General palaeontology, systematics and evolution (Vertebrate palaeontology)

Pelvic morphology of a tritylodontid (Synapsida: Eucynodontia) from the Lower Jurassic of China, and some functional and phylogenetic implications

Morphologie pelvienne d'un tritylodontidé (Synapsida: Eucynodontia) du Jurassique inférieur de Chine et quelques implications fonctionnelles et phylogénétiques

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A R T I C L E   I N F O

A B S T R A C T

Tritylodontids are specialised, herbivorous cynodonts whose exact phylogenetic position is controversial, with some authors regarding them as close relatives of mammaliaforms and others as members of the eucynodont clade Traversodontidae. The tritylodontid pelvis has been claimed to resemble that of mammaliaforms in having a narrow, rod-like ilium, but such claims have been strongly challenged because of the incompleteness of previously available tritylodontid pelvic material. However, a partial tritylodontid skeleton from the Lower Jurassic of China preserves nearly complete examples of all three pelvic elements in addition to both femora, providing unprecedented insight into the structure of the trity-lodontid pelvis and the configuration of the hip joint. This specimen confirms that the iliac blade is rod-like, adding to the evidence for a close relationship between tritylodontids and mammaliaforms. Furthermore, femoral retraction appears to have been driven partly by gluteus musculature in tritylodontids, as in mammaliaforms.

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R É S U M É

Les Tritylodontidés sont des cynodontes herbivores spécialisés, dont la position phylogéné-tique est controversée, certains auteurs les considérant comme de proches parents des mammifères et d'autres comme des membres du clade eucynodonte des Traversodontidae. Le pelvis de tritylodontidé est considéré comme ressemblant à celui des mammifères, en raison de leur iliaque étroit en forme de tige, mais de telles considérations sont

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Fémur
Hanche

vigoureusement remises en question en raison de la pauvreté du matériel pelvien de trity-
lodontidé disponible antérieurement. Cependant, un squelette partiel de tritylodontidé du
Jurassique inférieur de Chine conserve des exemples de trois éléments pelviens presque
complets, associés aux deux fémurs, ce qui jette un regard sans précédent sur la structure
du pelvis de tritylodontidé et sur la configuration de la hanche. Ce spécimen confirme que
la lame iliaque a la forme d'une tige, ce qui ajoute de nouvelles données soutenant une
relation étroite entre tritylodontidés et mammifères. En outre, la rétraction fémorale paraît
avoir été dirigée en partie par le muscle fessier chez les tritylodontidés, comme chez les
mammifères.

1. Introduction

Tritylodontids are a clade of specialised, herbivorous, predominantly Jurassic cynodonts whose exact relationship to mammaliaforms has long been controversial (Abdala, 2007; Hopson and Kitching, 2001; Kemp, 1983; Liu and Olsen, 2010; Rowe, 1988; Simpson, 1959; Sues, 1985; Sues and Jenkins, 2006). The craniodental anatomy of tritylodontids is strikingly similar to that of mammaliaforms in some respects, but tritylodontids lack a dentary-squamosal articulation and a number of other advanced features present in mammaliaforms (Luo, 1994). Tritylodontid postcranial anatomy is more clearly mammaliaform-like (Kemp, 1983), although some of the resemblances are at least arguably superficial (Sues, 1985; Sues and Jenkins, 2006).

Based on dental similarities, Crompton and Ellenberger (1957) suggested that tritylodontids were closely related to the presumably herbivorous traversodontid cynodonts of the Triassic, which would imply that the former were only distantly related to mammaliaforms. The hypothesis of phylogenetic proximity between traversodontids and tritylodontids was accepted, and in some cases elaborated upon, by a number of subsequent authors (e.g. Crompton and Jenkins, 1973; Hopson and Barghusen, 1986; Sues, 1985), but obtained its firmest support from a phylogenetic analysis by Hopson and Kitching (2001) that placed tritylodontids among traversodontids within the larger clade Cynognathia. Mammaliaforms, by contrast, were found to be members of the other major lineage of cynodonts, Probainognathia. However, Kemp (1983) argued that tritylodontids were closely related to mammaliaforms rather than to traversodontids, emphasizing the strong resemblances in postcranial morphology between the first two groups. Several phylogenetic analyses (Abdala, 2007; Liu and Olsen, 2010; Rowe, 1988; Wible, 1991) have provided support for slightly different versions of this alternative hypothesis of tritylodontid affinities. The most recent and comprehensive of these analyses (Abdala, 2007; Liu and Olsen, 2010) have upheld Hopson and Kitching's (2001) dichotomy between cynognathians and probainognathian, but have moved tritylodontids into the latter group in a position close to mammaliaforms.
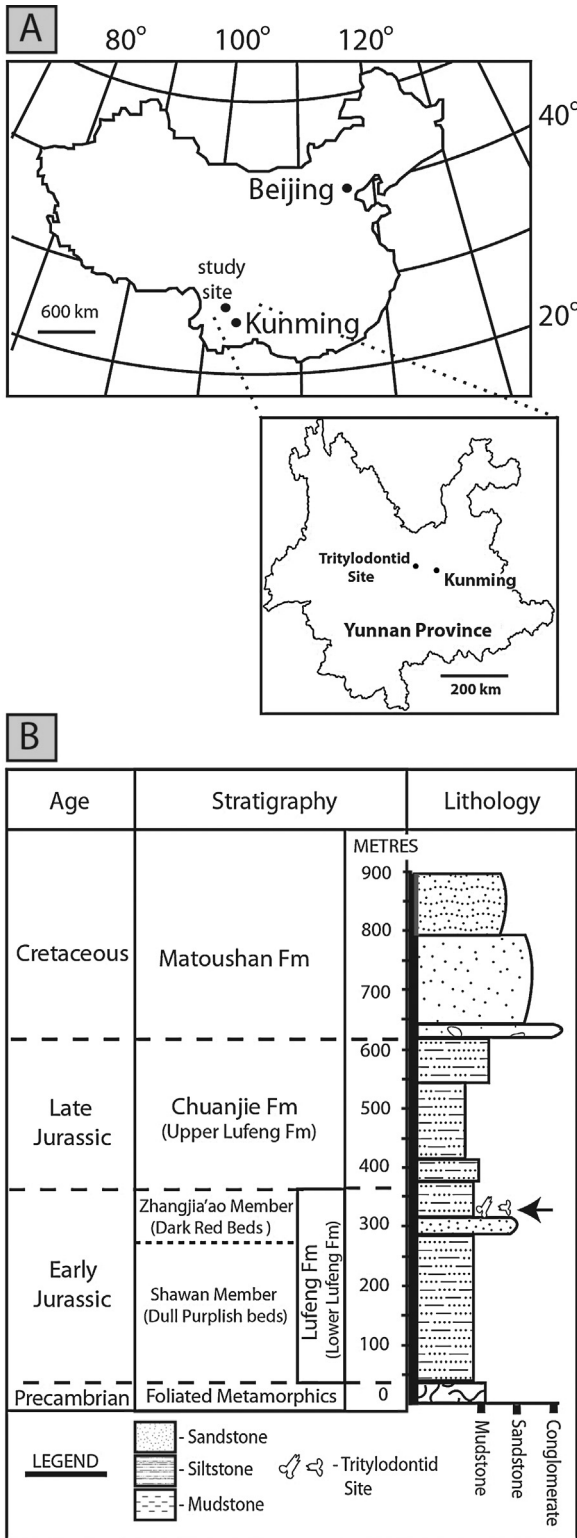
This paper describes a newly collected partial tritylodontid skeleton, including a number of dorsal, sacral and caudal vertebrae, much of the pelvis, and both femora, from the Lower Jurassic of China. Although taxonomically indeterminate, the specimen is of interest because of the novel information it provides regarding the anatomy of the tritylodontid pelvis, some aspects of which have been either controversial or simply unknown. In particular, the degree to which the tritylodontid ilium resembles that of mammaliaforms is a disputed point within the broader debate over whether the two groups display phylogenetically significant similarities in postcranial morphology. Kühne (1956) reconstructed the ilium of *Oligokyphus* as closely reminiscent of the mammaliaform condition, with a narrow preacetabular blade and no definite posterior process. However, Sues and Jenkins (2006) noted that this reconstruction was based on fragmentary material, and that a posterior process was in fact preserved in some *Oligokyphus* specimens and in a juvenile individual of *Kayentatherium* figured by Lewis (1986). The shape of an intact posterior process has not been described in detail for these genera or any other tritylodontid, making comparisons to other groups difficult, and the shape of the preacetabular blade of the tritylodontid ilium remains incompletely known (Sues and Jenkins, 2006). The new Lufeng specimen largely resolves these uncertainties, and shows that the tritylodontid pelvis and hip joint were strikingly mammaliaform-like in structure and presumed function.

