

A juvenile anuran from the Lower Cretaceous Jiufotang Formation, Liaoning, China

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Abstract

A disarticulated partial skeleton of a juvenile anuran is reported from the Lower Cretaceous Jiufotang Formation, Jehol Group, in Liaoning Province, China. The individual has a premaxilla with a tall, wide bifurcate alary process and a well-defined palatine process; a maxilla without pre- or postorbital processes; and no contact between the squamosal and the maxilla. The centra of the presacral vertebrae are notochordal. The urostyle (with transverse processes) and the pelvic girdle are proportionally short, and the hind limbs are long (including proportionally long femur, tibiofibula, and proximal tarsals), and the tibiofibula is considerably longer than the femur. Comparison with other frogs suggests the hindlimb proportions of the Jiufotang frog are similar to those of anurans that are primarily saltatory. Although body proportions and other osteological features distinguish the Jiufotang anuran from other Jehol taxa, its immaturity and fragmentary preservation preclude detailed discussion of its systematic position. Nonetheless, this frog documents not only the first fossil anuran from the Aptian Jiufotang Formation of China, but also the most recent Mesozoic anuran currently known from China.

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1. Introduction

Rocks of the Lower Cretaceous Jehol Group are best exposed in northeastern China, especially in western Liaoning Province, northern Hebei Province, and southeastern Nei Mongol (Inner Mongolia) Autonomous Region. The Jehol Group contains a diverse vertebrate assemblage represented by exquisite specimens, including feathered dinosaurs, primitive birds and mammals, and early angiosperms (Chang et al., 2003). Amphibians also constitute an important part of the biota, with at least eight described species (Wang and Evans, 2006). These include five anuran taxa from Liaoning Province:

Callobatrachus sanyanensis Wang and Gao, 1999 and *Liaobatrachus grabau* Ji and Ji, 1998 from the locality of Sihetun; “*Dalianbatrachus mengi*” Gao and Liu, 2004 from Huangbanjigou (probably a junior synonym of *Mesophryne beipiaoensis*; Wang and Evans, 2006); *Mesophryne beipiaoensis* Gao and Wang, 2001 from Heitzigou (all Jianshangou Bed, lower Yixian Formation); and *Yizhoubatrachus macilentus* Gao and Chen, 2004 from Hejiaxin (Dawangzhangzi Bed, middle Yixian Formation). A froglet is also known from Daohugou in Nei Mongol, from a horizon that is certainly lower than those of the Yixian Formation, although the debate continues as to whether or not it should be referred to the Jehol Group (Wang, 2004). Most anuran taxa from the Jehol Group are represented by only a single specimen. The exception is *Mesophryne*, which, at a single site in Lujiatun (Liaoning, Lujiatun Bed, basal Yixian Formation), is represented by

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a few dozen individuals. There are also additional, as yet undescribed anurans from several localities. One of these forms the basis of the present paper.

2. Geology and material

The specimen described herein is in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing. The incomplete skeleton includes parts of the skull, axial skeleton, pelvis and hind limbs, but only the latter two regions are articulated. The frog was collected from a new locality near the village of Xierhuqiao, Yixian County, Liaoning. The fossil horizon consists of tuffaceous lacustrine mudstones, silty sandstones and sandstones, and can be referred to the Jiufotang Formation of the Jehol Group (Wang and Zhou, 2003). This is the horizon that overlies the Hauterivian–Barremian Yixian Formation and is considered to be of Aptian age (Wang and Zhou, 2003). The same locality has also yielded fossil remains of plants, insects, fish, turtles, and a caudipterid dinosaur, but none of these has been named formally. Although poorly preserved, this specimen documents not only the first fossil anuran from the Jiufotang Formation, but also the youngest record of Chinese Mesozoic anurans. It also deserves description with respect to its osteological characteristics, which provide further information on the early evolution of frogs in China.

3. Systematic palaeontology

Class: Amphibia Linnaeus, 1758
 Subclass: Lissamphibia Haeckel, 1866
 Superorder: Salientia Laurenti, 1768
 Order: Anura Rafinesque, 1815

Genus and species indet.

Figs. 1–3

General preservation conditions (Fig. 1). The specimen is an incomplete skeleton split into part (IVPP V13235A) and counterpart (IVPP V13235B) on a block of dark grey mudstone. The anterior parts of the body, including the skull and vertebral column, are scattered in a mass, and the forelimbs and most of the pectoral girdle are missing. The pelvic girdle and hind limbs are approximately in their natural positions, with the right leg slightly detached. The feet are preserved, but partially disarticulated, with the right one being relatively more complete than the left. The following bones are found on IVPP V13235A: two complete premaxillae; the anterior part of the left maxilla with teeth, and the broken posterior portion of the right; most of the right squamosal with only the otic ramus broken; a nearly complete right pterygoid and part of the left; the middle portion of the right frontoparietal; most of the dorsally exposed pelvic girdle including both ilia, a possible fragmented ischium; a nearly complete but dorsally compressed urostyle; two nearly complete femora and tibiofibulae; a nearly complete right tibiale and fibulare; scattered

fragments of vertebral centra and neural arches including the arches of the atlas and the sacrum; and metatarsal and phalangeal bones from both feet. There is also a broken piece of a possible dentary with an anterior tip and posterior portion, and a bone fragment that might belong to one of the angulosplenials.

IVPP V13235B preserves the following bones or their impressions: most of the left pterygoid; the main body of the right maxilla with teeth and the posterior ramus of the left; parts of both the right and the left frontoparietals, with detached centra imbedded on their ventral surfaces; a nearly complete compound right cleithrum and suprascapula; fragmented parts of both ilia exposed in ventral view; portions of both femora and fragments of both tibiofibulae; part of the right fibulare; and scattered metatarsals and phalanges of the left foot. On each slab there are also bone fragments that are not identifiable. The following descriptions are based on superimposed line drawings of each slab made to render the bones as complete as possible.

