

ARCHOSAURIFORM POSTCRANIAL REMAINS FROM THE EARLY TRIASSIC KARST DEPOSITS OF SOUTHERN POLAND

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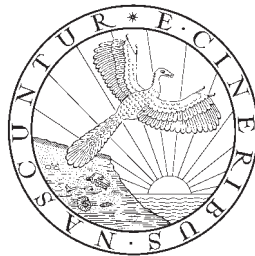
Postcranial bones of archosauriform reptiles from the Early Triassic karst deposits of southern Poland (Czatkowice 1 locality, Kraków Upland) have been assigned to two genera and species *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003 and *Collilongus rarus* gen. et sp. n. *Osmolskina* dominates the Czatkowice 1 fauna. Its postcranium is shown to be close to that of the Anisian South African *Euparkeria capensis*, the postcranial characters making an even stronger case than those of the skull. This similarity confirms the unity of the tetrapod fauna across Early Triassic Pangea. The exact relationships of *Collilongus*, based only on cervical vertebrae, remains unknown. The list of archosauriform synapomorphies, encompassing only skull characters according to current knowledge, is supplemented by one postcranial character: the sacral rib facet at least partly overlapping the medial wall of the acetabulum.

Key words: basal Archosauriformes, early Triassic, microvertebrates, Poland.

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INTRODUCTION

The main focus of this paper is a detailed description of the postcranial anatomy of a small euparkeriid reptile, *Osmolskina czatkowicensis* Borsuk-Białynicka *et al.* 2003, from the Early Triassic karst deposits of the Czatkowice 1 locality near Kraków, southern Poland (Paszkowski and Wieczorek 1982). Its skull bones have been described elsewhere (Borsuk-Białynicka and Evans 2009a).

Although reconstructed from disarticulated bones, this reptile significantly supplements the early fossil record of Archosauriformes. The term Archosauriformes (*sensu* Gauthier 1986 = Archosauria *sensu* Romer 1956), including Archosauria *sensu stricto* and some basal groups, is here preferred over the Archosauria *sensu lato* of many authors (*e.g.*, Juul 1994 and Gower and Wilkinson 1996). This terminological choice better corresponds, in our opinion, to the distinguished position of crown group archosaurs within the more inclusive clade.

Osmolskina czatkowicensis belongs to a diverse small vertebrate assemblage including three other diapsids, as well as procolophonids, amphibians (Borsuk-Białynicka *et al.* 1999) (among them a pre-frog salientian *Czatkobatrachus polonicus*; Evans and Borsuk-Białynicka 1998, 2009), and fish. This assemblage displays extensive similarities at a suprageneric level with Gondwanan Olenekian to Anisian faunas, a pattern that probably dates back to the Permian uniformity of tetrapod faunas across Pangea. However, the absence of therapsids from the Czatkowice 1 assemblage is noticeable. According to current knowledge (Shishkin and Ochev 1993; Lozovsky 1993), the north-south continuity of the Pangean tetrapod fauna was disturbed, then interrupted, at the Permo-Triassic boundary, by aridisation of the climate. This led to the development of a broad arid belt that extended across the majority of North and South America, central and northern Africa, and eastern Europe including the East European Platform and Cis-Urals, as well as Poland. A lack of therapsids is distinctive for the Olenekian faunas of this belt. Archosauriform remains are variously distributed over the belt. The North American Torrey and Wupatki Member of the Moenkopi Formation, correlated with the Late Olenekian (Morales 1993), have yielded no archosauriform body fossils at all but rich archosauriform ichno-fossils are present. Archosauriforms only appear in the Anisian Holbrook member of the Moenkopi Formation (the raiusuchid *Arizonasaurus* Nesbitt, 2005). Further to the East, the European Bundsandstein, the Middle and Upper part of which are roughly Olenekian in age, has yielded the long-spined *Ctenosauriscus* (Krebs 1969), dated as early Late Olenekian (Ebel *et al.* 1998), but probably related to *Arizonasaurus* (Nesbitt, 2003, 2005) and rather poorly known. In contrast, the Cis-Uralian Permian to Triassic tetrapod succession (Shishkin and Ochev 1993) has yielded a rich archosauriform assemblage, with a material assigned to proterosuchids, erythrosuchids, euparkeriids and raiusuchids (Sennikov 1995 and references therein). The absence of common archosaurian elements across Olenekian Euramerica, in contrast to the uniformity of its temnospondyl fauna, suggests (Shishkin and Ochev 1993) that terrestrial life was confined to isolated realms separated by aquatic barriers. The specific environment of the Czatkowice 1 karst region in the early Late Olenekian (Paszkowski 2009; Shishkin and Sulej 2009) is consistent with a certain degree of faunal endemism.

Osmolskina is the dominant archosauriform of the Czatkowice 1 assemblage. It is the second euparkeriid genus reported from the Laurasian part of Pangea, *Dorosuchus* Sennikov, 1989 from the Anisian of Russia, being the first one. Proterosuchids and erythrosuchids were apparently absent from Czatkowice 1, and raiusuchids have yet to be recognized with any certainty. Raiusuchids are a problematic group currently considered crurotarsians (Gower 2000; Gower and Nesbitt 2006), hence Archosauria *sensu stricto* (under the definition accepted herein), and are mainly middle through late Triassic in age. Their presence in the Olenekian, strongly suggested by Russian authors (Sennikov 1995 and references therein; Gower and Sennikov 2000), implies a still earlier split of the Archosauria. This is why the question of their presence in the earliest Late Olenekian (Shishkin and Sulej 2009) Czatkowice 1 assemblage is of great interest. While the archosauriform bones are readily distinguishable from the non-archosauriform ones, uncertainty as to the range of variability within *O. czatkowicensis* raises a problem of conspecificity of the Czatkowice 1 archosauriform material as a whole. Whether or not any archosauriforms other than euparkeriids (= “*Euparkeria* grade archosauriforms”) occurred in the Early Triassic Czatkowice 1 assemblage is a question we address in the present paper.

All Supplements are on-line under the address [http://www.palaeontologia.pan.pl/SOM/PP65-Borsuk-Białynicka and Sennikov.pdf](http://www.palaeontologia.pan.pl/SOM/PP65-Borsuk-Bialynicka%20and%20Sennikov.pdf)

Institutional abbreviations. — GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; PIMUZ, Paläontologisches Institut und Museum der Universität, Zürich, Swit-

zerland; PIN RAS, Paleontological Institute Russian Academy of Sciences Moscow, Russia; SAM, South African Museum, Cape Town, Republic of South Africa; SMNS, Staatliche Museum für Naturkunde Stuttgart, Germany; ZPAL, Institute of Paleobiology Polish Academy of Sciences, Warsaw, Poland.

Acknowledgments. — Mariusz Paszkowski and Józef Wieczorek (Jagiellonian University) discovered the Czatkowice 1 breccia, and kindly offered it for study to Teresa Maryńska and the late Halszka Osmólska who transferred it to the senior author (MBB). MBB is indebted to following persons and institutions that allowed the study of archosauriform material in their collections: Rupert Wild at the Staatliche Museum für Naturkunde Stuttgart, Germany; Michael Maish at the Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany, and Helmut Mayr at the Bayerische Staatssammlung für Paläontologie und Historische Geologie, München, Germany. Many thanks are due to Susan E. Evans for her continued help and critical comments during these studies, and to Caroline Northwood (La Trobe University, Victoria, Australia) who was the first to make some order in the postcranial archosaurian remains from Czatkowice 1. Thanks are also due to the following staff members of the Institute of Paleobiology, Polish Academy of Sciences in Warsaw: Ewa Hara for preparation of the material, Marian Dzięwiński for photographs, Cyprian Kulicki for SEM micrographs, and Alexandra Hołda-Michalska for preparing computer illustrations. The research of the senior author was partly supported by the State Committee of Scientific Research, KBN grant No 6 PO4D 072 19. The junior author was supported by the Russian Foundation for Basic Research, project N.N. 05-05-65146, 08-05-00526, 07-05-00069, and by the Program 15 of the Presidium of the Russian Academy of Sciences “The Origin of the Biosphere and Evolution of the Geo-Biosystems”, Subprogram II.

GEOLOGICAL SETTING

Czatkowice 1 was the largest of the karst forms developed in the Carboniferous Limestone quarry and including bone breccia. For the details of geological setting see Paszkowski and Wieczorek (1982), Paszkowski (2009), and Cook and Trueman (2009). The vertebrate assemblage extracted from the Czatkowice 1 breccia, includes both terrestrial and amphibious animals and some fish (Borsuk-Białynicka *et al.* 1999). Based on the *Parotosuchus* fauna (Shishkin and Sulej 2009), the most precise age dating for Czatkowice 1 breccia is an earliest Late Olenekian (corresponding to the lowermost Yarenskian stage). Probably, the material of Czatkowice 1 breccia was deposited in a freshwater pool, developed within a collapsed paleodoline (Paszkowski 2009) within an oasis, in an otherwise arid Central European Scythian environment (Ochev 1993; Shishkin and Ochev 1993). The Czatkowice 1 assemblage is distinguished by the small size of the component taxa, and this is consistent with the endemic character of a small oasis. Alternatively it could merely be a depositional artefact.

MATERIAL AND METHODS

The material comes from a single fissure exposure, referred to as Czatkowice 1 (Paszkowski and Wieczorek 1982; Paszkowski 2009). The bone breccia was prepared chemically in acetic acid. The material consists of about hundred more or less complete postcranial bones, and many hundreds of fragments. The bones are disarticulated, and mostly damaged or broken into pieces (some of which were glued back together). The relatively low level of abrasion suggests rather gentle transport over, at most, a short distance (Cook and Trueman 2009). Most of the material is stored in the Institute of Paleobiology, Polish Academy of Sciences, with some specimens in the Museum of the Earth, Polish Academy of Sciences.

General morphology, size and frequency, corresponding to those of skull bones (Borsuk-Białynicka and Evans 2009a) form the basis for identification of the postcranial bones of *Osmolskina* amongst the main bulk of the material. Three problems that appear are: a possible size overlap with the second, generally smaller, diapsid from the same material (Borsuk-Białynicka and Evans 2009b), questionable conspecificity of the archosauriform bones from Czatkowice 1, and poor discrimination between ontogenetic and taxonomic vari-

ability. The small number of adequately preserved specimens made any statistical test impossible to apply. Only a few measurements approximate variability ranges (Supplements 1 and 2).

Only mature vertebrae were eventually chosen for measurements, their maturity being determined on the basis of fusion of neurocentral sutures (Brochu 1996). The age criteria are less precise in the case of long bones. Their size variability is here considered in terms of continuous ontogenetic growth, but the poor preservation of the articular ends suggests a taphonomic bias towards the accumulation of immature specimens at least in this bone category.

The mesopodial bones present a very special problem. Among the numerous small bones of the Czatkowice 1 material, the proximal elements of the tarsus (astragalus and calcaneum) are specific enough to be recognized, and even assigned to particular taxa, but distal tarsals and carpals are extremely difficult to discriminate from one another and to assign with any confidence. The combination of different kinds of variability, such as hand and foot length disparity, and inter-podial and individual variation, makes the reconstruction of the extremities speculative. The known *Euparkeria* foot structure has been used as a reference. The phalanges are the best preserved and most abundant postcranial elements. As such, they represent the best material for statistical studies, but these are relegated to future comparative studies in the frame of the whole Czatkowice 1 assemblage.

The character list summarized by Juul (1994) and modified according to information available from the *Osmolskina* remains, incomplete as it is, has been used in the present paper (Appendix 4). As *Osmolskina* does not differ from *Euparkeria* in those characters for which it can be scored, its inclusion into the matrix does not change it in any way. Analysis of this matrix by cladistic computer programs is thus redundant. Simple statistical methods have been used for taxonomical problems.

The terminology used for the orientation of the long bones follows Gower (2003) in applying the terms: ventral for the flexor side, and dorsal for the extensor side. The terms lateral and medial will be used for the side views of the bones, corresponding to semierect position of appendages. Anterior and posterior are sometimes used to give more precision in the description of the details.

Some terms that refer to vertebral structure, such as posterior centrodiapophyseal crest and posterior centroparapophyseal crest, are from Wilson (1999).

The term "grade" used herein refers to the taxa that share the same combination of plesiomorphic and apomorphic characters but no synapomorphy unique for them.

SYSTEMATIC BACKGROUND

The Archosauria *sensu* Gauthier 1986 (= Avesuchia of Benton 1999) are restricted to the most recent common ancestor of Aves and Crocodylia and all its fossil and extant descendants. Several taxa once considered basal archosaurs belong to a more inclusive taxon, Archosauriformes (Gauthier 1986). One of the character states excluding taxa from the crown group is the lack of a posteriorly deflected calcaneum synapomorphic of Archosauria (Juul 1994, p. 38). Instead, they retain a plesiomorphic, virtually transverse orientation of the tarsus. Gower and Wilkinson (1996) found general agreement in the sequence of basal archosauriform groups recovered by consecutive cladistic analyses (Serenó and Arcucci 1990; Sereno 1991; Parrish 1993 and Juul 1994). According to all these authors, the Proterosuchidae is the outermost archosauriform taxon, the Erythro-suchidae are to be located one step more crownward, followed by the Early Anisian South African *Euparkeria* and the Middle to Late Triassic South American Proterochampsidae (Gower and Wilkinson 1996).

The genus *Euparkeria* was erected and first described by Broom (1913a, b), later by Houghton (1922), and then by Ewer (1965). Huene (1920) first used the family name Euparkeriidae to include *Euparkeria* and *?Browniella* (*contra* to Huene's *Broomiella*), a questionable genus subsequently synonymized with *Euparkeria* (Houghton 1922, Ewer 1965). Huene gave no family diagnosis and did not further comment on the new family, but it has been used to include several subsequent genera such as *Dorosuchus* (Sennikov 1989) from the Anisian of Russia, as well as *Turfanosuchus* (Young 1973), *Wangisuchus* (Young 1964), and *Halazhaisuchus* Wu (1982), all from the Anisian of China. Two of these, *Turfanosuchus* and *Wangisuchus* have been shown to have a crocodylian-like ankle joint (Gower and Sennikov 2000), which excludes them from the Euparkeriidae. *Dorosuchus* (Sennikov 1995) is known from a braincase and isolated postcranial bones.

Among proterosuchid taxa recorded in the literature, only four genera are adequately preserved and described, with their attribution supported by phylogenetic analysis (Gower and Sennikov 1997). They are as follows: *Archosaurus*, the only Permian proterosuchid; the Early Olenekian South African *Proterosuchus* (Broili and Schroeder 1934; Cruickshank 1972); the Early Triassic *Fugusuchus* from China (Cheng 1980; Gower and Sennikov 1997); and the Anisian *Sarmatosuchus* from Russia (Sennikov 1994; Gower and Sennikov 1997). *Chasmatosuchus* Huene, 1940 and *Gamosaurus* Otschev, 1979, possible proterosuchian taxa from the Olenekian of Russia, were based only on vertebral material (Supplement 3), and their attribution remains problematic. *Vonhuenia* Sennikov, 1992, with its low braincase and an iliac blade that does not extend anteriorly, might be a proterosuchid.

Erythrosuchids are adequately known from rich Russian, South African, and Chinese materials (*Garjainia*, *Erythrosuchus*, and *Shansisuchus* respectively). The affiliation of two additional Russian taxa, *Chalishevia* Otschev, 1980 and *Uralosaurus* Sennikov 1995, based on fragmentary material, is less certain.

The raiusuchids are another group represented in the Triassic of Russia, but mostly by vertebrae. Raiusuchid affinity has been demonstrated in three cases, those of *Vytshegdosuchus zheshartensis* Sennikov, 1988, *Tsylmosaurus jakovlevi* Sennikov, 1990, and *Scythosuchus* (Sennikov 1999), but attribution of other genera (*Dongusuchus*, *Energosuchus*, *Jaikosuchus*, *Jushatyria*, see Supplement 3) remains tentative (Gower and Sennikov 2000). Four of these genera, *Tsylmosuchus*, *Vytshegdosuchus*, *Jaikosuchus* (Sennikov 1995), and *Scythosuchus* (Sennikov 1999), come from the Olenekian, and the occurrence of *Tsylmosuchus* in the Early Olenekian demonstrates an unexpectedly early appearance of the archosauriform crown-group Archosauria.

SYSTEMATIC PALEONTOLOGY

Clade Archosauromorpha Huene, 1946

Clade Archosauriformes Gauthier, 1986

Family **Euparkeriidae** Huene, 1920

Provisional diagnosis. — Basal archosauriforms differing from crown-group Archosauria in the lateral orientation of the calcaneal tuber and the unossified medial wall of the otic capsule. They share a vertical orientation of the basisphenoid and the absence of an astragalocalcaneal canal with all archosauriforms except proterosuchids. They differ from erythrosuchids in the lighter construction of the skeleton, relatively smaller skull, and generally more elongate cervical vertebrae (centrum length/depth usually around 1.4–1.6 instead of 0.4–1.0 in erythrosuchids).

Remarks. — Among the numerous characters *Osmolskina* shares with *Euparkeria*, none can be shown to be synapomorphic at family level. However, a combination of primitive and derived archosauriform character states places the two genera in exactly the same position on the cladogram of Archosauriformes. This, in combination with a general similarity of body form, leads us, with reservation, to accord them family status within Euparkeriidae Huene, 1920. The differences between *Osmolskina* and *Euparkeria* are here regarded as generic. Among them, only one, the localization of the coracoid foramen, is uncontentious; the others are dependent on the accuracy of the reconstructions.

Generic composition. — *Euparkeria* Broom, 1913, *Osmolskina* Borsuk-Białynicka *et* Evans, 2003, most probably *Dorosuchus* Sennikov, 1989.

Occurrence. — Olenekian to Anisian of Pangea (localities in Europe and South Africa).

Genus *Osmolskina* Borsuk-Białynicka *et* Evans, 2003

Diagnosis. — As for the species.

Osmolskina czatkowicensis Borsuk-Białynicka *et* Evans, 2003

Holotype: The fragmentary maxilla ZPAL RV/77; Borsuk-Białynicka and Evans 2003, fig. 2A.

Type horizon: Early Late Olenekian.

Type locality: Czatkowice 1, southern Poland.

Material. — Numerous disarticulated postcranial bones (see Borsuk-Białynicka and Evans 2009a, for skull details). Catalogued postcranial specimens are: 63 measured vertebrae (Supplement 1); twelve scapulae: ZPAL RV/881–885, 902, 1161, 1261, 1282–1286; eight coracoids: ZPAL RV/890–891, 903, 1166–1169, 1311; eleven humeri ZPAL RV/1164, 1262–1263, 1266–1272, 1277; ten ilia: ZPAL RV/630, 678, 679, 911–913, 918, 919, 924, 925; four ischia: ZPAL RV/887–889, 892; five pubes: 905–907, 909, 910; fifteen femora: ZPAL RV/938–940, 1252, 1254, 1264, 1287–1302, 1304; 18 tibiae: ZPAL RV/1165, 1171, 1176, 1177, 1221, 1222, 1257–1260, 1265, 1303, 1306, 1317–1321, fragmentary radius ZPAL RV/1232 and ulnae ZPAL RV/1230 and 1279; fragmentary fibulae ZPAL RV/1182, 1225, 1247; numerous tarsal bones, of which the astragalus: ZPAL RV/811, a calcaneum ZPAL RV/810, and a fourth distal tarsal ZPAL RV/812 are catalogued and figured.

Measurements. — Appendix 1, Supplement 1.

Occurrences. — Type locality only.

Emended diagnosis. — An euparkeriid similar to *Euparkeria capensis*, but smaller, having a modal skull length of about 60 mm, modal femur and tibia length about 40 mm and 30 mm, respectively. *Osmolskina czatkowiczensis* differs from *Euparkeria* in having a slightly overhanging premaxilla (but less so than in proterosuchids) that was weakly attached to the maxilla (with no peg and socket articulation developed), and was probably separated from it by a slit-like additional antorbital space; in having a subquadrangular nasal process of the maxilla, and in having a barely recessed antorbital fenestra. In *O. czatkowiczensis* the preorbital part of the skull is less elongated than in *Euparkeria* which is best expressed in maxilla proportion, the maximum maxilla length to depth being 5:1 in *O. czatkowiczensis* (7:1 in *E. capensis*). The estimated tooth count is 13 in both species. The premaxillary body is finer in *O. czatkowiczensis* (maximum length to depth 10:3) than in *E. capensis* (10:4). The posterolateral process of the premaxilla slopes at an angle of about 50° in *O. czatkowiczensis* while being almost vertical in *E. capensis*. In *O. czatkowiczensis* the orbit is more rounded while tapering ventrally in *E. capensis*. The mandible of *O. czatkowiczensis* does not increase in depth posteriorly unlike that of *Euparkeria*. *O. czatkowiczensis* differs from *Euparkeria* in the shorter humerus, more twisted femur (distal to proximal end angle in *Osmolskina* about 55°, in *Euparkeria* 32°), the extremely anterior position of the coracoid foramen or notch and less compressed teeth. Compared to *Dorosuchus* (femur about 90 mm, tibia about 70 mm in length, femur twist about 40°), *Osmolskina* is smaller and has a more twisted femur.

VERTEBRAL COLUMN

General features. — All regions of the vertebral column of *Osmolskina czatkowiczensis* are represented in Czatkowice 1 material. The vertebral centra are holochordal and slightly amphicoelous, with slightly concave but not recessed lateral flanks. Neurocentral sutures are evident only in the smaller vertebrae. The dorsal surface of each centrum bears a deep pit, both longitudinal and transversal sections of the centrum being V-shaped. The vertebrae look rather short and tall, but the centrum length to posterior height ratio usually exceeds that of *Euparkeria capensis* (Appendices 1 and 2). It varies (Supplement 2) from 1.0–1.38 in the axis, increases to about 1.4–1.6 in postaxial cervicals, and decreases to 1.3–1.4 at the transition between the neck and thorax. It increases again to about 1.5–1.7 in dorsals, decreasing to about 1.56 in the first sacral centrum, and then to 1.38 in the second sacral and the short caudals of the tail base. The caudals get increasingly longer and slimmer down the tail. The parapophysis and diapophysis remain separate throughout most of the dorsal series. Intercentra were probably present within the cervical series, and probably absent in the dorsal series.

Atlas/axis complex. — The atlas consists of the intercentrum and paired neural arches (Fig. 1B, G). Isolated intercentra (*e.g.*, ZPAL RV/397 and 1149) are fairly frequent in the material. The largest and most frequent intercentrum type has been tentatively attributed to *Osmolskina* on the basis of size and neural arch fit. It is a transversally elongated, dorsally concave, beam of bone, with dorsally curved ends (Fig. 1B, C). The anterior surface bears a concave facet (Fig. 1B) for the occipital condyle, dorsolaterally flanked by two others facets for the neural arches (Fig. 1G). Much less concave is the posterior facet for the axis intercentrum which itself is unknown, as is the proatlas. The paired atlantal neural arches match the intercentrum (ventrally) and the paired, circular facets of the axis (posterodorsally) (Fig. 1G).

The axis (Figs 1A, 2A) is represented by seven specimens, all rather small. The centrum is short (Supplement 1), high, and triangular in transverse section owing to a prominent ventral crest with excavated flanks and a blunt edge. With the ventral crest aligned horizontally, and both the anterior and posterior faces of the centrum ori-

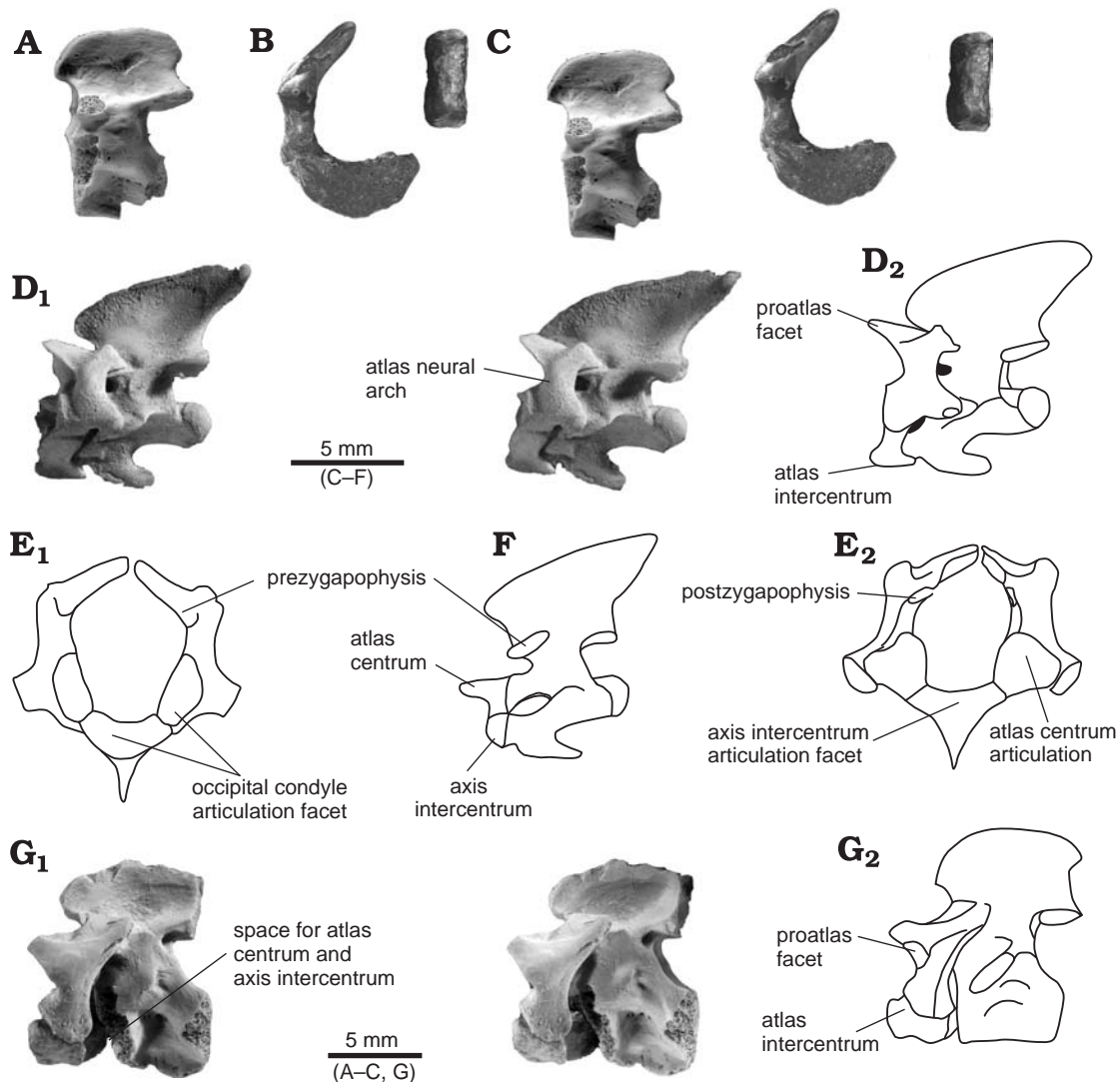


Fig. 1. A–C, G. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. A. Axis ZPAL RV/570, in left lateral view. B. Atlas intercentrum with right neural arch ZPAL RV/1149, in cranial view. C. Atlas intercentrum ZPAL RV/397, in ventral view. G. Axis ZPAL RV/672 combined with atlas neural arch and atlas intercentrum, in left lateral view. D–F. *Ctenosaura* sp. (Squamata), ZPAL RI/8, Recent. D. Atlas and axis in left lateral view. E. Atlas intercentrum and neural arches in cranial (E₁) and caudal (E₂) views. F. Axis with atlas centrum and axis intercentrum in left lateral view. A–D₁, G₁, SEM stereo-pairs.

ented vertically, the dorsal surface of the centrum slopes posteroventrally (Fig. 1A). The neural canal is slightly flattened bilaterally. The dorsal margin of the neural spine is longer than the neural arch, and it overhangs the postzygapophyses which themselves protrude posterior to the centrum. The dorsal margin of the spine curves downward so that its anterior and posterior apices are slightly hooked. The spine extends into two posteriorly concave crests on the postzygapophyses which delimit a triangular cleft for the interspinous ligaments and muscles. The prezygapophyses bear flat circular facets, one half-way up each neural arch, to receive the neural arches of the atlas. The axial centrum is unfinished anteriorly where it should contact the odontoid process (*i.e.*, atlas centrum). In *Osmolskina*, in contrast to crocodiles, the odontoid process remains free from the axis even when the neurocentral sutures close. Neither the atlas centrum nor the axis intercentrum have yet been identified.

