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RESEARCH

Dentary–squamosal jaw articulation in a late surviving tritylodontid synapsid from the Early Cretaceous of Western Siberia, Russia

Alexander O. Averianov[1] · **Alexey V. Lopatin**[2] · **Dmitry A. Slobodin**[3] · **Pavel P. Skutschas**[4] · **Olga N. Vladimirova**[3]

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Abstract

The late Early Cretaceous (Aptian) tritylodontid synapsid *Xenocretosuchus sibiricus* from Western Siberia, Russia, exhibits a dentary–squamosal contact formed by a distinct condyloid process. This is a new case of independent development of the dentary–squamosal jaw articulation in synapsids, after that observed in derived ictidosaurs and mammaliaforms. The articular process of the dentary is remarkable for its length and is separated by a deep cleft from the condyloid process in *Xenocretosuchus*. It is hypothesised that the former covered the quadrate and the postdentary bones dorsally. The main function of the quadrate and the postdentary bones was sound transmission, suggesting that the dentary–squamosal articulation played the main role in load bearing in *Xenocretosuchus*. This is supported by the extreme development of the mandibular middle ear in *Xenocretosuchus* which may be related to the fossorial adaptations seen in the late surviving tritylodontids.

Keywords Craniomandibular joint · Early Cretaceous · Morphology · Russia · Synapsida · Western Siberia

Introduction

The craniomandibular joint, consisting of the squamosal glenoid and the dentary condyle, is one of the most striking features of modern mammals. All other tetrapods have a plesiomorphic, “reptilian” jaw joint between the quadrate bone on the skull and the articular bone on the mandible. The primary “reptilian” jaw joint in mammals is transformed into the chain of ear ossicles, including the incus (former quadrate) and malleus (former articular). This transformation is now well documented in the fossil record (Crompton 1972; Allin 1975; Allin and Hopson 1992; Kielan-Jaworowska et al. 2004; Luo and Manley 2020). A recent detailed study of derived non-mammaliaform probainognathian cynodonts from the Upper Triassic of South America based on microcomputed tomography scanning of three-dimensional preserved specimens showed homoplastic evolution of the jaw joint in the lineage approaching Mammaliaformes (Rawson et al. 2024). According to this study, a dentary–squamosal contact evolved independently in ictidosaurs (*Riograndia* plus tritheledontids (Crompton 1963; Angielczyk and Kammerer 2018) and mammaliaforms. Although the dentary–squamosal jaw articulation has been described

✉ Alexander O. Averianov
dzharakuduk@mail.ru

Alexey V. Lopatin
alopat@paleo.ru

Dmitry A. Slobodin
d.a.slobodin@mail.ru

Pavel P. Skutschas
p.skutschas@spbu.ru

Olga N. Vladimirova
ovlad-5@mail.ru

[1] Zoological Institute, Russian Academy of Sciences, Universitetskaya nab., 1, Saint Petersburg 199034, Russia

[2] Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya Str. 123, Moscow 117647, Russia

[3] Kuzbass State Museum of Local Lore, Prospekt Sovetskiy 51, Kemerovo 650000, Russia

[4] Department of Vertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Universitetskaya nab., 7–9, Saint Petersburg 199034, Russia

for the Early Jurassic *Tritylodon* from South Africa (Fourie 1968), this interpretation has not been confirmed by subsequent studies (Jasinoski and Chinsamy 2012; Rawson et al. 2024), and Rawson et al. (2024) confirmed the absence of a dentary–squamosal contact in tritylodontids as a whole based on the well-preserved specimens of *Oligokyphus* from the Lower Jurassic of Great Britain.

Here we confirm the presence of a dentary–squamosal contact in a tritylodontid, based on a well-developed and separate condyloid process in the Early Cretaceous *Xenocretosuchus sibiricus* from Western Siberia, Russia. Re-evaluating the literature, we also suggest that a similar condyloid process and dentary–squamosal contact is present, but was not previously recognised, in the Middle Jurassic tritylodontid *Polistodon* from China (He and Cai 1984). Tritylodontids are derived probainognathian cynodonts characterized by enlarged, continuously growing incisors and multicusped, horizontally replaced postcanines (Angielczyk and Kammerer 2018; Melo et al. 2019). Their postcranial skeleton suggests fossorial adaptations (Mao et al. 2021). The group are best known from the Jurassic of the northern continents, Africa, and Antarctica, while their isolated teeth have been found in the Upper Jurassic of Central Europe (Hennig 1922). Tritylodontids survived into the Early Cretaceous in Russia, Japan, and China (Tatarinov and Maschenko 1999; Lopatin and Agadjanian 2008; Matsuoka et al. 2016; Mao et al. 2021), making them the youngest group of non-mammalian synapsids in the fossil record. *Xenocretosuchus* lived in an ecosystem favourable to relict tetrapod taxa, such as stem salamanders, protosuchian and shartegosuchid crocodyliforms, ceratosaurian theropods, and docodontan mammaliaforms (Averianov et al. 2023a, 2024; Skutschas et al. 2024), but dominated by an advanced ceratopsian dinosaur *Psittacosaurus sibiricus* (Averianov et al. 2006; Podlesnov et al. 2023).

Our results document a new case of independent evolution of a mammal-like dentary–squamosal contact in close mammalian relatives and confirm the high evolutionary lability of this morphological structure.