Description. The premaxillae (Fig. 2A, B) are entirely preserved on Block A. Each has a smooth anterior surface and a tall bifurcate alary process (= dorsal process, facial process) that curves posterolaterally. The taller ramus of the process is about two-thirds the width of the premaxilla (ca. 3 mm), giving the bone a narrow appearance in anterior view. A well-defined palatine process is present on the medial edge of the bone, and seems slightly shorter than the shorter ramus of the alary process. The lateral and medial ends of the partes dentalis of each premaxilla are truncate, with no complex articulation surface. There are eight and nine teeth preserved on the right and left premaxilla, respectively, but up to 15 tooth positions on each bone if the teeth were tightly spaced. All teeth are monocuspid, and of about equal height.

The maxilla (ca. 12 mm long; Fig. 2C–E) has a smooth, rectangular facial process (max. height ca. 2 mm) with no prominent pre- or postorbital processes. Its anterior end (for the lateral articulation with the premaxilla) is prominent, but as preserved is smooth and edentulous, as is the posterior end. Teeth occur on the anterior two-thirds of the bone. A well-developed palatal shelf (=lamina horizontalis; Sanchíz, 1998) is visible on the exposed medial sides of both maxillae on Block B. The maxillary teeth are tall and slender, with up to 45 tooth positions on each bone if the teeth were tightly spaced.

As preserved, the frontoparietals (total length ca. 7 mm) have smooth dorsal surfaces and a thickened and almost straight lateral edge, the middle portion of which rolls slightly ventrally to embrace the lateral wall of the braincase in life. The medial edge of each frontoparietal is concave anteriorly but not posteriorly, indicating that the two frontoparietals may have met in the posterior midline, but there was a large gap (fenestra) between the two bones anteriorly.

The squamosal is triradiate with a short, pointed zygomatic ramus, a long ventral ramus, and the broken base of the otic ramus. Because the zygomatic process is short, it is unlikely that it articulated with the maxilla in life. The ventral,