The size and shape of the axial neural spine in *Osmolskina* are similar to those of *Euparkeria* (Ewer 1965, p. 402, fig. 7c), but the neural arch pedicels of *Osmolskina* are deeper (Fig. 3A, B), so that the neural arch as a whole is taller and the anterior zygapophyses are placed relatively more dorsally.

Postaxial presacral vertebrae. — The postaxial cervicals (Fig. 2C–F, H) display a steep posteroventral slope of the dorsal surface of the centrum as does the axis, so that the anterior and posterior faces of the

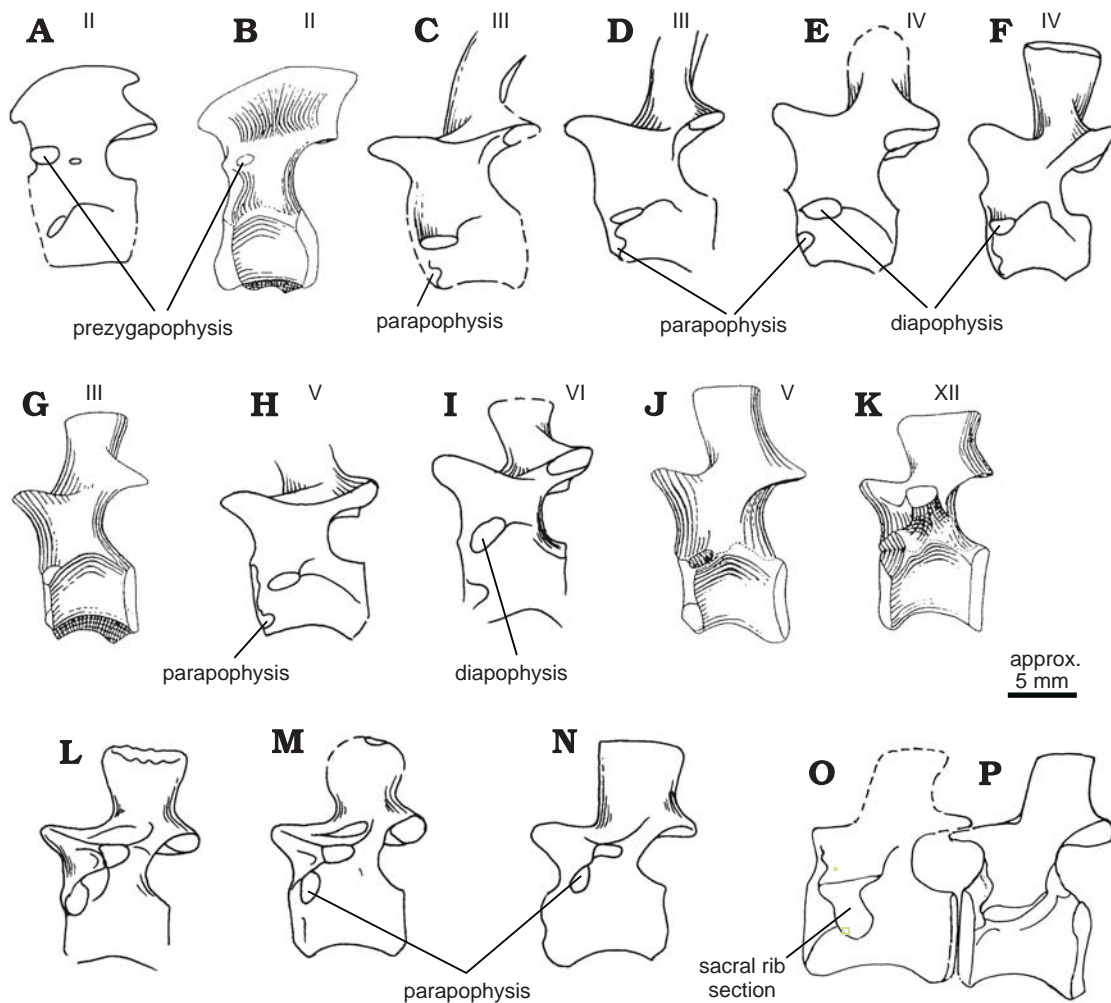


Fig. 2. A, C–F, H, I, L–P. *Osmolskina czatkowicensis* Borsuk-Białynicka et Evans, 2003, Early Triassic of Czatkowice 1, Poland. A. Reconstruction of the axis on the basis of ZPAL RV/570 and 637. C, D. Two possible third cervicals: ZPAL RV/635 (C) and ZPAL RV/636 (D). E, F. Two possible fourth cervicals: ZPAL RV/577 (E) and ZPAL RV/571 (F). H. A possible fifth cervical ZPAL RV/573. I. A possible sixth cervical ZPAL RV/607. L–N. Three roughly consecutive dorsals: ZPAL RV/633 (L), ZPAL RV/632 (M), and ZPAL RV/575 (N). O. First sacral ZPAL RV/642. P. Second sacral ZPAL RV/640. B, G, J, K. *Euparkeria capensis* Broom, 1913 (after Ewer 1965). B. Axis. G. Third cervical. J. Fifth cervical. K. Dorsal vertebra. Left lateral view.

centrum are offset in relation to one another. This slope is manifested in the anterior view of centra (Fig. 3A, B, D), so that both the posteroventral profile of the centrum and posteroventral margin of the neural arch are exposed in the cervicals, but not in the dorsals. In dorsal vertebrae the posterodorsal margin of the centrum is visible (Fig. 3F, H). The neck had probably an elevated rest position, but it levelled out within the anterior part of the dorsal series. Cervical centra bear an acute ventral keel (that fades posteriad beginning about the middle of the dorsal series). Because of the keel, the anterior facet of the centrum tends to be subtriangular, but it may be subpentagonal (because of the diapophyses) or even subseptagonal (because of parapophyses), while changing to subcircular in posterior dorsals (Fig. 3F, H), partly as a preservational effect. However, some cervical centra of *Osmolskina* type have the ventral side more flattened than usual, the ventral keel being little more than slight ridge along the blunt surface of the centrum. This is tentatively regarded as an intraspecific variability, but it remains poorly understood.

The ventral profile of the cervical centra is concave along the longitudinal axis and beveled both anteriorly and posteriorly (Figs 2D, F, 5F, G) to enclose triangular intercentral spaces. These may have housed intercentra, but could also result from poor ossification of the margins of the articular surfaces. However, the spaces are absent or very small in the dorsal region.

The neural arches are almost equal in length throughout the column. The neural spines are usually damaged. In cervicals, they are subquadrangular, much taller than long. The spine tops are rarely preserved, but

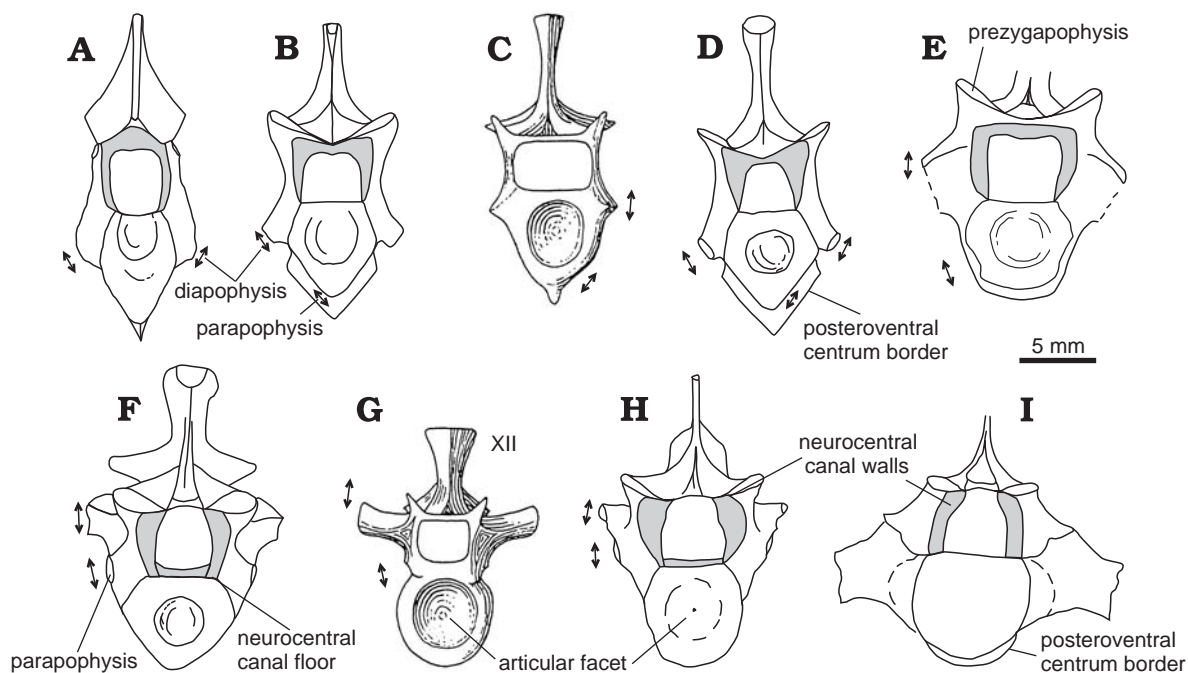


Fig. 3. **A, B, D–F, H, I.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A.** Axis ZPALRV/570. **B.** Cervical IV ZPALRV/577. **D.** Cervical IV ZPALRV/571. **E.** Posterior cervical ZPALRV/634. **F.** Anterior dorsal ZPALRV/633. **H.** Posterior dorsal ZPALRV/575. **I.** First sacral based on ZPALRV/639 and 642. **C, G.** *Euparkeria capensis* Broom, 1913 (after Ewer 1965). **C.** Cervical III. **G.** Dorsal. Cranial view; arrows denote the positions of diapophyses and parapophyses.

the presence of spine tables is documented in some cervical and anterior dorsal vertebrae (*e.g.*, ZPAL RV/1229; Fig. 4H). In some better preserved specimens the height of the spine is almost half the total height of the vertebra. The position of the neural spines changes along the column. By comparison with *Euparkeria*, the *Osmolskina* cervicals with anteroventrally sloping spines are considered to be anteriormost of the series (Fig. 2C, D). In the middle of the series, the spines became vertical (Figs 2E, F, 5F), and then sloped posteroventrally in the last cervicals (Figs 2H, I, 5G), and possibly in the anterior dorsals. Based on this reasoning, specimen ZPAL RV/573 (Fig. 4A) which has a more posteroventrally sloping spine than other cervicals, would be a posterior cervical, but it is longer than would be expected at the cervical-dorsal transition. Its position is therefore questionable. Anterior dorsals have lower, more vertical spines. When preserved the dorsal and sacral spines are subvertical and have no spine tables (Fig. 4B, C).

The anterior and posterior zygapophyses are subhorizontal and bear ovoid facets. Anteriorly, they sit at the anterior corners of a triangular shelf, apex posterior, that is laterally delimited by low subhorizontal crests converging toward the spine base. The articular facets are separated from each other by an incision, while uniting at the base by a dorsally concave blade that received a ventrally convex projection bridging the postzygapophyses, but an accessory articulation probably did not exist. The postzygapophyses protrude only slightly beyond the posterior edge of the centrum, but more so than do the prezygapophyses on the other side of the vertebra. They are suspended dorsally on the crests that converge toward the spine base. The crests delimit a deep triangular cleft that presumably received intervertebral ligaments. The articular facets are usually more or less oblique ventromedially, while being apparently more horizontal in the posterior half of the dorsal series.

As usual for reptiles, the cervicals have the diapophyses situated about the level of the neurocentral suture and close to the anterior margin of the centrum, whereas they are more posteriorly positioned on the dorsals, and lie on the neural arch. In the cervicals, the diapophyses are strongly protuberant and curve ventrolaterally towards the parapophyses so that the lateral walls of the centra are excavated. In dorsal vertebrae, the diapophyses extend horizontally, but their lateral extent is unknown because the distal parts are always damaged. On cervicals, the posterior border of the diapophysis passes into the centrodiaophyseal crest, concave both ventrally and laterally, that roofs the lateral excavation of the centrum. On the dorsals, the diapophysis is supported by three crests: the centrodiaophyseal crest reduced to a straight posterolateral border of the

diapophysis, an anterior crest extending to the prezygapophysis, and a ventral crest extending to the parapophysis (Figs 2L–N, 4B).

In cervicals, the parapophyses are situated very low, just above the level of the keel, and far anterior, so that they touch the border of the centrum (Figs 2C–F, 3B, D). As the anterior central region is usually damaged, the presence of the parapophyses is marked by a wavy margin. In the anterior dorsals, the parapophyses are positioned beyond the neurocentral suture (Fig. 3E, F) and then gradually more and more posterodorsally along the dorsal series (Fig. 2N). The gap between the parapophysis and diapophysis, bridged by the sharp crest, gradually decreases. In posterior dorsals, the diapophysis and parapophysis are close together (Fig. 4C), but the exact vertebral level at which they fuse cannot be determined.

Among 32 sufficiently well preserved archosauriform postaxial cervicals considered mature, the *Osmolskina* cluster encompasses 26 vertebrae (Appendix 2). Limited as they are, their measurements show a normal distribution (Figs 22, 23). Within this uniform group, there is some variation in central section whereby additional crests lateral to the ventral sagittal crest (posterior centroparapophyseal lamina of Wilson 1999) may be absent or variably developed. Nesbitt (2005) described similar variability within the vertebral series of *Arizonasaurus babbittini*. Depending on the presence v. absence of the lateral crests the ventral side of the centrum is narrow to acute or rather broad. However, no correspondence between this variability and the position of the vertebra along the spine has been observed.

Sacral and caudal vertebrae. — Among numerous sacrals attributed to *Osmolskina czatkowicensis*, two morphotypes, corresponding to the first and second sacral, have been recognized, both of them with conjoint sacral ribs. Both sacral centra are rather long (see Supplement 1C). The anterior articular facet of the first sacral centrum (Fig. 4D) often appears very broad, in contrast with the subcircular shape of the dorsal centra and that of the second sacral. This condition results from the large size and anterior position of the first sacral rib, as exposed by damage (see Gower 2003, p. 51 and fig. 25, for a similar structure in *Erythrosuchus*). The dorsal surface of the first sacral centrum slopes slightly posteroventrally (Fig. 3I), but there is no equivalent slope in the second sacral vertebra. Sacral ribs completely fuse with the centrum before the ossification of their distal ends and those of the neural spines.

In the first sacral the length of the base of the diapophysis almost equals that of the neural arch, the latter being relatively short and the former more expanded than in presacral vertebrae. The diapophysis is completely fused with a parapophysis that is unexpectedly low and anterior in position, given its posterodorsal position in the last dorsals. Together, the diapophysis and parapophysis create a subvertical facet that extends from a point at about half the height of the neural arch onto the dorsolateral side of the centrum. The second sacral rib is less deep, and more horizontally extended than the first one, and it does not invade the centrum as much. The distal ends of the sacral ribs are never preserved, but their general shape, subvertical in the first sacral and subhorizontal in the second (Fig. 2O, P) correspond to the sacral facet on the ilium (Fig. 10A₂, A₃).

The anterior caudal centra (Fig. 4F) are no longer than those of the dorsals, and correspond to them in proportions and overall shape (Supplements 1C, 2E–G). They are ventrally beveled, and probably bore chevrons. In the first caudal, the base of the transverse process retains a horizontal position and is equal to the neural arch in length. Posteriorly, the processes become shorter and thinner (Fig. 4F). They level with the base of the neurocentral canal. Attributed posterior caudals of *Osmolskina* (e.g., ZPAL RV/1300, 1301) become very narrow and elongate as the spines and diapophyseal crests are gradually reduced.

Chevron bones. — The largest of the numerous, usually damaged, chevron bones from Czatkowice 1 material, are considered to belong to archosauriforms. The chevrons are more than twice the length of the caudal centrum in *Proterosuchus vanhoepeni* (Cruickshank 1972) and are even longer in *Ticinosuchus ferox* (Krebs 1965), but no measurements are available for *Euparkeria capensis* (Ewer 1965). Given an estimated mean length of about 8.5 mm for the caudal vertebrae in *Osmolskina* (Supplement 1C), the expected length of the chevrons would be over 20 mm. ZPAL V/1349 (Fig. 4I) is a chevron that corresponds to this size range. It consists of a pair of distally fused haemal arches with a bilaterally flattened distal end. The arches are linked proximally by a dorsally concave transverse bar homologous to the intercentrum. The specimen thus closely corresponds to Ewer's (1965) description for *Euparkeria*, but this is not a phylogenetically useful element.

Osteoderms. — Numerous osteoderms of a fairly uniform size (about 5 mm in length) occur in the Czatkowice 1 material (Fig. 5B, C, H–O). They are mostly symmetrical, more or less cordate, the apex anterior (orientated by comparison with *Ticinosuchus* and *Euparkeria* Krebs 1976, pp. 62 and 70 respectively),

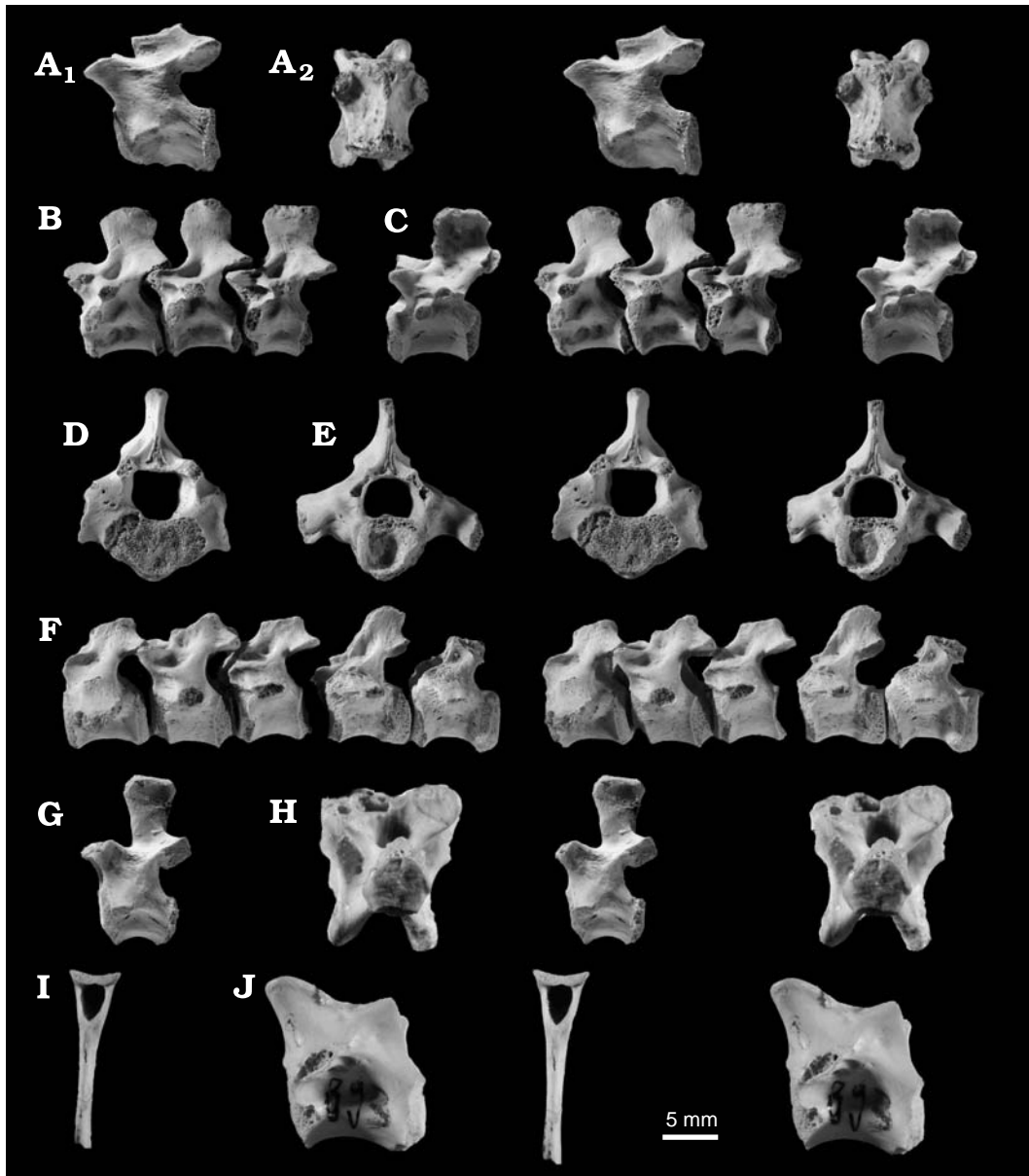


Fig. 4. A–L. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. A. Cervical vertebra ZPAL RV/573. B. Middorsal vertebrae ZPAL RV/572, 632, 633 in a possible sequence. C. Posterior dorsal vertebra ZPAL RV/572. D. First sacral ZPALRV/639. E. Second sacral ZPALRV/640. F. Possible series of consecutive caudals ZPAL RV/659, 657, 658, 576, 660. G. Midcervical vertebra ZPAL RV/571. H. Spine table in anterodorsal vertebra ZPAL RV/1348. I. Chevron ZPAL RV/1349. J. *Collilongus rarus* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Postcervical vertebra ZPAL RV/893. Left lateral (A₁, B, C, F, G, J), ventral (A₂), cranial (D, E), and dorsal (H) views. Stereo-pairs.

and incised at a posterior end (Fig. 5C, I, O). They vary in shape from very narrow to equilateral triangles. They have a more or less concave ventral surface and a longitudinal dorsal crest extending along the sagittal axis. Both surfaces are pitted, and many show traces of resorption. The anterior tip of the osteoderm is bordered posteriorly by a transverse furrow, and is slightly upturned (Fig. 5C₂, M), forming a tubercle that matches a small fossa on the posteroventral tip of the preceding osteoscuta (Fig. 5O). The resulting articulation is similar to that described by Ewer (1965, p. 414) in *Euparkeria*, and suggests these elements formed a single row of osteoderms with no trace of a transition from an unpaired to a paired arrangement. Nor is there any trace on these elements of a lateral overlap or any straight border that could have made a sutural contact with neighbouring scutes. They may belong to an unpaired series of the anterior neck or posterior tail, but it is difficult to envisage a smooth transition between the unpaired and paired rows of osteoderms, similar to that reconstructed in *Ticinosuchus* (Krebs 1965, 1976, p. 62)). Alternatively they may belong to a flank series.