Institutional abbreviations: **KOKM**, Kuzbass State Museum of Local Lore, Kemerovo, Russia; **PIN**, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

Materials and methods

The Shestakovo localities are situated around Shestakovo village in Chebula rayon of Kemerovo oblast – Kuzbass, Western Siberia, Russia (Fig. 1). The Shestakovo 1 locality is a high cliff along the right bank of Kiya River 1.5 km downstream of Shestakovo village (GPS coordinates: N 55° 54.60′, E 87° 56.90′). It was discovered in 1953 by geologist A.A. Mossakovsky. Extensive

Fig. 1 Geographic setting of Shestakovo 1 and 3 localities

work at this locality began after the discovery of a mammalian jaw in 1995 (Maschenko and Lopatin 1998). The Shestakovo 3 locality was discovered in 1995 by geologists from Tomsk State University at a road cut south of Shestakovo village (GPS coordinates N 55° 52.94′, E 87° 59.58′; Fig. 1). Since 2014, large-scale annual excavations at the Shestakovo 3 locality have been carried out by the Kuzbass State Museum of Local Lore (Lopatin et al. 2015; Averianov et al. 2023c).

Paleomagnetic studies conducted in the basins of the Kiya, Chulym, and Serta rivers have shown that the Ilek Formation, including the Shestakovo strata, has positive magnetization, which excludes the Neocomian (Berriasian–Hauterivian) age of these deposits (Pospelova and Larionova 1971). Recent data from spore-pollen spectra indicate the Aptian age of the Ilek Formation (Bugdaeva et al. 2017). The stratigraphic sections at Shestakovo 1 and 3 localities were described previously by Podlesnov et al. (2018) and Averianov et al. (2023c).

Specimen KOKM 25576 was scanned with a resolution of 27 µm using a Neoscan 80 X-ray microtomograph at the Center of Collective Use "Taxon" of the Zoological Institute of the Russian Academy of Sciences. The scanning parameters included a voltage of 110 kV, a current of 37 µA, a camera exposure of 2411 milliseconds, a rotation step 0.2°, and frame averaging of 7. The resultant data set comprised a stack of 3983 images, with a resolution of 2752 × 2752 pixels. Segmentation, surface rendering and the three-dimensional model of KOKM 25576 were conducted using in the Avizo Lite 2019.1 program (Thermo Fisher Scientific, Waltham, Massachusetts, USA). The morphological illustrations were prepared using Meshlab v. 2023.12.

Systematic palaeontology

Synapsida Osborn, 1903
Therapsida Broom, 1905
Cynodontia Owen, 1861
Probainognathia Hopson, 1990
Mammaliamorpha Rowe, 1988
Tritylodontidae Cope, 1884
Xenocretosuchus Tatarinov and Maschenko, 1999

Xenocretosuchus sibiricus Tatarinov and Maschenko, 1999
Figures 2, 3, 4 and 5

Holotype: PIN 4463/2, right upper molariform tooth.

Referred specimen: KOKM 25576, a nearly complete edentulous right dentary.

Localities and horizon: Shestakovo 1 (holotype) and Shestakovo 3 (KOKM 25576), Kemerovo oblast – Kuzbass, Russia (Fig. 1). Ilek Formation, Lower Cretaceous (Aptian).

Comments: *Xenocretosuchus sibiricus* is represented by numerous isolated postcanine teeth and rare isolated