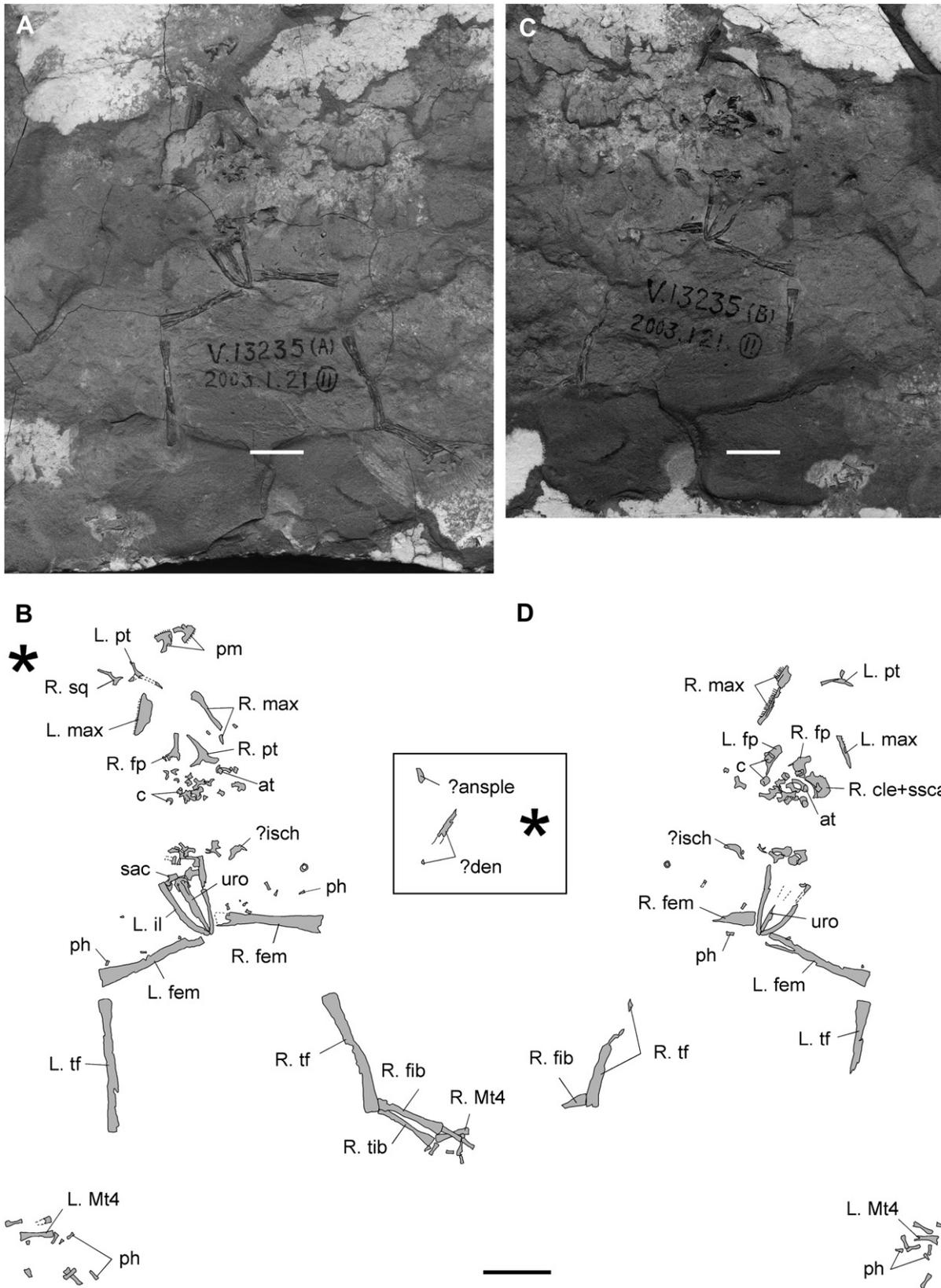


Fig. 1. Juvenile frog skeleton, IVPP V13235, from the Jiufotang Formation, Jehol Group, Xierhuqiao Village, Yixian County, Liaoning, China. A, B, IVPP V13235A, mainly dorsal view; C, D, IVPP V13235B, mainly ventral view. ansple, angulosplenial; at, atlas; c, centrum; cle + ssc, cleithrum + suprascapula; den, dentary; fem, femur; fib, fibulare; fp, frontoparietal; il, ilium; isch, ischium; L., left; Mt4, Metatarsal IV; max, maxilla; ph, phalanx; pm, premaxilla; pt, pterygoid; R., right; sac, sacrum; sq, squamosal; tf, tibiofibula; tib, tibiale; uro, urostyle. Scale bars represent 10 mm.

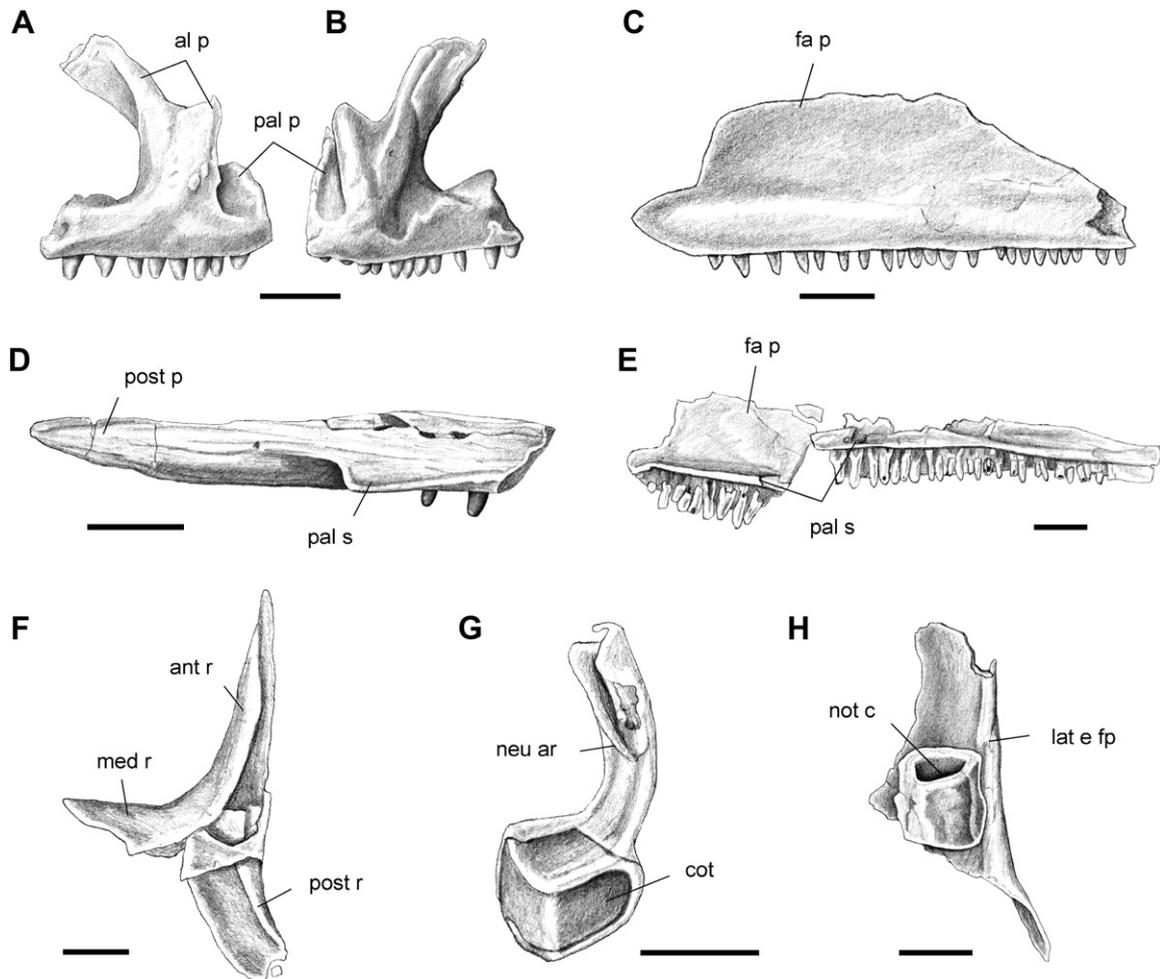


Fig. 2. Juvenile frog skeleton, IVPP V13235A, B; skeletal elements. A, B, right and left premaxilla respectively in anterodorsal view. C, D, anterior and posterior parts respectively of the left maxilla in lateral and medial views. E, posterior part of the right maxilla in medial view. F, right pterygoid in ventral view. G, left half of the atlas in anterior view. H, a detached centrum embedded in the ventral surface of a fragment of the left frontoparietal. al p, alary process; ant r, anterior ramus; cot, cotyle; fa p, facial process; lat e fp, lateral edge of frontoparietal; med r, medial ramus; neu ar, neural arch; not c, notochordal canal; pal s, palatal shelf; pal p, palatine process; post p, posterior process; post r, posterior ramus. All scale bars represent 1 mm.

quadrate, ramus is much longer (ca. 4 mm) than the zygomatic one by about four times. The otic ramus seems to be more robust than the zygomatic ramus.

