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The first crocodylomorph from the Mesozoic of Turkey (Barremian of Zonguldak) and the dispersal of the eusuchians during the Cretaceous

Stéphane Jouve^{a,b,*}, Volkan Sarıgül^c, J.-Sébastien Steyer^b and Sevket Sen^b

^aSorbonne Universités, UPMC, CR2P, 4 Place Jussieu, 75005 Paris, France; ^bCentre de Recherches sur la Paléobiodiversité et les Paléoenvironnements, UMR 7202 CNRS-MNHN-UPMC, 8 rue Buffon, CP38, Muséum national d'Histoire naturelle, 75005 Paris, France; ^cMuseum of Texas Tech University, 4th Street, Box 43191, Lubbock, Texas, 79409, USA

(Received 7 February 2017; accepted 26 September 2017)

A new crocodylomorph from the upper Barremian İncigez Formation of Zonguldak (NW Turkey) is described for the first time based on jaw and limb bone elements from the collection of the Istanbul Technical University. The material is attributed to *Turcosuchus okani* gen. et sp. nov. according to a unique combination of character states, such as a strong heterodonty, composed of non-spatulated teeth, a maximum of 10 teeth posterior to the symphysis, a sigmoidal dorsal margin of the dentary in lateral view, and a splenial excluded from the symphysis. An updated phylogenetic analysis of crocodylomorphs confirms that this new taxon belongs to the Hylaeochampsidae, and that it forms a relatively robust clade with the derived *Unasuchus*, *Acynodon*, *Iharkutosuchus* and *Hylaeochampsia*. *Turcosuchus* also presents some anatomical convergence with bernissartids, allodaposuchids, basal globidontans and other crocodylians. *Turcosuchus okani* is one of the earliest, but not basal hylaeochampsids, and the first known Early Cretaceous eusuchian outside Europe and North America. Our results support the clear geographical segregation between the Late Cretaceous tribodont eusuchians: basal globidontans in North America, and hylaeochampsids in the Tethyan area.

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Keywords: *Turcosuchus okani*; Hylaeochampsidae; Eusuchia; Turkey; phylogeny; palaeobiogeography

Introduction

Fossil tetrapod studies in Turkey are mostly restricted to Cenozoic mammals. Only a few Permian to Cretaceous tetrapod remains have been described so far, which include jaw fragments of the Late Cretaceous *Mosaurus hoffmani* (Bardet & Tunçözü 2002), footprints of a Permian captorhinid (Gand *et al.* 2011) and pelvic remains of a Late Triassic ichthyosaur (Mouanga *et al.* 2011) in north-western Anatolia. This is in addition to the recent south-eastern Anatolian discoveries of temnospondyls from the Middle Permian and Lower Triassic and mosasaur fragments from the Upper Cretaceous deposits, respectively (Yılmaz *et al.* 2014; Fortuny *et al.* 2015). The study of fossil archosaurs in Turkey is also in its infancy; only poorly preserved jaw fragments, teeth and a caudal vertebra of a phytosaur(s) from the Upper Triassic Çenger Formation (western Taurides, SW Turkey) have been described so far (Buffetaut *et al.* 1988). These specimens, together with new material collected by Olivier Monod (Géosciences Orléans, France), and one of our team (JSS), will be studied in detail (Steyer *et al.* in prep.).

The new material described here consists of jaw and limb bone elements found by one of our team (SS) in the palaeontological collections of the Istanbul Technical University (İstanbul Teknik Üniversitesi, İTÜ). It was collected from Gelik (Zonguldak district, NW Turkey) several decades ago, but no referral to the collection date or exact locality and horizon is reported. The collector is anonymous, but a preliminary identification was probably made during the late 1960s or 1970s by Cazibe Sayar (today a retired palaeontologist from İTÜ). This material represents the first Mesozoic crocodylomorph from Turkey. A detailed description is given here, as well as an updated phylogenetic analysis of eusuchian crocodylomorphs to test the position of this new taxon within the clade. The resulting consensual topology is calibrated in time and space to discuss biogeographical scenarios dealing with the evolution of the basal eusuchians.

Geological setting and locality

The geological framework of Zonguldak displays an interrupted but enduring depositional history, ranging from the

*Corresponding author. Email: jouvestephane@yahoo.fr

Carboniferous to the Eocene (Fig. 1). The Carboniferous rocks of Zonguldak are represented by the famous coal deposits, clustered under the name Zonguldak Formation (Tüysüz 1999) that constitutes the only Palaeozoic unit of the area. Sedimentation restarted after a long hiatus with the platform carbonates of the Kimmeridgian–Berriasian İnalı Formation that is unconformably overlain by the Barremian–Albian Lower Cretaceous sequence (e.g. Tüysüz 1999; Tüysüz *et al.* 2004; Hippolyte *et al.* 2010, 2015; Okan Tüysüz pers. comm. 2016). The lower portion of the Lower Cretaceous transgressive sequence initiates with the terrestrial basal clastics of the upper Barremian İncigez Formation, then continues with the limestones and dolostones of the Kapuz Formation and the marls of the Kilimli Formation which represent a shallow marine environment. The Öküşmedere and Çengellidere formations, described in the eastern part of Zonguldak (e.g. Derman 1990; Derman & İztan 1997), are considered here as the consecutive lateral equivalents of the Kapuz and Kilimli formations. The sequence continues with the Aptian–Albian siliciclastics of the Velibey and Sapça formations and terminates with the marls of the Tasmaca Formation, accentuating the shifting trend in sedimentation. The final phase of the Zonguldak sedimentary sequence corresponds to the Upper Cretaceous–Eocene transgressive sequence, including volcano-clastic rocks and pelagic carbonates (e.g. Tüysüz 1999; Tüysüz *et al.* 2012).

Together with the Zonguldak and İnalı formations, the basal portion of the Lower Cretaceous sequence is exposed around Gelik, a small town in the Zonguldak district, located east of Zonguldak city centre (Fig. 1). The Zonguldak and İncigez formations are the only two terrestrial deposits around Gelik. The exact locality of the specimen is unknown, but as the collection label mentions the Zonguldak district, it must have been collected from the Barremian İncigez Formation of Gelik (Fig. 1).

Systematic palaeontology

Crocodylomorpha Hay, 1930 *sensu* Nesbitt 2011

Neosuchia Clark in Benton & Clark, 1988

Eusuchia Huxley, 1875 *sensu* Brochu 2003

Family Hylaeochampsidae Andrews, 1913

Genus *Turcosuchus* gen. nov.

Etymology. Derived from the Latin words ‘*Turcus*’ meaning Turk or Turkish, and ‘*suchus*’ meaning crocodile.

Type species. *Turcosuchus okani* sp. nov.

Diagnosis. As for the type and only known species.

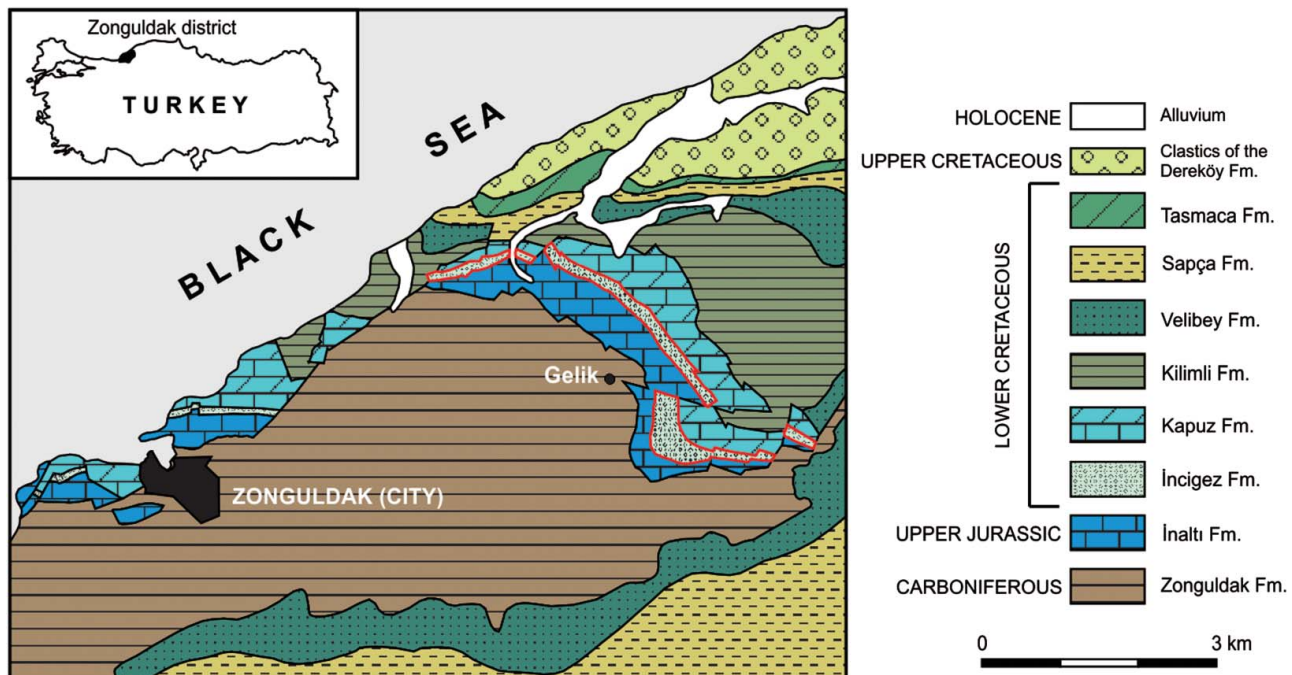


Figure 1. Geological map of the Zonguldak district (NW Turkey) including the location of Gelik (modified after Tüysüz 1999). The lithological borders of the İncigez Formation around the town of Gelik are highlighted in red, from where *Turcosuchus okani* was possibly collected.

