

THE EARLY TRIASSIC STEM-FROG *CZATKOBATRACHUS* FROM POLAND

SUSAN E. EVANS and MAGDALENA BORSUK-BIAŁYNICKA

Evans, S.E. and Borsuk-Białynicka, M. 2009. The Early Triassic stem-frog *Czatkobatrachus* from Poland. *Palaeontologica Polonica* **65**, 79–105.

Czatkobatrachus polonicus Evans et Borsuk-Białynicka, 1998 is a stem-frog from the Early Triassic karst locality of Czatkowice 1 (southern Poland). It was described and named on the basis of a small collection of vertebrae, ilia, and forelimb bones, with subsequent description of the scapulocoracoid. Further skeletal elements have now been recovered. Here we present a complete overview of the available material of *Czatkobatrachus*, give an extended diagnosis of the genus, and provide an assessment of its relevance to our understanding of the early stages of salientian evolution. *Czatkobatrachus* has an anuran type ilium, a urodelan-like scapulocoracoid, unfused epipodials, a moderately shortened presacral column, and a very short tail of separate caudal vertebrae. The strongly ossified ends of the proximal limb bones suggest terrestrial life. The skull is unknown.

Key words: Stem-frogs, Anura, Salientia, Lissamphibia, Triassic.

Susan E. Evans [ucgasue@ucl.ac.uk], Research Department of Cell and Developmental Biology, UCL, University College London, Gower Street, London, WC1E 6BT, UK.

Magdalena Borsuk-Białynicka [borsuk.b@twarda.pan.pl], Instytut Paleobiologii PAN, Twarda 51/55, 00-818 Warszawa, Poland.

Received 17 November 2006, accepted 15 September 2008



INTRODUCTION

Czatkobatrachus polonicus Evans *et* Borsuk-Białynicka, 1998 is a stem-frog described from the Early Triassic microvertebrate locality of Czatkowice 1 in southern Poland (Paszkowski and Wieczorek 1982). It is the earliest lissamphibian known from Northern Pangaea, and only the second recovered from Triassic deposits, the roughly contemporaneous salientian *Triadobatrachus massinoti* (Piveteau 1936) from Madagascar being the first. To date, only a few postcranial bones of *Czatkobatrachus* (ilia, distal humeri, ulnae, vertebrae, scapulocoracoid) have been described (Evans and Borsuk-Białynicka 1998; Borsuk-Białynicka *et al.* 1999; Borsuk-Białynicka and Evans 2002). Incomplete as they are, the remains of *Czatkobatrachus* are generally similar to those of *Triadobatrachus* but are significantly smaller and appear more derived (or at least better ossified) in rib, vertebral structure and limb morphology.

The objective of the present paper is to describe newly discovered material of *Czatkobatrachus polonicus*, as well as give a more detailed description of skeletal elements only briefly discussed in the original paper, most notably parts of the vertebral column and limbs.

Institutional abbreviations. — MNHN, Museum National d'Histoire Naturelle, Paris, France; UCMP, University of California, Museum of Paleontology, Berkeley, USA; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Acknowledgments. — The authors are indebted to the team of the Institute of Geology, Jagiellonian University, Kraków, and particularly Józef Wieczorek and Mariusz Paszkowski who discovered, and generously transferred the bone breccia from Czatkowice 1 to the Museum of the Earth and the Institute of Paleobiology, Polish Academy of Sciences, Warsaw. Our thanks are due also to the late Halszka Osmolska (Institute of Paleobiology) and Teresa Maryańska (Museum of the Earth) for access to materials in their care; Jean-Claude Rage (Museum d'Histoire Naturelle, Paris), for access to high-resolution casts of the holotype of *Triadobatrachus massinoti*; A.G. Jacobson (University of Texas, Austin) for information on head development in amphibians; Borja Sanchez (Natural History Museum, Madrid) for information on vertebral development; and Carl Gans (University of Texas, Austin) and Farish Jenkins Jr (Harvard University), for discussions on the functional morphology of early frogs. We are grateful to the referees: F. Jenkins Jr and Zbyněk Roček (Charles University Prague). Critical comments of the latter helped us to improve the final version of the manuscript. Ewa Hara (Institute of Paleobiology) carried out the acid preparation of the Czatkowice 1 breccia; Cyprian Kulicki (Institute of Paleobiology) performed the scanning electron microscope photography.

GEOLOGICAL SETTING

The Triassic deposits filling the karst fissures developed in the Early Carboniferous limestones at Czatkowice 1 (southern Poland) were discovered by a team from the Jagiellonian University, Kraków, and were first described by Paszkowski and Wieczorek (1982). The material described herein comes from the largest of the karst fissures called Czatkowice 1. This material has been dated as probably Early Olenekian in age (Borsuk-Białynicka *et al.* 2003). A more detailed account of the geology may be found elsewhere in this volume (Cook and Trueman 2009; Paszkowski 2009).

MATERIAL AND METHODS

The bone material from the karst deposits of Czatkowice 1 consists of the completely disarticulated skeletons of several small vertebrates, most of them reptiles (Borsuk-Białynicka *et al.* 1999). Salientian postcranial bones are easily discriminated from reptilian ones by their anatomical structure, further supported by their size range (all but one of the Czatkowice 1 reptiles are larger as adults); their frequency (*Czatkobatrachus* remains are comparatively scarce); and the type of bone tissue in terms of surface appearance. The skeletal ele-

ments were compared with those of both extant and fossil frogs, particularly the earliest known Jurassic frogs: *Notobatrachus degiustoi* Reig, 1955 and *Vieraella herbsti* Reig, 1961 (Báez and Basso 1996), and *Prosalirus bitis* Shubin *et* Jenkins, 1995 (Jenkins and Shubin 1998). Most informative was a comparison with the Early Triassic Malagasy basal salientian *Triadobatrachus massinoti* (Piveteau, 1936) (Rage and Roček 1989; Roček and Rage 2000).

The puzzling absence of skull bones cannot be explained as the effect of chemical preparation in acetic acid, because equally small and fine reptilian elements are perfectly preserved. It may be partly an artifact of the relative scarcity of *Czatkobatrachus* remains overall. Although all crown-group frogs have lost the lower dentition, most basal taxa, as well as many neobatrachians, retain teeth in the maxilla, and these toothed elements are both common and distinctive in microvertebrate assemblages, even when fragmented. Nonetheless, despite a careful scrutiny of all toothed elements from Czatkowice 1, none are attributable to *Czatkobatrachus*. Rage and Roček (1989) found no trace of teeth in *Triadobatrachus*, but only the most posterior part of the maxilla is preserved, and no teeth are expected in this part (Roček personal communication 2007).

The scanning electron microscope was used extensively for illustrations and studies of surface texture. Terminology used follows Sanchiz (1998).

PHYLOGENETIC BACKGROUND

No-one has ever seriously doubted the monophyly of Anura, and although the status of *Triadobatrachus* as a stem-frog has occasionally been challenged (*e.g.*, Hecht 1960), most authors accept also the monophyly of Salientia, including *Triadobatrachus*, and now *Czatkobatrachus*, along with crown-group Anura (*e.g.*, Duellman and Trueb 1986; Milner 1988; Rage and Roček 1989; Sanchiz 1999; Roček 2000; Carroll 2007; Anderson *et al.* 2008). There is also a general consensus that Salientia were derived from temnospondyl, or more precisely dissorophoid, ancestors (Bolt 1969, 1977, 1991; Bolt and Lombard 1985; Daly 1994; Milner 1988, 1990, 1993; Carroll 1999; but see Laurin and Reisz 1997; Laurin *et al.* 2000; Yates and Warren 2000; Anderson *et al.* 2008).

The monophyly of the Lissamphibia as a whole (Salientia, Caudata and Gymnophiona) was proposed by Parsons and Williams (1962, 1963), Szarski (1962), and Bolt (1969), and has been supported by many authors (*e.g.*, Milner 1988; Rage and Janvier 1982; Gauthier *et al.* 1989; Trueb and Cloutier 1991; Cannatella and Hillis 1993; Ford and Cannatella 1993; McGowan and Evans 1995; Gardner 2000). Others have rejected or questioned lissamphibian monophyly (*e.g.*, Shishkin 1973; Bolt and Lombard 1985; Carroll and Holmes 1980; Carroll 1999; Carroll *et al.* 1999), and the debate is ongoing. The recovery and description of early representatives of major lissamphibian lineages are clearly critical to the discussion of their ancestry.

SYSTEMATIC PALEONTOLOGY

Class **Amphibia** Linné, 1758

Order **Salientia** Laurenti, 1768

Family uncertain

Genus ***Czatkobatrachus*** Evans *et* Borsuk-Białynicka, 1998

Czatkobatrachus polonicus Evans *et* Borsuk-Białynicka, 1998

Holotype: ZPAL Ab IV/7, a right ilium.

Type horizon and locality: Olenekian karst deposits at Czatkowice Quarry (locality 1), Kraków region, Poland.

Material. — 76 catalogued specimens, including 15 presacral vertebrae, 2 sacral vertebrae, 9 scapulo-coracoids, 11 humeri, 2 ulnae, 19 ilia, 5 femora.

Emended generic and specific diagnosis. — Small stem-frog (less than 50 mm snout-vent length) that resembles *Triadobatrachus* and all other salientians in having an anteriorly extended iliac shaft. It resembles

Triadobatrachus and differs from crown-group anurans in retaining relatively long neural arches, unfused epipodials, a series of unfused caudal vertebrae instead of an urostyle (Lynch 1973; Trueb 1973; Sanchiz 1998), a scapulocoracoid that is a single ossification, and an ilium with very strong dorsal prominence and a slender elongate shaft, rounded in cross-section. It differs from *Triadobatrachus* in having a long slender scapular blade (short and broad in *Triadobatrachus*), in having a single atlas ossification with no trace of rib facets (bipartite atlas with a rib processes reported in *Triadobatrachus* by Rage and Roček 1989, and Roček and Rage 2000, but see below for different view), in having a higher level of ossification, long fused posterior transverse processes and sacral ribs, fully ossified components in elbow joint, ischium fused to ilium (the last feature unique within the Salientia; Roček, personal communication 2007) despite its much smaller size, and in having longer, more slender limbs. As reconstructed, the ilio-sacral joint of *Czatkobatrachus* has a morphology quite distinct from that of *Triadobatrachus*, in that the sacral rib is short and fused to the vertebral centrum (rather than free and posteriorly elongate), and has an expanded distal end that is both dorsoventrally and anteroposteriorly bifurcate, with a posterior notch and groove. *Czatkobatrachus* also differs from *Triadobatrachus* and resembles many crown-group frogs in having a fully ossified, capitate eminence (*eminentia capitata*) that equals or exceeds 60% of the width of the distal end of humerus, and asymmetrical epicondyles (ulnar epicondyle larger). It differs from crown-group frogs in having the anterior margin of atlas pedicel notched for the exit of the first spinal nerve and spinal nerve notches or foramina in some posterior vertebrae, and in retaining an ossified remnant of the pubis, fused to the body of the pelvis and perforated by an obturator canal.

Occurrence. — Only type locality.

VERTEBRAL COLUMN

The vertebral column of *Czatkobatrachus* is represented by isolated elements that have been ordered (Fig. 4B) partly on the basis of morphology (neural arch and centrum length, posterior zygapophysial size, transverse processes, and the presence or absence of free ribs) and partly by comparison with *Triadobatrachus* (Fig. 4A). On this basis, the atlas (Fig. 1), anterior, middle and posterior presacrals (Fig. 2), sacrals (Fig. 3), and caudals have all been identified. They are all fully ossified, and share a distinctive domed neural arch, a weak dorsal midline ridge, and a cylindrical perichordal (ectochordal) centrum perforated by a large unconstricted notochordal canal. The anterior zygapophyses are horizontal and vary in size along the column. Between them, the anterior border bears a deep V- or U-shaped notch that extends to the level of the base of the transverse processes. Behind the notch, there are bilateral depressions, some more marked than others, that mark the attachment of intervertebral muscles or ligaments. More posteriorly, the neural arch becomes strongly domed but curves down at the posterior margin. This posterior margin is usually slightly indented, but in the vertebrae immediately following the sacrum, it develops a small median process (Fig. 2C, G). The centrum is rounded in cross-section. Seen in anterior view, however, the lateral walls of the cylinder are usually thicker than the dorsal and ventral walls, giving the centrum a slightly depressed shape (see *e.g.*, Fig. 2A₁, C₁). In general morphology, the vertebrae closely resemble those of *Triadobatrachus*, except that the transverse processes, and in some cases the ribs, are fused to the vertebra rather than free. A few specimens (*e.g.*, ZPAL AbIV/6, Fig. 2A₁, A₂) show a bulbous region part way along the transverse process that marks the point of fusion, although subsequent remodelling apparently removes this to leave a single smooth, but actually compound, process.

Atlas. — Three atlantes have been recovered (ZPAL Ab IV/15, 112, and 126). None of these preserves a complete neural arch, but ZPAL Ab IV/126, the right half of an atlas, retains the neural arch pedicel and its posterior tip (Fig. 1B). The centrum is shorter than it is wide and fully notochordal. Anteriorly, the atlas bears paired, subcircular cotyles for the exoccipital condyles (Fig. 1A₂). As these surfaces are anterolaterally directed it suggests that the articular surfaces of the occipital condyles were themselves divergent. There is no interglenoid tubercle and the interglenoid region is perforated by an almost unconstricted notochordal canal (Fig. 1A₂, A₃). The neural arch pedicels are narrow but the edges are intact and are located at about the mid-length of the centrum. This centrum obviously corresponds to an intercentrum, even if the pleurocentrum contributed to its posterior part. There is no hint of the bipartite structure that has been interpreted for *Triadobatrachus* (Rage and Roček 1989), nor any trace of an atlantal rib (Fig. 1A). In ZPAL AbIV/126,

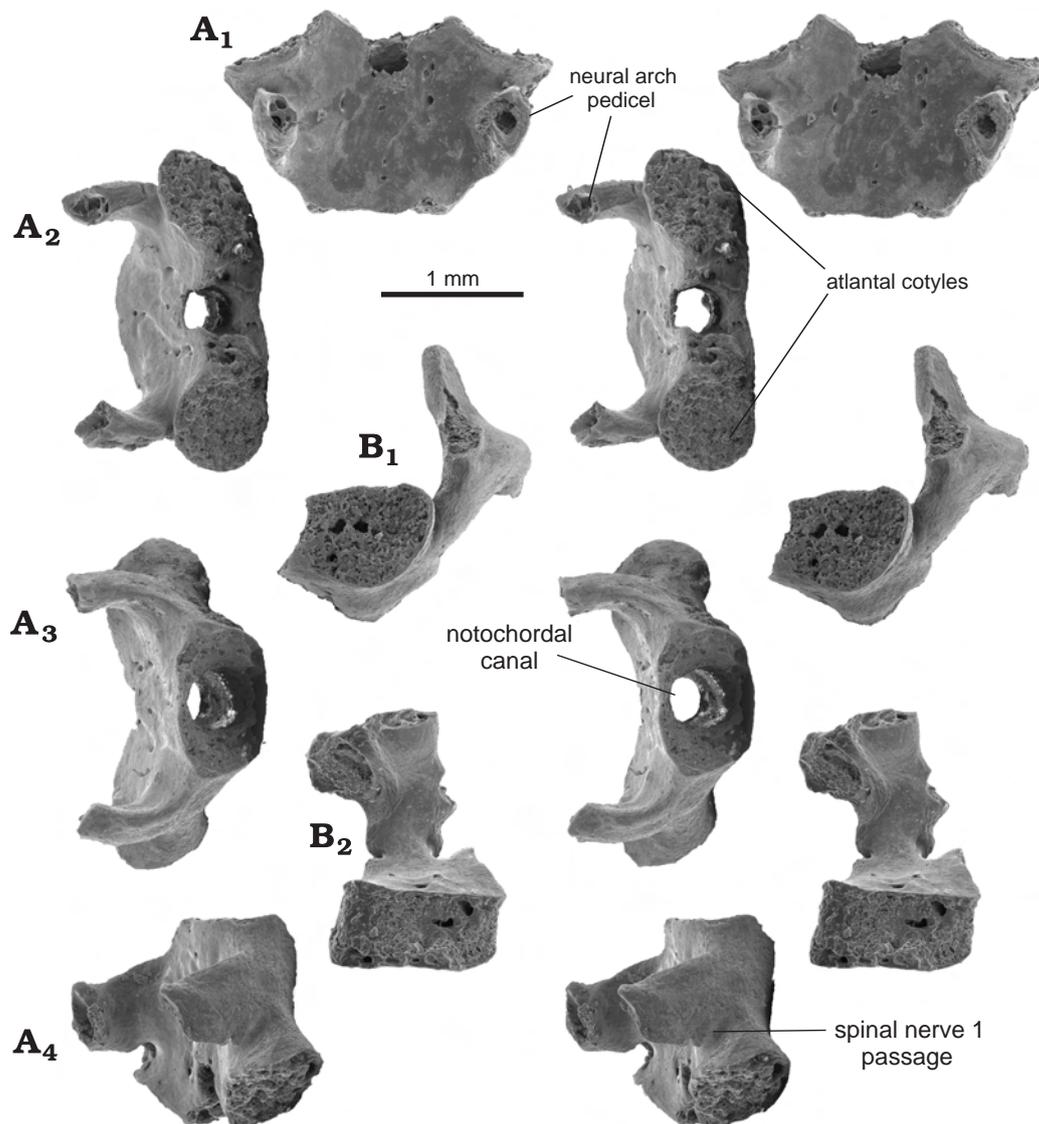


Fig. 1. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A.** Atlas ZPAL Ab IV/15, in dorsal (A_1), cranial (A_2), caudal (A_3), and left lateral (A_4) views. **B.** Atlas ZPAL IV/126, in cranial view (B_1) and medial view of the left neural arch pedicel (B_2). SEM stereo-pairs.

