Cretaceous Research 149 (2023) 105573

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

A new species of *Eopteranodon* (Pterodactyloidea, Tapejaridae) from the Lower Cretaceous Yixian Formation of China

Xinjun Zhang [a, b], Shunxing Jiang [b], Alexander W.A. Kellner [c], Xin Cheng [d], Fabiana R. Costa [e], Xiaolin Wang [b, f, *]

[a] *College of Paleontology, Shenyang Normal University, Shenyang, Liaoning 110034, China*
[b] *Key Laboratory of Vertebrate Evolution and Human Origins of Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China*
[c] *Laboratory of Systematics and Taphonomy of Fossil Vertebrates (LAPUG), Departamento de Geologia e Paleontologia, Museu Nacional/Universidade Federal do Rio de Janeiro, Quinta da Boa Vista s/n, São Cristóvão, Rio de Janeiro 20940-040, Brazil*
[d] *College of Earth Sciences, Jilin University, Changchun 130061, China*
[e] *Laboratory of Vertebrate Paleontology and Animal Behavior, Center for Natural and Human Sciences, Federal University of ABC, Alameda da Universidade s/n, São Bernardo do Campo, Anchieta, SP 09606-045, Brazil*
[f] *University of Chinese Academy of Sciences, Beijing 100049, China*

A R T I C L E I N F O

Article history:
Received 24 October 2022
Received in revised form
12 April 2023
Accepted in revised form 26 April 2023
Available online 5 May 2023

Keywords:
Pterosauria
Tapejaridae
Eopteranodon
Yixian Formation
Lower Cretaceous
China

A B S T R A C T

The Tapejaridae is an exquisite toothless pterodactyloid clade of pterosaurs that flourished in the Jehol Biota with well-developed premaxillary and dentary crests, large nasoantorbital fenestra and downward rostrum. Since *Sinopterus dongi* has been reported from the Jiufotang Formation, most of the Chinese tapejarids were discovered from this geological unity. *Eopteranodon lii*, the first tapejarid from the Yixian Formation, was formerly referred to the Pteranodontidae and is now assigned to the Tapejaridae. Here, *Eopteranodon yixianensis* sp. nov. is reported from this latter formation as differing from all other known tapejarids by largest rostral value (10.88); the nasoantorbital fenestra is not as long as that of other tapejarids (accounting for 35% of the skull length). Furthermore, the skull's length/height ratio is ~5.67; the lower bony crest occupies ~42% of the total mandibular length; the humerus and the fourth wing phalanx length ratio is ~2.17 and the downturn rostral angle is ~17°. New data on the evolution (morphology and geographical origin) of the group is also provided.

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1. Introduction

The Tapejaridae comprises toothless pterosaurs with large nasoantorbital fenestrae and developed cranial crests (Wellnhofer and Kellner, 1991; Cheng et al., 2020) that have already been recorded in Brazil (Kellner and Campos, 1988, 1994; Kellner, 1989, 2013; Pinheiro et al., 2011; Manzig et al., 2014; Cheng et al., 2020; Canejo et al., 2022; Martill et al., 2020a, 2020b), China (Wang and Zhou, 2002; Li et al., 2003; Lü and Yuan, 2005; Lü et al., 2006a, 2006b, 2006c, 2007, 2016; Zhang et al., 2019; Shen et al., 2021; Zhou et al., 2022), Spain (Vullo et al., 2012), Morocco (Martill et al., 2020b) and United Kingdom (Martill et al., 2020a). Since *Sinopterus dongi*, the first Chinese tapejarid reported in the early twentieth century (Wang and Zhou, 2002), many well preserved others (Li et al., 2003; Lü and Yuan 2005; Lü et al., 2006a, 2006b, 2007, 2016; Liu et al., 2014; Zhang et al., 2019; Shen et al., 2021; Zhou et al., 2022) have been found in quick succession. Interestingly, all described Chinese tapejarid specimens were discovered in the Jiufotang Formation, and for most tapejarids from China the skull is not described in detail.

Eopteranodon lii is a small edentulous pterosaur with a wing-span of ~1.37 m (including pectoral girdle) from the Lower Cretaceous Yixian Formation in Beipiao, Liaoning (Lü and Zhang, 2005). The holotype is split into part and counterpart, each containing several bone fragments, and bears an elongated edentulous skull and short cervical vertebrae similar to those of *Pteranodon*. However, as pointed out by Lü and Zhang (2005), the deltopectoral crest of the humerus is quite distinctive from that of the Pteranodontoidea (Kellner, 2003), which makes it unlikely to belong to this clade (Lü and Zhang, 2005). A second skeleton without the skull was referred to *E. lii* based on the ratios of the postcranial elements, and no further reason was given for this assignment (Lü et al., 2006a). Some concluded that *Eopteranodon* is mostly similar

* Corresponding author.
E-mail address: wangxiaolin@ivpp.ac.cn (X. Wang).

https://doi.org/10.1016/j.cretres.2023.105573
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to *Chaoyangopterus*, thus probably representing a junior synonym of *Chaoyangopterus* (Wang and Zhou, 2006; Wang and Dong, 2008). Others recovered this species as a member of the Tapejaridae (Andres and Ji, 2008; Vullo et al., 2012), and some researchers have examined the holotype of *E. lii*, the only specimen with preserved cranial elements, and concluded that the upper and lower jaws have been misidentified (Wang et al., 2017). *Eopteranodon lii* was then considered a junior synonym of *S. dongi* based on similar skull characters and proportions of the postcranial bones (Wang et al., 2017).

Here we present a new tapejarid specimen (IVPP V 14190) from Jianshangou bed of the Lower Cretaceous Yixian Formation in Heitizigou, Beipiao, Chaoyang, Liaoning (see the detailed site in Wang et al., 1998, 1999). The age of this horizon is ~125 Ma (He et al., 2004), dated to the Barremian/Aptian boundary (Cohen et al., 2013). The new specimen was formerly mentioned by Wang and Zhou (2006), but no detailed description was then presented. It is preserved in grey-whitish shale, and almost all elements are well articulated in their natural position. When compared to other Chinese tapejarids, the skull of this new tapejarid is well preserved so that a more detailed description on this element can be provided. We have also compared and discussed the similarities and differences between the new specimen and the holotype of *E. lii*, "*Sinopterus gui*", "*Sinopterus lingyuanensis*", *Sinopterus atavismus, S. dongi*, "*Huaxiapterus jii*", "*Huaxiapterus*" *corollatus* and "*Huaxiapterus*" *benxiensis* (Wang and Zhou, 2002; Li et al., 2003; Lü and Yuan, 2005; Lü and Zhang, 2005; Lü et al., 2006b, 2007, 2016; Wang et al., 2017; Zhang et al., 2019).

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2. Institutional abbreviations

BMNHC, Beijing Museum of Natural History, Beijing, China; BXGM, Benxi Geological Museum, Benxi, China; D, Dalian Natural History Museum, Dalian, China; GMN, Geological Museum of Nanjing, Nanjing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; JPM, Jinzhou Museum of Paleontology, Jinzhou, China; MN, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; SDUST, Shandong University of Science and Technology, Qingdao, China; XHPM, Dalian Xinghai Palaeontological Museum, Dalian, China; ZMNH, Zhejiang Museum of Natural History, Zhejiang, China.

3. Systematic paleontology

Pterosauria Kaup, 1834.
Pterodactyloidea Plieninger, 1901.
Tapejaridae Kellner, 1989.
Eopteranodon Lü and Zhang, 2005.
Type species: *Eopteranodon lii* Lü and Zhang, 2005.

Locality and horizon: Beipiao, Chaoyang, Liaoning, China; Lower Yixian Formation, Lower Cretaceous (Barremian/Aptian boundary).

Revised diagnosis: *Eopteranodon* presents the autapomorphic character of a premaxillary sagittal crest above the nasoantorbital fenestra forming a semicircular expansion. It can be distinguished from other tapejarids by the following combination of characters: skull longer and lower; rather short (only contact with jugal's topmost part) and anteroventrally-oriented medial nasal process; RV (rostral value; Kellner, 2010) high.

Eopteranodon lii Lü and Zhang, 2005.

Holotype: An incomplete skeleton housed at the Beijing Museum of Natural History (BMNHC- Ph000075, previously known as BPV-078), Beijing, China.

Referred specimen: A nearly complete skeleton lacking the skull housed at the Dalian Natural History Museum (D 2526), Dalian, China.

Locality and horizon: Beipiao, Chaoyang, Liaoning, China; Lower Yixian Formation, Lower Cretaceous (Barremian/Aptian boundary).

Revised diagnosis: *Eopteranodon lii* presents the autapomorphic characters of a RV = 6.60. It can be distinguished from other tapejarids by the following combination of characters: a downturn angle of ~13°; fourth phalanx of the wing finger are long.

Eopteranodon yixianensis sp. nov.

Etymology: Yixian refers to the fossil horizon where the holotype was discovered.

Holotype: Almost complete skeleton housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP V 14190), Beijing, China (Fig. 1).

Locality and horizon: Heitizigou, Beipiao, Chaoyang, Liaoning, China; Lower Yixian Formation, Lower Cretaceous (Barremian/Aptian boundary).

Diagnosis: *Eopteranodon yixianensis* is a tapejarid pterosaur with the following autapomorphies: RV = 10.88; short nasoantorbital fenestra (35% of the length between the tip of the premaxilla and squamosal). It can be distinguished from other tapejarids by the following combination of characters: a downturn rostral angle ~17°; skull's length/height ratio ~5.67; lower bony crest occupying ~42% of the total mandibular length; humerus and the fourth wing phalanx length ratio ~2.17.

4. Description and comparisons

4.1. Generalities

The specimen is flattened- a common condition of tapejarid pterosaurs from Liaoning, China. The skull is laterally exposed on its left side and slightly squashed (Fig. 1). It is also overlapped at its mid portion by right metacarpal IV and the first wing phalanx that completely folds at the articulation with this metacarpal and thus runs over the skull just below and parallel to metacarpal IV. As the right forelimb is folded, the subsequent second phalanx overlaps the cervical sequence at its mid portion, obscuring the fourth and fifth cervical vertebrae, and although some other overlapping bones can be seen (e.g., left forearm over pelvis and right femur), the overall shape of mostly all of the post-cranial bones can be easily recognizable.