The triradiate pterygoid (Fig. 2F) has a robust posterior ramus, a short medial ramus, and a long slender anterior ramus that extends anterolaterally to meet the maxilla.

A thin, elongated broken piece of bone on Block A may be part of a dentary. To its left is a thicker bone with depressions on its surface that might represent a fragment of an angulosplenic, the bone that forms the main body of the lower jaw with the dentary.

Elements of the vertebral column are scattered around the middle part of the block, making it difficult to identify each presacral. However, the atlas is characteristic in having large cotyles for articulation with the occipital condyles of the skull. The atlas of the Jiufotang anuran is split into two parts (one posterior to the right pterygoid on Block A, one posterior to the right cleithrum/suprascapula on Block B; Fig. 2G), and each part has a long curved neural arch perpendicular to a horizontally expanded base on which the cotyle is situated. The surface of the cotyle is coarse and flat, and is surrounded by

a thin rim of bone (Fig. 2G). This is almost certainly a juvenile condition, the articular surface being incompletely ossified in this animal and finished in cartilage. The surface has a square to ovoid outline but narrows medially, although it is not possible to say whether or not the articular surface continued onto the intercotylar area.

Other presacrals are preserved in three pieces, with the centra and two halves of the neural arch separated from one another. At least seven vertebral centra are preserved, mostly on Block B. They are short with a large notochordal canal surrounded by a thin cylinder of bone suggesting ectochordal/perichordal development (Fig. 2H). This resembles the notochordal condition (sensu Cannatella, 1985) of many basal frogs. The neural arches, as preserved, are short and wide with prominent zygapophyses. Their transverse processes range in length and width. These fragments of presacral vertebrae are arranged in a mass in the presacral part of the skeleton behind the skull elements. Whether free ribs were present or not cannot be determined owing to poor preservation of the region.

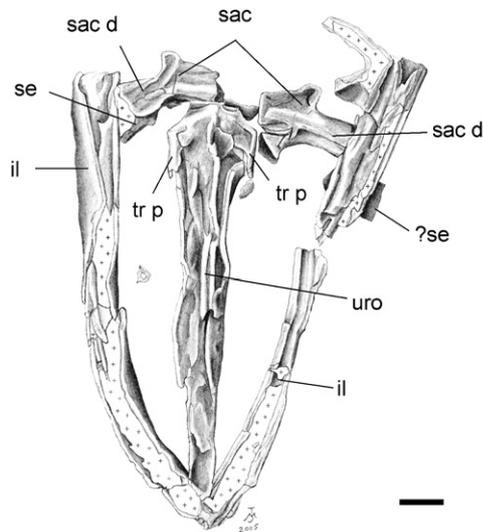


Fig. 3. The pelvic region of IVPP V13235A. il, ilium; sac, sacrum; sac d, sacral diapophysis; se, sesamoid; tr p, transverse process; uro, urostyle. Scale bar represents 1 mm.

The sacrum (Fig. 3) is preserved in halves, each with half of the neural arch, half of the centrum, and a sacral diapophysis. The neural arch is short and wide, and bears an anterior, but not a posterior, zygapophysis. The half centrum is partially obscured on each side by matrix and the urostyle but, from the structure of the urostyle (described below), bears a weak condyle. The sacral diapophysis is dorsoventrally thin, only slightly expanded at its distal end (visible on the more fully exposed left side), and bears a dorsal groove for the sacroiliac ligament (Emerson, 1982). Because both halves of the sacrum have been somewhat displaced in relation to the urostyle, their original orientation cannot be reconstructed. In any event, orientation can change intraspecifically (Báez and Nicole, 2004), as can the degree of flaring of the distal tips.

Below the distal end of the left sacral diapophysis is a strongly calcified or weakly ossified wedge of material (the colour and texture differ from that of fully ossified bones on this specimen). A similar structure lies behind the diapophysis on the right side, beneath the iliac shaft. These are tentatively identified as the sesamoid bones associated with the sacroiliac ligaments (Emerson, 1982). Emerson described three conditions of the sacroiliac joint: Type I in which the sacral diapophyses were greatly expanded anteroposteriorly with a hooklike sesamoid within a broad sacroiliac ligament; Type IIA with an only slightly expanded sacral diapophysis and a wedge-shaped sesamoid with a long and relatively broad sacroiliac ligament; and Type IIB with a rodlike sacral diapophysis, rounded in cross-section, associated with an ovoid sesamoid and a narrow, short ligament. Although the sesamoid in the Jiufotang frog seems to be under the diapophysis rather than at its tip, the structure of both diapophyses and sesamoids matches Emerson's Type IIA most closely. This type occurs in Discoglossidae but is also the most common type in neobatrachian frogs (Emerson, 1982).

Though compressed and crushed, the robust urostyle (ca. 9 mm long) appears to have a low dorsal crest, at least in its

anterior part (Fig. 3). Behind this the crest seems to be double, but this may mean that the urostyle arch has not fully developed in this region. Anteriorly, the urostyle is bicotylar, although only the right cotyle has been exposed (the left is under the partial sacral of that side). Anterolaterally, the urostyle bears paired transverse processes. These extend first laterally then posteriorly to lie parallel to the shaft of the urostyle. Dorsomedial to the base of each is a small accessory tubercle.

Only one pectoral element has been recognised with any confidence and this is the right cleithrum/suprascapula complex. This bone (ca. 4 mm wide) is blade-shaped, with a thickened and arched anterior edge. Other fragmentary elements in the same region could be parts of the more ventral pectoral elements but they cannot be identified with any confidence. No elements of the forelimbs are preserved, except for some phalanges in the anterior half of the specimen that might belong to either of the two hands.

