A stem-group frog from the Early Triassic of Poland

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Described on the basis of disarticulated postcranial bones (vertebrae, humeri, ilia) from karst deposits of Scythian age at the locality of Czatkowice in the Kraków Upland, Poland, *Czatkobatrachus polonicus* gen. et sp. n. is the first salientian known from the Triassic of the Northern part of Pangea. It may be only slightly younger (about 5 MA) than *Triadobatrachus massinoti* (Piveteau, 1936) from Madagascar, the only Early Triassic salientian known hitherto. *Czatkobatrachus* resembles *Triadobatrachus* but is more derived in some features of the vertebrae and elbow joint. It provides evidence of a global distribution of stem-frogs at the very beginning of the Mesozoic, and suggests that the origin of the group must be sought in the Permian.

Key words: Anura, Lissamphibia, Salientia, Triassic, Poland.

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Introduction

Frogs (Anura) form a successful and very distinctive component of the modern biota. Their early history, however, remains very poorly known and this complicates discussion of their origins, evolution, and relationships. Until now, the Triassic record has been based on a single specimen, *Triadobatrachus*, from the Early Triassic of Madagascar (Rage & Roček 1989), but the morphological, temporal (50 Ma) and geographical gap between it and the earliest true frogs is considerable. The latter are currently represented by a small group of Early to Middle Jurassic taxa – *Prosalirus* (Shubin & Jenkins 1995) from the Early Jurassic of North America, the slightly younger *Vieraella* and *Notobatrachus* from Argentina (Baez & Basso 1996), and the Middle Jurassic *Eodiscoglossus* from England (Evans *et al.* 1990). Like modern frogs, these Jurassic taxa were short-bodied and tail-less, with long hind limbs. *Triadobatrachus*, in contrast, was relatively long-bodied, had short hind limbs, and retained at least six tail vertebrae, although it shares a small suite of characters with the younger taxa – most notably the anteriorly-elongated blade of the ilium. Clearly, there is a substantial hiatus in the early record of Salientia (Milner 1988), and the recovery of additional Triassic material is a priority.

Czatkowice is a limestone quarry in the Kraków Upland region of Poland. The microvertebrate material described here comes from a single fissure, Czatkowice 1 (Paszkowski & Wieczorek 1982). The karstification phase during which the infillings of Czatkowice 1 were deposited may have lasted from the Late Permian to the Early Triassic, but ended when the entire region was submerged by the Röth Transgression at the end of the Scythian (about 238 Ma). Czatkowice 1 is yielding a diverse Early Triassic microvertebrate assemblage including a range of reptiles (procolophonids, lepidosauromorphs, prolacertiforms and basal archosaurs), as well as fish and amphibians. Amphibian bones are extremely rare, but they include elements which show morphological features unique to the Salientia.

Institutional abbreviations: MNHN – Museum National d'Histoire Naturelle, Paris; ZPAL – Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Description

Amphibia Linné, 1758
Salientia Laurenti, 1768
Family indet.
Czatkobatrachus gen. n.

Type species: *Czatkobatrachus polonicus* sp. n.

Derivation of name: From the type locality of Czatkowice near Kraków, Poland, and Greek *batrachos* – a frog.

Diagnosis. — As for the species.

Range. — Early Triassic of Poland.

Czatkobatrachus polonicus sp. n.

Derivation of name: From the country of origin, Poland.

Holotype: ZPAL Ab.IV/7, a partial right ilium (Figs 1B, 2A).

Other illustrated specimens: ZPAL Ab.IV/3 partial right humerus (Fig. 2B, C); ZPAL Ab.IV/6 presacral vertebra (Fig. 3A); ZPAL Ab.IV/8 (Fig. 3E) and ZPAL Ab.IV/10 (Fig. 3B) sacral vertebrae; ZPALAb.IV/15 atlas centrum (Fig. 3F, G); ZPAL Ab.IV/20 caudal vertebra (Fig. 3C, D); ZPALAb.IV/23 partial ulna (Fig. 2D). Other referred material: ZPAL Ab.IV/2, Ab.IV/12, Ab.IV/13, partial right humeri; Ab.IV/4, Ab.IV/5, Ab.IV/9, Ab.IV/18, Ab.IV/19, Ab.IV/21, partial left ilia; Ab.IV/17, partial right ilium; Ab.IV/16, partial left ilium and fused ischium; Ab.IV/11, Ab.IV/14, presacral vertebrae; Ab.IV/22 caudal vertebra; and further humeral (4) and vertebral (11) specimens as yet uncatalogued.