Some dark spots of soft tissue can be distinguished close to the elements of the right wing and to a less extent at the posterior region of the skull of the specimen, mainly around the sclerotic ring inside the orbit and close to the parietal crest (Fig. 1). A mixture of fibers is also observed in different directions between humerus, radius and ulna on the right side (Fig. 2A), a feature regarded as common in pterosaur wing membranes (e.g., Kellner, 1996). Although no different pattern is recognized from that of a bunch of fibers running parallel to each other, in some areas the wing membrane tissue shows a reticulated pattern. Indeed, the superimposition of distinct layers of actinofibrils due to a taphonomic artefact (i.e., dorsoventral compression) produces a reticular pattern and is seen in both non-pterodactyloids (e.g., *Jeholopterus*, *Pterorhynchus*) and pterodactyloids (e.g., tapejarids; Kellner, 1996), which would suggest a wide occurrence of multi-layered actinofibrils in the wing membrane of pterosaurs (Kellner et al., 2010).

Judging for the overall aspect of the specimen, it seems that it arrived at the bottom of the water column complete and was buried

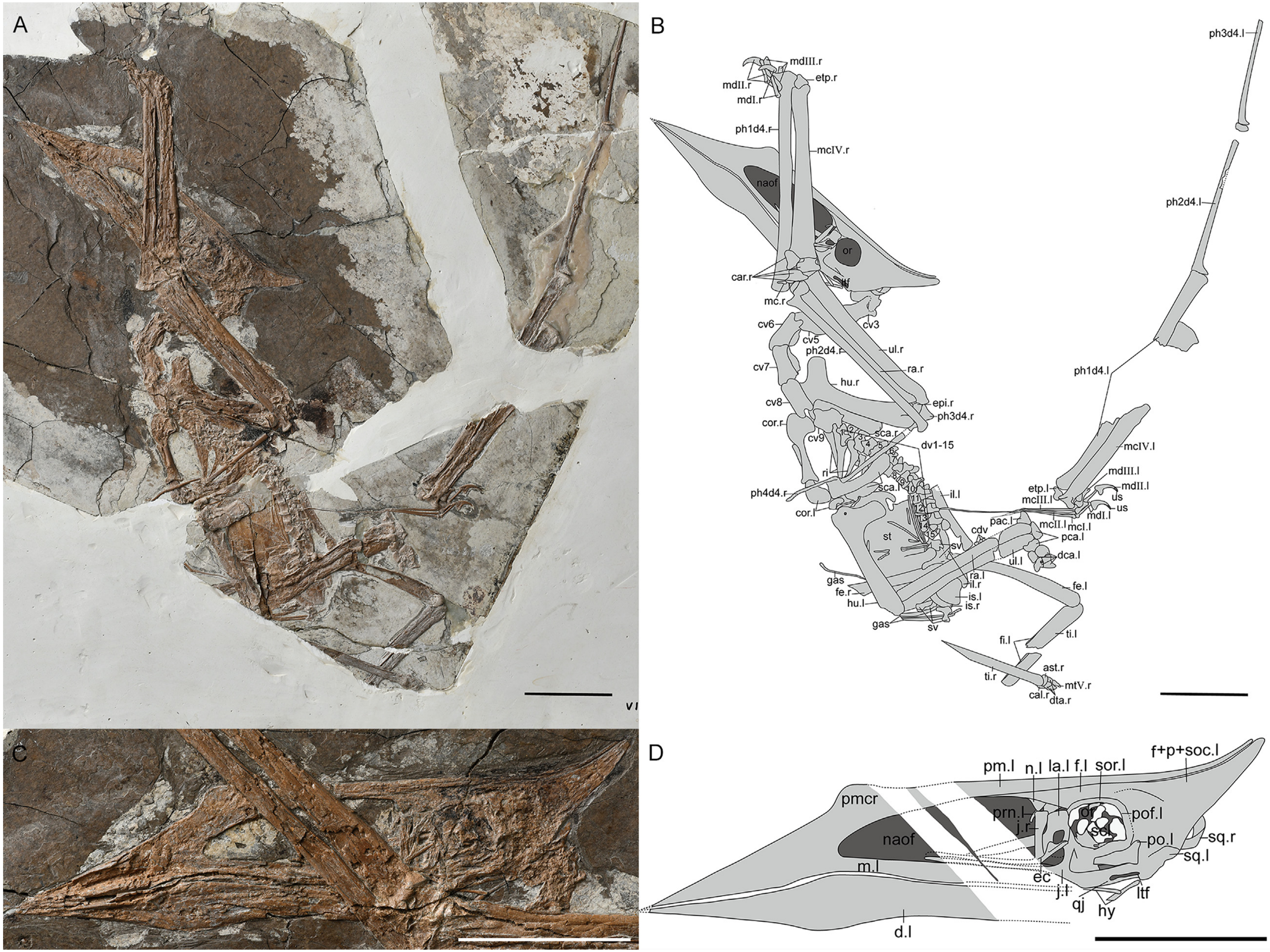

Fig. 1. *Eopteranodon yixianensis* IVPP V 14190. Photo (A) and line drawing (B) of the nearly complete skeleton. Photo (C) and line drawing (D) of the skull. Abbreviations: ast, astragalus; cal, calcaneum; car, carpal; cdv, caudal vertebra; cor, coracoid; cv3–9, cervical vertebrae 3–9; d, dentary; dca, distal carpal; dta, distal tarsal; dv, dorsal vertebra; ec, ectopterygoid; epi, epiphysis; etp, extensor tendon process; f, frontal; fe, femur; fi, fibula; gas, gastralia; hy, hyoid bone; hu, humerus; il, ilium; is, ischium; j, jugal; la, lacrimal; l, left; ltf, lower temporal fenestra; m, maxilla; mcI–III, metacarpals I–III; mcIV, metacarpal IV; mdI–III, manual digits I–III; mtV, metatarsal V; n, nasal; naof, nasoantorbital fenestra; or, orbit; p, parietal; pac, preaxial carpal; pca, proximal carpal; ph1d4-ph4d4, first-fourth phalanx of manual digit IV; pm, premaxilla; pmcr, premaxillary crest; po, postorbital; pof, postfrontal; pphd1-4, phalanges of the pedal digits 1–4; ppu, prepubis; prn, processus nasalis; pu, pubis; qj, quadratojugal; r, right; ra, radius; ri, rib; sca, scapula; scl, sclerotic ring; soc, supraoccipital; sor, supraorbital; sq, squamosal; st, sternum; sv, sacral vertebra; ti, tibia; ul, ulna; us, ungual sheath. Scale bars: 50 mm.

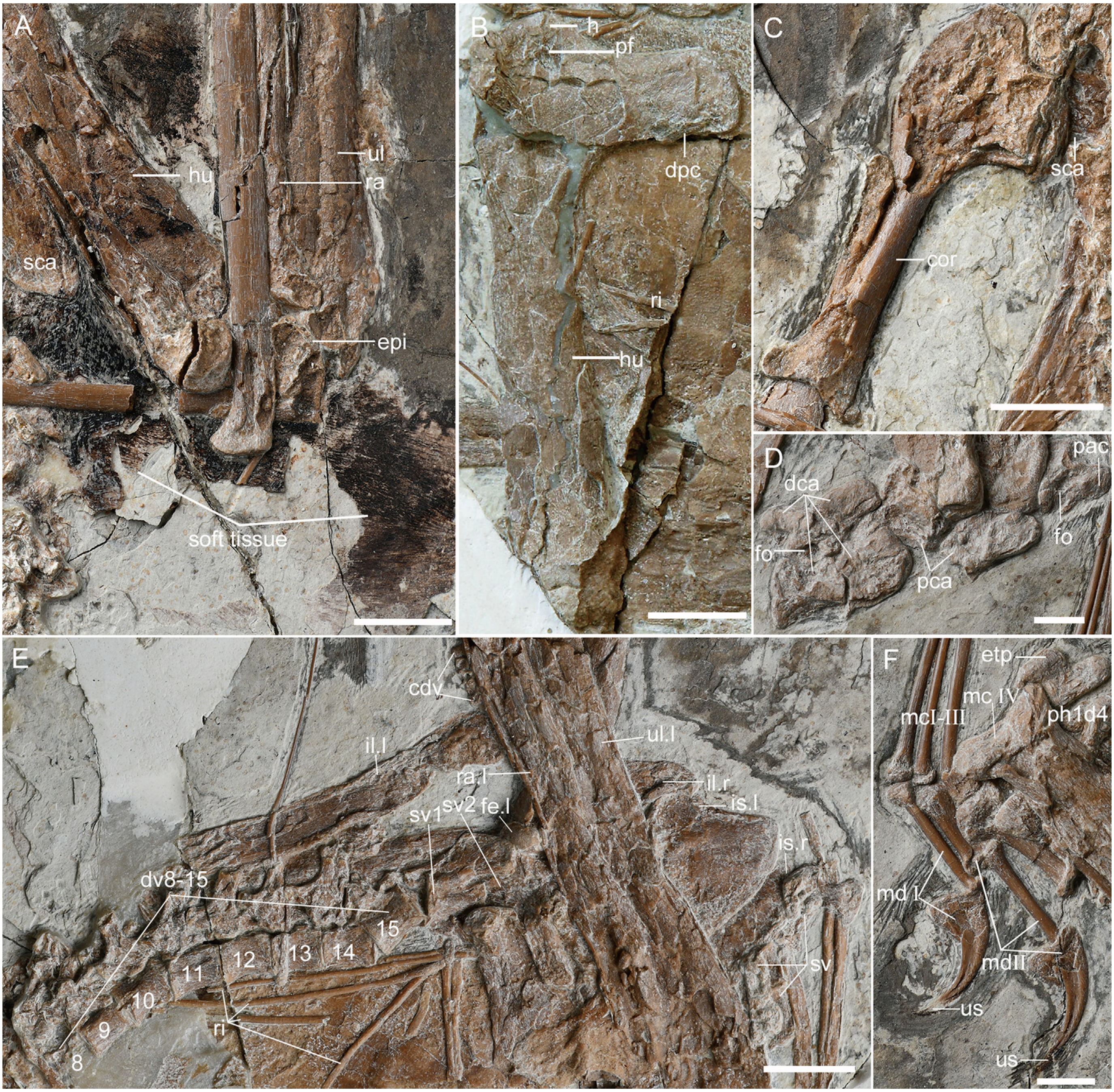

Fig. 2. Close-up of *Eopteranodon yixianensis* IVPP V 14190. A, soft tissue; scale bar: 10 mm. B, left humerus in medial view; scale bar: 10 mm. C, right coracoid in lateral view; scale bar: 10 mm. D, carpal region; scale bar: 5 mm. E, dorsal vertebrae and pelvic girdles; scale bar: 10 mm. F, metacarpals I-IV and manual digits; scale bar: 5 mm. Abbreviations: dpc, deltopectoral crest; fo, foramen; h, head; others see the caption in Fig. 1.

rapidly, which would thus have avoided the dismemberment of the carcass. The predominant darkish ton of the matrix could suggest a reducing environment. Furthermore, as to judge for the bone texture of several bones (e.g., left femoral head) and the unfused nature of others, such as the scapula and coracoid, the epiphysis of the humerus, the extensor tendon process of the first wing phalanx, carpals, sacral vertebrae, pelvic girdle, fibula and tibia and tarsals (Figs. 1–2), the specimen accounts for a juvenile individual (Bennett, 1993; Kellner, 2015).