2. Materials and methods

This study is based on CXPM C2019 2A235, a partial tritylodontid skeleton from the Lower Jurassic Lufeng Formation (formerly known as the Lower Lufeng Formation) of Lufeng County, Chuxiong Prefecture, Yunnan Province, China (Fig. 1). A cast of this specimen is housed at the IVPP, as IVPP FV 1970. The specimen is disarticulated, apart from a few articulated and semi-articulated vertebrae, but comprises bones that were found in a single stratigraphic layer in an area measuring less than 0.5 m^2. The bones are proportionate to one another in size, and do not include duplicate elements. Some have been affected by distortion, breakage, and/or surface wear, and many are stuck together in small clusters. The elements include 17 vertebrae from the dorsal, sacral and caudal parts of the column, some neural arch and rib fragments, a fragment of the left scapula, the left pubis and ischium, parts of both ilia, and both femora.

The specimen was used to investigate the muscular mechanism of hip retraction in tritylodontids, based on the assumption that the femur would have been held in a partially abducted position in normal walking as in extant small non-cursorial mammals (Jenkins, 1971a). The left femur of CXPM C2019 2A235 was physically manipulated within the acetabulum to confirm that retraction through an angle of about 90° in this abducted position was plausible. The articulated femur and pelvis were reconstructed

Fig. 1. Location and stratigraphy of tritylodontid site. A. Maps showing that the site is located to the northwest of Kunming in Yunnan Province, China. B. Composite stratigraphic section through the study area in the Lufeng Basin, showing the position of the tritylodontid specimen in the Dark Red Beds (Zhangjia'ao Member) of the Lufeng Formation.
Fig. 1. Localisation et stratigraphie du site à tritylodontidés. A. Cartes montrant la localisation du site au nord-ouest de Kunming dans la province de Yunnan, Chine. B. Coupe stratigraphique combinée à travers la zone d'étude dans le bassin de Lufeng montrant la position du spécimen de tritylodontidé dans les Dark Red Beds (membre Zanglia'ao de la formation de Lufeng).

in lateral view, in hypothetical postures representing successive stages of femoral retraction during the stance phase of locomotion. The approximate trajectory of the gluteus musculature that would have extended from the ilium to the greater trochanter of the femur (Romer, 1922) was then plotted on the diagrams, in order to determine whether this musculature would have had a substantial retractor moment arm about the hip joint as in extant mammals and presumably other mammaliaforms. "Mammalian" rather than "reptilian" terminology is used to designate muscles in this paper, but the "reptilian" homologue of each muscle is given in parentheses the first time each muscle is mentioned. Muscle homologies and nomenclature mainly follow Romer (1922).

Institutional abbreviations. **CXPM**, Chuxiong Prefectural Museum, Chuxiong, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MCZ**, Museum of Comparative Zoology, Cambridge, USA.

Anatomical abbreviations. ac, anterior condyle; **af**, acetabular facet; **cl**, crista lateralis; **cm**, crista medialis; **ds**, dorsal shelf; **ep**, epipubic bone; **f.**, facet for articulation with specified bone; **fh**, femoral head; **fo**, fossa; **gf**, gluteus fossa; **gt**, greater trochanter; **ib**, ischial buttress; **if**, iliacus fossa; **il**, ilium; **is**, ischium; **it**, ischial tuberosity; **itf**, intertrochanteric fossa; **lp**, lateral process; **lr**, lateral ridge; **lt**, lesser trochanter; **pc**, posterior condyle; **pdp**, posterodorsal process; **pe**, pectineal eminence; **poz**, postzygapophysis; **pr**, posterior ridge; **prz**, prezygapophysis; **pt**, pubic tubercle; **pu**, pubis; **ra**, rib attachment area; **rs**, rounded shelf; **S1–3**, sacral vertebra 1–3; **sc**, supraacetabular crest; **sf**, sacral fenestra; **sr**, sacral rib; **tp**, transverse process; **vg**, ventral groove; **vk**, ventral keel.

3. Geological background and sedimentology

Investigations into the Mesozoic stratigraphy of the Lufeng Basin over the last 75 years have resulted in a wealth of information regarding the Lufeng Formation (formerly called the Lower Lufeng Formation), which is exceptionally rich in fossil vertebrates. Analysis of palynomorph, invertebrate, and vertebrate fossils from the Lufeng Formation (Fang et al., 2000; Irmis, 2004; Sun and Cui, 1986; Wu and Chatterjee, 1993; Young, 1941) indicates that this unit is Early Jurassic (Sinemurian) in age, rather than Late Triassic as formerly believed (e.g. Young, 1947). In particular, the association of sauropodomorphs, tritylodontids, mammaliaforms, protosuchids, ornithischians and neotheropods in the Lufeng fauna strongly supports

the revised age assessment through faunal similarities with other Lower Jurassic continental successions, such as the Upper Elliot/Clarens formations of South Africa, the Kayenta Formation of Arizona, and the Forest Sandstone of Zimbabwe (Erikkson, 1985; Olsen and Sues, 1986; Sanabria, 2001; Weishampel et al., 2004).

The Lufeng Formation has been divided into two primary sub-units, the lower Dull Purplish Beds (Shawan Member) and the upper Dark Red Beds (Zhangjia'ao Member). Although both units are fossiliferous, the Dark Red Beds have yielded considerably more vertebrate remains, including CXPM C2019 2A235. The specimen was discovered 28.5 m above the basal contact of the Dark Red Beds (Fig. 1B). The base of the Dark Red Beds is characterised by a distinctive, green sandstone bed (actually a series of amalgamated beds) with a thickness of 10–20 m, and the tritylodontid site is located ~16.5 m above the top of this unit in a well-exposed cliff roughly 100 m north of the stream. The locality can be confidently assigned to "stratum 5" of Luo and Wu (1994). The specimen was recovered from a brownish grey (Munsell colour 5YR4-1) mudstone with weak horizon development, abundant slickensides, and clay cutans. These features suggest that the tritylodontid skeleton was preserved in the Bs horizon of a moderately well developed palaeosol that is best characterised as a vertisol (sensu Mack et al., 1993).

The overall sedimentology of the lower portion of the Dark Red Beds or Zhangjia'ao Member is generally indicative of a semi-arid fluvial-floodplain setting. Moderate to intense soil development is demonstrated by the abundance of moderate to well-developed palaeosols through much of the stratigraphic succession. The presence of well-developed B horizons, commonly with slickensides, clay cutans, blocky peds, and calcium carbonate nodules, provides a basis for diagnosing these palaeosols as dominantly vertisols and calcic vertisols. Thin sheet-like sandstone bodies are abundantly interspersed throughout the sequence and interpreted as crevasse splays, whereas rare medium-to-coarse-grained tabular sandstone bodies from 1.5–3 m thick (and up to 9 m thick) that preserve planar laminations (with parting lineation), small-medium trough cross stratification and current ripple cross lamination are interpreted as shallow, braided fluvial channels. Overall, the succession appears to represent a palaeosol-dominated, semi-arid distal floodplain setting.

4. Description of the specimen

CXPM C2019 2A235 represents a large tritylodontid, the relatively undistorted right femur measuring 95 mm in length. None of the vertebrae (Fig. 2) displays clear neurocentral sutures, and the second and third sacral vertebrae (S2–S3) are at least partially fused together. However, S1 is not fused to S2, nor are the pelvic elements fused to either the sacrals or each other. This apparently intermediate level of skeletal fusion suggests that the specimen may represent a subadult.