the posterodorsal margin bears a postzygapophysis (Fig. 1B₂). Above and lateral to the cotyles the surface of the centrum bears a shallow groove that leads into a small notch in the anterior margin of the pedicel (Fig. 1A₄). This matches the groove and notch (or foramen) found in the atlas of most salamanders and caecilians for the passage of the first spinal nerve although this is the first time the condition has been recorded in a salientian. Ritland (1955a) describes the nerve as running in front of the arch and above the centrum in the modern *Ascaphus*, but no obvious canal or incision is shown in his fig. 2.

Postatlantal presacral vertebrae. — Given the general similarity between the vertebrae of *Czatkobatrachus* and *Triadobatrachus*, it is likely that the vertebral column was of similar length. Using the criteria listed above, the presacral vertebrae can be roughly divided into anterior, middle and posterior elements.

Anterior presacrals are represented by several specimens (*e.g.*, ZPAL AbIV/6, 108–110; Figs 2A, B, 4). They have centra and arches shorter (anteroposteriorly) than those that follow them. Their zygapophyses are expanded and the transverse processes are robust, ovoid in cross-section (longest axis dorsoventral), and end in a pitted surface to which a free rib would have been attached — although immovably. ZPAL AbIV/108 (Fig. 2B₂) is an example of this morphology, and would have been located in an anterior position (Fig. 4B). In crown-group frogs presacrals 2–4 usually bear enlarged transverse processes/ribs to provide support for

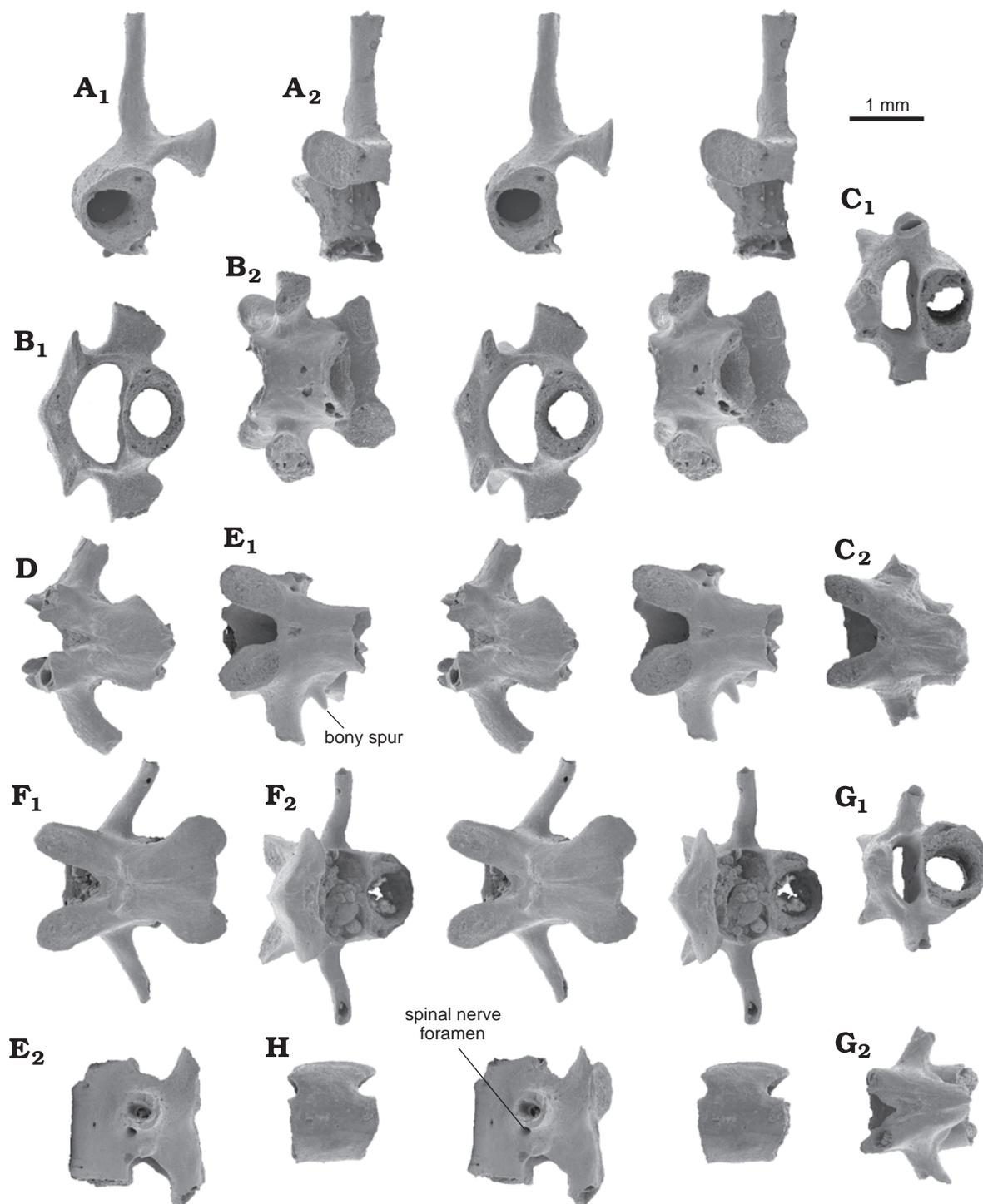


Fig. 2. *Czatkobatrachus polonicus* Evans et Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A.** Anterior dorsal ZPAL Ab IV/6, in caudal (A₁) and dorsal (A₂) views. **B.** Anterior dorsal ZPAL Ab IV/108, in caudal (B₁) and ventral (B₂) views. **C.** Anterior caudal ZPAL Ab IV/135, in posterior (C₁) and dorsal (C₂) views. **D.** Posterior presacral ZPAL Ab IV/127, in dorsal view. **E.** Directly presacral or anterior caudal vertebra ZPAL Ab IV/115, in dorsal (E₁) and left lateral (E₂) views. **F.** Middle presacral vertebra ZPAL IV/128, in dorsal (F₁) and caudal (F₂) views. **G.** ?the second caudal vertebra ZPAL Ab IV/134, in caudal (G₁) and dorsal (G₂) views. **H.** Posterior caudal ZPAL AB IV/20, in left lateral view. SEM micrographs; all but C₁, C₂, G₁, G₂ stereo-pairs.

the pectoral girdle. Of these, the strongest rib/process is usually that of presacral 3 (*e.g.*, Ritland 1955a). The condition in the Malagasy stem-frog *Triadobatrachus* is similar although whether the vertebra bearing the largest rib is presacral 3 or 4 depends on the interpretation of the atlas as single or bipartite. According to our

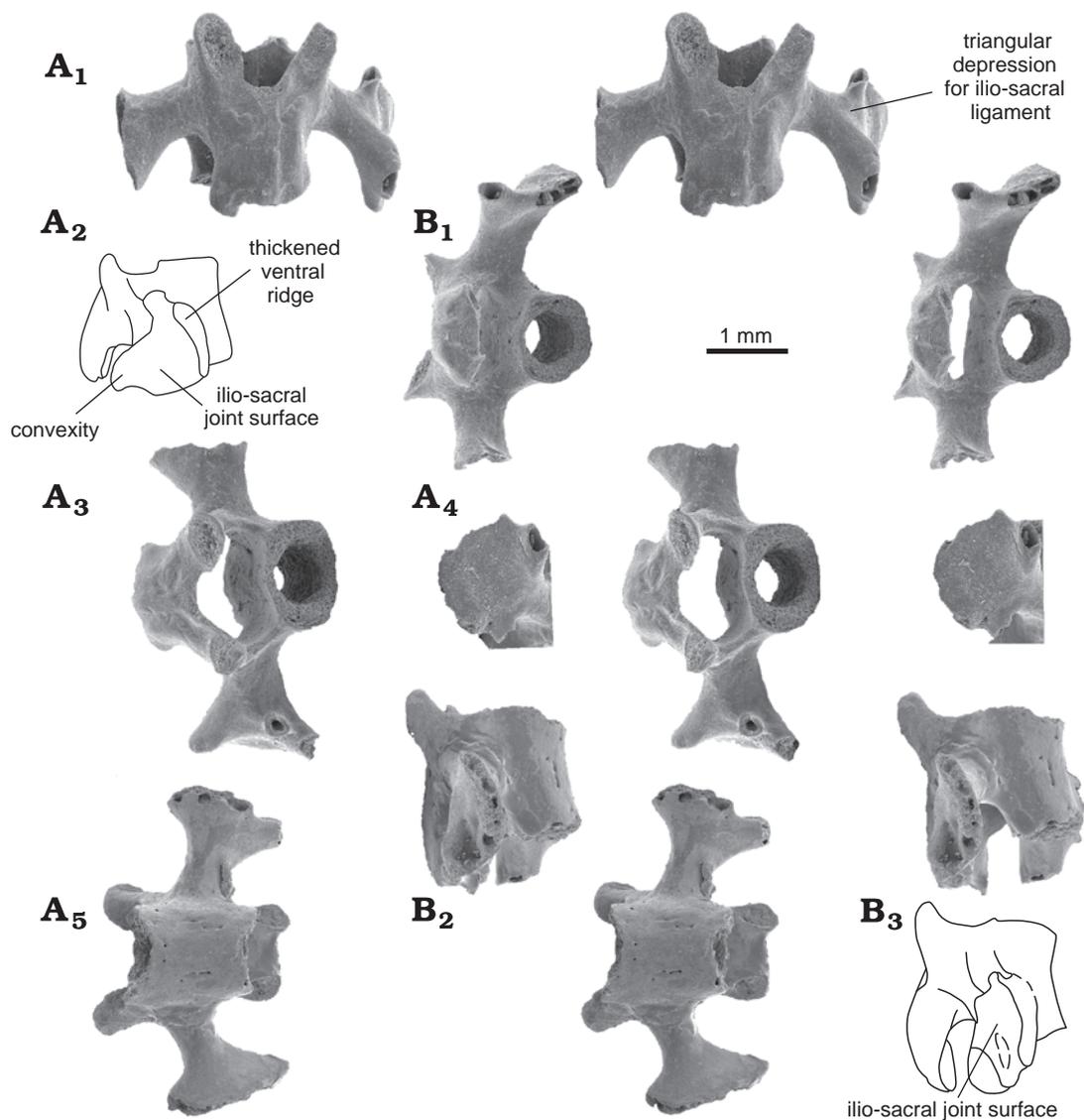


Fig. 3. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A.** Sacral vertebra ZPAL Ab IV/79, in dorsal (A_1), caudal (A_3), and cranial (A_5) views; right iliac surface in lateral view (A_2 , A_4). **B.** Sacral vertebra ZPAL Ab IV/76, in caudal view (B_1); right iliac surface in lateral view (B_2 , B_3). All but A_2 and B_2 SEM stereo-pairs.

interpretation, it is presacral 4 (Fig. 4A). Amongst the Polish material, specimen ZPAL ABIV/6 bears the longest transverse process, probably including a fused rib. In the reconstruction (Fig. 4), this element has been located posterior to ZPAL AbIV/108, which had either the third or fourth position, the exact number of anterior vertebrae being unknown. The length of processes and their dorsoventral flattening suggest they supported the pectoral girdle as they do in crown-group frogs.

Strong bifurcate ribs and/or uncinat processes (Ritland 1955a) are found on the third presacral of the Jurassic *Vieraella* and *Notobatrachus* (Báez and Basso 1996), and isolated ribs of similar morphology have also been described and illustrated for the Jurassic *Prosalirus* (Jenkins and Shubin 1998). In the living *Ascaphus*, the second rib is generally the largest and possesses a sharp, posterolaterally directed uncinat process, but the fourth rib is sometimes equally large. This compares closely with the structure in *Leiopelma* (Ritland 1955a) and discoglossids. The bifurcations that relate to the attachment of muscles connecting the scapula to the spine (*m. serratus*, Ritland 1955a), have not been recorded in *Czatkobatrachus*.

A third set of vertebrae (*e.g.*, ZPAL AbIV/11, 14, 26, 128, and 146; for the latter two see Figs 2F, 4B) show a fairly consistent morphology and are the most common. The neural arch is longer than it is wide (unlike the more anterior presacrals), and this is matched by a slightly longer centrum. The transverse processes

are shorter than those on ZPAL AbIV/6, are distally subcircular in section, vary in width, and are directed posterolaterally. The anterior zygapophyses vary slightly in shape, but seem to have decreased in size towards the rear of the column.

A fourth group of vertebrae, *e.g.*, ZPAL AbIV/8 and 10, tentatively considered a sacral by Evans and Borsuk-Białynicka (1998, fig. 3B, E), and ZPAL AbIV/127 (Fig. 2D) is characterised by a somewhat shorter arch and centrum than those of the mid-trunk, smaller postzygapophyses that are closer to the midline (distinguishing them from anterior presacrals) and a more robust posteriorly curved transverse processes probably with no free ribs contacting them. We interpret these elements as posterior presacrals.

ZPAL AbIV/115 (Fig. 2E) has two unusual features. The first is a small additional bony spur (Fig. 2E₁) on the left side between the transverse process and the posterior margin of the pedicel (on the right only a slight tuberosity). The second is the presence of a distinct foramen, possibly for a spinal nerve, perforating the neural arch pedicel on each side behind the transverse process (Fig. 2E₂). From its morphology, this vertebra is a posterior presacral or an anterior caudal (Fig. 4B). Rage and Roček (1986) reported that such foramina were not visible in *Triadobatrachus*.

Sacrum. — Two almost complete sacral vertebrae have been recovered, ZPAL AbIV/76 and 79 (Fig. 3B, A), and ZPAL AbIV/123. The main body of the bone is slightly shorter than that of the presacrals, but is otherwise similar in morphology. The arch has a low midline ridge and is slightly domed (Fig. 3A₁). The horizontal anterior zygapophyses are ovoid, long axis slightly divergent, and the U-shaped notch more open than in presacrals (Fig. 3A₁). Postzygapophyses are present (as in some basal frogs, *e.g.*, *Ascaphus*, Ritland 1955a) but small and more closely placed than in most presacrals. The centrum is spool-shaped like those of other vertebrae and shows a normally developed posterior joint surface (*i.e.*, no specialised sacro-caudal articulation). The notochordal canal continued into the tail (Fig. 3A₃, B₁).

