milner, 1987; Bardet & Godefroit, 1995): robust recurved crown with a sub-circular basal cross-section (maximum height/diameter of NMP Ob-00082 = 84.8/34 mm). Evaluating the generic validity of *Polyptychodon* is beyond the scope of this paper. However, the dental features evident in the Bohemian Cretaceous Basin pliosauromorph teeth are essentially plesiomorphic (see character polarizations in O'Keefe, 2001; T. Sato, unpub. thesis, University of Calgary, 2002; Druckenmiller & Russell, 2008; Smith & Dyke, 2008; Ketchum & Benson, 2010) and resemble those of other large-skulled Cretaceous taxa such as *Brachauchenius* Williston, 1903 (Schumacher, 2008) and *Kronosaurus* Longman, 1924 (Kear, 2005*b*).

Additional dentigerous elements including the symphyseal region of a mandible (NMP Ob-00045, NMP Ob-00073) from Bílá Hora and a premaxillary section of snout (NMP Ob-00019) from the Jizera Formation at Zámostí (Middle–Upper Turonian; Zahálka, 1903; Čech *et al.* 1980) are also consistent with large-skulled *Polyptychodon*-like pliosauromorphs. The decorticated mandible (NMP Ob-00045, NMP Ob-00073; Fig. 3e) is exposed in ventral aspect (the dorsal surface is obscured by matrix) and preserves a 15 mm deep tooth impression with distinctive branching ridges that extend to the apex (Fig. 3f). Both the anterior and posterior extremities of the mandible have been broken off, as has the left posterior ramus. Nonetheless, the preserved element is still quite large being 644 mm long, but remarkably slender with a maximum height/width of 80.5/181 mm. The symphysis is formed by the splenials and dentaries, which enclose an anterior projection of the angular (continuing anteriorly to within *c.* 40 mm of the symphyseal contact). There is no evidence of mandibular constriction or ventral keeling as occurs in plesiomorphic pliosauromorphs such as *Rhomaleosaurus* Seeley, 1874 (see O'Keefe, 2001; Druckenmiller & Russell, 2008; Smith & Dyke, 2008).

Although badly damaged, the Zámostí premaxillae (NMP Ob-00019: Fig. 3g–i) represent a weakly-tapered section of snout. Six alveoli are preserved with three teeth still *in situ*; maximum tooth height/diameter is 110/36.2 mm. Like the Bílá Hora mandible (NMP Ob-00073) NMP Ob-00019 is slender, being 137.9 mm long but only 95.5/152.5 mm high/wide at the midline, and could perhaps indicate a longirostrine skull (similar to that reconstructed for *Brachauchenius* by Albright *et al.* 2007*a*; Schumacher, 2008; and *Megacephalosaurus* by Schumacher *et al.* 2013). The dorsal surface of NMP Ob-00019 is heavily worn, making it difficult to establish whether the inter-premaxillary suture was elevated into a midline ridge as occurs in many plesiosaurians (e.g. *Umoonasaurus* Kear, Schroeder & Lee, 2006; Druckenmiller & Russell, 2008; Smith & Dyke 2008). Posteriorly, the premaxillae enclose a central cavity (filled with matrix) that might correspond to a cranial sinus.

Other diagnostic plesiosaurian remains from the Bohemian Cretaceous Basin include the parietal-squamosal region of a large skull (NMP Ob-00043; 200.1/158 mm in maximum preserved length/width) listed as '*Iserosaurus*' (Bayer, 1905) from probable Bílá Hora Formation rocks near Třemošnice (Lower or Middle Turonian; Čech *et al.* 1980). NMP Ob-00043 is exposed in dorsal view (Fig. 3j) with some unidentifiable elements, possibly the atlas-axis and components of the basicranium. The bone surfaces are badly damaged; however, the inter-parietal suture and area surrounding the pineal opening are discernable. Most importantly, there is no evidence of a squamosal bulb. This is a distinctive feature of many pliosauroids (e.g. *Peloneustes* Lydekker, 1889*b*; Andrews, 1913; Ketchum & Benson, 2011) but is conspicuously absent in Cretaceous taxa including *Leptocleidus* Andrews, 1922 (Druckenmiller & Russell, 2008; Kear & Barrett, 2011), *Brachauchenius* (Carpenter, 1996; Albright