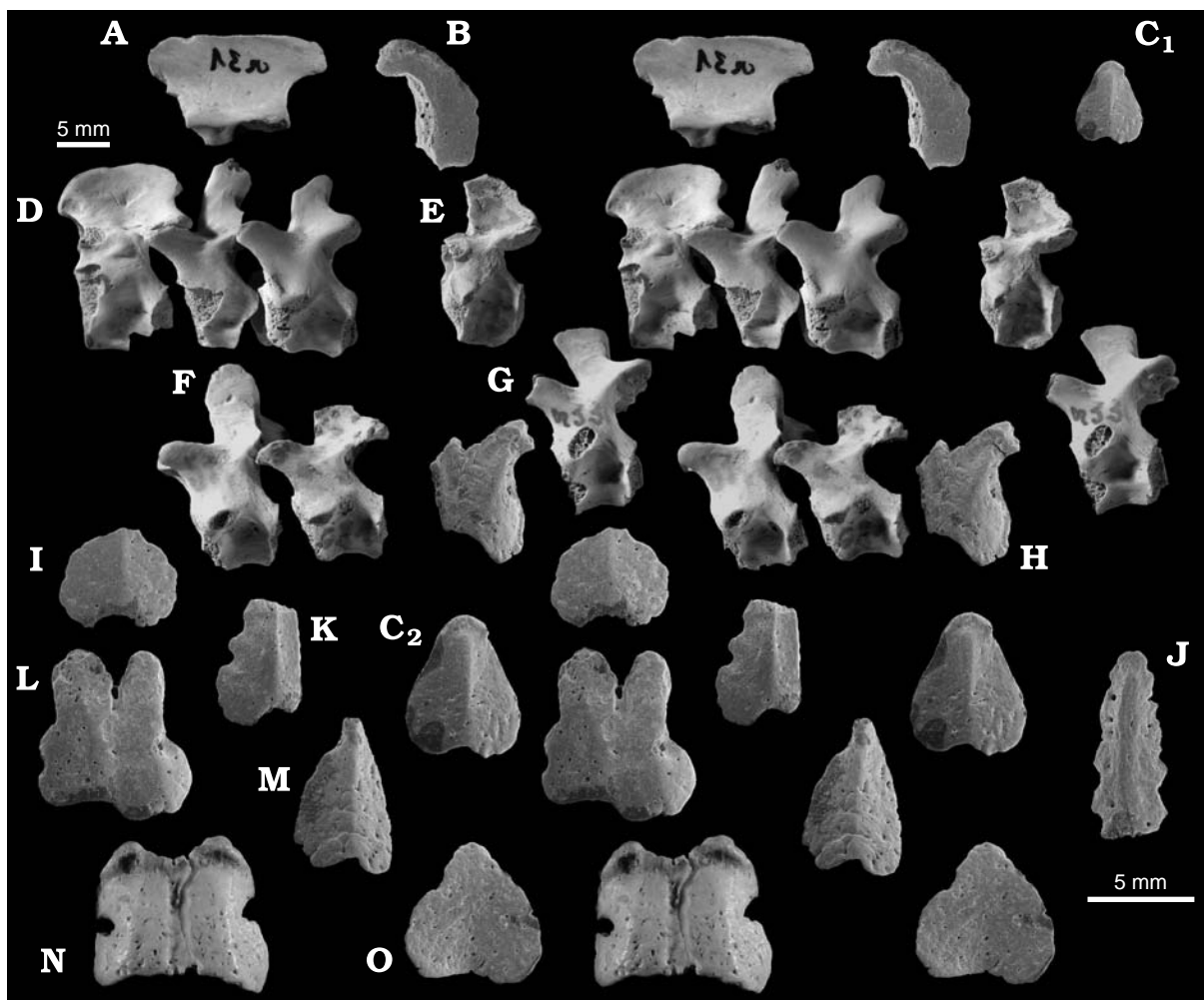


Fig. 5. Archosauriform remains, Early Triassic of Czatkowice 1, Poland. **A**. *Collilongus rarus* gen. et sp. n. Neural spine of axis ZPAL RV/587. **C–G, I, J, M, O**. *Osmolskina czatkowicensis* Borsuk-Białynicka et Evans, 2003. **C**. Simple osteoderm ZPAL RV/1338 in natural size (**C₁**), enlarged (**C₂**). **D**. Axis ZPAL RV/570, with two postaxial cervical vertebrae ZPAL RV/635 and 636 in a possible sequence. **E**. Cervical vertebra ZPAL RV/637. **F**. A possible sequence of midcervicals ZPAL RV/577 and 681. **G**. Posterior cervical vertebra ZPAL RV/607. **I, J, M, O**. Osteoderms: ZPAL RV/1342 (**I**), ZPAL RV/1341 (**J**), ZPAL RV/1339 (**M**), and ZPAL RV/1335 (**O**). **B, H, K, L, N**. Archosauriformes gen. indet. **B**. Left side of a compound osteoderm ZPAL RV/1345. **H**. ZPAL RV/1344. **K**. ZPAL RV/1336. **L**. ZPAL RV/1337. **N**. ZPAL RV/1340. Left side (**A, D–G**) and dorsal (**B, C, H–O**) views. SEM micrographs; all but **C₁** stereo-pairs.

Some small, very narrow specimens (e.g., ZPAL RV/1341) might belong to the unpaired posterior tail armour (Fig. 5J). Much less numerous are asymmetric osteoderms bearing a paramedian, instead of a median, keel and having one straight border (Fig. 5K) to make a sutural contact with a contralateral osteoderm. These elements closely correspond to the description of *Euparkeria* osteoderms (Ewer 1965, p. 414). They are usually strongly angled, the parasagittal part being rather narrow, thus indicating a slender back, the lateral part extending down the body flank. The third morphotype is represented by fused pairs of slightly asymmetric elements that are the largest and heaviest osteoderms (Fig. 5L, N). Some of these heavy osteoderms display a laterally twisted tip (Fig. 5B) that is rather difficult to interpret. One possibility is that such osteoderms fused with others to form an unpaired (e.g., cervical) shield of a type known in some crocodiles (Rogers 2003). They seem to be a variant of the fused pair (Fig. 5L, N).

The extremely small percentage of the heavy compound osteoderms (Fig. 5B, L, N) and the high percentage of the perfectly symmetric ones might reflect systematic differences. On the size and frequency criteria, the osteoderms of the first morphotype are tentatively considered to belong to *Osmolskina czatkowicensis*. If it is true, the dorsal armour over the vertebral column in *O. czatkowicensis* would be essentially unpaired, which is at odds with the data on *Euparkeria* armour (Ewer 1965; Krebs 1976). A close similarity between

osteoderms of the small, asymmetrical, morphotype described above (Fig. 5K) and those described by Ewer (1965) suggests paired construction of the armour over the spine, probably within the trunk, but the heavy compound osteoderms are relegated to Archosauriformes gen. indet.

PECTORAL GIRDLE AND FORELIMB

Scapula. — The archosauriform scapulae from the Czatkowice 1 material are elongate bones (Fig. 6G) about three times longer than wide at the distal end, and widening at the glenoid. The best preserved specimen, ZPAL RV/902 (Fig. 6H), exceeds 34 mm in length, and is about 11 mm in distal width.

The bone is medially concave (Fig. 7A) but becomes flatter towards the distal end. It suggests the thorax was fairly deep and narrow. The coracoid surface tapers anteriorly but is usually damaged. The glenoid facet is roughly semicircular and is perpendicular to the posterior border of the scapula (Figs 6F, 7A). More dis-

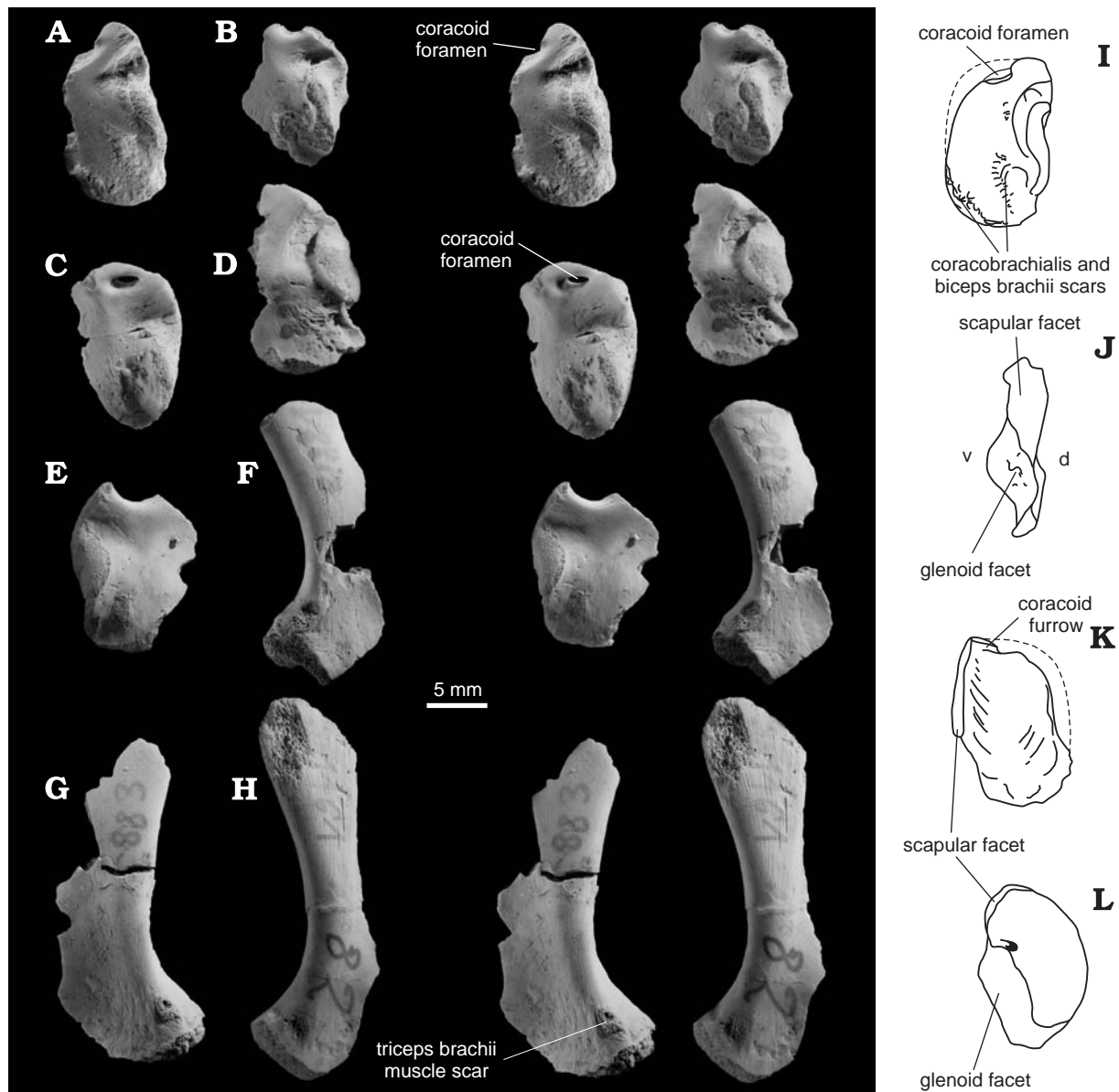


Fig. 6. A–K. *Osmolskina czatkowicensis* Borsuk-Białynicka et Evans, 2003, Early Triassic of Czatkowice 1, Poland. A–D. Left coracoids: ZPAL RV/903 (A), ZPAL RV/1169 (B), ZPAL RV/1311 (C), and ZPAL RV/1166 (D). E. A fragment of right coracoid ZPAL RV/1167 with largely open coracoid foramen. F. Right scapula ZPAL RV/881. G. Left scapula ZPAL RV/883. H. Right scapula ZPAL RV/1161. I. Left coracoid. J. Articular border of the left coracoid. K. Left coracoid. L. *Erythrosuchus africanus* Broom, 1905. Left coracoid (after Gower 2003, fig. 29). Ventral (A–E, I), lateral (F–H), and dorsal (K, L) views. A–H, stereo-pairs.

tally, this border arches strongly posteriorly, but becomes straighter distally. ZPAL RV/881 (Fig. 6G), shows that the proximal region was antero-posteriorly much wider (Fig. 7A₃) than preserved in most specimens, as it was in *Euparkeria* (Fig. 7E). The bone thins anteriorly, but probably gets thicker again (as does the scapular facet of the coracoid (Fig. 6J) to create a cavity on the lateral side of the scapula, anterior to the glenoid. Directly above and posterolateral to the proximal end, there is a scar probably left by the scapular head of the triceps muscle (Figs 6G, 7A).

The best preserved scapulae cluster about 30 mm in length, but there are many smaller specimens that are too fragmentary to be measured. There is no indication of heterogeneity in the sample, so the morphology described above may safely be ascribed to *Osmolskina*. Based on skull to scapula length proportions in *Euparkeria* (Appendix 1), the scapula appears relatively longer in *Osmolskina*. However, direct comparisons (Fig. 7A, E) show that the difference is not significant.

Coracoid. — The coracoid is considerably longer (15–21 mm N = 3) than wide (10–13 mm N = 3), and has thickened lateral and posterior borders (Fig. 6). Both the anterior and medial borders are usually damaged. As a rule, the fracture passes through the coracoid foramen, leaving it as an incision rather than an enclosed perforation. The slightly concave surface of the bone is considered dorsal. It is sculptured by posteriorly converging V-shaped ridges. The other side is a folded ventral or external surface. The folds probably correspond to what Ewer (1965, p. 407) described in *Euparkeria* as radiating struts buttressing the articular facets of the lateral border. The anteriormost of these supports the elongated scapular facet, extending down the anterior half of the coracoid (Fig. 6A–D, I), the middle one supports the glenoid, and the posterior one makes the coracoid blade more resistant to breakage. The scapular facet tapers posteriad and broadens at the anterior end (Fig. 6J). Its posteroventral half faces laterally and forms a complicated pitted facet that contributed to a glenoid. It has a swollen ventral border (*e.g.*, Figs 6A, 7A₃) that probably served for the attachment of the joint capsule. The swelling is bordered by two furrow-like depressions, exactly as it is in *Euparkeria*. The anterior one bears circular traces probably left by the origin of the supracoracoideus muscle. In rare instances, there is a vascular foramen or a trace of perforation (ZPAL RV/1169; Fig. 6B) in this concavity. The posteroventral surface of the coracoid bears two rugosities, lateral and posteromedial, probably for the coracobrachialis and the biceps brachii muscle respectively (Fig. 6I).

The coracoid foramen usually appears as a subhorizontal furrow (Fig. 6A, I) that incises the anterior border. The furrow enters ventrally, well anterior to the glenoid, and then slopes dorso-laterally to continue onto the dorsal surface of the bone (Fig. 6K). Only in rare specimens is the passage fully enclosed anteriorly. ZPAL RV/1168 (Fig. 6C) is an example, but the closing bridge is anteriorly damaged and none of the original bone edges are preserved. Specimens ZPAL RV/903 and 1168 (Fig. 6A and C respectively) are better preserved anterolaterally, and show that the usually missing anterior part of the coracoid was not extensive. This indicates a comparatively anterior position of the foramen, far from the posterior margin of the bone. ZPAL RV/1167 suggests that there was no anterior part (Fig. 6E), and the coracoid passage was open.

In terms of outline, *Osmolskina* coracoids are exactly the same as those of *Euparkeria* (Ewer 1965) and other basal archosauriforms such as *Sarmatosuchus* (Gower and Sennikov 1997, fig. 10), *Erythrosuchus* (Gower 2003), and the rauisuchids *Batrachotomus* (Gebauer 2004), *Ticinosuchus* (Krebs 1965), and *Postosuchus* (Long and Murry 1995). The *Osmolskina* coracoid (Fig. 7A₃) differs from that of *Euparkeria* (Fig. 7E₁) in that the glenoid part is more elongate relative to the preglenoid portion than in the latter (as presented by Ewer's 1965, fig. 9), while being similar to *Erythrosuchus* and *Sarmatosuchus* in this respect. A comparison with *Erythrosuchus africanus* is noteworthy. In this species (Gower 2003, fig. 29), the glenoid facet is widely exposed in dorsal view (Fig. 6L) in contrast to *Osmolskina* where it is almost hidden under the lateral border (Fig. 6K). This means a difference in position of either the coracoid, which is more probable, or the humerus. In *Osmolskina*, the coracoid probably angled ventromedially, suggesting a bilaterally flattened thorax, whereas *Erythrosuchus* had a more horizontally placed coracoids, indicating a more dorsoventrally flattened ribcage. As reconstructed by Ewer (1965, fig. 9) in *Euparkeria*, the coracoid was subhorizontal in orientation, but it is much more oblique in her fig. 20. The putative differences between *Osmolskina* and *Euparkeria* in the length and orientation of the glenoid (the glenoid being much shorter and more posterior in orientation in *Euparkeria*) might be artefacts.

Osmolskina is distinguished from all other basal Archosauriformes, and from most outgroup taxa (the rynchosaur *Hyperodapedon* is an exception; Benton 1983), in that the coracoid foramen is situated close to the anterior border of the coracoid and is anteriorly open in at least some cases. This difference (the foramen

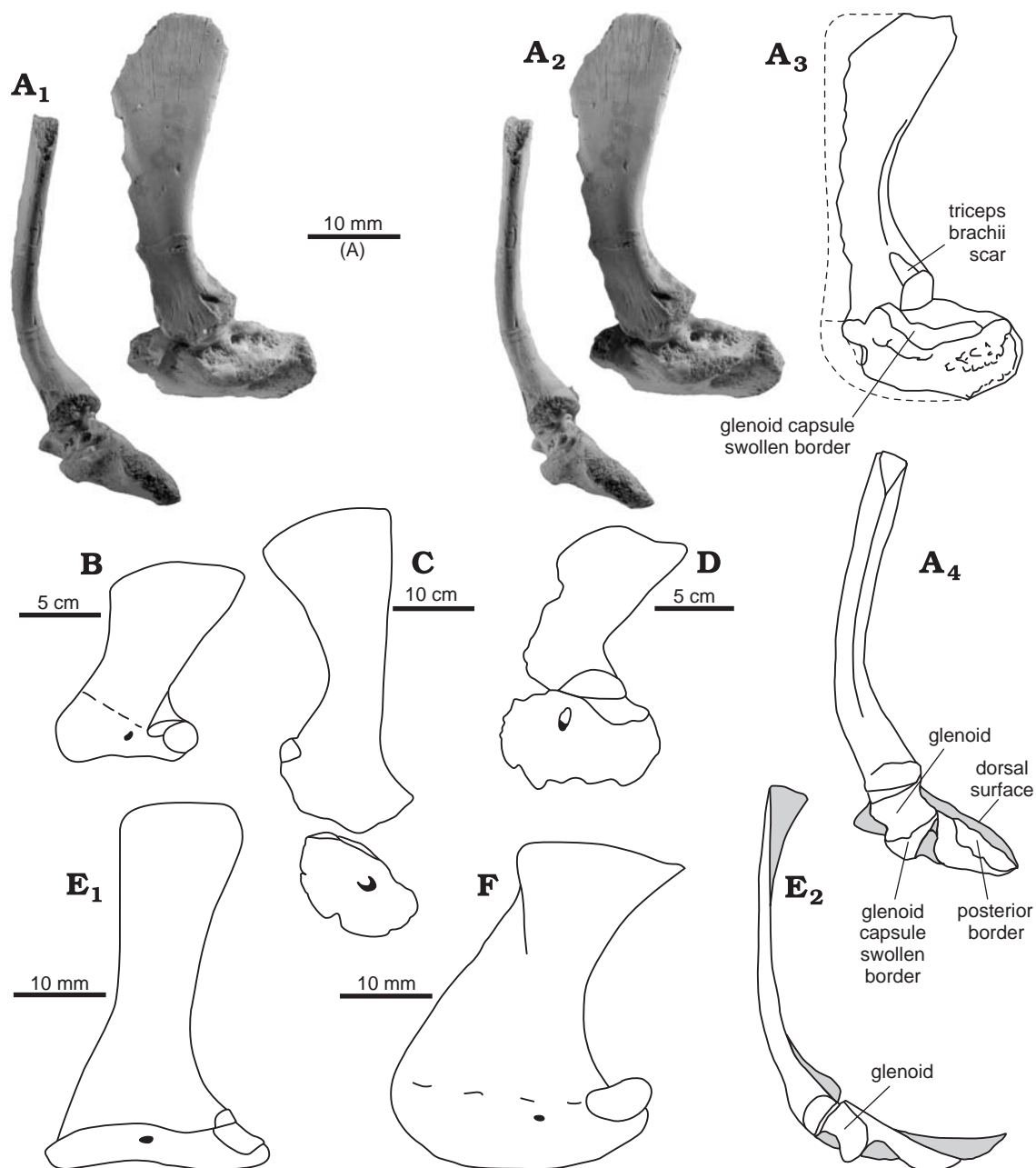


Fig. 7. Left scapulocoracoids. **A.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Combined from ZPAL RV/903 (scapula) and ZPAL RV/902 (coracoid). **B.** *Proterosuchus vanhoepeni* (Haughton, 1924) (after Cruickshank 1972). **C.** *Erythrosuchus africanus* Broom, 1905 based on Gower (2003, fig. 29). **D.** *Sarmatosuchus otschevi* Sennikov, 1994 (after Gower and Sennikov 1997). **E.** *Euparkeria capensis* Broom, 1913 (after Ewer 1965). **F.** *Prolacerta broomi* Parrington, 1935 (after Gow 1975). All but A₁, A₄, E₂ in left side view. A₁, A₄, E₂ in posterior view. A₁, A₂, stereo-pairs.

enclosed or open anteriorly) may well be ontogenetic, as demonstrated *e.g.*, by Currie and Carroll (1984) in the younginiform reptile *Thadeosaurus colcanapi*, but the decidedly anterior position is certainly an apomorphy of *Osmolskina*. Interestingly, anterior emargination of the coracoid is a phytosaurian character (Romer 1956; Westphal 1976; Chatterjee 1978; Long and Murry 1995, fig. 30), but an anterior position of the coracoid foramen is also found in the rauisuchid *Arizonasaurus babbitti* (Nesbitt 2005, fig. 27).

Humerus. — All Czatkowice 1 humeri of a size consistent with *Osmolskina* (see Appendix 1) display essentially the same structure. They are derived in terms of a weak twist of the shaft, a weak enlargement of the extremities, and the absence of both entepicondyle and ectepicondyle foramina. The proximal articular head is protuberant, and probably earlier to ossify than the internal tuberosity and the most proximal part of the

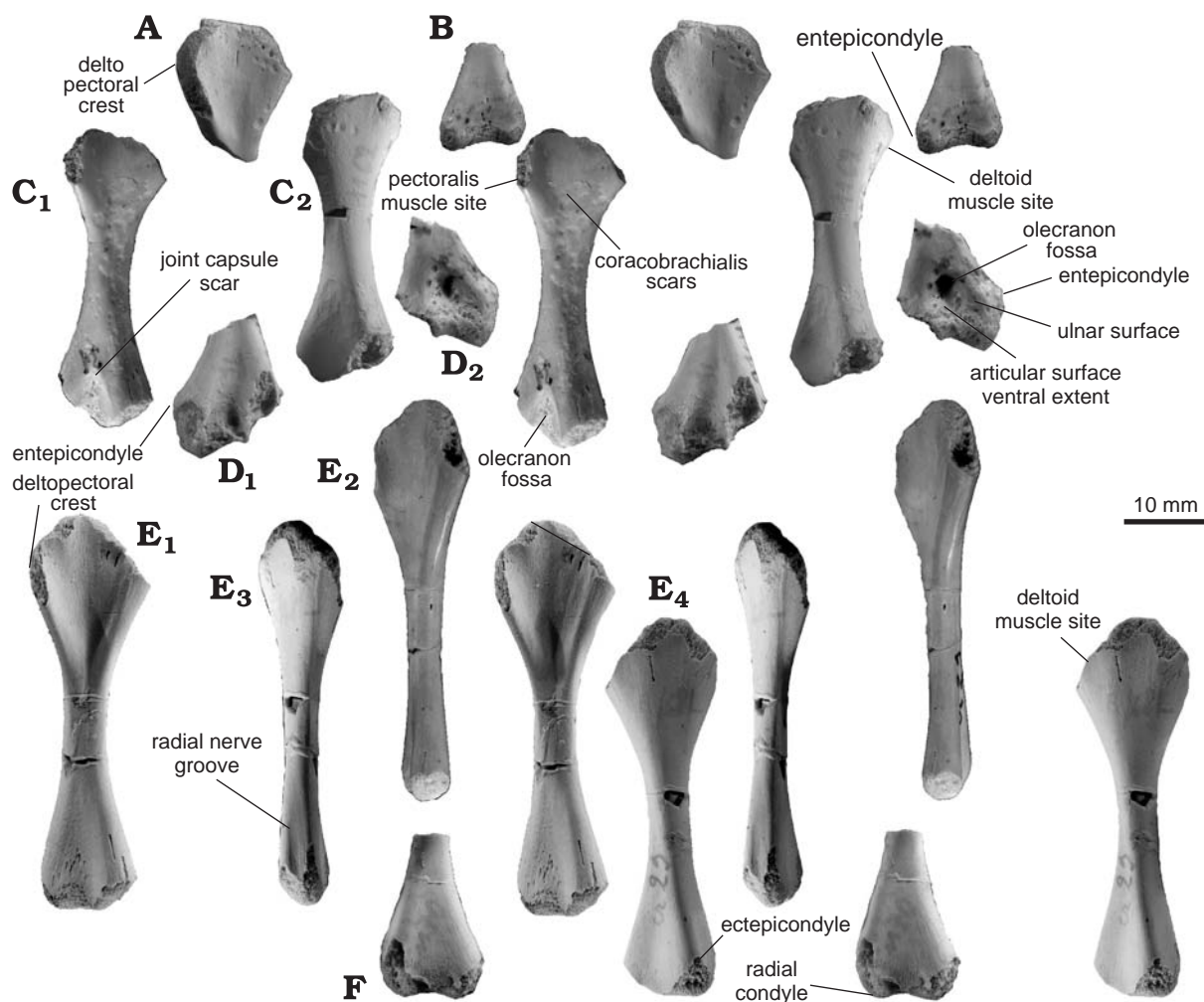


Fig. 8. **A, C, D.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A.** Proximal end of the right humerus ZPAL RV/1172, in ventral view. **C.** Left humerus ZPAL RV/1262 (reversed), in proximal ventral (**C**₁) and proximal dorsal (**C**₂) views. **D.** Distal end of the right humerus ZPAL RV/1164, in dorsal (**D**₁) and ventral (**D**₂) views. **B, E, F.** Archosauriformes gen. indet., Early Triassic Czatkowice 1, Poland. **B.** Distal end of the right humerus ZPAL RV/1173, in dorsal view. **E.** Right humerus ZPAL RV/877, in proximal ventral (**E**₁), distal medial (**E**₂), distal lateral (**E**₃), and proximal dorsal (**E**₄) views. **F.** Distal part of the left humerus ZPAL RV/1170, in dorsal view. Stereo-pairs.

deltopectoral crest which are less ossified and always damaged. The concave ventral surface of the proximal end bears slight scars that probably relate to the insertion of the coracobrachialis muscle. The dorsal face is slightly convex.

Humeral lengths and proportions, both suggest the presence of two morphotypes in the Czatkowice 1 material. The first morphotype is shorter and more robust, the second one is longer and slimmer. Based on rough estimates from damaged bones, most humeri cluster between 25 and 36 mm in length, which corresponds to the first morphotype. On the basis of frequency we consider it as belonging to *O. czatkowicensis*. The longest and best preserved specimen, ZPAL RV/877 (Fig. 8E) represents the second morphotype. It exceeds the next in length by more than 20% and is more slender. The possibility of negative allometry during ontogeny (McGowan 1999), the humerus becoming more slender with increasing length, is improbable. The longer morphotype, although more closely similar in proportions to *Euparkeria capensis*, is relegated to *incertae sedis*.