Diagnosis. — A small frog-like amphibian (about 50 mm snout-vent length), showing the following combination of derived character states: ilium with very prominent dorsal tuberosity; atlantal centrum single and without rib facets, anterior cotyles well spaced and slightly divergent; most or all presacral vertebrae bearing long slender transverse processes; sacral rib robust, posterolaterally curved, fused to vertebral

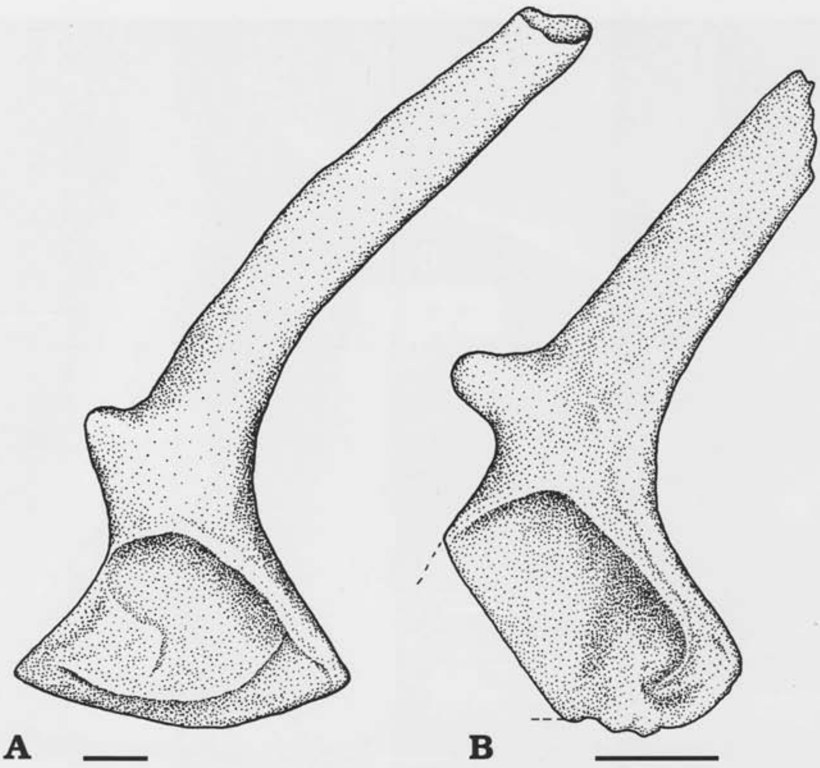

Fig. 1. **A**. *Triadobatrachus massinoti* (Piveteau, 1936), right ilium, MNHN, MAE 126. **B**. *Czatkobatrachus polonicus* gen. et sp. n., right ilium, holotype ZPAL Ab.IV/7. Scale bars 1mm.

centrum; slender humerus with a distinct olecranon scar and a well-ossified single distal humeral condyle, the width of which equals or exceeds 60% of the width of the distal humeral head; humeral condyle asymmetrically placed (medial epicondyle larger than lateral one).

Comparisons. — *Czatkobatrachus* resembles *Triadobatrachus* and all other known salientians in having an anteriorly elongated iliac blade and holocentrous vertebrae; it resembles *Triadobatrachus* and differs from all other known salientians in retaining relatively long vertebral neural arches, unfused epipodials, and unfused caudals. It also resembles *Triadobatrachus* in the shape of the ilium with its prominent dorsal tuberosity (Fig. 1) although the acetabulum is relatively wider and the tubercle more prominent in the Polish form. *Czatkobatrachus* differs from *Triadobatrachus* and resembles other more derived salientians in having the sacral ribs fused to the vertebrae, in having long slender transverse processes on the trunk vertebrae (free ribs therefore absent or very reduced), and in having a single atlantal centrum (bipartite in *Triadobatrachus*, see Rage & Roček 1989) which lacks any trace of rib facets. *Czatkobatrachus* also resembles some derived frogs, and differs from *Triadobatrachus*, *Vieraella*, *Prosalirus*, and *Notobatrachus*, in having a fully ossified elbow joint (ossified humeral radial condyle and ossified ulnar olecranon) although the polarity of this character is uncertain.