cast (NMP Ob-00122) of a ridged enamel crown. (e) Mandible (NMP Ob-00080) in ventral view, with enlargement of (f) tooth impression. Premaxillary section of snout (NMP Ob-00019) in (g) ventral, (h) lateral and (i) posterior views and (j) the parietal-squamosal section of a skull roof (NMP Ob-00043). (k) Pliosaurid-like vertebral centrum (NMP Ob-00020) in ventral view. Elements of an elasmosaurid skeleton: (l) two articulated cervical vertebral exposed in cross-section (NMP Ob-00109); (m) a caudal vertebra in ventral view and (n) scapula in lateral view, both enlarged from (o) a reassembled series of associated blocks (RMT PA 1477). Scale bars represent 10 mm in (a, f); 30 mm in (b–d, l, m); 50 mm in (k, n); 100 mm in (g–j, o); 200 mm in (e). Abbreviations: cav (m) – caudal vertebra shown in (m); ics – internal cranial sinus; scp (n) – scapula shown in (n); sym – symphysis; vnf – ventral nutrient foramina.

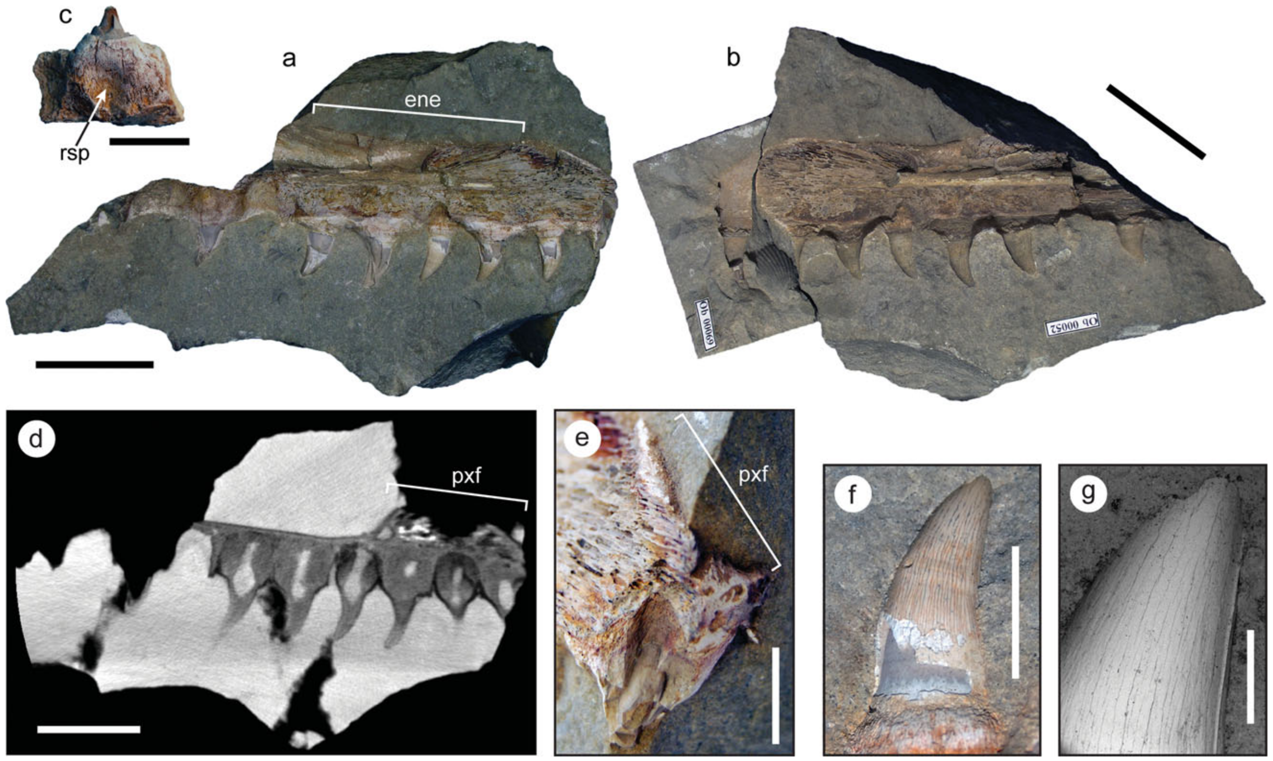

Figure 4. (Colour online) Diagnostic aquatic squamate fossils from the Bohemian Cretaceous Basin, Czech Republic. Tethysaurine maxilla (NMP Ob-00052, NMP Ob-00069, NMP Ob-00088) split into (a) part and (b) counterpart sections; (c) removed tooth base (NMP Ob-00071); (d) CT generated cross-section image through NMP Ob-00088 revealing extent of the premaxillary contact; (e) anterior view of premaxillary contact; (f) enlargement of the fourth maxillary tooth crown from NMP Ob-00088; and (g) SEM image of the fourth maxillary tooth showing the smooth enamel surface and posterior carina. Scale bars represent 50 mm in (a, b, e); 10 mm in (c, d, f); 4 mm in (g). Abbreviations: ene – embayment for external nasal aperture; pxf – premaxillary facet; rsp – resorption pit.