Both ilia (ca. 11 mm long; Fig. 3) are preserved but they have been dorsoventrally crushed and do not provide any details of their structure. The left bone seems also to have been rotated slightly, suggesting that the interiliac joint may not have fused. The ilia underlie the sacral diapophysis and would have been suspended from them by the sacroiliac ligament described above. The ischium is not in situ, but may be represented by a semicircle of bone that is split between the two blocks and lies anterior and to the right of the pelvis on the main block.

The frog has long legs in relation to its body proportions (using maxillary length as a substitute for skull length). The tibiofibula (20 mm long) is considerably longer than the femur (16.5 mm), and the proximal tarsals are also long (fibulare 10.2 mm, tibiale 9.4 mm). Metatarsal IV (5 mm long) has similar proportions to those of other Mesozoic frogs from China (see Table 1 and discussion below).

4. Discussion

4.1. Developmental stage

Anuran development has been well studied with the recognition of a fairly consistent series of osteological changes leading up to metamorphosis, and then a long postmetamorphic period involving growth and more minor changes in bone shape (e.g., Trueb, 1985; Wiens, 1989; Pügener and Maglia, 1997; Wild, 1997, 1999; Maglia and Pügener, 1998; Sheil, 1999; Trueb et al., 2000). These osteological changes have also been examined in some fossil frog taxa for which a large enough sample is known (e.g., Roček, 2003; Báez and Nicole, 2004).

The Jiufotang frog is small compared to other Mesozoic anurans from China (Table 1), and shows some characteristics that are usually associated with immaturity: weakly ossified vertebrae in which the neural arches are incomplete across the midline and unfused to the centra; a large frontoparietal fenestra; separate tibiale and fibulare; no ossified tarsals (although these only ossify late in maturity, if at all); and

probably incomplete fusion of the ilia at their symphysis (because the left seems to have rotated slightly around its long axis). In contrast, the premaxillae and maxillae are complete and bear teeth; the squamosals and pterygoids are fully formed with ossified rami; the sacro-urostylar and sacroiliac joints are formed; the urostyle is well ossified and the hypochord has already been incorporated into the bone; and the sacroiliac sesamoid seems to be either strongly calcified or partly ossified.

Based on developmental studies on the cranial ossification sequences of modern frogs (e.g., Hanken and Hall, 1984; Wiens, 1989; Púgener and Maglia, 1997; Wang, 1997; Trueb et al., 2000), the frontoparietal bones are always among the first bones to begin to ossify in the skull. The pterygoids and squamosals appear relatively late. In the discoglossid *Bombina orientalis*, both bones begin ossification after metamorphosis (Hanken and Hall, 1984; Maglia and Púgener, 1998); in *Discoglossus*, the squamosal first appears before metamorphosis and the pterygoid after (Púgener and Maglia, 1997); in *Spea*, *Rhinophrynus*, *Xenopus* and *Pipa*, both bones first appear before metamorphosis (Trueb, 1985; Wiens, 1989; Trueb et al., 2000). Maxillary teeth do not erupt until the end of metamorphosis (e.g., Púgener and Maglia, 1997; Yeh, 2001; Báez and Nicole, 2004). In the Jiufotang anuran, the pterygoid and squamosal bones are not only present but also appear fully formed (with their rami), and the maxillary and premaxillary teeth have developed. Together, these features suggest that the Jiufotang anuran is postmetamorphic. This is further supported by the fully developed urostyle, well-ossified ilia, fully fused tibia and fibula, and the ossification of all metatarsals and phalanges.

However, vertebral development in the Jiufotang anuran is incomplete. The transverse processes are strongly developed and fused to the neural arch laminae, but the latter are not fused across the midline. Ventrally, the centra are represented by thin cylinders of bone but these are free of the arches. The atlantal and sacral halves remain separate. In living anurans, the vertebral parts (both halves of the neural arch and the centrum) typically appear and then fuse (neural arch halves to centra and then neural arch laminae across the dorsal midline to roof the neural canal) in an anterior–posterior sequence, although the precise timing of these events varies interspecifically (Wiens, 1989; Blanco and Sanchíz, 2000; Trueb et al., 2000; Zbyněk Roček, pers. comm. 2005). In the pelobatid *Spea* (Wiens, 1989), the arches fuse with the centra and the neural arch laminae fuse across the midline before metamorphosis, but the transverse processes ossify after the laminae and neurocentral sutures have fused. In the leptodactylid *Chacophrys* (Wild, 1999), the sacral centrum is encircled in bone by the end of metamorphosis but presacral neural arches fuse postmetamorphically. In the hyperossified leptodactylid *Ceratophrys cornuta* (Wild, 1997), the sacrum is completed postmetamorphosis, and the adult vertebral condition is not reached until the subadult stage. In *Pipa* (Trueb et al., 2000) the vertebral column is not fully ossified until well after metamorphosis.

Thus, most evidence suggests that the Jiufotang anuran is a young postmetamorphic individual (large frontoparietal fenestra, unossified epiphyses, unfused tibiae and fibulae,

incomplete ossification of the vertebral column). The only feature in conflict with this assessment is the strong calcification or ossification of the sacroiliac sesamoids, a condition typically found only in mature or hyperossified frogs (Z. Roček, pers. comm. 2005). However, few authors mention this structure in developmental studies and the variability in its ossification pattern remains unknown. Its development is likely to reflect that of the associated sacrum and pelvis, and these are already robust in the Jiufotang anuran.