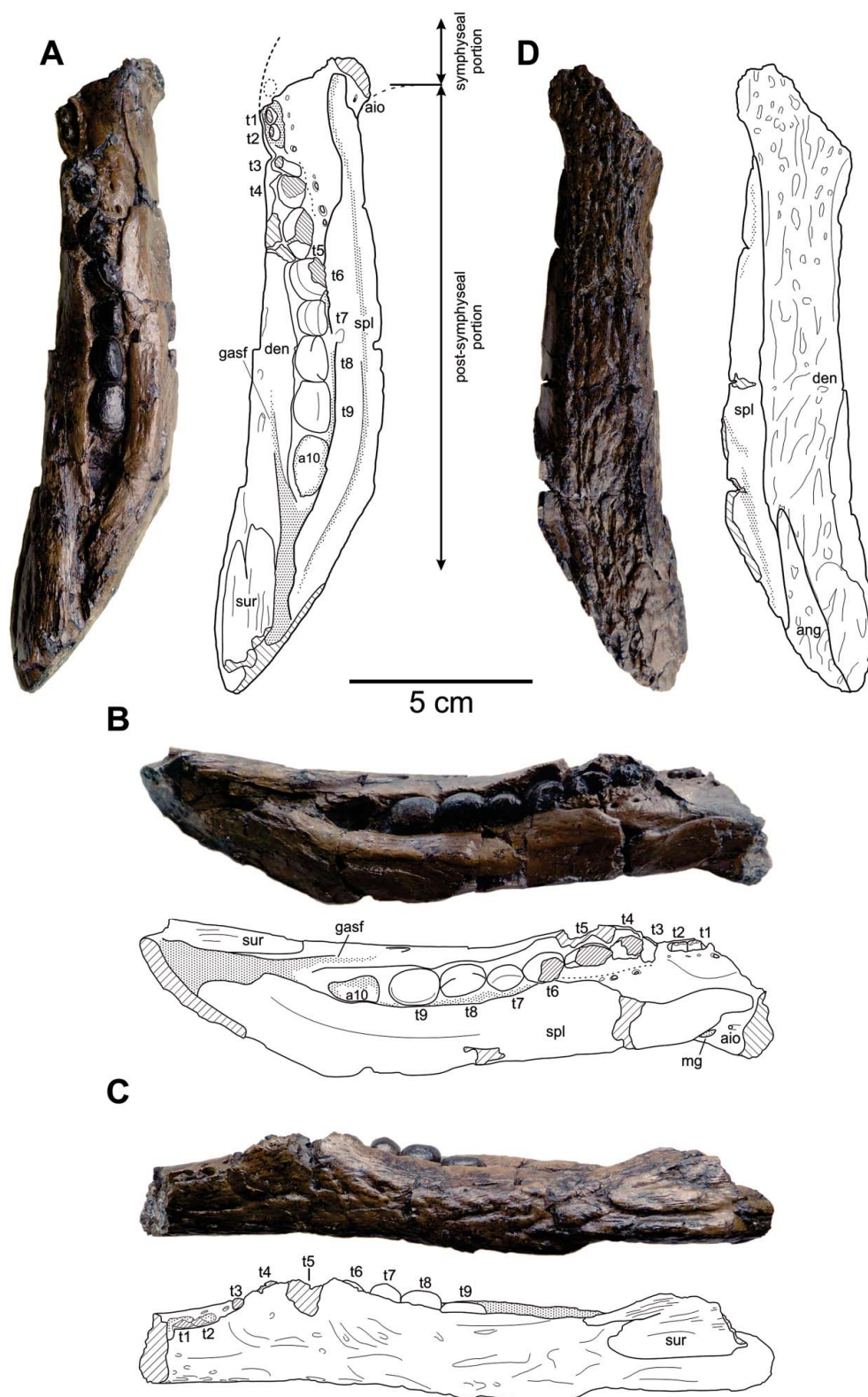


Figure 2. *Turcosuchus okani* gen. et sp. nov., holotype, İTÜ-Z1, anterior portion of the left hemimandible, Barremian, Gelik, Zonguldak district, Turkey, in: **A**, dorsal; **B**, dorsolingual; **C**, labial; and **D**, ventral views. The hatching indicates the damaged areas and dashed lines denote the inferred orientation of the symphyseal portion. Abbreviations: aio, anterior intermandibularis oralis foramen; ang, angular; a10, 10th preserved tooth alveolus; den, dentary; gasf, groove of the anterior surangular foramen; mg, Meckelian groove; spl, splenial; sur, surangular; t1–9, preserved teeth (1st to 9th).

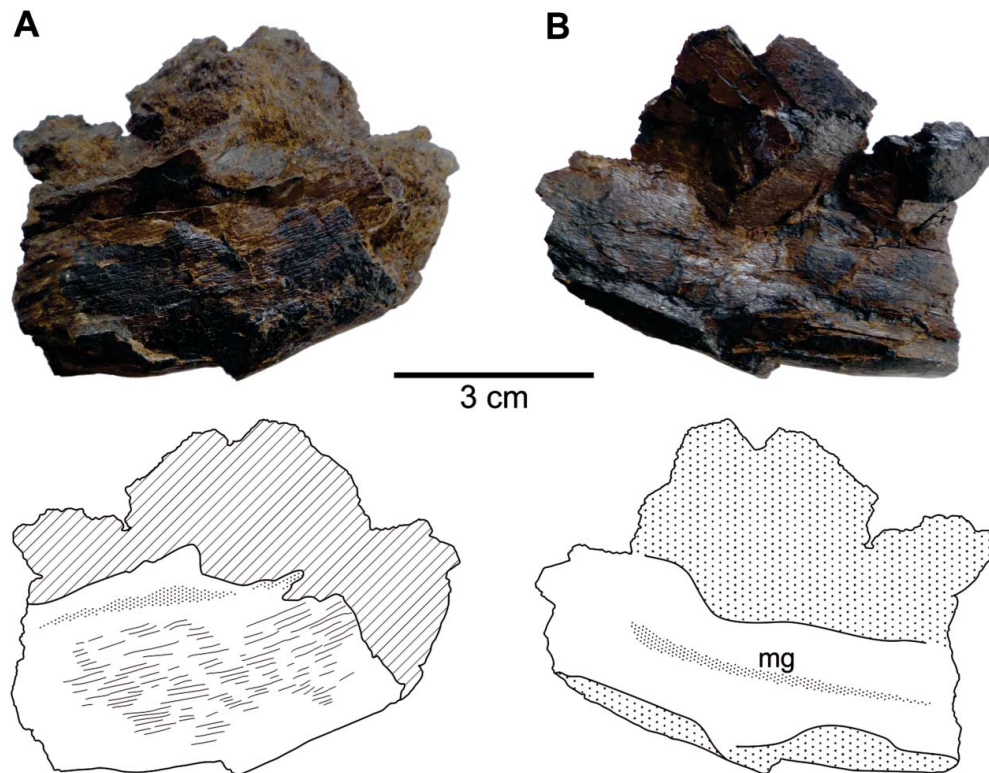


Figure 3. *Turcosuchus okani* gen. et sp. nov., holotype, İTÜ-Z1, posterior portion of the left hemimandible, Barremian, Gelik, Zonguldak district, Turkey, in: **A**, labial; and **B**, lingual views. The hatching indicates the damaged areas. Abbreviation: mg, Meckelian groove.

Turcosuchus okani sp. nov.
(Figs 2–6)

Etymology. Named in honour of Okan Tüysüz, Turkish structural geologist, who solved the problem of the stratigraphical provenance of the specimen studied here.

Holotype. Collection number İTÜ-Z1, partial left dentary with attached splenial and part of surangular, posterior fragment of left mandible, undetermined piece of a jaw bone yielding a portion of a tooth row, proximal portion of the right humeral shaft, distal portion of the left tibial shaft.

Type locality and horizon. Gelik area, Zonguldak district, the exact locality and horizon are unknown but the material is from the late Barremian İnciğez Formation (see above).

Diagnosis. Hylaeochampsid with the following combination of characters: strong heterodonty in size and shape; last three dentary teeth tribodont; at least two conical teeth anterior to the 8th tooth from the distal end; no spatulated morphology observed in any tooth; dental row closely packed, except a diastema between the 8th and 9th tooth from the distal end; 10 teeth or less in post-symphyseal dentary row; sigmoidal dorsal margin of

dentary in lateral view with two concave surfaces; splenial excluded from the symphysis.

Description and comparisons.

Preservation. The bones are a dark colour, reflecting the anoxic early diagenetic conditions where the cavities, a result of the degradation of the organic matter, are filled by pyrite (Pfretzschner 2004). Pyrite crystals are easily noticeable, even on the bone surfaces, as little pale yellow dots.