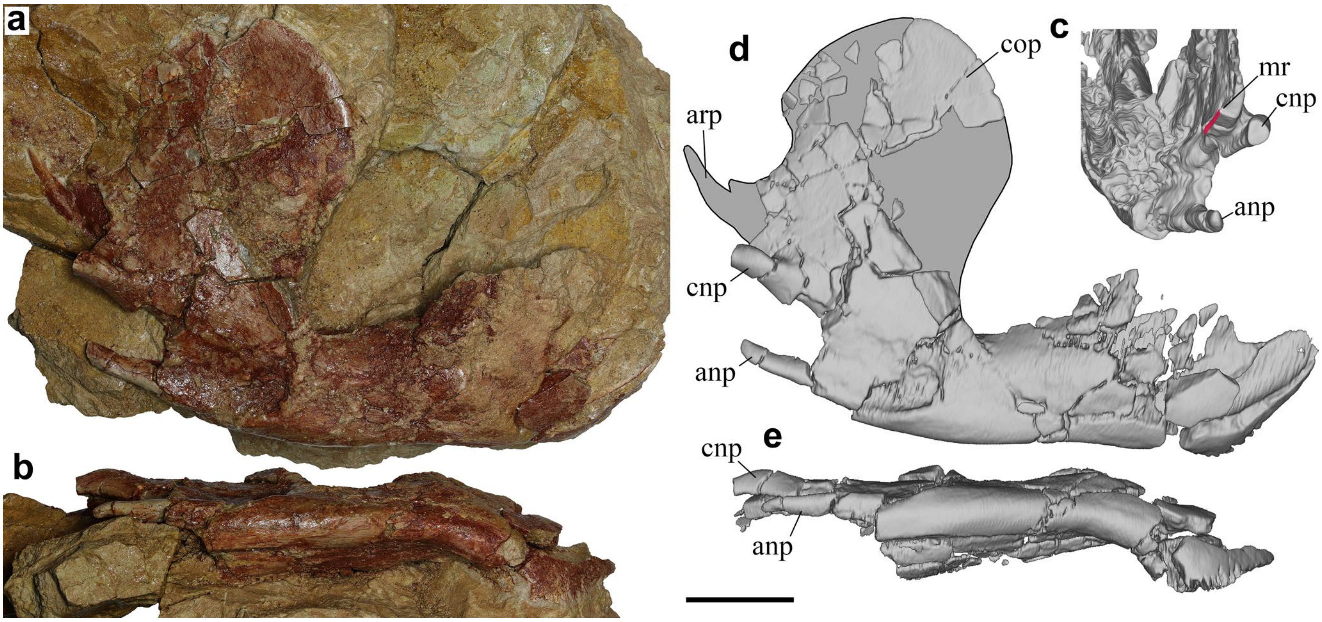

Fig. 2 Photographs (**a, b**) and surface renderings based on high resolution CT scans (**c–e**) of *Xenocretosuchus sibiricus*, KOKM 25576, right edentulous dentary from Shestakovo 3, Kemerovo oblast – Kuzbass, Russia; Ilek Formation, Lower Cretaceous (Aptian). **a**. lateral view; **b**. ventral view; **c**. posteromedial view; **d**. lateral view, with the outline of the coronoid and articular processes restored from the imprint; **e**. ventral view. Abbreviations: **anp**, angular process; **arp**, articular process; **cnp**, condyloid process; **cop**, coronoid process; **mr**, medial ridge (highlighted by red). Scale bar equals 3 cm

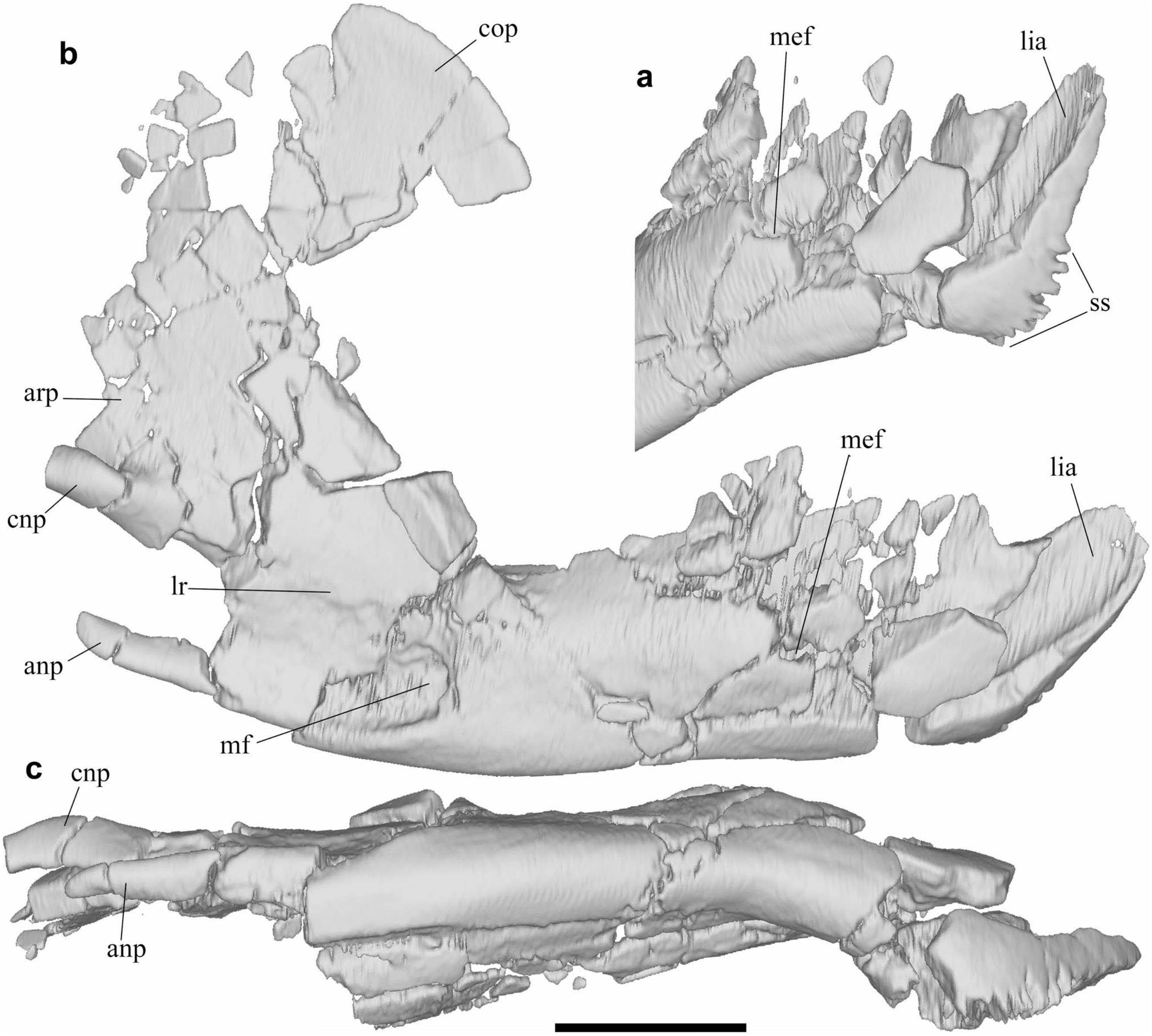

Fig. 3 Surface rendering based on high resolution CT scans of *Xenocretosuchus sibiricus*, KOKM 25576, right edentulous dentary from Shestakovo 3, Kemerovo oblast – Kuzbass, Russia; Ilek Formation, Lower Cretaceous (Aptian). **a**. anterolateral view of anterior end; **b**. lateral view; **c**. ventral view. Abbreviations: **anp**, angular process; **arp**, articular process; **cnp**, condyloid process; **cop**, coronoid process; **lia**, lower incisor alveolus; **lr**, lateral ridge; **mef**, mental foramen; **mf**, masseteric fossa; **ss**, symphyseal suture. Scale bar equals 3 cm