4.2. Skull

The skull (~164.5 mm in length – from squamosal to premaxilla) with toothless jaws is laterally exposed in left view (Fig. 1, Table 1), and considering the flattened nature of its preservation, it is not possible to properly delineate the limits of cranial bones. Despite the fact of its mid portion being overlapped by the right metacarpal IV and first wing phalanx, as already mentioned, it is possible to observe the full extent of the nasoantorbital fenestra, which is the

Table 1
Measurements of the skull elements of *Eopteranodon yixianensis* IVPP V 14190 (in mm).

Elements	Values
Skull length (from the tip of premaxilla to end of the parietal crest) (Lskull)	186.89
Skull length (from the tip of premaxilla to squamosal) (Lsq-pm)	164.50
Rostral length (Lros)	62.00
Skull height (excluded the posterior part of the premaxillary crest) (Hskull)	29.02
The perpendicular height from the ventral margin of the upper jaw to the most anterior point of the nasoantorbital fenestra	5.70
Nasoantorbital fenestra length (Lnaof)	57.60
Nasoantorbital fenestra height (Hnaof)	22.00
Diameter of the orbit	17.72
Mandibular length (Lman)	131.74[a]
The length from the tip of the mandible to the deepest bony crest (Ltip- deepest bony crest)	55.70
Dentary height (at the deepest point of the dentary crest)	15.13

[a] Approximate or estimated value.

Table 2
Comparisons of the skull of the Tapejaridae specimens from western Liaoning of China.

Elements	Lskull/Hskull	RV	Lnaof/Lsq-pm	Lros/Lsq-pm	Lnaof/Hnaof	L (the upward curved posterior sagittal crest)/Lsq-pm	Ltip- deepest bony crest/Lman
S. atavismus IVPP V 23388	–	4.98	–	–	3.91 (estimate)	–	27%
S. dongi IVPP V 13363 (Holotype)	4.27	4.68	42%	33%	2.44	0.25	38%
E. lii BMNHC- Ph000075 (Holotype)	–	6.60	–	–	–	–	–
E. yixianensis IVPP V 14190 (Holotype)	5.67	10.88	35%	38%	2.62	0.25	42%
"*H*". *corollatus* ZMNH M 8131 (Holotype)	4.15	4.52	–	–	–	–	43%
"*H*". *benxiensis* BXGM V 0011 (Holotype)	4.06	5.60	47%	33%	3.39	0.56	–

Measurements of *Sinopterus atavismus* from Zhang et al. (2019), *S. dongi* from Wang and Zhou (2002), *E. lii* from Lü and Zhang (2005), *"H". corollatus* from Lü et al. (2006b), *"H". benxiensis* from Lü et al. (2007). Abbreviations: L (the upward curved posterior sagittal crest) is the length of the upward curved posterior sagittal crest; others see the caption in Table 1.

largest skull opening (57.6 mm in length). Skull's length/height ratio is 5.67 – higher than that of other Chinese tapejarids (Table 2), which indicates that it has a longer and lower skull.

Compared to the skull length, the nasoantorbital fenestra is not as long as that of other tapejarids, accounting for 35% of the skull length (Table 2), whereas reaching over 45% in Brazilian tapejarids (Kellner, 2004, 2013), and about 42% in *S. dongi* (Wang and Zhou, 2002) and 47% in "*H*". *benxiensis* (Lü et al., 2007) (Table 2). Compared to *S. dongi*, this opening is also reduced in height (~22 mm in length), with a length/height ratio (2.62) slightly different from that of *S. dongi* (2.44) (Wang and Zhou, 2002), "*H*". *benxiensis* (3.39) and *S. atavismus* (3.91) (Zhang et al., 2019) (Table 2). The length/height ratio of the nasoantorbital fenestra is 2.2 in *Tupandactylus navigans*, but only 1.6 and 1.67 in *Tapejara wellnhoferi* and *Caupedactylus ybaka*, respectively (Frey et al., 2003; Kellner, 2013). It bears a triangular shape, with a straight posterior margin and an anterior one narrower than that of *S. dongi*, *"S. gui"*, "*Huaxiapterus jii*", "*Huaxiapterus*" *corollatus*, "*H*". *benxiensis* and *S. atavismus*. The lower temporal fenestra is small, elongated (slit-like) and presents a fossa/concavity ventral to it, which is also observed in other tapejarids (Kellner, 2004, 2013). The rostral value (RV = ros-l/aen-h), which is an index to measure the elongation of the rostrum (Kellner, 2010), is 10.88, higher than that of *S. dongi* (4.68), "*H*". *corollatus* (4.52), "*H*". *benxiensis* (5.60), *E. lii* (6.60) and *S. atavismus* IVPP V 233888 (4.98) (Table 2).

The entire orbit is slightly lower than the dorsal rim of the nasoantorbital fenestra, a similar condition to that found in tapejarids. The orbit accounts for 11% of the skull length, a similar proportion to that found of *S. dongi* (10%) (Wang and Zhou, 2002), and is piriform, a common feature in tapejarids (Kellner, 1989; Wang and Zhou, 2002; Frey et al., 2003; Manzig et al., 2014). There are many irregularly shaped pieces of sclerotic ring inside the orbit. The dorsal and posterolateral margins are rounded, which are made up of the supraorbital and postfrontal elements. The supraorbital is a flattened thin bone that has a faint groove marking the border with the frontal.

The premaxilla of *E. yixianensis* is elongated and extends backward. It fuses with the maxilla as no suture is observed between these elements. The rostrum is relatively long and occupies ~38% of the skull length, which is longer than that condition of 33% in *S. dongi* and "*H*". *benxiensis* (Table 2) and similar to that of *Caupedactylus* (39%) (Kellner, 2013). The dorsal margin of the rostrum is straight as in "*H*". *corollatus*, "*H*". *benxiensis*, *S. atavismus* and *E. lii*., whereas it is slightly concave in *S. dongi*, *"S. gui"*, "*H. jii*" and *"S. lingyuanensis"* (Fig. 3). The rostrum projects straight and downward, which is synapomorphy of the Tapejarinae (Kellner and Campos, 2007), forming a ~17° angle (Fig. 3G), but lack a downturned curvature. This angle varies in other tapejarids such as *S. atavismus* XHPM 1009 (16°), *S. dongi* (10°), "*H*". *corollatus* (18°), *"S. jii"* (16°), *"S. lingyuanensis"* (15°), *Caiuajara dobruskii* (30°–42°), *Tapejara wellnhoferi* (20°–25°), *Tupandactylus navigans* (21°–22°), *Tupandactylus imperator* (27°), *Caupedactylus ybaka* (19°), *Afrotapejara zouhrii*and *Wightia declivirostris* (12°) (Martill et al., 2020). In addition, three unmeasured tapejarid angles have been added, which are "*H*". *benxiensis* (15°) (Fig. 3I), *"S. gui"* (20°) (Fig. 3A), and *E. lii* (13°) (Fig. 3E). This anteriorly-directed rostrum missing any downward inclination is also found in *Thalassodromeus* and *Tupuxuara* (Kellner and Campos, 2002, 2007).

A common feature of tapejarids that is also found in *E. yixianensis* is the presence of a sagittal crest. In this species it starts above the level of the anterior margin of the nasoantorbital fenestra from where it extends backwards until slightly after the occipital region. The premaxilla bears a long posterodorsal process that forms the dorsal margin of the posterior sagittal crest, which ends slightly bent upwards. A semicircular expansion at the premaxillary crest close and above the anterior margin of the nasoantorbital fenestra (Fig. 3G) is also observed in *E. lii* (although more robust) (Fig. 3E), but not in *S. dongi* (Fig. 3D), *"S. gui"* (which is regarded as a junior synonym of *S. dongi*) (Fig. 3A), *S. atavismus* (Fig. 3B), "*H. jii*" (which is regarded as a synonym of *S. dongi*) (Fig. 3F) and *"S. lingyuanensis"* (Fig. 3C). This expansion gives the dorsal margin of the skull a sigmoid configuration formed by the

