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A NEW TRITYLODONTID FROM THE UPPER JURASSIC SHISHUGOU FORMATION OF THE JUNGGAR BASIN (XINJIANG, NW CHINA)

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ABSTRACT—A new tritylodontid cynodont, *Bienotheroides ultimus* sp. nov., is described from the Upper Jurassic Shishugou Formation of Jiangjunmiao in the northeastern Junggar Basin of Xinjiang (NW China). The type consists of a partial skeleton, including teeth, a partial skull, and a considerable portion of the postcranium. It is identifiable as *Bienotheroides* because of the structure of the upper molars and the characteristically deep zygomatic arch. It is distinguished from *Bienotheroides zigongensis* from the Middle Jurassic of the Junggar Basin particularly by characters of the forelimb, including a humerus that shows little torsion of the proximal and distal ends. *Bienotheroides ultimus* is the last of the Chinese tritylodontids known so far, and apart from *Xenocretosuchus* from the Lower Cretaceous of Russia and an unnamed form from the Lower Cretaceous of Japan, it is the last non-mammalian therapsid known in the entire fossil record.

INTRODUCTION

The tritylodontids are a small family of advanced non-mammalian eucynodonts of probably herbivorous habit, which made their first appearance in the uppermost Triassic (Fraas, 1866; Hennig, 1922; Simpson, 1928) and diversified rapidly during the Early Jurassic. They peristed into the Middle Jurassic with only a few genera: *Stereognathus* Charlesworth, 1854, from the Stonesfield Slate (= Stonesfield Member of the Sharp's Hill Formation) of England (Owen 1871; Simpson 1928) and the Great Estuarine Series of Scotland (both dated as Bathonian; Waldman and Savage, 1972) and *Bienotheroides* Young, 1982, from the Shaximiao Formation of Sichuan (Young, 1982; Sun 1984, 1986; Sun and Li, 1985) and the Wucaiwan Formation of Xinjiang, China (Sun and Cui, 1989), which are regarded as Middle Jurassic in age. In this paper we describe the first definite record of a Late Jurassic tritylodontid. It is from the Shishugou Formation of Xinjiang, China, which overlies the Wucaiwan Formation in the eastern and northeastern part of the Junggar Basin and is generally regarded as of Late Jurassic age (Currie and Zhao, 1993). The specimen is referrable to the hitherto exclusively Middle Jurassic genus *Bienotheroides*. As will be shown below, it represents, however, a new species.

Recently, Tatarinov and Matchenko (2000) described some teeth from the Lower Cretaceous of Russia as a new genus of tritylodontid, *Xenocretosuchus*, and Matsuoka and Setoguchi (2000) described some isolated teeth from the Kuwajima Formation (dated as Berriasian-Valanginian) of Japan. Apart from these exceptional records, the new specimen of *Bienotheroides* is the stratigraphically youngest non-mammalian therapsid known, and it is therefore of particular general interest, as it definitely extends the range of the Tritylodontidae into the Upper Jurassic in Central Asia.

Institutional Abbreviation—NIGPAS, Nanjing Institute for Geology and Palaeontology, Academia Sinica, China.

SYNAPSIDA
THERAPSIDA
CYNODONTIA
Family TRITYLODONTIDAE Cope, 1884
Genus *BIENOTHEROIDES* Young, 1982

Type Species—*Bienotheroides wanhsienensis* Young, 1982

BIENOTHEROIDES ULTIMUS sp. nov.

Holotype—NIGPAS-SGP 1, a partial skeleton, including two incisors, one upper molar, a partial skull with most of the right zygomatic arch and a considerable part of the postcranium (Figs. 1–5).

Type Locality—About 35 km north of Jiangjunmiao near the Road 216 from Qitai to Ertai, 44° 48′ 45″ N, 90° 02′ 43″ E, northern Qitai County, eastern Junggar Basin, Xinjiang Uygur Autonomous Region, People's Republic of China.

Horizon—Shishugou Formation, Upper Jurassic, about 30 m above the main fossil wood horizon (upper log-bearing horizon of McKnight et al., 1990).

Etymology—From Latin ultimus = ultimate, referring to the fact that this is the geologically youngest Chinese non-mammalian therapsid.

Diagnosis—Potential autapomorphies not shared by other members of the genus *Bienotheroides*: stapedial process of quadrate slender and directed medially, dorsal quadrate facet for contact with petrosal very small, humerus with only very slight torsion of proximal and distal ends (about 20°); additional features that might be useful for identification: upper molars with convex anterior margin (may be ontogenetic), trochlea of humerus directed totally distally, radius with wide and non-angular distal end.

Description

Dentition—Only two fragmentary incisors and the almost complete crown of an upper molar remain of the dentition. Both incisors are only represented by apically and basally broken portions of the root. They show an almost circular cross-section and a large pulp cavity.

The molar (Fig. 1C) is from the right maxilla, probably from the anterior or middle rather than from the posterior part of the tooth series. There are three longitudinal rows of cusps, as usual in tritylodontids. The labial row consists of two cusps only, in contrast to *Bienotheroides wanhsienensis*, but as in *B. zigongensis* (Sun, 1986). The middle row consists of three cusps, as does the lingual row, as in other species of *Bienotheroides*.