Dorsal vertebrae. A total of 11 vertebrae appear to belong to the dorsal part of the backbone, which reportedly contains 19 vertebrae in *Kayentatherium* (Lewis, 1986; Sues and Jenkins, 2006). As in *Kayentatherium*, there is no

evidence for a sharp distinction between thoracic and lumbar parts of the dorsal series. One well-preserved vertebra (Fig. 2A) closely matches Kühne's (1956: fig. 45A) reconstruction and description of an anterior thoracic vertebra of *Oligokyphus*, having a small centrum, a backswept neural spine, and a small laterally directed process located slightly dorsal to the neurocentral junction on the anterior part of the neural arch. This process is separate from the articular area for the rib, and must have been associated with muscle or tendon attachment (Sues and Jenkins, 2006). The width of the anterior articular surface (19 mm) slightly exceeds the length of the centrum (17 mm), in contrast to the condition in *Oligokyphus* (Kühne, 1956), and considerably exceeds the height of the anterior articular surface (14 mm). A second vertebra appears similar in structure, but is badly dorsoventrally compressed.

Most of the remaining nine dorsal vertebrae are poorly preserved to varying degrees. Their positions within the column are difficult to determine, although they presumably come from the middle and posterior parts of the dorsal series. Their centra are slightly longer than those of the anterior dorsals, ranging up to 21 mm in length, and the articular surfaces are higher in proportion to their width. Two of the centra (Fig. 2B) bear prominent midline keels. The neural arch of one of the mid-to-posterior dorsals bears a small lateral process like that present in one of the anterior dorsals. The area for rib attachment is an elongate, inclined, anteriorly positioned facet near the level of the neurocentral junction, and the zygapophyses are tilted to an angle that is intermediate between horizontal and vertical. The only two intact neural spines are low, only slightly posteriorly inclined, and minimally expanded at their tips. In adult *Kayentatherium*, by contrast, the apices of the middle and posterior dorsal neural spines are conspicuously expanded (Sues and Jenkins, 2006).

Sacral vertebrae. Three sacral vertebrae are present (Fig. 2D–E), fewer than the four postulated by Kühne (1956) for *Oligokyphus* and reported by Lewis (1986) for *Kayentatherium*. One of the sacrals is detached from the others, and resembles the dorsal vertebrae in having large prezygapophyses whose articular surfaces are directed dorsomedially. This vertebra probably represents S1, and appears to articulate with the more anterior of two partially fused sacrals that can accordingly be identified as S2 and S3. It is likely that an S4 was present, as in *Kayentatherium* and *Oligokyphus*, but is missing or indistinguishable from the caudals.

The anterior and posterior articular surfaces of the centra of the preserved sacrals are wider than high, and the centra are about as long as those of the largest dorsals. Each centrum bears a single ventral keel, but the sharpness of the keel decreases from S1 to S3. In contrast to the prezygapophyses of S1, the intact left prezygapophysis of S2 is small, tapers to a point anteriorly, and has a transversely concave articular surface.

The ribs of S1 are less anteroposteriorly broad than those of S2 and S3, and do not appear to contact the ribs of S2 when the two vertebrae are placed in articulation. The distal part of each rib flares posteriorly into an expanded area whose lateral edge is concave in the ventral direction and inclined to face slightly anteriorly. This edge would
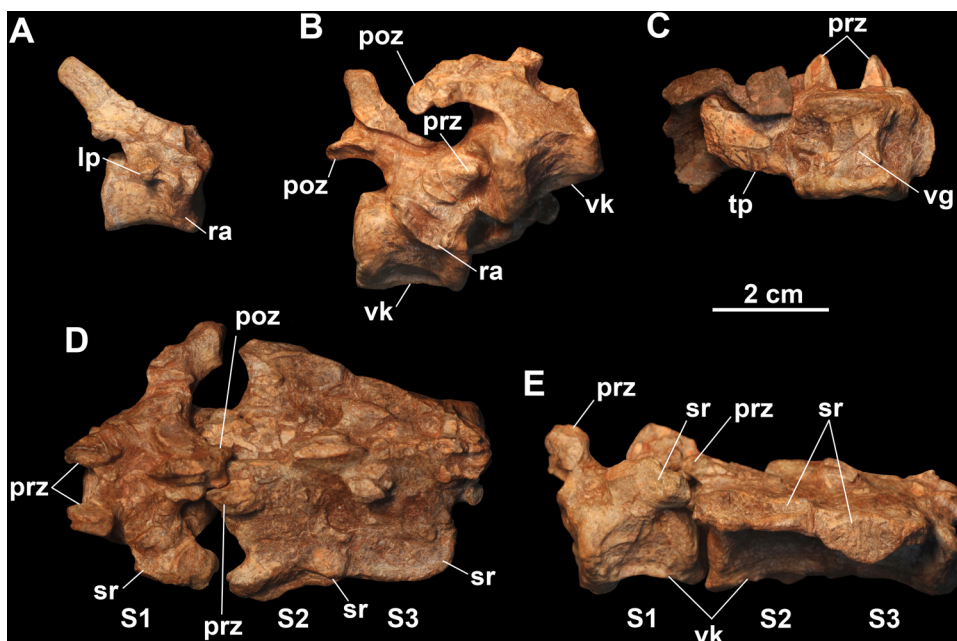
Fig. 2. Representative vertebrae of Lufeng tritylodontid specimen CXPM C2019 2A235. A. Anterior dorsal vertebra in right lateral view. B. Posterior dorsal vertebrae, one in right lateral view and the other in oblique posterior and right lateral view. C. Anterior caudal vertebra in ventral view. D–E. Sacral vertebrae 1–3 in dorsal (D) and left lateral (E) views. Neural arch fragment adhering to vertebra darkened for clarity in (C).

Fig. 2. Vertèbres représentatives du spécimen de tritylodontidé de Lufeng CXPM C2019 2A 235. A. Vertèbre dorsale antérieure en vue latérale droite. B. Vertèbres dorsales postérieures, l'une en vue latérale droite, l'autre en vue postérieure oblique et en vue latérale droite. C. Vertèbre caudale antérieure en vue ventrale. D–E. Vertèbres sacrées 1–3 en vues dorsale (D) et latérale gauche. (E). Fragment de l'arc neural adhérant à la vertèbre assombrie pour plus de visibilité en (C).

presumably have contacted the ilium. The ribs of S2 and S3 are broad and sheet-like even proximally, but expand slightly near their tips to contact one another and enclose a sacral foramen. The lateral articular surface formed by the rib of S2 is oblong and dorsoventrally narrow, whereas that formed by the rib of S3 is slightly broadened by a convex ventral expansion. The total length of the surface formed by the three sacrals for contact with the ilium is about 5 cm.

Caudal vertebrae. Three vertebrae appear to be from the proximal part of the tail, and are generally similar to the proximal caudal vertebrae of *Oligokyphus* (Kühne, 1956). Their centra each bear on the ventral surface a shallow longitudinal groove flanked by two ridges, and are slightly shorter (about 18 mm) than those of the posterior dorsal vertebrae. The articular surfaces of the centra are nearly flat, and considerably wider than high. The prezygapophyses are widely spaced and dorsomedially directed. The caudal vertebrae bear broad transverse processes, the best preserved of which (Fig. 2C) ends abruptly at a straight lateral edge. The posterior edge of this transverse process has a slight anterolateral inclination, whereas the anterior edge is slightly concave and forms a small anterior prominence at its lateral end.

Dorsal ribs. Only a few rib fragments are preserved. Two well-preserved proximal fragments are present, and are both single-headed.

Scapula. A piece of bone flattened against the left side of a dorsal vertebra (Fig. 3P) represents the blade of the left scapula, exposed in medial view. The scapula is preserved in an inverted position, with the dorsal edge pressed

against the ventral part of the centrum of the vertebra. The dorsal part of the blade of the scapula is subtriangular in medial view as in *Kayentatherium* (Sues and Jenkins, 2006), but the dorsal margin is less strongly convex than in that taxon and the posteriorly directed prominence seen at the posterodorsal corner of the scapula of *Kayentatherium* is absent in CXPM C2019 2A235. In *Bienotheroides*, the posterodorsal corner of the scapula also lacks a prominence (Sun and Li, 1985), but appears more rounded than in CXPM C2019 2A235. Unlike in both *Kayentatherium* and *Bienotheroides*, the posterior margin of the scapula of CXPM C2019 2A235 is sinuous in medial view, being slightly convex dorsally but concave ventrally. The posterior edge of the blade forms a sharp, laterally prominent crest, whose posterior surface bears a shallow concavity that may represent a poorly developed equivalent of the postscapular fossa as seen in *Kayentatherium* (Sues and Jenkins, 2006) but apparently not in *Bienotheroides* (Sun and Li, 1985). The glenoid and acromial portions of the scapula are broken away.