4.2. Comparison with other Jehol anurans of China

The Jiufotang anuran from Liaoning shows the following features: (1) maxillae with no pre- or postorbital processes and no contact with squamosal; (2) large frontoparietal fenestra; (3) lack of dermal sculpture on skull bones; (4) presacral vertebrae with notochordal centra; (5) slightly expanded sacral diapophyses; (6) premaxillae with high, wide bifurcate alary process and well-defined palatine process; (7) large atlantal cotyles; (8) well-calcified sesamoid bones associated with Type IIA sacroiliac joint; (9) bicondylar sacro-urostylar articulation; (10) urostyle with distinct, posteriorly angled, transverse processes; (11) proportionally long femora, tibiofibulae and proximal tarsals, with tibiofibulae considerably longer than femora (Fig. 1); (12) proportionally short pelvis. Of these features, 1–5 are subject to change through ontogeny, but 6–12 may prove useful for comparison.

To date, five monotypic anuran genera (*Liaobatrachus grabau* Ji and Ji, 1998, *Callobatrachus sanyanensis* Wang and Gao, 1999, *Mesophryne beipiaoensis* Gao and Wang, 2001, *Dalianbatrachus mengi* Gao and Liu, 2004, and *Yizhoubatrachus macilentus* Gao and Chen, 2004) have been described from the Yixian Formation of the Jehol Group, but *Dalianbatrachus mengi* is almost certainly a junior synonym of *Mesophryne beipiaoensis* (Wang and Evans, 2006). In general appearance, the new Jiufotang frog differs from the anurans from the Yixian Formation in having proportionally longer hind limbs and a shorter pelvis. Table 1 shows comparative data. In order to minimize the possible influence of ontogenetic variation, a juvenile specimen (IVPP V12541) of *Yizhoubatrachus macilentus* was used in addition to the larger holotype, but other taxa lack specimens of different age. We estimated the maximum SPL of our new frog as 38 mm, but it could have been smaller than this. The first groups of proportions compare the lengths of the leg bones against SPL (Lines 9–12 in Table 1). These suggest that the new frog has a proportionally longer femur (Fem), tibiofibula (Tf) and fibulare (Fib) than the other Chinese taxa. As Metatarsal IV (Mt4) is of similar relative length in all specimens (including the mature and immature *Yizhoubatrachus*), it was used as a standard against which to examine the proportions of the urostyle and ilium. The results suggest that the new frog has proportionally the shortest urostyle (Uro) and ilium (Il) of the Chinese taxa (Lines 13 and 14), but has a tibiofibula that is considerably longer than the femur, and proportionally more elongate proximal tarsal segments (Lines 15 and 16).

Table 1
Measurements and selected proportions of Chinese Mesozoic anurans (in mm); *represents a maximum estimate

		<i>Callobatrachus sanyanensis</i>	<i>Liaobatrachus grabaui</i>	<i>Mesophryne beipiaoensis</i>	“ <i>Dalianbatrachus mengi</i> ”	<i>Yizhoubatrachus macilentus</i>	<i>Y. m.</i> V12541	New frog V13235
1	SPL	93	70	70	77*	62*	41*	38*
2	Femur	34.0	29.0	30.0	32.0	24.0	15.2	16.5
3	Tibiofibula	35.0	29.0	29.0	32.0	22.0	14.5	20.0
4	Fibulare	20.0	16.0	17.4	19.0	12.5	7.8	10.2
5	Ilium	31.0	22.0	26.0	27.0	19.6	14.8	11.1
6	Urostyle	27.0	22.0	21.0	26.0	19.0	?	9.1
7	Maxilla	20.4	?	18.0	17.0	16.1	12.3	11.5
8	Metatarsal IV	10.8	9.6	10.0	10.0	7.6	4.6	5.0
9	Fem/SPL	0.37	0.41	0.43	0.42	0.39	0.37	0.43
10	Tf/SPL	0.38	0.41	0.41	0.42	0.35	0.35	0.53
11	Fib/SPL	0.22	0.23	0.25	0.25	0.20	0.19	0.27
12	Mt4/SPL	0.12	0.14	0.14	0.13	0.12	0.11	0.13
13	Uro/Mt4	2.50	2.29	2.10	2.60	2.50	?	1.82
14	Il/Mt4	2.87	2.29	2.60	2.70	2.58	3.22	2.22
15	Tf/Fem	1.03	1.00	0.97	1.00	0.92	0.95	1.21
16	Fib/Fem	0.59	0.55	0.58	0.59	0.52	0.51	0.62

Measurements for the first five taxa are taken from the holotype specimen, with an extra juvenile specimen representing *Yizhoubatrachus*. See text for further explanation.

With respect to non-metric characters, the Jiufotang anuran differs from *Yizhoubatrachus* in the absence of a preorbital process on the maxilla and the presence of a wide (rather than narrow) alary process on the premaxilla; and it differs from *Mesophryne* in the lack of a postorbital process on the maxilla and of a squamosal/maxillary contact. However, at least some of these characters could be influenced by ontogeny.

4.3. Phylogenetic position and lifestyle

Crown-group anurans have been recorded from a range of Jurassic and Cretaceous localities around the world, although relatively few of these specimens are articulated (see Sanchíz, 1998 for a fairly comprehensive listing). They include basal taxa (e.g., the Jurassic *Prosalirus* Shubin and Jenkins, 1995, *Vieraella* and *Notobatrachus* Báez and Basso, 1996), early discoglossoids (e.g., the Middle Jurassic–Early Cretaceous European *Eodiscoglossus* Hecht, 1970) and basal pipoids (e.g., *Cordicephalus*, *Shomronella*, *Thoraciliacus*; Nevo, 1968; Estes et al., 1978; Trueb, 1999; Trueb and Báez, 2006).

The fragmentary nature and immaturity of the Jiufotang specimen limit comparisons and preclude any definitive discussion of its phylogenetic position. Two features suggest this was a relatively primitive frog: the notochordal vertebral centra and the retention of transverse processes on the urostyle. A bicondylar sacro-coccygeal articulation is found in a wide range of frogs, but is more derived than the planar articulation of basal taxa like *Prosalirus* (Jenkins and Shubin, 1998). The pattern of sacroiliac suspension is closest to Emerson’s (1982) Type IIA, found in discoglossoids and many neobatrachians. The proportionally longer hind limbs are suggestive of many neobatrachian frogs, but are not exclusive to these and are matched by some discoglossoids.