The anterior cusp of the labial series is broken, whereas the posterior one is complete. Both are well developed. The posterior labial cusp is somewhat higher than the middle cusp of the median series. The anteromedial cusp is very small and sur-

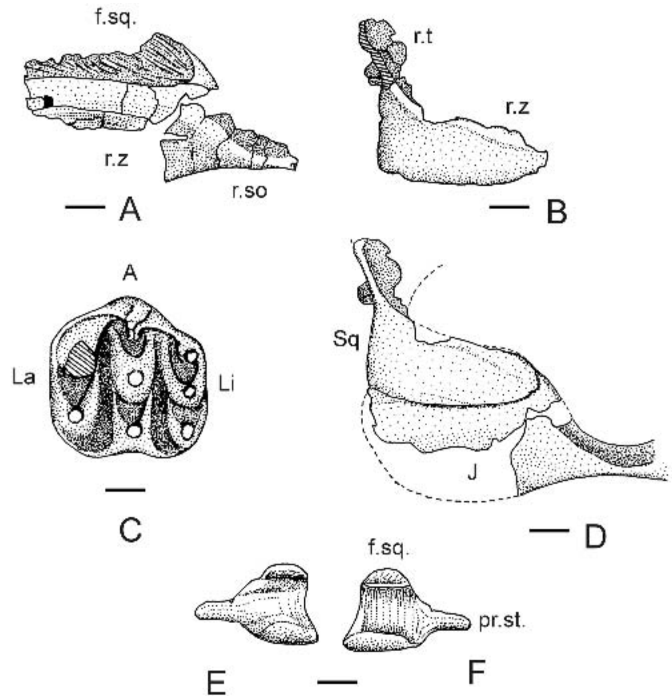

FIGURE 1. *Bienotheroides ultimus* sp. nov., holotype (NIGPAS-SGP 1), cranial elements. **A**, right jugal in lateral view. **B**, right squamosal in lateral view. **C**, right upper molar in occlusal view. **D**, restoration of right zygomatic arch in lateral view. **E–F**, right quadrate in (**E**) posterior and (**F**) anterior view. **Abbreviations**: **Ant**, anterior; **f. sq.**, facet for squamosal; **J**, jugal; **La**, labial; **Li**, lingual; **pr. st.**, stapedial process; **r. so.**, suborbital ramus; **r. t.**, temporal ramus; **r. z.**, zygomatic ramus; **Sq**, squamosal. Scale bar for A–B and D–F equals 10 mm; for C it equals 2 mm.

rounded laterally by ridges that extend from the base of the middle cusp of the median series, as in *B. zigongensis*. A ridge runs up the anterior face of the anteromedian cuspule and another one extends lingually from the base of the cuspule and connects it with the base of the anterolingual cusp.

The central median cusp is tall and its tip curves slightly anteriorly, as in the other large cusps. It is slightly lower than the posterior labial, but distinctly higher than the posterior median and the lingual cusps. The posterior median cusp corresponds in shape to the central median cusp, but is slightly lower.

The lingual series consists of a small anterior cuspule, which, in contrast to the rather blunt anteromedian cuspule, is markedly pointed. The central lingual cusp corresponds in shape to the other larger cusps, but is lower, the posterior lingual cusp is even smaller but well pointed.

There is no cingulum. The labial and lingual cusp series are approximately equidistant from the median series, giving the cusp pattern a very regular appearance. The general shape of the molar is almost rectangular. The middle part of the anterior margin, at the level of the anteromedian cuspule, extends, however, anteriorly with a distinct convexity, a feature that is regularly observed in upper cheek teeth of *Oligokyphus* (Kühne, 1956), but not in *Bienotheroides*.

Skull—There are only a few, but highly diagnostic skull elements. Best preserved is a large part of the right zygomatic arch (jugal and squamosal; Fig. 1A, B, D). Apart from this, both quadrates (Fig. 1E, F) and a large part of the skull roof are identifiable, the latter being poorly preserved and showing little detail.

The jugal (Fig. 1A, D) is incomplete but can be largely reconstructed. It very much resembles the other species of *Bienotheroides* and, to a lesser extent, *Bocatherium* (Clark and Hopson, 1985). The suborbital ramus is incomplete anteriorly and the contact with the maxilla and lacrimal can not be established. However, the ramus is wide and dorsoventrally flattened anteriorly, becoming triangular in cross-section posteriorly before turning into the deep zygomatic ramus of the jugal. It is reinforced by a strong lateral and dorsomedial ridge, between which the dorsal surface is concave and inclined laterodorsally. The ventral surface is gently convex, the medial surface slightly concave. The subtemporal portion of the jugal is nearly complete dorsally and posteriorly, but only its anteroventral margin is preserved. The jugal was an unusually high, dorsoventrally expanded element as in other species of *Bienotheroides*. The dorsal preserved half of the zygomatic ramus of the jugal is occupied by the extensive sutural facet for the squamosal. The medial surface of this part of the bone is smooth and gently convex.

The squamosal (Fig. 1B, D) preserves most of its zygomatic portion and can be articulated with the jugal. The zygomatic ramus of the bone is narrow anteriorly, but then expands rapidly, forming a high, thin plate with a slight medial curvature. When jugal and squamosal are articulated (Fig. 1D), they together form a very deep zygomatic arch which is very reminiscent of that of both *Bienotheroides wanhsienensis* and *B. zigongensis*. Only a small part of the posterior border of the temporal fenestra is preserved, which is formed by a mediolaterally expanded flange of bone. The posterior surface of the squamosal shows only the dorsalmost extremity of the so-called meatus auditorius externus. The region for suspending the quadrate and quadratojugal is entirely missing.