Ilium. The ilium is strikingly like those of mammaliaforms in overall morphology. The acetabular region is well preserved in both ilia (Fig. 3A–D, G), and the blade of the right ilium is preserved to a distance of 21 mm beyond the acetabulum. An additional fragment (Fig. 3E–F), 23 mm in length, probably belongs to the right ilium. If the vertebral column had the sinuous curvature typical of mammals, the iliac blade would have extended anterodorsally from the acetabular region in life.
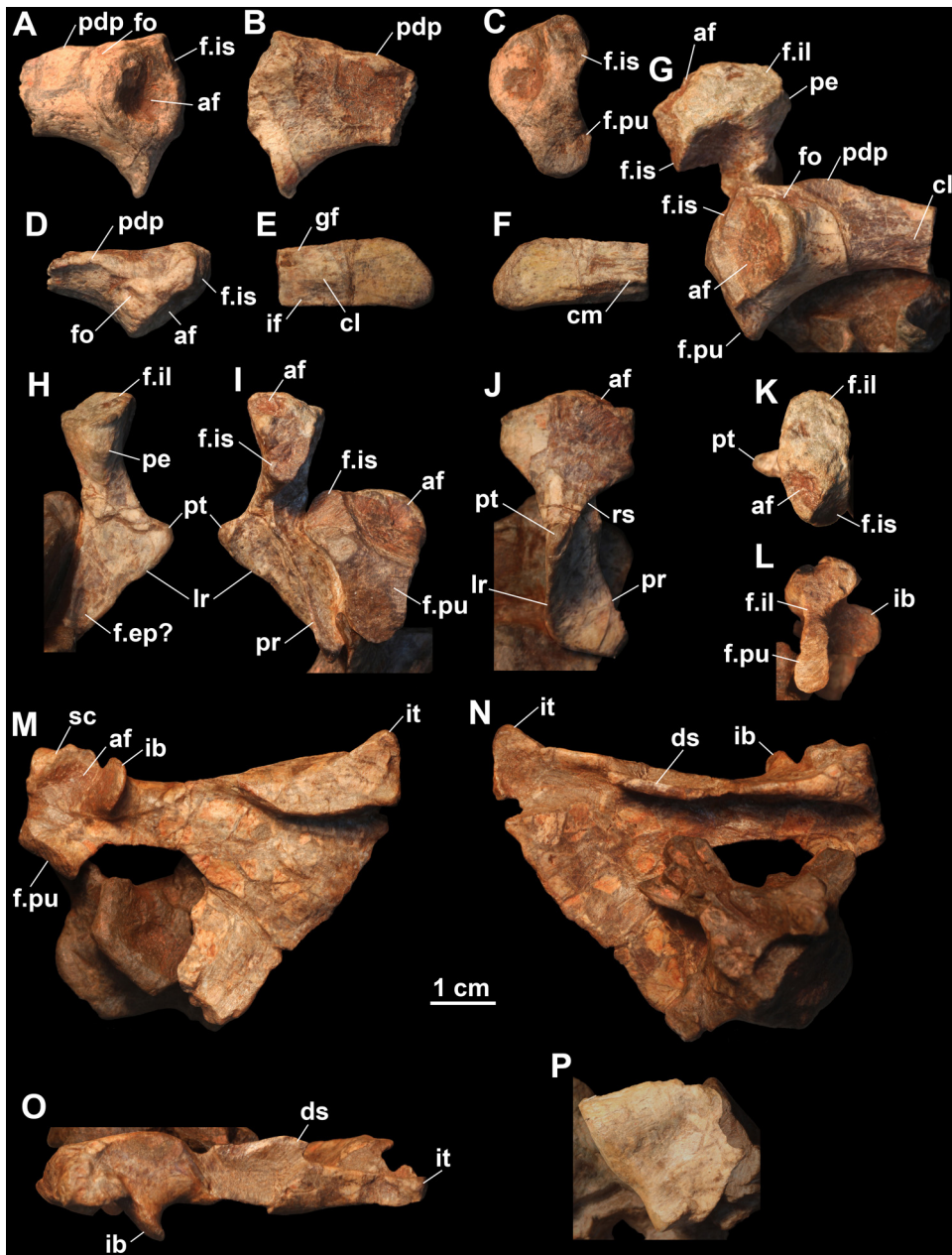
Fig. 3. Pelvic and pectoral girdle elements of Lufeng tritylodontid specimen CXPM C2019 2A235. A–D. Posterior part of left ilium in lateral (A), medial (B), posterior (C) and dorsal (D) views. E–F. Anterior end of left iliac blade in lateral (E) and medial (F) views; G, posterior part of right ilium in lateral view and dorsal part of left pubis in approximate medial view. H–K. Left pubis in anterior (H), posterior (I), lateral (J) and dorsal (K) views. L–O. Left ischium in anterior (L), lateral (M), medial (N) and dorsal (O) views. P. Left scapula in medial view. Additional elements adhering to some bones have been darkened for clarity.

Fig. 3. Éléments de la ceinture pelvienne et pectorale du spécimen de tritylodontidé de Lufeng, CXPM C2019 2A235. A–D. Partie postérieure de l'iliaque gauche en vues latérale (A), médiale (B), postérieure (C) et dorsale (D). E–F. Terminaison antérieure de la plaque iliaque gauche en vues latérale (E) et médiale (F). G. Partie postérieure de l'iliaque droit en vue latérale et partie dorsale du pubis gauche en vue approximativement médiale. H–K. Pubis gauche en vues antérieure (H), postérieure (I), latérale (J) et dorsale (K). L–O. Ischium gauche, en vues antérieure (L), latérale (M), médiale (N) et antérieure (O). P. Scapula gauche en vue médiale. Des éléments additionnels adhérant à certains os ont été assombris pour plus de visibilité.

The acetabular surface of the ilium is approximately semi-circular in outline, as in the mammaliaform *Morganucodon* (Jenkins and Parrington, 1976). The lateral edge of the acetabular surface is strongly convex, forming a supraacetabular buttress that lies anterodorsal rather than dorsal to the acetabulum (Fig. 3A). In the left ilium, the acetabular surface is unevenly concave, in that the central part of the surface forms a deep, bowl-like depression that is sharply delimited by raised rims. The acetabular surface of the right ilium appears somewhat damaged. The flat,

posteroventrally facing pubic facet has a wide, rounded ventral end and a narrow dorsal end that is confluent via a narrow strip of bone with the ventral end of the ischial facet (Fig. 3C). The ischial facet is weakly convex from dorsal to ventral, and slightly narrower than the pubic facet.

The iliac blade is dorsoventrally narrow and mediolaterally compressed, with a "rod-like" morphology similar to that seen in early mammaliaforms such as *Morganucodon* (Jenkins and Parrington, 1976) and in the non-mammaliaform probainognathians *Therioherperton* and *Prozostrodon* (Bonaparte and Barberena, 2001). The blade appears almost entirely equivalent to the considerably broader preacetabular part of the iliac blade of basal (non-eucynodontian) cynodonts (Jenkins, 1971b; Kemp, 1980a), basal (non-traversodontid) cynognathians (Jenkins, 1971b) and traversodontids (Bonaparte, 1963; Jenkins, 1970; Kammerer et al., 2008; Kemp, 1980b; Liu and Powell, 2009). In tritylodontid ilia, the only remnant of the postacetabular part of the primitive blade is generally a "posterior" process that takes the form of a small flange on the posterior part of the dorsal edge of the bone, although this structure is usually poorly preserved (Sues and Jenkins, 2006). In CXPM C2019 2A235, the posterior process is preserved nearly intact on both ilia (Fig. 3A–B, D, G), and clearly takes the shape of a long, low convexity separated from the dorsal edge of the ischial facet by a concave area of bone. In at least one juvenile individual of *Kayentatherium*, a more distinct, posterolaterally directed process appears to be present (Lewis, 1986: fig 2; Sues and Jenkins, 2006), but this structure is nevertheless modest in size and its morphology remains to be fully documented.