Mandible. The left hemi-mandible is almost completely preserved, except in its symphyseal and articular regions. Although this hemi-mandible is dorsoventrally compressed and slightly distorted, it is still discernible that the dentary is mediolaterally narrow, with a consistent width throughout, and that it undulates laterally prior to the symphysis (Fig. 2A, B). The lateral and lateroventral sides of the preserved portion of the dentary are ornamented with small pits, and a set of parallel-lying ridges (Fig. 2C, D). As visible in the lateral view, the sinusoidal dorsal margin consists of two concave surfaces that are demarcated by the higher dorsal margin on which the 5th preserved tooth is erupted (Fig. 2C). Although slightly deformed, it is also discernible that the anterior curvature is deeper than the posterior one, and that the anterior teeth

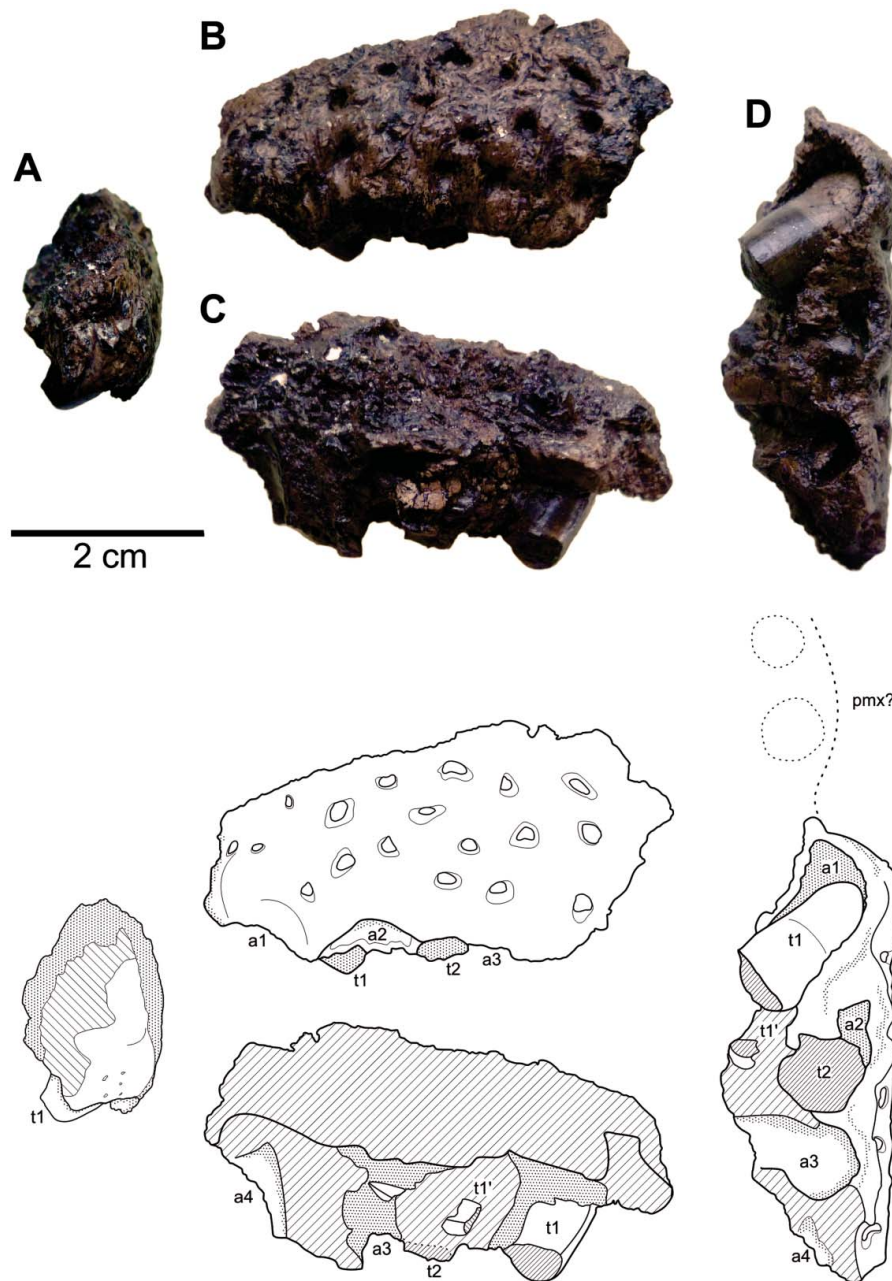


Figure 4. *Turcosuchus okani* gen. et sp. nov., holotype, İTÜ-Z1, portion of a left maxilla or right dentary, Barremian, Gelik, Zonguldak district, Turkey, in: **A**, anterior; **B**, labial; **C**, lingual; and **D**, dorsal views. The hatching indicates the damaged areas. Abbreviations: a1–4, preserved alveoli numbered front to back; t1–2, preserved teeth; t1', broken apical side of the preserved teeth.

are slightly oriented anterolaterally. The posterior margin of the dentary is also gently curved from the 6th to the most posterior preserved alveoli, with the dentary being slightly laterally depleted. These mandibular curvatures are observed, more or less deep, in nearly all neosuchians, but they are weak or absent in *Iharkutosuchus makadii* Ösi *et al.*, 2007, *Unasuchus reginae* Brinkmann, 1992 and *Pietraroiasuchus ormezzanoi* Buscalioni *et al.*, 2011. The dorsal surface of the mandible is narrow medial to the

tooth row and just posterior to the symphysis, the mandibular branch being nearly as wide at this level as more posteriorly. The medial margin of the dentary is narrow in hylaeochampsids, such as *Acynodon iberoccitanus* Buscalioni *et al.*, 1997, *Iharkutosuchus makadii* Ösi *et al.*, 2007 (SJ, pers. obs.) and *Bernissartia fagesii* Dollo, 1883, and forms a wide anterior dorsal plate in the basal globidontans, such as *Brachychampsia montana*, Gilmore 1911 (Sullivan & Lucas 2003), *Allognathosuchus* spp. (Brochu

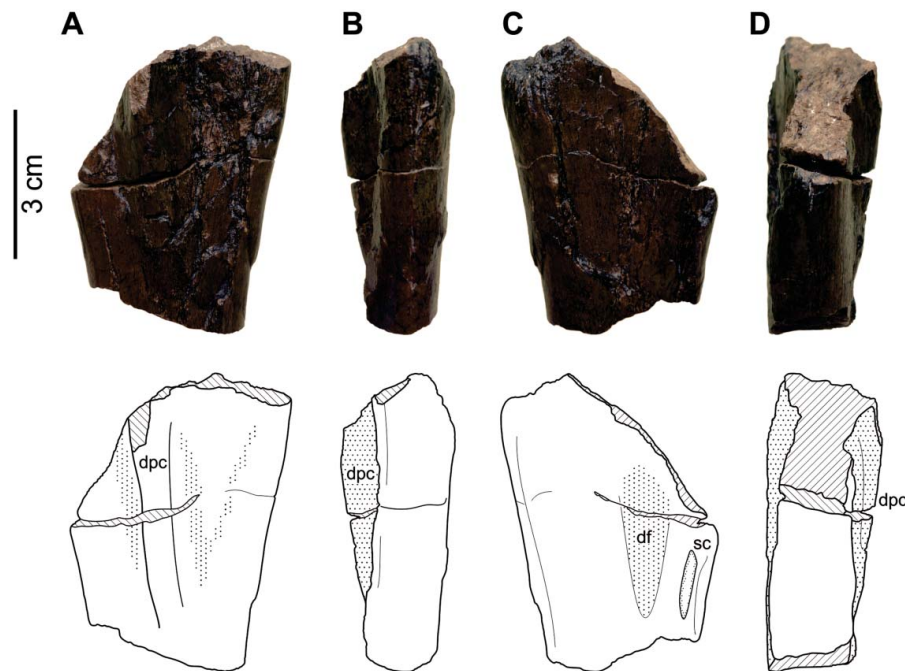


Figure 5. *Turcosuchus okani* gen. et sp. nov., holotype, ITÜ-Z1, proximal portion of the right humeral shaft, Barremian, Gelik, Zonguldak district, Turkey, in: **A**, ventral; **B**, medial; **C**, dorsal; and **D**, lateral views. The hatching indicates the damaged areas. Abbreviations: df, dorsal fossa; dpc, distalmost portion of the deltopectoral crest; sc, muscle scar for Mm. teres major and latissimus dorsi.

2004) and *Stangerochampsia mccabei* Wu *et al.*, 1996. A set of foramina called the ‘special foramina’ by Edmund (1957) are visible immediately lingual to the dental arcade. The row of these foramina can be tracked along the preserved anterior portion of the dentary, to the splenial overlaps around the 5th preserved tooth. The ventral part of the mandible is crushed and the anterior acute process of the angular is visible on the ventral side: it penetrates between the splenial and dentary, and reaches the level of the anterior margin of the last alveolus (Fig. 2D).