Both quadrates are present, but only the right one is complete (Fig. 1E, F). It is very different from the quadrate of basal tritylodontids, such as *Oligokyphus* (Kühne, 1956) by the lack of a well-developed dorsal process and dorsal angle (Luo and Crompton, 1994). Instead it ends dorsally with a flattened facet for articulation with the anterior paroccipital process of the petrosal, as in *Kayentatherium* and *Bienotheroides* (Sues, 1986; Luo and Crompton, 1994). This dorsal contact facet is unusually small, as compared to other tritylodontids, about half the size of the same structure of *Bienotheroides zigongensis*, and less than 1/3 in proportion to those of *Oligokyphus*, *Kayentatherium* and *Bienotherium* (Z.-X. Luo, pers. comm., 2003). It is completely preserved, except for a tiny portion of the posteromedial margin. The margin of the bone between the dorsal facet and the stapedial process is intact. The medial (stapedial) process is, in contrast to *Oligokyphus* but in close agreement with *Bienotheroides zigongensis*, slender and elongate (Sun and Cui, 1989). It is completely preserved. The main difference to *B. zigongensis* is that in this taxon the stapedial process extends distinctly mediodorsally, whereas it is directly medially oriented in *B. ultimus*. The articulatory trochlea is wide transversely and reaches considerably upwards both on the anterior and posterior surface of the bone. The lateral margin of the dorsal plate of the quadrate is only very slightly concave, the concavity marking the facet for the quadratojugal.

Apart from these well preserved skull elements, there is a large portion of the dorsal skull roof, which contains much of the parietals and even the anterodorsal margin of the right orbit. The parietals form a very narrow, long sagittal crest to which the frontals appear to contribute anteriorly. Directly anterior to this crest, there is a depression on the skull roof bordered by anteriorly diverging frontal ridges as in *Bienotheroides wanhsienensis*. The anterolateral margin of the frontal, which takes part in the formation of the orbital border, is strongly thickened into a marked hump that indicates the posterior border of the orbit. The orbit appears to be very small from what remains of the other circumorbital elements (nasal, lacrimal). The skull remains allow an estimate of the length of the skull from the posterior end of the squamosal to the anterior orbital margin, which amounts to approximately 85 mm. As the snout is very short in other known specimens of *Bienotheroides*, it appears unlikely that the entire skull was more than 100 mm long. This agrees well with the size of the other specimens of *Bienotheroides*, which are only marginally larger.

Some additional fragments, which might represent parts of the skull and lower jaw, are too incomplete to be interpreted with confidence. A large fragment appears to represent part of the coronoid process of the right dentary. The dorsal end of the left coronoid process is preserved in situ within the remnants of the left fenestra temporalis.

Vertebral Column—There are remains of 17 presacral vertebrae, which are largely represented by the centra only. The neural arches were not tightly sutured to either the cervical or thoracic centra, so they are usually only represented by fragments.

Five vertebral centra are clearly cervical. They are short and wide (Fig. 2A–D, G–H). The anteriormost of these, probably the third cervical, is 8 mm long and 12 mm wide anteriorly (Fig.2 A–C). The anterior surface of the centrum is rather flat, the posterior one slightly convex. These almost flat articulatory surfaces are characteristic for all the preserved presacrals. The ventral surfaces of the cervicals are rather flat and bear no or only a slight keel (Fig. 2B, D, G). The length/width ratio of the cervicals and thoracics increases posteriorly. A middle thoracic centrum, out of a series of four articulated elements, is 14 mm long, but only 13 mm wide anteriorly and 12 mm posteriorly. The anterior height of the centrum is 10 mm, the posterior height 9.5 mm. The thoracic centra are all slightly expanded anteriorly and posteriorly and constricted at mid-length (Fig. 2K–Q). The ventral surfaces are well rounded (Fig. 2L, P). There are neither ventral nor lateral ridges. The five best-preserved thoracic vertebrae, which appear to be from the middle of the series, show at least part of the neural arches. The diapophysis and parapophysis are well separated (Fig. 2I, J). The parapophyses start at the neurocentral suture, the centrum expanding below it into a small lateral lip which supports the parapophysis (Fig. 2I, K). The parapophysis is extensive and inclined posterodorsally. It almost truncates the anterior margin of the neural arch. The diapophyses are small and circular and situated on short transverse processes (Fig. 2I–J). The prezygapophyses are only preserved in a single vertebra. They are closely spaced and have concave articulating facets, which are strongly medially inclined. They extend only marginally anterior to the centrum. A postzygapophysis is preserved in another vertebra. It extends well beyond the posterior margin of the centrum. The small, convex articulatory facet is strongly inclined laterally. There is no complete processus spinosus in situ, but there are some fragments that have been found in association. They indicate that the processus spinosi were rather short and slender. The thoracic vertebrae of *B. zigongensis* figured by Sun and Li (1985) appear to be more posterior in the series than those preserved in *B. ultimus*. Nevertheless, the much smaller size of the parapophyses and the more robust build of the entire neural arch in the *B. zigongensis* vertebrae is strikingly different.