As a preliminary exploration of the possible significance of its hind limb proportions, we compared the Jiufotang frog to

other living and fossil taxa using a ternary diagram (Fig. 4). Our methodology follows that of Gatesy and Middleton (1997) and is not elaborated here to save space.

The Early Triassic dissorhoid *Micropholis* (Schoch and Rubidge, 2005), one of the two outgroups of this analysis, has a proportionally long femur, short tibiofibula and small fibulare, the general morphology of primitive tetrapods. It plots in cell 1, away from anurans (cells 3–8). Close to it (in cell 2) is the second outgroup, the Lower Triassic stem-frog *Triadobatrachus* (Rage and Roček, 1989), whereas the Middle–Upper Jurassic anuran *Notobatrachus* (Báez and Basso, 1996) plots in cell 4, closer to other frogs, despite the long femur. The Lower Jurassic *Prosalirus* (Shubin and Jenkins, 1995) plots in cell 8, near the centre of the anuran cluster, suggesting that it has generalized anuran leg proportions.

Among living frogs, the basal *Ascaphus* has a proportionally short femur and a long fibulare and plots close to the main anuran cluster in cell 7. *Leiopelma* is more problematic in that although the smaller of two specimens plots within the main cluster (in cell 8), its larger conspecific (in the lower right corner of cell 7) has a proportionally longer tibiofibula and fibulare in relation to the femur.

The discoglossids, including the Middle Jurassic–Early Cretaceous *Eodiscoglossus*, the Early Cretaceous *Wealdenbatrachus*, and the Palaeogene *Latonia* (Sanchíz, 1998), and the living bombinatorids have a relatively short femur and group mainly in the lower three cells (6–8), but *Barbourula* is aberrant (left edge of cell 3) in having an unusually short fibulare and relatively long femur and long tibiofibula. Among “mesobatrachians”, the pelobatids have a proportionally short fibulare and long femur (cells 3, 4 and 6), but the pelodytids are more generalised (cells 7 and 8). Among fossil pipoids, palaeobatrachids plot with pelobatids, whereas other taxa (e.g., *Cordicephalus*, *Thoraciliacus*; Nevo, 1968; Trueb, 1999) generally plot in cells 3, 4, 5 and 8, and thus overlap extant swimming