The splenial forms most of the medial margin of the dentary (Fig. 2A, B). The anterior tip of the splenial is curved medially and terminates as a high lamina above the Meckelian canal. The splenial covers most of the Meckelian groove where only a tiny extent becomes visible anteriorly (Fig. 2B). The splenial is excluded from the symphysis, as in most hylaeochampsids, such as *Pietraroiasuchus ormezzanoi*, *Acynodon adriaticus* Delfino *et al.*, 2008b, *A. iberoccitanus* (Martin 2007), and in some blunt toothed globidontans, such as *Brachychampsia montana*, *Kuttanacaiman iquitosensis* Salas-Gismondi *et al.*, 2015 and *Caiman wannlangstoni* Salas-Gismondi *et al.*, 2015. In contrast, the splenial participates in the symphysis in *Unasuchus reginae* and *Iharkutosuchus makadii*, and in the non-eusuchian *Bernissartia fagesii*. The posterior dorsal surface of the splenial, situated medially to the last three alveoli, is distinctly swelled and forms a lip-shaped crest. This thickening on the splenial is different from that observed in the basal globidontans *B. montana*, *Allognathosuchus* spp., *Globidentosuchus brachyrostris*

Scheyer *et al.*, 2013, *K. iquitosensis* and *Stangerochampsia mccabei*, in which the splenial forms a prominent shelf that overhangs medially its ventral surface. The posterior intermandibularis oralis foramen, which may perforate the splenial in its midpart, cannot be detected due to the poor preservation of the splenial. Instead, a tiny anterior foramen, visible on the lingual surface of the anteriormost preserved part of the dentary, is interpreted as the possible anterior intermandibularis oralis foramen (Fig. 2A, B), but it cannot be excluded that it was only an accessory foramen as observed in some alligatoroid specimens (SJ, pers. obs.).

A shallow anteroposterior groove extends lateral to the last alveolus on the *Turcosuchus* mandible (Fig. 2A, B). It is interpreted as the groove of the anterior surangular foramen and suggests that this foramen is located dorsally on the surangular. This groove also separates the dorsal and ventral processes of the surangular: although the dorsal anterior process is not preserved, the ventral anterior process is elongated anteriorly, as is the case in alligatoroids (Brochu 1997, 1999), and in the hylaeochampsids *Acynodon iberoccitanus* (SJ, pers. obs.) and *Iharkutosuchus makadii* (Ösi *et al.* 2007), and in both species *Pachycheilosuchus trinquei* Rogers, 2003 (Buscalioni *et al.* 2011) and *Shamosuchus djadochtaensis* Mook, 1924 (Pol *et al.* 2009) recently described as hylaeochampsids (Narváez *et al.* 2016). The anterior extent of the ventral surangular processes does not reach the posteriormost mandibular tooth, as in tribodont globidontans like *Brachychampsia* spp. (Williamson 1996), *Allognathosuchus* spp. and *S. mccabei*.

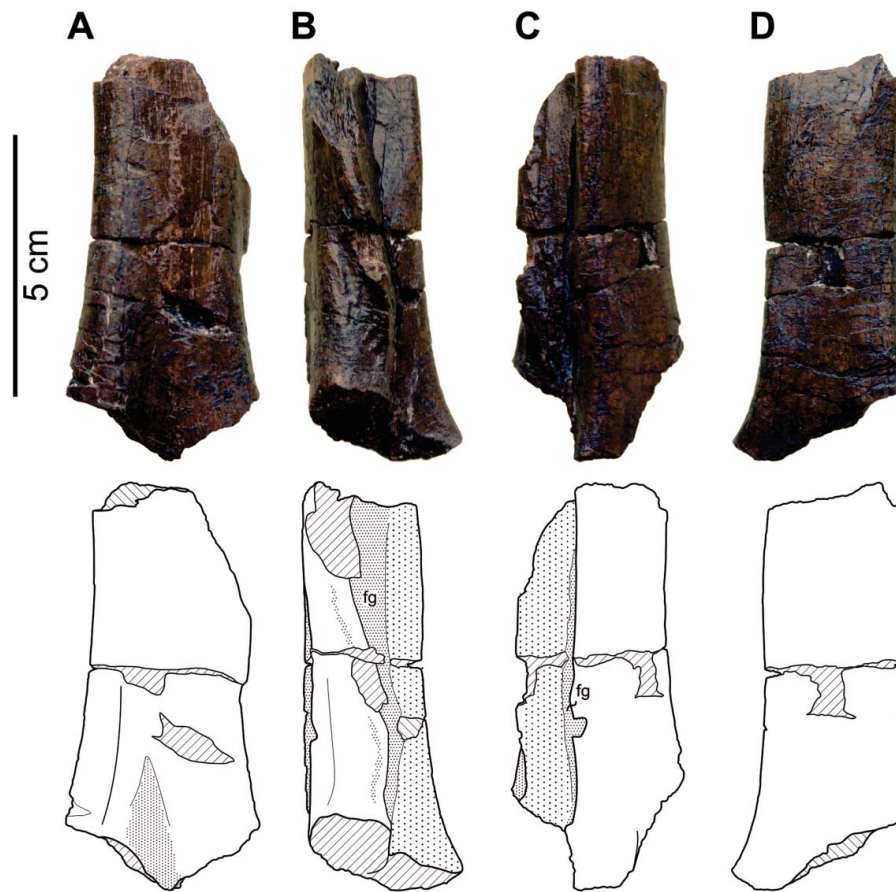


Figure 6. *Turcosuchus okani* gen. et sp. nov., holotype, İTÜ-Z1, distal portion of the left tibial shaft, Barremian, Gelik, Zonguldak district, Turkey. **A**, anterior; **B**, lateral; **C**, posterior; **D**, medial views. The hatching indicates the damaged areas. Abbreviation: fg, fibular groove.

The posterior portion of the lower jaw is poorly preserved and consists almost exclusively of the angular (Fig. 3). Striations on its lateral side possibly indicate the insertion area of the *M. pterygoideus ventralis*, the main jaw adductor muscle in neosuchians (Holliday & Witmer 2007; Ősi 2014). The slightly concave medial side of the angular represents the posterior part of the Meckelian groove.

Undetermined jaw fragment. The second element which yields a portion of the tooth row is a fragment of an unidentifiable jaw bone. The anterior side of the jaw fragment is slightly curved medially (Fig. 4A), where the lateral side is ornamented with distinct pits, and the lateral margins of the alveoli are slightly concave (Fig. 4B, C). These preserved alveoli are rounded, as in most crocodylians (Brochu 2004), and are not confluent with each other. A conical and bicarinate tooth lacking most of the apical portion is preserved in the first alveolus, whereas the second alveolus contains a very fragmented and slightly displaced tooth (Fig. 4D). The missing apical portion of the first tooth is embedded within the crushed remains of the second tooth (Fig. 4C, D). Although broken in half, the crown of the first

preserved tooth measures about 1.65 cm, with a root about 0.8 cm long. The mesiodistal and labiolingual diameters of the broken section are 0.7 cm and 0.5 cm, respectively. No basal constriction is present. The third tooth socket is empty, and only a small portion of the mesial side of the fourth alveolus is preserved.

Dentition. The preserved dental row corresponds to the post-symphyseal region of the dentary and bears nine teeth and a posterior tooth socket (Fig. 2A, B). This pattern resembles that of derived hylaeochampsids, in which only 10 or fewer teeth occur on the post-symphyseal dentary. The dental pattern of *Turcosuchus okani* is strongly heterodont: the first three preserved teeth are slender and oval in cross section. They are followed by four more robust conical and bicarinate teeth whose morphology is very similar to the first preserved tooth on the undetermined jaw bone. The two subconical and blunt posterior teeth are typical of the tribodont condition (Buffetaut & Ford 1979); the same morphology is also inferred for the missing last tooth. These tribodont teeth have a mesiodistal diameter of about 1 cm, but the penultimate is the largest preserved tooth (Supplemental Appendix 1). It cannot

be excluded that the last tooth is the largest (the last alveoli is extremely deformed), as in *A. prenasalis* Loomis, 1904 and *Allognathosuchus mooki*. In *I. makadii*, *U. reginae*, *B. fagesii*, *A. iberoccitanus* and *B. montana*, the largest is the penultimate (Supplemental Appendix 1). The apical surfaces of the tribodont teeth are smooth and no ornamentation is observed. Distal and mesial carinae are present in all teeth of adequate preservation, even on the first tribodont tooth that reflects a transitional morphology. The penultimate tooth is too abraded to identify any carina. No true serration is observed (pseudozipodonty, e.g. Prasad & Lapparent de Broin 2002). The root and crown are demarcated by a deep constriction in the last two preserved teeth, and with a shallower constriction for the tooth just anterior, as is observed in globidont neosuchians (Ösi 2014). These teeth are large, almost smooth, with an ovoid contour in dorsal view, and consistently differ from that which is observed in *Bernissartia fagesii*. In the latter species, the tribodont teeth are smaller, bear numerous vertical wrinkles, and have a typical kidney shape (Buffetaut & Ford 1979; Mazin *et al.* 2009). The poor preservation of the anterior teeth does not allow confirmation of the existence of constriction.

The teeth are tightly placed on the tooth row. The first and second preserved alveoli seem to be confluent but a slight interalveolar space is visible between the second and the third preserved teeth. In all the hylaeochampsids, the distance between the teeth is constant, and without diastema. In *Turcosuchus okani*, the teeth posterior to the 4th preserved tooth are closely packed, with no confluent alveoli, contrary to that which is observed in many alligatoroids. In possible hylaeochampsids *Pachycheilosuchus trinquei* and *P. ormezzanoi* the posterior teeth are more spaced. These posterior teeth probably did not occlude the upper ones.