In spite of variation (see below), the basic, highly unusual, morphology of the sacral transverse processes (diapophyses) is the same. The processes are short and strong, proximally almost circular in cross-section, but they expand and bifurcate distally, in both dorsal and anterior/posterior views (Fig. 3A₁, A₃, B₁). The posterodorsal margin of the process extends first laterally and then curves strongly posteriad (to be continued further in cartilage, as shown by a pitted, unfinished surface). The anteroventral margin of the process angles slightly posterolaterally and then curves anteriorly. Between these margins, the dorsolateral surface of the process bears a triangular depression (or furrow) that opens outward into a large distal concavity facing laterally (Fig. 3A₁) or dorsolaterally (Fig. 3B₂, B₃). The concavity creates a subhorizontal passage oriented anteroventrally, and open posteriorly (Fig. 3A₂, B₃), that could have admitted the anterior tip of the ilium (the diameter of which is consistent). It is bordered ventrally by the thickened, shelf-like edge of the process and posterodorsally by a convexity (Fig. 3A₂, A₄, B₂). However, its surface is completely smooth, without the pitting that characterises a surface bearing joint cartilages (*e.g.*, that of the pelvic acetabulum). Rather, the morphology suggests that the tip of the ilium was suspended in position by ligaments, the chief of which ran from the dorsomedial surface of the transverse process in the triangular depression noted above (as in the type IIA iliac suspension of Emerson 1979). A small anterior tubercle may have limited forward movement (Figs 3A₄, B₂, 4C₂). However, given the importance of sesamoid cartilages in the ilio-sacral articulation of extant frogs (Emerson 1979, 1982), there is a possibility that the distal concavity of the sacral processes included a sesamoid which allowed a more anterior position of the ilium (Fig. 4C₁) or a shift of the ilium shaft relative to the sacrum. The position of the iliac facet varies (see above) from directly lateral facing (Fig. 3A₁, the distal flange particularly broad dorsoventrally Fig. 3A₂), to dorsolateral (Fig. 3B₂, the distal flange dorsoventrally less extensive Fig. 3B₃). However, according to Ritland (1955a, p. 138), “no other parts of the skeleton of *Ascaphus* are subject to greater variation than the sacrum and the coccyx”, and the variability of the sacral processes in *Czatkobatrachus* is most probably intraspecific. There is nothing to suggest a ventral position of the ilium joint with respect to the sacrum in *Czatkobatrachus*, but the arrangement of the iliosacral joint offers a perfect transitional stage towards an eventual position of the ilium ventral to the sacrum. Acquisition of this ventral position was an important element in the evolution of the anuran locomotor apparatus (Shubin and Jenkins 1995), already present in the Early Jurassic species *Prosalirus bitis*. The arrangement of the ilio-sacral joint was markedly different from that reconstructed for *Triadobatrachus* (Rage and Roček 1986) in which the ilium simply abuts the lateral surface of a sacral transverse process that is not fused to the body of the vertebra. In its larger size (relative to body size), the complete fusion of the sacral ribs, and the larger, more complex, ilio-sacral contact, the sacrum of *Czatkobatrachus* appears to be better adapted to terrestrial locomotion.

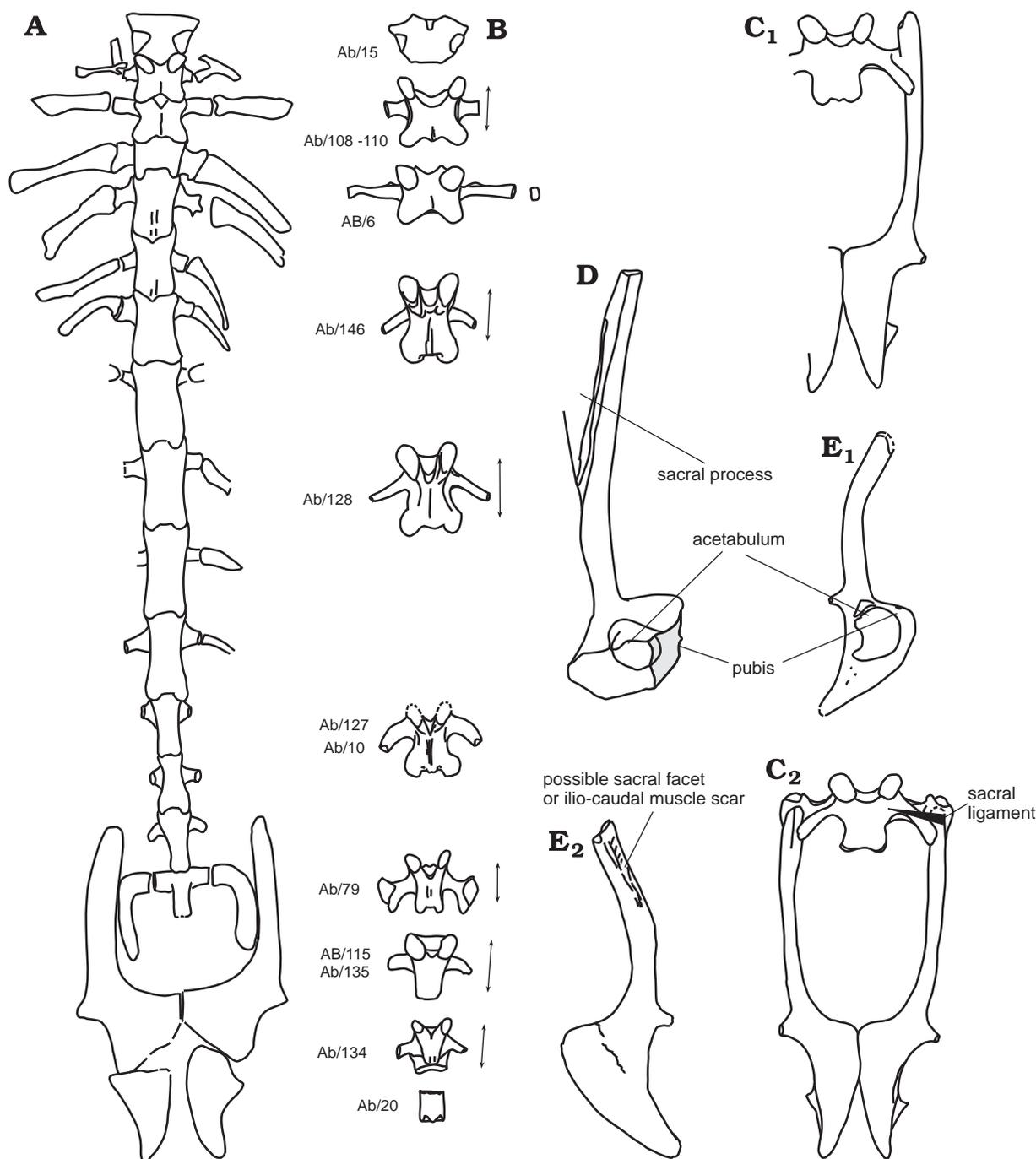


Fig. 4. **A.** *Triadobatrachus massinoti* (Piveteau, 1936), Early Triassic of Madagascar. Vertebral column with pelvis according to Rage and Roček (1989) with a hypothesised reinterpretation of two anterior cervicals based on *Czatkobatrachus* structure. **B.** **C.** **E.** *Czatkobatrachus polonicus* Evans et Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **B.** Vertebrae arranged in natural sequence. **C.** Possible sacro-pelvic configuration with a connective tissue pad filling up the distal concavity of the sacral transverse process (C_1), the same with the distal end of the ilium located in the concavity (C_2). **E.** Reconstruction of right innominate bone, in lateral (E_1) and medial (E_2) views. **D.** *Pelobates fuscus* ZPAL Ab III/6, Recent, right innominate bone and sacral process in lateral view. All but D, E in dorsal view.

Caudal series. — In all crown-group frogs, the caudal vertebrae are fused into an elongated urostyle, although some (*e.g.*, the Jurassic *Notobatrachus*) are recorded as retaining one free caudal vertebra behind the sacrum (Báez and Basso 1996) and the condition occurs as a variant in the living *Ascaphus* (Ritland 1955a). In *Triadobatrachus*, however, the caudal vertebrae are unfused and form a short series of at least

6 small vertebrae showing a sharp posterior decrease in diameter and a reduction in the neural arch and transverse processes. Posterior caudals are thus little more than double cylinders. We have recovered two kinds of caudal element from Czatkowice 1 (*e.g.*, ZPAL AbIV/134, 135, and 20; Evans and Borsuk-Białynicka 1998; Fig. 2C, G, H, respectively), and we interpret *Czatkobatrachus* as having had a short tail like that of *Triadobatrachus*, rather than a urostyle. Anterior postsacrals (*e.g.*, ZPAL AbIV/134 and 135, Fig. 2C, G) resemble posterior presacrals in having a relatively short arch and centrum and a thickened transverse process, but differ in that the postzygapophyses are even smaller and lie close to the midline on a tapering posterior spur. Further posteriorly, the transverse processes are reduced and then lost. As represented by ZPAL AbIV/20 (Fig. 2H), posterior caudals also lack anterior or posterior zygapophyses, and their anteriorly and posteriorly tapering arches would have been held together by ligaments.

The robustness of the transverse processes of the vertebrae immediately in front of and behind the sacrum suggests they were involved in some way with the support of the ilium, perhaps providing additional attachment points for stabilising ilio-lumbar and sacro-coccygeal musculature (Emerson and de Jongh 1980).

PECTORAL GIRDLE AND LIMB

Scapulocoracoid. — The pectoral girdle of *Czatkobatrachus polonicus* has been described in detail elsewhere (Borsuk-Białynicka and Evans 2002), but its morphology is summarised here for completeness.

The bone is represented by many fragmentary specimens, the most complete of which is ZPAL AbIV/26 (Fig. 5A). It is a single ossification and consists of a subtriangular ventral plate and a narrow blade that widens distally along its vertebral border to about twice the proximal width, although no specimen has the distal end preserved. The scapular blade is unusually long and slender (ZPAL AbIV/29, Fig. 5B). In life, it was inclined posterodorsally, its axis making an angle of about 65° with the long axis of the coracoid plate.

A large glenoid cavity occupies much of the postero-ventral region of the scapulocoracoid, extending well posteriorly. It is subcircular in outline, much deeper dorsoventrally than is usual in lower tetrapods, and is hemispherical rather than funnel shaped (in contrast to urodeles). It faces directly laterad, in contrast to the posterolateral orientation in non-lissamphibian temnospondyls. A distinct anteroventral glenoid tubercle seems to belong to the scapular component of the glenoid and contributes a small articular surface to its anteroventral border.

Anterodorsal to the glenoid is a large supraglenoid foramen that forms a subvertical cleft partly separating the glenoid region of the scapula from its acromial part, homologous and similar in position to the scapular cleft of *Anura* (Borsuk-Białynicka and Evans 2003; Carroll 2007). The acromial part is a long, laterally (or slightly anterolaterally) flattened process extending ventrally from the scapula, of which it is an integral part. Ventral to the supraglenoid foramen, the acromial process fuses with the procoracoid part (anteroventrally), and with both the scapular and coracoid parts of the glenoid (posteroventrally). Separating the procoracoid region from the coracoid, the supracoracoid foramen leads into a short canal directed toward the supraglenoid foramen. Both open on the medial surface of the scapula in the subscapular fossa. The procoracoid region faces almost laterally, but the coracoid itself turns ventromedially to lie at an angle of about 110° to the plane of the scapula. Its ventromedial margin ends in a strip of unfinished bone that would have been continued in cartilage in life (Fig. 5C), rather than forming a transverse bar as it does in anurans. The retention of the supracoracoid foramen, which is included within the scaphoid fenestra in anurans, provides further evidence that an independent coracoid bar was not yet developed. Furthermore, it suggests that the arciferal contact of the *Czatkobatrachus* scapulocoracoids was of a caudate rather than anuran pattern. No clavicles have been identified for *Czatkobatrachus*, but they were probably present, given the high degree of ossification of the skeleton, and their retention in *Triadobatrachus* (Rage and Roček 1989). These elements have been lost in caudates, but in arciferal frogs, clavicles are necessary to retain the structural integrity of the girdle, given the mobility of the epicoracoid cartilages with respect to each other during locomotion (Emerson 1983). Their possible role in *Triadobatrachus* and *Czatkobatrachus* remains obscure.

Humerus. — The humerus was one of the first bones to be recognised for *Czatkobatrachus* because it is characteristically salientian. The majority of specimens preserve only the distal ends (*e.g.*, ZPAL AbIV/2–3, 12–13, and 55), but ZPAL Ab IV/78 is a complete humerus that permits a detailed description and also a discussion of forelimb-hind limb ratios.

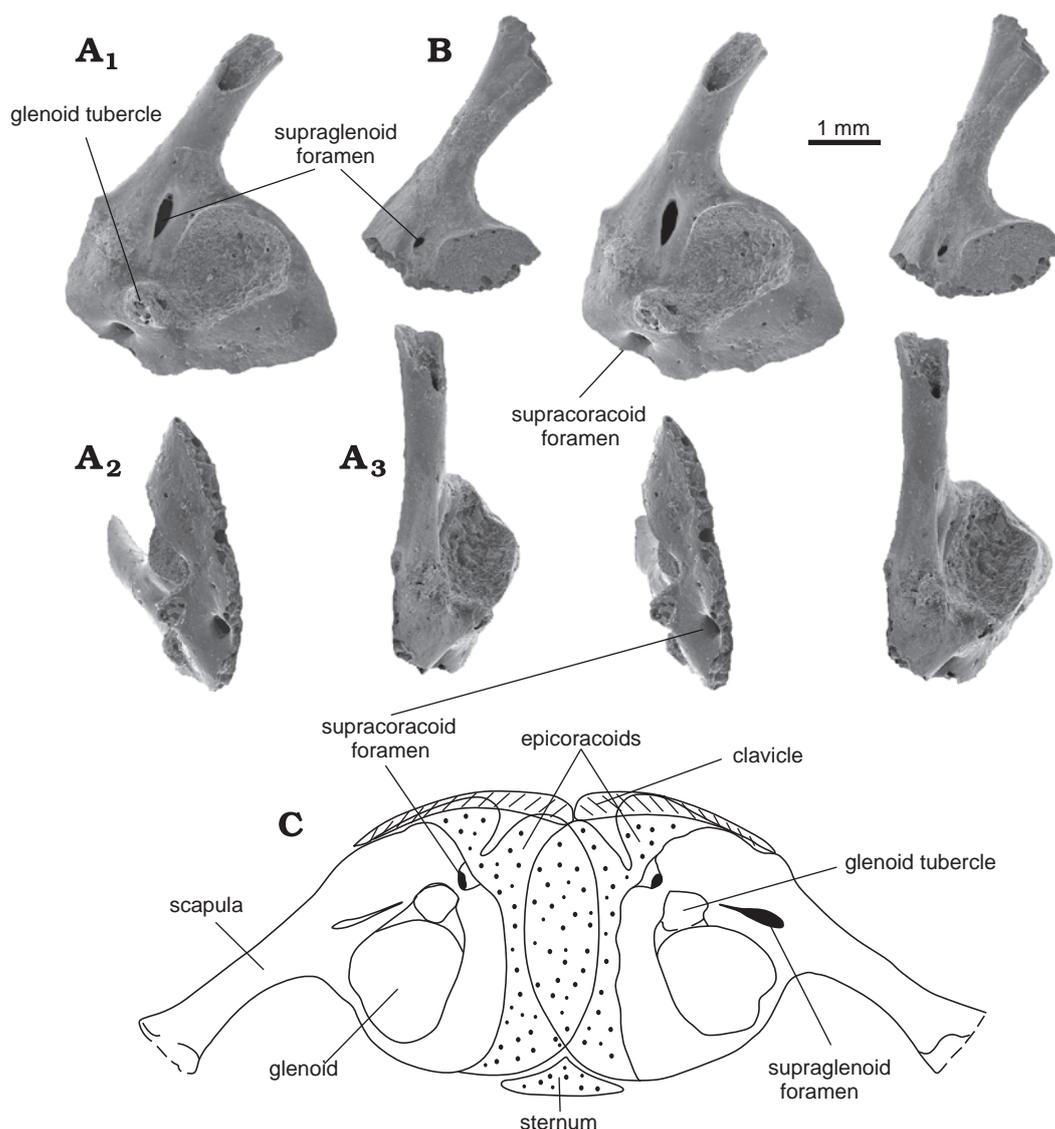


Fig. 5. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A.** Left scapulo-coracoid ZPAL Ab IV/26, in lateral (**A**₁), ventral (**A**₂), and anterior (**A**₃) views. **B.** Left scapula ZPAL AB IV/29, in lateral view. **C.** Reconstruction of pectoral girdle in ventral view. All but C SEM stereo-pairs.