incisors and postcranial bones from the Shestakovo 1 and 3 localities. All morphometric and morphological differences in a sample of tritylodontid postcanine teeth from the Shestakovo 1 and 3 localities can be explained by individual or ontogenetic (positional) variation and therefore all these teeth are assigned to the same taxon. Since the alveolar furrow on the specimen KOKM 25576 corresponds in size to isolated lower postcanine teeth of *X. sibiricus*, and only one taxon of Tritylodontidae is known in Shestakovo localities, the specimen KOKM 25576 is assigned here to *X. sibiricus*. This specimen is the only known dentary belonging to this taxon. *Xenocretosuchus* has been considered a junior subjective synonym of *Stereognathus* Charlesworth (1855) based on the close similarity of the postcanine teeth (Averianov et al. 2017). Here we adopt a more conservative taxonomy, as *Xenocretosuchus* may differ in anterior dentition and mandibular morphology (the latter unknown for *Stereognathus*). The Aptian *X. sibiricus* is contemporaneous with *Fossiomanus sinensis* Mao, Zhang, Liu et Meng, 2021 from the Aptian Jiufotang Formation of Liaoning, China (Mao et al. 2021). Both represent the youngest fossil record of the non-mammalian synapsids. The exact age of *Xenocretosuchus kolossovi* Lopatin et Agadjanian, 2008 from the Lower Cretaceous Batylykh Formation of Yakutia, Russia (Lopatin

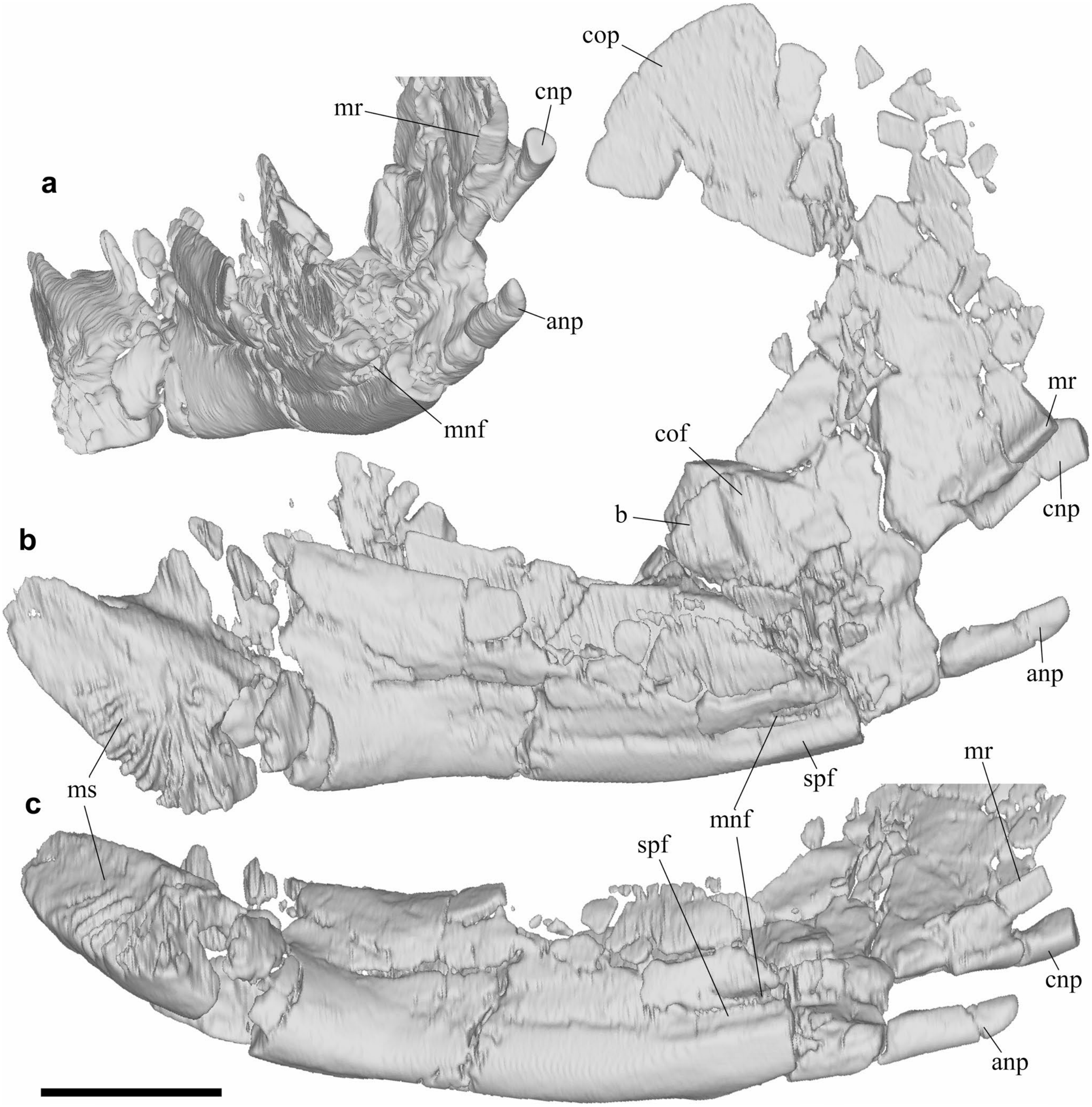

Fig. 4 Surface rendering based on high resolution CT scans of *Xenocretosuchus sibiricus*, KOKM 25576, right edentulous dentary from Shestakovo 3, Kemerovo oblast – Kuzbass, Russia; Ilek Formation, Lower Cretaceous (Aptian). **a**. posteromedial view of posterior end; **b**. medial view; **c**. ventromedial view. Abbreviations: **anp**, angular process; **b**, boss; **cnp**, condyloid process; **cof**, coronoid facet; **cop**, coronoid process; **mnf**, mandibular foramen; **mr**, medial ridge; **ms**, mandibular symphysis; **spf**, splenial facet. Scale bar equals 3 cm

and Agadjanian 2008) is uncertain. It could be as young as Aptian–Albian, based on the presence of a eutriconodontan *Gobiconodon* sp. (Averianov et al. 2023b). *Fossiomanus* was distinguished from all other tritylodontids by having a zigzag suture on the mandibular symphysis (Mao et al. 2021). This suture is also present in *Xenocretosuchus* (see Description and comparison), but *Xenocretosuchus* differs from *Fossiomanus* in having two pairs of upper incisors.