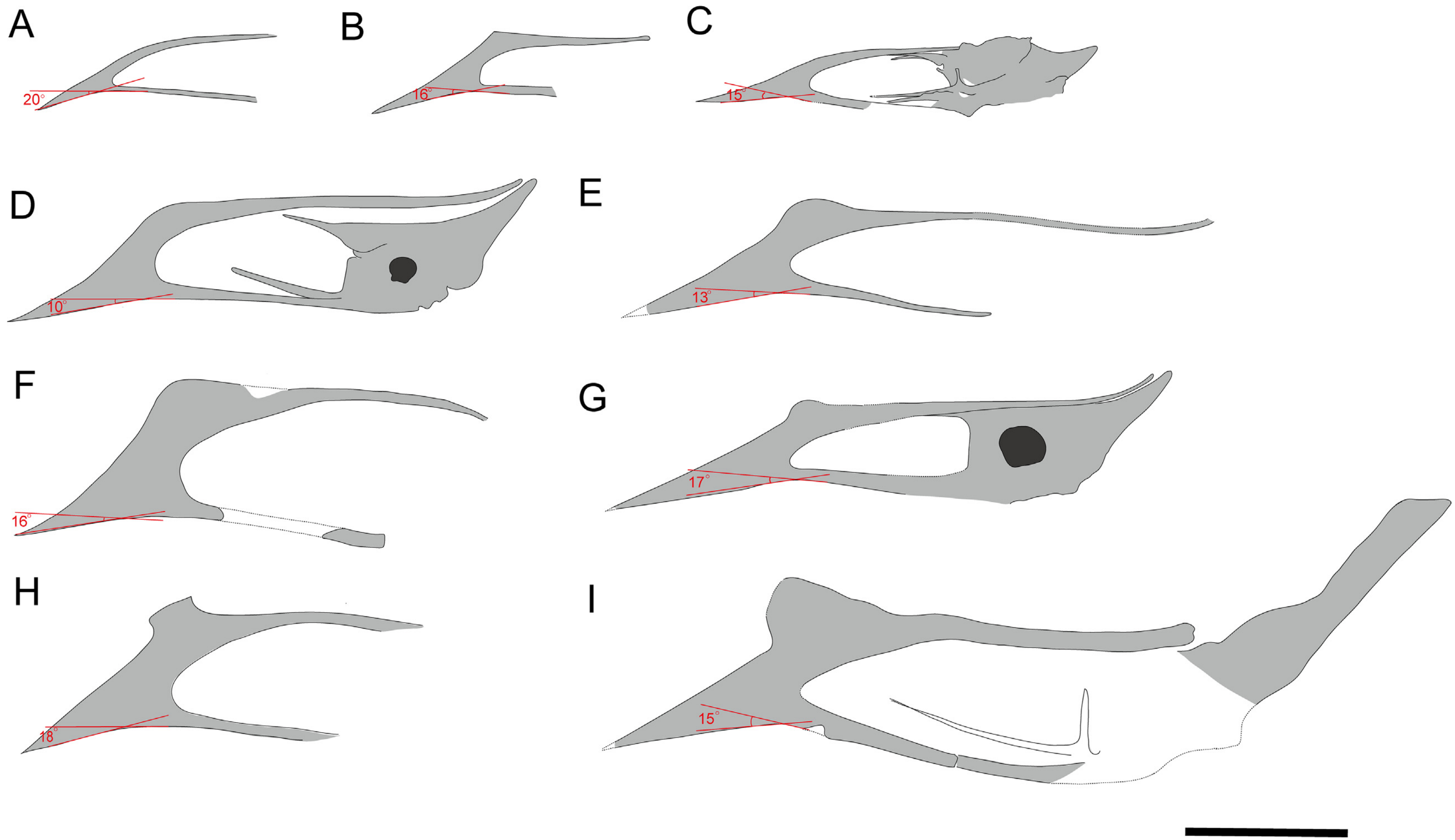

Fig. 3. Comparison of skull morphology of known Chinese tapejarids. A, "*Sinopterus gui*" (BMNHC-Ph000074, previously BVP 077) (Li et al., 2003); B, *Sinopterus atavismus* (XHPM 1009) (Lü et al., 2016); C, "*Sinopterus lingyuanensis*" (JPM-2014-005) (Lü et al., 2016); D, *Sinopterus dongi* (IVPP V 13363) (Wang and Zhou, 2002); E, *Eopteranodon lii* (BMNHC- Ph000075) (Lü and Zhang, 2005); F, "*Huaxiapterus jii*" (GMN-03-11-001) (Lü and Yuan, 2005); G, *Eopteranodon yixianensis* (IVPP V 14190); H, "*Huaxiapterus*" *corollatus* (ZMNH M 8131) (Lü et al., 2006b); I, "*Huaxiapterus*" *benxiensis* (BXGM V 0011) (Lü et al., 2007). Dashed lines are reconstructed portions of the skull. Scale bar: 50 mm.

concave shape of the skull anterior to the crest that begins convex and then becomes straight when extending more posteriorly until curving upwards in a concave shape. "*Huaxiapterus*" *corollatus* has a quadrangular-shaped process that is perpendicular to the dorsal margin of the rostrum, which is located above the anterior margin of the nasoantorbital fenestra (Lü et al., 2006b) (Fig. 3H). "*Huaxiapterus*" *benxiensis* bears an extended forward ladder shaped process at the cranial crest just above the anterior margin of the nasoantorbital fenestra (Lü et al., 2007) (Fig. 3I).

The lateral surface of the maxilla is broken and the place of the lateral expansion is not well preserved. Moreover, its posterior portion where it articulates with the skull cannot be observed as it is overlapped by the folded right wing. Consequently, no further information can be added regarding this element.

The nasal has a short (only contact with jugal's topmost part), anteroventrally-oriented medial nasal process, differing from the condition found in *S. dongi* and *"S. lingyuanensis"*, which bears a long (almost reaching the ventral margin of the skull) and almost perpendicular process. This bone starts below the dorsal margin of the nasoantorbital fenestra, and is barely exposed in lateral view and overlaid by the anterior process of frontal, which is long with a sculptured lateral surface and whose limits are hard to establish. The frontal seems to take part of the large sagittal crest. In addition, the sagittal crest is also partially formed by the parietal and supraoccipital, but the boundary of the parietal, frontal and supraoccipital is difficult to determine (Fig. 1). The ratio of the upward curved posterior sagittal crest to the skull length is about 0.25, which is consistent with *S. dongi* and smaller than "*H*". *benxiensis* (0.56) (Table 2).

The lacrimal forms the posterodorsal margin of the nasoantorbital fenestra and attaches to the lower end of the orbit. The surface of this bone is poorly preserved, but we can see that it is fenestrated.

The postorbital is preserved on the left side. It is a triangular bone that contacts the jugal and squamosal ventrally. Both squamosals are preserved, and the left one remained in its natural position. It extends ventrally and participates in the dorsocaudal margin of the lower temporal fenestra. The right one was dislocated towards the occiput in medial side. The jugals are partially preserved, with the left one more complete than the right one. The maxillary process is elongated, slender and participates in the ventral margin of the nasoantorbital fenestra; the lacrimal process is flattened, slightly anteriorly directed (as in *S. dongi*), overlain by the lacrimal and separates the nasoantorbital fenestra from the orbit; and the postorbital process separates the orbit from the lower temporal fenestra, which was detected in the micro-CL image (Fig. 4A, B) quite vertical between the maxillary process and the lacrimal process. The lacrimal process preserved in a ~80° with the postorbital process.

The quadratojugal is a small bone fused with the jugal. It extends anteroventrally from the anterior margin of the lower temporal fenestra. Between the left and right jugals there is an incomplete ectopterygoid that forms part of the anteromedial margin of the pterygoid fenestra, which is similar to that of *Caupedactylus ybaka* (Kellner, 2013).

The dentary crest is placed just below the high point of the mandible in *Eopteranodon*, similar to the position of this crest in *Sinopterus* and different from that of *Tapejara* and *Caiuajara*, in which it is slightly displaced forward regarding the most pronounced curvature of the mandible. This crest in *Eopteranodon* is not deep as in *Tapejara* (Wellnhofer and Kellner, 1991), *Europejara* (in which this crest is also much more anteriorly placed; Vullo et al., 2012) or *Caiuajara* (Manzig et al., 2014), but shallow and with a similar length of that of the Chinese tapejarids (Wang and Zhou, 2002; Li et al., 2003; Lü and Yuan, 2005; Lü et al., 2006b, 2007, 2016; Zhang et al., 2019). The low bony crest extends from the tip of the mandible to a point about 42% from the posterior end. The ratio is similar to that of "*H*". *corollatus*, larger than that of other Chinese tapejarids (Table 2). The dorsal margin of the dentary is convex, slightly posterior of the ventral crest. Other mandibular bones cannot be delineated. At last there are two thin, rod-like bones beneath the lower jaw that seems to belong to the hyoid apparatus.

4.3. Axial skeleton

The axial skeleton series of *E. yixianensis* is articulated and accounts for 24 presacral vertebrae (29 with sacrals) as follows: 9 cervical vertebrae, 15 dorsal vertebrae, 5 sacral vertebrae and caudals whose number is unknown. The right second wing phalanx overlaps the cervical sequence, obscuring the fourth and fifth cervical vertebrae.

In the posterior part of the skull both atlas and axis can be observed, but they are far too destroyed, with most of the external bone surface severely eroded in a way that nothing can be said about their specific features. Most of the cervical vertebrae also have the lateral surface broken, but it can be seen that they are moderately elongated. The length/minimum width ratio of cervical 6 is 2.85 (Table 3), slightly higher than that of *S. dongi* (21.19/9.64 ≈ 2.20), but lower than in "*H*". *benxiensis* (3.13) (Lü et al., 2007). Neural spines are comparatively tall regarding the lower condition found in the Archaeopterodactyloidea or the reduced condition in the Azhdarchidae, and blade-like. Pneumatic foramina that are commonly found in derived pterodactyloid pterosaurs (e.g., Buchmann and Rodrigues, 2019) could not be identified due to the compaction of the neck of this specimen. In any case, if present, they were not very well developed as observed in some azhdarchoids (e.g., Kellner et al., 2019).

Fifteen dorsal vertebrae are clearly discernible and are all rotated laterally, exposing it from left lateral view and slightly ventral (Fig. 2E). As the notarium is not formed, it is not possible to know if dorsal vertebrae fuse and form this structure in more mature individuals. The seventh and eighth dorsal vertebrae are not well preserved. Transverse processes tend to be on the anterior half of the vertebra. The last vertebra of the dorsal series (the fifteenth vertebra) has broader processes in comparison to those of more anterior ones.

The size of the first sacral vertebra is similar in size to that of dorsals, with broad processes. The second sacral is much larger than that of the first one, also bearing broad processes (Fig. 2E). Besides these two, there are three more sacral vertebrae- two ventral to the ischia (with elongated centra) and one ventroposteriorly placed, which accounts for a total of at least five sacrals, but it is possible that this number could be higher than five (Fig. 2E).

There are three small elements that could be interpreted as the neural spines of the caudal vertebrae and a centrum of a caudal vertebra. These neural spines are low and narrow along the midline of the neural arch (Fig. 2E).

Three ribs are placed near the vertebral column. They are long, double-headed, and arched dorsally and slightly curved caudally. The sternum is present, but severely damaged and displaced from its original position. Despite that, it can be said that it is a big and thin bony plate, with some of its areas showing the internal surface with many pits (granulated area). The gastralia is v-shaped.