et al. 2007*a*), *Megacephalosaurus* (Schumacher *et al.* 2013) and *Polyptychodon* (Owen, 1851; Welles & Slaughter, 1963).

Identifiable plesiosaurian postcranial elements include a large dorsal centrum (NMP Ob-00020: maximum length/width/height = 82.8/97.9/65.6 mm; Fig. 3k) from the Bílá Hora Formation at Bílá Hora that lacks ventral nutrient foramina (*foramina subcentralia sensu* Storrs, 1991). Druckenmiller & Russell (2008) suggested that this condition might be unique to *Brachauchenius* and *Kronosaurus*.

Ekrt *et al*. (2012) gave a brief account of '*Cimoliasaurus teplicensis*' (Fritsch, 1906) from the Teplice Formation at Hudcov (Upper Turonian; Wiese *et al.* 2004). This disarticulated skeleton incorporates probable dorsal and caudal centra (Fig. 3m), ribs and an incomplete scapula (Fig. 3n) that have been embedded in a plaster panel mount (RMT PA 1477; Fig. 3o). Some articulated cervical (Fig. 3l) and dorsal vertebral centra (NMP Ob-00098, NMP Ob-00100, NMP Ob-00109) are also known from the same locality. The latter are only visible in cross-section but the cervicals (NMP Ob-00109) are clearly longer than wide (length/width = 46/39 mm) with small, centrally positioned ventral nutrient foramina and platycoelous articular surfaces. Similar states have been used to define Elasmosauridae (Welles, 1943, 1952; Brown, 1981, 1993; Bardet *et al.* 1999; O'Keefe, 2001; T. Sato, unpub. thesis, University of Calgary 2002; Druckenmiller & Russell, 2008; Vincent *et al.* 2011). The scapula of RMT PA 1477 is exposed in lateral view and is missing most of its dorsal blade, but likewise conforms to the general morphology of elasmosaurids (e.g. *Hydrotherosaurus*: Welles, 1943, p. 241, plate 23*a*; *Albertonectes* Kubo, Mitchell, Henderson, 2012; Kubo *et al.* 2012, p. 563–564, fig. 6B).

3.c. Aquatic squamates

The mosasauroid maxilla described by Zázvorka (1965) was recovered from exposed bedrock during excavations in a garden (J. Hurych, pers. comm. 2012) in the village of Dolní Újezd (part of Přibyňoves) in E Bohemia. The landscape surrounding Dolní Újezd is covered by loessic brown soil, although Middle Turonian Jizera Formation limestones extend in a NW–SE-trending band *c.* 3 km to the west (Stárková & Opletal, 1998; Adamovič *et al.* 2000). The Dolní Újezd maxilla has been split through its lateral wall to form a part (NMP Ob-00088; Fig. 4a) and counterpart (NMP Ob-00052, NMP Ob-00069; Fig. 4b). A tooth (NMP Ob-00071; Fig. 4c) has also been removed from NMP Ob-00088 to show the expanded bony base of attachment and a posterolingual resorption pit (indicative of mosasauroids; Bell, 1997; Caldwell &

Palci, 2007). The maxilla is 181.5/35 mm long/high but lacks its posterior extremity. Its anterodorsal margin is shallowly embayed between the third and sixth tooth positions to accommodate the external bony nasal aperture. The premaxilla suture is just visible anteriorly (Fig. 4d), and is delimited anteriorly by the fourth tooth position as evidenced from CT images (Fig. 4e) generated at the Czech Technical University in Prague. Caldwell (1999, 2000) and Bardet *et al*. (2003*b*) used projection of the premaxilla–maxilla suture beyond the fourth maxillary tooth position to define Mosasauridae; a more posterior termination is evident in derived forms (Bell, 1997). Makádi *et al*. (2012) also listed restriction of the premaxilla–maxilla contact anterior to the midline of the fourth maxillary tooth position as a diagnostic feature of the primitive mosasauroid clade Tethysaurinae. NMP Ob-00088 preserves nine alveoli with seven pleurodont teeth (c. 15 mm in crown height) *in situ*. The crowns are posteromedially curved (Fig. 4f) and weakly oval in cross-section. The exposed labial enamel surfaces are smooth with weak unserrated carinae (Fig. 4g), similar to those of tethysaurines such as *Tethysaurus* Bardet, Pereda Suberbiola & Jalil, 2003*b*, *Russellosaurus* Polcyn & Bell, 2005 and *Pannoniasaurus* Makádi, Caldwell & Ősi, 2012.