There are also numerous remains of ribs, some of them well preserved, but they are all fragmentary and can at present not be brought into a meaningful series (Fig. 2E, F). The distal ends of all the ribs are slender, usually to an extreme degree, ending as if cut off in a very slight thickening (Fig. 2E). Only some far posterior, single-headed ribs are expanded for their entire length, as those figured by Sun and Li (1985) for *B. zigongensis*, but generally differentiation of the thoracal ribs appears to be slight, as in *Oligokyphus* (Kühne, 1956) but in contrast to many more basal cynodonts.

Shoulder Girdle—The shoulder girdle is represented by the glenoid region of the left scapula (Fig. 3B, C) and an incomplete (?) right clavicle (Fig. 3A). The scapula has detached from the coracoid elements and shows a corrugated surface for contact with the coracoid, which is generally oval in shape but drawn out into a narrow tip medially (Fig. 3C). The glenoid is oriented at an angle of about 45° to the contact with the coracoid and opens laterally and slightly posteriorly (Fig. 3B, C) and articulates well with the isolated caput of the left humerus. Above the glenoid, the scapular blade constricts considerably. The acromial region is already missing.

The clavicle preserves the medial end and most of the horizontal ramus of the shaft, but the ascending distal portion is entirely missing. The bone expands slightly at the medial end and shows a roughened ventral surface there (Fig. 3A). The horizontal ramus then remains more or less flat for some distance, becoming continuously narrower laterally until it turns into an anteromedially flattened blade which, at its lateralmost preserved end, shows already an indication of dorsal curvature.

Forelimb—The right humerus is almost complete with the proximal ends of radius and ulna still in articulation (Fig. 4A–D). The distal end of the radius is also present, but strongly weathered and incomplete. The left forelimb is represented by fragments of the proximal and almost the entire distal end of the humerus (Fig. 3D–F), the proximal end of the ulna and the nearly complete radius (Fig. 3G–I).

The humerus is generally of typical tritylodontid shape. It differs, however, considerably from all hitherto described tritylodontids, and in fact all other cynodonts, by the fact that the proximal and distal end show only very little torsion, approximately 20°, so that they come to lie almost in the same plane (Fig. 4B–D). This is certainly no effect of distortion, as the humerus is three-dimensionally preserved.

The proximal end of the humerus is approximately rectangular and dominated by the large caput humeri (Fig. 4A–D). The caput does not protrude above the proximal outline of the humerus. On the dorsal surface it extends about 11 mm distally (Fig. 4D), whereas it does not extend on the ventral surface at all (Fig. 4C). The crista deltopectoralis is incomplete. It extends distally for almost exactly half the length of the humerus, being developed as a thin and narrow plate of bone (Fig. 4C, D). The posteroproximal surface of the proximal end shows a marked concavity on the dorsal side. A marked ridge extends on the dorsal surface from the caput humeri distally until it merges in the moderately developed lateral ectepicondylar ridge at the distal end of the bone (Fig. 4D). The ventral surface is largely slightly concave; a ridge extends from the distal end of the crista deltopectoralis to the ventrolateral surface of the epicondylus ulnaris (Fig. 4C).

The distal end of the humerus is dominated by the large, almost symmetrically developed radial and ulnar epicondyles (Figs. 3D–F, 4B–D). There is a well developed foramen entepicondyloideum, but no indication of a foramen ectepicondyloideum. The ulnar and radial articulations are well differentiated. The capitellum is almost entirely restricted to the ventral and distal surfaces of the humerus (Fig. 3D–F), whereas the trochlea extends slightly onto both the dorsal and ventral surfaces, but is also essentially directed distally (Fig. 3D–F).

The proximal end of the ulna shows a large and well-developed olecranon ulnae for attachment of the m. triceps, which extends about 15 mm proximal to the articular facet for the humerus (Fig. 4B–D). Proximally, the olecranon is expanded into a strongly convex, anteroposteriorly elongated surface. The posterior surface of the olecranon is deeply concave, much more so than the anterior surface. Strong lateral ridges are found both anteriorly and posteriorly for the entire length of the olecranon and extend, less clearly developed, along the ulnar shaft as far as it is preserved. At the anterior surface, just distal to the humeral articulation, a strongly developed bony flange marks the tuberositas ulnae, which in mammals is the insertion for the m. brachialis and m. biceps brachii (Fig. 4B, C). The shaft of the ulna distal to the sigmoid fossa is anteroposteriorly flattened.