Also the proximal and distal ends detached from the shafts display two different morphologies, the more expanded ends (Fig. 8A, D) matching the shorter bones (Fig. 8C) belonging to *O. czatkowicensis* and *vice versa* (Fig. 8B, F and E). The distal end of *O. czatkowicensis* (Fig. 8D), has a more protruberant entepicondyle than the second morphotype (compare Fig. 8D and E). The flattening of one of its sides corresponds to the position of the radial nerve groove that usually runs laterally and separates the ectepicondyle from the supinator muscle origin. The other side, which is thus considered medial, is evenly convex in section, and ex-

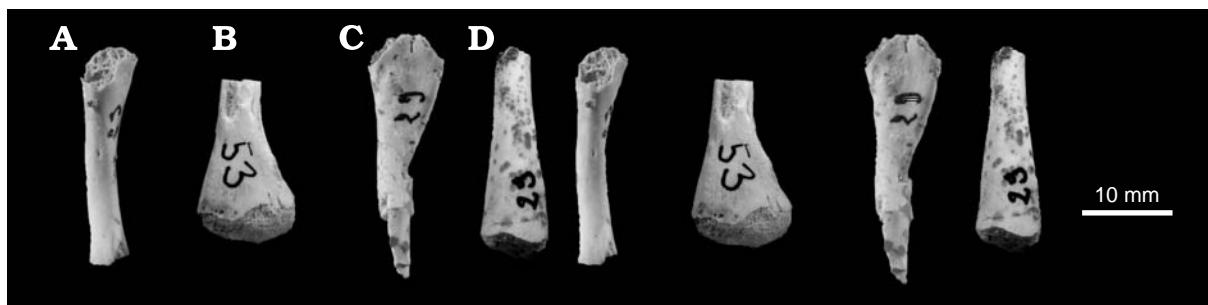


Fig. 9. **A, C, D.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A.** Proximal part of the left ulna ZPAL RV/1230, in ventromedial view. **C.** Proximal part of the left ulna ZPAL RV/1179, in medial view. **D.** Distal part of the radius ZPAL RV/1235. **B.** Archosauriformes gen. indet., Early Triassic Czatkowice 1, Poland. Distal part of the radius ZPAL RV/1232. Stereo-pairs.

tends into the entepicondyle. The central part of the articular surface extends onto the lateral wall of the ulnar condyle, and only slightly onto the ventral surface of the bone (Fig. 8D₂). The preserved part probably received the ulna. The radial condyle is broken off. There is a deep concavity proximal to the trochlea, corresponding to the olecranon fossa on the ventral side of the bone. Attributed to Archosauriformes, ZPAL RV/1170 (Fig. 8F) has a shallower olecranon fossa, and a less prominent entepicondyle, suggesting that this specimen belongs to the longer morphotype (ZPAL RV/877; Fig. 8E).

The twist in the proximo-distal axis is roughly 30–40° for the whole Czatkowice 1 archosauriform group, being slightly more in the shorter ones, assigned to *O. czatkowicensis*, and slightly less in the longest bone. The deltopectoral crest is always smoothly rounded and has its apex at a point roughly 20% down the length of the humerus. In spite of some differences, both Czatkowice 1 humeral morphotypes correspond to a lightly built animal and are closely similar to those of *Euparkeria*.

Radius. — Several fragments (*e.g.*, ZPAL RV/1231, 1233, 1234, 1235; Fig. 9D) of slender columnar bones with slightly convex articular ends are considered to be the distal parts, possibly less than half the length, of the radius. The bones are featureless, circular in section, and only slightly waisted. They are considered to belong to *O. czatkowicensis* because they are more numerous and smaller than the second morphotype from the Czatkowice 1 material (ZPAL RV/1232; Fig. 9B).

Ulna. — Only those ulna fragments that have the proximal part preserved (ZPAL RV/1178, 1179) are readily recognizable (Fig. 9A, C), but no specimen has its articular surface and olecranon preserved. The distal parts are less characteristic anatomically and have yet to be recognized. On the basis of Ewer's (1965) data on *Euparkeria*, and specimens of crocodile antebrachii (ZPAL RI/75, 76), the acute proximal apex is regarded as medial, and the two blunt ones are considered dorsal and lateral. The proximal parts of the ulna are short along the dorsoventral axis and expanded transversally, being slightly concave ventrally and convex dorsally. Proximally, the dorsal wall turns into a blunt margin that probably continued as an olecranon. The ulnar head is triangular in transverse section. As a whole, the bone is twisted, the ventral concavity probably facing towards the radius, as it does in the crocodylian antebrachium. Mid-shaft, the transverse section becomes circular. Distally, the shaft is twisted at about 50° to the proximal end, the ventral surface of the bone passing into the lateral side of the distal end. These specimens match the size of radii and humeri assigned to *O. czatkowicensis*.

PELVIC GIRDLE AND HINDLIMB

The pelvis is represented by more than 100 iliac specimens of which about ten are complete, and by a large number of fragmentary pubes and ischia, none of them complete.

Ilium. — The subtriangular iliac blade and subcircular acetabular region (Fig. 10) are separated by an antero-posteriorly constricted neck, at the level of the dorsal half of the acetabulum. The preacetabular process of the iliac blade hardly extends beyond the anterior margin of the iliac neck. The postacetabular process is a stout elongate blade that is triangular in lateral aspect and tapers posteriad, slightly excavated ventrally in its distal half. The ventrolateral margin of the excavation is thickened and featureless. The ventromedial margin is acute and protrudes mediad. Bordered by these two margins, the elongate ventral excavation is a possible site of

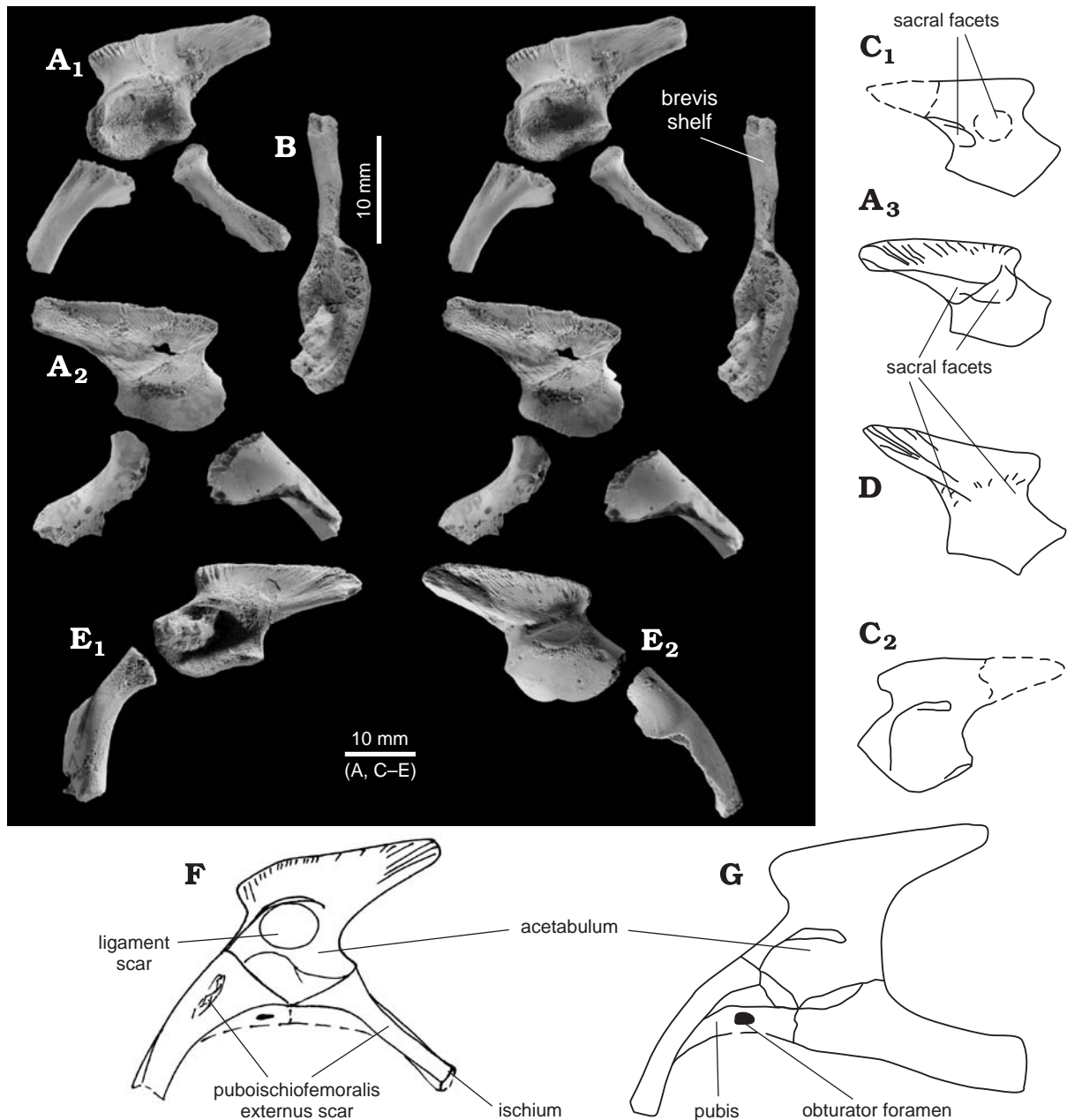


Fig. 10. **A, B, E, F.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A.** Right pelvis (reversed) combined from different individuals: ZPAL RV/678 (ilium), ZPAL RV/910 (pubis), and ZPAL RV/908 (ischium), in lateral (**A₁**) and medial (**A₂**) views; **A₃**, the same ilium in medial view. **B.** Left ilium ZPAL RV/630, in ventral view. **E.** Left ilium ZPAL RV/630 combined with a reversed right pubis ZPAL RV/905, in lateral (**E₁**) and medial (**E₂**) views. **F.** Reconstruction of the left pelvis, in lateral view. **C.** *Dorosuchus neoetus* Sennikov, 1989. Left ilium, in medial (**C₁**) and lateral (**C₂**) views, after Sennikov (1995). **D, G.** *Euparkeria capensis* Broom, 1913. **D.** Left ilium, in medial view, after Ewer (1965). **G.** Left pelvis, in lateral view, after Ewer (1965). **A, B,** stereo-pairs.

origin of the caudifemoralis brevis muscle (Romer 1923; Hutchinson 2001). This position is essentially the same as that of the “brevis shelf” (Romer 1927; Gauthier 1986; Novas 1996), as demonstrated by Langer and Benton (2006, fig. 9) in the dinosaurs. In the dinosaurs the brevis shelf extends more anterior and faces more ventrolateral than ventral, while being more distal, tapering toward the acetabulum (Fig. 10B), and facing ventrally in *Osmolskina*. According to Novas’s (1996) definition, the brevis shelf is “a prominent shelf on the posterolateral margin of the iliac blade, placed external to the posteroventral margin”, which corresponds to its lateral inclination. In *Osmolskina* the surface is more or less horizontal and its medial margin corresponds to the posteroventral one of the Dinosauria. Novas (1996) supported the view that the lateral of the two margins of the

brevis shelf was a neomorphic structure, whereas the medial margin was original. The presence of the shelf, although narrower and less excavated, in *Osmolskina* is more consistent with Hutchinson's (2001) view that the shelf is a pre-existing (*i.e.*, plesiomorphic) structure which was subjected to variability in the archosauriform evolution. The ventromedial margin continues towards the middle of the anterior sacral rib scar, and it probably received the second sacral rib. The ventral profile of the posterior iliac process makes an open angle (about 120°) with the posterior wall of the acetabulum.

A major part of the acetabulum is produced by the ventral portion of the ilium. Its ventral border bears elongated articular facets for the pubis and ischium, the axes of which close an angle of about 120°. The apex of the angle protrudes ventrally, exactly as it does in most basal Archosauriformes (Charig and Sues 1976), but hardly so in *Shansisuchus* (Young (1964, fig. 41). It also protrudes in basal archosaurs such as parasuchians and aetosaurs (Krebs 1976; Long and Murry 1995) on the one hand and in *Lagerpeton* (Sereno and Arcucci 1993) on the other. In all these taxa, the pubis and ischium facets touch each other leaving no space for an acetabular perforation, in contrast to *Marasuchus* where they are wide apart (Sereno and Arcucci 1994). In *Osmolskina*, the ischium and pubis facets are subperpendicular to the plane of the acetabulum, which suggests a vertical position of the ilium. In contrast, in raiisuchids, the facets face ventrolaterally (personal observation on *Batrachotomus kupferzellensis* SMNS 80273, and *Stagonosuchus nyassicus* GPIT 325, see also Gebauer 2003), which is consistent with a subhorizontal position of the ilia (Bonaparte 1984; Parrish 1986).

In *Osmolskina*, the lateral surface of the iliac blade is slightly concave, but anteriorly, it turns into a convex surface facing anterolateral. This angulation is not associated with the presence of the rugose swelling or crest in contrast to most raiisuchid ilia (Gower 2000). A thick, laterally protruding supraacetabular ridge overhangs the acetabulum. It encircles the acetabulum anterodorsally, and protrudes mostly above the acetabulum, while leaving its posterior side open with no trace of an antitrochanter (*e.g.*, see Sennikov 1995, pp. 63–64 for terminological discussion). Two circular scars of porous bone marking the attachment of the ilio-femoral ligaments are situated within the acetabulum. The larger one, about one third the diameter of the acetabulum, occupies the ventral-most position, the second slightly smaller one, is dorsal and directly underlies the supraacetabular ridge.

The acetabular portion of the ilium is medially convex. Its dorsal part bears a flat, step-wise subcircular sacral facet facing dorsomedially (Fig. 10A₂, A₃). The facet passes onto the iliac blade and is radially ridged. Posterior to it, there is a triangular scar for the posterior sacral rib bordered dorsally by a longitudinal crest that passes into the ventro-medial border of the posterior process.

The dorsal border of the ilium is thin and bears heavy striations (Fig. 10A₁). They are most likely traces of tendons of the axial muscles, particularly of longissimus dorsi and iliocostalis muscles that fill the gap between the ilium and the neural spines (Romer 1956, p. 317). Anteriorly, the striations are vertical. They attenuate posteriorly to become distinct again on the lateral side of the posterior process. They also occur on the medial surface of the iliac blade and are oriented in a similar fan-shaped manner, subvertical in the anterior part then increasingly oblique.

The fairly large sample of ilia from Czatkowice 1 attributed to archosauriforms is morphologically quite uniform, and does not suggest any taxonomic heterogeneity. As there is more than one archosauriform taxon in the Czatkowice 1 material (see p. 316), this suggests that the ilium must have been identical in all of them. It seems useful to stress that the morphology differs from that of the raiisuchids (Sennikov 1988, Gower and Sennikov 2000) in the absence of a buttress above the rim of the acetabulum, a character unique to this group (Parish 1993, Gower 2000), and in the weak, rather than strong (Gower 2000), dorsal reorientation of the anterior sacral facet that indicates a weak, instead of strong, ventral deflection of the sacral ribs.

Comments: In the overall shape of the iliac blade, the iliac contribution to the acetabulum, the shape and depth of the acetabulum, and the development of the supraacetabular ridge, the *Osmolskina* ilium (Fig. 10A) corresponds to that of *Euparkeria* (Fig. 10G) as well as to that of *Dorosuchus neoetus* (Fig. 10C₂). This type of ilium is typical of archosauriforms in that (1) the acetabulum is deep, overhung by an anterodorsal, but mostly dorsal, supraacetabular ridge, and (2) the sacral facets are situated on the ventral (acetabular) and anterior parts of the ilium whereas they lie above the acetabulum level in prolacertiforms, and posterodorsal to it in lepidosaurs (Borsuk-Białynicka 2008). The non-perforated state of the acetabulum, and the weak development of the anterior process of the blade (Fig. 10A, E), both suggest a basal position for *Osmolskina* within the Archosauriformes.

Pubis. — All pubic specimens are damaged, and are usually represented by their middle sections. None has the acetabular part preserved. A roughly estimated length for the best preserved specimen, ZPAL

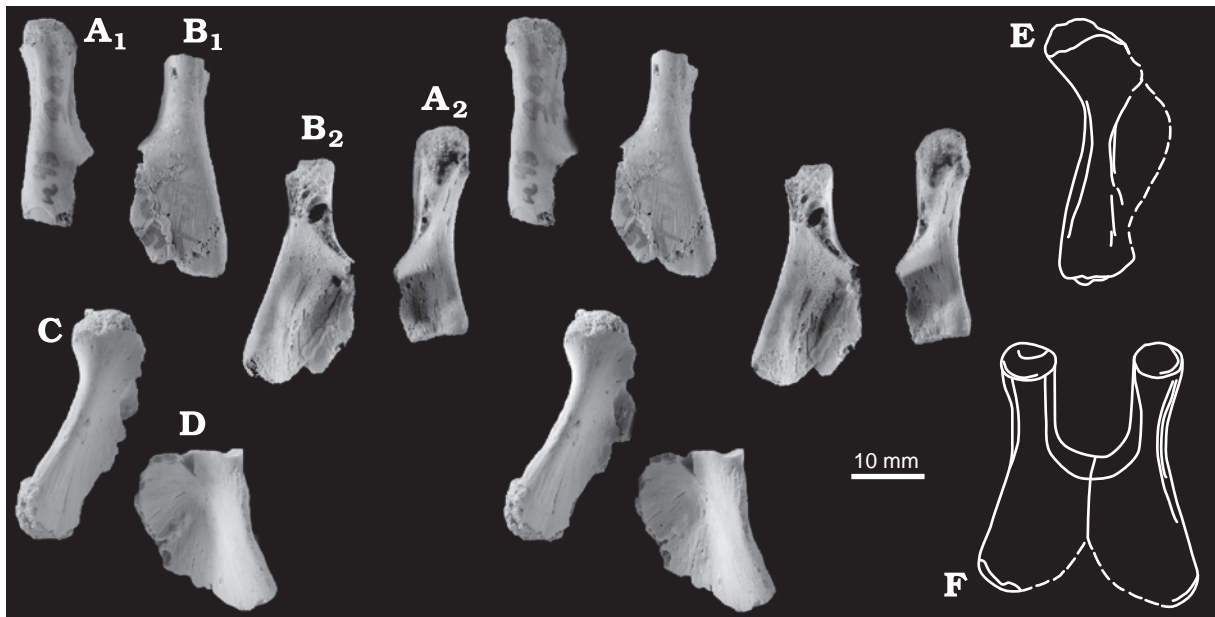


Fig. 11. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A.** Right pubis ZPAL RV/905. **B.** Left pubis ZPAL RV/906. **C.** Right ischium ZPAL RV/908. **D.** Distal part of the left pubis ZPAL RV/904. **E.** Reconstruction of pubis of both sides with a symphysis based on ZPAL RV/905 and 906. **F.** Reconstruction of right ischium based on ZPAL RV/908. Anterior (A_1 , B_1), posteroventral (A_2 , B_2), anteroventral (C), posteroventral (D), anteroventral (E), and anterodorsal (F) views. A–D, stereo-pairs.

RV/906, is about 20–25 mm. The pubis is bilaterally flattened proximally, but distally it passes into the medial symphyseal blade that forms the so called “pubic apron” (Fig. 11A, B, F). As a whole the bone is bowed antero-ventrally. The proximal part extends towards the ischium. A pubic foramen or an incision is expected to occur in that region, but neither it nor the pubic symphysis is ever preserved. Laterally, the proximal end of the bone bears a scar that probably reflects the origin of the puboichiofemoralis externus muscle.

Ischium. — The columnar shaft of the ischium is straight in posterior aspect but is arched transversely. The concave surface was probably oriented ventrolaterad in life, but the structure of this part of the pelvis is far from clear. Two specimens (ZPAL RV/908 and 892) are both 20 mm in length. Numerous fragmentary specimens are about the same size. The acetabular end is heavy. As suggested by the remnants of the acetabular part, the bone extended straight posteroventrad whereas the pubis turned more sharply ventrad. The shaft extends into a medial blade (Fig. 11C, E) that thins toward a symphyseal part, never fully preserved in the Czatkowice 1 material. The lateral border of the ischium bears rugosities that probably relate to the origin of the puboischiofemoralis externus muscle (Fig. 11C). They are situated about the mid-length of the bone.

Femur. — Femora are amongst the most common elements in the postcranial material from Czatkowice1, but even the largest are incomplete (Fig. 12A, G) with the proximal and distal ends always damaged. Very few specimens (*e.g.*, ZPAL RV/1188 and 1189; Fig. 12E and F respectively) preserve the region of the head. Contrary to expectations, they belong to the smallest individuals, but morphologically they are identical with the larger bones in the sample. The distal ends are more numerous but always detached from the shafts.

The *Osmolskina* femur (Fig. 12C) is similar to that of *Euparkeria* (Fig. 12D) and of *Dorosuchus* (Fig. 12I), but seems more twisted. It is expressed by a proximal end relatively narrow (Fig. 12C) in distal ventral view as compared to *Euparkeria* (Fig. 12D). The roughly estimated angle between the main axis of the distal end and that of the proximal end is as much as 55° in *Osmolskina*, compared to 25° in *Erythrosuchus* (Gower 2003, p. 63), slightly more than this in *Euparkeria* (32° according to Ewer 1965, p. 413), about 40° in *Dorosuchus* (Sennikov 1989) and up to 60° in crocodiles (*Crocodylus niloticus* ZPAL RI/76 and juvenile *Alligator* sp. ZPAL RI/74).

The proximal part of the shaft is widely subtriangular in transverse section, the ventrally located fourth trochanter (site of attachment of caudifemoralis musculature, Romer 1923), being at the top of the triangle. The

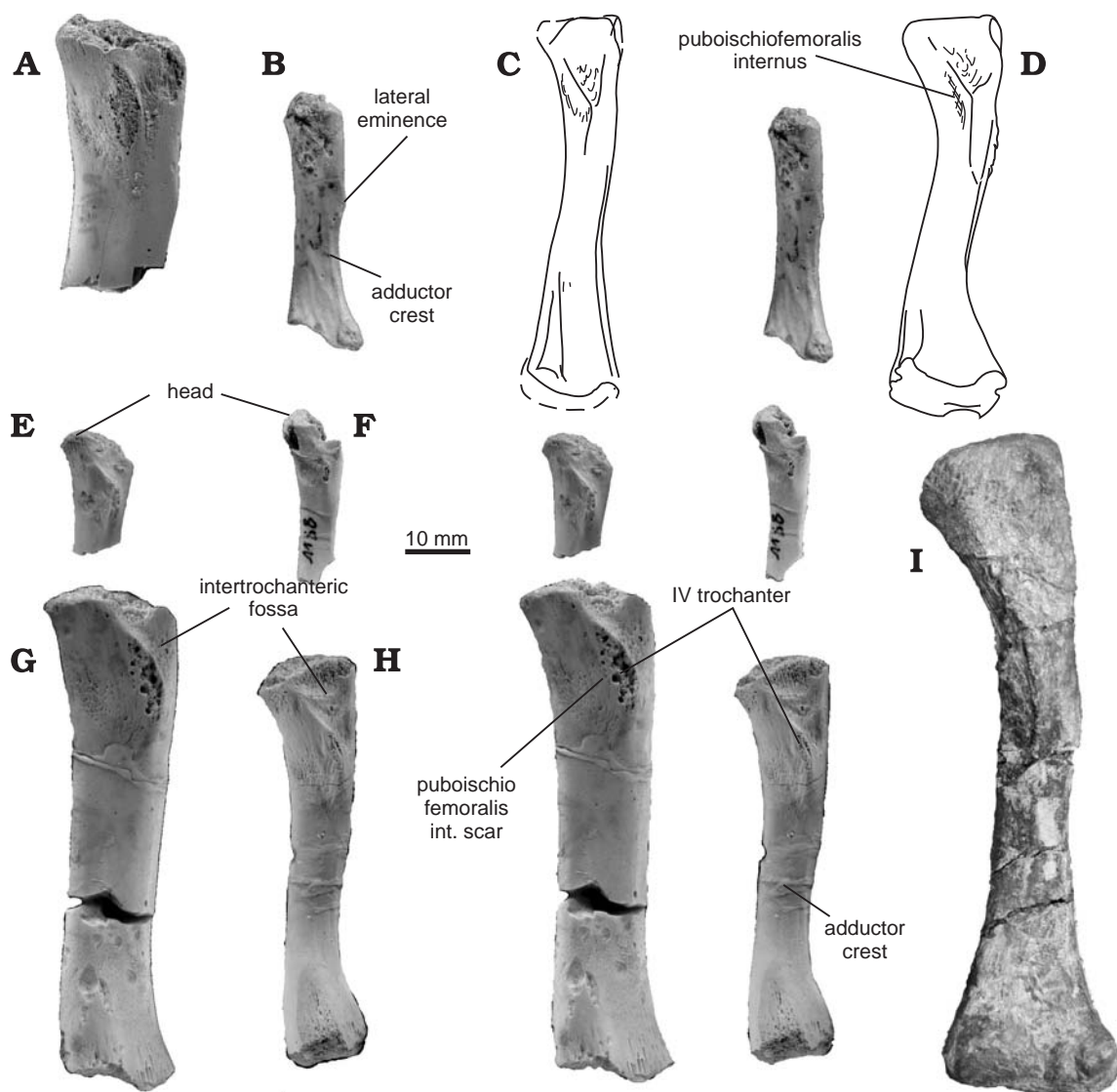


Fig. 12. Right femora. **A, G.** Archosauriformes gen. indet. **A.** Proximal part ZPAL RV/1174 (left reversed). **G.** ZPALRV/1332. **B, C, E–H.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B.** ZPAL RV/1184 (left reversed). **C.** Reconstruction of the bone. **E.** Proximal end ZPAL RV/1189 (left reversed). **F.** Proximal part ZPAL RV/1188. **H.** ZPALRV/940. **D.** *Euparkeria capensis* Broom, 1913 (left reversed), drawing after Ewer (1965, fig. 31). **I.** *Dorosuchus neoetus* Sennikov, 1989 PIN/1579/61, in distal ventral view. All but I in proximal ventral view. B, E–H, stereo-pairs.

distal end is roughly quadrangular in transverse section. The presence of an intercondylar fossa (Fig. 13G) on the dorsal side, and of the popliteal space on the ventral side (Fig. 13F) make both sides of the distal end slightly concave. The posterior (or lateral) surface bears a short furrow extending along its ventral border.