4. Palaeobiogeographical and biostratigraphical conclusions

Although fragmentary, the Turonian marine amniote remains from the Bohemian Cretaceous Basin contribute an important record of early Late Cretaceous faunal diversity from the northern Tethyan margin. Identifiable higher-level taxa such as protostegid sea turtles (archytypal in pre-Coniacian strata; Hirayama, 1997), possible polycotylid and elasmosaurid plesiosaurs and tethysaurine mosasauroids represent lineages that were widespread during this timeframe, and conform with documented finds from elsewhere along the northern/eastern European platforms (see summarative lists in Welles, 1962; Persson, 1963; Bardet & Godefroit, 1995; Storrs *et al.* 2000; Karl, 2002; Bardet *et al.* 2008) and the contiguous North African rim of the Mediterranean Tethys (e.g. Bardet *et al.* 2003*a*, *b*; Buchy *et al.* 2005*b*; Buchy, 2006; Tong *et al.* 2006). Ekrt *et al.* (2008) concluded that Turonian teleost fish assemblages from the Bohemian Cretaceous Basin were compositionally Boreal in character, and reflected a common pelagic distributional range (based on palaeogeographical reconstructions; Ziegler, 1988) across the northern European shelf sea. Conversely, macroinvertebrate taxa seem to have been mixed, with high-latitude Boreal forms (e.g. allocrioceratid and collignoniceratid ammonites; Weise & Voigt, 2002) occurring in conjunction with distinctive Tethyan benthic elements (Kollmann *et al.* 1998).

The Boreal affinities of Bohemian Cretaceous Basin assemblages become noticeably more pronounced during the Late Turonian, following the onset of marked climatic cooling (Voigt & Wiese, 2000). How this event would have affected coeval pelagic marine amniotes is unclear. Certainly though, early mosasauroid radiations seem to have been influenced by water temperature (Jacobs *et al.* 2005; Bardet *et al.* 2008), with Turonian tethysaurines in particular displaying a low-mid palaeolatitudinal distribution (from *c.* 45° N to 30° S latitude; Jacobs *et al.* 2005) extending from North Africa (*Tethysaurus*, Morrocco; Bardet *et al.* 2003*b*), across the palaeo-Atlantic into the Western Interior Seaway of North America (*Russellosaurus*, Texas; Polcyn & Bell, 2005) and southwards to the Gondwanan margin of South America (*Yaguarasaurus*, Colombia; Páramo-Fonseca, 2000). The recognition of probable tethysaurine mosasauroids from Middle–Upper Turonian sequences in the Bohemian Cretaceous Basin is therefore not surprising; indeed, the group seems to have persisted within the mid-latitude Northern European Platform region up until the Maastrichtian (e.g. *Pannoniasaurus*, Hungary; Makádi *et al.* 2012).

The co-occurrence of mosasauroids and large-bodied, macrophagous pliosauromorphs (cf. *Polyptychodon* sp.) in the Middle–Upper Turonian Jizera Formation also emphasizes the compositional similarity of Bohemian Cretaceous Basin assemblages to their mid-latitudinal equivalents in North America (e.g. VonLoh & Bell, 1998). Unfortunately, poor stratigraphical control of the Bohemian Cretaceous Basin fossils limits determination of a clear temporal overlap. Nevertheless, both mosasauroids and large predatory pliosauromorphs are known to have co-existed for a brief interval based on the well-constrained North American records (Schumacher, 2011). Significantly, the last definitive incidences of *Polyptychodon*-like fossils in the Northern European Platform are stratigraphically coincident (e.g. Czech Republic, Germany, England: Milner, 1987; Sachs, 2000), implying a simultaneous global extinction and wholesale replacement of the last plesiosaurian megacarnivores by derived mosasauroids during Late Turonian times.

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