Description and comparison

Specimen KOKM 25576 is an almost complete right edentulous dentary (Figs. 2, 3, 4 and 5). The anterior end

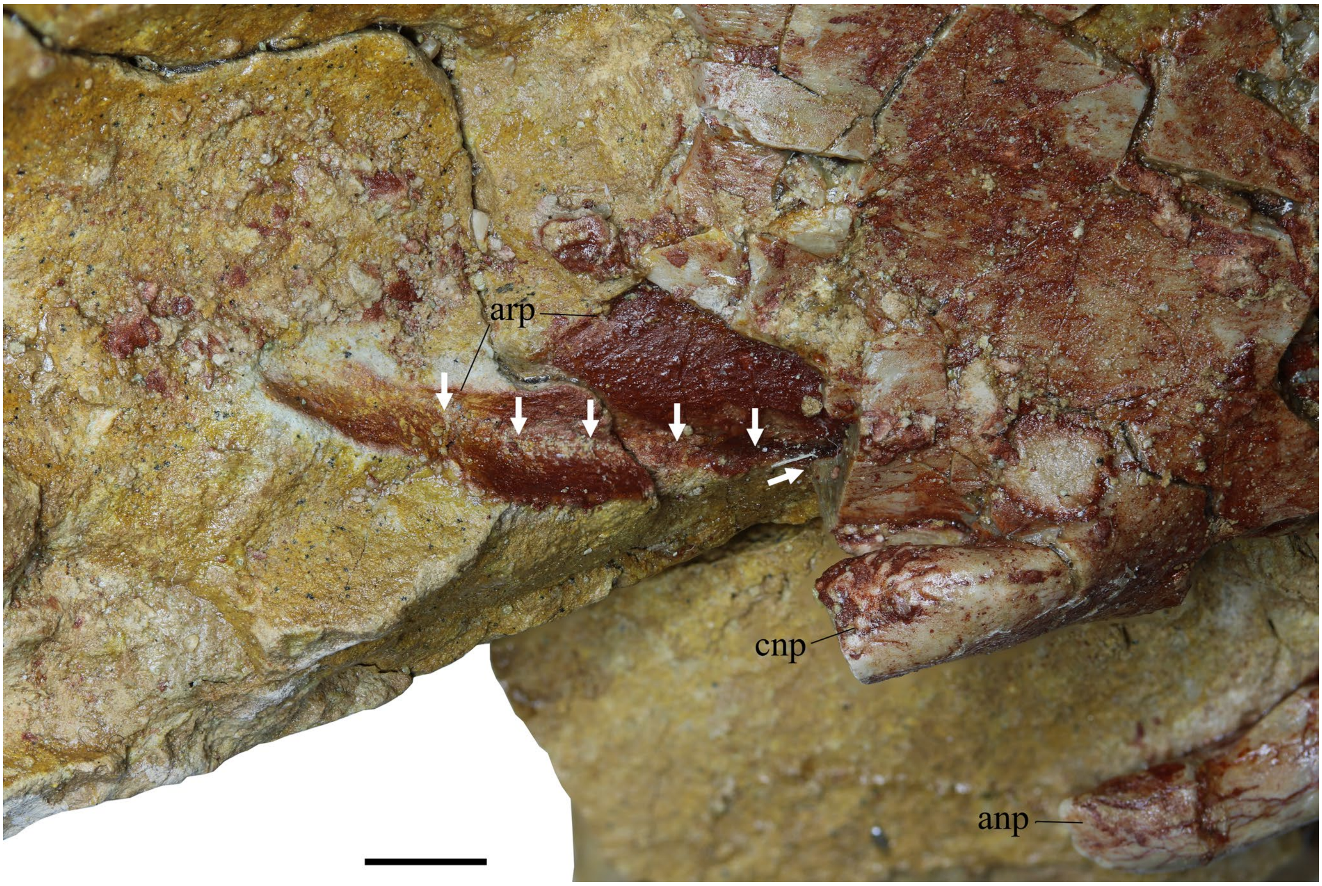

Fig. 5 A close-up photograph of the articular and condyloid processes in lateral view of *Xenocretosuchus sibiricus*, KOKM 25576, right edentulous dentary from Shestakovo 3, Kemerovo oblast – Kuzbass, Russia; Ilek Formation, Lower Cretaceous (Aptian). Arrows indicate the medial ridge and its imprint. Abbreviations: **anp**, angular process; **arp**, articular process; **cnp**, condyloid process. Scale bar equals 5 mm

of the dentary is detached and partially displaced from the rest of the mandible. The alveolar margin is partially destroyed medially and laterally. The posterior tip of the condyloid process is absent. The coronoid process is largely destroyed, but its outline can be reconstructed from the imprint (Figs. 2d and 6b). The total length of the dentary, between the anterior tip of the dentary and the posterior end of the articular process (preserved as an imprint), is 89.0 mm.