On the ventral surface, a triangular sculptured region, extending over a proximal one fifth the length of the shaft, and tapering distally (Fig. 13F), corresponds to the intertrochanteric fossa, the site of attachment of puboischiofemoralis externus (Romer 1922, 1923). The fourth trochanter lies at the apex of a sharp V-shaped crest, widely open anteriorly and pointing towards the tail. It is weakly expressed, and lies at no more than the proximal 1/4 of the femur length, slightly more proximal than in *Euparkeria*, and slightly more distal than in *Dorosuchus*. Anteromedial to the trochanter, a subcircular scar probably marks an attachment point of a part of the puboischiofemoralis muscle. The adductor crest extends diagonally along the ventral side of the shaft, beginning from the fourth trochanter and fading out at the ectepicondyle. Distally the adductor crest is confluent with a sharp crest that follows the lateral border of the bone. Proximally, at about one third the length of the shaft, this border produces an eminence (Figs 12B, 13F, G) which gives the bone a slightly humped lateral profile. In *Erythrosuchus*, the iliofemoralis muscle was inserted proximal of this eminence and the

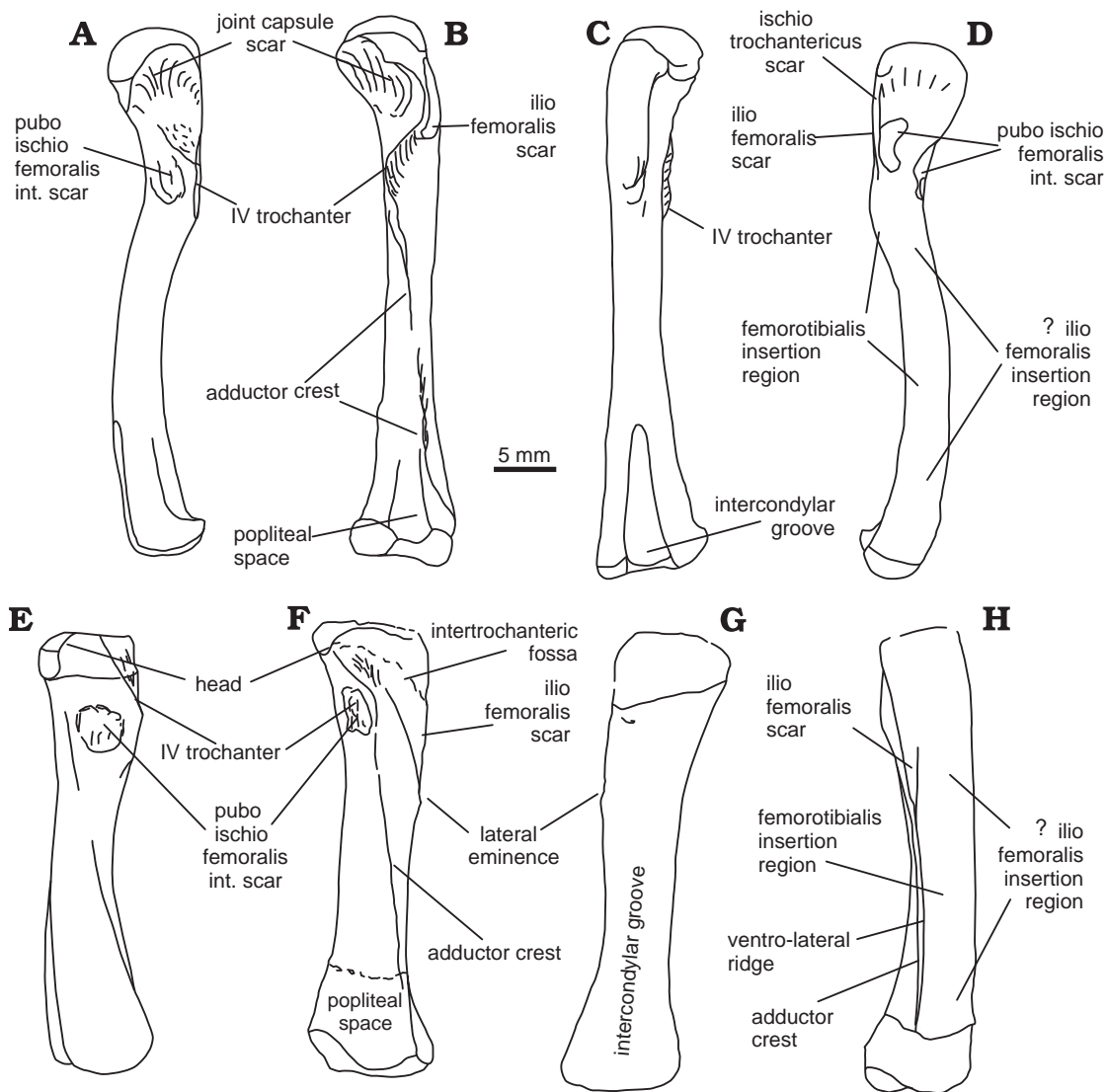


Fig. 13. **A–D**. Extant juvenile *Alligator* sp. Right femur ZPAL RI/74. Muscle scars according to Romer (1923). **E–H**. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice I, Poland. Right femur. Distal medial (A, E), distal ventral (B, F), distal dorsal (C, G), and distal lateral (D, H) views.

femoro-tibialis muscle distal of it (Gower 2003, fig. 34). The dorsal surface of the femur in *Osmolskina* (Fig. 13G) is quite smooth.

The *Osmolskina* femora range in size. The modal length is estimated at about 40 mm, but fragments of larger individuals show that the bone may have attained twice this length. As estimated for one of the more complete bones, ZPAL RV/940, the length to width index is about 4.5 for both proximal and distal ends. In 26 specimens, the width of the proximal end measured directly above the fourth trochanter, is mostly between 9 and 11 mm. Some much larger specimens reach 15–19 mm in width (Fig. 12A, G). They are separated by a hiatus (Supplement 2H and Fig. 14) from the rest of the sample, and, on this basis, are relegated to Archosauriformes gen. indet., but they cannot be distinguished from the femora attributed to *O. czatkowicensis* on any morphological features.

The dorso-ventral flattening of the proximal part of the shaft is expressed by the ratio of the bi-lateral diameter to the dorso-ventral diameter, and is 1.4:1 in ZPAL RV/940 and 1.7:1 in one of the largest femora, ZPAL RV/1174. This either shows negative allometry (the flattening increasing in ontogeny) or systematic difference. According to Parrish (1986), the femora are markedly anteroposteriorly (= dorsoventrally) flattened in both ornithosuchids and rauisuchids while being more nearly circular in other archosauriforms. The width to height ratio is 1:1 in both the older and the younger *Crocodylus niloticus* (ZPAL RI/76 and 75 respectively) examined.

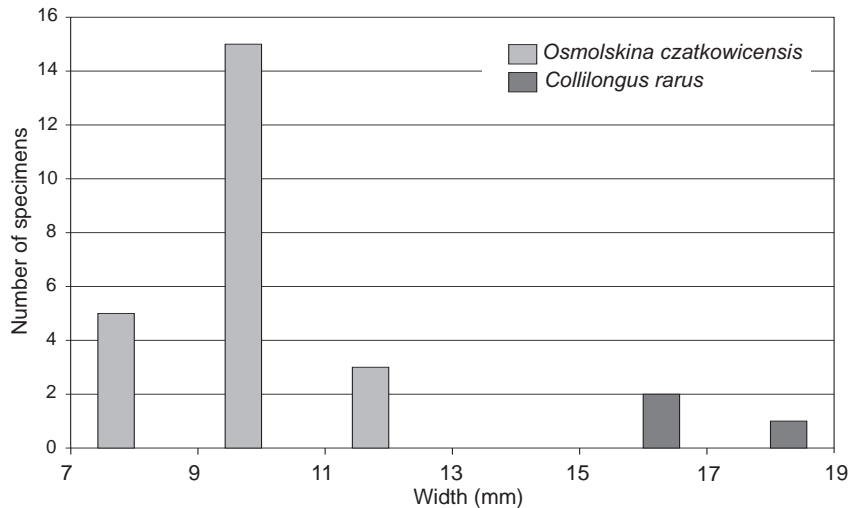


Fig. 14. Frequency distribution of femur width. Archosauriformes from the Early Triassic Czatkowice 1, Poland.

Tibia. — All the archosauriform tibia from Czatkowice 1 are simple long bones that are slightly expanded at both ends, especially proximally, the transverse section being a flattened oval rather than a circle. They are represented by several fairly well preserved but never complete specimens (Fig. 15A–C), and numerous fragments. The roughly estimated lengths suggest the same hiatus in the variability ranges of this bone as in the case of the femur. Moreover, the size differences combine with morphological differences that suggest the variability has systematic significance.

The main morphotype, about 30 mm in length, and flattened dorso-ventrally, is considered to belong to *Osmolskina*. The shorter side of the *Osmolskina* tibia bears a distinct oval muscle scar probably left by the puboischiotibialis muscle. In lizards, the tendon of this muscle inserts on the medial wall of the tibia near the proximal end (Romer 1942). The side bearing this scar is thus considered medial, and the flattening of the bone is correspondingly dorso-ventral. A similar scar that appears (although not described) on the medial side of the tibia in *Euparkeria* (Ewer 1965, fig. 32) and in *Erythrosuchus* (Gower 2003, fig. 35B), is considered homologous. One of the larger surfaces of the shaft, which is slightly convex, is considered dorsal. The opposite side, which is slightly concave, is ventral. A vertical crest extending from the proximal end of ZPAL RV/1221 (Fig. 15B₃, B₄) for a short distance down the ventrolateral side of the shaft probably denotes the fibular contact. The proximal and distal articular surfaces are never preserved. In *Euparkeria* (Ewer 1965, fig. 32) the proximal end of the tibia bears a rough triangular field tapering distally and laterally which may reflect the attachment of the common tendon of the knee joint extensors (extensor tibialis, ambiens and femoro-tibialis), and is thus a substitute of the cnemial crest. No such field occurs in *Osmolskina*.

Fibula. — The fibula has been reconstructed (Fig. 16E) from two sets of fragments considered as proximal and distal parts (Fig. 16A, C respectively). They come from the same sample, correspond in size and state of preservation, and are probably complementary to each other. The bone is very narrow, the shaft being flat on one side, considered ventral, and slightly convex in transverse section on the opposite side. The flat wall (Fig. 16E₁, E₃) is bordered by faint crests. The flattening continues over both parts of the fibula thus providing a basis for reconstruction. The anterior trochanter (*i.e.*, iliofibularis trochanter of Parrish 1986) protrudes from the shaft at around one third its length. It makes the bone crooked. As reconstructed, the fibula is slightly bowed medially and the distal end is enlarged.

According to Sereno (1991), the anterior trochanter of the fibula in basal archosauriforms is represented by an oval rugosity or a low vertical crest, in contrast to the strongly protruding trochanter in most basal crurotarsians (phytosaur, ornithosuchids, aetosaurs, rauisuchids and primitive crocodylomorphs) that makes the fibula crooked in shape. As illustrated by Sereno (1991, fig. 21), the shape of the fibula in *Euparkeria* is speculative, because it is only preserved distally. Ewer (1965) did not comment on this feature. Reconstructed from Czatkowice 1 material, the fibula corresponds in length to the tibiae of *Osmolskina czatkowicensis*, and is tentatively assigned to this species. However its crooked appearance resembles basal crurotarsians rather than *Proterosuchus* (Cruickshank 1972) and most erythrosuchids (Charig and Sues

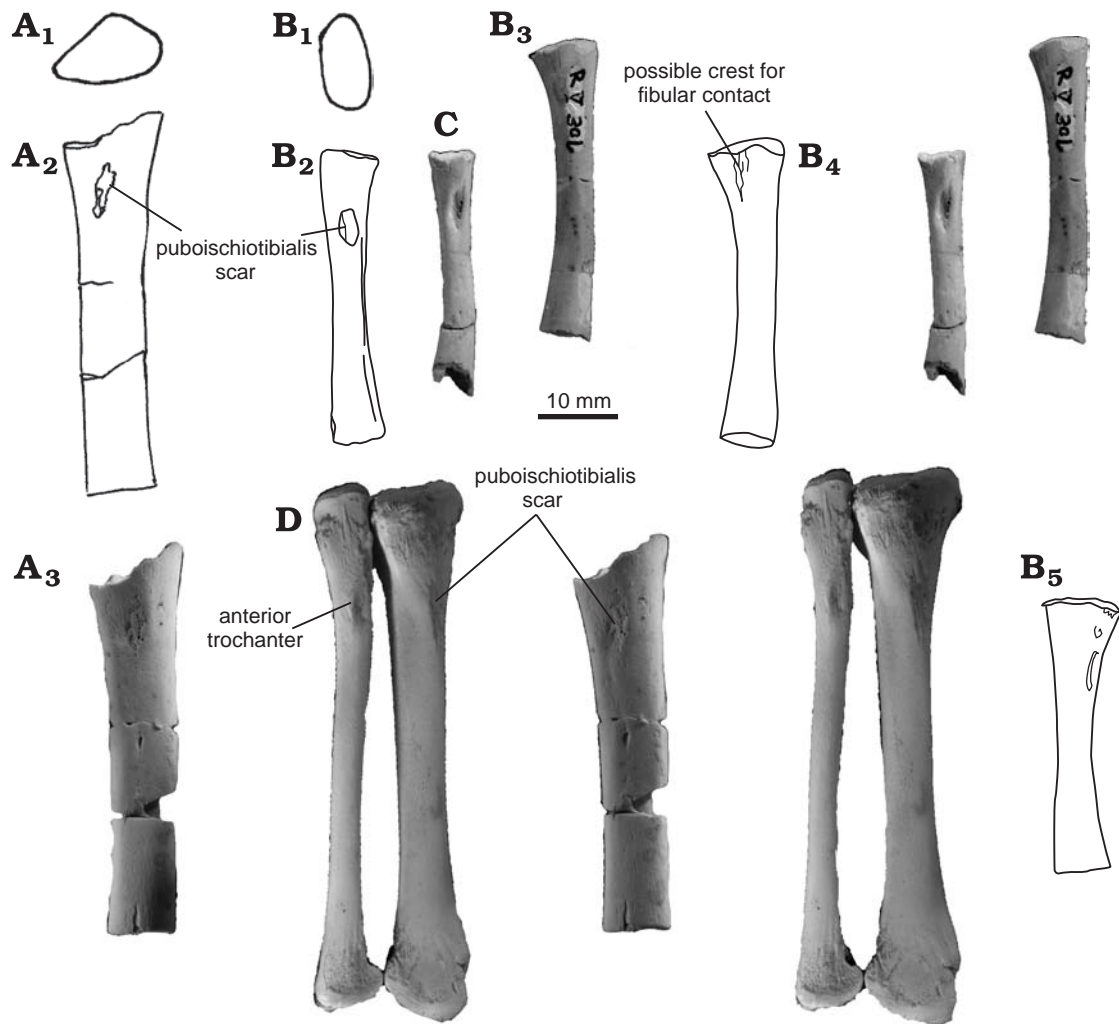


Fig. 15. **A.** Archosauriformes gen. indet. 2003, Early Triassic of Czatkowice 1, Poland. Tibia ZPAL RV/1175, in ?medial view (A_2 , A_3). The outline of the proximal end with medial side down (A_1). **B.** **C.** *Osmolskina czatkowicensis* Borsuk-Białynicka et Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B.** Right tibia ZPAL RV/1221, in medial (B_2) view; with the outline of the proximal end with medial side down (B_1); the same tibia in lateral (B_3 , B_4) and dorsal (B_5) views. **C.** Left tibia ZPAL RV/1222, in medial view. **D.** Extant crocodile *Crocodilus niloticus*, crus ZPAL RI/76. A_3 , B_3 , C, D, stereo-pairs.

1976) as far as they are known. As reconstructed, the fibula suggests either that the crooked shape appeared in basal archosauriforms, or that it does not belong to *Osmolskina* and demonstrates the presence of the crurotarsians in the material.

Tarsus. — Among the very small disarticulated tarsal and carpal elements in the Czatkowice 1 material, the largest, most frequent, and least variable in size are considered to belong to *Osmolskina czatkowicensis*. They usually look like small bodies of spongiosa mostly lacking a surface of finished bone. If preserved at all, the joint facets are damaged all around the margins. However, a few more complete specimens (an astragalus: ZPAL RV/811, a calcaneum ZPAL RV/810, and a fourth distal tarsal ZPAL RV/812) permit a more detailed description. Other than the fourth, the distal tarsals have not been identified.

The astragalus is an ovoid body bearing two slightly concave proximal facets for the fibula and tibia, respectively, on the proximolateral and proximomedial sides. They are approximately perpendicular to each other and separated by a nonarticular surface. This surface is slightly concave in its transverse axis. It extends from the dorsal surface to the ventral one, turning distally into the ventral groove system (Cruickshank 1978, 1979; Sereno 1991; Gower 1996), and running down the ventral surface to end at the distolateral corner in a deep pit (referred to as the “perforating foramen component of the astragalus groove system” by Gower 1996). The exact shape of the ventral groove system is difficult to assess, because of poor preservation of the surface.

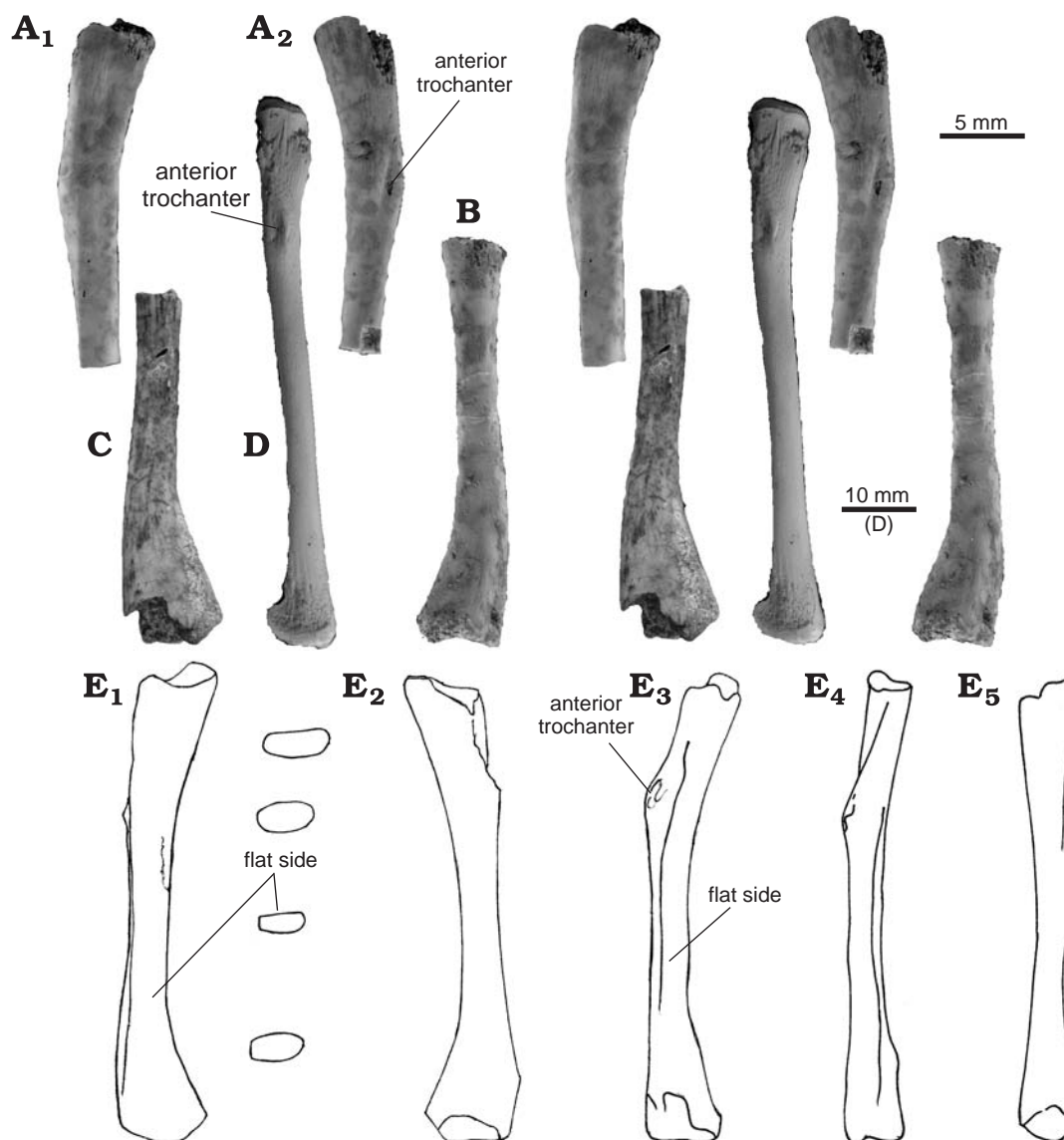


Fig. 16. **A, B, C, E.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. Possible left fibula. **A.** Proximal part ZPAL RV/1225. **B.** Almost complete shaft ZPAL RV/1247 with the distal end. **C.** Distal part ZPAL RV/1182. **E.** Reconstruction of the whole bone. **D.** *Crocodilus niloticus*, left fibula ZPAL RI/76. Ventral (**A₁**, **C**), dorsal (**A₂**, **B**, **D**, **E₂**) views; **E₁**, ventral view and transverse sections on different levels (ventral side upwards); ventro-lateral (**E₃**), lateral (**E₄**), and medial (**E₅**) views. **A–D**, stereo-pairs.

In the lateral half of the dorsal surface, finished bone is sometimes preserved in a slightly concave and pitted field (Fig. 17A) (dorsal hollow of Gower 1996). The tibial facet is a transversely widened oval (Fig. 17) whereas the fibular facet is subcircular with the lateral part of the outline slightly concave (Fig. 17F). Distally the fibular facet passes along the lateral side of the bone into a calcaneal facet (Fig. 17B) of approximately the same diameter. The calcaneal facet faces distolaterally. It is incised posteriorly by the distolateral branch of the ventral groove mentioned above (Fig. 17B). Apart from this, there is no indication of any subdivision of this facet into dorsal and ventral parts as recognized in *Proterosuchus* (Sereno 1991, fig. 3D). Neither is there any astragalo-calcaneal canal. Obviously, the pit of the ventral groove is a rudiment of this canal. The calcaneal facet is saddle-shaped and slightly convex (Fig. 17B), along the antero-posterior axis (because ventrally it turns toward the perforating foramen of the ventral groove system). The posterior incision probably received the ventromedial process of the calcaneum (Fig. 18B₃, E), the joint allowing a slight mobility in two planes.

The distal facets of both astragalus and calcaneum contribute to the articular surface for distal tarsal four (Figs 17J, 18B₃, B₂), as they do in *Erythrosuchus* and *Euparkeria* (Gower 1996). If properly identified here, the facet for distal tarsal four covers the medial one third of the distal surface of the astragalus. It is almost flat

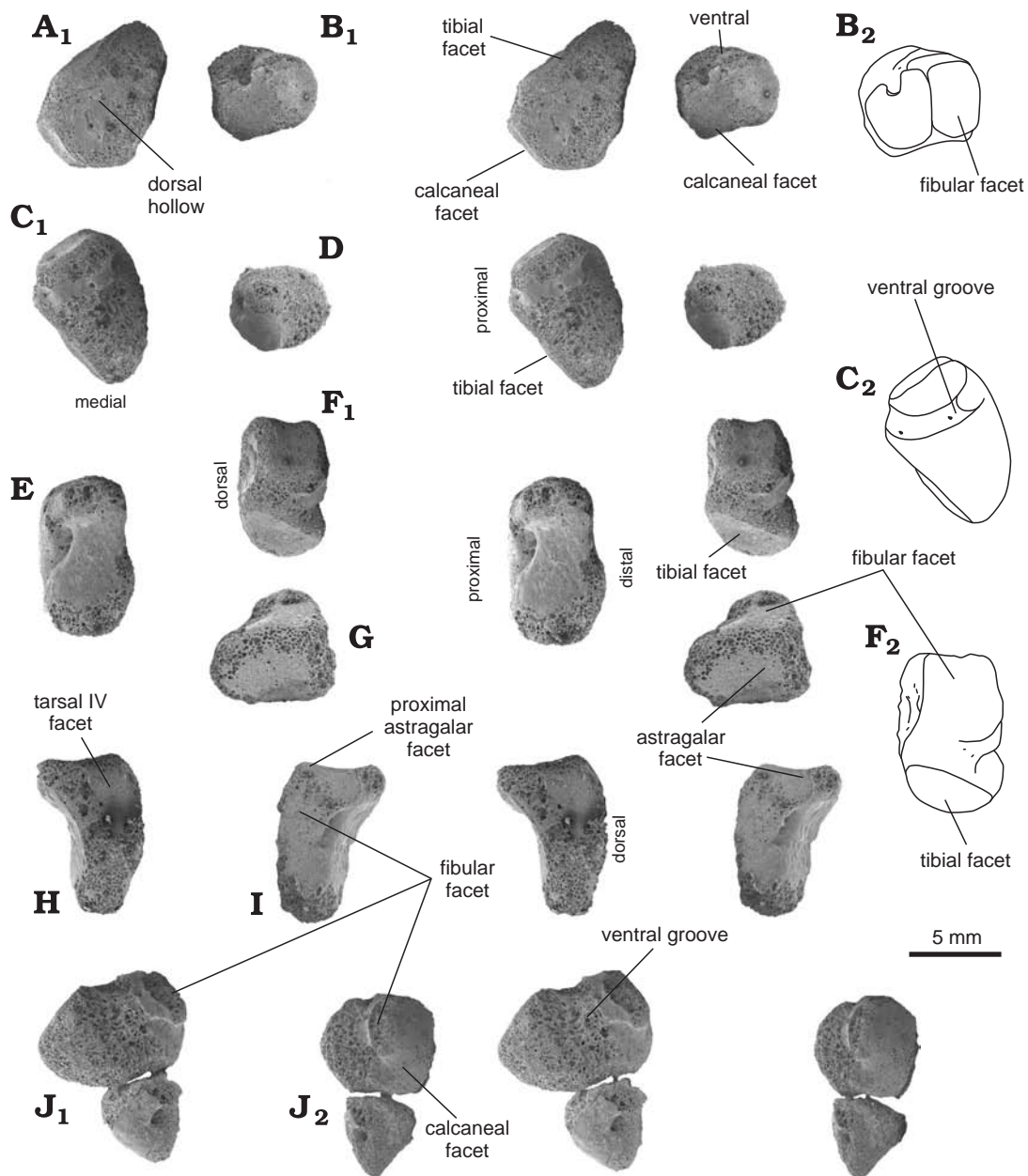


Fig. 17. *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **A–C, F.** Right astragalus ZPAL RV/811. **D.** ?Right distal tarsal IV ZPAL RV/812. **E.** Left calcaneum ZPAL RV/810. **G–I.** Left calcaneum ZPAL RV/810. **J.** Right astragalus ZPAL RV/811 combined with ?right distal tarsal IV ZPAL RV/812. Dorsal (A), lateral (**B₁**, **B₂**, **J₂**), ventral (C, E, **J₁**), proximal (D, I), proximolateral (F), medial (G), and distal (H) views. All but **B₂**, **C₂**, **F₂** SEM stereo-pairs; **B₂**, **C₂**, **F₂** corresponding schemes.

and subtriangular in outline. The remaining two thirds of the distal astragalus form an ovoid surface that is distally convex. This surface extends onto the ventral side. Faint subdivisions probably mark the separation of facets for tarsal III and metatarsals II and I, as in *Euparkeria* (Fig. 19C).