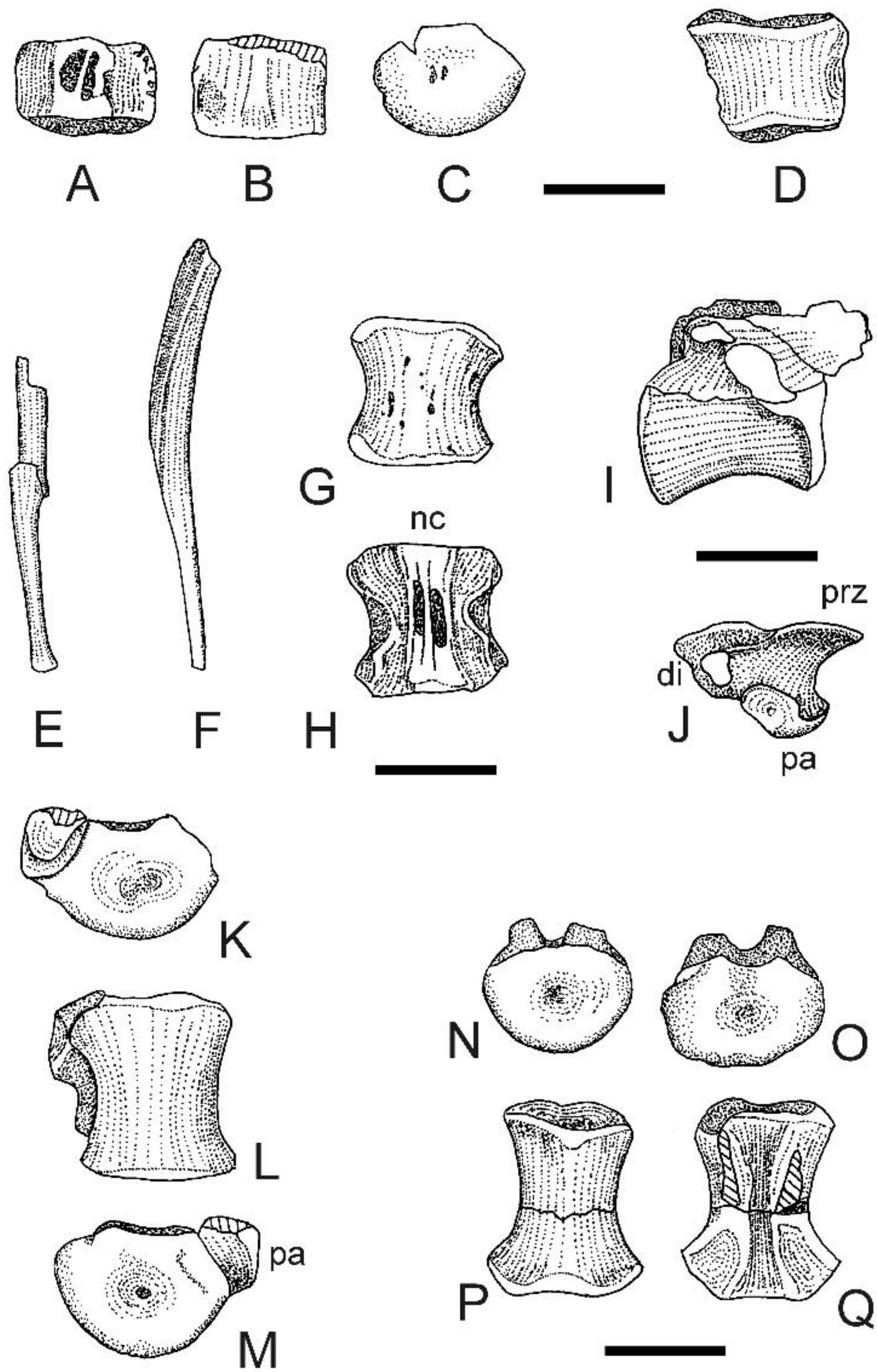

FIGURE 2. *Bienotheroides ultimus* sp. nov., holotype (NIGPAS-SGP 1), axial skeleton. **A**–**C**, anterior cervical centrum in (**A**) dorsal, (**B**) ventral and (**C**) posterior views. **D**, middle cervical centrum in ventral view. **E**, distal end of anteror thoracic rib. **F**, shaft of anterior thoracic rib. **G**–**H**, posterior cervical centrum in (**G**) ventral and (**H**) dorsal views. **I**, right lateral view of thoracic vertebra with part of the neural arch preserved. **J**, partial neural arch in right lateral view. **K**–**M**, thoracic vertebra in (**K**) anterior, (**L**) ventral and (**M**) posterior view. **N**–**Q**, thoracic vertebra in (**N**) anterior, (**O**) posterior, (**P**) ventral and (**Q**) dorsal views. **Abbreviations**: **di**, diapophysis; **nc**, neural canal; **pa**, parapophysis; **prz**, prezygapophysis. Scale bars equal 10 mm.