ZPAL AbIV/78 (Figs 6 and 7A) is a complete left bone roughly 11 mm in length and a little over 0.5 mm in width at its narrowest point. The proximal and distal ends are gracile, separated by a long and slender shaft. The proximal end has a dorsoventrally flattened terminal condyle that is much more tightly co-ossified with the shaft than is usual in extant frogs (*e.g.*, *Rana*, *Bufo*, and *Pelobates*). A ventral humeral crest (*crista humeralis ventralis*; of Sanchiz 1998) is present but is very low both proximally and distally. However, in the extant *Rana* the proximal part of the crest is intimately connected with the articular condyle, protruding over it proximally, and sharing its delayed ossification. No such connection is evident in *Czatkobatrachus*, but the crest looks proximally unfinished. The relative weakness of the crest may reflect the size of the associated musculature. The muscles that attach to the crest (*mm. pectoralis*, *deltoideus*, *coracobrachialis*, *supracoracoideus*, *scapulo-humeralis*, *dorsalis scapulae*, *latissimus dorsi*; Ritland 1955b) are mostly postural muscles, supporting the body in standing. If the body was light, strong musculature may not have been necessary. The scars of the pectoralis muscle — on the crest edge, and that of the deltoideus, on the anterior side of the crest, are the only ones tentatively recognized here (Fig. 6B₁, C) on the basis of *Ascaphus* structure (Ritland 1955a).

The humeral shaft is circular in cross-section, but is otherwise featureless. It expands gradually into a slender distal end. Ventrally there is a large capitae eminence (65% or more than the total width of the distal

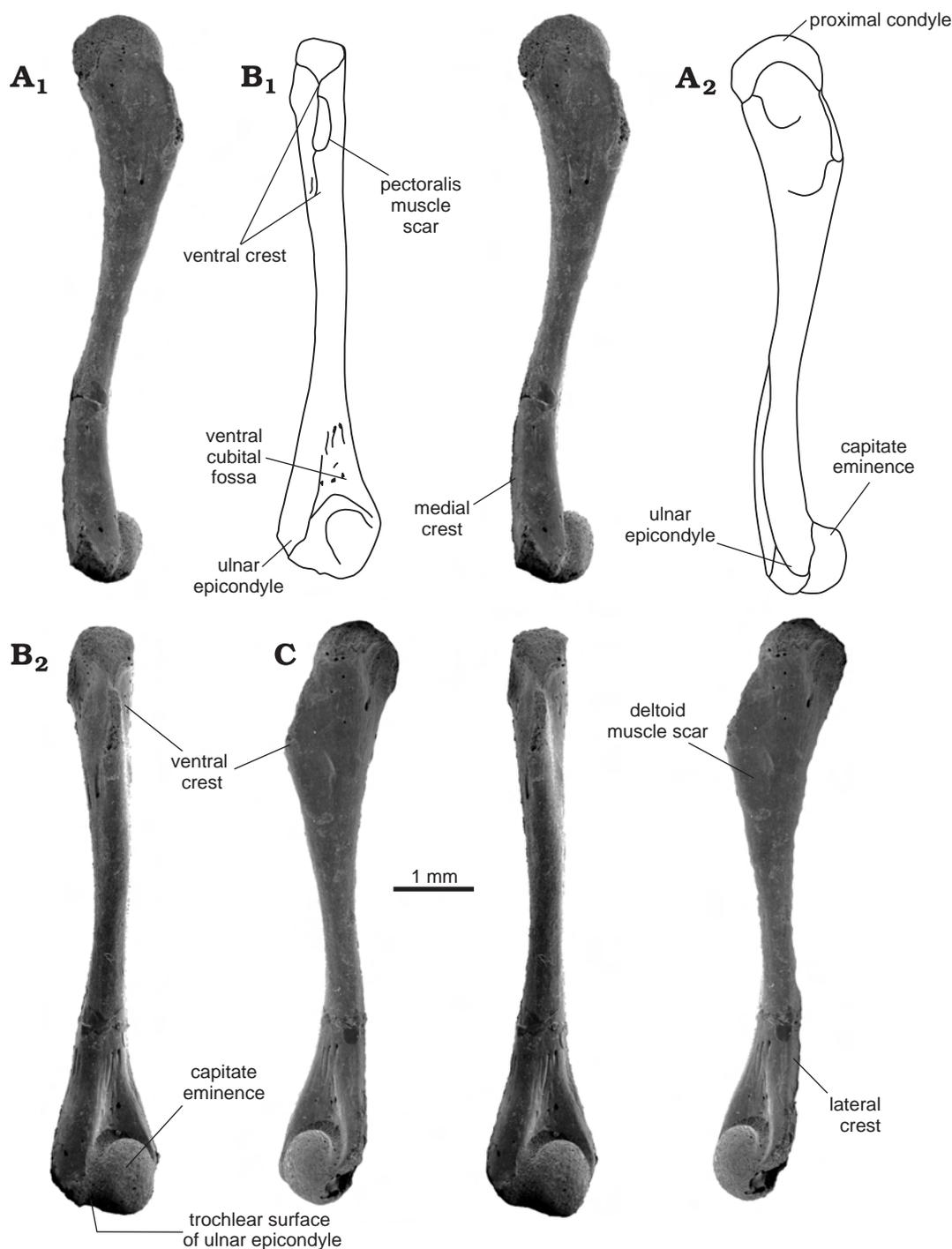


Fig. 6. *Czatkobatrachus polonicus* Evans et Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. Left humerus ZPAL Ab IV/78, in posterior = medial (A), ventral (B), and anterior = lateral (C) views. A₁, B₂, C, SEM stereo-pairs.

end). The remaining some 35% of the distal end is occupied by the ulnar epicondyle, contacting the eminence ventrally through a small trochlear surface (Figs 6B, 7A₃). Dorsally, there is a short triangular olecranon scar (Fig. 7B). The radial epicondyle — the site of origin of many extensor muscles (*e.g.*, *mm. extensor carpi radialis*, *extensor carpi ulnaris*, *extensor digitorum communis longus*), is very small (suggesting weak extensor muscles) while the ulnar epicondyle (mostly for flexor muscles) is more prominent. These differences may relate to sexual behaviour (amplexus) and may be subject to sexual dimorphism (Roček, personal communication 2007). The longitudinal medial and lateral distal muscle crests are quite feeble (Fig. 6A, C), and thus the forelimbs were probably not heavily muscled.

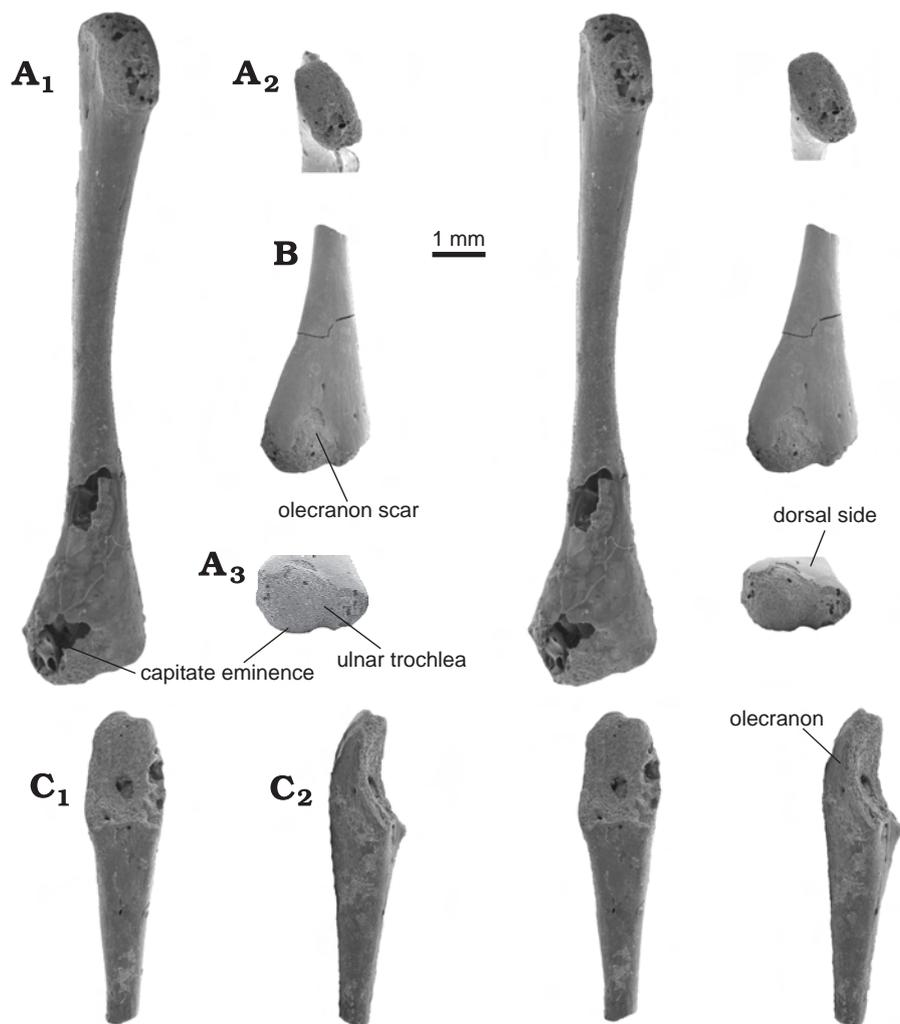


Fig. 7. *Czatkobatrachus polonicus* Evans *et* Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A.** Left humerus ZPAL Ab IV/78, in dorsal view (A₁), proximal end (A₂), and distal end (A₃). **B.** Distal part of the left humerus ZPAL Ab IV/55, in dorsal view. **C.** Ulna ZPAL Ab IV/22, in anterior (C₁) and lateral (C₂) views. SEM stereo-pairs.

Antebrachium. — The ulna of *Czatkobatrachus* is represented by three specimens of the proximal end (*e.g.*, ZPAL AbIV/22, Fig. 7C). Like the humerus, the bone is well ossified with a strong elongated olecranon process, providing the lever arm for the triceps muscle (*m. anconeus*; Duellman and Trueb 1986) and a concave articular surface for the humeral articulation. The elbow joint seems to have been stable. No radius has been recognized as yet.

PELVIC GIRDLE AND HIND LIMB

Pelvic girdle. — The pelvic girdle of *Czatkobatrachus* is represented by many distinctive ilia (some 18 specimens), some specimens having the puboischiadic plate fused in place (*e.g.*, ZPAL AbIV/111 and 129; Fig. 8D and B, respectively). At the time of the original description (Evans and Borsuk-Białynicka 1998), the most complete ilium was the holotype, ZPAL AbIV/7, but more complete specimens have been found subsequently. ZPAL AbIV/114 (Fig. 8A) is one of the most complete, the delicate iliac shaft usually breaking at or close to its junction with the acetabular region. The acetabular region is expanded, with a large shallow lateral acetabular surface, little development of a supra-acetabular buttress, and no extension of the anterior or posterior acetabular margins (into *partes descendens* or *ascendens*; Sanchiz 1998). The medial surface is smooth with no trace of an interiliac synchondrosis. The most obvious feature is a large protruding dorsal prominence (also present in *Triadobatrachus*; Rage and Roček 1989, fig. 3) for the gluteus magnus muscle or

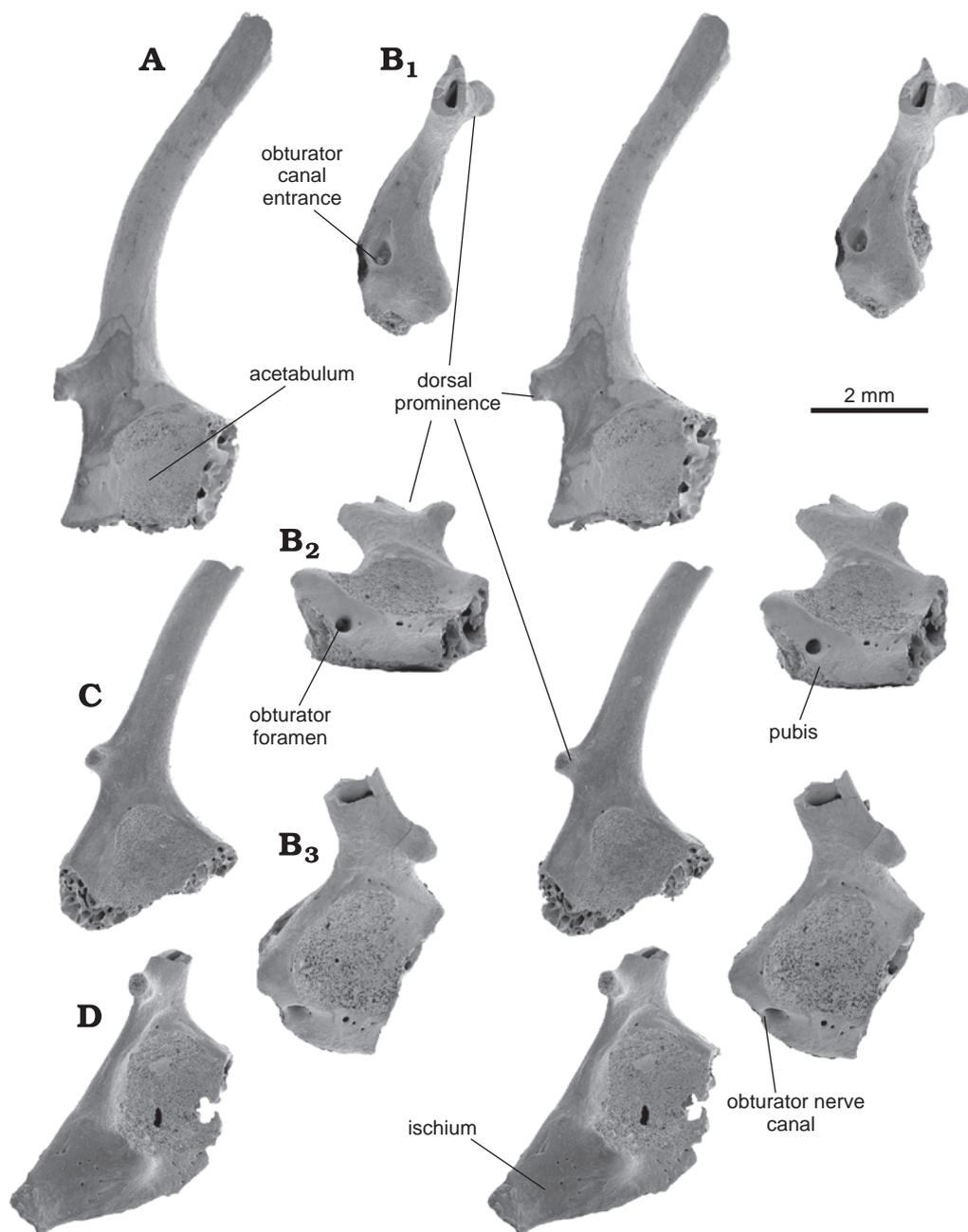


Fig. 8. *Czatkobatrachus polonicus* Evans et Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. **A.** Right ilium ZPAL Ab IV/114, in lateral view. **B.** Left acetabulum ZPAL Ab IV/129, with proximal part of ilium and pubis preserved, in anterior (B_1), medial (B_2), and reversed lateral (B_3) views. **C.** Right ilium ZPAL Ab IV/54, in lateral view. **D.** Right acetabulum ZPAL Ab IV/111 with proximal part of ilium and ischium preserved, in lateral view. SEM stereo-pairs.

for its accessory tendon (Ritland 1955b; Duellman and Trueb 1986). The iliac shaft is somewhat longer than that of *Triadobatrachus* (6.5 versus 4.9 times dorsal vertebral lengths), and is more slender. The shaft is ovoid in cross section with no traces of either crests or rugosities, except for a faint trace on the dorsomedial side of the distal end (Fig. 4E₂), left by the sacral transverse process or by the ilio-caudal muscle. As described for *Triadobatrachus* (Rage and Roček 1989, p. 11), the end of the shaft is open and hollow. It was presumably completed by a cartilaginous plug or extension of some form.