The calcaneum (Fig. 17E, G–I) is a wedge-shaped bone with an almost flat dorsal face and a concave ventral face; the medial portion of the bone protrudes ventrad (corresponding to medial posterior pyramid of Cruickshank, 1979 and Cruickshank and Benton 1985). The best preserved specimen, ZPAL RV/810, is largely surfaced with compacta. The orientation of the bone is based on comparative data from Sereno (1991) and Gower (1996). The ventral surface of the calcaneum bears a step-like groove directly below the proximal edge of the bone (Fig. 17E, I). This groove is perforated by a large vascular foramen. The same structure in *Erythrosuchus africanus* is referred to as a proximoventral groove (Gower 1996; p. 354). According to the

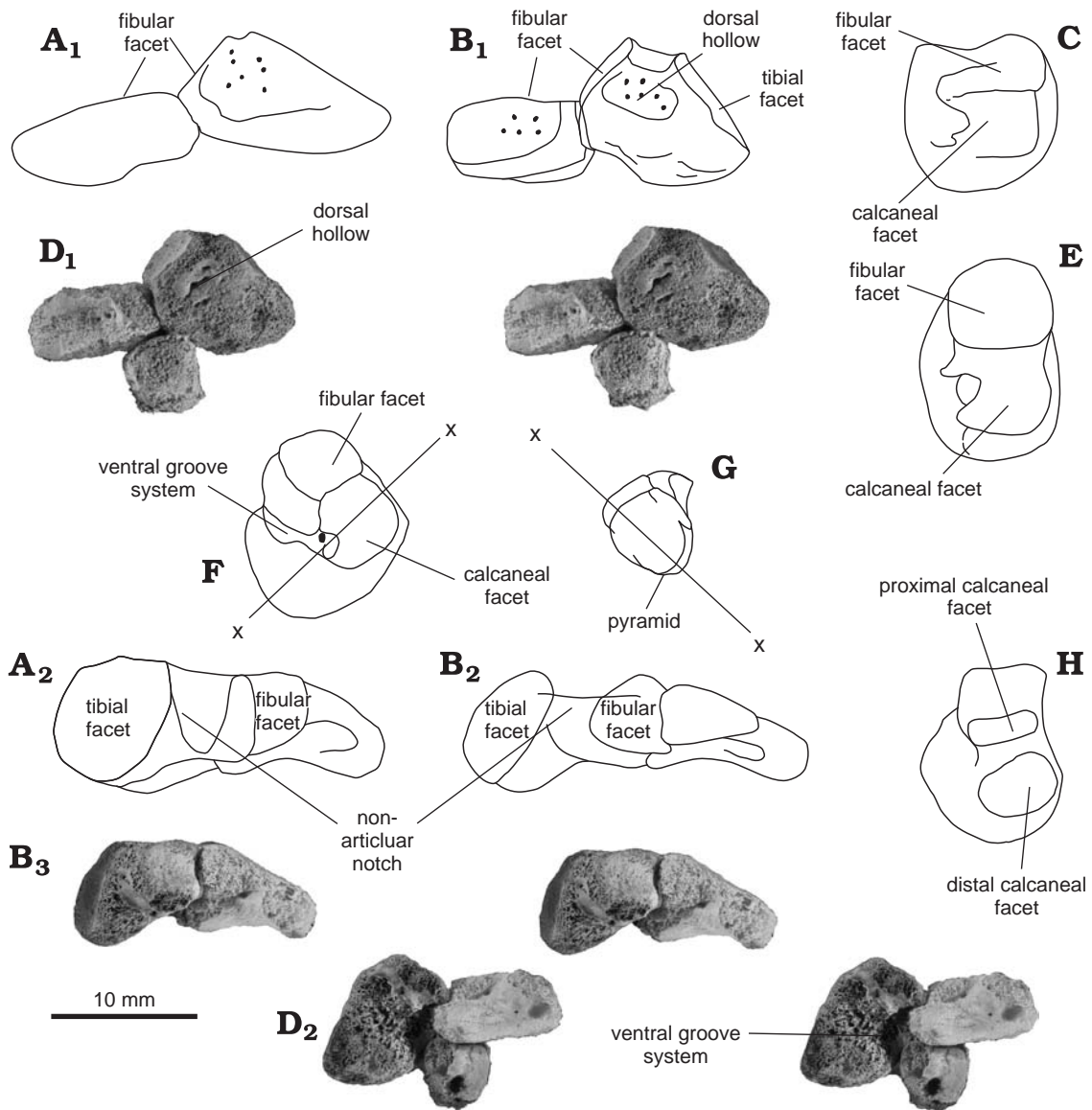


Fig. 18. **A, C.** *Euparkeria capensis* Broom, 1913. Right astragalus and calcaneum. **B, D–G.** *Osmolskina czatkowicensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B.** Right astragalus and calcaneum. **D.** Right astragalus ZPAL RV/811 combined with calcaneum ZPAL RV/1253 and distal tarsal IV ZPAL RV/812. **E, F.** Right astragalus. **G.** Right calcaneum. **H.** *Proterosuchus vanhoepeni* (Haughton, 1924), right astragalus. A₁, A₂, C, H after Sereno (1991), but A₁ slightly changed. Dorsal (A₁, B₁, D₁), proximal (A₂, B₂), ventral (D₂), directly lateral (C, E, H), distolateral (F), and medial (G) views. B₃ D₁, D₂, SEM stereo-pairs.

latter author this groove, which is also present in other erythrosuchids and in *Proterosuchus*, probably housed soft tissue binding the fibula to the calcaneum on the plantar surface of the foot. The dorsal part of the bone is covered by a slightly concave surface of compacta perforated by small nutrient canals.

The proximal surface of the calcaneum bears a flat, subtriangular facet that would have combined with the fibular facet of the astragalus to receive the fibula. The fibular facet is extended laterally and then ventrally (Figs 17I, 18B₂, B₃). The extension is covered with a sheet of compacta, and is medially separated by the proximoventral groove mentioned above. The groove extends along and below the posterolateral border of the facet.

The astragalar facet on the calcaneum (Fig. 17G, I) is subrectangular and slightly saddle-shaped. It is weakly convex in the shorter proximodistal axis and slightly concave along the subhorizontal axis (Fig. 18F: X-X axis). It extends onto the ventrally protruding part of the calcaneum (Fig. 17G) to articulate with the incision on the corresponding calcaneal facet of the astragalus, along the X-X axis (Fig. 18F). This articulation

results in the fibular facet of the calcaneum being turned a little posteroventrally from the plane of the astragalus. There would have been a limited mobility at this joint in the horizontal plane, around a vertical axis, and probably some in a vertical plane, but no subdivision of the tarsus into crus-connected and pes-connected units is evident.

The lateral portion of the calcaneum is featureless. The tuber is directed laterally and only slightly ventrad. The lateral half of the distal surface (Fig. 18B₃) lacks compacta whereas the medial half bears two facets. Of these, a narrow semilunar facet situated on the medial border of the bone is probably just an extension of the astragalar facet, and suggests a slight vertical mobility within the astragalo-calcaneal joint, as does a similar extension on the proximal side of the astragalar facet. A large flat surface lateral to the semilunar facet would have combined with the facet on the astragalus to receive distal tarsal four (Fig. 17H).

The width of calcaneum (8 specimens) varies from 7–13 mm, but the majority (7 specimens) cluster between 7–9 mm (Appendix 1). Again, as in the case of long bones, there is a hiatus within the size range, but the largest specimen (ZPAL RV/1281) does not differ from the remaining specimens in morphology.

Only one specimen of distal tarsal four (DT4), ZPAL RV/812, is sufficiently well preserved for description (Figs 18D, J, 19C). It is a pyramidal bone with one subtriangular flat facet covered with compacta that matches the distal facet of the best preserved astragalus, ZPAL RV/811. If this is a correct interpretation, then the adjacent slightly convex surface of the pyramid is for the calcaneum, whereas the base of the pyramid, covered with compacta and perforated by one deep pit, should be oriented ventrally. This would match the distoventral surface of the DT4 in *Erythrosuchus* as illustrated by Gower (1996, fig. 4B). Articulated in this way, DT4 leaves medial and lateral spaces that must have received DT3 and Metatarsal V respectively.

Comments: The reconstruction of the tarsus in *Osmolskina czatkowicensis* is broadly based on Cruickshank (1979) and Gower (1996), the latter describing the erythrosuchid ankle, the minute details of which provide a basis for homology. Only one calcaneum, ZPAL RV/1281, definitely exceeds the normal size range of the tarsal elements (Appendix 1), thus supporting the idea of sample heterogeneity, but the majority of tarsal bones are more or less uniform in size. The close match in size and shape of the respective articular facets (ZPAL RV/811 and 1253), albeit in different individuals, allows the reconstruction (Figs 18J and 19C).

According to this reconstruction, the overall structure of *Osmolskina* tarsus, including the relative widths of the distal articular surfaces of the calcaneum and astragalus (Serenio 1991) and lateral direction of the tuber calcanei, resembles that of other basal grade archosauriforms (Parrish 1993; Juul 1994). *Osmolskina* shares this structure with *Euparkeria* (Fig. 19A, C), proterochampsids (Cruickshank 1979), and erythrosuchids (Gower 1996), while differing from the latter mainly in size dependent details. It differs from that of *Proterosuchus* in having a relatively smaller calcaneum and in the absence of an astragalocalcaneal canal, the plesiomorphic features retained by *Proterosuchus*, and lost in all the remaining archosauriforms.

In *Osmolskina* the relative width of the astragalus to the calcaneum lies at roughly 1.12 (9 mm to 8 mm respectively), and 1.2 in *Euparkeria* (according to Ewer 1965, fig. 32), the difference being negligible. The astragalus and calcaneum are almost level distally, except for the distal concavity for distal tarsal four, but proximally, the astragalus protrudes strongly to contact the crus obliquely rather than terminally. The distal ends of the crural bones are never complete, but were probably also oblique to match the tarsus, as they are in crocodiles (Fig. 15D). The astragalus of *Osmolskina* shows no evidence of a depression at the medial end of the tibial facet (a feature mentioned by Gower 1996, p. 365, point 4).

The calcaneal facet of the astragalus in *Osmolskina* is quite similar to that illustrated for *Euparkeria* (Serenio 1991, fig. 4D), with a shallow pit incising the posterior margin (in the distolateral branch of the ventral groove system). In both genera, the shape of the ventromedial calcaneal protrusion that was received into a corresponding notch on the astragalus (Fig. 18C, E) is similar. This, in turn, suggests a similar, limited, range of mobility.

In *Osmolskina* the tibial and fibular facets of the astragalus are well separated from each other by the non-articular notch. The *Euparkeria* pes is represented by three articulated specimens; the unnumbered specimen of Broom (Ewer 1965, see also Broom 1913, pl. LXXV), SAM 6049, and GPTI 1681/1 (previously SAM 7698). According to Gower (1996, p. 365), the notch does not separate the fibular and tibial facets in *Euparkeria*. However, the stereophotographs of SAM 6049 (Ewer 1965) and Broom's (1913) unnumbered specimen (Ewer 1965, fig. 30 and Fig. 19C herein) as well as personal observations by one of us (MBB) on GPTI 1681/1, all suggest the facets may in fact be separated in the South African taxon.

In Broom's specimen (Fig. 19C), the proximal tarsals seem to be twisted counter-clockwise. We consider that the proximal tarsals turned as a single unit, instead of being disarticulated (contrary to Ewer 1965).

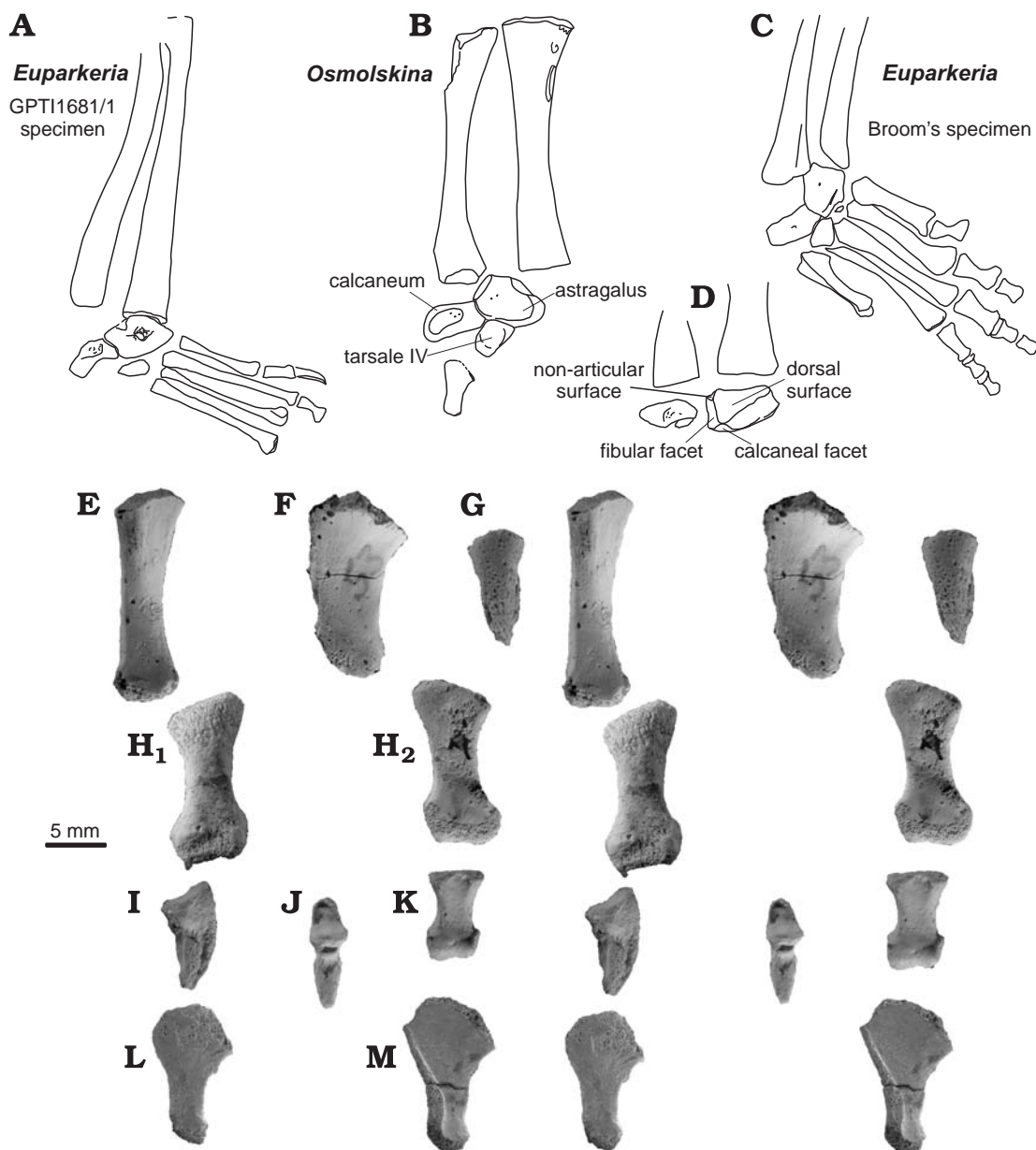


Fig. 19. **A, C, D.** *Euparkeria capensis* Broom, 1913. **A.** Right crus and pes after GPIT 1681/1 (MBB's sketch drawing). **C.** Right crus and pes of Broom's (1913) specimen (after Ewer 1965, fig. 30). **D.** Distal part of right crus and partial tarsus of SAM 6049 (after Ewer 1965, fig. 32). **B, G–M.** *Osmolskina czatkowiczensis* Borsuk-Białynicka *et* Evans, 2003, Early Triassic of Czatkowice 1, Poland. **B.** Reconstruction of the right crus, partial tarsus and Vth metatarsal. **G.** Ungual ZPAL RV/1244. **H.** Metatarsal ?I ZPAL RV/1238. **I.** Ungual ZPAL RV/1241. **J.** Ungual ZPAL RV/1242. **K.** A phalanx ZPAL RV/1243. **L.** Vth metatarsal V ZPAL RV/1247. **M.** Vth metatarsal ZPAL RV/1246. **E, F.** Archosauriformes gen. indet., Early Triassic of Czatkowice 1, Poland. **E.** Right metatarsal III or IV ZPAL RV/1236. **F.** Vth metatarsal ZPAL RV/1237. Dorsal (A–E, G, H₁), ventral (H₂, J, K), and side (I, L, M) views. All but A–D stereo-pairs.

Based on stereo-photographs of SAM 6049 (Ewer 1965, fig. 32), our interpretation (Fig. 18D) agrees with that of Gower (1996, p. 365) (in that the facet marked with a dot (Ewer l.c.) is for the calcaneum, and the one facing to the left is for the fibula) with one difference: what is a blunt proximo-lateral corner of the astragalus in Ewer's illustration is, in our opinion, the non-articular surface that separates fibular and tibial facets. The absence of this surface would be a significant difference between these otherwise similar genera, because its presence in *Osmolskina* is quite evident.

In the astragalus of *Osmolskina* (Fig. 18E), the fibular facet is broadly exposed in lateral view while being barely visible in *Euparkeria* (Fig. 18C) according to Sereno (1991, fig. 18). This suggests the astragalus is shallower in *Euparkeria* than in *Osmolskina*, and much less proximally protuberant. However, both SAM

6049 and Broom's unnumbered specimen (Fig. 19C) demonstrate that *Euparkeria* is quite similar to *Osmolskina* in the angulation of the crural facets and the degree of proximal protrusion of the astragalus (see also Gower 1996, p. 365).

In summary, the *Osmolskina* tarsus structure seems to be essentially the same as that in *Euparkeria*.

Metapodia and phalanges. — Within the small sample of more or less complete metapodia, five bones are recognized as metatarsals, and only one as a metacarpal. The metatarsals are longer and stouter than the metacarpal, but the size range is unknown and some overlap between them is possible. Specimen ZPAL RV/1236 (Fig. 19E), considered a possible right metatarsal III, is 18 mm long and about 3.5 mm in minimum width. It is thus longer than estimated on the basis of skull to metapodia length proportions (Appendix 1). The proximal end is oval with a dorso-laterally directed axis, probably to overlap metatarsal IV.

Two specimens, ZPAL RV/1238 (Fig. 19H) and ZPAL RV/1239, are considered right metatarsals I. Both are stout bones about 11 mm in length and 3.7 in minimum width. The proximal articular facets are flat and triangular, the apex of the triangle directed dorsad. The putative lateral margin faces dorsomedially, perhaps to allow an overlap by metatarsal II. The distal end is markedly enlarged bilaterally. The medial condyle is more prominent, the end appearing slightly asymmetrical in dorsal aspect. Collateral ligament pits are present on each side wall. The distal articular facet extends slightly further ventrally than dorsally, but the latter surface bears a concavity, referred to as an extensor depression (in the manus Sereno 1993). The long axis of the bone is slightly ventrally concave, especially in the distal part.

Among the metatarsals V of the Czatkowice 1 material, the largest specimens are considered archosauriform. Two specimens, ZPAL RV/1346 and 1347 (Fig. 19), match the *O. czatkowicensis* tarsus in terms of size (Fig. 19C), and are tentatively considered to belong to this species. A third, ZPAL RV/1237, is similar in morphology but about 25% longer and much stouter may be not conspecific. In accordance with Robinson's (1975, p. 464) terminology, the most probable metatarsal V of *Osmolskina* is both hooked and inflected. The hooking (*i.e.* medial angulation of the proximal end amounting to 90° in lizards) is about 70° in *Osmolskina*. The long axis of the shaft is rather straight in the transverse plane with both sides symmetrically concave. The inflexion (*i.e.* plantar-dorsal angulation of the long axis, Robinson 1975) is expressed by a ventral convexity of the bone in the long axis (and a corresponding dorsal concavity). The inflexion increases the lever arm of the fifth digit flexors and is functionally similar to a convexity of the whole plantar side of the foot in lower tetrapods that serves as a pulley for the foot flexors (Schaeffer 1941; Robinson 1975). The lateral plantar tubercle that forms the protruding tip of the inflexion in lizards (and a partial substitute for the tuber calcanei of mammals, Robinson 1975) is represented in *Osmolskina* by an elongate tuberosity that borders the lateral side of the shaft. This served for the insertion of the femorotibial head of the gastrocnemius muscle, and probably for the fifth digit abductor and some parts of the peroneus muscle. There is no medial tubercle but the articular facet for DT4 (Fig. 20L) protrudes toward the plantar side, in contrast to lizards where it is angled dorsally relative to the proximal part of the metatarsal. The outer process of metatarsal V in *Osmolskina* is less protuberant than in lizards, but still developed.

Some shorter, flattened metapodia that are slightly bowed to one side (*e.g.*, ZPAL RV/1243; Fig. 19H) are considered metacarpal I or V. The outline of the proximal end is dorsoventrally depressed and ellipsoid, as in *Varanus niloticus* (ZPAL RI/31) and *Euparkeria* (Ewer 1965, fig. 10I). In *Varanus*, metacarpals I and V are slightly bowed towards the axis of the hand.

Manual and pedal phalanges are strongly waisted directly above their bilaterally expanded distal ends. As in metapodia, these ends bear deep collateral ligament pits on each side. The proximal surface is concave, but varies in its depth and symmetry, asymmetric facets probably belonging to outer digits. In some specimens the proximal surface is slightly subdivided. Dorsally, it is flanked by a protrusion (for the common digital extensor) that makes the articular surface deeper and subtriangular. In some specimens the whole surface extends ventrally to assure greater dorsiflexion.

The largest unguals of the Czatkowice 1 material range in size but are consistent in morphology. Most of them might belong to *Osmolskina czatkowicensis*. They are generally less bilaterally flattened, and less acute (Fig. 19G, J) than the small unguals of the Czatkowice 1 material (Fig. 19I), but vary in the degree of flattening, the depth of concavity and its symmetry. They are readily distinguishable by their porous surface texture, suggesting the presence of a particularly strong germinative layer of the keratinized claw. Extending along the distal 2/3 of both sides, deep furrows fastened the claw to the unguis. Relatively narrower unguals, probably belonging to side digits have a slightly asymmetrical proximal facet subdivided by a longitudinal ridge and bordered by a proximally protruding dorsal process for the common digital extensor tendon.

Family uncertain

Genus *Collilongus* gen. n.

Type species: *Collilongus rarus* gen. et sp. n.

Derivation of the name: From Latin, *collum* — neck, *longus* — long.

Diagnosis. — As for the species.

Collilongus rarus gen. et sp. n.

Holotype: Cervical vertebra ZPAL RV/580.

Type horizon: Early Olenekian.

Type locality: Czatkowice 1, southern Poland.

Derivation of the specific name: From Latin, *rarus* — rare in Czatkowice 1 material.

Material. — Four cervicals: ZPAL RV/579, 580, 581, 596; ?four dorsals: ZPAL RV/584, 585, 588, 694; one sacral ZPAL RV/1369; and twelve caudals: ZPAL RV/583, 594, 661, 662, 663, 1362, 1363, 1364, 1365, 1366, 1367, 1368.

Measurements. — Appendix 1, Supplement 1.

Diagnosis. — A small archosauriform. Cervical centra 12–13 mm in adult length, smaller than in any other known archosauriforms except euparkeriids. From known euparkeriids it differs in having more elongate and cylindrical cervical centra, and costal articulations barely protruding from the body of the centrum, while resembling the East European rauisuchids *Tsylmosaurus*, *Vytshegdosuchus*, and *Dongusuchus* except in smaller size. Weak development of ventral crests makes the vertebrae most similar to those of *Tsylmosuchus*, but posteroventral obliquity of the centrum is less. In cervicals the centrum length to posterior depth index is about 2.07 except at the transition between cervical and dorsal series where it drops to 1.8. In caudals it ranges from 1.9 to 3.7 and increases down the tail.

Range. — Olenekian.

VERTEBRAL COLUMN

The atlas/axis complex. — The atlas/axis complex has not been identified except for an isolated axis spine ZPAL RV/587 (Fig. 5A) that is lower and more elongate than that of *Osmolskina*.

Postaxial cervicals. — The postaxial cervical centra are elongate cylinder-shaped and slightly amphiceolous (Fig. 20A, B, D, E, Supplement 1A). The ventral sagittal crest is absent. Cervical centra are not beveled. They slope at an angle of about 4–9° to an axis perpendicular to the articular surfaces, and there is no obvious gradation of this feature. The articular ends of the centra protrude ventrad. The diapophysis and parapophysis protrude only slightly from the body of the centrum and are quite close to its anterior border. The diapophysis is supported by a posteriorly extending crest (posterior diapophyseal lamina of Wilson 1999) that is much less ventrally concave than in *Osmolskina*. Below the crest, the lateral wall is not excavated. The posterior centroparapophyseal crest (Wilson 1999) is developed in anterior cervicals.

The neural canal is subquadrangular in outline. The subhorizontal prezygapophyseal facets are more elongate than those of *Osmolskina* and converge slightly ventro-medially. Their lateral borders pass into sharp crests that converge posteriad to fuse at the base of the spine. Between them is a triangular, non-articular shelf with a concavity for the interspinous ligament at the base of the spine. Extending from the postzygapophyses, the crests, analogous to the anterior ones, produce a high, narrow, triangular concavity. The spine is always damaged, but specimen ZPAL RV/579 (Fig. 20A) shows it to be almost as high as the vertebra itself, with a straight anterior margin. It is supported by the posterior half of the arch. One problematic specimen, ZPAL RV/893 (Fig. 20M), that exceeds the size range of *Osmolskina* but is shorter than most *Collilongus* cervicals (ratio 1.8) might be a transition vertebra between the elongate cervical and much shorter dorsal vertebrae. Some morphological features, such as the more protuberant diapophyses, more ventrally concave posteroventral diapophyseal lamina, and excavated ventrolateral centrum wall, might be, at least partly, centrum length dependent.