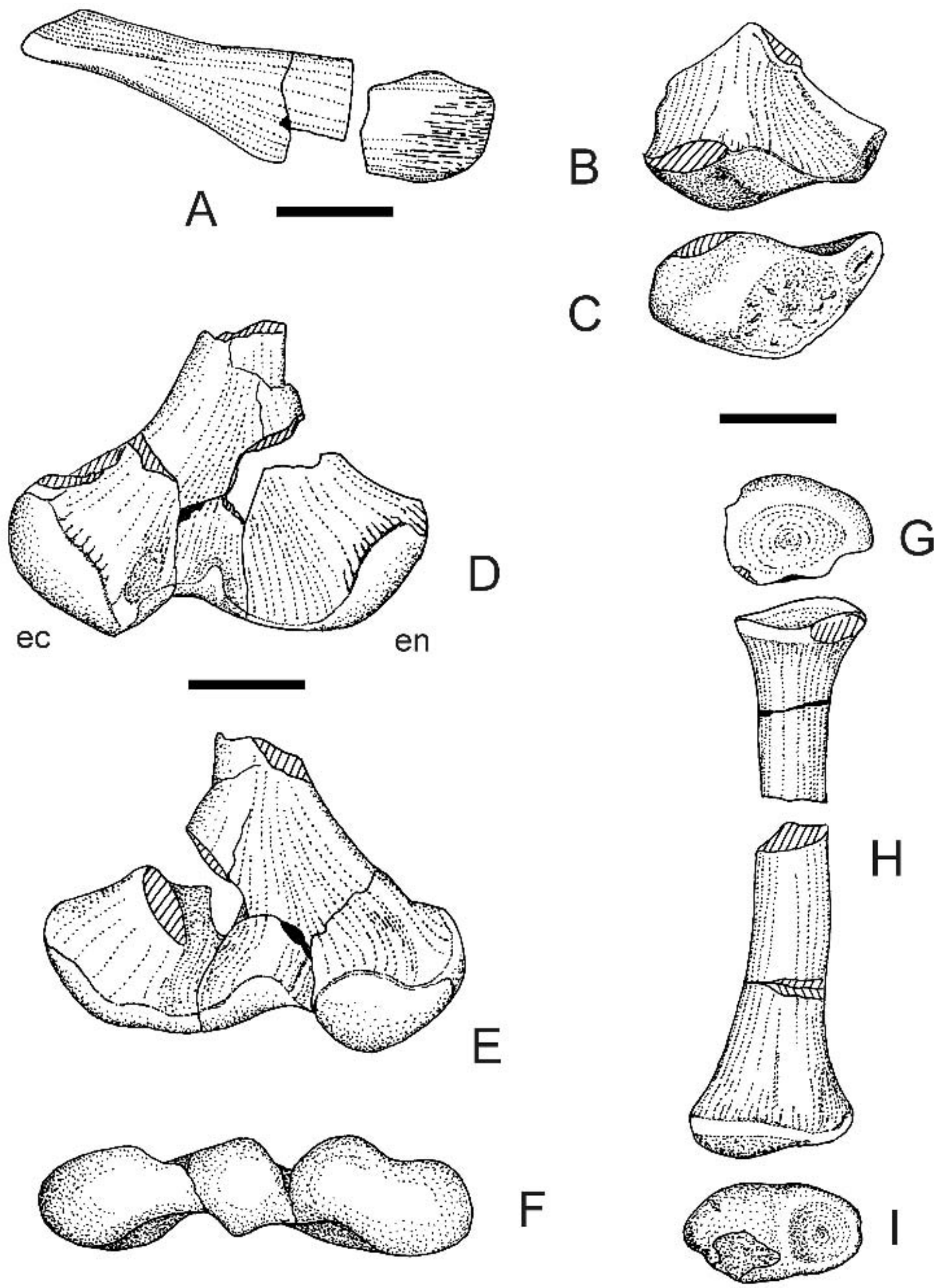

FIGURE 3. *Bienotheroides ultimus* sp. nov., holotype (NIGPAS-SGP 1). Shoulder girdle and forelimb elements. **A**, incomplete right clavicle in ventral view. **B**–**C**, glenoid region of left scapula in (**B**) lateral and (**C**) proximal views. **D**–**F**, distal end of left humerus in (**D**) dorsal, (**E**) ventral and (**F**) distal views. **G**–**I**, left radius in (**G**) proximal, (**H**) anterior and (**I**) distal views. **Abbreviations**: **ec**, ectepicondylus; **en**, entepicondylus. Scale bars equal 10 mm.

The radius is slender and elongate with a slightly expanded proximal and wide distal end (Fig. 3G–I). The proximal articulation with the humerus is cup shaped and anteroposteriorly elongated (Fig. 3G); medially it turns into the small, strongly convex articular facet with the ulna (Figs. 3G, H, 4C, D). The distal end is transversely expanded and shows a clear division of the articular facets for radiale and intermedium (Fig. 3I). The entire facet is almost flat and does not extend up the shaft of the bone on either side, so that the distal margin is almost straight (Fig. 3H), whereas it is strongly medioproximally inclined in *B. zigongensis* (Sun and Li, 1985), where it is also much wider. The slender radial shaft is almost essentially straight and has a rounded cross section in the middle, which becomes anteroposteriorly flattened distally.

Pelvic Girdle—Even though there remains little of the posterior half of the skeleton, there are parts of all three pelvic elements, the almost complete right ilium (and the weathered acetabular portion of the left one), the proximal end of the right pubis and much of the left ischium. All the elements remain separate and show roughened and corrugated sutural contact surfaces.