4.4. Pectoral girdle and forelimb

The scapula/coracoid length ratio is ~1.10, similar to that of "*S. gui*" (1.29) (Li et al., 2003), "*H.*" *corollatus* (1.23) (Lü et al., 2006b), *S. atavismus* IVPP V 23388 (1.25) (Zhang et al., 2019), *S. dongi* IVPP V

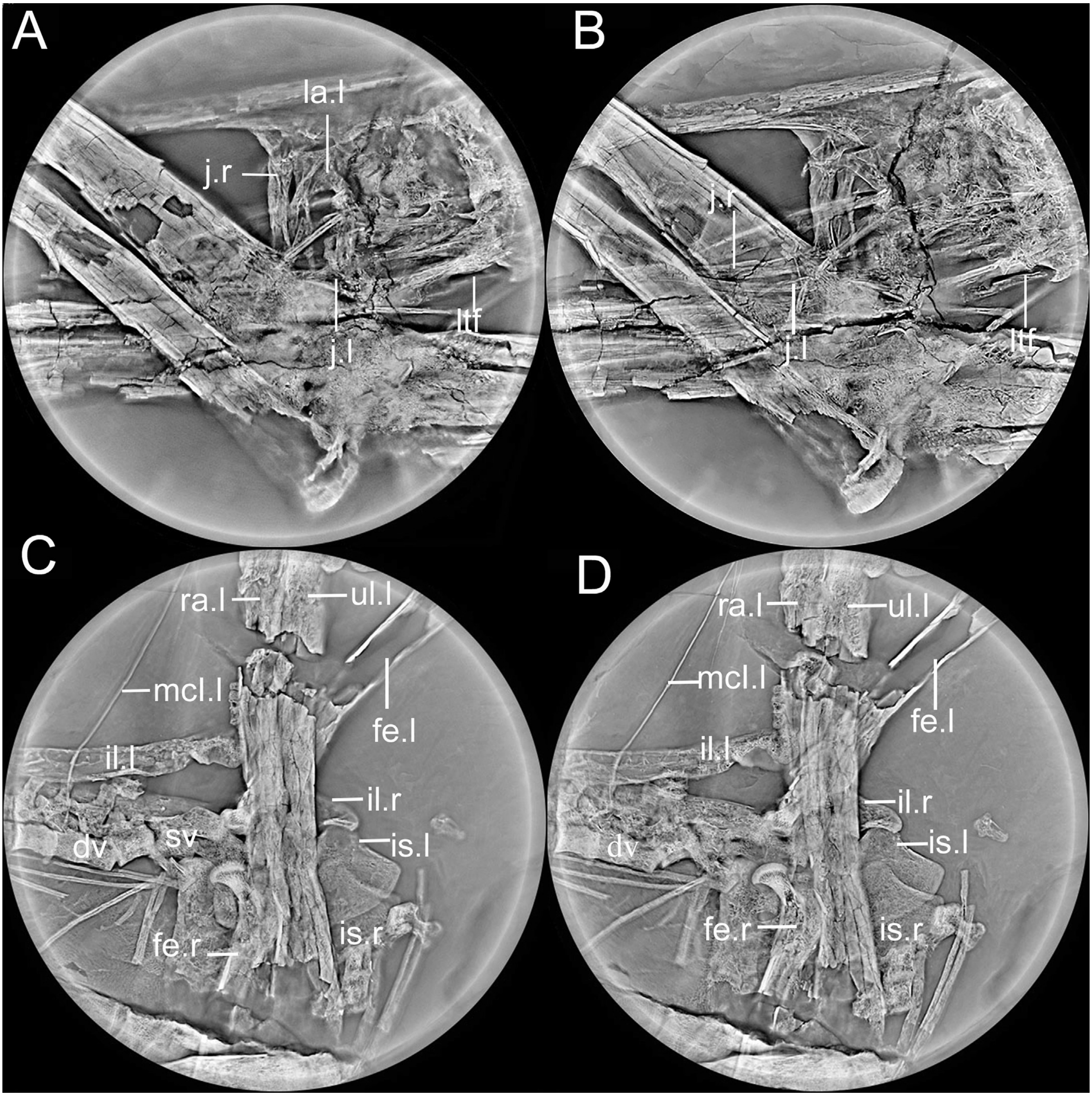

Fig. 4. Micro-CL images of *Eopteranodon yixianensis* IVPP V 14190. A and B, the skull region; C and D, the pelvic region.

Table 3
Measurements of the vertebral column elements of *Eopteranodon yixianensis* IVPP V 14190 (in mm).

Elements	Values
Length of cervicals 3–9 (between pre- and postzygapophyses)	16.26[a], –, –, 20.37, 22.86, 20.28, 17.62[a]
Minimum width/height of cervicals 3–9	9.30[a], –, –, 7.15, 8.33, 9.04, 7.12[a]
Centrum length of dorsals 8–15	6.37, 5.49, 6.23, 6.04, 6.04, 5.70, 5.97, 5.97
Centrum length of sacral 1	6.37

[a] Approximate or estimated value; – not preserved.

13363 (1.11) (Wang and Zhou, 2002), *E. lii* D 2526 (1.15) (Lü et al., 2006a), *S. dongi* D 2525 (0.97) (Lü et al., 2006c) and *Sinopterus* SDUST-V1012 (1.13) (Zhou et al., 2022). The scapula is elongated and slightly longer than the coracoid. The ventral margin of the coracoid has a deep flange. The articulation of the coracoid and sternum is strongly concave.

The left humerus is preserved in medial view, and the right one is exposed in lateral view. Humerus and ulna length ratio is 0.73, similar to that of *S. dongi* (0.66) (Wang and Zhou, 2002), "*S. gui*" (0.66), *Sinopterus* SDUST-V1012 (0.67) (Zhou et al., 2022), "*H. jii*" (0.68) (Lü and Yuan, 2005), "*H*". *corollatus* (0.70) (Lü et al., 2006b) and *S. atavismus* (0.71) (Lü et al., 2016), and slightly lower than that of "*H.*" *benxiensis* (0.77) and *"S. lingyuanensis"* (0.83) (Lü et al., 2016), but higher than that of *E. lii* (0.63). Humerus and metacarpal IV length ratio is 0.72, almost the same as that of "*S. gui*" (0.71), and higher than that of *S. dongi* (0.61) (Wang and Zhou, 2002), "*H. jii*" (0.60) (Lü and Yuan, 2005), "*H*". *corollatus* (0.52) (Lü et al., 2006b), "*H*". *benxiensis* (0.68), *S. atavismus* (0.67 (Lü et al., 2016), and *E. lii* (0.65), but lower than that of *"S. lingyuanensis"* (0.83) (Lü et al., 2016). The left deltopectoral crest extends anteriorly and is perpendicular to the shaft, which is similar to *S. atavismus* (Zhang et al., 2019), *S. dongi* (Shen et al., 2021), *Sinopterus* SDUST-V1012 (Zhou et al., 2022) and *Caupedactylus ybaka* (Kellner, 2013). However, the other side is at a slightly oblique angle to the humeral shaft, anteroventrally. This is similar to *Tapejara wellnhoferi* (Eck et al., 2011), *Caiuajara dobruskii* (Manzig et al., 2014) and *Tupandactylus navigans* (Beccari et al., 2021). The above situation is probably caused by preservation. The dorsal and ventral margins of the deltopectoral crest are parallel to each other, a common feature in the Tapejaridae (Eck et al., 2011; Zhang et al., 2019). In addition, the left humerus shows a well-developed pneumatic foramen on the base of the deltopectoral crest, close to the proximal articulation (Fig. 2B). Such foramen is commonly observed in azhdarchoid pterosaurs (e.g., Kellner et al., 2019). Distally, the right humeral shaft is slightly curved. Near the distal end of the right humerus there is an unfused humeral epiphysis, which was related to the ontogenetic stage of *E. yixianensis* (Fig. 2A).

The ulna and radius are worse preserved on the left side, but their shafts are more intact at the right side. The ulna diameter is about 1.5 as long as that of the radius at midshaft, which is only visible in the micro-CL image (Fig. 4C, D).

At the left side four distal and two proximal carpals, all unfused, as well as one preaxial carpal, can be identified. Distal carpals can be seen in distal view and are formed by four parts, all unfused in this specimen but forming a quadrangular-shaped unit. A pneumatic foramen is visible in one of these distal carpals (Fig. 2D). The two proximal carpals are presumably the ulnare (next to the distal carpals) and the radiale. The preaxial carpal is a small bone with a pneumatic foramen (Fig. 2D). There is no trace of both pteroids neither sesamoids.

Regarding the metacarpal region, the shafts of metacarpals I-III are plastically deformed in some parts. Metacarpal I thickens first and then becomes thin, and subsequently gets thick again. Metacarpals II and III change from fine to coarse. Regarding the length, metacarpal I is 78.80 mm, slightly shorter than metacarpal IV (Table 4). It is worth mentioning that metacarpal I is not complete (some of its parts were broken), but it might have reached the length of metacarpal IV and articulated with the carpal if completed. Compared to metacarpal I, metacarpals II and III are reduced. While metacarpal III is shorter than II, metacarpals II and III are longer than half the length of metacarpal IV.

The first phalanges of manual digits I to III are progressively thicker. In terms of length, the first phalanx of digit I is longer than that of digit II, but similar to that of digit III (Table 4). The first phalanx of digits I-III has a distinct process in the proximal portion, and the process of the first phalanx of digits III is more developed (Fig. 2F). Manual claws are large, and the unguals are curved and present a horny sheath (Fig. 2F).