Outside Tritylodontidae, a small prominence corresponding to the posterior process is present in *Prozostrodon* (Bonaparte and Barberena, 2001), and apparently even in the early mammaliaform *Erythrotherium* (Jenkins and Parrington, 1976: fig. 13A). The postacetabular part of the iliac blade is somewhat reduced in the traversodontid *Exaeretodon* (Bonaparte, 1963) and particularly in a basal cynodont specimen described by Broom (1948) under the name "*Leavachia*", now considered a subjective junior synonym of *Procynosuchus* (Hopson and Kitching, 1972; Kemp, 1980a; Kammerer and Abdala, 2009). In both cases, however, the postacetabular part of the iliac blade is above the acetabulum and directed approximately posteriorly, rather than resembling the posterior process of the tritylodontid ilium in being anterior to the acetabulum and either strongly posterodorsally aligned or reduced to a dorsal convexity. In *Exaeretodon*, the postacetabular part of the blade is also proportionally much larger than the posterior process of the ilium appears to be even in juvenile *Kayentatherium* (Lewis, 1986: fig. 2).

Lateral to the concave area between the posterior process and the acetabulum, and bordering the margin of the acetabulum, the left ilium of CXPM C2019 2A235 bears an area of rugosity whereas the right ilium forms a smaller, sharply defined fossa with an irregular outline. In the right ilium, the blade extends far enough beyond the acetabulum that the posterior parts of the crista lateralis and crista medialis reported by Kühne (1956) in *Oligokyphus*, and also present in the indeterminate tritylodontid ilium MCZ 8835 (Sues and Jenkins, 2006) are evident.

The anterior iliac fragment (Fig. 3E–F) measures 23 mm in length and more likely belongs to the right ilium than to the left, based on preliminary comparisons to undescribed tritylodontid ilia in IVPP field collections from the Jurassic of northwestern China. The posterior end of this fragment is 9 mm deep dorsoventrally, making it slightly but distinctly shallower than the anterior end of the posterior fragment of the right ilium (10 mm). However, the anterior fragment deepens anteriorly, attaining its maximum dorsoventral depth of 10 mm at a point slightly posterior to the tip. In MCZ 8835 and *Kayentatherium* (MCZ 8812) the blade of the ilium is proportionally dorsoventrally deeper than in CXPM C2019 2A235 (Sues and Jenkins, 2006), as in *Bienotheroides* (Maisch et al., 2004). In MCZ 8835, however, the blade is dorsoventrally constricted at a point just anterior to the acetabulum.

The total length of the intact ilium is difficult to estimate, but a figure of about 7 cm seems plausible. Assuming the anterior fragment indeed belongs to the right ilium, the tip of the iliac blade is more prominent ventrally than dorsally. The crista lateralis, interpreted by Kühne (1956) in *Oligokyphus* as dividing a dorsally placed gluteus fossa from a ventrally placed iliacus fossa, is weakly developed in this part of the ilium and terminates about 13 mm posterior to the tip. The anteriormost part of the lateral surface is flat, and prominent relative to the dorsal and ventral fossae. The crista medialis terminates at about the same level as the crista lateralis, but it is much more prominent. The ventromedially directed surface below the crista medialis is flat, whereas the dorsomedially directed surface above the crista is slightly concave. There are no distinct indications of sacral rib attachment on the medial surface of either ilium.

Pubis. The left pubis of CXPM C2019 2A235 (Fig. 3G–K) is almost intact, although its symphyseal edge is obscured through contact with the medial surface of the right ilium. The anterior part of the dorsal end of the pubis forms a slightly rugose, anterodorsally directed, U-shaped articular surface for the ilium. The posterior part of the dorsal end of the pubis forms a narrow, medially located, tongue-like surface that would have articulated with the ischium and faced posterodorsally and slightly medially. Lateral to the area of contact between the iliac and ischial facets is a small concave area that represents the pubic contribution to the acetabulum (Fig. 3K). The concave area has a subtriangular outline and is bordered posteriorly by a small, pyramid-like prominence of bone. The acetabular surface of the pubis would face approximately dorsally in the articulated pelvis, is not associated with a laterally projecting buttress, and is considerably smaller than the acetabular surface formed by the ilium.

The lateral surface of the head (dorsal portion) of the pubis (Fig. 3J) has a rhomboid shape and narrows ventrally towards the base of a blade-like, anteroposteriorly narrow pubic plate that is directed medially and posteriorly as well as ventrally. The anteroposteriorly narrow pubic plate is separated from the dorsal part of the bone by a distinct neck, and the anterior part of the plate is strongly everted so that what is presumably the morphological equivalent of the anterior edge of the primitive pubic plate is directed laterally. The prominent apex of this

everted portion of the pubis is dorsally positioned, lying just below the neck. Kühne (1956) identified the apex of a similar everted flange in *Oligokyphus* as a pubic tubercle, and regarded the everted arrangement as primitive. A broadly similar configuration is present in *Therioherpeton* (Bonaparte and Barberena, 2001) and in the traversodontids *Exaeretodon* (Bonaparte, 1963) and *Andescynodon* (Liu and Powell, 2009).

In CXPM C2019 2A235, the pubic tubercle lies at the ventral corner of the rhomboid lateral surface of the head of the pubis. The posteroventral edge of the rhomboid surface forms a low, rounded shelf that stands out from the more subdued adjacent part of the pubic plate and terminates at the pubic tubercle. The lateral and medial faces of the head of the pubis both curve smoothly into the narrow, transversely convex anterior face, which forms a low, rounded eminence adjacent to the anterior margin of the iliac facet. This eminence is similar in position to the pectineal process of monotremes and marsupials, and may represent the origin of *M. pectineus* (homologous to part of *M. puboischiofemoralis internus*).

The pubic plate is complex in structure but has a roughly subtriangular cross-section, with anterior, posterolateral and posteromedial surfaces separated by well-defined ridges. The lateral ridge separating the anterior and posterolateral surfaces is continuous with the distal edge of the pubic tubercle, and represents the everted anterior edge of the primitive pubis. Ventral to the pubic tubercle, the lateral ridge gradually recedes in prominence as in *Exaeretodon* (Bonaparte, 1963), giving the relatively flat anterior surface of the blade (Fig. 3H) a triangular shape as it tapers to a rounded ventral point that also represents the anterior end of the short ventral edge of the pubis.

The ventralmost part of the anterior surface bears a distinct, subrectangular depression that may represent either a preservational artefact or an articular facet for an epipubic bone. The equivalent facet takes the form of a fossa in extant monotremes and dasyurid marsupials (Kielan-Jaworowska, 1975), and epipubic bones have been previously reported in the tritylodontid "*Tritylodontoideus*" (Fourie, 1962, 1963) but never adequately documented.

The posterolateral and posteromedial surfaces of the pubic plate are separated by a slightly irregular posterior ridge, which is as thin and sharp as the lateral ridge but somewhat less prominent. The posterior ridge begins distally at the posteroventral tip of the pubic plate, which is slightly damaged, and extends proximally to intersect the rounded shelf formed by the posteroventral edge of the rhomboid lateral surface of the head of the pubis.

The posterolateral surface of the pubis is concave between the lateral and posterior ridges, and is twisted so that its proximalmost part faces posteriorly whereas its distalmost part faces laterally. The whole surface is also tilted somewhat ventrally, as a result of the medial deflection of the pubic plate as a whole. The posteromedial surface of the pubic plate is partly obscured by contact with the right ilium, but appears flat and anteroposteriorly narrow. The medial ridge separating the posteromedial and anterior surfaces does not seem to be as prominent as the lateral and posterior ridges.

Ischium. The left ischium of CXPM C2019 2A235 (Fig. 3L–O) is nearly complete, although parts of this bone have undergone obvious distortion. The ischium is the largest of the three pelvic bones, and consists of a sizeable acetabular portion, a narrow neck, and a broad, subtriangular plate. Except at the dorsal margin, which is folded medially, the neck and plate of the ischium are mediolaterally thin. In the articulated pelvis, the neck of the ischium would have extended approximately posteriorly from the acetabular region and at most slightly ventrally, approximating the mammaliaform condition (Jenkins and Parrington, 1976). The orientation of the ischium appears similar in *Oligokyphus* (Kühne, 1956) and in the traversodontids *Luangwa* (Kemp, 1980b) and *Menadon* (Kammerer et al., 2008), though in *Exaeretodon* (Bonaparte, 1963) and *Andescynodon* (Liu and Powell, 2009), the ischium appears to slope more ventrally.