The right ilium (Fig. 5A) is slender without any considerable

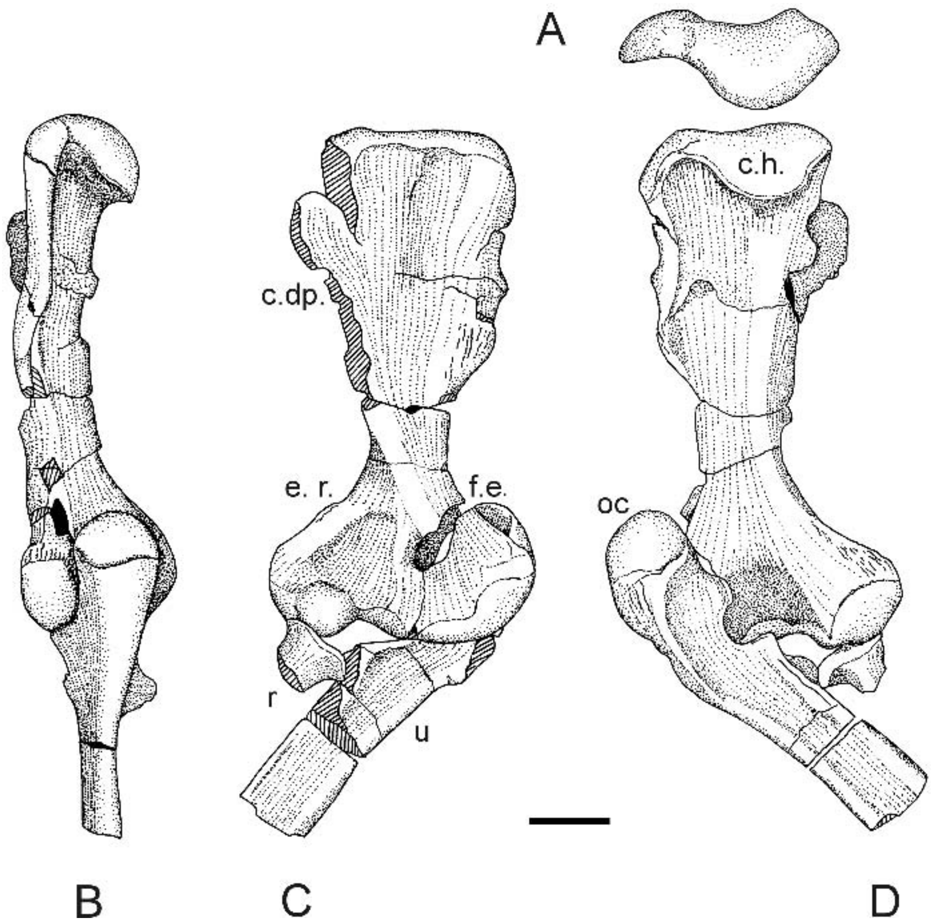

FIGURE 4. *Bienotheroides ultimus* sp. nov., holotype (NIGPAS-SGP 1). Right humerus and elbow in articulation. **A**, proximal view of humerus. **B**–**D**, humerus and elbow articulation in (**B**) lateral, (**C**) ventral and (**D**) dorsal views. **Abbreviations**: **c. dp.**, crista deltopectoralis; **c. h.**, caput humeri; **e. r.**, ectepicondylar ridge; **f. e.**, foramen entepicondyloideum; **oc**, olecranon; **r**, radius; **u**, ulna. Scale bar equals 10 mm.

anterior or posterior expansion dorsal to the acetabulum, of which it forms a section of about 120°. A strong dorsal ridge extends from a point slightly anterior to the middle of the dorsal margin of the ilium's portion of the acetabulum to the preserved dorsal end of the bone, as in *Oligokyphus* (Kühne, 1956). Posterior to this ridge, the dorsal surface is flat but strongly inclined posteromedially; anterior to it, it descends even more steeply anteromedially. The distal third of the preserved medial surface of the bone is strongly roughened, certainly for the attachment of the sacral ribs.

The proximal end of the pubis (Fig. 5A), which can be perfectly articulated with the ilium, shows little more than the acetabular portion of the bone. The ventral margin of the acetabulum is complicated by a cotylus-like indentation close to the posterior margin of the bone, smaller than the portion of the same cotylus which is found in the acetabular margin of the ischium (see below).

The left ischium (Fig. 5B) is very similar to that of *Oligokyphus*, as illustrated by Kühne (1956). It forms a considerable part of the acetabulum, of similar size to the portion contributed by the ilium and much larger than that formed by the pubis. The posteroventral margin of the acetabulum has a deep cotyloid indentation, which extends almost to the contact with the ilium, i.e., it is much more pronounced than in *Oligokyphus*. The dorsal margin of the ischiadic blade is almost entirely preserved. It is slightly concave. The ventral margin is only partially preserved, but what remains shows that the bone became markedly constricted posterior to the acetabular part, but farther posterior was expanded considerably into a dorsoventral blade. The posterior margin of the ischium is completely straight. Its posterodorsal corner is pronounced, but not as much as Kühne (1956) shows for *Oligokyphus*.

Hindlimb—The only identifiable element of the hindlimb is an almost complete right tibia (Fig. 5C–F), lacking only a small portion of the shaft.

The tibia is very reminiscent of that of *Oligokyphus* (Kühne, 1956). The proximal end is expanded mediolaterally (Fig. 5C–E), the articulatory facet for the femur being gently convex and somewhat extended posterolaterally. The shaft is moderately slender and mediolaterally flattened (Fig. 5C, E). It is almost straight. The distal end is slightly expanded with a distinct posterolateral and ventral protrusion (Fig. 5C, E, F).

DISCUSSION

The specimen described above clearly is a representative of the genus *Bienotheroides* Young, 1982, one of the most advanced tritylodontids known (Clark and Hopson, 1985), forming a clade with *Stereognathus* from the Middle Jurassic of Great Britain and *Bocatherium* from the Lower Jurassic of Mexico (and, possibly, also *Xenocretosuchus* from the Lower Cretaceous of Siberia, which closely resembles *Stereognathus* in dental morphology). The specimen is identifiable as *Bienotheroides* by the structure of the single preserved upper cheek tooth, which agrees almost