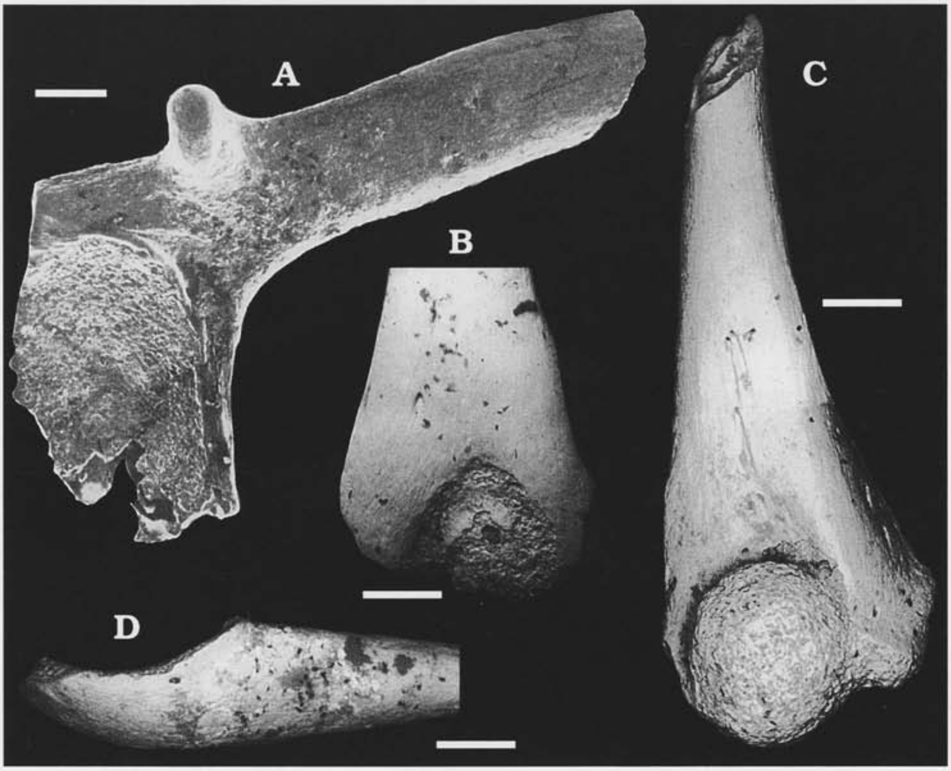

Fig. 2. *Czatkobatrachus polonicus* gen. et sp. n., isolated bones. **A**. Holotype right ilium, ZPAL Ab.IV/7, lateral view. **B**, **C**. Partial right humerus, ZPAL Ab.IV/3, in partial dorsal (**B**) and ventral (**C**) views. **D**. Ulna, ZPAL Ab.IV/23, side view of olecranon region. All SEM micrographs; scale bars 0.5 mm.

Discussion

Attribution of the material. — The Czatkowice material is dissociated and attribution of specimens to *Czatkobatrachus* is made on the basis of resemblance to other primitive salientians and modern frogs. The atlas, humeri and ilia are distinctively salientian in their morphology. The post-atlantal vertebrae share a common structure (ectochordal centra in which the dorso-lateral margins bear a comma-shaped thickening, relatively elongated neural arches, no trace of neurocentral sutures, small size and delicate build) and clearly belong to a single genus. The form of the centrum is identical to that of the attributed atlas, and the vertebrae are compatable in size with the ilia and humeri. They also show a close general resemblance to the vertebrae of *Triadobatrachus*. The thin cylindrical ectochordal centrum is quite different from the more robustly built centrum of a small reptile (e.g., a notochordal lepidosauromorph), and quite different from that of small temnospondyls (to which the other amphibian material from the locality has been attributed). The vertebrae can therefore be referred to *Czatkobatrachus* with some confidence. In most presacral vertebrae, the transverse processes are broken, but ZPAL Ab.IV/ 6 (Fig. 3A) preserves a long narrow process