Regarding the manual digit IV, the extensor tendon process is unfused with the straight and elongated first phalanx of the wing finger. Both proximal ends of the second and third phalanges have a shoe-like shape. The fourth phalanx is a little bit curved. The ph2d4 and ph1d4 length ratio is 0.85, the same as that of "*S. lingyuanensis"* (Lü et al., 2016), higher than in *S. dongi* (0.73) (Wang and Zhou, 2002), "*H. jii*" (0.79) (Lü and Yuan, 2005), "*H*". *corollatus* (0.61) (Lü et al., 2006b), "*H*". *benxiensis* (0.75), *S. atavismus* (0.79) and *E. lii* (0.75). The ph3d4 and ph1d4 length ratio is 0.52, similar to that of *S. dongi* (0.54), but lower than that of "*H. jii*" (0.58), "*H*". *benxiensis* (0.57), *S. atavismus* (0.58) (Lü et al., 2016), *"S. lingyuanensis"* (0.63) (Lü et al., 2016), and higher than in "*H*". *corollatus* (0.39) (Lü et al., 2006b) and *E. lii* (0.47) (Lü and Zhang, 2005). The ph3d4 and ph2d4 length ratio is 0.61, which is quite similar to that of *E. lii* (0.63) (Lü and Zhang, 2005), "*H*". *corollatus* (0.64) (Lü et al., 2006b), and lower than that of *S. dongi* (0.73) (Wang and Zhou, 2002), *"S. lingyuanensis"* (0.74) (Lü et al., 2016), "*H. jii*" (0.72) (Lü and Yuan, 2005), "*H*". *benxiensis* (0.76) and *S. atavismus* (0.73) (Lü et al., 2007). Humerus and the fourth wing phalanx length ratio is 2.17, which is lower than that of "*H*". *corollatus* (2.34) (Lü et al., 2006b) and *Sinopterus dongi* D 2525 (2.51) (Lü et al., 2006c), but higher than other Chinese tapejarids (Fig. 5). The ph1d4 and ph4d4 length ratio is 3.84, which is lower to that of "*Huaxiapterus*" *corollatus* (4.99) (Lü et al., 2006b) and "*H*". *benxiensis* (5.00) (Lü et al., 2007), higher than other Chinese tapejarids (Fig. 5). The ph3d4 and ph4d4 length ratio is 1.98, which is lower than that of "*H*". *corollatus* (2.04) (Lü et al., 2006b), "*Huaxiapterus jii*" (2.04) (Lü and Yuan, 2005) and G, *Sinopterus dongi* D 2525 (2.47) (Lü et al., 2006c), higher than other Chinese tapejarids (Fig. 5). *E. yixianensis* is also a small edentulous pterosaur with a wingspan of ~1.25 m (including pectoral girdle), close to the size of *S. dongi* IVPP V 13363 (wingspan ~ 1.2 m) and *E. Lii* D2526 (wingspan ~ 1.364 m), much larger than "*S. gui*" (wingspan ~ 0.6 m) (Kellner and Campos, 2007), *S. atavismus* XHPM 1009 (wingspans ~ 0.83) and *"S. lingyuanensis"* (wingspans ~ 0.87 m), and smaller than "*H.*" *corollatus* (wingspans ~ 1.56 m) (Lü et al., 2006b), "*H. jii*" (wingspan ~ 1.60 m) (Lü and Yuan, 2005) and "*H.*" *benxiensis* (wingspan ~ 1.7 m, adult).

4.5. Pelvic girdle and hindlimb

The pelvic girdle is mostly overlapped by left radius and ulna, and some pelvic elements such as left ischium and ilium got displaced. The right ilium is exposed in medial view and the proximal tip is missing. The postacetabular process of the right ilium is partially overlapped by the left radius and ulna, and we can see that it was short and gradually narrows, but the caudal tip is still rounded (Figs. 2E, 3C, D), similar to that of *S. atavismus* (Zhang et al., 2019) and *Sinopterus* SDUST-V1012 (Zhou et al., 2022). The left ilium is exposed in lateral view and has a long preacetabular process (Fig. 2E). The left ischium is exposed in lateral view and the right one in medial view. The ischium is a broad, thin subtriangular bone whose caudal margin is predominantly concave and the ventral margin is convex (Fig. 2E), similar to that of *Tapejara wellnhoferi*, *S. atavismus* and *Sinopterus* SDUST-V1012 (Eck et al., 2011; Zhang et al., 2019; Zhou et al., 2022).

Both femora are partially preserved, with the left one far more complete than the right one such as the case of the tibia. The left femur and tibia are articulated and exposed in medial view. The right femoral head is well developed and round, which can be detected in the micro-CL image (Fig. 4C, D). Humerus and femur length ratio is 0.88, similar to that of the holotype of *E. lii* (0.88), *E. lii* D 2526 (0.86) (Lü et al., 2006a), *S. dongi* (0.81) (Wang and Zhou, 2002), "*S. gui*" (0.91) (Li et al., 2003), "*H. jii*" (0.79) (Lü and Yuan, 2005), "*H.*" *corollatus* (0.86) (Lü et al., 2006b), " *H.*" *benxiensis* (0.78) and *S. atavismus* (0.82) (Zhang et al., 2019), but lower than that of *"S. lingyuanensis"* (1.31) (Lü et al., 2016). Ulna and femur

Table 4
Measurements of the postcranial bones of *Eopteranodon yixianensis* IVPP V 14190 (in mm).

Elements	Left	Right
Scapula	39.67	41.09
Coracoid	35.99	40.58
Humerus	70.70	66.66[b]
Ulna	86.71[b]	97.00
Radius	84.52[b]	96.94
Metacarpal IV	91.05[b]	98.47
Metacarpal I—III	76.21, 50.34, 59.36	–, –, –
First to second phalanx of manual digit I	11.20, 10.59	12.72, 10.72
First to third phalanx of manual digit II	8.59, 10.34, 11.39	5.05[b], 11.48, 10.23
First to fourth phalanx of manual digit III	12.30, 5.04[b], -, -	11.39, 3.59[b], -, -
First to fourth phalanx of manual digit IV	94.05[b], 82.49[b], 60.28[b], -	125.12, 106.51, 64.53, 33.00[a]
Ilium	57.15[b]	41.46[b]
Femur	80.24	54.73[b]
Tibia	60.95[b]	62.76[b]
Metatarsal V	–	6.21

[a] Approximate or estimated value.
[b] Preserved length; - not preserved.

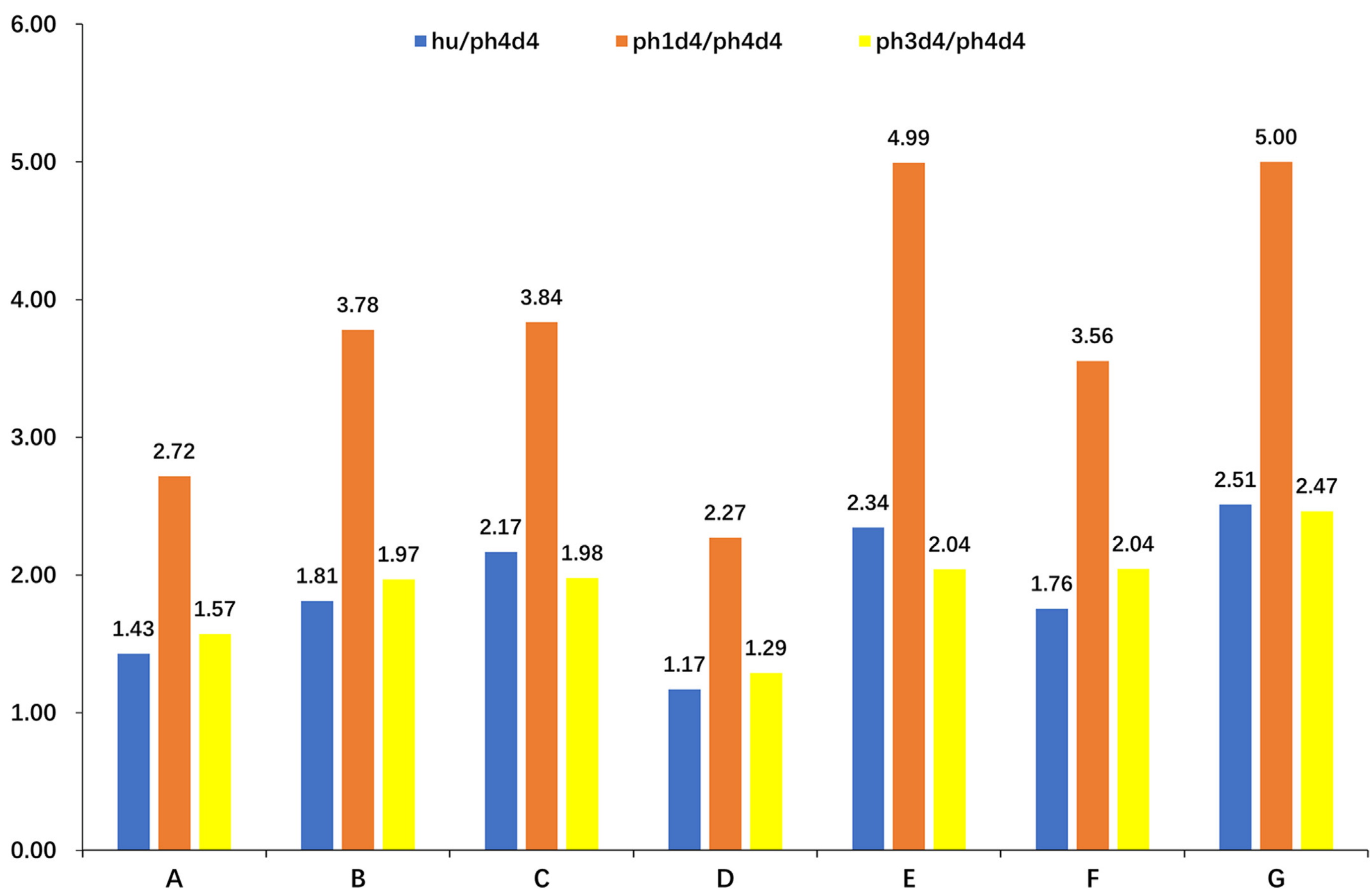

Fig. 5. Histogram of ratios of humerus, first, and third phalanx of the wing finger to fourth phalanx of the wing finger in Chinese tapejarids. A, *Sinopterus atavismus* XHPM 1009 (wingspan ~0.83 m) (Lü et al., 2016); B, *Sinopterus dongi* IVPP V 13363 (wingspan ~1.2 m) (Wang and Zhou, 2002); C, *Eopteranodon yixianensis* IVPP V 14190 (wingspan ~1.25 m); D, *Eopteranodon lii* D 2526 (wingspan ~1.364 m) (Lü et al., 2006a); E, "*Huaxiapterus*" *corollatus* ZMNH M 8131 (wingspan ~1.56 m) (Lü et al., 2006b); F, "*Huaxiapterus jii*" GMN-03-11-001 (wingspan ~1.60 m) (Lü and Yuan, 2005); G, *Sinopterus dongi* D 2525 (wingspan ~1.7 m) (Lü et al., 2006c).

length ratio is 1.24, similar to that of *S. dongi* (1.22) (Wang and Zhou, 2002), "*S. gui*" (1.30), " *H. jii*" (1.20) (Lü and Yuan, 2005), "*H*". *corollatus* (1.23) (Lü et al., 2006b), "*H*". *benxiensis* (1.06) (Lü et al., 2007) and *S. atavismus* (1.20) (Zhang et al., 2019); lower than that of *E. lii* (1.40); but much higher than that of "*S. lingyuanensis*" (0.63) (Lü et al., 2016). The tibia is straight. It tends to be thinner from proximally to distally, same as *S. dongi* (Shen et al., 2021). The fibula is very thin, and only the distal portion of the left fibula can be seen because of its state of preservation. The astragalus, calcaneum and distal tarsals are all preserved and unfused. The astragalus is a sub-rectangular bone whose edges are rounded, the same condition as that of *S. atavismus* (Zhang et al., 2019). The outermost distal tarsal is sub-triangular. Only a hook-shaped, short right metatarsal V is preserved.