Specimens ZPAL AbIV/16, 111, and 129 add further to our knowledge of pelvic structure, and in combination with the ilia permit a complete reconstruction of the pelvis. ZPAL AbIV/129 (Fig. 8B₃) preserves the almost square anteroventral tip of the pelvic plate. This is thickened in anterior view (Fig. 8B₁) and grooved. In the upper part of the groove, hidden in direct medial view, there is a large foramen. This leads into a short

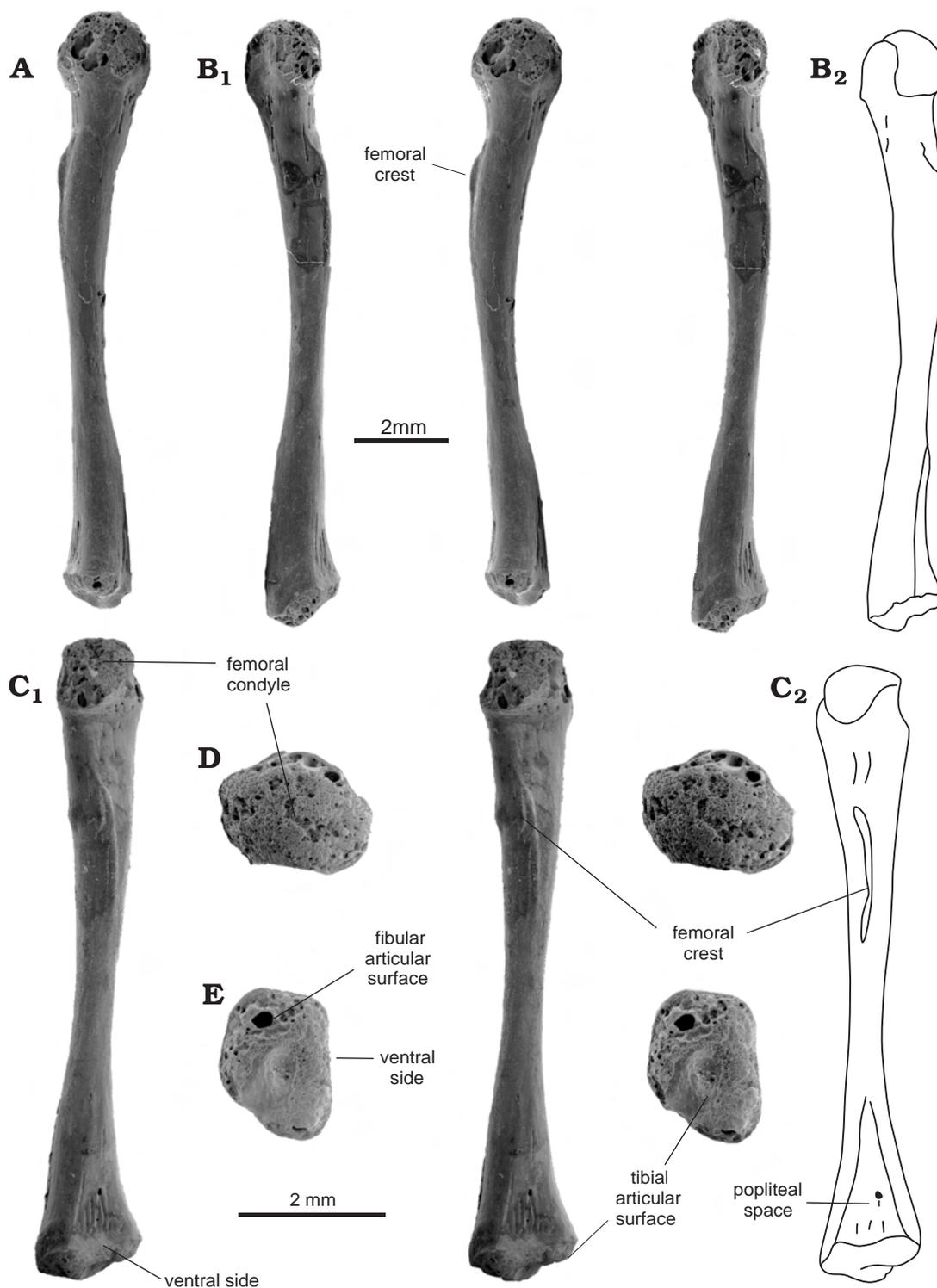


Fig. 9. *Czatkobatrachus polonicus* Evans et Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. Left femur ZPAL AB IV/25, in anterior (A), posterior = lateral (B), ventral (C), proximal (D), and distal (E) views. All but B₂, C₂ SEM stereo-pairs.

canal that runs through the anterior pelvic margin at roughly 45 degrees and emerges on the lateral surface (Fig. 8B₃) just below the anterior rim of the acetabulum. This canal is not present in crown-group anurans and is not described for *Triadobatrachus*, but from its course and position must have carried the obturator nerve and blood vessels from out of the pelvic cavity. In non-lissamphibian temnospondyls and amniotes, this canal perforates the pubis, suggesting that the anterior corner of the pelvic plate in *Czatkobatrachus* is an ossified remnant of this bone (cartilaginous in crown-group frogs), not a calcified prepubis as found in

Ascaphus and *Xenopus* (Ritland 1955a). Posteriorly, ZPAL AbIV/16 (not figured) and 111 (Fig. 8D) preserve the almost complete posteroventral, ischiadic part of the pelvic plate. They show that the acetabular surface is not rounded in the complete pelvis but instead has a posterior triangular extension formed by the ischium. This, in turn, suggests that there was an anteroposterior component to the femoral movement as well as the dorsoventral one. The triangular ischium closely resembles the same element in *Triadobatrachus*, except that the ischium is free from the rest of the pelvis in the Malagasy genus.

In crown-group frogs, the two halves of the adult pelvis meet posteroventrally at a steep angle, with a deep synchondrosis of the pubo-ischiadic plate that may or may not extend to the base of the ilium. As described by Green (1931) for *Rana*, this synchondrosis deepens gradually during development, with only the edges of the pubo-ischiadic plate meeting initially but then incorporating more and more of the plate until the two halves are completely fused. This articulation is not discussed for *Triadobatrachus* (Rage and Roček 1989). The only visible articular surface on the pubo-ischiadic plate of the Polish form is a recessed pitted strip along the ventromedial margin (Fig. 8B₂). The two pelvic plates clearly met at an angle (a horizontal orientation would render the pelvis too wide), but with a relatively weak synchondrosis, like that of the larval *Rana*.

Femur. — The only hind limb element to be identified with any certainty is the femur (Fig. 8), but a second element closely matches the fibulare (Fig. 10) of modern frogs. No conjoined tibiofibulae have been recovered. Since these are among the most characteristic and common frog elements preserved in microvertebrate assemblages, we are confident that in *Czatkobatrachus*, as in *Triadobatrachus*, these two bones were not fused.

The femur is represented by two complete specimens, ZPAL AbIV/25 (Fig. 9) and 125, and several fragments. By comparison with the modern *Bufo punctatus*, the complete specimens are both right femora. However, the attribution of femora to right or left can be somewhat problematic, because of the lack of landmarks, and the variability of bone curvature in extant frogs. In *Rana*, the bone is S-shaped in a dorso-ventral plane, but is curved in both dorso-ventral and lateral planes in *Bufo*, and in only one plane in *Pelobates*. Perhaps the type of locomotion, and the size have a bearing on this character, but the relationships are obscure. In *Czatkobatrachus*, the femur is only slightly bowed dorsoventrally (dorsally concave Fig. 9A, B), and probably twisted, the axes of the ends being subperpendicular to each other. The torsion is less obvious in *Bufo* but is difficult to observe in extant frogs because their epiphyses are usually lost. In contrast to them, *Czatkobatrachus* femora have completely fused epiphyses and their articular surfaces are at least partly finished (although in life they were certainly coated with articular cartilage).

ZPAL Ab IV/25 (Fig. 9) is long and slender, ca. 12.5 mm in total length with small proximal and distal ends of equal width (ca. 2 mm). The shaft is 0.8 mm at its narrowest point. The femur is thus only slightly longer than the humerus and of very similar proportions. The proximal end bears a proximally convex, slightly bilaterally flattened, condyle (Fig. 9D). The femoral crest (corresponding to the trochanter) extends down the ventral surface beginning proximally from a point about 1/5 of the femoral length and fading out at about 3/5 femoral length. By comparison with extant frogs (*Ascaphus* as illustrated by Ritland



Fig. 10. *Czatkobatrachus polonicus* Evans et Borsuk-Białynicka, 1998, Early Triassic of Czatkowice 1, Poland. Possible fibulare ZPAL Ab IV/138, in proximal (A) and lateral (B) views. SEM stereo-pairs.

1955a, b), the crest is for the attachment of hip muscles (*mm. pectineus, gluteus minimus, iliofemoralis, pyriformis, quadratus femoris, and obturator externus*; Ritland 1955b). The distal end has its surface differentiated (Fig. 9E). By comparison with a *Bufo* femur, a large concavity in the anteroventral part of distal surface was probably for the tibia, whereas a second, posterior, convexity articulated in some way with the fibula. As noted above, there is no evidence that the crural bones were fused.

Possible additional element. — ZPAL AbIV/138 (Fig. 10) is a long bone of similar overall morphology and bone type (density and surface texture) to that of the other limb elements of *Czatkobatrachus*, but it is much shorter than either the humerus or femur (roughly 45% of the femoral length). Like the femur, the shaft is bowed, with one edge almost straight and the other strongly concave. Both heads are compressed, with a possible distal head broader than the proximal one. This bone does not show any obvious match to either of the epipodials in *Triadobatrachus* (and is relatively shorter) or modern frogs (where they are rounded but always co-ossified), although it does show some resemblance to the epipodials of salamanders. The closest match in a modern frog is to the fibulare, one of the two ankle bones that become elongated in crown-group frogs. These bones are apparently only slightly elongated in *Triadobatrachus* so their extension in *Czatkobatrachus* would represent an advance, although it would be consistent with the generally longer and more gracile limbs of the Polish form.

CHARACTER ANALYSIS

Axial length. — Crown-group frogs are characterised by a very short vertebral column (typically 6–9 presacrals, Griffiths 1963; Kluge and Farris 1969; Lynch 1973). The number of presacral vertebrae in *Czatkobatrachus* but it was probably similar to that of *Triadobatrachus* (14–15), because their vertebrae are very similar both in length and morphology. If this is correct, then the body axis of basal salientians was much shorter than that of many outgroup taxa (*e.g.*, 19–24 in branchiosaurs, Boy and Sues 2000), a shortening that would have involved a reduction in the number of trunk somites (Richardson *et al.* 1998). The recently described amphibamid *Gerobatrachus* has 17 presacrals, intermediate between the primitive condition and that in basal salientians (Anderson *et al.* 2008).

The first spinal nerve. — The notch in the anterior margin of the atlas in *Czatkobatrachus* is reminiscent of the morphology of crown-group salamanders (but not stem taxa) and caecilians. In salamanders and caecilians the atlantal foramen transmits a spinal nerve, but the identity and homology of this nerve is still disputed. According to Duellman and Trueb (1986), the first spinal nerve (here called the transatlas nerve to avoid confusion later) emerges through the atlas in salamanders, but between the atlas and second presacral in frogs. Deuchar (1975), however, argued that the disposition of the anterior spinal nerves in frogs is similar to that in salamanders, the difference being that the first nerve (between the occiput and atlas; sometimes called the suboccipital nerve, *e.g.*, Mookerjee 1930, 1931; Fox 1954) usually gets lost in anuran metamorphosis. Whether this nerve really exists in frogs, and which nerve, if any, is its equivalent in salamanders and caecilians is a problem on which *Czatkobatrachus* structure sheds some light. This, however, requires a brief diversion into cranial embryology.

In the embryonic amphibian head, there are four segments (somitomeres) (Jacobson 1993 and personal communication 2003), three preotic and one subotic. These are followed by two postotic somitomeres that become the first two somites. A preoccipital arch forms between the first and second of these (somitomeres 5 and 6), the occipital arch forms between the second and third somite (somitomeres 6 and 7), and the atlas arch forms between the third and fourth somites (somitomeres 7 and 8) (Goodrich 1911; Wake and Lawson 1973).

According to Jacobson (1993) the first spinal nerve emerges from the third somite, and thus at the level of the anterior part of the atlas (see Burke *et al.* 1995 for different opinion). Francis (1934) claimed that salamanders had a still more anterior nerve (in front of the atlas, in addition to the transatlas nerve), equivalent, according to him, to the suboccipital nerve, and thus to the spinal nerve 1. The transatlas nerve would thus correspond to spinal nerve 2 (although Francis chose to designate it as spinal nerve 1 as it was the first nerve visible in the adult). However, Wake and Lawson (1973) found no evidence for the existence of any nerve in front of the atlas in salamanders, and identified the suboccipital nerve with the transatlas nerve, as spinal nerve 1, with nerve 2 passing behind the atlas. This is the homology accepted herein.

This accepted homology also agrees with the pattern of innervation of the atlanto-occipital muscles, and with morphology. The transatlas nerve of salamanders has only a ventral root, and the first spinal nerve in frogs has lost the dorsal root and dorsal root ganglion during metamorphosis (Mookerjee 1930, 1931; Fox 1954). Wake and Lawson (1973) also suggested that the first spinal nerve originally lay in front of the atlas arch in salamanders (within the range of the third somite), moving back into the atlas pedicel through time (possibly to protect it from the cranio-cervical joint surfaces). A similar process has been assumed by Ritland (1955a) in crown-group frogs (*e.g.*, *Rana* and *Xenopus*) in which the fibers of the first spinal nerve fuse with the spinal nerve 2 (Ritland 1955, pp. 160–163) completely losing their individuality during metamorphosis, except in *Ascaphus* and *Leiopelma* in which they are very much reduced. According to Ritland (1955a, p. 163) “the way in which change may occur at any level of the cord is by a gradual shift of fibers to the next posterior exit from the spinal canal”.

The alternative scenario by Francis (1934) would require that the second spinal nerve moved forwards through the atlas from back to front (to become transatlas nerve *i.e.*, his spinal nerve 1 in adults). This is not the pattern seen in the embryonic development of salamanders, where the notch in the front edge of the atlas gradually becomes enclosed (*e.g.*, Mookerjee 1930, 1931). The same transition is seen in salamander evolution where an anteriorly open notch (SEE) may present an intermediate stage between the unnotched condition in some karaurids (Evans *et al.* 1988, SEE personal observations) and the perforating foramen of crown-group urodeles (SEE). The presence of a notch in the anterior margin of the atlas in *Czatkobatrachus* provides evidence that the condition in stem-frogs was not dissimilar to the condition in most salamanders, with the first spinal nerve (= suboccipital nerve, *i.e.*, transatlas nerve) notching the anterior margin of the atlas. A fully enclosed atlantal foramen is also found in basal caecilians (Jenkins and Walsh 1993; Evans and Sigogneau-Russell 2001), and could be a basal lissamphibian feature. However, the absence of either a notch or foramen in the stem-caudate *Marmorierpeton* (Evans *et al.* 1988, and SEE personal observations) renders this character problematic, as does the two-state condition (anterior incision or closed foramen) in salamanders, and its ontogenetic variation.