Dorsals. — The assignment of dorsal vertebrae to *Collilongus rarus* is based on large size, and is only tentative. ZPAL RV/584, 585, 588, and 663, exceed the observed size range of *O. czatkowicensis* (Supplement 1B). The dorsal centra are slightly more bilaterally flattened than the cervical centra. They have a faint

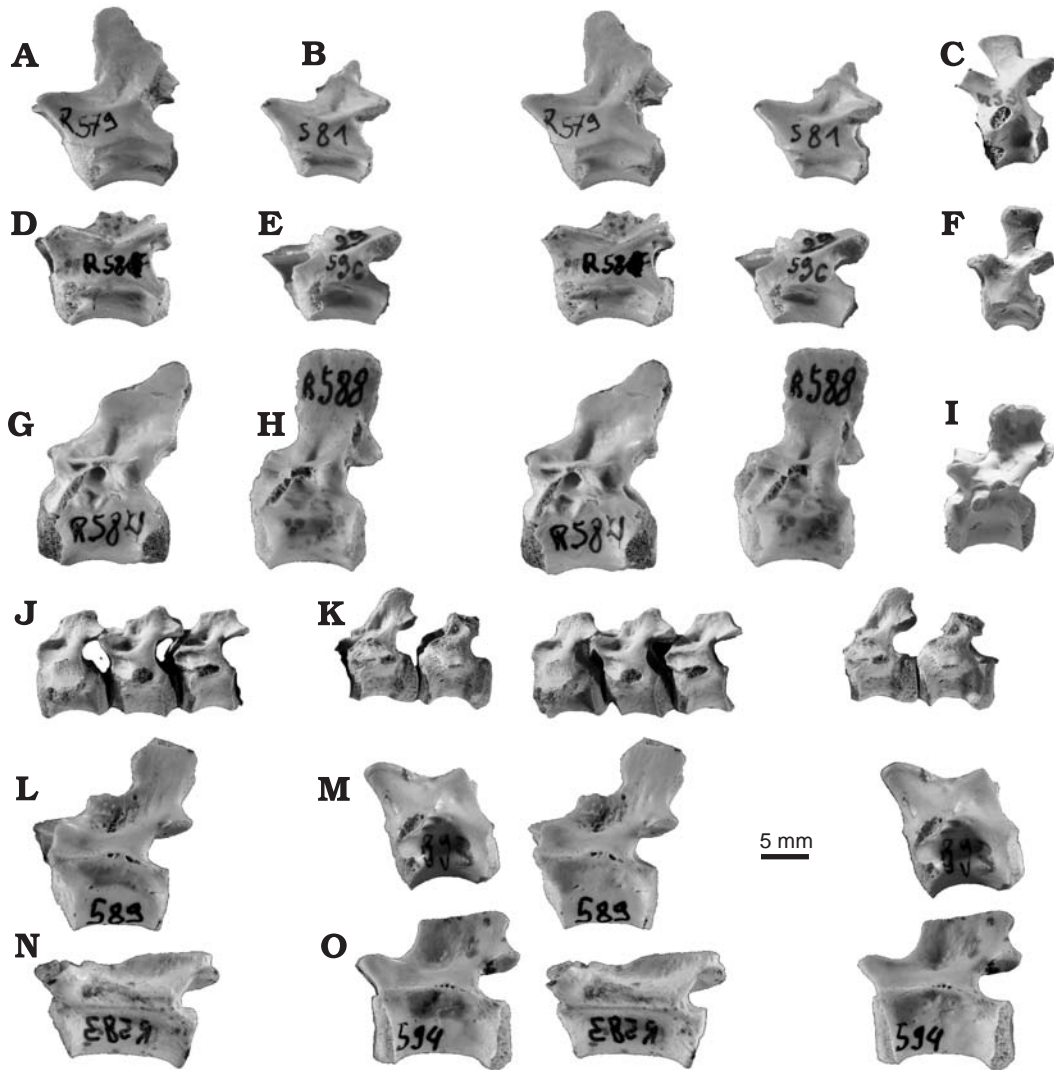


Fig. 20. A, B, D, E, G, H, L–O. *Collilongus rarus* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Cervical vertebrae: ZPAL RV/579 (A), ZPAL RV/581 (B), ZPAL RV/580 (D), and ZPAL RV/596 (E). Dorsal vertebrae: ZPAL RV/584 (G) and ZPAL RV/588 (H). L. Anterior caudal vertebra ZPAL RV/589. M. Posterior cervical vertebra ZPAL RV/893. N. Midcaudal vertebra ZPAL RV/583. O. Anterior caudal vertebra ZPAL RV/594. C, F, I–K. *Osmolskina czatkowicensis* Borsuk-Białynicka and Evans, 2003, Early Triassic of Czatkowice 1, Poland. C. Posterior cervical vertebra ZPAL RV/607. F. Midcervical vertebra ZPAL RV/571. I. Posterior dorsal vertebra ZPALRV/572. J. Anterior caudals in possible natural sequence ZPAL RV/659, 657, 658. K. Slightly more posterior caudals in a possible natural sequence ZPAL RV/576, 660. Left side view. All but C, F, I stereo-pairs.

sagittal crest and are not beveled. As preserved in ZPAL RV/588 (Fig. 20H), the neural spine is as high as the vertebra itself and $2/3$ as long at the base. It is subrectangular with a narrow top.

Caudals. — Large sized sacra such as *e.g.*, and 1369 are tentatively considered to belong to *Collilongus rarus*. In ZPAL RV/1369 the large oval scars left by the diapophyses are situated at the level of the neural arch base and cover almost the whole length of the arch. The specimen corresponds in size to caudals attributed to *Collilongus rarus* and may be a posterior sacral vertebra. With a ratio 1.39 the specimen is much shorter than the caudals that increase in length down the tail. There is no finished bone on the articular surfaces.

In anterior caudals, the spines are large (Fig. 20L, O), tall blades sloping posteriad, supported by the whole length of the neural arch, but further caudally, the spines become low crests supported by narrow postzygapophyses (Fig. 20M). With increasing length and slenderness of the centra, the diapophyses are gradually reduced to crests. Ventral crests appear at some distance from the sacrum, and are doubled for chevron attachment. The borders of the articular surfaces protrude ventrally. Otherwise, the centra are straight ventrally along the sagittal axis. The articular facets of the centra are U-shaped and deeper than wide,

the centra being more bilaterally flattened than they are in *Osmolskina*. As usual, the neural canal is relatively smaller than in dorsals.

Comments. — The vertebrae of *Collilongus rarus* approximate prolacertiform type vertebrae in the proportions of the cervical centra (Appendices 2 and 3), but their short, tall neural spines contrast with the elongated crest-like prolacertiform type cervical neural spines. Prolacertiform vertebrae in the Czatkowice 1 material (Borsuk-Białynicka *et al.* 1999) belong to animals of much smaller size (about 6 mm cervical centrum length and a length-to-height proportion of about 4.0). The other archosauriform type dorsal, sacral, and caudal vertebrae are tentatively associated with the cervicals. Their conspecificity is highly likely. All the vertebrae in this series are mature as shown by the completely closed neurocentral sutures.

In their elongate shape, the cervical vertebrae of *Collilongus* most closely resemble those of Olenekian raiisuchids from Russia, and particularly those of the group including *Tsylmosuchus*, *Vytshgedosuchus*, *Dongusuchus*, and *Energosuchus*. Sennikov (1999) considered six species: *T. samariensis*, *T. jakovlevi*, *T. donensis*, *V. zheshartensis*, *D. efremov*, and *E. garjanovi*, to be consecutive members of the same phylogenetic line, ranging from Early Olenekian to Ladinian (Supplement 4). This hypothesis is based on the common possession of elongate cervical vertebrae with a central axis sloping posteroventrally at 6–20° (Supplement 4); a concave ventral centrum profile; and diapophyses and parapophyses that hardly protrude from the centrum. As these taxa are represented by isolated bones, no other feature can be used to unite them. Just two species, *T. jakovlevi* and *V. zheshartensis*, include fragmentary ilia with a supra-acetabular buttress that approximates the raiisuchid condition (Sennikov 1995; Gower and Sennikov 2000), and this forms the basis for the raiisuchid attribution of the whole group. *Collilongus* cervical vertebrae are much smaller and less sloping (1 to 9°), less waisted, and slightly less ventrally concave, but otherwise quite similar to those of any of these apparent raiisuchids. However, no synapomorphy can be named to support their relationships.

Family, gen. et sp. indet.

Osteoderms. — Heavy, compound osteoderms (Fig. 5B, H, K, L, N) are provisionally excluded from *Osmolskina czatkowicensis*.

FORELIMB

Humerus. — The almost complete specimen ZPAL RV/877 (Fig. 8E) is the longer and more slender of the two morphotypes recognized in Czatkowice 1 material. Detached proximal ends (ZPAL RV/1174, 1276) and detached distal ends (ZPAL RV/1161–1163, 1170, 1173) (Fig. 8B, F) probably belong to the same morphotype. All these specimens are less extended transversely than are the corresponding parts in *Osmolskina*, and are better ossified even in relatively small specimens (*e.g.*, Fig. 8B). The less deeply excavated olecranon fossa and the less protruding entepicondyle, also suggest these specimens belong with the longer morphotype (ZPAL RV/877; Fig. 8D). For a detailed discussion see p. 298).

Radius. — A distal radius end, ZPAL RV/1232 (Fig. 9B), 11 mm in distal width and much more waisted than that of *Osmolskina* is considered phylogenetically distinct.

HINDLIMB

Femur. — Specimens ZPAL RV/1132, 1174 (Fig. 12A, G), and the distal femoral end, ZPAL RV/1254, may not be conspecific with *Osmolskina czatkowicensis*, because they exceed it in size. However, their fragmentary preservation precludes their morphological distinction from those assigned to *Osmolskina*, and they remain *incertae sedis* among the Czatkowice 1 archosauriform assemblage.

Tibia. — In both length and width, the tibia ZPAL RV/1175 (Fig. 15A) is about 50% larger than comparable elements of *Osmolskina* (Fig. 15B, C). It differs also in being less waisted, with a more flattened shaft. Furthermore, the puboischiotibialis scar on the proximal end is situated in the middle of the larger surface in contrast to *Osmolskina* where it lies on the narrower side. The size difference thus combines with morphological differences.

Fibula. — As reconstructed herein (Fig. 16) on the basis of specimens ZPAL RV/1180–1182, this fibula type corresponds to *Osmolskina* in size, but is distinctive in the strong protrusion of the anterior trochanter. This makes it appear crooked, a feature tentatively considered to be characteristic of basal crurotarsians (Sereni 1991). Despite the striking slenderness, this element may suggest the presence of a basal crurotarsian in the Czatkowice 1 assemblage.

Calcaneum. — ZPAL RV/1281 is a calcaneum that exceeds the expected upper size limit for *O. czatkowicensis* by 50%.

Comments. — These aberrant bones excluded from the *O. czatkowicensis* hypodigm might belong to *Collilongus rarus*, as suggested by their size and number, but this attribution is tentative.

DISCUSSION

HETEROGENEITY OF CZATKOWICE 1 ARCHOSAURIFORM FAUNA

Archosauriform postcranial bones are the largest and most frequent within the bulk of Czatkowice 1 material. Most of them were assigned to *Osmolskina czatkowicensis* (Borsuk-Białynicka and Evans 2003), but some elements (*e.g.*, vertebrae, humeri, femora, tibiae and a calcaneum) that exceed the typical size range of *O. czatkowicensis*, and are separated from it by a hiatus (Appendices 1 and 2, Figs 14 and 21–24), are considered to represent a second distinct, morphotype.

The heterogeneity of the material is best documented by morphometric analysis of vertebral centra. A frequency distribution of centrum length, and of the length to posterior depth index suggests bimodality of the samples. This is most obvious in the case of cervicals (Appendix 2, Supplement 2A, B). The main group, displaying a more or less normal distribution, considered to belong to *Osmolskina czatkowicensis*, is separated by a hiatus from rarer specimens of much larger size (Fig. 21) and elongate proportions (Fig. 22) that are assigned to *Collilongus rarus* gen. et sp. n. The heterogeneity is also expressed by the caudals. In the mixed sample, the anterior caudal centra display a more or less normal distribution, while revealing a slight bimodality (Fig. 23) or a large variance along the tail.

Among long bones, only the tibia definitely combines differences in size and morphology. The largest tibia (ZPAL RV/117; Fig. 15A₁) is distinguished by both the shape of its transverse section (Fig. 15B₁) and the position of the puboischiotibialis muscle scar (p. 305), and is thus considered distinct from *Osmolskina czatkowicensis*.

There are thus at least two archosauriform taxa in the Czatkowice 1 assemblage.

PHYLOGENETIC VALUE OF CENTRUM PROPORTIONS

Centrum proportion is often the most noticeable feature in damaged disarticulated vertebrae, and the one most readily defined precisely. Appendix 2 includes frequency distributions of the centrum length to posterior depth index across the available archosauriform material (mostly Russian Triassic material, PIN RAS, Supplements 3, 4) and from the literature (Krebs 1965; Gebauer 2004; Sennikov 1995 and references therein; Gower and Sennikov 2000; Young 1964).

The cervical vertebrae (Fig. 24) show a roughly bimodal distribution, the main peak occurring about a length/depth index value of 1.4–1.6, the second above 2.0. *Osmolskina* contributes to the main peak of the curve along with the proterosuchids, but this means simply that it shares centrum proportions common to many Early Triassic archosauriforms. With its length/depth index in the range 1.4–1.6, *Osmolskina* has slightly longer cervical centra, and *Collilongus* has them still more elongate than *Euparkeria* (Appendix 2).

The erythrosuchid sample is included in the left slope of the curve (Fig. 24) with a modal value about 0.8 for cervicals and slightly more than this (about 0.9) for dorsals. Interestingly, some Middle Triassic rauisuchids (*Batrachotomus* and *Stagonosuchus*), and the putative proterosuchid *Sarmatosuchus*, display almost erythrosuchid proportions of cervicals (Appendix 2). This suggests centrum proportions reflect function more than affinity, although monophyletic groups do usually have some general adaptations in common.

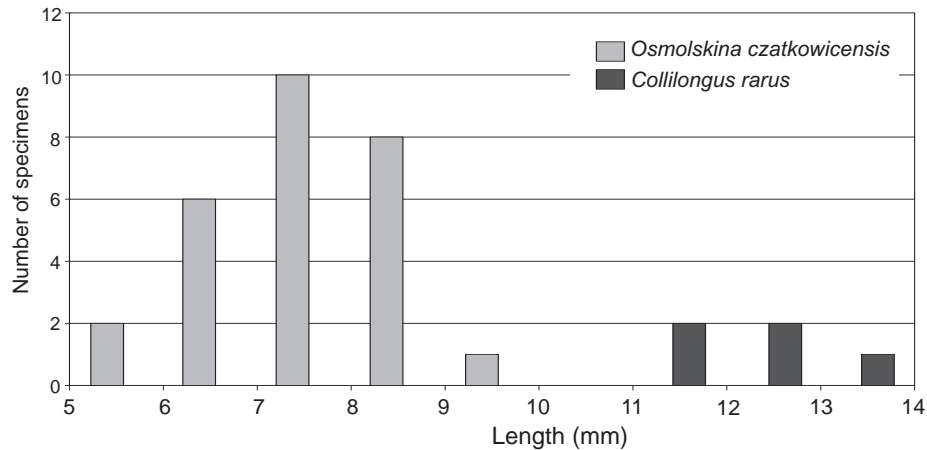


Fig. 21. Frequency distribution of cervical centrum length in Archosauriformes from the Early Triassic of Czatkowice 1, Poland.

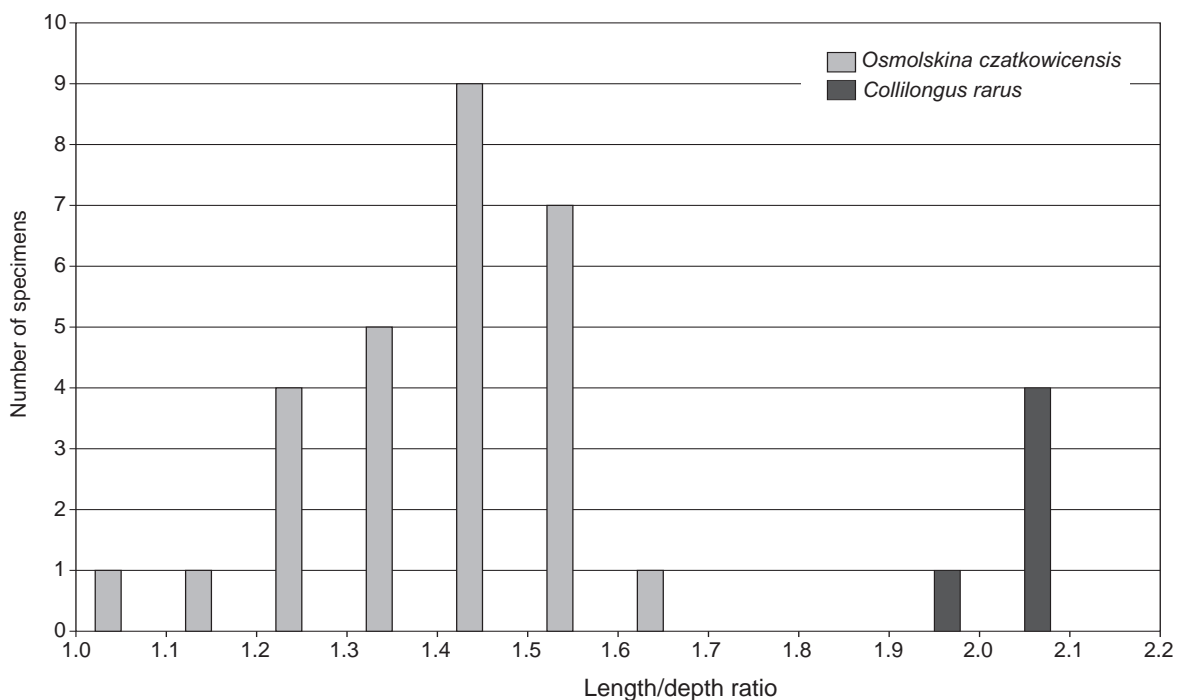


Fig. 22. Frequency distribution of vertebral index (cervical centrum length to posterior depth) in Archosauriformes from the Early Triassic of Czatkowice 1, Poland.

Collilongus matches the variability range of four Russian “rauisuchid” (*sensu* Gower and Sennikov 2000) genera, *Tsylmosuchus*, *Vytshgedosuchus*, *Dongusuchus*, and *Energosuchus*, that have been considered to form a clade (Sennikov 1990). Although not representative in statistical terms, these five genera (including *Collilongus*) correspond to the right side of the frequency curve (2.1–2.2; Fig. 25, Appendix 2). They are unique among Triassic archosauriforms in their elongate neck, which might be indicative of relationship. Other possible Eastern European “rauisuchids”, *Jaikosuchus*, *Vjushkovisaurus*, and *Scythosuchus* (Sennikov 1995, 1999), have centrum proportions that differ less from those of Early to early Middle Triassic archosauriforms (Supplement 4). Their centra are more elongate than those of the earliest proterosuchids *Archosaurus* and *Vonhuenia*, but resemble Olenekian proterosuchids like *Chasmatosuchus* and *Gamosaurus*.

The relative lengths of the postaxial cervical centra have been discussed in a slightly different context by Sereno (1991, p. 34 and table 1), and were subsequently included into Juul’s (1994) data matrix. According to these authors, the elongation of the anterior neck vertebrae is a synapomorphy of the Ornithodira. The Russian material (Supplements 3, 4) shows that the same has occurred, obviously independently, in some

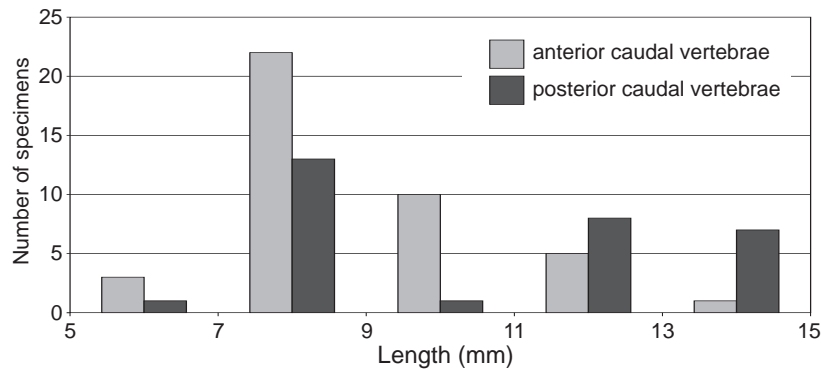


Fig. 23. Frequency distribution of caudal centrum length in Archosauriformes from the Early Triassic of Czatkowice 1, Poland.

“rauisuchids”. This does not undermine Sereno’s synapomorphy (according to Gower and Wilkinson 1996: “a derived character should not be unique to a clade to provide evidence for that clade”). Sereno (1991) also claimed that, in most basal archosauriforms, cervical centra were subequal or shorter than the average middorsal centrum. Our material is not sufficient to comment definitively on the relative lengths of cervical and dorsal vertebrae, but we support the relative shortening of the neck vertebrae at the origin of Archosauriformes. Strongly elongate cervical vertebrae prevail (Appendix 3) in the consecutive outgroups of the Archosauriformes (Evans 1988), as represented by “prolacertiforms” (recently considered paraphyletic; Dilkes 1998; Müller 2004; Borsuk-Białynicka and Evans 2009b) such as *Prolacerta*, *Macrocnemus*, *Tanystropheus*, and *Megalancosaurus*, but also in the most primitive diapsids, Araeoscelidia. In those taxa, the cervical centrum length/depth index oscillates between 2 and 3.7 (reaching the value 11.3 in *Tanystropheus*), while being much less in the proterosuchids. According to limited data on the proterosuchids, mainly of the Tatarian–Induan age (Supplements 3, 4), the initial cervical centrum index ranged between 1.2–1.5, up to 1.8 at most. At the same time, skull length that reaches only 40% to 55% of the trunk length in “prolacertiforms” (exceptionally only 31% in *Tanystropheus*), rises as high as 66% to 85% in those basal archosauriforms for which data are available (Appendix 3).

FUNCTIONAL CONSIDERATIONS

A negative correspondence between head size and neck length is known in vertebrate anatomy. The interference of various functional, biomechanical, and phylogenetic factors tends to obscure this association which is most evident in extreme cases, such as the disproportionately heavy skull and correspondingly short cervical region of erythrosuchids (see also elephants). Scarce as they are, the data available (Appendix 3) suggest that an allometric increase in skull size could have been a selective agent driving neck length reduction as a possible novelty at the origin of archosauriforms. Once head to body proportions had reached equilibrium and stabilized, there was a further radiation in neck length and mobility, as shown by the variability of Triassic archosauriforms.

A possible scenario is as follows: in the earliest diapsids, a trend to neck elongation might have been advantageous for sensory monitoring of the environment. This trend was sometimes reversed in heavy-skulled animals (Appendix 3, column 4), such as rhynchosaurs (Benton 1983) and trilophosaurs (Carroll 1988). In the same way, in archosauriforms, the allometric growth of skull (Appendix 3, columns 6–12) could have been recompensed by shortening of the neck, the requirements for better environmental monitoring having been satisfied mainly by a facultative bipedality which itself have been substantially enhanced by the improvement of biomechanical parameters of the ilio-sacral joint (Borsuk-Białynicka 2008).

The advantages of erect posture for fast locomotion have been stressed many times in the literature (Bakker 1971; Bonaparte 1971; Charig 1972; Parrish 1986), but extant tetrapod studies demonstrate that a sprawling gait might be equally efficient in tetrapod manoeuvrability and speed of locomotion (Sereno 1991 and references therein). The choice between gait types in diapsid phylogeny could have been haphazard from the point of view of locomotion, the primary adaptive agent being orientation. According to the scenario we propose, bipedality was first selected to improve environmental control, whereas an erect posture followed it

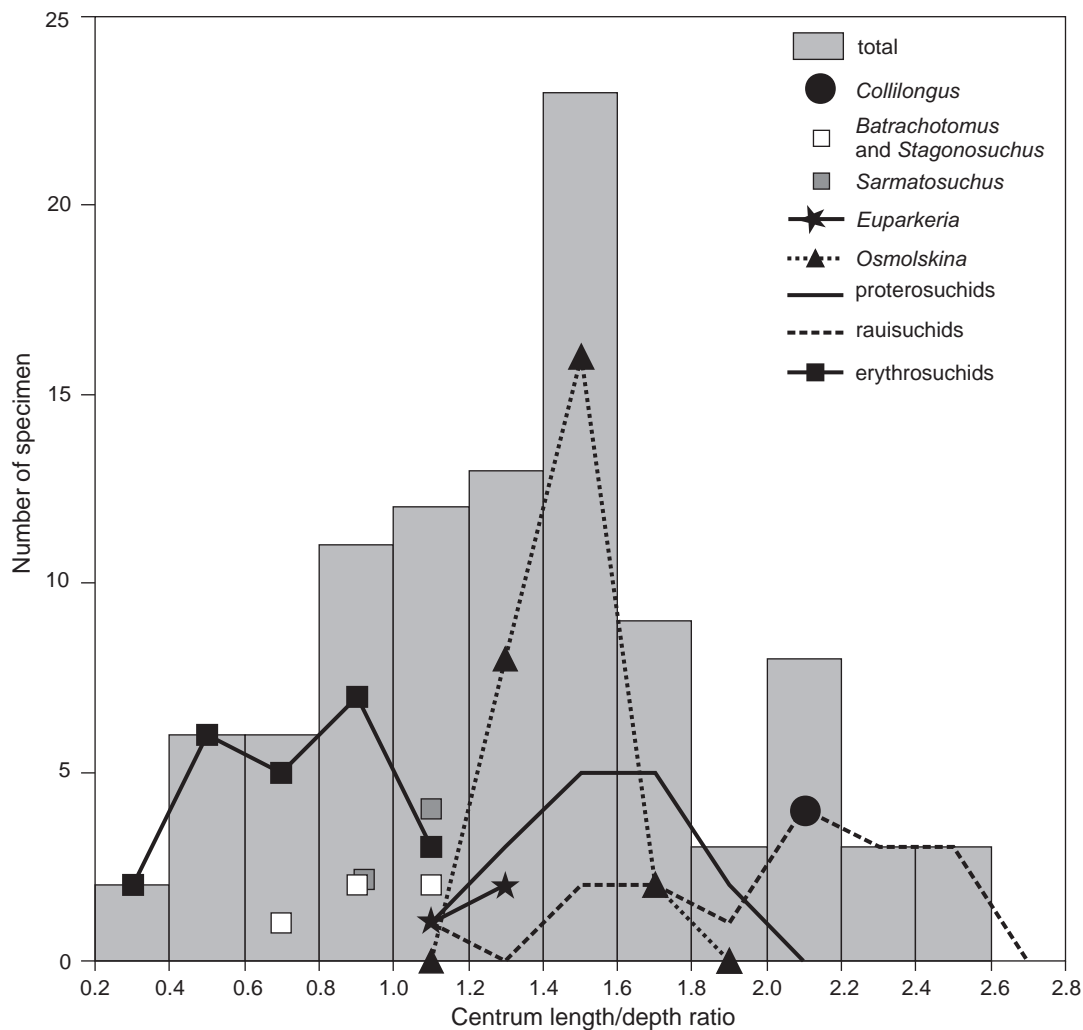


Fig. 24. Frequency distribution of cervical centrum length to posterior depth index in basal archosauriforms and raiusuchids.

in some groups. Sereno's (1991) statement that "erect posture may be a prerequisite for bipedalism" clearly concerns obligate bipedalism only.