5. Discussion

The Tapejaridae clade erected by Kellner (1989) provided three diagnostic characteristics to distinguish these peculiar edentulous pterosaurs: a sagittal crest that extends from the anterior portion of the skull backwards, a downturned rostrum (much prominent in *Tapejara* and thus regarded as an autapomorphy to this genus) and a huge nasoantorbital fenestra. Two characters particularly unite the tapejarids from China: a sculptured frontal and a spike-like crest directed upwards and backwards. The new specimen shares all the abovementioned tapejarid characteristics, being thus assigned to this clade.

The holotype of *E. lii* can be assigned to the Tapejaridae because of the large nasoantobital fenestra, a developed cranial crest and a downturned rostrum. This is also the first tapejarid from the Yixian Formation. It seems to represent a juvenile specimen (due to the lack of fusion of several elements) at Ontogeny Stage 2 (OS2) (Lü and Zhang, 2005; Kellner, 2015). Its size is close to that of *S. dongi* (Wang and Zhou, 2002) and the new specimen (IVPP V 14190). In addition, there are also differences between *E. lii* and *Sinopterus*. The skull is lower and longer than *Sinopterus*; the RV is 6.60, which is much larger than that of all members of *Sinopterus* (Table 2). Therefore, we consider *E. lii* as a member of the Tapejaridae clade different from *Sinopterus*.

Lü and Zhang (2005) listed the following distinguishing features when they firstly established *E. lii*: ① early small edentulous pterosaurs; ② straight deltopectoral crest of the humerus, with upper and lower edges nearly parallel; ③ wing metacarpal slightly longer than ulna; ④ ratio of wing metacarpal and first phalanx of the wing finger (mcIV/ph1d4) = 0.76; ⑤ wing metacarpal subequal in size to second phalanx of the wing finger (mcIV/ph2d4 ~ 1). Later, Lü et al. (2006a) identified a new skeleton without the skull as *E. lii*, and added two distinguishing features: ⑥ ratio of the length of deltopectoral crest to humerus ~0.25; ⑦ ratio of second phalanx of the wing finger and first phalanx of the wing finger ~0.76. The characteristics listed by Lü and Zhang (2005) apply to all tapejarids and do not serve the purpose of distinguishing this group. Therefore, they have been removed. The ratio of the postcranial bones listed in features ⑥ and ⑦ is similar to that of other tapejarids and neither distinguishes this group, being thus deleted.

The new specimen (IVPP V 14190) shares some features with *E. lii*, such as longer and lower skulls (Fig. 4), with a length-height ratio of 5.67, higher than that of *Sinopterus* species (Table 2), as well as the premaxillary sagittal crest above the nasoantorbital fenestra forming a semicircular process (Fig. 4E, G). Besides, the new specimen differs from other *Sinopterus* specimens by bearing a short (only contact with jugal's topmost part), anteroventrally-oriented medial nasal process, differing from the condition found in *S. dongi* and "*S. lingyuanensis*", which bears a long (almost reaching the ventral margin of the skull), almost perpendicular process; skull's length/height ratio is ~5.67, which is higher than in other *Sinopterus* species; the nasoantorbital fenestra is not as long as that of other *Sinopterus* species, accounting for 35% of the skull length, whereas reaching over 42% in *Sinopterus* species (Table 2). Therefore, the new specimen can be assigned to the *Eopteranodon* genus.

The most significant difference between the new specimen and *E. lii* is that the rostral value of the former is 10.88, which is much higher than that of the latter (6.60) (Table 2), suggesting that the new specimen has a longer rostrum. Besides, the downturn angle of the new specimen is ~17°, higher than that of *E. lii* (13°) (Fig. 4). The low bony crest extends from the tip of the mandible to a point about 42% from the posterior end. The ratio is similar to that of "*H*". *corollatus*, larger than that of other Chinese tapejarids (Table 2). There are also some postcranial ratio differences between the new specimen, *E. lii* and *Sinopterus* species. Humerus and the fourth wing phalanx length ratio of *E. lii* is ~1.17, which is much lower than the new specimen and *Sinopterus* species; first and the fourth wing phalanx length ratio of *E. lii* is ~2.27, which is much lower than the new specimen and *Sinopterus* species; third and the fourth wing phalanx length ratio of *E. lii* is ~1.29, which is lower than the new specimen and *Sinopterus* species (Fig. 5). This indicates that the fourth phalanx of the wing finger of *E. lii* was relatively long. Therefore, the establishment of *E. yixianensis* sp. nov. with the holotype of IVPP V 14190 is justified.

Compared to the Chinese tapejarids from Jiufotang Formation, the skulls of *Eopteranodon* species are longer and lower. Considering that *Eopteranodon* was recovered from older layers, we assume that longer and lower skulls are more "basal" characteristics in this group. At the same time, compared to all Chinese tapejarids, the skulls of the South American species of this group are shorter and higher, as well as younger in age, which suggests that the skull morphology might has changed from long and low to short and high. From the point view of morphology and stratigraphic age, "Eurasia" (Europe + Asia) is regarded as the most likely area of origin for the group.

Moreover, the anterior projection of the premaxillary crest in *E. yixianensis* forms a semicircular process, a similar condition to that of *E. lii* (Fig. 4E, G). While the crest of *S. atavismus* is pointed in the middle part of its dorsal margin (Fig. 4B), the premaxillary crest of *S. dongi* is smooth in the same position (Fig. 4D, C, A, F). *S. corollatus* shows a quadrangular-shaped process that is perpendicular to the dorsal margin of the rostrum (Fig. 4H). *Sinopterus benxiensis* has an extended forward ladder shaped process on the cranial crest located above the anterior margin of the nasoantorbital fenestra (Fig. 4I), which suggests that the premaxillary crest has a wide range of types in Chinese tapejarids. This difference may be caused by interspecific differences, rather than the single gender differences previously thought.

Eopteranodon yixianensis also provides some other important information about tapejarids. The total number of dorsal vertebrae is poorly known in tapejarids. Zhou et al. (2022) speculated that the 15 dorsal vertebrae of *Sinopterus* SDUST-V1012 possibly represent a complete dorsal series. There are also 15 complete dorsal vertebrae preserved in *E. yixianensis*. The Brazilian tapejarid specimen MN 6558-V has 12 complete dorsal vertebrae (Cheng et al., 2020). Besides, the jugals can be confirmed as a triradiate element by micro-CL image, which is consistent with "*S. lingyuanensis*" (Lü et al., 2016), but it is reported as a tetraradiate type in the Brazilian tapejarids (Wellnhofer and Kellner, 1991). These variations possibly also reflect the evolutionary patterns of the dorsal series and jugals in tapejarids, and need to be further examined with additional specimens in future studies.

6. Conclusions

A new species of the Tapejaridae, *Eopteranodon yixianensis* sp. nov. has been erected based on the new specimen IVPP V 14190. From the perspective of anatomical changes in the skeleton of the tapejarids, there may be the following evolutionary trends: the skulls have evolved from long and low to short and high; the number of dorsal vertebrae evolved from more to less; the jugal has evolved from a triradiate type to a tetraradiate type. The reasons for the above changes are currently unclear, and more specimens are needed for further research. Besides, we regard that the variations in the shape of the premaxillary crest of the Chinese tapejarids appear to be related to interspecific differences.

Data availability

Data will be made available on request.

Acknowledgements

We thank Long Xiang for preparing the specimen and Wei Gao for photos. We also thank Dr. R. Vullo and Dr. E. Koutsoukos for their kind comments on the early version of the manuscript. This work is supported by the National Natural Science Foundation of China (42288201, 42072028, 42072017), the Strategic Priority Research Program (B) of Chinese Academy of Sciences (XDB26000000), the Scientific Research Foundation of Shenyang Normal University, China (BS202309) and the Youth Innovation Promotion Association CAS (2019075). FRC thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for support (grant No. 421772/2018-2). AWAK acknowledges the support of the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ # E-26/201.095/2022), and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq #313461/2018-0; #406779/2021-0; #406902/2022-4).

References

Andres, B., Ji, Q., 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. Palaeontology 51, 453–469.

Beccari, V., Pinheiro, F.L., Nunes, I., Anelli, L.E., Mateus, O., Costa, F.R., 2021. Osteology of an exceptionally well-preserved tapejarid skeleton from Brazil: revealing the anatomy of a curious pterodactyloid clade. PLoS One 16 (8), e0254789.

Bennett, S.C., 1993. The ontogeny of *Pteranodon* and other pterosaurs. Paleobiology 19, 92–106.

Buchmann, R., Rodrigues, T., 2019. The evolution of pneumatic foramina in Pterosaur Vertebrae. Anais da Academia Brasileira de Ciências 91, e20180782.

Canejo, L., Holgado, B., Weinschütz, L.C., Ricetti, J.H.Z., Wilner, E., Kellner, A.W.A., 2022. Novel information on the cranial anatomy of the tapejarine pterosaur *Caiuajara dobruskii*. PLoS One 17 (12), e0277780.