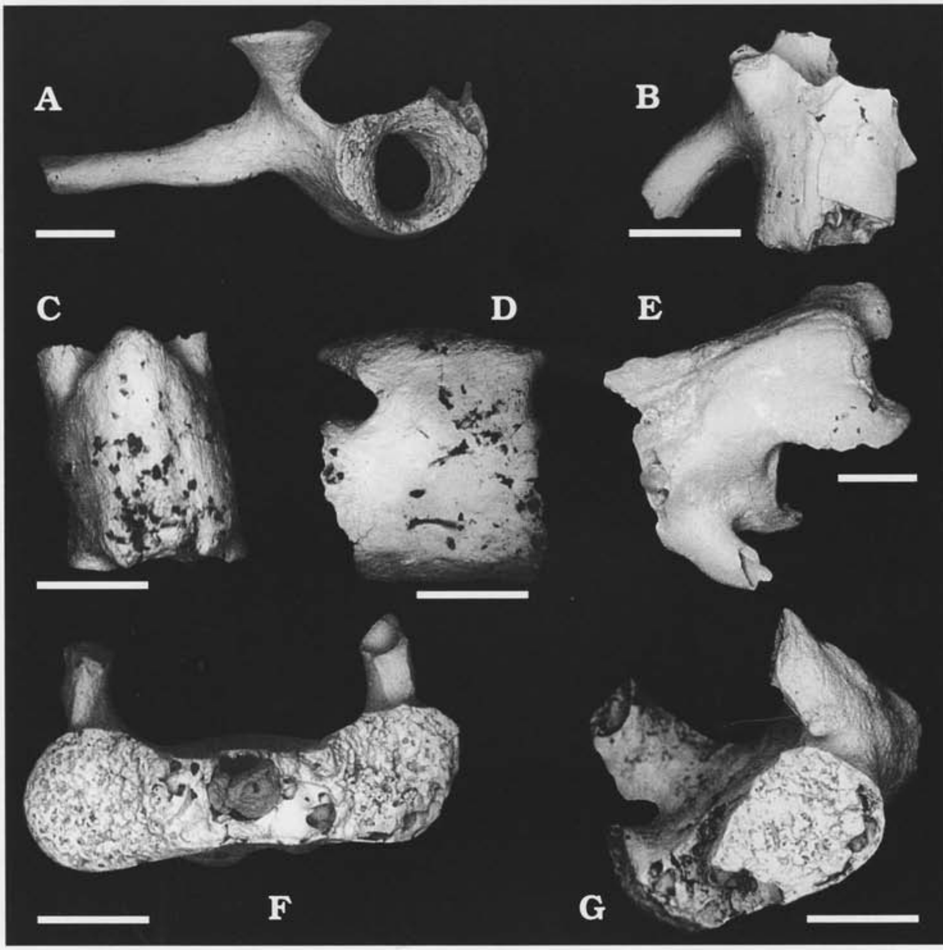

Fig. 3. *Czatkobatrachus polonicus* gen. et sp. n., isolated bones. **A**. Presacral vertebra, ZPAL Ab.IV/6, anterior view. **B**. Sacral vertebra, ZPAL Ab.IV/10, dorsal view. **C**, **D**. Caudal vertebra, ZPAL Ab.IV/20 in dorsal (**C**) and left lateral (**D**) views. **E**. Sacral vertebra, ZPAL Ab.IV/8, left lateral view. **F**, **G**. Atlas, ZPAL Ab.IV15 in anterior (**F**) and antero-lateral (**H**) views. All SEM micrographs; scale bars 0.5 mm.

culminating in a slightly expanded unicapitate tip which may have supported a small free rib such as that of living discoglossid frogs. The sacral transverse processes are very robust and are directed posterolaterally (Fig. 3B, E). The general shape again resembles that of *Triadobatrachus*, except that the ribs are fused to the centrum. Finally, there are two small vertebrae (ZPAL Ab.IV/20 and Ab.IV/22, Fig. 3C, D) which share the common central morphology but are much smaller and lack either transverse processes or proper zygapophyses. They resemble the tiny caudal vertebrae of *Triadobatrachus* and suggest that *Czatkobatrachus* also retained a small tail. A single ulna with a fully ossified olecranon (Fig. 2D) is tentatively attributed to *Czatkobatrachus* since this is the only animal in the deposit known to have an ossified distal humeral condyle (Fig. 2B, C), and the size and curvature of the olecranon provide