Subdivision of the atlas. — Rage and Roček (1989) and Roček and Rage (2000) interpreted the atlas of *Triadobatrachus* as being bipartite, with a single arch but with the centrum divided into anterior and posterior parts, and with a dichoccephalous atlas rib (see also Estes and Reig 1973) meeting both components. This would be an unusual morphology, and it is certainly not the condition in *Czatkobatrachus* where the atlantal centrum is a single entity with a short neural arch bearing the postzygapophysis but no rib. According to Shishkin (2000, pp. 543–544) one of the few apomorphies that can be attributed with confidence to temnospondyls (including lissamphibians, Duellman and Trueb 1986) is the absence of transverse processes on the atlantal neural arch. Fusion of the first two vertebrae can occur in frogs (*e.g.*, palaeobatrachids, rhinodermatids, brachycephalids, and some bufonids, myobatrachids, and pipids, Duellman and Trueb 1986, p. 470; rarely in *Ascaphus*, Ritland 1955a), and is probably associated with a strong shortening of both the centra and neural arches (Ritland 1955a, fig. 4). Such fusion does lead to the presence of a transverse process, but it is associated with the second vertebral segment. Contrary to the opinion of Rage and Roček (1989), the neural arches were certainly present on the first two vertebrae in *Triadobatrachus*, as shown by what is probably the pedicel of atlantal arch, and by the postzygapophyses on the second vertebra (Fig. 4A). The state of preservation of *Triadobatrachus* does not permit a full understanding of its neck structure. The second vertebra of *Triadobatrachus* is damaged (Roček and Rage 2000, fig. 3), but what remains appears to be quite consistent with the morphology of the same element in *Czatkobatrachus* (Fig. 4A).

Tuberculum interglenoideum. — As most frogs, *Czatkobatrachus* lacks an interglenoid tubercle between the atlantal cotyles, having instead a flat surface perforated by the notochord. However, an anterior median process reported by Báez and Basso (1996, p. 143) in *Notobatrachus* and a nubbin-like process in the same position of *Prosalirus* (Jenkins and Shubin 1998, p. 500 and fig. 3A) may represent remnants of the interglenoid tubercle. The tubercle is present in most crown group salamanders (secondarily lost in some paedomorphic taxa, *e.g.*, batrachosauroids, Estes 1981), in albanerpetontid amphibians (SEE personal observations), in stem-caecilians (Jenkins and Walsh 1993; Evans and Sigogneau-Russell 2001), and in the derived amphibamid *Gerobatrachus* (Anderson *et al.* 2008). It is absent in the Middle Jurassic karaurid *Marmorierpeton* (Evans *et al.* 1988), but has been described as present in the Upper Jurassic *Karaurus* from Kazakhstan. Its presence might be a synapomorphy linking caecilians, crown-group salamanders and albanerpetontids (*e.g.*, Feller and Hedges

1998; but see Hay *et al.* 1995), or, given its presence in *Gerobatrachus* (Anderson *et al.* 2008), a character of *Gerobatrachus* and Batrachia (*sensu* Anderson *et al.* 2008). This would require a subsequent reversal in crown-group caecilians, in salientians, and in *Marmorerpiton*. However, the tubercle can also occur in other amphibian lineages (*e.g.*, some microsaur, Carroll and Gaskill 1978), and it may be of functional significance.

Caudals. — On present evidence, the fusion of the caudal vertebrae to form the urostyle is a derived character of crown-group Anura, although some early taxa retained a single postsacral vertebra in front of the urostyle (*e.g.*, some *Notobatrachus*, Báez and Basso 1996). According to Ritland (1955a), the extant *Ascaphus* also retains a strong tendency for the possession of discrete post-sacral vertebrae. In *Czatkobatrachus* the presence of discrete caudals is considered plesiomorphic, as is their presence in *Triadobatrachus*, but the reduced caudal number they probably share is derived. The widely open notochordal canal in *Czatkobatrachus* caudals implies the persistence of the notochord into the tail.

Transverse processes/ribs. — Developmental studies on living frogs (Blanco and Sanchiz 2000) have shown that the transverse process and small free rib, where present, are part of the same anlagen. Differences between clades reflect different degrees and patterns of ossification. In neobatrachian frogs, the transverse process ossifies as a single unit and fuses to the vertebral body. Three extant families (ascaphids, discoglossids and pipids: Trueb 1973), and virtually all Mesozoic anurans (Roček 2000, including *Vieraella*, *Notobatrachus*, *Prosalirus*, *Eodiscoglossus*), retain small ribs on the anterior presacrals. In *Triadobatrachus*, all vertebrae, except the atlas (but see Rage and Roček 1989 for different opinion) bear free ribs, and no vertebra has more than a short transverse process to which the rib attaches. This is presumably the primitive salientian condition since it is also found in stem caudates (Evans, unpublished data). *Czatkobatrachus* resembles primitive modern frogs in having short transverse processes that probably contacted free ribs (not yet recognized, but interpreted from the pitted terminal surfaces of the processes) on a few anterior presacrals (ZPAL Ab IV/108–110), but fused ones on posterior vertebrae (ZPAL Ab IV/6, 10, 127, 128, 146) as shown by areas of incomplete fusion in ZPAL AB/IV/6 (Fig. 2A). These processes are directed laterally in some anterior vertebrae and posteriorly in most of the others; they are slender mid-trunk, but become thickened immediately in front of and behind the sacrum. The state of transverse processes/ribs in *Czatkobatrachus* is here considered derived.

Pectoral girdle. — The pectoral girdle of *Czatkobatrachus* has been reconstructed (Borsuk-Białynicka and Evans 2002) as a pair of undivided scapulocoracoid plates ventrally connected in an arciferal manner (Fig. 5C), no clavicle, cleithrum or sternum fragments having been identified. Crown-group frogs, with both arciferal and firmisternal girdles, have a separate scapula and coracoid. This is in contrast to non-liss-amphibian temnospondyls (Borsuk-Białynicka and Evans 2002 and references herein) and to caudates that have a single scapulocoracoid, this state being considered plesiomorphic. Within Anura, more basal clades like Ascaphidae, Discoglossidae and Pipidae display short scapulae, in contrast to neobatrachian frogs where the scapula may be longer and more slender (Trueb 1973), but never to the extent seen in *Czatkobatrachus*. In ascaphids and pipids the scapulae are proximally uncleft while being cleft or bicapitate in almost all other frogs (Trueb 1973). The widely held opinion (*e.g.*, Trueb 1973) that short uncleft scapulae are primitive for frogs has been challenged by the structure of the scapulocoracoid in *Czatkobatrachus*. Its elongate scapular blade is proximally perforated by the supraglenoid foramen. This separates the anterior acromial part from the posterior, glenoid part, and is most probably homologous to the scapular cleft (Borsuk-Białynicka and Evans 2002) or a scapular cleft *in statu nascendi*.

Trueb (1973) stated explicitly that the arciferal type of pectoral girdle was plesiomorphic for salientians, and that firmisterny is derived. Emerson (1983) was more cautious. However, the consistently arciferal structure of the caudate pectoral girdle suggests that this is the plesiomorphic state, and we accept this view. Firmisterny is derived, and is probably better as a shock-absorbing device. Although earlier reconstructions of *Triadobatrachus* (Rage and Roček 1989) suggested it had a tripartite pectoral girdle like that of modern frogs, our studies have shown that the pectoral girdle of the Malagasy specimen might be reinterpreted as a single structure (Borsuk-Białynicka and Evans 2002) like that of *Czatkobatrachus*.

Ilium and ilio-sacral joint. — An elongate anteriorly directed ilium is synapomorphic for the Salientia (*Triadobatrachus* included) and is shared by *Czatkobatrachus*, but its contact with the sacrum is probably still plesiomorphic or intermediate. Emerson (1979) was probably the first to realize that the ilia articulate ventral to the sacrum in extant frogs. They do also in *Notobatrachus* (Báez and Basso 1996, fig. 13). As re-

constructed herein, the contact in *Czatkobatrachus* occurs between the medial surface of the ilium and the lateral concavity of the sacral process whereas the anteroventral extension of the transverse process props the ilium from the ventral side. However, a posterior extension of the transverse process does overlap the ilium shaft dorsally and may represent a rudiment of the modern configuration.

Puboischiadic plate. — In salamanders, the pubis is unossified and the same is generally true of frogs (Trueb 1973), although Ritland (1955a) reported it as ossified or calcified in *Ascaphus* (calcified according to Trueb 1973). It is also ossified in all pipids (Roček, personal communication 2007). In albanerpetontids (McGowan and Evans 1995) an ossified pubis remains, providing evidence that it was still present in the lissamphibian ancestor (assuming monophyly), although Anderson *et al.* (2008) report it as unossified in the amphibamid *Gerobatrachus* (but this could be due to immaturity). In living frogs, the pubis is restricted to a small unossified region of the ventral pelvic plate between the ilium and ischium. The pelvis of *Czatkobatrachus* thus represents an intermediate stage in which the pubis has been greatly reduced (as in modern frogs) but remains ossified. It is also intermediate in the presence of the perforating canal.

In amniotes and in most non-lissamphibian temnospondyls, the ossified pubis contains a conspicuous foramen for the obturator nerve and its accompanying blood vessels. In salamanders, this nerve supplies a puboischiofemoralis internus muscle on the inner face of the pelvis (Francis 1934) and then sends branches to puboischiofemoralis externus on the outside. The nerve is said to be reduced in salamanders compared to other tetrapods (Noble 1922) and is absent in living frogs (Green 1931; Ritland 1955a), with its role taken over by a branch of the femoral nerve. This change has been linked to metamorphosis, when there is a loss of some spinal nerves (Green 1931). The presence of a homologue of the obturator canal in *Czatkobatrachus* implies retention of the nerve. This would be consistent with the fact that there has been less reduction of the presacral region in *Czatkobatrachus* than in crown group frogs.

Sacro-caudal joint. — According to Trueb (1973) the anuran sacro-urostylar joint is subject to considerable variation. Most crown-group frogs have a bicondylar sacro-urostylar joint, and this was regarded as primitive by Trueb (1973, see also Duellman and Trueb 1986). However, the Jurassic *Prosalirus*, and the extant *Ascaphus* and *Leiopelma*, retain a simple fibrocartilaginous intercentral connection that is identical to those within the presacral column. This condition is considered to be more primitive by Jenkins and Shubin (1998), and is that found in *Czatkobatrachus*. The *Czatkobatrachus* sacrum retains postzygapophyses, as a plesiomorphic character, as does *Notobatrachus* (Báez and Basso 1996). These are absent in *Prosalirus* (Jenkins and Shubin 1998) and in most extant frogs (Trueb 1973; exceptions include some extant pelobatids and discoglossids).

Limb bones. — Both the humerus and femur display a strikingly anuran morphology that may be at least partly size-dependent. Which, if any, of their characters are synapomorphic for *Czatkobatrachus* and crown-group anurans is a question that requires more extensive studies of the out-groups. The large capitate eminence of the anuran humerus is shared not only by caudates and albanerpetontids (SEE personal observations) but also by the Dissorophioidea and by a more-inclusive group of temnospondyls (the Euskelia of Yates and Warren 2000), and is thus plesiomorphic at the level of Lissamphibia. The size and shape of the ventral crest of the humerus is also similar in both anurans and caudates, but salientians lack the dorsal crest of the humerus, that bears an attachment for the humeral retractor (subscapularis muscle) in caudates. The slender elongate salientian-type femur bears a low ventral crest for the attachment of hip muscles (*mm. pectineus, gluteus, iliofemoralis, pyriformis, quadratus femoris*, and *obturator externus*; Ritland 1955b) instead of the protruding finger-like trochanter serving the same function in caudates. The development of prominent humeral and femoral crests is probably derived for salamanders, with salientians showing the primitive state.

FUNCTIONAL MORPHOLOGY

General axial characters. — Shortening the axial skeleton limits its capacity for lateral undulation during locomotion and implies that both *Czatkobatrachus* and *Triadobatrachus* had already modified their locomotor strategy towards a gait in which there was a greater dependency on the limbs.

Transverse processes. — Reduction of lateral mobility of the vertebral column in *Czatkobatrachus* is also supported by the fusion and, sometimes, by elongation of transverse processes, which suggest the spine was more stiffened in the horizontal plane than that of *Triadobatrachus*. Enlargement of the peri-sacral transverse processes may be associated with strengthening of the ilio-lumbaris (anteriorly) and of caudal musculature homologous to coccygeo-iliacus and coccygeo-sacralis (posteriorly) (Emerson and De Jongh 1980). These may have provided additional support and stabilisation to the ilio-sacral articulation during locomotion (see also for lumbo-dorsal fascia below).

Caudal vertebrae. — The reduction of the tail in *Triadobatrachus*, and presumably also in *Czatkobatrachus* (see above), shows that these animals had moved away from a primarily undulatory mode of locomotion, for which the tail is of great importance. Despite the absence of the urostyle in both these animals, the juxtaposition of a shortened tail between elongate, anteriorly directed ilia may, according to Jenkins and Shubin (1998), represent a primitive stage in the evolution of the anuran caudopelvic musculature linkage. We concur with this view. The absence of any ridges or tuberosities on the cylindrical terminal caudal elements suggests they were not tightly held together and probably retained some flexibility (but see also the information on transverse processes above).

Elements of the caudopelvic mechanism. — Saltation is, without doubt, the most distinctive feature of crown-group frogs and was present in the earliest known and most primitive anuran taxa (*Prosalirus*, *Vieraella*, *Notobatrachus*). The key finding of Emerson and De Jongh (1980) was that the typical anuran saltation mechanism requires a body divided into two components — anterior (head, forelimbs, presacral column and sacrum) and posterior (pelvis, urostyle and hind limbs) separated by a joint (sacro-urostyler) that permitted dorsoventral flexion and extension. In jumping, the sacro-urostyler joint extends to bring the sacrum, presacral series and head into line with the urostyle and the long axis of the ilia.

Sacro-caudal joint. — In extant frogs a loss of sacral postzygapophyses and the development of a bicondylar, uniaxial, joint between the sacral centrum and the urostyle (Jenkins and Shubin 1998) allow for extension-flexion movements in the sacro-urostyler joint. In *Czatkobatrachus*, the retention of both a simple sacro-caudal joint and sacral postzygapophyses do not exclude, but do limit, the potential for dorsoventral excursion of the spine at this joint (Jenkins and Shubin 1998). Modern anurans that lack this capacity also lack true saltation, and have locomotor patterns involving walking, swimming, climbing, or burrowing. This is likely to have been the case for *Czatkobatrachus*.

Ilium. — The presence of an elongate ilium, the shaft of which extends well anterior to the level of the acetabulum, obviously contributed to the stiffening of the posterior body segment. This important element of the frog-type locomotory mechanism had already developed in *Czatkobatrachus* and, to a lesser degree (Fig. 4), in *Triadobatrachus*. The rotation and elongation of the iliac shaft, that occurs prior to metamorphosis in extant frogs (Green 1931), was also one of the first postcranial characters developed in salientian phylogeny. As this iliac elongation evolved well before true saltation, its selective advantage remains obscure, particularly as it now functions in many different locomotory types including jumping, walking, and swimming.