The proximal end of the ischium (Fig. 3L) forms a narrow, oblong, anteroventrally directed facet for articulation with the pubis. The ventral part of the anteriorly directed facet for the ilium is also narrow, but the dorsal part of the facet swells laterally to form a prominence with a convex edge. The acetabular part of the ischium (Fig. 3M) is a broad, shallow, laterally directed concavity bounded dorsally by a low, posteriorly tapering supraacetabular crest extending from the prominence on the iliac facet. The acetabular concavity is bounded posteriorly by a large tab-like buttress that extends laterally and slightly posteriorly. The flat articular face of this ischial buttress is accordingly directed anteriorly and slightly laterally, and is dorsoventrally narrow with a broadly rounded lateral end.

The neck of the ischium is long and dorsoventrally shallow in lateral view (Fig. 3M), as in *Therioherpeton* (Bonaparte and Barberena, 2001). In the tritylodontid *Dinnebitodon* (Sues and Jenkins, 2006) and the traversodontids *Exaeretodon* (Bonaparte, 1963), *Luangwa* (Kemp, 1980b), *Menadon* (Kammerer et al., 2008) and *Andescynodon* (Liu and Powell, 2009), the neck is deeper in proportion to its length, making it appear less sharply defined.

The distal part of the ischium flares ventrally, and to a small degree dorsally, to form a thin but extensive plate. The posterodorsal corner of the plate forms a distinct, dorsally directed ischial tuberosity, and a similarly well-defined tuberosity appears to be present in *Bienotheroides* (Maisch et al., 2004) but not in *Luangwa* (Kemp, 1980b), *Menadon* (Kammerer et al., 2008), *Therioherpeton* (Bonaparte and Barberena, 2001) or *Erythrotherium* (Jenkins and Parrington, 1976). The ischial plate extends ventrally as an oblong sheet of bone that narrows slightly towards its contact with the pubis. The ventralmost part of the ischial plate is broken away. However, placing the pubis and ischium in approximate articulation shows that the obturator foramen was much larger than in the basal cynognathian *Cynognathus* (Jenkins, 1971b) or the traversodontid *Exaeretodon* (Bonaparte, 1963), and more polygonal than round in outline.

The dorsal shelf of the ischium extends anteriorly to reach the acetabular part of the bone (Fig. 3O). The dorsal surface of the shelf is distorted, except near the acetabulum, but differs from the corresponding surface in early mammaliaforms (Jenkins and Parrington, 1976), typical
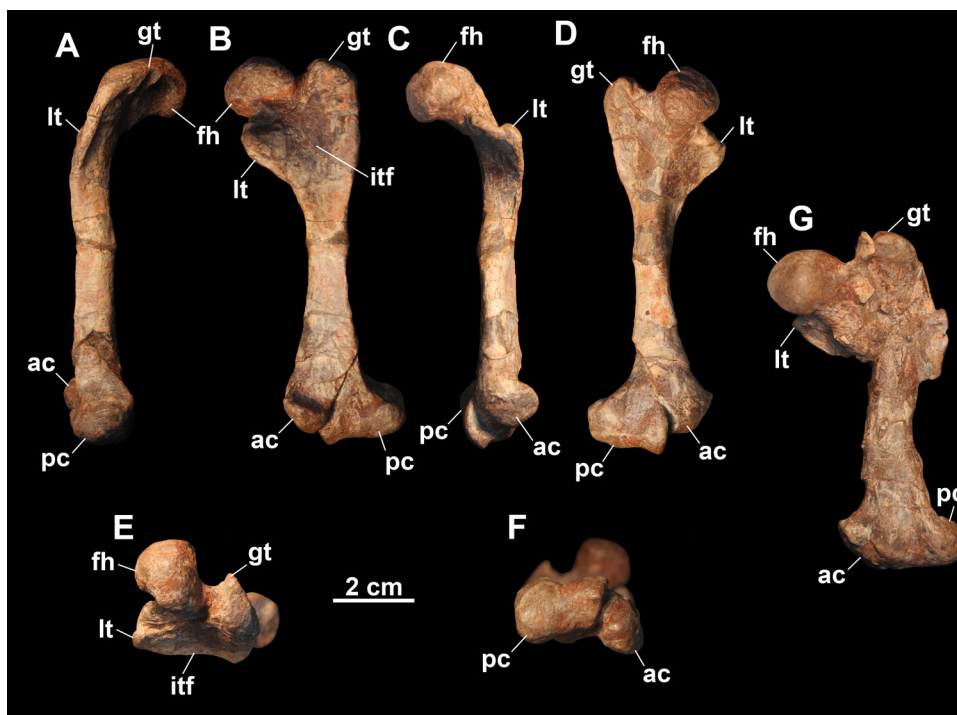
Fig. 4. Femora of Lufeng tritylodontid specimen CXPM C2019 2A235. A–F. Right femur in posterior (A), ventral (B), anterior (C), dorsal (D), proximal (E) and distal (F) views. G. Left femur in dorsal view.

Fig. 4. Fémurs du spécimen de tritylodontidé de Lufeng, CXPM C2019 2A235. A–F. Fémur droit en vue postérieure (A), ventrale (B), antérieure (C), dorsale (D), proximale (E) et distale (F). G. Fémur gauche en vue dorsale.

non-mammaliaform cynodonts (Jenkins, 1970, 1971b; Kammerer et al., 2008; Liu and Olsen, 2009), and even *Dinnebitodon* (Sues and Jenkins, 2006) in that no groove is present in the neck region.

Femur. Both femora are present. The following description is based mainly upon the better-preserved right femur (Fig. 4A–F), and follows convention by describing the femur as though this bone extended laterally from the hip with the extensor surface directed dorsally. The left femur (Fig. 4G) appears to have been compressed proximodistally, and the expanded proximal portion of the bone has been deflected anteriorly relative to the shaft. By contrast, the right femur is nearly pristine, although the posterior part of the distal end has been slightly displaced relative to the rest of the bone. The anteroposterior width of the distal end is about the same in both femora, measuring 32 mm in the right femur and 31 mm in the left, but the minimum shaft widths of the two femora are considerably different at 9 mm and 11 mm, respectively. These proportions give the right femur a surprisingly gracile appearance relative to both the left femur and most tritylodontid femora that have been illustrated in the literature (Sues and Jenkins, 2006, fig. 5.17; Sun and Li, 1985, fig. 11; Young, 1947: fig. 20). However, the right femur of CXPM C2019 2A235 appears similar in its proportions to the femur of *Oligokyphus* as reconstructed by Kühne (1956: fig. 58), suggesting that there may be genuine variability among tritylodontids with respect to femoral robustness.

The head of the femur projects proximally, dorsally and slightly anteriorly, has convex dorsal and proximal surfaces, and is much more dorsally prominent and distinct from the adjacent part of the femur than is the case in basal cynodonts (Jenkins, 1971b; Kemp, 1980a), basal cynognathians (Jenkins, 1971b), traversodontids (Bonaparte, 1963; Jenkins, 1970; Kemp, 1980b; Liu and Powell, 2009), and even *Therioherpeton* (Bonaparte and Barberena, 2001) and the tritheledontid *Irajatherium* (Martinelli et al., 2005). In these characteristics, the femoral head of the present specimen resembles the corresponding structure in most other tritylodontids (Kühne, 1956; Sues and Jenkins, 2006; Sun and Li, 1985; Young, 1947) and in early mammaliaforms (Jenkins and Parrington, 1976), although our observations of a specimen referred to the tritylodontid *Bienotheroides wansienensis* (IVPP V7906; Sun and Li, 1985) indicate that the head of the femur protrudes anteroproximally rather than dorsally and is not sharply set off from the rest of the bone. Sues and Jenkins (2006) noted an important difference between the tritylodontid and mammaliaform conditions, in that the femoral head is hemi-ovoid rather than hemispherical in tritylodontids. In CXPM C2019 2A235, the femoral head is elongated along an anterodorsal–posteroventral axis as in other tritylodontids, the long axis of the head measuring about 130% of the length of the short axis.

The proximal part of the femoral shaft takes the shape of a wide, distally tapering triangle owing to the presence of

flange-like greater and lesser trochanters, which resemble those of most other tritylodontids in general morphology and position (Sues and Jenkins, 2006). The greater trochanter forms a triangular, proximodorsally directed apex that lies posterior to the head of the femur and is separated from it by a slight notch, whereas the apex of the lesser trochanter is anteroventrally directed and more distally positioned. The ventral surface of the proximal portion of the femur bears a broad, shallow inter-trochanteric fossa.