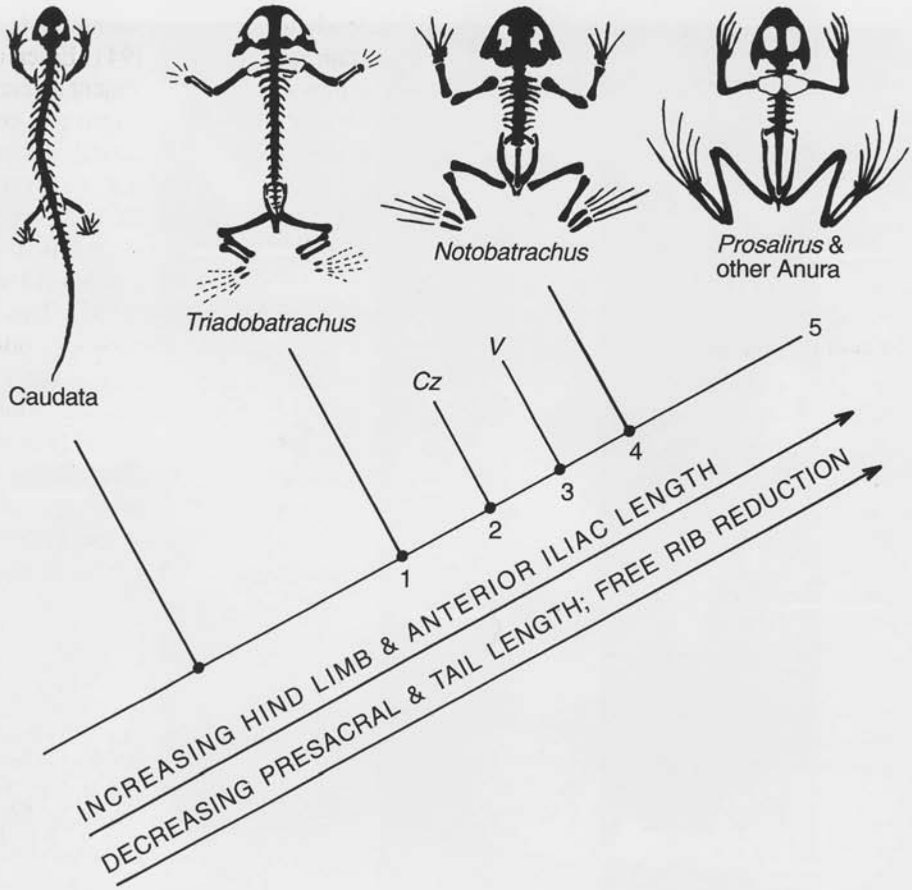

Fig. 4. Diagram (based on Baez & Basso 1996) showing hypothesized relationships of early salientians with the addition of *Czatkobatrachus* and *Prosalirus*: 1 – Salientia, pelvis with anteriorly directed iliac blade; single distal humeral condyle; reduction of tail; 14 or fewer presacral vertebrae; 2 – Unnamed node (Cz = *Czatkobatrachus*), elongate transverse processes on some or all presacrals, sacral rib fused to vertebral centrum; single atlantal centrum; no atlantal ribs; 3 – Unnamed node (V = *Vieraella*), shortened presacral neural arches, loss of tail, fusion of radius+ulna, tibia+fibula; 4 – Unnamed node, 9 or fewer presacral vertebrae, coccyx present; hind limb substantially longer than fore limb; 5 – Anura, well ossified sphenethmoid; no separate caudal vertebra between sacrum and coccyx.

a good match. If the attribution is correct then, as in *Triadobatrachus*, the ulna and radius remained unfused.

Phylogenetic discussion. — Allowing for the limited characters available, *Czatkobatrachus* can be fitted into a recently published cladogram of early frogs (Baez & Basso 1996) as a sister group of *Vieraella*, *Notobatrachus*, *Prosalirus*, and other crown-group anurans (Fig. 3, node 2). The development of the transverse processes may be a synapomorphy at the level of node 2, suggesting a reduction in rib size with a concomitant reduction in the *iliocostalis* musculature in favour of *iliolumbaris* and *longissimus dorsi* muscles. This in turn may signal the beginnings of an evolutionary shift away from predominantly undulatory movements of the body towards a locomotor style in which dorso-ventral movements had a more important role (Hinsche 1941; Emerson & De Jongh 1980; Emerson 1982). *Czatkobatrachus* thus appears to document an early post-*Triadobatrachus* stage in salientian evolution where the presacral vertebral column remained comparatively long (based on the length of individual neural arches), a short tail was retained, and the epipodials remained separate, but elongate transverse processes and fused sacral ribs provided added presacral stability and improved transfer of thrust from the hind limb. The presence of near contemporaneous salientian remains in both northern and southern continents provides confirmation of a pan-Pangean distribution of Salientia by the Early Triassic (Shubin & Jenkins 1995). This in turn supports the idea that the origins of the Salientia, and – by implication – of other lissamphibian lineages (salamanders, caecilians, albanerpetontids), must be sought in the Permian, a view supported by the molecular data (e.g., Salthe & Kaplan 1966). Whether Lissamphibia is monophyletic (Milner 1988; Trueb & Cloutier 1991) or not (Carroll & Currie 1975), there must have been a period of evolution and diversification in the Permian and Early Triassic of which we currently have no knowledge. This highlights the paucity of the small freshwater/terrestrial tetrapod record and the need to identify and prospect early depositional environments suitable for their preservation.