Specimen KOKM 25576 belongs to an adult but not a senile individual judging by a short diastema between the lower incisor and postcanine teeth. In aged specimens of *Tritylodon* this diastema increases drastically and the postcanine tooth row is placed almost entirely medial to the coronoid process (Jasinoski and Chinsamy 2012).

The ventral margin of the mandibular body is sinusoidal in lateral or medial view, convex at the level of the anterior end of the coronoid process and the diastema, and concave between them. A similar sinusoid ventral profile is present in *Kayentatherium* (Sues 1986). The ventral margin of the mandibular body is straight to slightly convex in *Tritylodon* (Jasinoski and Chinsamy 2012) and convex in *Bienotherium*, *Oligokyphus*, *Bienotheroides*, and *Polistodon* (Young 1947; Kühne 1956; He and Cai 1984; Sun 1984). The dorsal (alveolar) margin of the mandibular body is straight in lateral or medial view, as it is typical for the tritylodontids. The depth of the mandibular body increases anteriorly, and is minimal at the anterior end of the coronoid process, as in *Bienotheroides* (Sun 1984). In *Tritylodon*, *Bienotherium*, *Oligokyphus*, *Kayentatherium*, and *Polistodon* the depth of the mandibular body is almost constant (Young 1947; Kühne 1956; He and Cai 1984; Sues 1986; Jasinoski and Chinsamy 2012).

The anterior end of the mandibular body is strongly arched medially, forming a long symphysis with the contralateral dentary (Fig. 3c). A similar condition is present in *Bienotherium* and *Bienotheroides* (Young 1947; Sun 1984; Watabe et al. 2007), while in *Kayentatherium* this arching is less pronounced and the mandibular symphysis is relatively shorter (Sues 1986). The mandibular symphysis is teardrop-shaped in medial view, with the long axis oriented at an angle of about 45° to the horizontal. A similar orientation of the mandibular symphysis

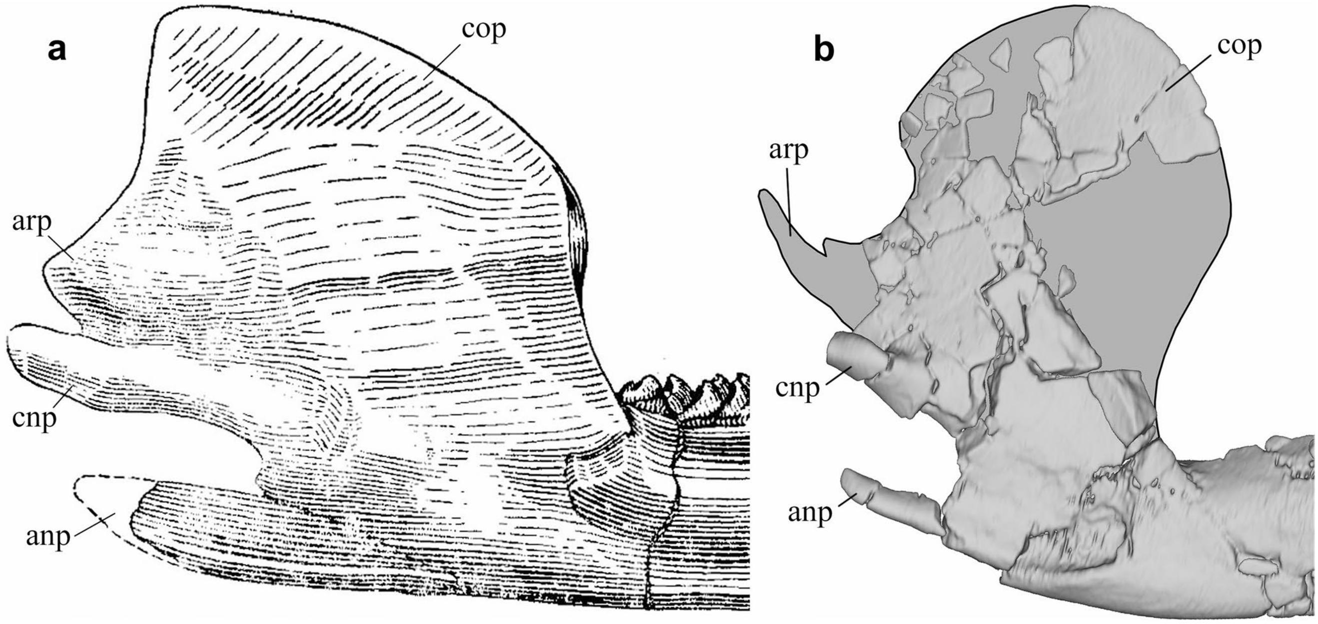

Fig. 6 Comparison of the mandibular ramus of *Polistodon* and *Xenocretosuchus* in lateral view. **a**. *Polistodon chuannanensis* from the Middle Jurassic Xiashaximiao Formation of Sichuan, China (based on He and Cai 1984: fig. 3 reversed); **b**. *Xenocretosuchus sibiricus*, based on KOKM 25576. Abbreviations: **anp**, angular process; **arp**, articular process; **cnp**, condyloid process; **cop**, coronoid process. Not to scale

is present in *Bienotherium*, *Kayentatherium*, and *Bienotheroides* (Hopson 1966; Sun 1984; Sues 1986), whereas the mandibular symphysis is more horizontal in *Tritylodon* and *Oligokyphus* (Kühne 1956; Jasinoski and Chinsamy 2012). The anteroventral part of the mandibular symphysis consists of high radiating ridges that form a zigzag suture in anterior view. The zigzag suture of the mandibular symphysis among the tritylodontids was previously reported only for *Fossiomanus* and it was considered a unique feature of this taxon (Mao et al. 2021). The rest of the mandibular symphysis is smooth. In ventral view, the mandibular body expands mediolaterally posteriorly, as in *Bienotherium* and *Bienotheroides* (Young 1947; Sun 1984), while in *Kayentatherium* this expansion is less pronounced (Sues 1986).