Cheng, X., Bantim, R.A.M., Sayão, J.M., Zhang, X.J., Jiang, S.X., Kellner, A.W.A., Wang, X.L., Saraiva, A.A.F., 2020. Short note on the vertebral column of the Tapejaridae (Pterosauria, Pterodactyloidea) based on a new specimen from the Crato Formation (late Aptian, Early Cretaceous), northeast Brazil. Journal of South American Earth Sciences. https://doi.org/10.1016/j.jsames.2020.102921.

Cohen, K.M., Finney, S.C., Gibbard, P.L., Fan, J., 2013. The ICS international chronostratigraphic chart. Episodes 36, 199–204.

Eck, K., Elgin, R.A., Frey, E., 2011. On the osteology of *Tapejara wellnhoferi* KELLNER 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE-Brazil. Swiss Journal of Palaeontology 130, 277–296.

Frey, E., Martill, D.M., Buchy, M.C., 2003. A new species of tapejarid pterosaur with soft-tissue head crest. Geological Society, London, Special Publications 217, 65–72.

He, H., Wang, X.L., Zhou, Z.H., Wang, F., Boven, A., Shi, G., Zhu, R., 2004. Timing of the Jiufotang Formation (Jehol Group) in Liaoning, northeastern China, and its implications. Geophysical Research Letters 31. https://doi.org/10.1029/2004gl019790.

Kellner, A.W.A., 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeastern Brazil. Anais da Academia Brasileira de Ciências 61, 439–445.

Kellner, A.W.A., 1996. Reinterpretation of a remarkably well-preserved pterosaur soft tissue from the Early Cretaceous of Brazil. Journal of Vertebrate Paleontology 16 (4), 718–722.

Kellner, A.W.A., 2003. Pterosaur phylogeny and comments on the evolutionary history of the group, vol. 217. Geological Society, London, Special Publications, pp. 105–137.

Kellner, A.W.A., 2004. New information on the Tapejaridae (Pterosauria, Pterodactyloidea) and discussion of the relationships of this clade. Ameghiniana 41, 521–534.

Kellner, A.W.A., 2010. Comments on the Pteranodontidae (Pterosauria, Pterodactyloidea) with the description of two new species. Anais da Academia Brasileira de Ciências 82, 1063–1084.

Kellner, A.W.A., 2013. A new unusual tapejarid (Pterosauria, Pterodactyloidea) from the Early Cretaceous Romualdo Formation, Araripe Basin, Brazil. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103, 409–421.

Kellner, A.W.A., 2015. Comments on Triassic pterosaurs with discussion about ontogeny and description of new taxa. Anais da Academia Brasileira de Ciências 87, 669–689.

Kellner, A.W.A., Campos, D.A., 1988. Sobre um Novo Pterossauro com Crista Sagital da Bacia do Araripe, Cretáceo Inferior do Nordeste do Brasil. Anais da Academia Brasileira de Ciências 60 (4), 459–469.

Kellner, A.W.A., Campos, D.A., 1994. A new species of *Tupuxuara* (Pterosauria, Tapejaridae) from the Early Cretaceous of Brazil. Anais da Academia Brasileira Ciências 66 (4), 467–473.

Kellner, A.W.A., Campos, D.A., 2002. The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. Science 297, 389–392.

Kellner, A.W.A., Campos, D.A., 2007. Short note on the ingroup relationships of the Tapejaridae (Pterosauria, Pterodactyloidea), vol. 75. Boletim do Museu Nacional Nova Série Rio de Janeiro-Brasil, pp. 1–14.

Kellner, A.W.A., Wang, X.L., Tischlinger, H., Campos, D.A., Hone, D.W.E., Meng, X., 2010. The soft tissue of *Jeholopterus* (Pterosauria, Anurognathidae, Batrachognathinae) and the structure of the pterosaur wing membrane. Proceedings of the Royal Society B-Biological Sciences 277, 321–329.

Kellner, A.W.A., Weinschütz, L.C., Holgado, B., Bantim, R.A.M., Sayão, J.M., 2019. A new toothless pterosaur (Pterodactyloidea) from Southern Brazil with insights into the paleoecology of a Cretaceous desert. Anais da Academia Brasileira de Ciências vol. 91 (Suppl. 2), e20190768.

Li, J.J., Lü, J.C., Zhang, B.K., 2003. A new lower Cretaceous sinopterid pterosaur from the western Liaoning Province, China. Acta Palaeontologica Sinica 42, 442–447. Pl.I.

Liu, D.X., Zhou, C.F., Wang, J.Q., Li, W.G., Wei, Q.W., 2014. New data on the cervical morphology of the Chinese tapejarine. Historical Biology. https://doi.org/10.1080/08912963.2014.885962.

Lü, J.C., Gao, C., Liu, J., Meng, Q., Ji, Q., 2006a. New material of the pterosaur *Eopteranodon* from the Early Cretaceous Yixian Formation, western Liaoning, China. Geological Bulletin of China 25, 565–571.

Lü, J.C., Jin, X., Unwin, D.M., Zhao, L., Yoichi, A., Ji, Q., 2006b. A new species of *Huaxiapterus* (Pterosauria : Pterodactyloidea) from the Lower Cretaceous of Western Liaoning, China with comments on the systematics of tapejarid pterosaurs. Acta Geologica Sinica 80, 315–326.

Lü, J.C., Liu, J., Wang, X., Gao, C., Meng, Q., Ji, Q., 2006c. New material of pterosaur *Sinopterus* (Reptilia: Pterosauria) from the Early Cretaceous Jiufotang Formation, Western Liaoning, China. Acta Geologica Sinica 80, 783–789.

Lü, J.C., Gao, Y., Xing, L., Li, Z., Ji, Q., 2007. A new species of *Huaxiapterus* (Pterosauria: Tapejaridae) from the Early Cretaceous of western Liaoning, China. Acta Geologica Sinica 81, 683–687.

Lü, J.C., Teng, F., Sun, D., Shen, C., Li, G., Gao, X., Liu, H., 2016. The toothless pterosaurs from China. Acta Geologica Sinica 90, 2513–2525.

Lü, J.C., Yuan, C., 2005. New tapejarid pterosaur from Western Liaoning, China. Acta Geologica Sinica 79, 453–458.

Lü, J.C., Zhang, B.K., 2005. New pterodactyloid pterosaur from the Yixian Formation of western Liaoning. Geological Review 51, 458–462. Pl.I.

Manzig, P.C., Kellner, A.W.A., Weinschütz, L.C., Fragoso, C.E., Vega, C.S., Guimarães, G.B., Godoy, L.C., Liccardo, A., Ricetti, J.H.Z., de Moura, C.C., 2014. Discovery of a rare pterosaur bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying reptiles. PLoS One 9, e100005.

Martill, D.M., Green, M., Smith, R.E., Jacobs, M.L., Winch, J., 2020a. First tapejarid pterosaur from the Wessex Formation (Wealden Group: Lower Cretaceous, Barremian) of the United Kingdom. Cretaceous Research 113 (2020), 104487.

Martill, D.M., Smith, R.E., Unwin, D.M., Kao, A., McPhee, J., Ibrahim, N., 2020b. A new tapejarid (Pterosauria, Azhdarchoidea) from the mid-Cretaceous Kem Kem beds of Takmout, southern Morocco. Cretaceous Research 112 (2020), 104424.

Pinheiro, F.L., Fortier, D.C., Schultz, C.L., Andrade, J.A.F.G., Bantim, R.A.M., 2011. New information on the pterosaur *Tupandactylus imperator*, with comments on the relationships of Tapejaridae. Acta Palaeontologica Polonica 56 (3), 567–580.

Shen, C., Pêgas, R.V., Gao, C., Kundrát, M., Zhang, L., Wei, X., Zhou, X., 2021. A new specimen of *Sinopterus dongi* (Pterosauria, Tapejaridae) from the Jiufotang Formation (Early Cretaceous, China). PeerJ 9, e12360.

Vullo, R., Marugán-Lobón, J., Kellner, A.W.A., Buscalioni, Á.D., Gomez, B., de la Fuente, M., Moratalla, J.J., 2012. A new crested pterosaur from the Early Cretaceous of Spain: the first European tapejarid (Pterodactyloidea: Azhdarchoidea). PLoS One 7, e38900.

Wang, X.L., Dong, Z.M., 2008. The Chinese fossil reptiles and their kin, second ed. Science Press, Beijing, p. 224.

Wang, X.L., Wang, Y.Q., Wang, Y., Xu, X., Tang, Z.L., Zhang, F.C., Hu, Y.M., 1998. Stratigraphic sequence and vertebrate-bearing beds of the Lower part of the Yixian Formation in Sihetun and neighboring area, western Liaoning, China. Vertebrata Palasiatica 36 (2), 81–101.

Wang, X.L., Wang, Y.Q., Jin, F., Xu, X., Wang, Y., Zhang, J.Y., Zhang, F.C., Tang, Z.L., Li, C., Gu, G., 1999. The Sihetun fossil vertebrate assemblage and its geological setting, western Liaoning, China. PalaeoWorld (11), 310–327.

Wang, X.L., Jiang, S.X., Cheng, X., 2017. Palaeovertebrata Sinica. Volume II: Fishes. Fascicle 4 (Serial no. 8): Basal Archosauromorphs, Crocodylomorphs, and Pterosaurs. Science Press, Beijing (in Chinese).

Wang, X.L., Zhou, Z.H., 2002. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy. Chinese Science Bulletin 47, 1521–1527.

Wang, X.L., Zhou, Z.H., 2006. Pterosaur assemblages of the Jehol Biota and their implication for the Early Cretaceous pterosaur radiation. Geological Journal 41, 405–418.

Wellnhofer, P., Kellner, A.W.A., 1991. The skull of *Tapejara wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, Northeastern Brazil. Mitteilungen der Bayerischen Staatssammlung für Palaontologie und Historische Geologie 31, 89–106.

Zhang, X.J., Jiang, S.X., Cheng, X., Wang, X.L., 2019. New Material of *Sinopterus* (Pterosauria, Tapejaridae) from the Early Cretaceous Jehol Biota of China. Anais da Academia Brasileira de Ciências 91, e20180756.

Zhou, C.F., Niu, T., Yu, D., 2022. New data on the postcranial skeleton of the tapejarid *Sinopterus* from the Early Cretaceous Jehol Biota. Historical Biology. https://doi.org/10.1080/08912963.2022.2042811.