Both trochanters differ in detailed morphology between the left and right femora. In the left femur, the apex of the greater trochanter is sharp and separated from the femoral head by only a narrow notch as in *Oligokyphus* (Kühne, 1956) and *Bienotherium* (Young, 1947), but in the right femur the notch is broader and the apex gentler as in *Bienotheroides* (Sun and Li, 1985). In the left femur, the lesser trochanter has a symmetrical appearance in dorsal or ventral view, in that the anteroproximal and anterodistal edges of the trochanter are similar in length, but in the right femur the apex of the trochanter is curved proximally and the anteroproximal edge is clearly shorter than the anterodistal one. The left femur resembles those of *Bienotherium* (Young, 1947) and IVPP V7906 (Sun and Li, 1985) in the structure of the lesser trochanter, whereas the right femur appears closer to *Oligokyphus* (Kühne, 1956) and the indeterminate tritylodontid femur MCZ 8838 (Sues and Jenkins, 2006). Surprisingly, the femur of the holotype of *Bienotheroides wansienensis* (IVPP V4734) differs from IVPP V7906, as well as from those of typical tritylodontids, in that the badly damaged lesser trochanter appears to project ventrally rather than anteroventrally. In CXPM C2019 2A235, at least some of the differences between the left and right femora undoubtedly reflect distortion of the latter, but it is also possible that the trochanter shape displays a high degree of plasticity in tritylodontids.

The distal end of the femur is anteroposteriorly expanded, and in the case of the left femur the degree of expansion is conspicuously greater in the posterior direction as in *Oligokyphus* (Kühne, 1956) and *Bienotherium* (Young, 1947). In contrast to MCZ 8838 (Sues and Jenkins, 2006), the femur possesses a patellar groove, although this structure is weakly developed. The popliteal space is flat. The distal condyles of the femur appear similar in form to the equivalent structures in *Bienotherium* (Young, 1947) and MCZ 8838 (Sues and Jenkins, 2006). The posterior condyle protrudes slightly farther dorsally than the anterior one, and in distal view the long axis of this condyle is approximately dorsoventral. The anterior condyle protrudes much farther ventrally, and the orientation of its long axis in distal view is posterodorsal–anteroventral.

5. Discussion

5.1. Taxonomic identification of CXPM C2019 2A235

Because the postcranium remains rather poorly known and poorly studied in non-mammaliaform cynodonts, no list of well-supported postcranial synapomorphies has been established for tritylodontids. Nevertheless, there is clear morphological evidence that CXPM C2019 2A235 is referable to this clade. The degree of narrowing of the iliac blade and reduction of the posterior process seen in this specimen is known only in tritylodontids, mammaliaforms, *Therioherpeton* and *Prozostrodon*, although it may also prove characteristic of some other probainognathians whose postcrania are poorly known at present. The proximal part of the femur is even more distinctively tritylodontid in character, taking into account differences between tritylodontids and mammaliaforms identified by Sues and Jenkins (2006). Only tritylodontids are known to possess a femoral head that is similar to that of mammaliaforms in being prominently set off from the shaft, but distinct from the mammaliaform condition in being hemi-ovoid rather than hemispherical. Similarly, the femur is mammaliaform-like in that the greater trochanter has a proximally directed apex separated by a concavity from the head of the femur, and in that the lesser trochanter is directed more anteriorly than ventrally. However, CXPM C2019 2A235 resembles previously described tritylodontids and differs from mammaliaforms in that the apex of the lesser trochanter is located well distal to that of the greater trochanter, and distal to the femoral head.

Further compelling, though circumstantial, evidence that CXPM C2019 2A235 represents a tritylodontid comes from the size and provenance of the specimen. Leaving aside tiny, problematic *Kunminia* (Young, 1947), the only synapsids that have been recovered from the Lufeng Formation are tritylodontids and mammaliaforms, and the known mammaliaforms are uniformly much smaller than CXPM C2019 2A235. By contrast, tritylodontids of varying sizes are a relatively abundant and diverse part of the vertebrate assemblage (Luo and Sun, 1994; Luo and Wu, 1994).

Most of the named tritylodontid taxa from the Lufeng Formation are known only from craniodental material, making morphological comparisons with CXPM C2019 2A235 impossible, and some of them may be synonymous. However, a femur of *Bienotherium yunnanense* from the Dull Purplish Beds described by Young (1947: fig. 20A) closely resembles the relatively undistorted right femur of CXPM C2019 2A235 in shape, and is only slightly smaller (72 mm in length, compared to 95 mm). Both *B. yunnanense* and the even smaller putative species *B. elegans* are known only from the Dull Purplish Beds. Luo and Wu (1994) referred to the stratigraphically low part of the Dark Red Beds from which CXPM C2019 2A235 was recovered as "stratum 5", and reported no described synapsids from this interval. Despite being from the Dark Red Beds, CXPM C2019 2A235 might represent a large, late-occurring individual of *B. yunnanense*, or of *B. elegans* if this taxon is valid. Similarly, CXPM C2019 2A235 might be a small individual of *B. magnum*, a very large putative species known from the overlying stratum 6 of the Dark Red Beds (Chow, 1962; Luo and Wu, 1994). However, the specimen is clearly too large to be referable to *B. minor* (Young, 1947) or *Oligokyphus lufengensis* (Luo and Sun, 1994) from the Dull Purplish Beds, or to *Yunnanodon* (Cui, 1976), *Dianzhongia* (Cui, 1981) or *Lufengia* (Chow and Hu, 1959) from stratum 6. It is also possible that CXPM C2019 2A235, evidently the first tritylodontid described from stratum 5, represents a new taxon.
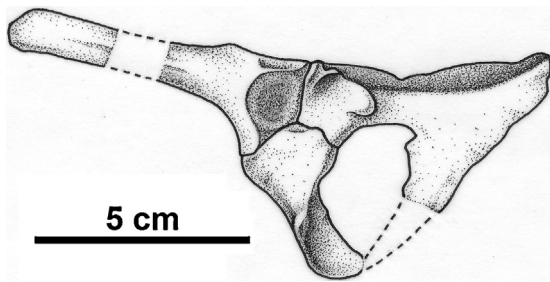
5 cm

5.2. Evolution of pelvic and femoral morphology in cynodonts

It is clear that the pelvis of CXPM C2019 2A235 (Fig. 5) is far closer to the mammaliaform than to the primitive cynodont condition, particularly in the narrow form of the iliac blade. The ridge-like dorsal and ventral edges of the anterior fragment of the right ilium are intact, and show unambiguously that this part of the ilium was not significantly wider than the posterior portion. The only indication of a posterior process is the slight convex-ity on the posterior part of the dorsal margin. In most other non-mammaliaform cynodonts in which the pelvis is known, excluding the probainognathians *Therioherpeton* and *Prozostrodon* (Bonaparte and Barberena, 2001) but including traversodontids (Bonaparte, 1963; Jenkins, 1970; Kammerer et al., 2008; Kemp, 1983; Liu, 2007; Liu and Powell, 2009), the ilium retains a dorsoventrally deeper blade and a larger posterior process. CXPM C2019 2A235 also resembles mammaliaforms such as *Morganucodon* (Jenkins and Parrington, 1976) in that the neck of the ischium is relatively long and narrow, although this feature is shared with *Therioherpeton* (Bonaparte and Barberena, 2001).

In general, tritylodontid pelvic morphology is rather poorly known, and it is not clear how widely the distinc-tive features seen in CXPM C2019 2A235 are shared with other taxa. As reconstructed by Kühne (1956), the iliac blade of *Oligokyphus* is at most slightly greater in pro-portional dorsoventral depth than that of CXPM C2019 2A235, despite being somewhat different in shape. The blade of an indeterminate tritylodontid ilium (MCZ 8835) from the Kayenta Formation also appears conspicuously narrow (Sues and Jenkins, 2006: fig. 5.16a, b), although this may be partly a result of damage. However, the ilium is very different in structure in some other tritylodon-tids, including *Kayentatherium* (Sues and Jenkins, 2006) and *Bienotheroides* (Maisch et al., 2004). The ilium is incom-pletely known in both taxa, but it is clear that the entire iliac blade is dorsoventrally deeper relative to both the length of the ilium and the depth of the posterior end of the bone than is the case in CXPM C2019 2A235. In both *Oligokyphus* (Kühne, 1956) and *Dinnebitodon* (Sues and Jenkins, 2006),

the neck of the ischium is broader than in CXPM C2019 2A235.