Postcrania. The material also consists of a partial right humerus and a partial left tibia. The partial right humerus preserves the proximal end and the bone shaft (Fig. 5). Only the distalmost portion of the deltopectoral crest is preserved on the ventral side, which is opposed by a proximally expanding fossa on the dorsal side. A small scar on the posterolateral side of the dorsal surface might have served as an insertion area for *Mm. teres major* and *latissimus dorsi* (Meers 2003). The partial left tibia consists of a distal fragment of triangular outline. A distinct groove, facing the fibula, is visible on its posterolateral side, as in most crocodylians (Nesbitt 2011, character 337) (Fig. 6). The distal articular surface is missing.

Phylogenetic analysis

Methods

The new material was included in an updated matrix of neosuchians, including 193 morphological characters and

107 ingroup taxa (Supplemental Appendices 2 and 3). *Goniopholis simus* Owen, 1878 was used as the outgroup taxon and *Unasuchus reginae* Brinkmann 1992, a crocodyliform with disputed taxonomic placement (Martin & Delfino 2010), was also included. The matrix was based on Brochu & Storrs (2012) and Narváez *et al.* (2015, 2016) with a few modifications in the coding. Character 106 was modified after Brochu & Storrs (2012). We added five characters to the matrix: character 190 was adopted from Salas-Gismondi *et al.* (2015, character 198), whereas the final four characters 190 to 193 are introduced here for the first time. Characters were weighted equally and multistate characters left unordered by following Fitch parsimony (Fitch 1971). The maximum parsimony analysis was conducted using TNT version 1.1 (Goloboff *et al.* 2003, 2008). Tree-space was searched by using the advanced search methods in TNT for 5000 random addition replicates. The default settings for the advanced search methods are changed to increase the iterations of each method per replicate, which now comprises 100 sectorial search drifting cycles, 100 ratchet iterations, 100 drift cycles, and 100 rounds of tree fusion per replicate. This tree-space search procedure was repeated for five different random start seeds. Nodal support was evaluated using Bremer support index, and the trees were manipulated with Mesquite (Maddison & Maddison 2011).



Results

The phylogenetic analysis generated 133 equally most parsimonious trees with a length of 807 steps (CI: 0.326; RI: 0.7875), and a strict consensus tree with 817 steps (CI: 0.322, RI: 0.7837) (Fig. 7; Supplemental Appendix 4). This strict consensus tree is globally congruent with previous results (e.g. Narváez *et al.* 2016). Accordingly, *Turcosuchus okani* belongs to Eusuchia. Within this large clade, *T. okani* is recognized as a member of the Hylaeochampsidae. It forms, together with *Pachycheilosuchus*, *Shamosuchus* and *Pietraroiasuchus*, the stem-group of a clade including *Unasuchus* and more derived hylaeochampsids (i.e. *Acynodon*, *Iharkutosuchus* and *Hylaeochampsia vectiana* Owen, 1874). The clade including *Turcosuchus okani* and more derived hylaeochampsids is supported by three synapomorphies (see remarks below): the posterior dentary, or maxillary teeth, are tribodont [character 190(1), convergent with basal globidontans and few other taxa], the largest dentary tooth in diameter is the penultimate tooth [character 106(1), convergent with basal globidontans], and 10 teeth or fewer on the post-symphyseal region [character 191(1), convergent with gavialoids and most of the crocodylians]. This clade is relatively robust, with a Bremer index of 4, whereas the Bremer index is 1 for Hylaeochampsidae, Eusuchia, and all more basal hylaeochampsids.

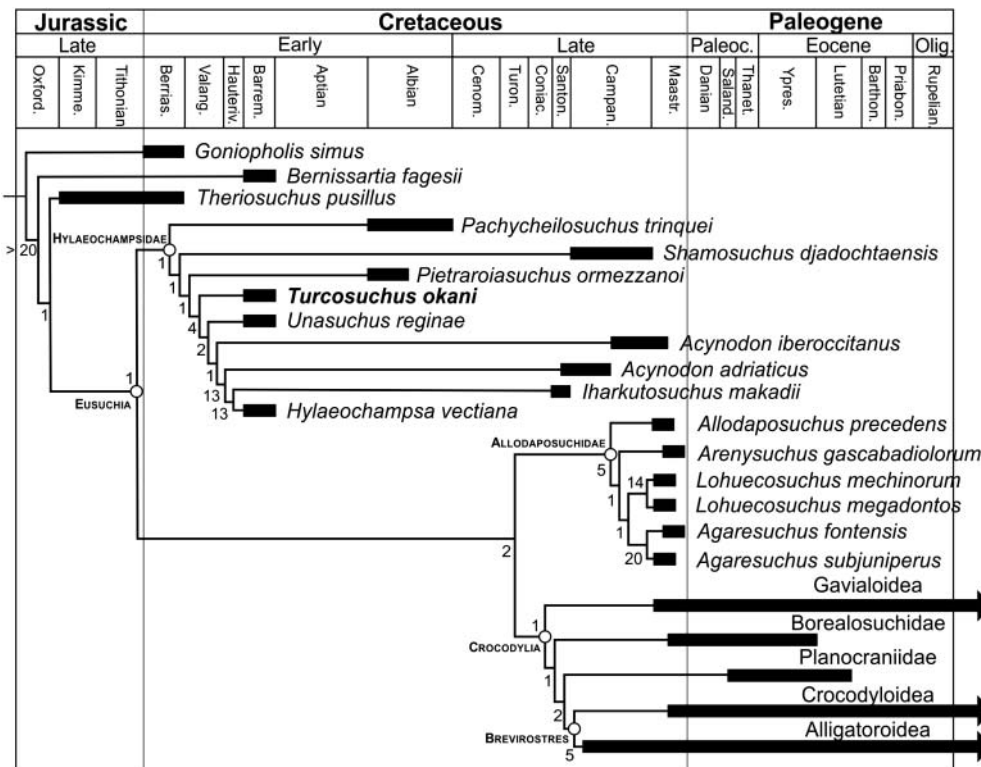


Figure 7. Phylogenetic position of *Turcosuchus okani* gen. et sp. nov. within crocodylomorphs. Calibrated cladogram based on a simplified strict consensus of 142 MPTs, tree lengths 817 steps (see text). CI = 0.325, RI = 0.7837. The black rectangles represent the stratigraphical distribution of each taxon. The geological time scale is from Gradstein *et al.* (2012).

Unasuchus reginae, the taxonomic position of which remains controversial within crocodylomorphs (Martin & Delfino 2010; Turner *et al.* 2016), is recognized here as a hylaeochampsid, more precisely as the sister-taxon of the clade comprising *Acynodon*, *Iharkutosuchus* and *Hylaeochampsia*. This clade is supported by only one synapomorphy: the dentary is linear between the 4th and the 10th alveoli [character 50(2)].

Discussion

Lower dentition of *Turcosuchus* and other eusuchians

Since the three synapomorphies shared by *Turcosuchus okani* and derived hylaeochampsids pertain to the lower jaw dentition (see above), dental patterns in non-marine neosuchians deserve further comments, starting with the concepts of heterodonty and tribodonty: heterodonty, which means having different kinds of teeth, is observed in various crocodyliforms and appears as an ecologically convergent character (Ösi 2014). Among neosuchians, the posterior teeth of bernissartids are tribodont, distinctly striated and kidney-shaped, and lateromedially compressed, while more anterior teeth are leaf shaped (Mazin *et al.*

2009). In most hylaeochampsids, these teeth are larger, not kidney-shaped, and less lateromedially compressed. In the possible hylaeochampsids *Pachycheilosuchus trinquei* and *Pietraroiasuchus ormezzanoi*, the dentition displays a homodont pattern with conical teeth of nearly the same size, whereas *Shamosuchus djadochtaensis* possesses conical anterior and more robust posterior teeth. In *Acynodon iberoccitanus* and *Iharkutosuchus makadii*, heterodonty is accentuated with spatulate and equidimensional anterior teeth and larger ovoid tribodont/molariform posterior teeth (Buscalioni *et al.* 1997; Martin 2007; Ösi *et al.* 2007), whereas in *Unasuchus reginae* and *Acynodon adriaticus*, the anterior teeth morphology is more conical, as in *Turcosuchus okani* (Brinkmann 1992; Delfino *et al.* 2008b) (Fig. 3). In alligatoroids, the teeth anterior to the tribodont ones are more or less conical.