The lateral side of the mandibular body becomes more convex posteriorly. Between the coronoid process and the alveolar margin, the dorsal side of the dentary is almost horizontal. A single relatively large mental foramen is located at the mid-height of the lateral side, at the most prominent point of its convex profile (Fig. 3b). It is slightly closer to the coronoid process than to the anterior end of the dentary. The mental foramen is oval, with the long axis slightly oblique to the horizontal. A similar mental foramen in a similar position is found in *Bienotherium*, *Oligokyphus*, *Kayentatherium*, and *Bienotheroides* (Young 1947; Kühne 1956; Sun 1984; Sues 1986; Sun and Cui 1989; Watabe et al. 2007). In *Tritylodon* there are two smaller mental foramina that are moved posteriorly during ontogeny by bone remodelling (Jasinoski and Chinsamy 2012). The mental foramen is very large in a single known juvenile specimen of *Bocatherium* (Clark and Hopson 1985).

The medial side of the mandibular body consists of a thin medial wall of the alveolar trough, which is convex medially, and a more flattened ventral part. Only a short anterior fragment of the postdentary trough is preserved. It is narrow dorsoventrally and continues anteriorly to the mandibular canal through the mandibular foramen, which lies below the preserved posterior end of the alveolar part of the dentary (Fig. 4b, c). Ventrally and anteriorly to the preserved anterior end of the postdentary trough there is a distinct longitudinal depression which probably represents the splenial facet. This facet continues anteriorly into a narrow Meckelian groove that disappears about halfway to the mandibular symphysis. The Meckelian groove extends to the mandibular symphysis in *Oligokyphus*, *Kayentatherium*, and *Bienotheroides* (Kühne 1956; Sun 1984; Sues 1986; Rawson et al. 2024). In *Bienotheroides* the splenial covers about the half of the mandibular body (Sun 1984). In *Oligokyphus* the splenial facet extends to the mandibular symphysis (Rawson et al. 2024).

At the anterior end of the dentary, close to the mandibular symphysis, there is a single large incisor alveolus. The incisor was semi-procumbent, oriented at approximately 45° to the horizontal line. The incisor alveolus is located anteromedial to the postcanine tooth row. All the postcanine teeth were placed in a single alveolar trough that was not divided into individual alveoli. The internal walls of the alveolar trough are flat and remarkably smooth. The alveolar trough deepens anteriorly.

The mandibular ramus consists of a very large coronoid process and smaller articular, condyloid, and angular processes (Figs. 2, 3 and 4). The anterior margin of the coronoid process is inclined anteriorly, with its greatest convexity extending anteriorly to its ventral margin (Fig. 2a, d), as in *Bienotherium* and *Bienotheroides* (Young 1947; Sun 1984). In *Tritylodon*, *Oligokyphus*, *Bocatherium*, and *Kayentatherium* the anterior margin of the coronoid process is vertical (Kühne 1956; Clark and Hopson 1985; Sues 1986; Jasinoski and Chinsamy 2012).

Most of the articular process is preserved as an imprint (Figs. 2a and d, and 5). The articular process is longer than in all other tritylodontids. It is posterodorsally curved and terminates in a pointed tip.

A condyloid process distinct from the articular process was depicted but not recognised for *Polistodon* (He and Cai 1984: fig. 3; Fig. 6a). The condyloid process is absent in all other known tritylodontids. Instead, they have a variably developed but usually weak lateral ridge extending anteroventrally towards the anterior end of the masseteric fossa (Young 1947; Kühne 1956; Sun 1984; Sues 1986; Rawson et al. 2024). In specimen KOKM 25576, there is a very weak lateral ridge anterior to the condyloid process.

The angular process is long and separated from the condyloid process by a deep incisura. A similar condition is present in *Polistodon* (He and Cai 1984; see also Fig. 6a). In *Bienotheroides*, the incisura is shallower, and the angular process is shorter (Sun 1984). In other tritylodontids, the incisura is absent, and the angular process is short to almost absent (Young 1947; Kühne 1956; Sues 1986; Jasinoski and Chinsamy 2012; Rawson et al. 2024).

The masseteric fossa is a shallow depression ventral to the lateral ridge. It is deepest along its anteroventral margin. Dorsal to the lateral ridge, the lateral aspect of the coronoid process is flat. The preserved ventral part of the anterior margin of the coronoid process is very thick laterally. On the medial side, there is a prominent “boss” at the anteroventral corner of the coronoid process, similar to that in *Tritylodon*, *Oligokyphus*, and *Bienotheroides* (Kühne 1956; Sun 1984; Jasinoski and Chinsamy 2012). Posterior to this “boss”, there is a strap-like depression of the coronoid facet, similar in outline to the coronoid bone in *Bienotheroides* (Sun 1984).

The medial ridge, dorsally bordering the trough for the postdentary bones, is robust in the middle part and extends posteriorly all the way to the end of the articular process, as judged by its impression (Fig. 5). The medial ridge is separated from the condyloid process by a deep cleft (Fig. 2c).