A recent analysis of tritylodontid inter-relationships based on a small number of characters (Watabe et al., 2007) agreed with older "hand-drawn" cladograms (Clark and Hopson, 1985; Sues, 1986) in placing *Oligokyphus* as a basal tritylodontid, *Bienotheroides* as a relatively derived one, and *Bienotherium* and *Kayentatherium* in intermediate positions. If CXPM C2019 2A235 is referable to *Bienotherium* or a more basal form, it is likely that the narrow type of ilium present in *Oligokyphus* and CXPM C2019 2A235 rep-resents the primitive tritylodontid condition whereas the broad type present in *Bienotheroides* and *Kayentatherium* is derived. This hypothesis regarding iliac evolution within Tritylodontidae will require further testing on the basis of both additional specimens with well-preserved pelves and further phylogenetic analyses, but CXPM C2019 2A235 corroborates the work of Kühne (1956) in conclusively demonstrating that a strikingly mammaliaform-like iliac morphology is characteristic of at least some tritylodontids.

The ilia of *Kayentatherium* and *Bienotheroides* are less clearly reminiscent of the mammaliaform condition, but the admittedly incomplete available information regarding the morphology of the ilium in these taxa provides no clear indication that the blade was as deep as in traver-sodontids or that a large posterodorsal process was present. The new evidence regarding tritylodontid pelvic structure from CXPM C2019 2A235 supports recent analyses (Abdala, 2007; Liu and Olsen, 2010) that have recovered trity-lodontids as close relatives of mammaliaforms. However, substantial character evidence conflicts with this hypothe-sis and instead favours the possibility that tritylodontids are specialised traversodontid cynodonts (Sues, 1985), a view supported by the analysis of Hopson and Kitching (2001).

5.3. The mechanism of femoral retraction in tritylodontids

An important functional shift in Permo-Triassic therap-sid evolution was the transition from a sprawling hindlimb posture to a more erect one (Blob, 2001; Gregory and Camp, 1918; Jenkins, 1971b; Kemp, 1980a, b; Romer, 1922), entailing a re-orientation of the femur from approx-imately horizontal during locomotion to steeply inclined. This transition was associated with the evolution of a mode of hip retraction driven partly by gluteus musculature (= M. iliofemoralis), extending from the ilium to the greater trochanter of the femur. As the iliac blade expanded ante-riorly and the greater trochanter became more prominent, the line of action of the gluteus came to pass posterior and dorsal to the centre of rotation (COR) of the hip joint. This provided the gluteus musculature with a short retractor moment arm, allowing it to contribute to propulsion dur-ing walking and running. By projecting dorsal to the COR, the greater trochanter was able to act as a retroarticular process with respect to the hip joint, making it possible for the gluteus musculature to retract rather than protract the femur despite originating anterior to the acetabulum.

This mechanism may have been incipiently present in traversodontids (Kemp, 1980b), in which the preacetabular
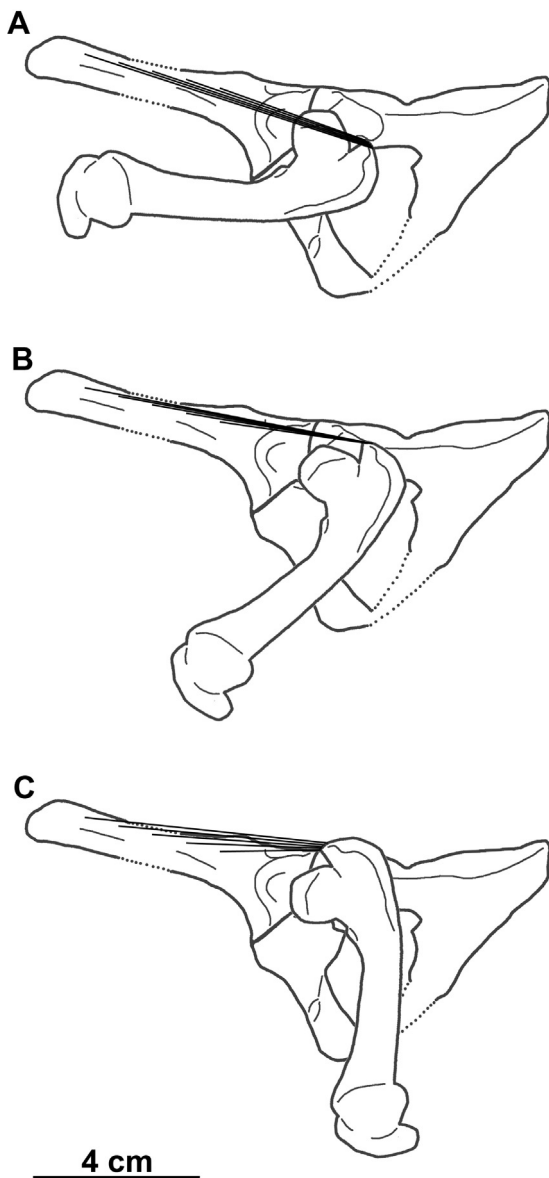
Fig. 6. Hypothetical mode of retraction of the hip joint during normal walking in the taxon represented by CXPM C2019 2A235, assuming a slightly simplified and idealised version of the pattern of hip kinematics described by Jenkins (1971a) in extant *Didelphis virginiana*. The femur is abducted about 40° from the sagittal plane throughout the stance phase of locomotion, and retracts through a 90° angle so that its orientation changes from anterolateral at the beginning of the stance phase (A) to ventrolateral at the end (C).

Fig. 6. Mode hypothétique de rétraction du « hip point » pendant la marche normale dans le taxon représenté par CXPM C2019 2A235, en assumant une version idéalisée et légèrement simplifiée du schéma de cinématique du « hip » décrit par Jenkins (1971a) dans *Didelphis virginiana* actuel. Le fémur est déplacé de 40° par rapport au plan sagittal pendant la phase de posture de locomotion, et se rétracte d'un angle de 90°, si bien que son orientation change d'antéro-latérale, au commencement, à ventro-latérale, à la fin de la phase de posture.

part of the ilium is anteriorly prominent. However, the ability of the gluteus musculature to act as a femoral retractor in traversodontids was clearly limited by the relatively distal position of the greater trochanter upon the femur. In CXPM C2019 2A235, by contrast, the apex of the greater trochanter projects almost as far proximally as does the femoral head. If the femur was held in a partially abducted position during locomotion, as is typical even in small extant non-cursorial mammals such as *Didelphis virginiana* (Jenkins, 1971a), the trochanter would actually have been situated farther dorsally than the femoral head in retracted femoral positions. Fig. 6 illustrates the potential for a degree of gluteus-driven retraction in CXPM C2019 2A235, assuming a pattern of hip kinematics similar to that described by Jenkins (1971a) for *D. virginiana*. At the beginning of the stance phase of a typical walking stride (Fig. 6A), the femur would have extended anterolaterally from the acetabulum, and the retractor moment arm of the gluteus musculature would have been minimal. In moderately (Fig. 6B) and highly (Fig. 6C) retracted positions attained later in the stance phase, however, the increasing elevation of the greater trochanter would have caused the gluteus musculature to move into a dorsal position relative to the hip COR and acquire a retractor moment arm.

The gluteus would evidently have contributed only to the later stages of hip retraction, as was probably also true in traversodontids (Kemp, 1980b) and is characteristic even of extant marsupials (Argot, 2002). As in these taxa, early retraction would have been driven by musculature originating on the ischium, which could have continued to play a role even as retraction continued and the gluteus musculature became engaged. Furthermore, the dorsoventral narrowness of the gluteus fossa of the iliac blade suggests that the gluteus musculature was limited in size, and therefore in ability to contribute forcefully to femoral retraction. In tritylodontids with broader ilia, such as *Kayentatherium* (Sues and Jenkins, 2006) and *Bienotheroides* (Maisch et al., 2004), the gluteus musculature was presumably larger and more important in locomotion.

The fact that the hip joint of tritylodontids was configured in a way that clearly facilitated involvement of the gluteus musculature in retraction underlines the fundamentally mammaliaform-like structure of the tritylodontid pelvis and femur. The presence of an anteriorly directed iliac blade and relatively high greater femoral trochanter in *Therioherpeton* (Bonaparte and Barberena, 2001) implies that gluteus-driven retraction would also have been feasible in this taxon, and the mechanism may have been widespread in probainognathians close to the origin of mammaliaforms.

Acknowledgements

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