Tribodonty, on the other hand, means having bulbous crushing teeth at the distalmost portion of the dental arcade: this condition occurs only in some heterodont eusuchians. Crushing posterior teeth are observed in *Turcosuchus okani* but also in bernissartids, *Unasuchus reginae*, derived hylaeochampsids and various alligatoroids (e.g. Lucas & Estep 2000; Martin 2007; Ösi *et al.* 2007, 2014; Delfino *et al.* 2008b; Sweetman *et al.* 2015). Because of this varied distribution among eusuchians,

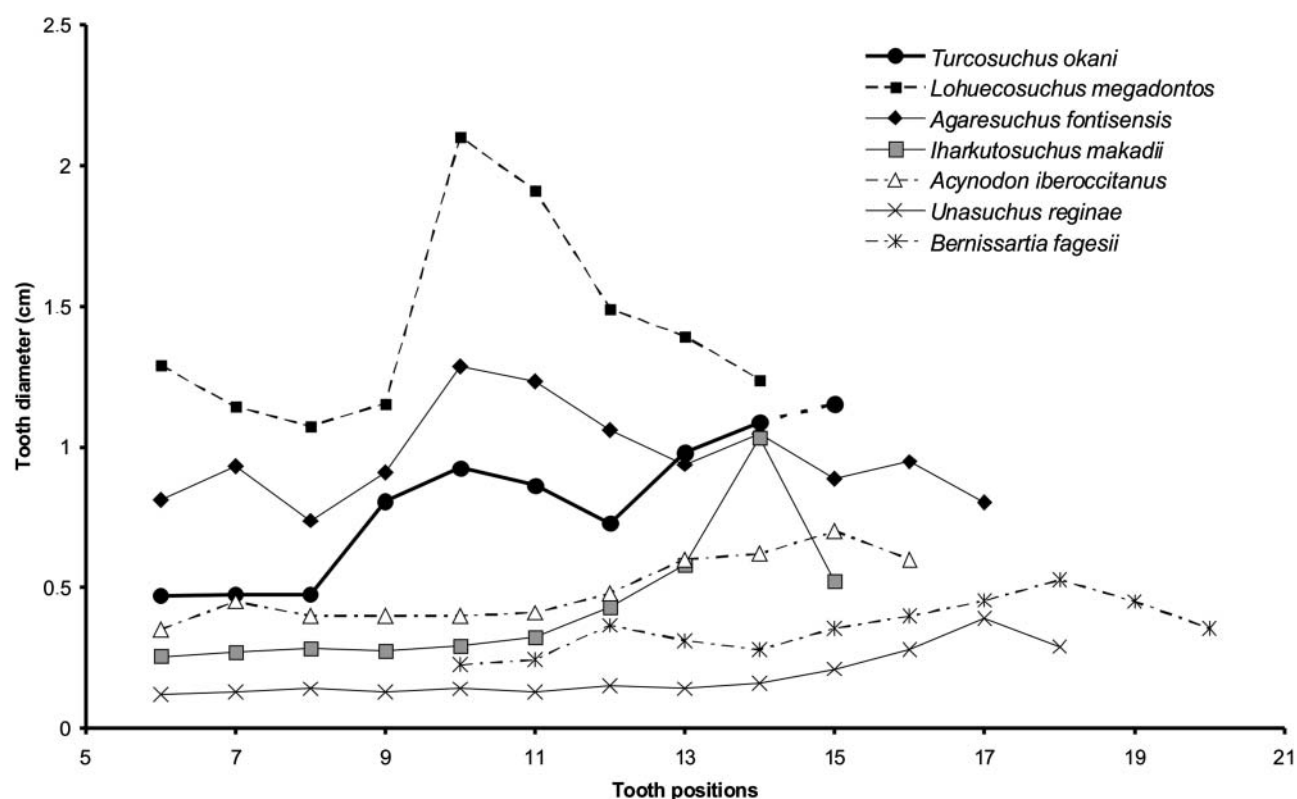


Figure 8. Tooth measurements (diameter versus position) of *Turcosuchus okani* gen. et sp. nov. compared with other basal eusuchians (Supplemental Appendix 1). Since the anterior portion of the mandible is unknown in *Turcosuchus okani*, the exact location of the preserved teeth in the tooth row is also unknown. Therefore, the largest anterior tooth in diameter is considered as the 10th as in allodaposuchids.

tribodonty should be considered as an ecological convergence related to a peculiar diet, and not as a clear diagnostic or autapomorphic character (Ösi 2014; Brochu *et al.* 2015). This situation explains possible misidentifications of some hylaeochampsids (e.g. *Acynodon*) as alligatoroids (e.g. Buscalioni *et al.* 1997; Martin 2007; Delfino *et al.* 2008b).

Numerous dental characters are convergences between blunt toothed eusuchians, basal globidontans, and derived hylaeochampsids, such as the shape of posterior teeth (character 190) and the size of the penultimate teeth that are the largest (character 106). Bernissartids also bear convergent tribodont teeth (character 106); this is the unique convergent character between *B. fagesii* and *T. okani*, but the largest tooth is not the penultimate. Moreover, the morphology of their teeth consistently differs from that which is observed in hylaeochampsids (see above). These tooth characters are related to diet, but others differ between hylaeochampsids, basal globidontans and bernissartids. Generally, the crocodylian lower dentition is characterized by an enlarged diameter fourth tooth and a second enlarged tooth positioned more posteriorly (character 51; see Brochu 2004 for further discussion). In derived hylaeochampsids the penultimate

crushing tooth is the largest [character 106(1)], so large in most derived hylaeochampsids that it is twice the diameter of the ultimate one [character 106(2)]. Although the exact positions of the first and second enlarged teeth are unknown in *Turcosuchus okani*, the penultimate crushing tooth, or maybe the unpreserved ultimate in the preserved dental row, is considered as the largest in diameter. In tribodont hylaeochampsids, the largest tooth is always a crushing one; it is the penultimate tooth in *Iharkutosuchus makadii* and *Unasuchus reginae*, *Acynodon iberoccitanus* (SJ, pers. obs.) and maybe in *Turcosuchus okani* (Fig. 8; Supplemental Appendix 1). The position of the largest dentary tooth varies in different globidontan species. It is the last one in *Alligator prenasalis* and *Allognathosuchus mooki* (Fig. 7B), and the penultimate in *Brachychampsa montana*. In *Bernissartia fagesii*, the largest tooth is neither the ultimate nor the penultimate, but the tooth just anterior.

Having 10 or fewer dentary teeth posterior to the symphyseal region [character 191(1)] remains the only dental character state shared by derived hylaeochampsids and *T. okani* and not convergent with any globidontan. This new character is proposed here based on the variation in the number of dentary teeth on the post-symphyseal

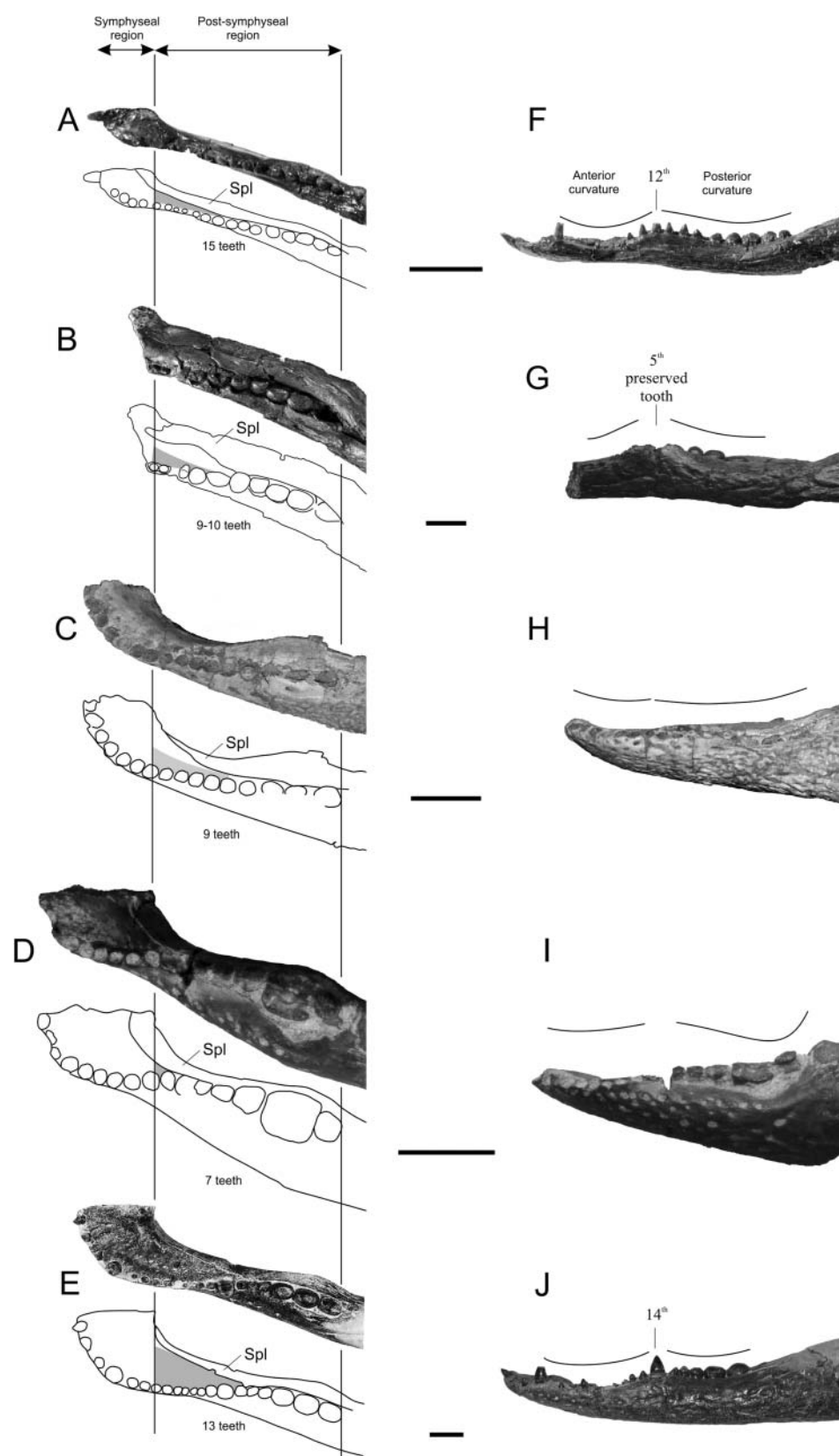


Figure 9. Comparison of the dental pattern in tribodont eusuchians and close relatives. **A, F**, *Bernissartia fagesii*, IRScNB R46, Bernissart, Belgium; **B, G**, *Turcosuchus okani*, İTÜ-Z1, Gelik, Turkey; **C, H**, *Acynodon iberoccitanus*, ACAP (uncat.), Fox-Amphoux, France; **D, I**, *Itharkutosuchus makadai*, MTM PAL2012.29.1, Itharkút, Hungary; **E, J**, *Brachychampsia montana*, SMP VP-1312, San Juan Basin, USA (from Sullivan & Lucas 2003). In A–E, the grey area corresponds to the dorsal surface of the post-symphyseal portion of the dentary. Curvatures on dentary with the second largest tooth in diameter, if present, are marked in F–J. Scale bars: 2 cm.