OSMOLSKINA RECONSTRUCTION PROBLEMS

Given the close similarity between *Euparkeria capensis*, a species known from several partly preserved but articulated skeletons, and *Osmolskina czatkowicensis*, based on disarticulated material, any detailed reconstruction of the latter should be referred to the former.

Ewer (1965) estimated there were 22 presacral in *Euparkeria*, 7 cervicals, 15 dorsals, 2 sacrals, and 30–40 caudal vertebrae. The numbers were probably similar in *Osmolskina* but its cervical centra were slightly longer than those of *Euparkeria* (Appendix 2). In spite of poor preservation and approximate measurements, the humerus of *Osmolskina* may be estimated as roughly 70% of femur length, similar to that in *Euparkeria* (68%, Ewer 1965, table 3). In *Euparkeria*, the tibia length is 82–83 % of femur length (Ewer 1965), which probably holds for *Osmolskina*. Other proportions cannot be estimated even roughly. The trunk to hind leg length proportion, indicative of locomotor type, remains unknown.

In *Euparkeria* spine tables are developed in the posterior cervical and anterior dorsal regions. These also occur (Fig. 4H) in some better preserved anterior dorsal vertebrae of *Osmolskina*, but they were probably absent from more posterior dorsal vertebrae (Fig. 4B, C). According to Ewer (1965), the spine tables provide attachment sites for tendons of the transversospinalis system, and their localization relates to relative mobility of particular vertebral regions rather than to the overlying scutes. They occur more posteriorly when the tail is

heavy and active (*e.g.*, as a weapon: *Stagonolepis*, Walker 1961), and in more anterior vertebrae when neck mobility is important (Ewer 1965). The importance of raising the anterior end of the column in facultative bipeds may explain the localization of spine tables in *Euparkeria* (Ewer 1965). This relation probably hold in *Osmolskina*.

Osmolskina (Fig. 7A₄) and *Euparkeria* (Fig. 7E₂) appear to differ in the angulation of the coracoid with respect to the scapula (as presented by Ewer's 1965, fig. 9). If it is correct, the rib-cage would be narrower in *Osmolskina* and might correspond to more elevated position of the thorax. However, the reconstruction (Ewer 1965) of *Euparkeria* as a facultatively bipedal animal (based on persuasive arguments *e.g.*, ratio of a hindlimb to thorax length and depth of the acetabulum) fits better with the narrow rib-cage we suggest for *Osmolskina*. The *Euparkeria capensis* specimen SAM 5867 illustrated by Ewer (1965, fig. 20) is distorted and Ewer's (1965, fig. 9) interpretation seems wrong.

The ilium of *Osmolskina* is exactly like that of *Euparkeria* (Ewer 1965; personal observation of GPIT 1681/1 by MBB), including the position of the sacral rib facets, the apparently subparallel (instead of dorsally divergent) iliac blades, and traces of sacroiliac ligaments. The ilia of both genera have a morphology that is typical of Triassic archosauriforms. The anterior sacral rib facet is situated directly on the medial wall of the acetabulum. According to Borsuk-Białynicka (2008) this is a prerequisite for bipedality. Given a proximal rather than directly medial orientation of the femoral head in both *Osmolskina* and *Euparkeria*, the resting position of the leg was sprawling rather than erect, and the bipedality could have been only facultative. The well developed fourth trochanter of the femur in both genera supports the view that they raised the body when running fast. In addition, the slender humeral proportions and absence of epicondyles also point to the frequent adoption of a more erect stance.

As reconstructed, *Osmolskina* has the tarsus essentially transversally aligned with the calcaneal tuber laterally directed, but the astragalocalcaneal canal has been lost. The ventromedial pyramid of the calcaneum was probably received into the notch on the calcaneal facet of the astragalus (Fig. 19B–D). The same was probably true of *Euparkeria*. Some amount of mobility was possible in this joint, but its range was rather limited. In both genera, the tarsus was mesotarsal in type as defined by Gower (1996) or MPM type in Cruickshank and Benton's terminology (1985). In *Osmolskina*, the distal facet of the astragalus extends dorsally (Fig. 18C), and the same is true of the distal facet of the tarsal IV, which indicates an essentially horizontal resting position of the pes.

THE PHYLOGENETIC POSITION OF *OSMOLSKINA*

The placement of *Osmolskina czatkowicensis* at the euparkeriid level of archosauriform phylogeny was based on a combination of derived and primitive braincase characters (Borsuk-Białynicka and Evans 2003, 2009a).

The Archosauriformes (*sensu* Gauthier 1986 equal to Archosauria *sensu* Romer 1956) have been diagnosed mainly on skull characters by consecutive authors (Benton 1985, Benton and Clark 1988, Gauthier *et al.* 1988, Juul 1994). From the extensive description of the archosauriform postcranium given by Romer (1956), most characters were shown to be valid for the less inclusive groups. Only two characters, the absence of the humeral ectepicondylar foramen that relates to reduction of ectepicondyle (or distal end of humerus reduced in width — as worded by Benton 1985, p.126), and the presence of the fourth trochanter on the femur, were included in the archosauriform diagnosis by Gauthier *et al.* (1988) and Benton and Clark (1988) respectively. Of these characters, only the second is uniquely derived, and only for the clade Archosauriformes less Proterosuchidae (Juul 1994, character 4). Both characters are locomotion dependent. Two further postcranial characters: the presence of an anterior iliac process (Juul 1994, character 8), and the presence of dorsal osteoderms (Juul 1994, character 14) have been considered synapomorphic for the same less inclusive clade (Archosauriformes less Proterosuchidae). The ventral pelvic elements (Charig 1972) and tarsus (*e.g.*, Krebs 1965; Cruickshank 1979; Cruickshank and Benton 1985; Sereno 1991; Gower 1996) have been widely discussed in relation to archosauriform evolution. The pubis and ischium have become increasingly elongate (ischium longer than iliac blade — character 10 of Juul 1994, p. 38) and directed more or less ventrad (character 33 of Benton and Clark 1988), but again the initial stages of these morphological changes have not been defined as discrete novelties that could be included into the archosauriform diagnosis.

Juul (1994) discussed character distribution within the Archosauriformes, and summarized the results of previous cladistic analyses (Benton and Clark 1988; Gauthier *et al.* 1988; Sereno and Arcucci 1990; Sereno 1991; Parrish 1993), including them in his own data matrix. The latter forms the basis for our discussion. From Juul's list we have chosen only postcranial characters, and only those preserved in *Osmolskina* (Appendix 4). The numbering of characters is after Juul (1994) except for a new character, numbered 0, introduced to the matrix in the present study.

Character 0. — Iliosacral joint above the level of the supraacetabular ridge (0), overlapping the dorsal half of medial wall of the acetabulum (1), overlapping the whole medial wall of the acetabulum (2).

The position of the sacral rib facet relative to that of the acetabulum, the former lying on the medial, the latter on the reverse side of the ilium, is difficult to study, and has been rarely described. Some recent dinosaur papers (Novas 1996, fig. 7; Langer and Benton 2006, fig. 7) include the respective illustrations. Rare data on prolacertiform-grade reptiles (*Prolacerta broomi*, Gow 1975, *Macrocnemus bassani*, Rieppel 1989, as well as MBB's personal observations on *Macrocnemus bassani*, specimens PIMUZ T2472, T4822, and T4355) show the iliosacral joint lying above the acetabulum level. In contrast, in both *Osmolskina* and *Euparkeria* (Ewer 1965, fig. 11, MBB personal observation on the GPTI specimen), the anterior sacral rib overlaps the dorsal half of the medial wall of the acetabulum, and the same is true of *Dorosuchus neoetus* (Sennikov 1995, fig. 19L). Cruickshank's illustration (1972, fig. 8) suggests the same position of the joint in *Proterosuchus vanhoepeni*. If this is correct, then the character appeared within the proterosuchids or in the common archosauriform ancestor. This evolutionary shift in iliosacral morphology was probably a crucial event at the origin of archosauriforms, which enhanced a development of bipedality (Borsuk-Białynicka 2008).

Once developed, this character remained quite stable. As illustrated by Huene (1960) in *Vjushkovia*, by Young (1964, fig. 41A, B) in *Shansisuchus*, and by Gower (2003) in *Erythrosuchus*, the erythrosuchid ilium has the iliosacral joint in exactly the same position. It was retained in basal archosaurs, as exemplified by *Turfanosuchus dabanensis*, a crurotarsian from China (Wu and Russell 2001, fig. 11), in ornithosuchids (Walker 1964, fig. 11E), in phytosaurs (MBB personal observation of *Nicrosaurus kapffi* SMNS 52971), aetosaurs (Long and Murry 1995, fig. 80), and rauisuchids (Long and Murry 1995, fig. 134; Nesbitt 2005, fig. 23, MBB personal observation on *Batrachotomus kupferzellensis* SMNS 80273). In the extant crocodiles the sacral facet extends still further ventrad to overlap the entire medial wall of the acetabulum. In Dinosauromorpha (*sensu* Sereno 1991) the morphology of the iliosacral joint gets more complex (Langer and Benton 2006), but the biomechanics of this joint are poorly understood. This character obviously needs further study.

All 27 of Juul's (1994) characters, that could be scored for *Osmolskina* (Appendix 4) match the states of *Euparkeria*. Of them only seven show the derived condition, and these are shared by basal archosauriforms less proterosuchids. Of the remaining 20 plesiomorphic character states that exclude both genera from the crown-group, the following are particularly significant. The calcaneal tuber (character 24, Juul 1994) is lateral in orientation instead of posteriorly angulated, the facet for distal tarsal IV on the calcaneum (character 25) is oriented distally and is fully separated from the fibular facet, instead of touching it, and the relative transverse diameters of the calcaneum and astragalus (corresponding to DD character of Sereno 1991, p. 50, and character 57 of Juul 1994) are close to the proterosuchid ratio.

The following characters of Juul's (1994) matrix deserve some comments.

Character 12. — Intertrochanteric fossa present (0) or absent (1). The intertrochanteric fossa displays a continuous spectrum of states in archosauriforms, depending on the development of the posterior branch of the ventral ridge system (Romer 1956), and of the fourth trochanter. In our opinion this fossa is quite distinct in *Osmolskina* (Fig. 13E, F), and closely corresponds to the state in *Euparkeria* (Ewer 1965, fig. 31) *contra* Juul (1994, pp. 34, 38; the expression "intertrochanteric fossa on humerus" is evidently a mistake) who considers the fossa to be absent in *Euparkeria*.

Character 13. — Primitive mesotarsal joint ("PM" of Chatterjee 1982: the astragalus and calcaneum tightly adhering to each other) (0); Modified primitive mesotarsal joint ("MPM" of Cruickshank and Benton 1985 — perforating astragalocalcaneal canal between astragalus and calcaneum lost) (1). MPM type was considered synapomorphic for archosauriforms less proterosuchids and erythrosuchids (Sereno 1991, p. 6, supported by Juul 1994), but it has been shown to be shared by erythrosuchids (Gower 1996). This character is important in placing *Osmolskina* above the proterosuchid node.

Character 19. — The presence (0) or absence (1) of a non-articular space between the crural facets on the astragalus, was scored "0" in *Euparkeria* by Juul (1994), who followed Sereno and Arcucci (1990) and Sereno

(1991). We support this scoring, contra Gower's (1996) opinion that *Euparkeria* possessed the contiguous crural facets characteristic of archosaurs. The presence of a non-articular space between the astragalar crural facets in *Euparkeria* is suggested by stereophotographs of SAM 6049 (Ewer 1965) and Broom's (1913) unnumbered specimen (Ewer 1965, fig. 30 and Fig. 19C herein), and verified by MBB's personal observation of GPTI 1681/1 (Fig. 19A). This interpretation is also supported by the retention of the primitive condition in *Osmolskina* (Fig. 17A), a genus morphologically close to *Euparkeria* in other respects. However, the character may sometimes vary at a generic level as demonstrated by Gower (1996) in the erythrosuchids.

Character 28. — Fibular facet of the astragalus concave (0) flexed (1) — the facet in *Osmolskina* is slightly saddle-shaped, concave in its proximo-distal aspect, convex dorsoventrally. In biomechanical terms this suggests a slight mobility in this articulation, but not any specialized joint. The information on this facet in *Euparkeria* is too vague to be used for comparison.

Character 39. — Absence (0) or presence (1) of a supraacetabular crest. There is a lack of clarity as to what is meant by "supra-acetabular crest proper" (Juil 1994, p. 13). An anterodorsal crest, that makes the acetabulum more concave, occurs even in *Proterosuchus* (Cruickshank 1972, p. 108, fig. 8a) but in this genus, exactly as in *Prolacerta* (Gow 1975), it extends "along the front rim of the acetabulum" rather than dorsally. In both *Osmolskina* and *Euparkeria* the supraacetabular crest is mostly dorsal to the acetabulum and protrudes laterad. Certainly, the differences between *Euparkeria* grade archosauriforms and derived archosaurs is just quantitative.

Character 47. — Absence (0) or presence (1) of a brevis shelf. An elongate ventrally facing slightly excavated surface medially bordered by an acute crest probably received caudifemoralis brevis muscle in both *Osmolskina* and *Euparkeria* (Ewer's 1965 illustrations and MBB personal observations of GPTI 1681/1). It is here regarded as a homologue of the "brevis shelf". Similar to that of *Marasuchus* (Langer and Benton 2006) it differs from that of most basal dinosaurs, which faces ventrolaterally and extends further anteriorly. *Osmolskina*, *Euparkeria*, and probably *Marasuchus* display an intermediate less derived state of the same character.

Characters 28, 39, 47. — Are considered questionable and have been omitted in the Appendix 4. The remaining characters of Juil's (1994) matrix, such as organization of the dermal armour, number of phalanges and most of the length ratios, percentages and details of the skeleton as a whole, as well as configurations of bones in the distal limb parts, are considered as unknown.

The close similarity between *Euparkeria* and *Osmolskina* poses the question of their generic distinction. To several discriminative skull characters of *Osmolskina* (main proportions, premaxilla overhanging, possible supplementary slit-like antorbital fenestra, poorly recessed main antorbital fenestra; Borsuk-Białynicka and Evans 2003, 2009a), considered significant at generic level, we may add only two postcranial features: the slightly longer cervical centra of *Osmolskina*, and the extremely anterior position of the coracoid foramen. Differences in size, stratigraphic age and geographic provenance, *Euparkeria* coming from the Anisian of the Gondwanan part of Pangea, *Osmolskina* from the Olenekian of the Laurasian part, tend to support a generic distinction, but we are aware of the arbitrary character of the decision.

Under a traditional classification, both genera *Osmolskina* and *Euparkeria* would be placed in the family Euparkeriidae Huene 1920, the Anisian *Dorosuchus* Sennikov, 1989, from Russia, about twice as large as *Osmolskina* and slightly more derived in femur structure, forming a third member (Sennikov 1995). Herein, we tentatively accept this formal solution. However, it should be stressed that this family is not supported by any shared derived characters, unless an apparently unique combination of plesiomorphic and apomorphic character states may be considered as such.

CONCLUSIONS

The early Late Olenekian (Shishkin and Sulej 2009) Czatkowice 1 fauna includes two archosauriform genera and species, *Osmolskina czatkowicensis* Borsuk-Białynicka et Evans, 2003 and *Collilongus rarus* gen. et sp. n.

Osmolskina czatkowicensis is the dominant animal in the Czatkowice 1 assemblage in terms of frequency, and exceeds all but *Collilongus* in size.

Osmolskina czatkowicensis shares a combination of plesiomorphic and apomorphic characters with the Anisian South African *Euparkeria capensis*, while differing in details of cranial and postcranial osteology,

mostly reconstructed in probabilistic terms, which are considered significant at generic level. In this situation any computer cladistic analysis including *Osmolskina* seems redundant.

No unique derived character has been found in support of the monophyly of Euparkeriidae. However, the combination of primitive and derived character states *Euparkeria* and *Osmolskina* share with each other is tentatively considered as synapomorphic. Both genera share the absence of the astragalocalcaneal canal with all archosauriforms less proterosuchids, but lack archosaur synapomorphies (posteriorly deflected tuber calcanei, and continuous fibular and IV tarsal facets of calcaneum). They are both lightly built carnivores sharing no synapomorphies with the heavily built erythrosuchids.

The hypothesis that an overlap, or partial overlap, of the medial wall of the acetabulum by the sacral rib facet, is synapomorphic for the Archosauriformes (Borsuk-Białynicka 2008) is supported. By analogy with lizards, this archosauriform novelty is considered to have enhanced bipedality, initially facultative, in this clade.

The rare *Collilongus rarus* gen. et sp. n., based on cervical vertebrae, is the largest animal in the Czatkowice 1 fauna. It is most similar to long-necked rauisuchids from Russia, particularly *Tsylmosuchus* from the Early Triassic of the Russian Platform (Sennikov 1995), but is much smaller than any of these. However, its rauisuchid affinities, though possible, cannot be established with certainty on the basis of known elements.

The similarities of the Czatkowice 1 fauna to contemporaneous (Olenekian *Czatkobatrachus*–*Triadobatrachus*) or almost contemporaneous (Olenekian *Osmolskina* – Anisian *Euparkeria*) Gondwanan faunas, may be a legacy of the uniformity of Permian teropod faunas throughout Pangea.

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APPENDIX 1

Postcranial size relations in *Euparkeria capensis* Broom, 1913, size estimations in mm for *Osmolskina czatkowicensis* Borsuk-Białynicka et Evans, 2003, and actual size ranges of *O. czatkowicensis* and *Collilongus rarus* gen. et sp. n. bones from Czatkowice 1. * roughly estimated values; N, observation number.

Character Taxon/ value	1. Skull length	2. Cervical centrum length	Ratio 1/2	3. Dorsal centrum length	Ratio 1/3	4. Scapula length	Ratio 1/4
<i>E. capensis</i> SAM5867 size range	87.0	8.5 8.5-9.0 N = 2	10.7	10.0 8.6–11.7 N = 27	8.7	37.4	2.3
<i>O. czatkowicensis</i> prediction	60.0	5.6		6.9		21	“
<i>O. czatkowicensis</i> actual size range		6.5-9.0 N = 22		6.8-10.0 N = 17		29–34 N = 7	–
<i>C. rarus</i> size range		6.5–13.0 N = 27	“	11.9 – 15.6 N = 4	“		

Character Taxon/ value	5. Humerus length	Ratio 1/5	6. Ilium length	Ratio 1/6	7. Femur length	Ratio 1/7	8. Tibia length	Ratio 7/8
<i>E. capensis</i> SAM5867 variability range	37.8 37.8–43.2 N = 2	2.1	33.1 29.5–37.8 N = 3	2.6	55.8 53.8–61.6 N = 3	1.54	47.8 44.1–51.0 N = 3	1.2
<i>O. czatkowicensis</i> prediction	29	“	23	“	39	“	28	“
<i>O. czatkowicensis</i> actual size range	25–36* N = 10				34–43* N = 4		28–36* N = 5	
<i>C. rarus</i> size range	45 N = 1	–	19.9–26.8 N = 15	–	70–76* N = 2	–	55* N = 1	–

Character Taxon/ value	9. Astragalus width	Ratio 8/9	10. Calcaneum width	Ratio 9/10	11. Mtt I, V	Ratio 8/11	12. Mtt II, III, IV	Ratio 8/12
<i>E. capensis</i> SAM6049	10	4.78	8.3	1.2	11.8–12.8 N = 3	3.7–3.9	17.7–21.7 N = 4	ca. 2.2–2.5
<i>O. czatkowicensis</i> prediction	6.9	“	5.7	“	7–7.5	“	11.2–13	“
archosauriform size estimations	7–10 N = 4		7–9 + 13.5 N = 7 + 1		10; 11.5; 15 N = 3		?16, ?18	

The predictions about the size of postcranial bones in *Osmolskina* are based on the skeletal proportions of *Euparkeria*, taking skull length as a reference point (Therrien and Henderson 2007). The skull length of *Osmolskina* was calculated from the most common skull bones (Borsuk-Białynicka and Evans 2009a) and is a rough approximation of the actual modal value. Data for *Euparkeria* are from the type specimen of *E. capensis* SAM 5867 (Ewer 1965, tables 2, 3, and illustrations). Ilium length, and tibia and tarsal widths calculated from information from the same paper.

APPENDIX 2

Frequency distribution of the index of vertebral centrum length (a) to posterior depth (d) in basal archosauriform and rauisuchid taxa. N = 99 postaxial cervicals.

Taxa a/d ratio classes	Protero-suchids	Sarmato-suchus	Erythro-suchids	<i>Eupar-keria</i>	<i>Osmols-kina</i>	<i>Colli-longus</i>	Raui-suchids	<i>Batra-chotomus Stagono-suchus</i>	Total
0.21–0.4			2						2
0.41–0.6			6						6
0.61–0.8			5					1	6
0.81–1.0		2	7					2	11
1.01–1.2	1	4	3	1	0		1	2	12
1.21–1.4	3			2	8		0		13
1.41–1.6	5				16		2		23
1.61–1.8	5				2		2		9
1.81–2.0	2				0	0	1		3
2.01–2.2	0				0	4	4		8
2.21–2.4	0					0	3		3
2.41–2.6	0						3		3
2.61–2.8							0		0

Proterosuchids including *Proterosuchus* (according to Cruickshank 1972, fig. 4) and *Archosaurus*, *Chasmatosuchus*, *Gamosaurus* (according to AGS).

Erythrosuchids including *Erythrosuchus* (after Gower 2003), *Garjainia*, *Vjushkovisaurus*, after AGS data (Supplement 4), *Shansisuchus* (after Young 1964, table 6).

Rauisuchids including *Ticinosuchus* (after Krebs 1965) and *Energosuchus*, *Jaikosuchus*, *Jushatyria*, *Vytshegdosuchus*, *Scythosuchus*, *Vjushkovisaurus* (according to AGS, Supplement 4).

APPENDIX 3

Skull to body proportion and centrum proportion indices in some diapsids.

	1	2	3	4	5	6
Genus Index	<i>Araeoscelis</i>	<i>Megalanco-saurus</i>	Prolacerti-formes	<i>Paradapedon</i>	<i>Trilopho-saurus</i>	<i>Protero-suchus</i>
Acetabulum – glenoid distance/ Skull length	3.9	2.09	1.83–2.5 <i>Tanystropheus</i> 3.2	2.26 skull short but heavy	3.8	1.37
Cervical centrum proportion index ranges)	2.0–3.33	aprox. over 4	2.0–3.2 <i>Tanystropheus</i> 3.69–11.3	0.67–0.86		1.27–1.3

	7	8	9	10	11	12
Genus Index	<i>Erythro-suchus</i>	<i>Vjushkovia</i>	<i>Garjainia</i>	<i>Euparkeria</i>	<i>Ornithosuchus</i>	<i>Silesaurus</i>
Acetabulum – glenoid distance/ Skull length	1.17	1.70	1.21	1.5	1.47	2
Centrum proportion index range (cervicals)	0.41–0.5	0.71–0.9	0.71–1.2	1.3–1.44	1.22–1.3	1.6–2.1

Rough measurements have been taken from illustrations by: 1, Reisz *et al.* (1984); 2, Renesto (2000); 3, Gow (1975), Chatterjee (1986), Rieppel (1989), Peyer (1937), Wild (1974); 4, Chatterjee (1974); 5, Gregory (1945); 6, Cruickshank (1972); 7, Charig and Sues (1976); 8, Huene (1960); 9, Ewer (1965); 11, Walker (1964); 12, Dzik (2003).

APPENDIX 4

List of character states mostly according to Juul (1994) scored for *Euparkeria capensis* (after Juul 1994; first place figure) and *Osmolskina czatkowicensis* (second place figure).

0. Character added: iliosacral joint above the level of the supraacetabular ridge (0), overlapping the dorsal half of medial wall of the acetabulum (1), overlapping the whole medial wall of the acetabulum (2): 1 1
4. Fourth trochanter absent (0), present (1): 1 1
8. Anterior process of iliac blade absent (0), present (1): 1 1
9. Pubic tuber anteroventrally directed (0), or strongly downturned in lateral aspect (1): 1 1
10. The ischium is not longer (0), or is longer than the iliac blade (1): 1 1
12. Intertrochanteric fossa present (0), or absent (1): 0 0
13. Ankle type PM (0), MPM (1), rotary crurotarsal (2), AM (3): 1 1
14. Dorsal body osteoderms absent (0) present (1): 1 1
19. Crural facets of the astragalus: separated by a non-articular surface (0), or continuous (1): 0 ?0
24. Orientation of calcaneal tuber lateral (0), or deflected more than 45° posterolaterally (1): 0 0
25. Articular surfaces for fibula and distal tarsal IV on calcaneum separated by a non-articular surface (0), continuous (1): 0 0
27. Hemicylindrical calcaneal condyle for articulation with fibula absent (0), present (1): 0 0 (the character corresponding to character 8 by Sereno 1991)
29. Calcaneal tuber shaft proportions taller than broad (0), broader than tall (1): 0 0
30. Calcaneal tuber distal end anteroposteriorly compressed (0), rounded (1), flared (2): 0 0
34. Accessory neural spine on mid caudal vertebrae absent (0), present (1): 0 0
36. Acetabulum laterally oriented (0), ventrally deflected (1), open ventrally (2): 0 0
42. Lesser trochanter on femur absent (0), weakly developed (1), or a spike or crest (2): 0 0
43. Prominent cnemial crest absent (0), present (1): 0 0
46. Number of sacral vertebrae two (0), two plus incipient third (1), three or more (2): 0 0
47. A brevis shelf absent (0), present (1): 0 0
48. Tibia femur length ratio 1.0 (0), more than 1.0 (1): 0 0
49. Fibula non-tapering and calcaneum unreduced (0), thin tapered fibula and reduced calcaneum (1): 0 0
51. Deltpectoral crest rounded (0), subrectangular (1): 0 0
56. Distal articular surface of the calcaneum: transverse width more (0), or less than 35% of that of astragalus: 0 0
57. Hooked proximal end of metatarsal V present (0), absent (1): 0 0
60. Acetabulum imperforate (0), semiperforate (1), largely perforate (2): 0 0
63. Proximal articular surface of the calcaneum convex or flat (0) or concave (1): 0 0
66. Hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae absent (0), present (1): 0 0
72. Dorsoventrally aligned median depression on distal end of tuber calcis absent (0) present (1): 0 0