The ilia of *Czatkobatrachus* and *Triadobatrachus* are distinctive in having a hypertrophied dorsal tubercle — dorsal prominence (according to Sanchíz's 1998 terminology). In extant frogs, the dorsal prominence is associated with the origin of the gluteus magnus muscle, a powerful extensor of the hip. The function of hip (and knee) extension in leaping is obvious, but it is less clear why this tubercle should be so enlarged in two taxa that were clearly not saltatory. In most frogs that possess a dorsal prominence, this structure is aligned with the iliac blade and is not protruding. It is, however, hypertrophied in living pipids and some bufonids, apparently in relation to the presence of an accessory tendon of the gluteus magnus muscle that attaches to it (Dunlap 1960; Emerson and Jongh 1980). This tendon is said to be a part of the dorsolumbar fascia and has a role in limiting movement of the urostyle in relation to the pelvic girdle. Both pipids and bufonids are locomotor specialists, swimming or walking respectively. Since they are not related, this is a convergent adaptation. The accessory tendon is not present in either *Ascaphus* or *Leiopelma*, and the same was presumably true of early crown group frogs as the dorsal prominence is not hypertrophied in *Prosalirus* (Jenkins and Shubin 1998), *Vieraella*, or *Notobatrachus* (Báez and Basso 1996). Whether the enlargement of the dorsal prominence of stem-frogs is comparable to that of pipids and bufonids is, of course, impossible to determine but it does suggest the gluteus magnus, or an accessory tendon, had an important role in stem-frog

locomotion, perhaps (as in the living taxa) in stabilisation of the pelvis against the sacrum and tail. This could have been important to taxa like *Czatkobatrachus* and *Triadobatrachus* in which the ilio-sacral joint was still very weak (see below).

Ilio-sacral joint. — Emerson (1979, 1982), Emerson and De Jongh (1980), and Jenkins and Shubin (1998) have dealt with this topic in some depth. The ilio-sacral joint of crown-group frogs is not a synchondrosis or an abutting joint as it is in most tetrapods. Instead, the sacral diapophysis lies above the iliac blade, suspending it by means of a specialised ligament system that frequently contains a sesamoid. Emerson (1982) described three principle types of ilio-sacral joint in frogs, ranging from the specialised joint of pipids (her type I) that permits fore-aft sliding between an expanded sacral diapophysis and a long ilium, to the mechanically simplest kind (her type IIB) in which the sacral diapophysis is only slightly dilated and the iliac blade is suspended from it by means of a ligament that runs from the distal end of the sacral rib to the ventral surface of the ilium. This arrangement, found in basal ascaphids and derived ranids (as well as the Jurassic *Prosalirus*, Jenkins and Shubin 1998), is said to maximise dorsoventral rotation of the pelvis on the sacrum and tends to limit movement to this plane. There is a variant of this arrangement (Type IIA) in which distally expanded sacral processes with arcuate distal edges are connected to the ilium by means of a ligament inserting dorsally near the base of the sacral rib. The difference between types II A and IIB in the position of the ligament origin reflect a difference in mobility, type IIA allowing for a lateral swing of the pelvis on the sacrum. This type, found mostly in walking frogs, tends to increase the range of protraction (and thus stride length), but at the expense of jumping ability (since the body would be less stable in the leap). It could be predicted that early frogs and stem-frogs might have an arrangement intermediate between type IIA and IIB, so that there was both dorso-ventral and lateral movement, permitting walking and imperfect jumping, in the absence of the specialised sacro-urostylar system. This is clearly not the condition in *Triadobatrachus* where the sacral ribs remain separate from the vertebral body and the distal ends are elongated, posteriorly directed processes that have a long abutting contact with the medial side of the ilium (Rage and Roček 1989), much like the arrangement in more basal amphibians. *Czatkobatrachus* has sacral diapophyses that are fused to the vertebral body. Each of them has a widely extended distal end containing a dorsolaterally to laterally facing concavity that probably received the ilium in a lateral (rather than ventral) position. A dorsal ligament furrow, extending medially, well towards the shaft of the sacral process, clearly recalls Emerson's type IIA and suggests lateral mobility rather than jumping. According to Jenkins and Shubin (1998), the ventral position of the ilia with respect to the sacral transverse processes in crown-group frogs positions the pelvis advantageously to transmit vertical thrust to the axial skeleton during jumping. A lateral, rather than ventral, position of the ilia with respect to sacral transverse process, as reconstructed for *Czatkobatrachus*, contributes to the hypothesis that this stem salientian was a walker rather than a jumper.

Musculoskeletal information. — Among the muscles that fire during the initial phase of take-off, and are positively correlated with the height of jump in extant frogs (Emerson and Jongh 1980), only *m. longissimus dorsi* could have functioned in frog style in *Czatkobatrachus*, i.e., to straighten the back, but this is its normal function. The short, rather strong transverse processes show that it was well developed. Two other muscles that contribute to the caudopelvic mechanism in extant frogs, the *mm. coccygeo-sacralis* and *coccygeo-iliacus*, were probably no different in morphology and function from their homologues in other tetrapods, as shown by the lack of a urostyle in *Czatkobatrachus*. The same is probably true of the pyriformis muscle that, in frogs, contributes to posteroventral rotation of the urostyle at take-off. In *Czatkobatrachus* it probably still acted like the caudifemoralis muscle of caudates, to retract the femur and flex what was left of the tail.

Pectoral girdle. — The nature of the arciferal pectoral girdle organization ascribed to *Czatkobatrachus* (Fig. 5C) is difficult to interpret in functional terms. According to Emerson (1983), the ventral cartilages of arciferal frogs rotate in a horizontal plane, but the exact biomechanical significance of this mobility remains obscure. There is no obvious correlation between locomotion type and girdle type, jumping frogs being both arciferal and firmisternal as are the hopping/walking types (Emerson 1983). In *Czatkobatrachus*, the slender proportions of the scapula are somewhat similar to those of some neobatrachians (*Bufo*, *Rana*, and *Rhinoderma*; Trueb 1973, fig. 2-9c, d, e), but also to the early Jurassic frog *Vieraella herbsti* (Báez and Basso 1996, figs 6, 7), and contrast with short scapulae of ascaphids, discoglossids and pipids (Trueb 1973, fig. 2-9i, j, g). The shape is also very different from that of *Triadobatrachus* (Rage and Roček 1989). This difference must

be interpreted in functional, rather than phylogenetic terms, but the function remains obscure. More conclusive is the structure of the glenoid discussed in detail elsewhere (Borsuk-Białynicka and Evans 2002). In essence, the structure of the glenoid, which is relatively large in vertical diameter, suggests a greater range of dorsoventral mobility for the forelimb than that of outgroup temnospondyl clades where forelimb movement was primarily horizontal. The directly lateral orientation of the glenoid results in a humeral resting position that was perpendicular to the body axis rather than oblique. This lateral orientation of the glenoid differs from the more posterolateral position of outgroup taxa and the more posterior position of crown-group frogs, but is similar to that of caudates. It has been tentatively interpreted as an early adaptation towards maintaining balance, preventing an animal burdened with a heavy head from falling forwards (Borsuk-Białynicka and Evans 2002). Overall, therefore, the scapulocoracoid of *Czatkobatrachus* suggests terrestrial locomotion in which the forelimbs had a role in raising the body off the ground.

Limb bones. — The humerus of *Czatkobatrachus* is slender and elongate, and apparently more strongly ossified than is usual in extant frogs. It has rather elaborate ends that are completely co-ossified with the shaft. The proximal end of the *Czatkobatrachus* humerus may have been more heavily loaded and subjected to a greater degree of stress, perhaps because the body was less balanced (although it was a very light animal). The distal end is also strongly ossified (as is the corresponding ulna joint) but is more closely similar in its morphology to that of extant frogs, except that the antebrachial bones were not fused. The asymmetry of the epicondyles in *Czatkobatrachus* is interesting, given that symmetrical radial and ulnar epicondyles, as found in *Ascapus* and *Notobatrachus* (Báez and Basso 1996), were thought to be primitive. However, in living frogs the development of the epicondyles, and of the associated medial and lateral crests, can be size and sex dependent (Ritland 1955a). Nonetheless, since the ulnar epicondyle provides the common origin for the flexor muscles of the hand, this movement may have been more important in *Czatkobatrachus*. The significant length and ossification of the olecranon reflects the size of the triceps muscles extending the elbow joint, an important action for anterior body elevation. This process is also well-developed in the amphibamid *Gerobatrachus* (Anderson *et al.* 2008).

Gans and Parsons (1965) suggested that stem-frogs may have waited for prey with the body propped up on the forelimbs, thrusting forward to grab food using the forelimbs as fixed points. The morphology of the *Czatkobatrachus* forelimbs would be consistent with this hypothesis.

According to Jenkins and Shubin (1998), the length of the femur in the earliest recorded crown-group frog, *Prosalirus*, is about 9.9 of that of a dorsal vertebra, with that in *Notobatrachus* at 8.5, *Bombina* at 8.1, *Bufo* at 7, and *Triadobatrachus* at 4.9 times the dorsal length. In *Czatkobatrachus*, as preserved, this value is around 6.5. *Czatkobatrachus* femur is longer and more slender than that of the Malagasy stem frog, but shorter than in crown-group leapers, although given the significantly longer vertebral centra of *Czatkobatrachus*, the difference is not significant. The humerus of *Czatkobatrachus* is unusually long (83%) in relation to femoral length, by comparison with *Triadobatrachus* (77%), *Bufo marinus* (75%), *Prosalirus* (70.6%), *Notobatrachus* (65%), and *Rana temporaria* (62.5%). Frogs moving primarily by saltation have relatively shorter fore-limbs than those, like *Bufo*, which do not.

CONCLUSIONS

The detailed study of the postcranial remains of the early Triassic genus *Czatkobatrachus* have not altered the original hypotheses (Evans and Borsuk-Białynicka 1998) with respect to the position of this genus in salientian phylogeny (Fig. 11). *Czatkobatrachus* shows a combination of primitive and derived character states that together place it between purported stem-lissamphibians (*e.g.*, *Gerobatrachus*) and crown-group anurans. However, its position with respect to *Triadobatrachus* remains unclear. Many of its characters (humeral morphology, ilio-sacral morphology, scapula shape, the fusion of the transverse processes) appear to position *Czatkobatrachus* above *Triadobatrachus* on the anuran stem, but these differences could relate to function and lifestyle, if *Triadobatrachus* were less terrestrial.

The most obvious derived characters shared by *Czatkobatrachus*, *Triadobatrachus* and the Anura relate to the pelvis (*i.e.*, the anteriorly elongate ilium and, consequently, posterior position of the acetabulum with

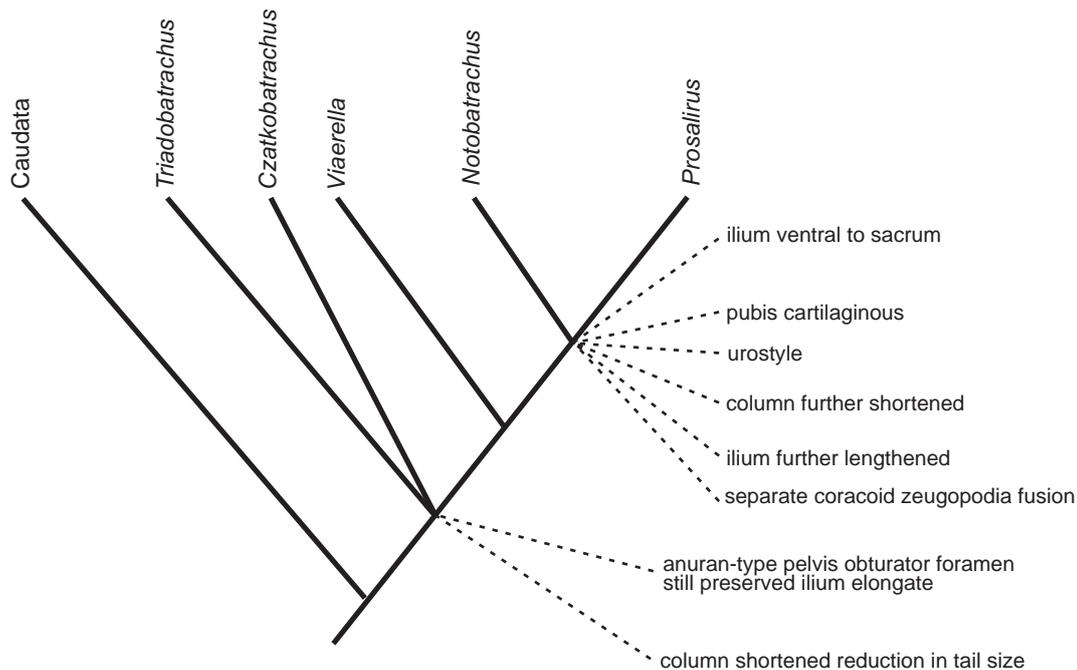


Fig. 11. A possible sequence of character states in salientian phylogeny. Phylogenetic diagram after Evans and Borsuk-Białynicka (1998).

respect to the ilio-sacral joint, and the reduced pubis). The ilium is less elongate than it is in the crown-group frogs but more so than in *Triadobatrachus*.

A shortened presacral column and the reduction in length of the tail, would be further synapomorphies of the Salientia, if our reconstruction, based on vertebra size and structure in *Czatkobatrachus*, is confirmed by the recovery of further articulated material. Similarly, long slender propodials and the loss of the interglenoid tubercle are also putative salientian synapomorphies. The posterior shift of the first spinal nerve, to a position that notches the anterior margin of the neural pedicel of the atlas, is an expression of a lissamphibian evolutionary trend.

Although the material is still limited, we have data on four key regions in the evolution of salientian locomotion: the axial skeleton, the pectoral girdle, the pelvis, and the limb proportions. These suggest *Czatkobatrachus* had taken the following steps:

(1) A shift in locomotor pattern away from lateral undulation toward greater dependence on the limbs (fusion of the ribs to the vertebrae, strong transverse processes, the tail probably reduced in length).

(2) The development of a slender scapula, and a large circular glenoid facing laterad within a basically arciferal pectoral girdle. These characters might be *Czatkobatrachus* autapomorphies related to the importance of the forelimbs in propping up the body, in a stage transitional between caudate-like locomotion and that of anurans. The strongly and fully ossified elbow joint suggests that this was an important part of the same functional complex for this small amphibian.

(3) The development of an anteriorly directed cylindrical iliac shaft, with a large dorsal prominence (associated with gluteus magnus or its stabilising tendon). The orientation of the iliac blade implies that thrust forces from the legs were already being directed anteriorly parallel to the body axis, even if the animal was not yet leaping. The ilio-sacral joint had been modified from an abutting cartilage covered joint into a primarily suspensory one, the two components being fastened by a ligament. The ilium was still positioned lateral to the sacral transverse process at the ilio-sacral joint, but was stabilised both dorsally and ventrally by parts of the sacral diapophysis. However, the posterodorsal convexity might represent a rudiment of the sacral flange that overlaps the ilium dorsally in crown-group frogs. The combination of a pelvis modified to transmit thrust anteriorly, with a weak ilio-sacral joint and a short but probably flexible tail, would have placed considerable reliance on the soft tissues holding these elements together. This may explain the increased size of the peri-sacral transverse processes and the enlargement of the dorsal prominence of the ilium (for a stabilising tendon of gluteus magnus).

(4) The development of longer, more gracile limbs without strong muscle attachment surfaces. The retention of fore- and hind limbs of similar length is a primitive character, compared to the disparity found in crown-group anurans. However, the elongation of the humeri, by comparison with both *Triadobatrachus* and crown-group frogs, may represent another autapomorphy of *Czatkobatrachus*, reflecting an unusual, transitional, locomotor pattern.

In combination, these features suggest *Czatkobatrachus* was a small agile terrestrial animal that walked, and perhaps hopped, with a stiffened back, and a reduced tail. It thus shows many of the morphological features predicted by Gans and Parsons (1965) for the ancestral stem-frog stage. *Czatkobatrachus* was substantially smaller than *Triadobatrachus*, was longer limbed, and would have been more agile. It was probably also more fully terrestrial, judging by the higher degree of ossification throughout the skeleton (even by comparison with basal crown-group taxa).