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Wczesnotriasowa pra-żaba z Polski

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Streszczenie

Czatkobatrachus polonicus gen. et sp. n. jest drugim w świecie, po *Triadobatrachus massinoti* (Piveteau, 1936), triasowym przedstawicielem linii filogenetycznej płazow bezogonowych (Anura). Jest on równocześnie pierwszym przedstawicielem tego odcinka filogenezy spoza Gondwany. Fragmenty szkieletu pozaczaszkowego zaliczone do *Czatkobatrachus polonicus* pochodzą z brekcji kostnej wypełniającej struktury krasowe rozwinięte w wapieniach karbońskich w kamieniołomie Czatkowice koło Krakowa. Brekcja ta tworzyła się w permsko-wczesnotriasowej fazie krasowienia wapieni, a końcem tej fazy była transgresja retu (Paszkowski & Wieczorek 1982). Zespół fauny, do którego należy *Czatkobatrachus* (Borsuk-Białynicka *et al.* w opracowaniu), jest więc najprawdopodobniej wieku scytyjskiego (wczesny trias).

Materiał kostny zaliczony do *Czatkobatrachus polonicus* składa się z ok. 40 okazów. Wśród nich są liczne lecz niekompletne kości biodrowe (Fig. 2A), kości ramienne (Fig. 2B, C) i kręgi, w tym kręgi krzyżowe (Fig. 3B, E), przedkrzyżowe (Fig. 3A), ogonowe (Fig. 3C, D) i dźwigacz (Fig. 3F, G) oraz pojedynczy fragment proksymalnego zakończenia kości łokciowej (Fig. 2D). Kości te zostały wybrane spośród setek luźnych okazów uzyskanych drogą preparacji chemicznej i przemywania wielu kilogramów brekcji.

Przynależność okazów do jednego gatunku opiera się na połączeniu w nich cech żabich (budowa kości biodrowych, ramiennych i dźwigacza, brak szwów między łukami a trzonami kręgów) z jednolitą budową i rozmiarami szczątków (trzony kręgów ektochordalne o podobnej długości i delikatnej budowie, różniące się od innych kregów tego zespołu faunistycznego) oraz podobieństwem względem rodzaju *Triadobatrachus* (np. rozmiary guzka grzbietowego Fig. 1).

Grupa Salientia, do której rodzaj *Czatkobatrachus* został zaliczony, obejmuje płazy bezogonowe (Anura), znane od jury i ich prymitywnych krewniaków, reprezentowanych dotąd wyłącznie przez *Triadobatrachus* z wczesnego triasu Madagaskaru. Jako drugi przedstawiciel triasowych Salientia *Czatkobatrachus* uzupełnia wiadomości na temat tego bardzo słabo poznanego etapu filogenezy, rzucając światło na proces ewolucyjny powstawania samych Anura. W kladogramie ilustrującym stosunki pokrewieństwa wczesnych Salientia (wg Baez & Basso 1996) lokuje się on jako pierwsza grupa zewnętrzna w stosunku do Anura (Fig. 4). Podstawą takiej lokalizacji jest wykształcenie wyrostków poprzecznych kręgów przedkrzyżowych związane z redukcją żeber (a zatem i ruchów bocznych kręgosłupa) uznane za synapomorfię *Czatkobatrachus* i Anura. Pod względem wykształcenia stawu łokciowego *Czatkobatrachus* jest także bardziej nowoczesny niż *Triadobatrachus,* który lokuje się jako dalsza grupa zewnętrzna. Tak skonstruowany kladogram wskazuje, że wydłużenie kości biodrowej i redukcja ruchów bocznych kregosłupa nastąpiła w linii płazow bezogonowych wcześniej niż zrosty podramienia i podudzia oraz powstanie urostylu. Stanowi to wskazanie dla przyszłych rekonstrukcji procesu powstawania żabiego sposobu lokomocji.

Laurazyjskie położenie stanowiska z *Czatkobatrachus* potwierdza światowy zasięg prymitywnych Salientia w triasie (ekstrapolowany wcześniej na podstawie rozmieszczenia jurajskich żab), implikując równocześnie długą, może permską, wcześniejszą historię tej linii płazów.