Discussion

The development of a long articular process of the dentary, extending posteriorly to the postdentary bones and reinforced by thick medial and lateral ridges is the first stage of morphological transformations leading to the establishment of the load-bearing dentary–squamosal articulation (Rawson et al. 2024). This stage was acquired by derived probainognathians, including tritylodontids (Kühne 1956; Sues 1986). This condition is hypertrophied in *Xenocretosuchus*: its articular process is distinctly longer than in any other tritylodontid (Fig. 2), with the medial ridge extending to the apex of this process (Fig. 5). This extended articular process in *Xenocretosuchus* probably covered the quadrate, as in the ictidosaur *Riograndia* (Rawson et al. 2024). The incipient (Romer 1969, 1970) or substantial (Crompton 1963) dentary–squamosal hinge in some probainognathians is formed by a thickened part of the lateral ridge of the dentary articular process. In the stem mammals *Sinoconodon* and *Morganucodon* the dentary condyle is formed by a mediolaterally extended posterior end of the articular process that incorporates the posterior extremities of the lateral and medial ridges (Kermack et al. 1973; Crompton and Sun 1985). The tritylodontids *Polistodon* and *Xenocretosuchus* show a third variant of the dentary–squamosal articulation: the posterior part of the lateral ridge is separated from the articular process by a deep cleft and forms a distinct condyloid process (Fig. 2).

The establishment of the dentary–squamosal contact in the tritylodontids requires a considerable dorsoventral expansion of the zygomatic arch because plesiomorphically the squamosal was placed well dorsal to the jaw articulation (Fig. 7a). The zygomatic arch is already extremely expanded in the Middle–Late Jurassic *Bienotheroides* (Sun 1984; Sun and Cui 1989; Liu et al. 2025). The specialisation of the condyloid process may have been caused by the intensification of the load-bearing function of the dentary–squamosal joint, while the quadrate–articular joint was specialised for sound transmission. The intensification of the hearing in *Polistodon* and *Xenocretosuchus* is evident from the considerable development of the mandibular middle ear in these taxa, exemplified by a deep incisura between the angular and condyloid processes (Figs. 2a and d, 6 and 7b). This incisura is significantly smaller in *Bienotheroides* (Sun 1984) and virtually absent in other tritylodontid taxa. The large development of the mandibular middle ear facilitates

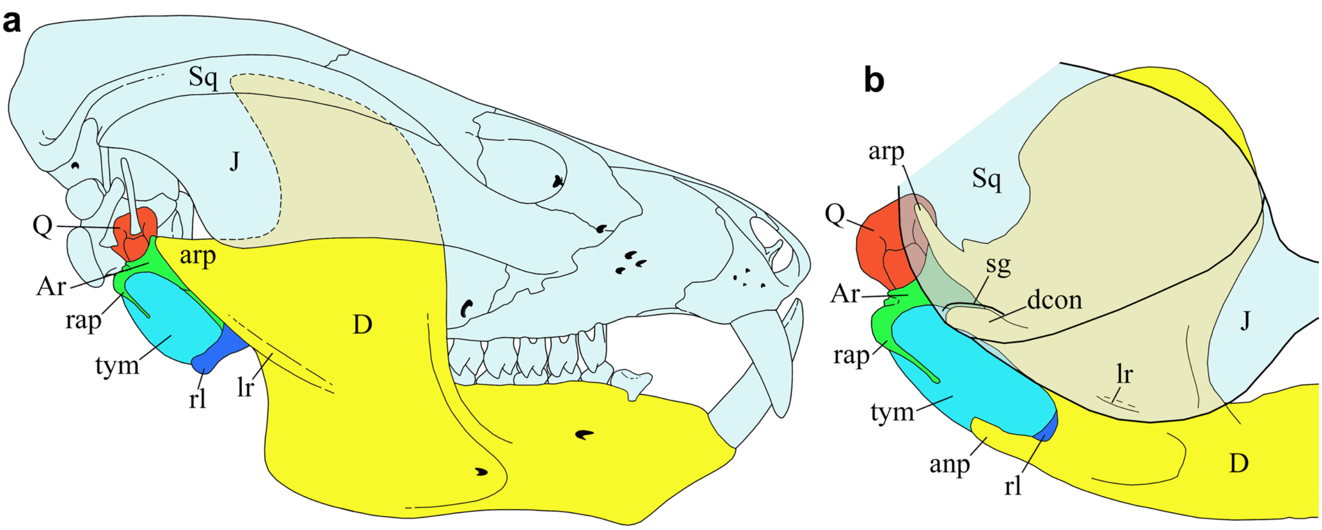

Fig. 7 Interpretation of jaw articulation in Tritylodontidae (lateral views). **a**. Early Jurassic *Kayentatherium wellesi*, skull (modified from Sues 1986: figs. 1; and 22); **b**. Early Cretaceous *Xenocretosuchus sibiricus*, posterior dentary and hypothetical reconstruction of associated structures, based on KOKM 25576. Abbreviations: **anp**, angular process; **Ar**, articular; **arp**, articular process; **D**, dentary; **dcon**, dentary condyle; **J**, jugal; **lr**, lateral ridge; **Q**, quadrate; **rap**, retroarticular process of articular; **rl**, reflected lamina of angular; **sg**, squamosal glenoid; **Sq**, squamosal; **tym**, tympanicum. Not to scale

the substrate sound transmission (Luo et al. 2016) and may be explained by the progressive fossoriality in the late surviving tritylodontids (Mao et al. 2021), including *Xenocretosuchus*.

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Author contributions A.O.A. and A.V.L. designed the research and wrote the main manuscript text. A.O.A. processed the CT data, created the virtual 3D reconstruction, and created the figures. D.A.S. and P.P.S. conducted the field work. O.N.V. organized the field work at Shestakovo 3 locality and curated specimens. All authors revised and commented on drafts of the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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