The reconstructed palaeoenvironment for *Czatkobatrachus* (Borsuk-Białynicka *et al.* 1999; Cook and Trueman 2009) was a small non-permanent water body (or group of such water bodies), surrounded locally by vegetation (oasis), but in a rather arid environment. This is precisely the environment envisaged by Hecht (1962) and Gans and Parsons (1965) for the stem-group frog stage. Food, in the form of insects, is likely to have been concentrated in the vegetation around the water, providing a focus for small vertebrates.

Together *Triadobatrachus* and *Czatkobatrachus* demonstrate that the evolution of the pelvis (elongate anteriorly directed blades, reduced pubis) and some aspects of the ilio-sacral joint (loosening of the ilio-sacral contact, development of a suspensory system), preceded the evolution of those features uniquely associated with saltation (the urostyle, fusion and elongation of the antibrachial and tibiofibular bones, a separate coracoid element and more parasagittal position of the fore-limb for jumping). The saltatory functional complex had evolved by the Early Jurassic (*Prosalirus* Shubin *et al.* 1995), but further Triassic material is needed in order to determine the sequence of intermediate steps. These may, in turn, shed light on the peculiar functional complex presented by *Czatkobatrachus*, as would the recovery of more of its Permian antecedents (*Geroatrachus* being an important recent addition). Since very few localities of appropriate age yield articulated specimens, microvertebrate localities like Czatkowice probably offer the best chance of filling the void.

REFERENCES

- Anderson, J.S., Reisz, R.R., Scott, D., Fröbisch, N.B., and Sumida, S.S. 2008. A stem batrachian from the Early Permian of Texas and the origin of frogs and salamanders. *Nature* **453**, 515–518.
- Báez, A.M. and Basso, N.G. 1996. The earliest known frogs of the Jurassic of South America: Review and cladistic appraisal of their relationships. *Münchener Geowissenschaftliche Abhandlungen A* **30**, 131–158.
- Blanco, M.J. and Sanchiz, B. 2000. Evolutionary mechanisms of rib loss in anurans: a comparative developmental approach. *Journal of Morphology* **244**, 57–67.
- Bolt, J.R. 1969. Lissamphibian origins: possible protolissamphibians from the Lower Permian of Oklahoma. *Science* **166**, 888–891.
- Bolt, J.R. 1977. Dissorophoid relationships and ontogeny, and the origin of the Lissamphibia. *Journal of Paleontology* **51**, 235–249.
- Bolt, J.R. 1991. Lissamphibian origin. In: H.-P. Schultze and L. Trueb (eds) *Origin of Higher Groups of Tetrapods: Controversy and Consensus*, 194–222. Comstock Publishing Associates, Ithaca and London.
- Bolt, J.R. and Lombard, R.E. 1985. Evolution of the tympanic ear and the origin of frogs. *Biological Journal of the Linnean Society* **24**, 83–99.
- Borsuk-Białynicka, M. and Evans, S.E. 2002. The scapulocoracoid of an Early Triassic stem-frog from Poland. *Acta Palaeontologica Polonica* **47**, 79–96.
- Borsuk-Białynicka, M., Cook, E., Evans, S.E., and Maryńska, T. 1999. A microvertebrate assemblage from the Early Triassic of Poland. *Acta Palaeontologica Polonica* **44**, 167–188.
- Borsuk-Białynicka, M., Maryńska, T., and Shishkin, M.A. 2003. New data on the age of the bone breccia from the locality Czatkowice 1 (Cracow Upland, Poland). *Acta Palaeontologica Polonica* **48**, 153–155.
- Boy, J.A. and Sues, H.-D. 2000. Branchiosaurs: larvae, metamorphosis and heterochrony in temnospondyls and seymouriamorphs. In: H. Heatwole and R. L. Carroll (eds) *Amphibian Biology, Volume 4, Palaeontology*, 1150–1197. Surrey Beatty and Sons, Chipping Norton.
- Burke, A.C., Nelson, C.E., Morgan, B.A., and Tabin, C. 1995. Hox genes and the evolution of vertebrate axial morphology. *Development* **121**, 333–346.

- Cannatella, D.C. and Hillis, D.M. 1993. Amphibian relationships: phylogenetic analysis of morphology and molecules. *Herpetological Monographs* **7**, 1–7.
- Carroll, R.L. 1999. The ancestry and interrelationships of modern amphibians. *Canadian Association of Herpetologists Bulletin* **13**, 2–7.
- Carroll, R.L. and Gaskill, P. 1978. The order Microsauria. *Memoirs of the American Philosophical Society* **126**, 1–211.
- Carroll, R.L. and Holmes, R. 1980. The skull and jaw musculature as guides to the ancestry of salamanders. *Zoological Journal of the Linnean Society* **68**, 1–40.
- Carroll, R.L., Kuntz, A., and Albright, K. 1999. Vertebral development and amphibian evolution. *Evolution and Development* **1**, 136–48.
- Cook, E. and Trueman, C. 2009. Taphonomy and geochemistry of a vertebrate microremains assemblage from the Early Triassic karst deposits at Czatkowice 1, southern Poland. *Palaeontologia Polonica* **65**, 17–30.
- Daly, E. 1994. The Amphibamidae (Amphibia: Temnospondyli), with a description of a new genus from the Upper Pennsylvanian of Kansas. *The University of Kansas Museum of Natural History Miscellaneous Publications* **85**, 1–55.
- Deuchar, E. 1975. *Xenopus: The South African Clawed Toad*. 246 pp. John Wiley and Sons, London.
- Duellman, W.E. and Trueb, L. 1986. *Biology of the Amphibians*. 669 pp. McGraw-Hill Book Company, New York.
- Dunlap, D.G. 1960. The comparative myology of the pelvic appendage in the Salientia. *Journal of Morphology* **106**, 1–76.
- Emerson, S.B. 1979. The ilio-sacral articulation in frogs: form and function. *Biological Journal of the Linnean Society* **11**, 153–168.
- Emerson, S.B. 1982. Frog postcranial morphology: identification of a functional complex. *Copeia* **1982**, 603–613.
- Emerson, S.B. 1983. Functional analysis of frog pectoral girdles. The epicoracoid cartilages. *Journal of Zoology, London* **201**, 293–308.
- Emerson, S.B. and De Jongh, H.J. 1980. Muscle activity at the ilio-sacral articulation of frogs. *Journal of Morphology* **166**, 129–144.
- Estes, R. 1981. Gymnophiona, Caudata. In: P. Wellnhofer (ed.) *Handbuch der Paläoherpetologie*, 2, 1–113. Gustav Fischer Verlag, Stuttgart.
- Estes, R. and Reig, O. 1973. The early fossil record of frogs; a review of the evidence. In: J.L. Vial (ed.) *Evolutionary Biology of the Anurans*, 11–63. University of Missouri Press, Columbia.
- Evans S.E. and Borsuk-Białynicka, M. 1998. A stem-group frog from the Early Triassic of Poland. *Acta Palaeontologica Polonica* **43**, 573–580.
- Evans, S.E. and Sigogneau-Russell, D. 2001. A stem-group caecilian (Lissamphibia: Gymnophiona) from the Lower Cretaceous of North Africa. *Palaeontology* **44**, 259–273.
- Evans, S.E., Milner, A.R., and Mussett, F. 1988. The earliest known salamanders (Amphibia: Caudata): a record from the Middle Jurassic of England. *Geobios* **21**: 539–552.
- Feller, A.E. and Hedges, S.B. 1998. Molecular evidence for the early history of living amphibians. *Molecular Phylogenetics and Evolution* **9**, 509–516.
- Ford, L.S. and Cannatella, D.C. 1993. The major clades of frogs. *Herpetological Monographs* **7**, 94–117.
- Fox, H. 1954. Development of the skull and associated structures in the Amphibia with special reference to the urodeles. *Transactions of the Zoological Society of London* **28**, 241–304.
- Francis, E.T.B. 1934. *The Anatomy of the Salamander*. 381 pp. Clarendon Press, Oxford.
- Gans, C. and Parsons, T.S. 1965. On the origin of the jumping mechanism in frogs. *Evolution* **20**, 92–99.
- Gardner, J. 2000. Revised taxonomy of albanerpetontid amphibians. *Acta Palaeontologica Polonica* **45**, 55–70.
- Gauthier, J., Cannatella, D., de Queiroz, K., Kluge, A.G., and Rowe, T. 1989. Tetrapod phylogeny. In: B. Fernholm, K. Bremer, and H. Jornvall (eds) *The Hierarchy of Life*, 337–353. Elsevier Science Publishers B.V., New York.
- Goodrich, E.S. 1911. On the segmentation of the occipital region of the head in the Batrachia Urodela. *Proceedings of the Zoological Society of London* **1911**, 101–120.
- Green, T.L. 1931. On the pelvis of the Anura: a study in adaptation and recapitulation. *Proceedings of the Zoological Society of London* **4**, 1259–1290.
- Griffiths, I. 1963. The phylogeny of the Salientia. *Biological Reviews of the Cambridge Philosophical Society* **38**, 241–292.
- Hay, J.M., Ruvinsky, I., Hedges, S.B., and Maxson, R.L. 1995. Phylogenetic relationships of the amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. *Molecular Biology and Evolution* **12**, 928–937.
- Hecht, M.K. 1960. The history of the frogs. *Anatomical Record* **138**, 365.
- Hecht, M.K. 1962. A reevaluation of the early history of the frogs. Part I. *Systematic Zoology* **11**, 39–44.
- Jacobson, A.G. 1993. Somitomeres: mesodermal segments of the head and trunk. In: J. Hanken and B.K. Hall (eds) *The Skull, Volume 1, Development*, 42–76. The University of Chicago Press, Chicago.
- Jenkins, F. Jr and Shubin, N. 1998. *Prosalirus bitis* and the anuran caudopelvic mechanism. *Journal of Vertebrate Paleontology* **18**, 495–510.
- Jenkins, F. Jr and Walsh, D.M. 1993. An early Jurassic caecilian with limbs. *Nature* **363**, 501–502.
- Kluge, A.G. and Farris, J.S. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* **18**, 1–32.
- Laurin, M. and Reisz, R.R. 1997. A new perspective in tetrapod phylogeny. In: S. Sumida and K.L.M. Martin (eds) *Amniote Origins*, 9–59. Academic Press, San Diego.
- Laurin, M., Girondot, M. and De Ricqlès, A. 2000. Early tetrapod evolution. *Trends in Ecology and Evolution* **15**, 118–123.
- Lynch, J.D. 1973. The transition from archaic to advanced frogs. In: J.L. Vial (ed.) *Evolutionary Biology of the Anurans*, 133–182. University of Missouri Press, Columbia.

- McGowan, G.J. and Evans, S.E. 1995. Albanerpetontid amphibians from the early Cretaceous of Spain. *Nature* **373**, 143–145.
- Milner, A.R. 1988. The relationships and origin of living amphibians. In: M.J. Benton (ed.) *The Phylogeny and Classification of the Tetrapods*, Vol. 1. *Systematics Association Special Volume* **35A**, 59–102. Clarendon Press, Oxford.
- Milner, A.R. 1990. The radiation of temnospondyl amphibians. In: P.D. Taylor and G.P. Larwood (eds) *Major Evolutionary Radiations*, 321–349. Clarendon Press, Oxford.
- Milner, A.R. 1993. The Paleozoic relatives of lissamphibians. *Herpetological Monographs* **7**, 8–27.
- Mookerjee, H.K. 1930. On the development of the vertebral column in Urodela. *Philosophical Transactions of the Royal Society of London B* **218**, 415–446.
- Mookerjee, H.K. 1931. On the development of the vertebral column of Anura. *Philosophical Transactions of the Royal Society of London B* **219**, 165–196.
- Noble, G.K. 1922. The phylogeny of the Salientia. I. The osteology and the thigh musculatur; their bearing on the classification and phylogeny. *Bulletin of the American Museum of Natural History* **46**, 1–87.
- Parsons, T.S. and Williams, E.E. 1962. The teeth of Amphibia and their relationship to amphibian phylogeny. *Journal of Morphology* **110**, 375–389.
- Parsons, T.S. and Williams, E.E. 1963. The relationships of the modern Amphibia: a reexamination. *Quarterly Review of Biology* **38**, 26–53.
- Paszkowski, M. 2009. The Early Triassic karst of Czatkowice 1, southern Poland. *Palaeontologia Polonica* **65**, 7–16.
- Paszkowski, M. and Wieczorek, J. 1982. Fossil karst with Mesozoic bone breccia in Czatkowice 1 (Cracow Upland, Poland). *Kras i speleologia* **3**, 32–38.
- Piveteau, J. 1937. Paléontologie de Madagascar. XXIII. Un Amphibien du Trias inférieur. *Annales de Paléontologie* **26**, 135–177.
- Rage, J.-C. and Janvier, Ph. 1982. Le problème de la monophylie des Amphibiens actuels, à la lumière des nouvelles données sur les affinités des Tetrapodes. *Geobios, Mémoire spéciale* **6**, 65–83.
- Rage, J.-C. and Roček, Z. 1989. Redescription of *Triadobatrachus massinoti* (Piveteau, 1936) an anuran amphibian from the Early Triassic. *Palaeontographica, Abteilung Paläozoologie-Stratigraphie* **206**, 1–16.
- Richardson, M.K., Allen, S.P., Wright, G.M., Raynaud, A., and Hanken, J. 1998. Somite number and vertebrate evolution. *Development* **125**, 151–160.
- Ritland, R.M. 1955a. Studies of the post-cranial morphology of *Ascaphus truei*. — Part I Skeleton and spinal nerves. *Journal of Morphology* **97**, 119–177.
- Ritland, R.M. 1955b. Studies of the post-cranial morphology of *Ascaphus truei*. — Part II Myology. *Journal of Morphology* **97**, 215–282.
- Roček, Z. and Rage, J.-C. 2000. The anatomical transformations from temnospondyl to proanuran stages. In: H. Heatwole and R.L. Carroll (eds) *Palaeontology: The Evolutionary History of Amphibians*, 1274–1294. Surrey Beatty and Sons, Chipping Norton, Australia.
- Sanchíz, B. 1998. Salientia. In: P. Wellnhofer (ed.) *Handbuch der Paläontologie* **4**, 1–275. Verlag Dr. Friedrich Pfeil, München.
- Shishkin, M.A. [Шишкин, М.А.] 1973. Морфология древних земноводных и некоторые проблемы эволюции низших тетрапод [The morphology of the early amphibians and some problems of the lower tetrapod evolution]. *Труды Палеонтологического Института АН СССР* **137**, 1–260.
- Shishkin, M.A. 2000. Evolution of the cervical vertebrae in temnospondyl amphibians and differentiation of the early tetrapods. *Palaeontological Journal* **34**, 534–546.
- Shubin, N.H. and Jenkins, F.A. Jr. 1995. An Early Jurassic jumping frog. *Nature* **377**, 49–51.
- Szarski, H. 1962. The origin of Amphibia. *Quarterly Review of Biology* **37**, 189–241.
- Trueb, L. 1973. Bones, frogs and evolution. In: J.L. Vial (ed.) *Evolutionary Biology of the Anurans*, 65–132. University of Missouri Press, Columbia.
- Trueb, L. and Cloutier, R. 1991. A phylogenetic investigation of the inter- and intrarelationships of the Lissamphibia (Amphibia, Temnospondyli). In: H.-P. Schultze and L. Trueb (eds) *Origin of the Higher Groups of Tetrapods — Controversy and Consensus*, 223–313. Cornell University Press, Ithaca.
- Yates, A.M. and Warren, A.A. 2000. The phylogeny of the “higher” temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society* **128**, 77–121.
- Wake, D.B. and Lawson, R. 1973. Developmental and adult morphology of the vertebral column in the plethodontid salamander *Eurycea bislineata*, with comments on vertebral evolution in the Amphibia. *Journal of Morphology* **139**, 251–299.