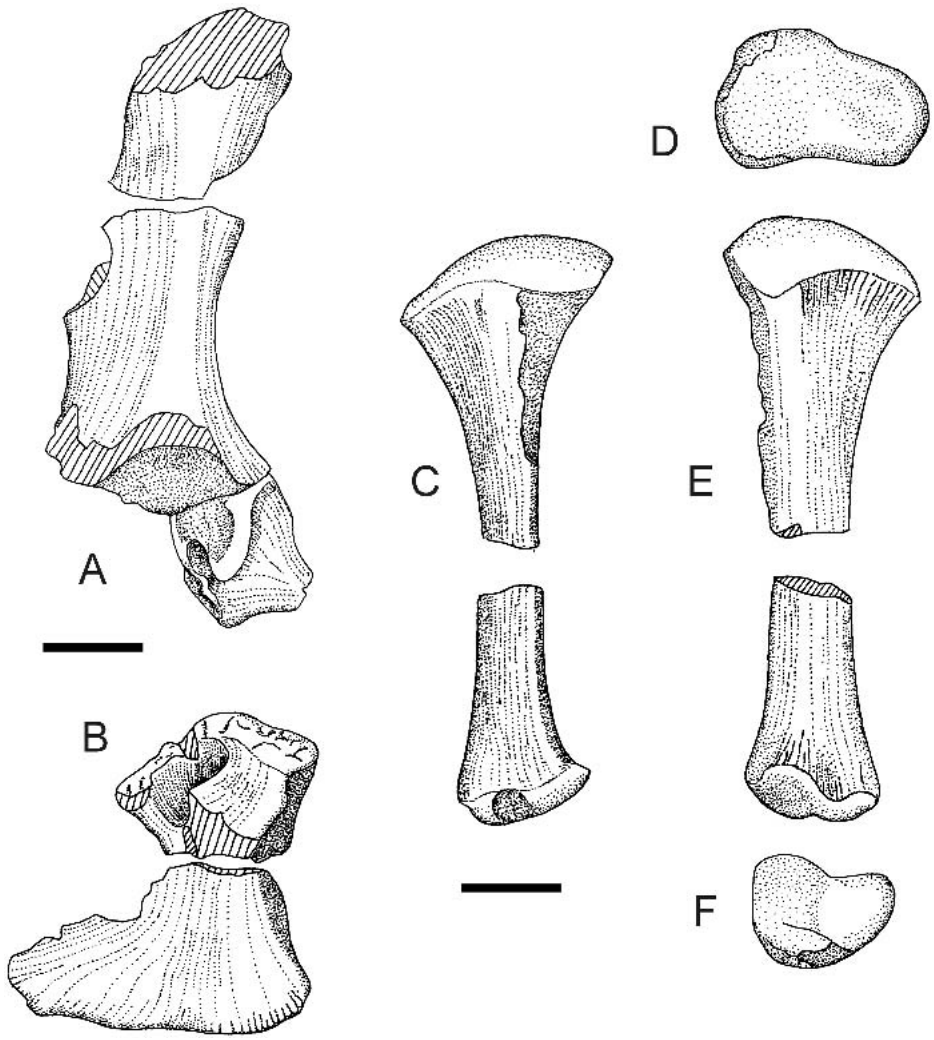

FIGURE 5. *Bienotheroides ultimus* sp. nov., holotype (NIGPAS-SGP 1). Pelvic girdle and hindlimb. **A**, right ilium and pubis in articulation, lateral view. **B**, left ischium in lateral view. **C**–**F**, right tibia in (**C**) medial, (**D**) proximal, (**E**) posterior and (**F**) distal views. Scale bars equal 10 mm.

perfectly with *Bienotheroides zigongensis*, and by the very deep, dorsoventrally expanded, plate-like subtemporal part of the zygomatic arch, which is one of the most characteristic autapomorphies of the genus.

The postcranial elements, as far as they are comparable, also show a close resemblance to *B. zigongensis* as described and illustrated by Sun and Li (1985), and the specimen would probably have been identified with that species were it not for several differences in morphology enumerated above, which, together with the younger stratigraphic age, indicate a specific separation. The anteriorly convex border of the upper cheek tooth is probably not a very diagnostic character. The morphology of the quadrate is, however, despite general resemblance, clearly different from that of *B. zigongensis*. Most importantly, the forelimb is well distinguished from this, as well as all other known cynodont species, by the small amount of torsion of the distal and proximal ends of the humerus, in which feature *B. ultimus* is more advanced and "mammal-like" than any other nonmammalian therapsid hitherto discovered. The morphology of the distal end of the humerus, with the directly distally directed trochlea, and the shape of the distal end of the radius are further clear differences from *B. zigongensis*. It therefore appears justified to erect a new species for the material from the Shishugou formation. Several features, such as the lack of co-ossification of neural arches and vertebral centra and, particularly, the endochondral shoulder girdle and the pelvic girdle elements strongly indicate that the holotype of *B. ultimus* is an immature animal. The differences enumerated above are, however, unlikely to be due to ontogenetic changes.

The late tritylodontid *Bienotheroides* was a long-lived representative of the family, being known from both Sichuan and Xinjiang and extending from the Middle into the Late Jurassic, as shown by the present specimen, which also provides some new information on several parts of the postcranial skeleton, such as the cervical vertebrae and pelvic and hind limb elements. *Bienotheroides ultimus* demonstrates that the group persisted into the Upper Jurassic in China and therefore helps to close the stratigraphic gap between the Middle Jurassic tritylodontids from Europe and Asia and the recently described, Lower Cretaceous species *Xenocretosuchus sibiricus* (Tatarinov and Matchenko, 1999) from Siberia and the Lower Cretaceous findings from Japan (Matsuoka and Setoguchi, 2000).

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