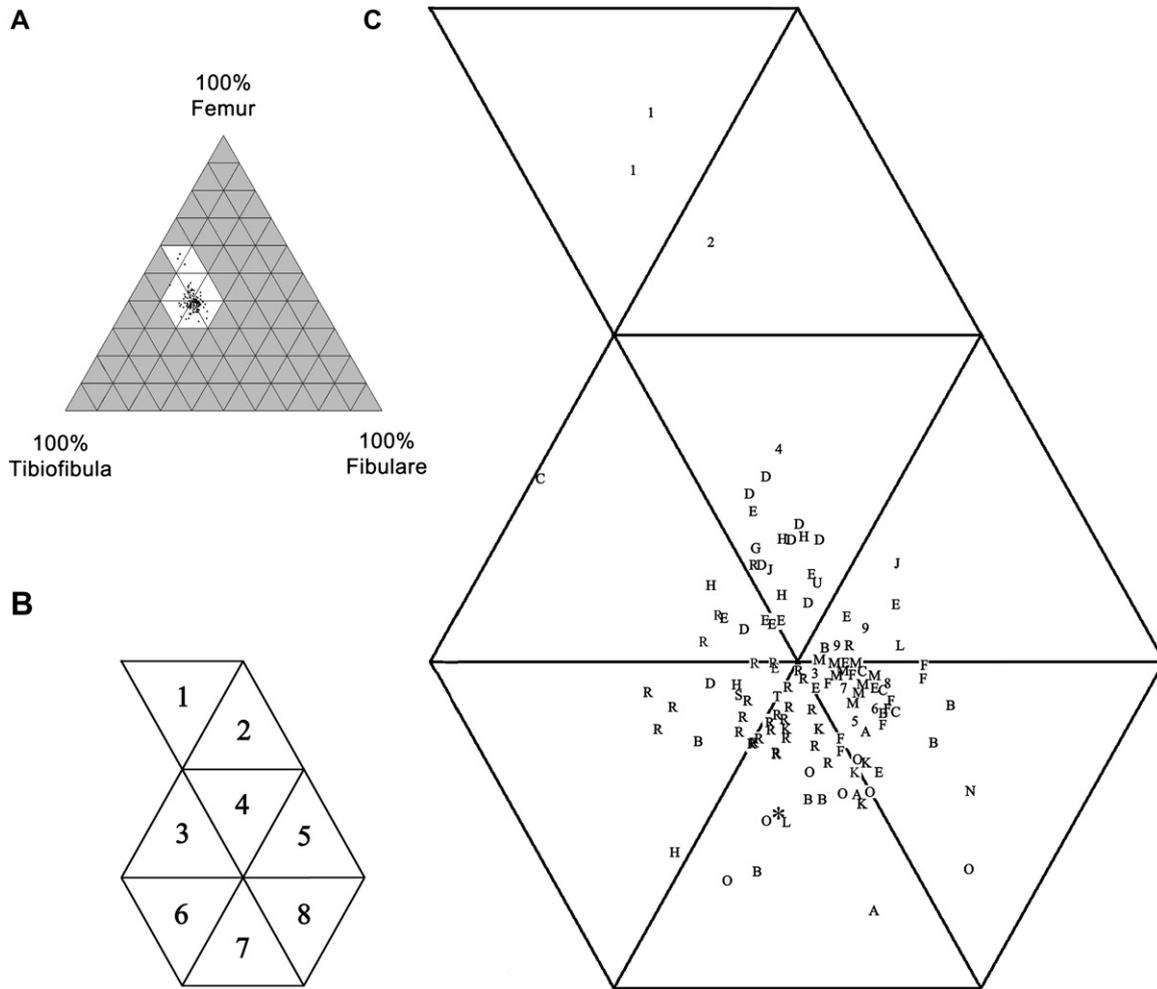


Fig. 4. Anuran and outgroup hindlimb proportions in ternary morphospace. Cells containing data are highlighted (in 4A, showing that frogs occupy only a small fraction of potential leg designs), labelled (in 4B), and enlarged to show detail (4C). Each abbreviation (in 4C) represents data from a single specimen. The new frog is shown with an asterisk (*). See text for further explanations. Abbreviations in 4C: 1, *Micropholis* (outgroup 1); 2, *Triadobatrachus* (outgroup 2); 3, *Prosalirus*; 4, *Notobatrachus*; 5, *Callobatrachus*; 6, “*Dalianbatrachus*”; 7, *Liaobatrachus*; 8, *Mesophryne*; 9, *Yizhoubatrachus*; A, Leiopelmatidae; B, Discoglossidae; C, Bombinatoridae; D, Palaeobatrachidae; E, other fossil pipoids; F, living pipids; G, Rhinophrynidae; H, Pelobatidae; J, Scaphiropodidae; K, Pelodytidae; L, Leptodactylidae; M, Bufonidae; N, Brachycephalidae; O, Hylidae; R, Ranidae; S, *Trichobatrachus*; T, Rhacophoridae; U, Microhylidae. Supplementary information refers to website: http://www.anat.ucl.ac.uk/research/evans/frogleg_appendix.pdf.

pipids (mainly cell 8), with femora and tibiofibulae of similar length.

Neobatrachian frogs vary in their limb proportions depending on whether they are predominantly walkers or jumpers. Most *Bufo* (predominantly walking) are tightly clustered in cell 8 with a near-equally proportioned femur and tibiofibula, whereas saltatory ranids and hylids have proportionally longer tibiofibulae (mainly in cells 3, 6 and 7). The two available leptodactylid taxa plot in cells 5 and 7. The fibulare is of similar length proportion in both, but whereas the femur is the longer element in *Ceratophrys* (a walker), it is the tibiofibula in *Leptodactylus* (a jumper).

In summary, and allowing for the limited sample, most of the anuran taxa plotted cluster phylogenetically but there is also a functional signal in that primarily saltatory taxa (e.g., ranids, hylids) plot mainly in cells 3, 6 and 7, whereas walkers (e.g., bufonids) and swimmers (e.g., pipids) plot in cells 5 and 8.

The previously described Jehol frogs form a relatively tight cluster in cells 5 and 8 (with walkers and swimmers). The basal discoglossid *Callobatrachus* (Wang and Gao, 1999; Wang, 2004), in particular, has leg proportions similar to those of the living *Alytes*. In contrast, the Jiufotang anuran has a relatively longer tibiofibula and fibulare and plots in cell 7, away from both the centre of the anuran cluster and from other Jehol frogs. It plots close to *Leptodactylus*, but also within the range of hylids and discoglossids (the closest discoglossids being *Latonia* and *Discoglossus*). It was therefore almost certainly saltatory.

Ideally, the comparison of the Jiufotang anuran would have been made with animals of similar developmental stage. Where possible we included data from immature anurans (e.g., of *Leiopelma*, *Eodiscoglossus*, *Palaeobatrachus*, *Eopelobates*, and *Xenopus*), but a broad spread of taxa was not available. We found some evidence that limb proportions change with age because the few small individuals in our study

generally plotted away from the adults. However, there was no common trend. In some taxa the contribution of the tibiofibula to overall leg length decreased with maturity (*Eopelobates*, *Palaeobatrachus*) whereas in others it increased (*Eodiscoglossus*, *Leiopelma*, *Xenopus*). In *Rana temporaria* the length of the fibulare increases at the expense of femoral length. Thus we are unable to predict whether or not the limb proportions of the Jiufotang frog would have changed with maturity, but the conclusion that it was primarily saltatory is unaffected.

4.4. Other implications

Until recently, there was a large hiatus between the Triassic temnospondyl amphibians of China and the Cenozoic (middle Miocene) frogs and salamanders from Shandong Province. The Yixian Formation (Hauterivian–Barremian; Wang and Zhou, 2003) amphibians have helped to fill this gap and the frog described herein extends the record a little further (Aptian; Wang and Zhou, 2003). As yet no Late Cretaceous frogs have been found in China although they are known from Mongolia and Central Asia (e.g., Roček and Nessov, 1993).

5. Conclusions

Based on developmental comparisons, the fossil frog from the Jiufotang Formation (Aptian, Early Cretaceous) in Liaoning, China, represents a postmetamorphic juvenile, probably far from maturity. The notochordal centra and the retention of urostylar transverse processes suggest that it belongs to a primitive lineage. On the basis of limb proportions, this frog was probably primarily saltatory (like many discoglossids and neobatrachians) although it has a generalized sacroiliac morphology (Type IIA; Emerson, 1982). Amongst Jehol frogs, limb and pelvic proportions, supported by premaxillary and maxillary characters, seem to distinguish the Jiufotang frog from older taxa encountered in the Yixian Formation. Less definitively, this combination of characters also separates the Jiufotang frog from non-Chinese taxa. However, this is based on very few robust characters and is complicated by the immaturity and fragmentary preservation of the specimen.

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