portion that varies comparing basal globidontans and derived hylaeochampsids. It is also the only number that can be defined in the *T. okani* dentition. The number of post-symphyseal teeth is always more than 10 [character 191(0)] in most of the outgroup members to Eusuchia and basal eusuchians (Fig. 9A). The plesiomorphic condition is seen in *Pachycheilosuchus tringuei* and *Pietraroiasuchus ormezzanoi*, which are considered as basal hylaeochampsids (Narváez *et al.* 2015). In more derived hylaeochampsids, there are 10 dentary teeth posterior to the symphysis in *Turcosuchus okani* (Fig. 9B), nine in *Acynodon iberoccitanus* (Fig. 9C), and seven in *Unasuchus reginae* and *Iharkutosuchus makadai* (Fig. 9D). A dental number higher than 10 is a plesiomorphic condition, visible in basal globidontans: *Brachychampsa montana* has 13 teeth (Sullivan & Lucas 2003) (Fig. 9E), *Stangerochampsa mccabei*, *Allognathosuchus mooki* (Lucas & Estep 2000) and *Alligator prenasalis* have 11 teeth, *Hassiacosuchus kayi* Mook, 1941 has 14 teeth, and *Wannaganosuchus brachymanus* Erickson, 1982 has at least 12 teeth. Some basal caimanines also bear posterior crushing teeth but their number of post-symphyseal teeth is higher than that of basal globidontans. There are 11 teeth posterior to the symphysis in *Globidentosuchus brachyrostris* (Scheyer *et al.* 2013), 12 in *Kuttanacaiman iquitosensis* (Salas-Gismondi *et al.* 2015), and 13 in *Eocaiman cavernensis* Simpson, 1933 (SJ, pers. obs.). The only exception is *Gnatusuchus pebasensis* Salas-Gismondi *et al.*, 2015 with its shovel-like mandible (and a very long symphysis) which bears only three teeth posterior to the symphysis (Salas-Gismondi *et al.* 2015). In *B. fagesii* the number of postsymphyseal teeth is very high with 15 teeth (Fig. 9A).

The poor preservation of *Turcosuchus okani* limits its number of attributed coded characters to 14 (i.e. 7.3% of the total character number in the matrix), and most of these are found to be convergent with basal globidontans. The only character scored for basal globidontans that is scored as plesiomorphic in *T. okani* concerns the anterior width of the post-symphyseal section of the dentary (character 193). The relevant portion is mediolaterally narrow [character 193(0)] in *Bernissartia fagesii* (Fig. 9A) and in most eusuchians like hylaeochampsids (Fig. 9B, C), even when the symphysis is long and wide, as in *Iharkutosuchus makadai* (Fig. 9D). In contrast, the medial expansion of the anterior post-symphyseal dentary is an apomorphy of globidontans that contributes to the wide mandibular symphysis of this group, as observed in *Brachychampsa montana* (Sullivan & Lucas 2003), *Allognathosuchus* spp. (Brochu 2004) and *Stangerochampsa mccabei* (Fig. 9E).

A rectilinear dental alignment of the posterior teeth is found in bernissartids (Fig. 9A, F) and in many eusuchians. This alignment is found in most of the eusuchians, but in basal globidontans (e.g. *B. montana*, *E. cavernosus*, *W. brachymanus* and *A. prenasalis*) the alignment of the

lingual side of the teeth is parallel to the mandibular medial axis at the level of four teeth anterior to the three last ones. The four posteriormost teeth curve laterally (Fig. 9E, J). In hylaeochampsids, most of the posterior teeth have their medial margin aligned and diverges laterally compare to the medial axis of the mandible and no posterior curvature is observed (Fig. 9B, C, G, H). In *I. makadai*, only the ultimate tooth has its medial margin laterally located in the tooth row (Fig. 9D, I). The damaged dentary of *T. okani* does not allow a precise observation, but at least the last five teeth (5th to 9th preserved teeth) and its ultimate alveoli (10th) are rectilinearly aligned (Figs 2A, 9G).

A similar pattern of alignment and divergence of posterior teeth on the lower jaw is also observed in the allodaposuchids *Lohuecosuchus megadontos* Narváez *et al.*, 2015 and *Agaresuchus fontisensis* Narváez *et al.*, 2016. The allodaposuchids and hylaeochampsids were previously considered as a monophyletic clade (e.g. Brochu 2013; Narváez *et al.* 2015), but a recent analysis suggests that the former group is more closely related to Crocodylia (Narváez *et al.* 2016). Therefore, it remains unresolved whether alignment and divergence of posterior dentary teeth is a synapomorphy of Allodaposuchidae + Hylaeochampsidae, or a homoplastic character within basal eusuchians.

The dorsal margin of the dentary is nearly straight in hylaeochampsids [character 50 (2)], including *Unasuchus reginae*, and is probably related to the absence of a larger tooth, even if in *A. iberoccitanus* and *I. makadai* a very weak elevation exists dividing the dorsal margin of the dentary in an anterior shallow curvature and a posterior straight tooth alignment (Fig. 9H, I). In contrast, the dorsal margin of the dentary is wavy in basal eusuchians like *Bernissartia fagesii* (Fig. 9F), in allodaposuchids (e.g. Narváez *et al.* 2015, 2016; Martin *et al.* 2016), basal globidontans such as *Brachychampsa montana* (Fig. 9J), and in most of the crocodylians. Although preservation damage on the lateral margin of *T. okani* exaggerates the peak height at the level of its largest tooth (fifth preserved tooth), its sigmoidal dorsal dentary margin appears to be unique among hylaeochampsids. This character state [50 (0)] is plesiomorphic among the tested neosuchians, and the linear dorsal margin of the dentary [50 (2)] is an apomorphy of the clade excluding *T. okani* and grouping *U. reginae* and more derived hylaeochampsids.

Palaeobiogeographical significance of *Turcosuchus*

The Cretaceous tribodont eusuchians are known in the northern hemisphere only, and they mostly come from Europe (Fig. 10; Supplemental Appendix 5). The two groups of basal eusuchians, Hylaeochampsidae and Allodaposuchidae, often considered as forming a monophyletic

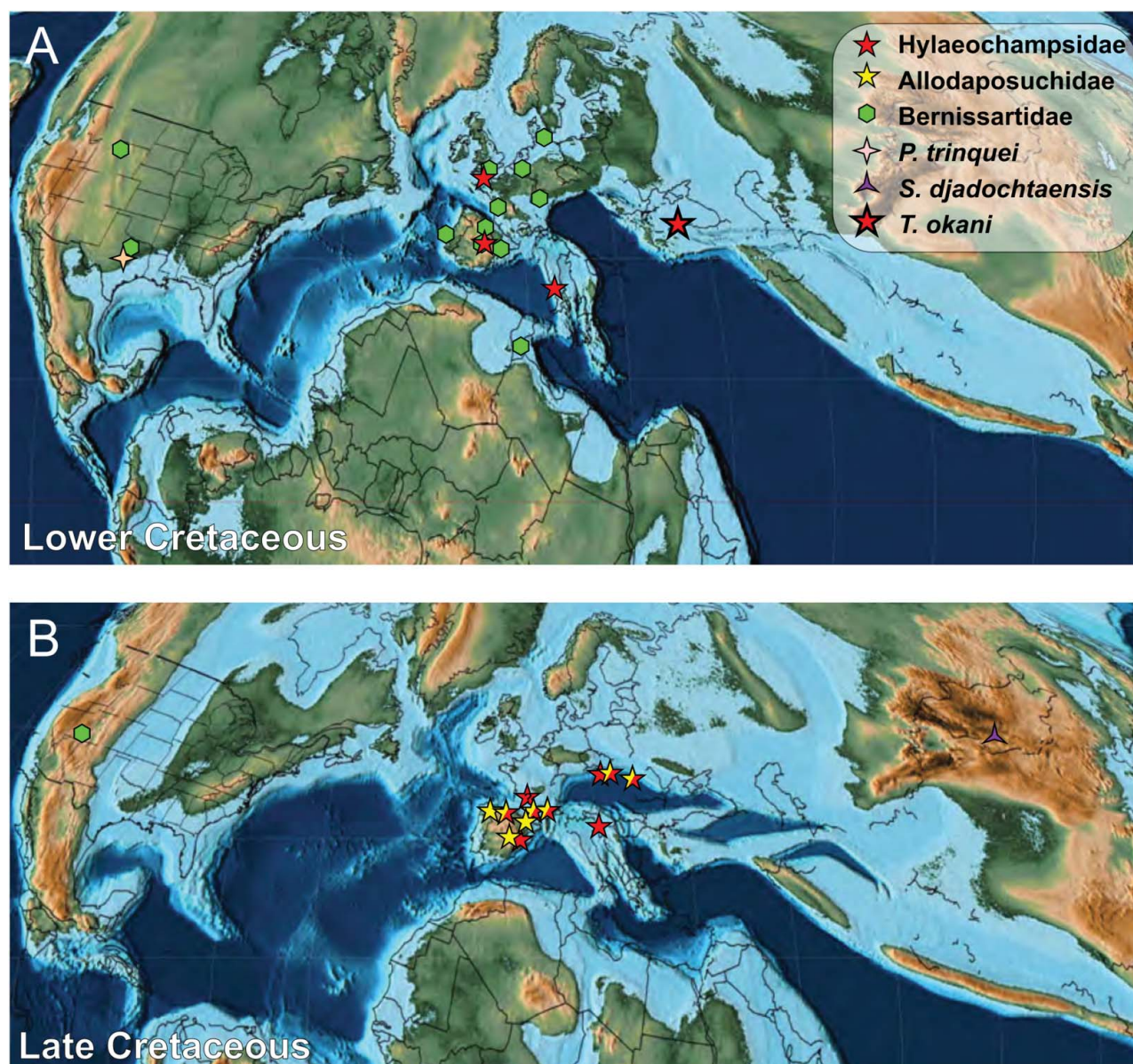


Figure 10. Distribution of blunt-toothed neosuchians Hylaeochampsidae, Allodaposuchidae and Bernissartidae during the Cretaceous Period (see text and Supplemental Appendix 5 for references). The Early Cretaceous (Barremian, **A**) and the Late Cretaceous (Coniacian–Santonian, **B**) maps are modified after Scotese (2014a, b).

group (e.g. Brochu 2013; Narváez *et al.* 2015), have a biogeographical history centred on the Tethys during the Cretaceous.

During the Barremian (Early Cretaceous), the clade is already centred in Europe, with only three occurrences in North America (see below) and a new occurrence with *T. okani* in Turkey. *Bernissartia*, being a non-eusuchian tribodont form, is well known in the Barremian of Belgium (e.g. Dollo 1883; Norell & Clark 1990) and Spain (Buscalioni *et al.* 1984, 2008; Buscalioni & Sanz 1990; Ortega *et al.* 2010), as well as England (Buffetaut & Ford 1979; Salisbury & Naish 2011), France (Martin & Delfino 2010), Switzerland (Monjon 2006), Denmark (Schwarz-Wings *et al.* 2009), and

North America (Winkler *et al.* 1990; Oreska *et al.* 2013) with fragmentary material. The early hylaeochampsid *Hylaeochampsia vectiana* is also known in the Barremian of England (Owen 1874; Clark & Norell 1992), whereas *Unasuchus reginae*, another hylaeochampsid according to our phylogenetic analysis, is known in the Barremian of Spain (Brinkmann 1992). Taking all these distributions into account, *Turcosuchus okani* represents, therefore, the first eastern occurrence of the eusuchians during the Barremian.

Interestingly, the two known Albian forms, *Pachycheilosuchus trinquei* from the Glen Rose Formation (Texas) and *Pietraroiasuchus ormezzano* from Italy, are younger than the oldest known hylaeochampsids, but more basal

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phylogenetically (Fig. 7). Moreover, *P. trinquei* is the most western hylaeochampsid (Fig. 10). This result should be considered with caution, as this taxon has been often considered as outside the eusuchians (e.g. Pol *et al.* 2009; Turner & Sertich 2010; Wilberg 2012, 2015).

During the Late Cretaceous (i.e. Santonian to Maastichtian), the hylaeochampsids (*Iharkutosuchus makadii* and *Acynodon* spp.) were mostly restricted to Europe (e.g. Buscalioni *et al.* 2001; Martin 2007; Delfino *et al.* 2008b; Martin & Delfino 2010), with the exception of the basal *Shamosuchus djadochtaensis* from Mongolia (Mook 1924). As for *P. trinquei*, the presence of such eastern hylaeochampsid, represented by *S. djadochtaensis*, should be considered with caution as this taxon is also considered as non eusuchian in many phylogenetic analyses (e.g. Pol *et al.* 2009; Turner & Sertich 2010; Adams 2014).

Allodaposuchids, on the other hand, are known in the Campanian–Maastichtian of southern France (Martin *et al.* 2016), Spain (Blanco *et al.* 2014, 2015; Puértolas-Pascual *et al.* 2014; Narváez *et al.* 2015, 2016) and Romania (Nopcsa 1928; Buscalioni *et al.* 2001; Delfino *et al.* 2008a). Their distribution is located in southern Europe only.

The discovery of *Turcosuchus okani* indicates the eastward radiation of the eusuchians already started during the Early Cretaceous. During the Late Cretaceous, the eastern extent of the group should be represented by *Shamosuchus djadochtaensis* from Mongolia, but is most likely represented by *Allodaposuchus precedens* from Romania and a gavialoid indet. from Crimea (e.g. Storrs & Efimov 2000; Martin & Delfino 2010) (Fig. 10). Moreover, the Barremian age of *T. okani* coincides with the earliest occurrence of the tribodont neosuchians such as *Bernissartia fagesii*, *Koumpiodontosuchus aprodokiti* Sweetman *et al.* 2015, *Hylaeochampsia vectiana* and *Unasuchus reginae* (Fig. 7). Therefore, the assignment of *T. okani* within the Hylaeochampsidae is congruent with the temporal and spatial distribution of this clade.

The oldest blunt-toothed globidontan taxa like *Brachychampsia*, *Stangerochampsia* and *Albertochampsia* were collected from the Campanian and Maastichtian of North America and are younger than the first hylaeochampsids and bernissartids (e.g. Erickson 1972; Wu *et al.* 1996; Sullivan & Lucas 2003). Nevertheless, they are contemporaneous with the latest hylaeochampsids. All these crushing toothed eusuchians are interpreted as having a similar omnivorous diet with durable, hard-shelled prey (Ösi 2014), as the extant *Caiman latirostris* (Ösi & Barrett 2011). With the clear identification of *Acynodon* as a hylaeochampsids and not an alligatoroid (Rabi & Ösi 2010; Turner & Brochu 2010; Brochu 2011), the geographical distribution of the Late Cretaceous tribodont eusuchians clearly shows a geographical segregation between tribodont globidontans, present in North America, and hylaeochampsids in the

Tethyan area. Both occupy a similar ecological niche related to their probable similar diet (Ösi 2014).

Conclusions

Turcosuchus okani gen. et sp. nov. from the Barremian of Gelik (Zonguldak district, NW Turkey) is described in this work based on partial jaw and long bone material. The morphology of its dentary, as well as its dentition pattern, show that *T. okani* is a hylaeochampsid, a result confirmed by our phylogenetic analysis which positions it within the clade. The tribodont condition of the posterior teeth, and the tribodont tooth being the largest in the tooth row, are synapomorphies that *Turcosuchus okani* shares with hylaeochampsids, but these character states also occur in other tribodont eusuchians. Having 10 or fewer teeth posterior to the symphyseal region is shared by derived hylaeochampsid taxa like *Turcosuchus okani*, *Acynodon* spp. and *Iharkutosuchus makadii*. It is also observed in gavialoids and most of the crocodyloids, while this number is higher in other tribodont eusuchians. The undulation of the jaw with a sigmoidal dorsal margin observed in *Turcosuchus okani* is also present in other eusuchians, but absent in derived hylaeochampsids. It differs from the basal taxa (e.g. *Pachycheilosuchus trinquei* and *Pietraroiasuchus ormezzanoii*) which have a homodont dentition, and from the derived taxa (e.g. *Iharkutosuchus makadii*) which have a strong heterodont dentition and a nearly straight dorsal margin of the lower jaw, and thus exhibits a unique combination of characters. In addition, *Turcosuchus okani* represents the only Early Cretaceous eusuchian discovered in Asia and suggests the eusuchians were more widespread than previously thought.

Acknowledgements

We would like to thank Okan Tüysüz (İTÜ) for his great help in understanding the geology of Zonguldak, A. M. Celal Şengör (İTÜ) for providing the workspace to VS for the description and drawings of the specimen, and Christopher Brochu (the University of Iowa) for his helpful comments and granting scientific material on neosuchians. SJ thanks Lorna Steel (Natural History Museum, London), as well as M. Rabi and Z. Szentesi (Hungarian Natural History Museum) for their help, hospitality and access to the collections and material. We would also like to thank Atila Ösi and an anonymous reviewer for their helpful comments, John Jones for the English grammar review and Sophie Sanchez for her help. SJ received support from the SYNTHESYS Project (<http://www.synthesys.info/>) financed by the European Community Research Infrastructure Action under the FP7 “Capacities” Program (HU-TAF-4866; GB-TAF-3366). We would like to thank

Mehmet Sakinç (İTÜ) for access to the İTÜ palaeontological collections in 2005.

Supplemental data

Supplemental material for this article can be accessed at: <https://doi.org/10.1080/14772019.2017.1393469>

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